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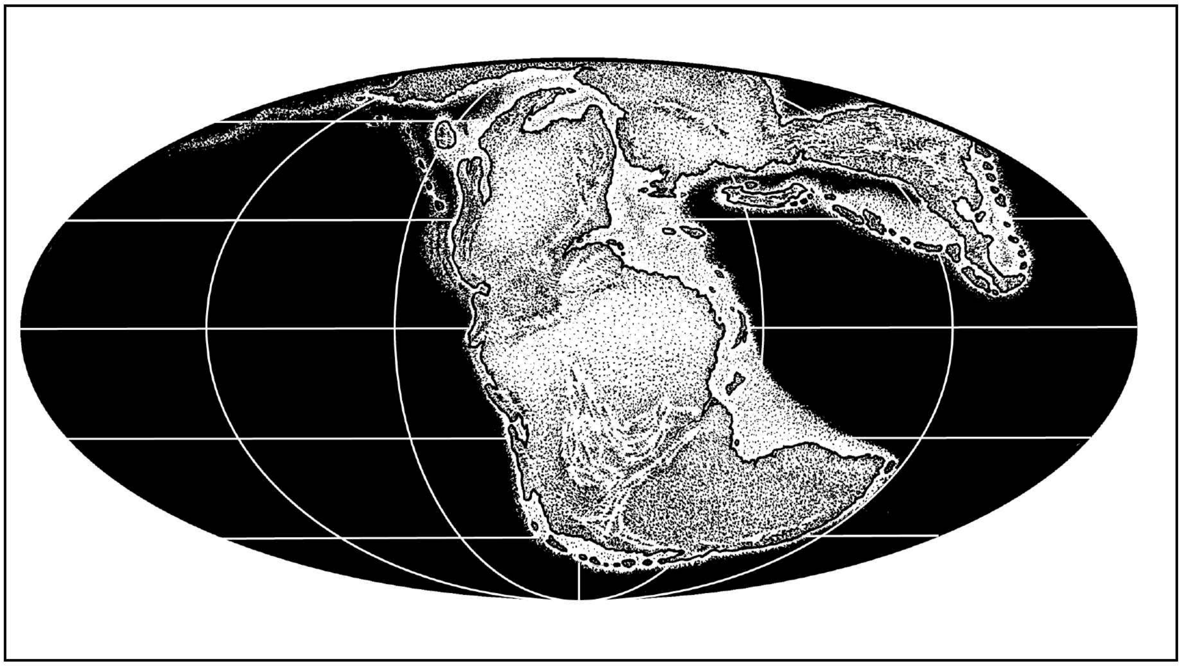
New Mexico Museum of Natural History & Science

A Division of the
DEPARTMENT OF CULTURAL AFFAIRS

The Global Triassic



edited by

Spencer G. Lucas and Justin A. Spielmann

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DEDICATION TO NORMAN J. SILBERLING AND E. TIMOTHY TOZER

It is both an honor and a pleasure to dedicate this volume to Norm Silberling and Tim Tozer, two of the great knights errant of the Triassic timescale. Nearly 30 years ago, in 1968, Norm Silberling and Tim Tozer published one of the classic mileposts along the path to a global Triassic timescale. Titled "Biostratigraphic classification of the marine Triassic in North America" (Geological Society of America, Special Paper 110), this work owed much to Norm and Tim's immediate predecessors, Si Mueller and Frank McLearn, who had amassed much of its underlying data. Nevertheless, it was Norm and Tim's masterful synthesis that established a standard Triassic ammonite zonation that has been tested and elaborated for decades and is still central to many aspects of the ongoing work on the Triassic timescale.

Born 28 November 1928 in Oakland, California, Norm Silberling grew up and was educated in northern California, ultimately receiving a Ph.D. in geology from Stanford University in 1957. Norm was a student of the legendary Si Mueller, who followed James Perrin Smith (Mueller's thesis advisor) in developing the phenomenal record of Triassic ammonoids known from Nevada. Before finishing his Ph.D., Norm saw service in the Korean War, where he was awarded two combat stars. After the Ph.D., his professional career began on the faculty of Stanford University, and then he moved in the 1970s to working for the U. S. Geological Survey, first in Menlo Park, California, then in Washington, D. C., and finally in Denver, Colorado, where he retired in the mid-1990s.

During Norm's scientific career he was never far from Nevada, though both Alaska and, ultimately, New Zealand also became field areas. From the 1950s through the 1970s, Norm's research evolved from ammonoid biostratigraphy to regional stratigraphy and ultimately into tectonics. Indeed, Norm was one of the key players in developing an understanding of what are variously called suspect (or allochthonous, or accreted or displaced) terranes, particularly based on his Alaskan work. His application of the terrane concept to the geology of western Nevada revolutionzed our understanding of the Mesozoic geological history of the Great Basin. Indeed, it is fair to say that Norm's contributions to tectonics are at least equal to his work on Triassic biostratigraphy.

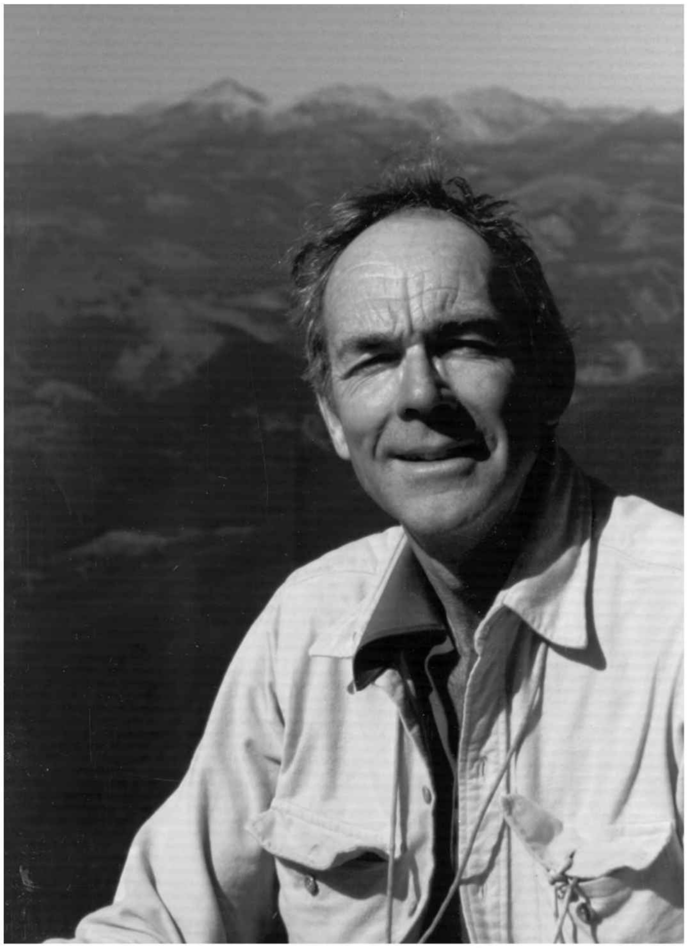
Thus, Norm Silberling has really had two careers as an earth scientist and contributed more to both than most contribute to a single career. He truly stands as one of the twentieth century's most important Triassic ammonite biostratigraphers, one of its most perceptive tectonicists and one of the most accomplished students of the geological history of western North America.

I (Spencer Lucas) worked with Norm in Sonora, Mexico, during the mid-1990s. Together, we collected the first Early Triassic ammonites found in Mexico, and Norm brought great clarity and wise caution to interpretation of the structural morass of the Caborca terrane from which lesser observers have mostly conjured tectonic fantasy. I can truly say that Norm is a fine gentleman and a gentle soul—soft spoken and well spoken, but with a penetrating intellect and vast experience that made him one the most valuable field collaborators of my career.

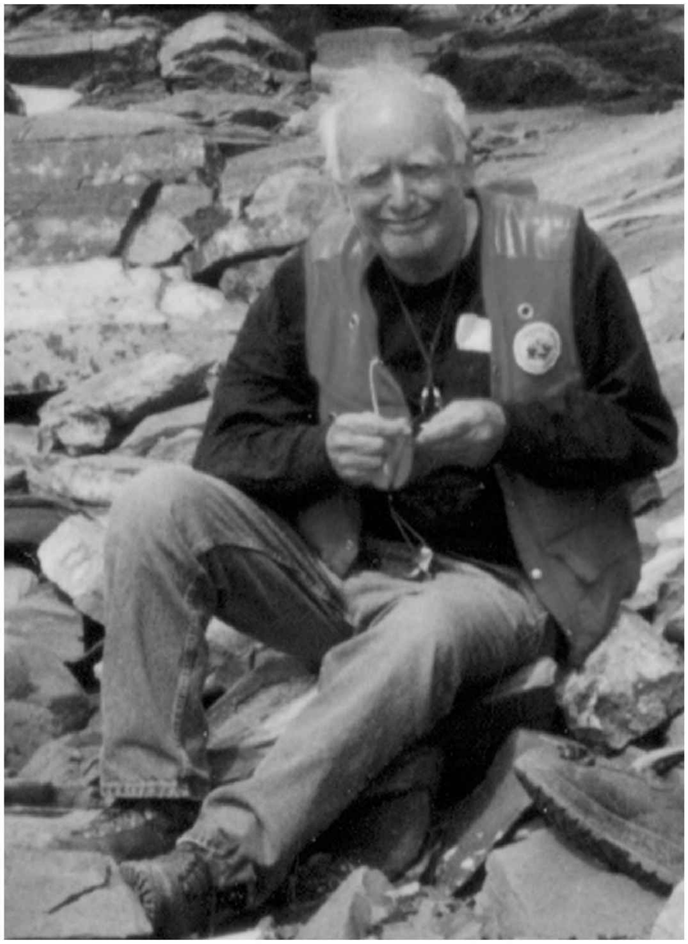
Tim Tozer was born 13 January 1928 in Potters Bar, England. In the 1940's, the family moved to Canada where Tim completed high school, after which he returned to the UK to attend University at Cambridge. After graduating in 1948, Tim travelled back to Canada to undertake PhD studies at the University of Toronto (1952), and then work as a lecturer at the University of Western Ontario (1948-1952). Starting in 1952, Tim then began over a half-century of work with the Geological Survey of Canada, first in Ottawa and later in Vancouver.

Tim's early research work in Canada involved Cretaceous-Paleocene nonmarine molluscs, but his interest became firmly focussed on the Triassic after meeting Frank McLearn, a GSC colleague and leading authority on the Triassic and its ammonoids, who retired the year Tim joined the GSC but kept active writing and mentoring Tim. Tim's first exposure to Triassic rocks was in the southern Yukon where he spent the 1953 season studying the Lewes River Group. That same year, he visited Cowichan Lake on Vancouver Island with George Jeletsky, and then Tyaughton Creek in south-central B.C. with Howard Tipper, both crucial areas for latest Triassic biochronology.

The major focus of Tim's fieldwork from the mid 1950's was not in the Cordillera but in the far north. Together with Ray Thorsteinson, a contemporary from the University of Toronto, he was to spend a decade exploring the Canadian Arctic Archipelago (1954-1964). This was pioneering work. The geology of the Arctic was largely un-



NORMAN J. SILBERLING



E. TIMOTHY TOZER

known, and Tim and Ray mapped vast tracts of the islands for the first time, establishing, among other things, the Mesozoic-Tertiary stratigraphy of the Sverdrup Basin. For Tim, this began with a 6 month field season by dog and sled; only later did Piper Super Cub aircraft become the mode of transport. Tim went on to establish the Lower Triassic stages and to define their constituent ammonoid faunas. This was to become the North American standard chronostratigraphy: Griesbachian, Dienerian, Smithian, and Spathian, aptly named after Arctic creeks that he had first named to commemorate distinguished researchers of the Lower Triassic.

Tim began work in northeast British Columbia in 1960, with a raft expedition on the mighty Liard River. This provided much Middle Triassic data to add to his knowledge of the Lower Triassic of the Arctic. In 1964, he visited Peace River Valley, treading in McLearn's footsteps and building on his legacy. Collaborative work with Norm Silberling began at this time – they were together in B.C. in 1965. Tim and Norm pushed forward with the marriage of Canadian and US Triassic data in a way that Si Muller and Frank McLearn never achieved simply because they never met. Tim was now in a position to produce his classic "Standard for Triassic Time" (1967), and shortly after that the joint landmark paper with Norm Silberling.

Tim travelled the world far and wide studying Triassic rocks and ammonoids, mastering his subject and meeting key players in the Triassic world. His fascination with the personalities of 19th century Triassic studies gave Tim's research a depth that few achieve – a view of the people behind the science. His famous 'pink book' - for which a GSC 'Miscellaneous Series' publication was invented! - lays out the unfolding drama of "The Triassic and its ammonoids: The Evolution of a Time Scale." This scholarly masterpiece is highly recommended reading.

Tim's foreign travels and international liaisons enriched his science with wide ranging correspondents and opportunities to host visiting scientists. It was during one such visit in the late 1970's with a Chinese colleague that he flew over Williston Lake to view the drowned Peace River Valley where Frank McLearn had worked in the 1930's, and that he had followed in 1964. It was here that Upper Triasssic ammonoid zonation was carefully pieced together prior to the valley being dammed and flooded (1967). Rather than see only remnants of the former outcrops, Tim was startled to see new exposures around the entire lake shore. He wasted no time and immediately planned fieldwork that I (Mike Orchard), having recently joined the GSC, was fortunate enough to become involved with: the following year (1980) Tim and I set off to explore entirely new, 'virgin' outcrop - 'dripping with ammonoids and bursting with conodonts'! This was undoubtedly the highlight of my early years with the GSC and hugely exciting for Tim, who now saw the somewhat synthetic ammonoid zonation laid out in clear succession. This was to be the beginning of our long collaboration intercalibrating the ammonoid and conodont scales. Over the next two decades we re-visited many of the sites in B.C. that Tim now knew to be pivotal in his biochronology, and some new ones like the Queen Charlotte Islands, where the pioneering George Mercer Dawson worked in the 1870's. On that occasion, Tim used Dawson's original field notes to locate unique localities – typical of Tim's scholarly approach. It was Tim's ammonoid zonation that truly laid the foundation for advancement in conodont biochronology. The impact of Tim's work is manifest in his monumental 1994 work "Canadian Triassic ammonoid faunas".

Tim's knowledge of Triassic rocks throughout western Canada eventually led to his consideration of Cordilleran tectonics. Why were there reefs in the Yukon and anomalous distributions of certain fossils? Tim is credited with introducing the notion of transported fossil assemblages, and in 1982 he represented his views in a landmark paper assessing plate and terrane movements in which he proposed paleolatidudes for circum-Pacific allochthonous terranes.

Tim's career achievements were recognised in 1989 by his paleontological peers when he received the Elkanah Billings Medal, awarded by the Geological Association of Canada for lifetime achievement in paleontological research. Four years later he received a rare honour with an appointment to membership of the Order of Canada, awarded by the Governor General of Canada for contributions "to our knowledge of the stratigraphy and structure of the Arctic Islands and the physical and biological state of our earth during the Triassic Period". Truly deserved.

—Spencer G. Lucas and Michael J. Orchard

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THE EARLY TRIASSIC CARBON, SULFUR AND NITROGEN ISOTOPE RECORD

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At the aftermath of the end-Permian mass extinction, Panthalassan ocean chemistry underwent profound changes, as outlined by geochemical, sedimentological and paleontological observations. The Early Triassic carbon, sulfur, nitrogen and strontium isotope records show patterns that, in concert, are unprecedented in earth history. The Early Triassic carbon isotope record is marked by three positive excursions, all located at, or close to stage/substage boundaries—Dienerian-Smithian (Induan-Olenekian), Smithian-Spathian, and Spathian-Anisian (Olenekian-Anisian)—as reported previously from sites located in the Tethyan realm. Carbon isotope data from marine sequences on the western margin of the North American continent show an identical pattern, confirming the global nature of Lower Triassic carbon isotope fluctuations. All three excursions are present in the Ursula Creek section in Northeast British Columbia (Williston Lake), and fully or partially recorded in several sections within the Thaynes Formation outcrop in the Western United States (Utah, Nevada and SE Idaho). As in the Tethys, these carbon isotope excursions stand out, not only by their abruptness, but also by their extreme magnitude, comparable only with Precambrian and Early Cambrian counterparts.

The high abundance of organic matter throughout the Ursula Creek section allowed us to provide a continuous nitrogen isotope profile for the entire Early Triassic and part of the Anisian. The $\delta^{15}N$ values are relatively constant for most of the section, but display a negative excursion of 1.5‰ across the Olenekian-Anisian boundary, mirroring the carbon isotope excursion. It indicates increased nitrate availability, consistent with the onset of an upwelling system indicated by the presence of phosphate nodules. While the nitrogen isotope anomaly is likely to be local, confined to the North American upwelling zone, it suggests a sudden increase in ocean productivity, in agreement with a positive excursion in carbon isotopes. Another remarkable feature of the Early Triassic stable isotope record is represented by a large sulfur isotope shift, as recorded in sedimentary sulfates, though its timing and relationship to the carbon isotope record is not well defined. Sulfur isotope profiles in the Moenkopi Formation in SW Utah and N Arizona show a major increase in $\delta^{34}S$ values from approximately 11‰ in the Lower Red Member (Smithian) to values as high as 30‰ in the Shnabkaib Member (Spathian). $\delta^{34}S$ values from the younger (Lower Anisian?) Moqui Member are relatively low, around 10‰, indicating a return to initial values and thus defining a positive excursion within the Spathian, possibly spanning the Spathian-Anisian boundary. Tentative correlations with the carbon isotope record from the Thaynes Formation, due to interfingering relationships between the Thaynes and Moenkopi formations, indicate a decoupling of the carbon and sulfur isotope cycles during the Smithian and Spathian (Olenekian). Although it is difficult to reconstruct a scenario that would account for all geochemical anomalies described above, the stable isotope record is consistent with an Early Triassic stratified, stagnant ocean, low latitudinal temperature gradients, large carbon isotope gradients between deep, anoxic and surface waters, and increased sulfate reduction in the anoxic zone that would lead to large fractionation of sulfur isotopes and formation of residual brines enriched in ^{34}S. A reorganization of the ocean circulation system and onset of vigorous upwelling currents at the end of the Early Triassic would mark the return to normal conditions and final recovery after the end-Permian mass extinction.

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THE TRACHYCERATIDAE FROM SOUTH CANYON (CENTRAL NEVADA): RECORD, TAXONOMIC PROBLEMS AND STRATIGRAPHIC SIGNIFICANCE FOR THE DEFINITION OF THE LADINIAN-CARNIAN BOUNDARY

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Abstract—South Canyon, type locality of the Lower Carnian *Trachyceras desatoyense* Zone of the North American Standard Scale, has been extensively sampled utilizing a bed-by-bed approach. The ammonoid rich Middle Member of the Augusta Mountain Formation (Star Peak Group) has been sampled at five sites, and preliminary data are presented. Suture line analysis permits the identification of the genus *Daxatina* from the lower part of the Middle Member and subsequently, this genus is reported for the first time from South Canyon. *Trachyceras*, also identified on the basis of its suture line, definitely occurs in the higher part of the studied interval, about 50 m from the base. This discovery of *Daxatina*, a genus almost identical to *Trachyceras* except for its ceratitic suture line, brings into question the definite taxonomical position of *Trachyceras desatoyense* Johnston, 1941, a species whose suture line is not known. Taxonomical analysis of South Canyon Trachyceratidae is also complicated by the very common occurrence in both *Daxatina* and *Trachyceras* of a preseptal layer, an inner layer of the test that tends to smooth the internal mold with respect to the outer surface of the test. The occurence of *Daxatina*, in conjunction with conodont and daonellid faunal analyses, support the correlation of the lower part of the Middle Member with the Upper Ladinian *Frankites sutherlandi* Zone of British Columbia.

INTRODUCTION

By tradition, the chronostratigraphy of the Triassic is mostly based on ammonoids, which provide the highest power of biochronologic resolution for the study of marine successions. This distinctive advantage of the ammonoids also holds true for resolving one of the major chronostratigraphic problems of the Upper Triassic Series, i.e., the definition of the GSSP of the Carnian Stage. Up till now only one candidate marker for this boundary has been suggested, and this is the appearance of the ammonoid *Daxatina* cf. *canadensis* at Prati di Stuores-Stuores Wiesen, in the Dolomites, Italy (Broglio Loriga et al., 1999). The correlatability of this particular bioevent and its calibration with conodont and bivalve events are still under evaluation. South Canyon (central Nevada, Fig. 1) is one of the three most interesting areas for the definition of the GSSP of the Carnian Stage, and the other site is the Spiti Valley (Tethys Himalaya, northern India; Balini et al., 1998, 2001). South Canyon is of great interest because it is the key-locality for intercontinental correlation with North America. However, ammonoids from this site were never studied with a bed-by-bed approach. Because of the great importance of this site, a joint research program based on bed-by-bed sampling of ammonoids, conodonts (M.J. Orchard) and bivalves (C.A. McRoberts) was started in 2002. A summary of the new data is presented in the Field Trip Guidebook (Balini et al., 2007), and the conodonts are described by Orchard and Balini (this volume). Herein, we describe in more detail certain facts and taxonomic problems concerning a key group for the definition of the Ladinian-Carnian boundary, i.e., the ammonoids of the Family Trachyceratidae Haug, 1894.

IMPORTANCE OF SOUTH CANYON FOR THE NORTH AMERICAN TRIASSIC

For more than 60 years South Canyon has been regarded as the best locality for the Lower Carnian in North America. It is the type locality of the *Trachyceras desatoyense* Zone, the first zone of the Lower Carnian of the North American Standard Scale (Silberling and Tozer, 1968; Tozer, 1994; Fig. 2), that is based on the ammonoid "fauna" described by Johnston in 1941. This "fauna" is of high diversity, consisting of 13 genera, 17 new species (among them *Trachyceras desatoyense*), and 5 taxa in open nomenclature, but until the work of Tozer (1994) it had not been recognized elsewhere in North America. Its position within the North American Standard Scale was not easy to define, and a few refinements were required (see also Balini et al. 2007, fig. 3). Johnston (1941) correlated the "fauna" with the Lower Carnian *Trachyceras aon* or *Trachyceras aonoides* zone of the Tethyan Triassic, but its position with respect to the typical Upper Ladinian ammonoid zones was not recognized until 1968, when Silberling and Tozer discovered elements of the *Frankites sutherlandi* Zone, the uppermost zone of the Upper Ladinian, several hundreds of feet below the *Trachyceras desatoyense* "fauna". The position of the *Trachyceras desatoyense* zone with respect to the other Carnian ammonoid zones was even more difficult to clarify. In 1968 Silberling and Tozer suggested time equivalence with the *Trachyceras obesum* Zone of British Columbia, a poorly documented zone also containing *Trachyceras s.s.* ammonoids (Tozer, 1967; Silberling and Tozer, 1968). This poorly defined zone was later revised by Tozer (1981 and 1994); *Trachyceras obesum* was moved to *Austrotrachyceras* Krystyn, 1979, and the discovery in British Columbia of a few *Trachyceras desatoyense* specimens below the *Austrotrachyceras obesum*

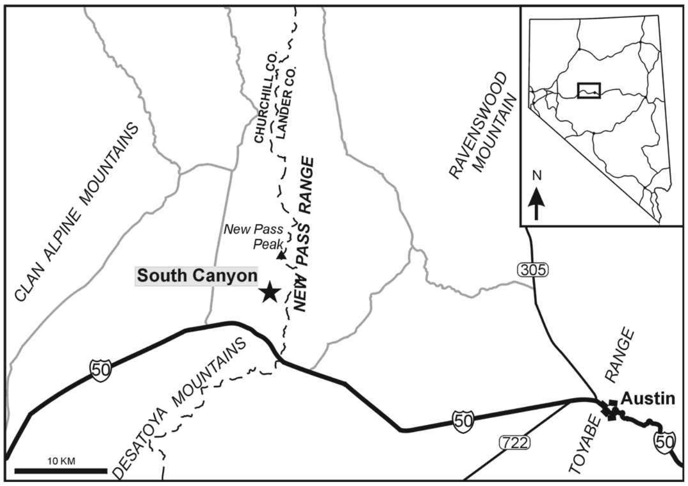

FIGURE 1. Location map of South Canyon in the New Pass Range (central Nevada).

		Ammonoid Zone	Type locality
CARNIAN	Lower	*Sirenites nanseni*	Ewe Mountain, BC
		Austrotrachyceras obesum	Ewe Mountain, BC
		Trachyceras desatoyense	South Canyon, Nevada
LADINIAN	Upper	*Frankites sutherlandi*	Boiler Canyon, BC
		Maclearnoceras maclearni	Fossil Gate, BC
		Meginoceras meginae	Boiler Canyon, BC

FIGURE 2. The North American Upper Ladinian–Lower Carnian ammonoid Standard Scale (Tozer, 1994). Except for the *Trachyceras desatoyense* Zone (shaded area) all zones are defined in British Columbia (BC).

Zone, definitively established the position of the *T. desatoyense* Zone as lowermost Carnian, below the *A. obesum* Zone.

THE STRATIGRAPHIC SUCCESSION AT SOUTH CANYON

The Triassic succession at South Canyon was briefly described by Silberling (1956). In 1977 Nichols and Silberling discussed lithostratigraphic classification and correlation, and they slightly modified the lithostratigraphy of the section. Figure 3 shows the synthetic log of the Triassic succession (see Balini et al., 2007, for descriptions of the lithofacies). Basically, the Augusta Mountain Formation is subdivided into three members. The Lower Member consists of thick-bedded to massive coral limestones, with intercalations of conglomerates in the lower part, and of shales in the upper part. The top of the Lower Member is very peculiar and consists of well bedded coquina-like brachiopod limestone beds, which testify to the drowning of the carbonate platform. The Middle Member, consisting of alternating marls and limestones, is capped by massive limestones of the Upper Member, which record the onset of carbonate platform conditions.

The Augusta Mountain Formation is rather fossiliferous. Foraminifers (Gazdzicki and Stanley, 1983), cnidarians (Roniewicz and Stanley, 1998) and bivalves (Waller and Stanley, 2005) were reported mostly from the Lower Member. Brachiopods are very abundant at the top of the member, but they have not been studied. Conodonts were reported from the Middle Member by Mosher (1968). Ammonoids occur in two fossil bearing intervals (Silberling and Tozer, 1968). The lower occurrence, recorded within the Lower Member (USGS Locality M2559), provided ammonoids representative of the *Frankites sutherlandi* Zone, while the upper occurrence, documented in the lower part of the Middle Member (USGS Locality M2560), is the ***stratum typicum*** of the *Trachyceras desatoyense* Zone. New data regarding ammonoids, conodonts and bivalves from the lower part of the Middle Member are briefly described by Balini et al. (2007) and by Orchard and Balini (this volume).

THE STUDIED SECTIONS

Sections

South Canyon is oriented approximately W-E and the Triassic succession strikes 120°-140° SE and dips 40°-60°SW. The beds dip with the slope on the northern side of the canyon, whereas they dip against the slope on the southern side. Details on the distribution of the outcrops are illustrated in Balini et al. (2007), but here we simply summarize that the Middle Member is soft weathering and is not very well exposed. The best outcrops are located on the northern side of the canyon (WGS84 coordinates 39°36'N, 117°30'W) because the debris cover is thinner than on the southern side. Natural outcrops are scattered, and bed-by-bed sampling of the stratigraphic section usually requires the removal of debris. Five sites were sampled during four field excursions from 2001 to 2006. These sites (labelled A, B, D, E and F) are distributed over a distance of less than 500 m along strike. The stratigraphic intervals exposed at the five sites are shown in Figure 4. Site A is more or less equivalent to USGS locality M2560 (N.J. Silberling, personal commun. to MB and JJ, 2001).

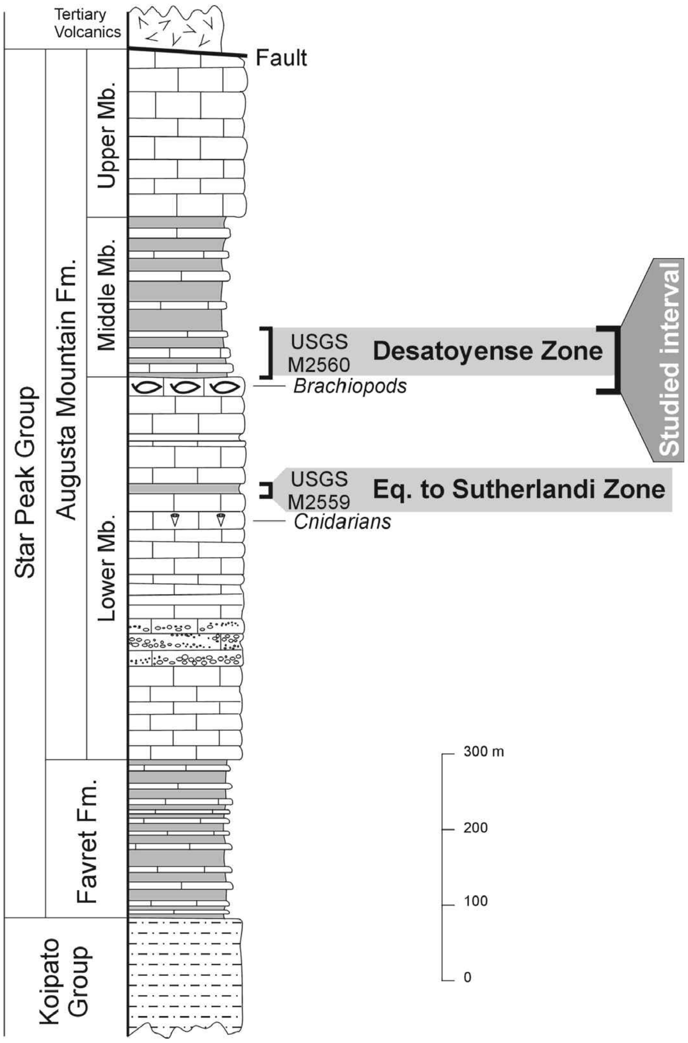

FIGURE 3. The Triassic succession at South Canyon. The stratigraphic section is slightly modified from Silberling (1956). The position of USGS localities M2559 and 2560 is described in Silberling and Tozer (1968).

Lithology

The upper part of the Lower Member and the lowermost 70 m of the Middle Member can be subdivided into the following four lithologic intervals (see also Balini et al., 2007; Fig. 4):

1) Lower Member. Gray crinoidal packstones in 20 to 50 cm thick beds.

2) Lower Member. Gray bioclastic, brachiopod rich, packstones in 10 to 20 cm thick beds, with rare marly interbeds. Thickness about 7 m.

3) Middle Member. Monotonous alternation of light gray to dark gray bioclastic marly mudstones and wackestones with gray marls. The mudstones-wackestones usually contain varying amounts of ammonoids, and sometimes brachiopods and bivalves. Brachiopods are more common in the lowermost part. Thickness about 65 m.

4) Middle Member. Interval dominated by gray mudstones in 30 to 50 cm thick beds, with some intercalations of up to 60 cm thick intervals of marly mudstones/calcareous marls in 1 cm thick beds and

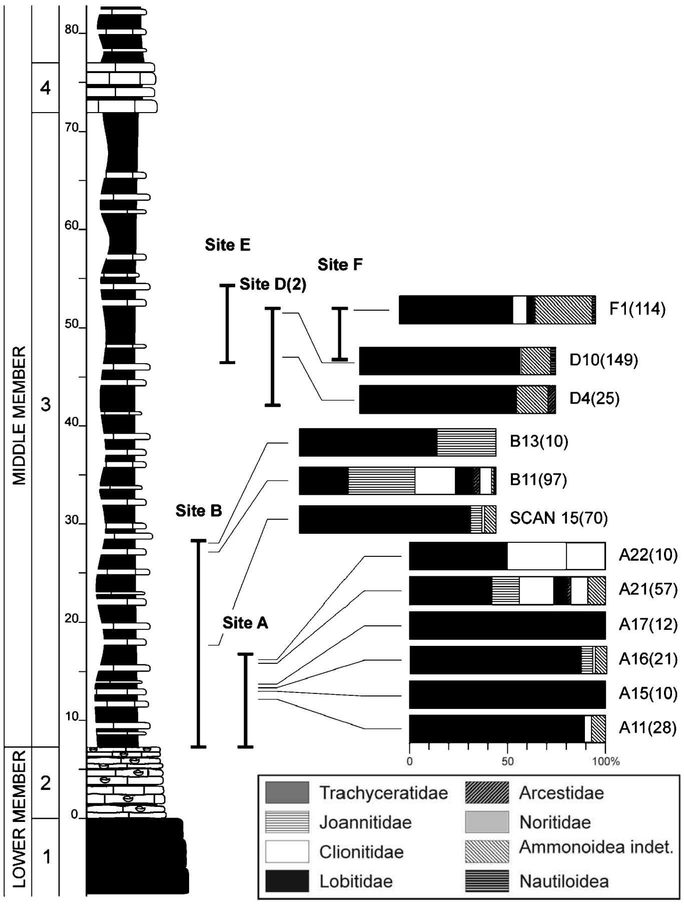

FIGURE 4. The lowermost part of the Middle Member of the Augusta Mountain Formation on the northern side of South Canyon showing the position of the stratigraphic intervals sampled at sites A, B, D (2), E and F, as well as the faunal composition of some cephalopod assemblages. Numbers at the right of the faunal bars show the designation number of the sample (section and # of bed) and, in parentheses, the total number of cephalopod specimens in the sample.

with marls.

Lithologic intervals 1-2 and 4 are much better exposed than the soft weathering interval 3, and have been used to define and compare the relative position of the studied sections.

Sampling

Sampling was conducted utilizing a bed-by-bed approach. All naturally or artificially exposed beds at the five sites were sampled. Occasionally, some beds exposed along side the sections were also sampled. These samples are plotted on the sections, but they are separate from samples taken within designated sections.

Sampling procedures assured almost no selection of specimens, and nearly all incomplete specimens were kept as well. Consequently, we may safely assume that sampling composition reflects the composition of the faunas recorded in the beds.

THE RECORD OF TRACHYCERATIDAE

Faunal Composition

In the studied sections nearly all beds are fossiliferous. Cephalopods are the most common megafossils, but brachiopods and bivalves are also common. Brachiopods are not only restricted to interval 2 (Fig. 4), but they are also found in the lower part of interval 3. Their frequency decreases, while the frequency of daonellids increases. A total of 1505 ammonoids have been collected thus far.

Ammonoids are found from the uppermost bed of the brachiopod packstones (interval 2) to the Middle Member. Faunal composition of the cephalopod assemblages is shown in Figure 4. Ammonoids belong to the families Trachyceratidae, Joannitidae, Clionitidae, Lobitidae, Arcestidae and Noritidae. Family indeterminate mainly includes rather incomplete specimens of small size with almost evolute coiling, which could be referred to either *Clionitites* (family Clionitidae) or *Hannaoceras* (family Trachyceratidae).

Trachyceratidae are undoubtedly the most frequent group of ammonoids, and they represent a little more than the 50% of the overall collection. Their dominance normally ranges between 50 to 80%. Only rarely it is lower than 40%, but on occasion they represent 100% of the assemblage. Faunal diversity at the family rank may change from bed to bed, and does not seem to be influenced by sample size. The faunas with the highest diversity are A21, B11, and F1, with 5 to 6 families, but sample D10 yielded the largest number of specimens, and includes only Trachyceratidae, as well as Nautiloids and specimens in open position (family indet.).

Family Composition

Although taxonomic analysis is still in progress, we do present some qualitative and semiquantitative data. Ammonoid families are represented by few to very few genera. Joannitidae, Clionitidae, Lobitidae and Noritidae are represented by only one genus each, *Joannites*, *Clionitites*, *Lobites* and *Neoclypites*, respectively. No definite examples of *Perrinoceras* (family Hungaritidae) and *Coroceras* (family Lobitidae) were collected even though these two genera were reported from South Canyon by Johnston (1941). The Trachyceratidae are only slightly more diversified. Most belong to the group of *Daxatina* and *Trachyceras* (Figs. 5-6), while *Hannaoceras* is much rarer. *Silenticeras* is represented by only one specimen from level D4, but the occurrence of *Frankites sutherlandi* from levels SCAN 14 and SCAN 15 is noteworthy (Fig. 5, Balini, in press). The first report of *Frankites* from South Canyon is of great bio- and chronostratigraphical significance, but it is treated in a separate contribution (Balini, in press). Here we focus on another group of Trachyceratidae very important for bio- chronostratigraphy, i.e., the group of *Daxatina* and *Trachyceras*.

TAXONOMIC PROBLEMS AFFECTING THE TRACHYCERATIDAE

Among the Trachyceratidae, the genera *Daxatina* Strand, 1919, and *Trachyceras* Laube, 1869 are morphologically very close. Both genera are characterized by a ventral furrow, dense ribs, several spiral rows of nodes and two rows of double-pointed ventral nodes bordering the furrow. Although *Daxatina* sometimes has triple pointed ventral nodes (e.g., *Daxatina canadensis* Whiteaves, 1889: Tozer, 1994, pl. 85, fig. 7), the only clear distinguishing difference between the two genera is the suture line, which is ammonitic in *Trachyceras*, and ceratitic in *Daxatina*, with occasional wrinkles on the external saddle (Tozer, 1994, p. 166, fig. 68e).

Taking into account that *Daxatina* is traditionally regarded as a latest Ladinian genus in North America, and that *Trachyceras* is accepted everywhere in the world as a typically Carnian ammonoid, the morphological similarities between the two genera suggest possible phylogenetic relationships. However, up till now bed-by-bed analysis of these relationships has not been done.

Even if the morphological similarities of *Daxatina* and *Trachyceras* may suggest intriguing and stimulating hints for future phylogenetic investigations, there is, however, a direct and somewhat depressing consequence: for specimens retaining the test, the separation of *Daxatina* and *Trachyceras* may be nearly impossible.

Given this complex background, it is clear that the South Canyon ammonoid record is of great interest. This is probably the only site in the

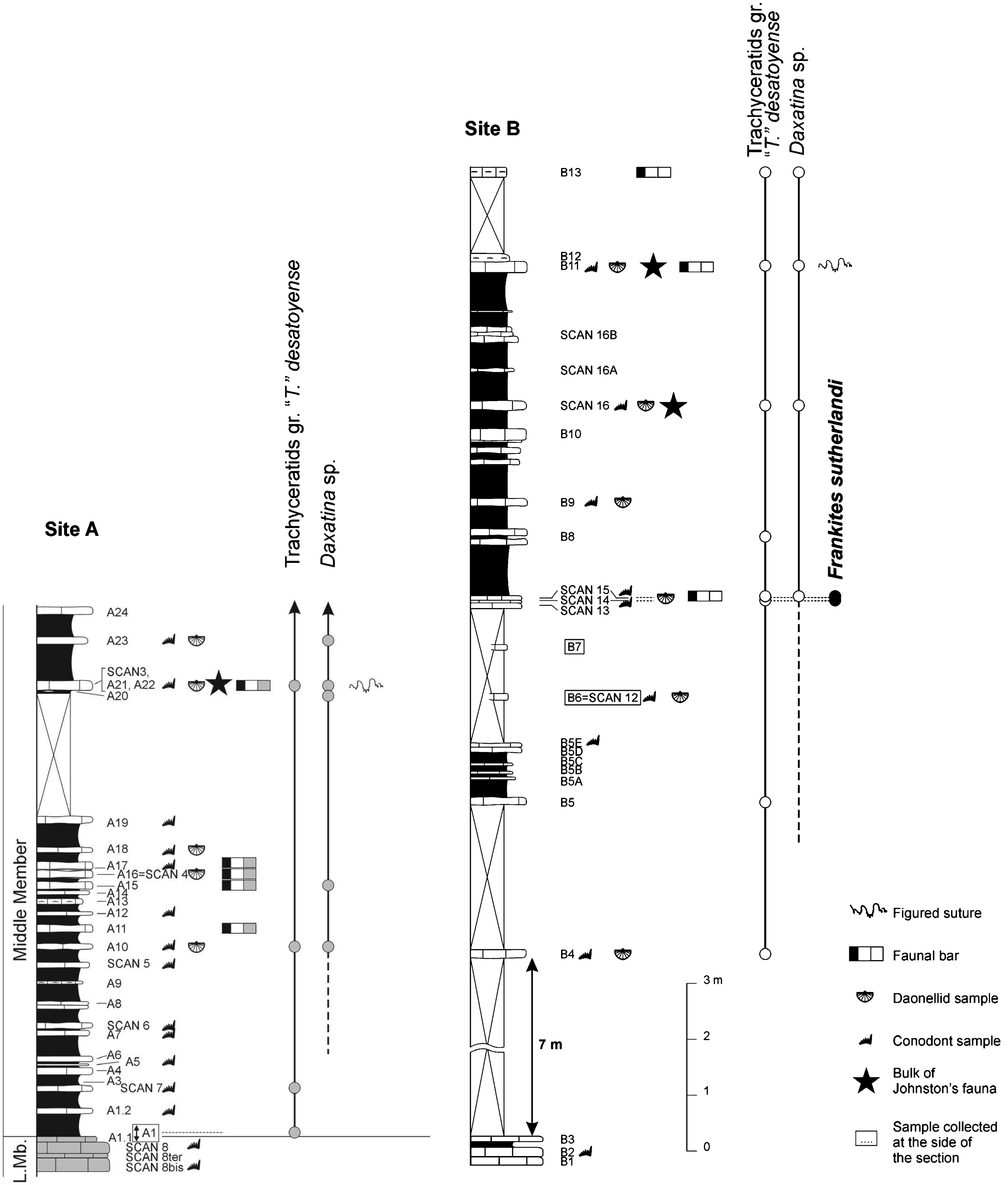

FIGURE 5. Stratigraphic sections sampled at sites A and B, with the distribution of some ammonoid taxa. Daonellid and conodont faunas are described in Balini et al. (2007).

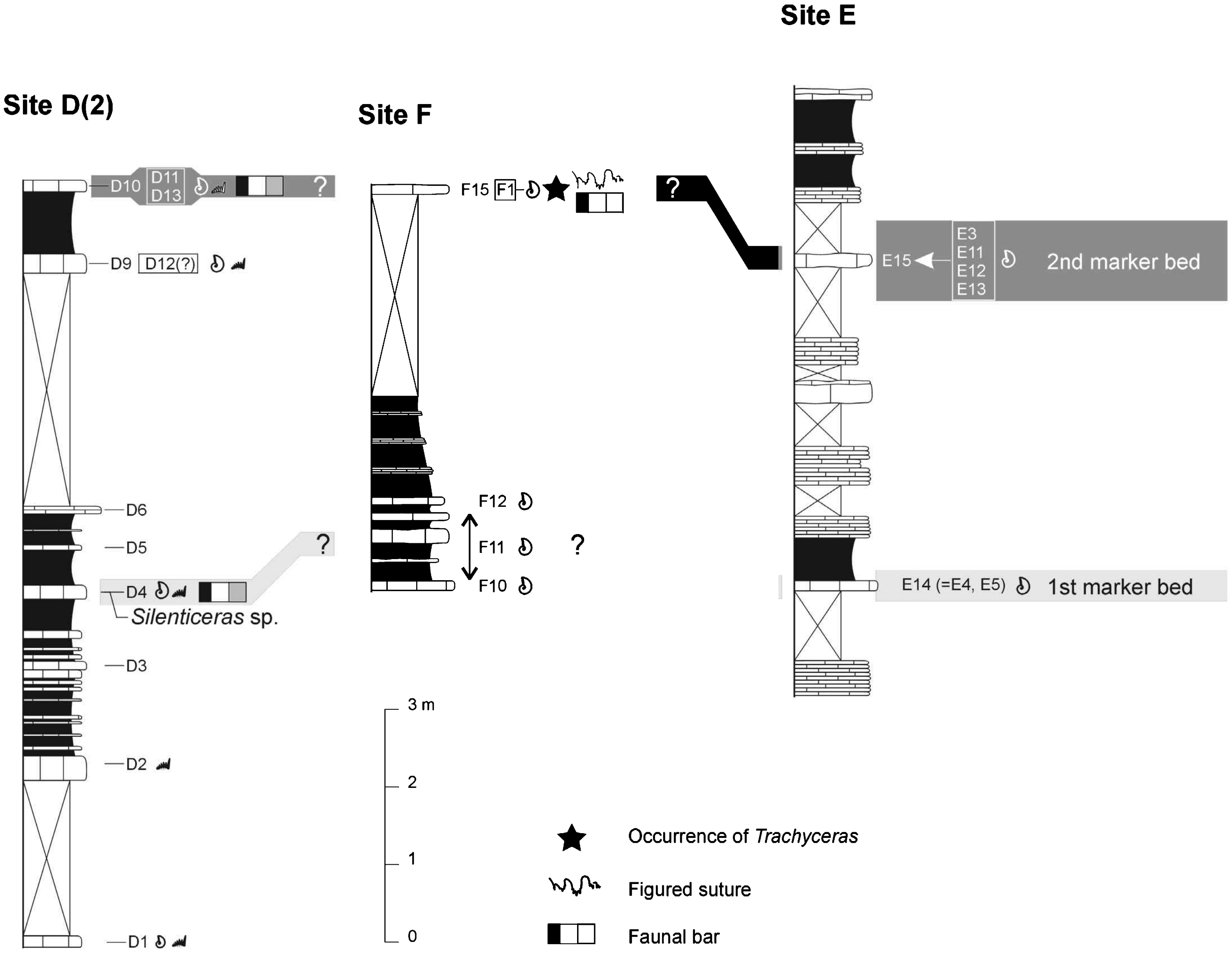

FIGURE 6. Stratigraphic sections sampled at sites D(2), E and F showing the position of the two most important fossil bearing levels. The two marker beds are briefly illustrated in Balini et al. (2007).

world with a very rich and uncondensed record of well preserved Trachyceratidae, in particular of the group of *Daxatina* and *Trachyceras*. At the present stage of work, the taxonomic revision of the ammonoid faunas of South Canyon is not yet complete. However, we present herein a few facts which are useful for the discussion on the GSSP of the Carnian Stage. We also illustrate some problems in order to show the direction of ongoing investigations.

Fact #1: *Daxatina* is Documented in the South Canyon Sections

At sites A and B, *Daxatina* is quite common and is represented by at least two groups. The first group exhibits a rather involute coiling and is very densely and finely ribbed (Fig. 7A-B). It includes some of the specimens classified by Johnston as *Trachyceras* cf. *T. aonoides*. The other group is more strongly ornamented and is probably represented by more than two species (Fig. 7C-E). The suture lines (Fig. 8) are clearly ceratitic, or just slightly crenulated.

Daxatina has been also found in the 2nd marker bed sampled at sites D(2) and E (Fig. 7E).

Fact #2: *Trachyceras* is also Documented in the South Canyon Sections

The sections sampled at sites D(2), E and F (Fig. 6) are characterized by two rather rich fossil bearing levels, which can be easily correlated, especially sites D(2) and E (Fig. 6). The lower level (levels D4= E14,E4 and E5) yields involute, compressed and densely ribbed Trachyceratidae, while the upper level (D10=E15, E3, E11, E12, E13) yields not only compressed and densely ribbed Trachyceratidae, but also the above mentioned coarsely ornamented *Daxatina* (Fig. 7E). These two marker beds are also probably exposed at site F (Fig. 6). The search for preserved suture lines has not met with much success in the 1st marker bed, while in the 2nd marker bed *Daxatina* (level D10 and E3) and two groups of ammonoids with an ammonitic suture have been identified (Figs. 9-10). The first group (Figs. 9-10A) exhibits a suture that is undoubtedly ammonitic, even if it is not as deeply indented as in typical *Trachyceras aon*. This group fits much better with *Trachyeras* than with *Daxatina* because the latter never displays true indentitions of the saddles. The second group possesses a more indented suture (Fig. 10B) and is conspecific with the specimen classified as *Trachyceras* (*Trachyceras*) cf. *T. desatoyense* Johnston by Silberling (1956, fig.2B). However, this second group of *Trachyceras* does not agree with the types of *Trachyceras desatoyense*, since it exhibits a narrow venter and an almost subtriangular whorl section (M.B. pers. observation of specimens housed at NMNH, Washington).

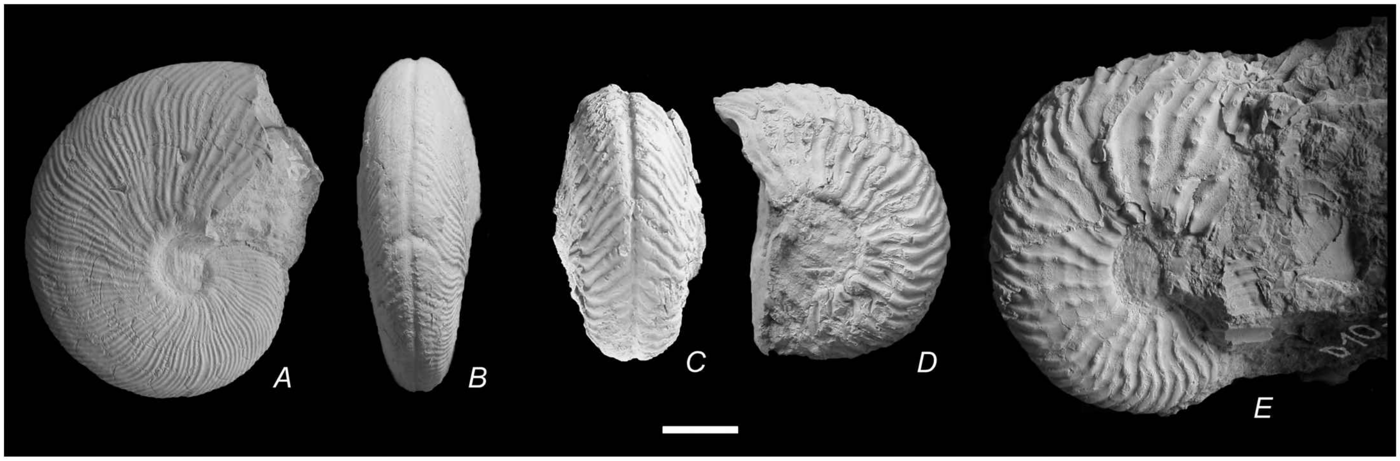

FIGURE 7. Examples of *Daxatina* from South Canyon. **A**, specimen B11-76, internal mould of phragmocone, lateral view. **B**, same specimen, ventral view. **C**, specimen B11-95, phragmocone, ventral view. **D**, same specimen, lateral view. **E**, specimen D10-70, body chamber, lateral view. Bar scale is 1 cm.

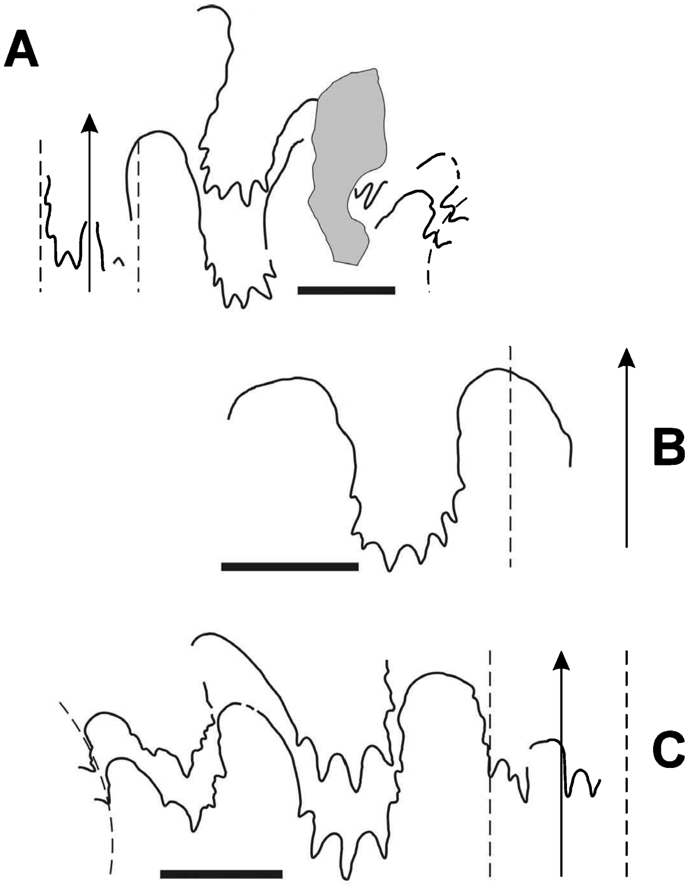

FIGURE 8. Suture lines of *Daxatina* specimens. **A**, specimen A22-8. **B**, specimen B11-95 (see also Figure 7C). **C**, specimen B11-66. Shaded area is covered by test. Bar scale is 0.5 cm.

Question #1 and #2: Where is and What is *Trachyceras desatoyense* Johnston, 1941?

These questions cannot be answered at the present time. The type specimens of *Trachyceras desatoyense* retain the test, and their suture lines are unknown. Moreover, Johnston did not select as the holotype one of his beautifully preserved, relatively large sized specimens such as pl. 68, fig. 4, but instead, chose one of the smallest specimens (pl. 67, fig. 4-5), which is a juvenile.

The preservation of the test should not represent a problem for the understanding of the internal mold, because for ammonoids the internal mold normally reflects almost exactly the morphology of the outer surface of the test. Unfortunately, this is not true for the South Canyon Trachyceratidae. *Frankites*, *Daxatina*, and *Trachyceras* specimens in the collection exhibit, almost as a rule, a thick and well developed preseptal layer (Fig. 11) in the innermost part of the body chamber, as well as on the phragmocone. This structure of the shell was described by Tozer (1972) for *Frankites*, but this is the first report for *Daxatina* and *Trachyceras*. Figure 11 includes some examples of specimens possessing a preseptal layer. In some specimens (Fig. 11A-B) two layers can be recognized, while other specimens apparently have three layers (Fig. 11C-D). Further investigation is necessary to clarify the structure and ontogenetic meaning of this double or multilayered feature.

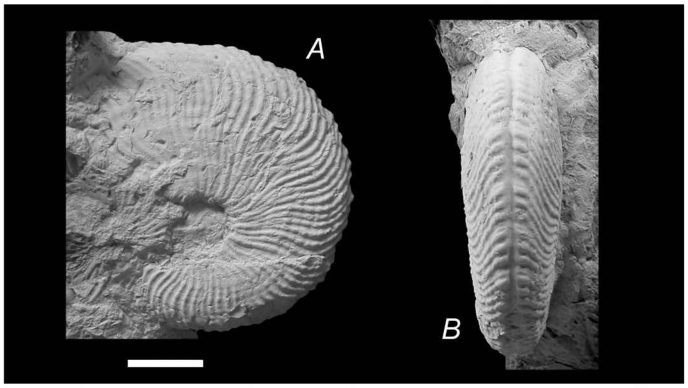

FIGURE 9. Example of *Trachyceras* from level F1, specimen F1-54 (see also Figure 10A) preserved as internal mold with preseptal layer. **A**, lateral view. **B**, ventral view showing rounded instead of double pointed ventral nodes. Bar scale is 1 cm.

From a taxonomic point of view, the preseptal layer precludes a direct comparison between the internal mold and outer surface of the test because the internal mold may be much smoother than the outer surface (Fig. 11D). When the preseptal layer is present, the septa are imprinted onto it, and not on the (outer) test. This structural feature does not have a "smoothing" influence on the indentitions of the suture lines. Specimen F1-54 (Fig. 10A) possesses a preseptal layer, and its suture line was drawn from the surface of the internal mold. Notwithstanding this feature, its suture line is definitely ammonitic.

STRATIGRAPHIC SIGNIFICANCE OF THE NEW DATA

Results from the recent investigations conducted at South Canyon on ammonoids, conodonts and bivalves, in cooperation with M.J.

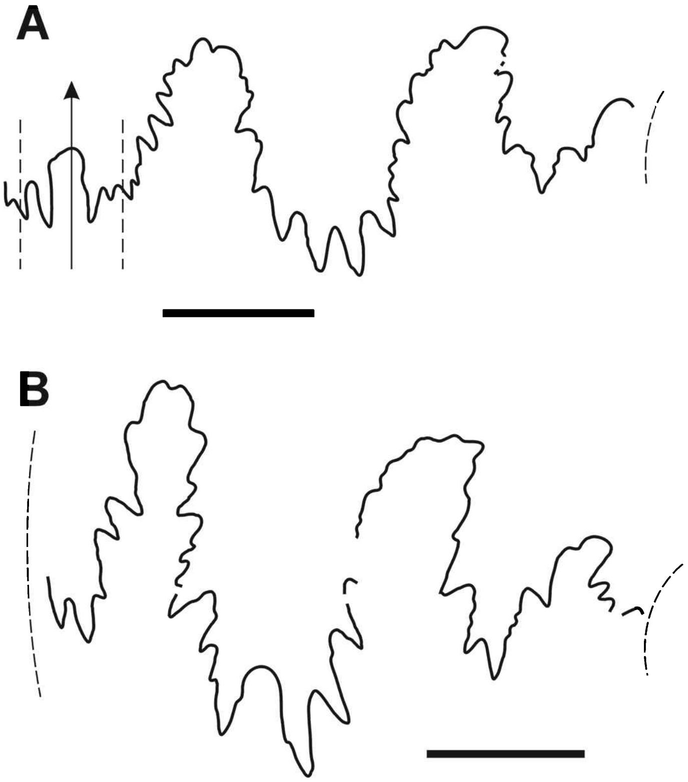

FIGURE 10. Suture lines of *Trachyceras* specimens. **A**, specimen F1-54. **B**, specimen F1-1, submature, probably conspecific with *Trachyceras* (*Trachyceras*) cf. *T. desatoyense* Johnston, Silberling 1956 (non Johnston, 1941). Bar scale is 0.5 cm.

Orchard and C.A. McRoberts (Balini, in press; Balini et al., 2007; Orchard and Balini, this volume), necessitate a modification in the correlation of the South Canyon succession with British Columbia. The lower part of the Middle Member of the Augusta Mountain Formation exposed at site A and B is now correlated with the upper part of the *Frankites sutherlandi* Zone of British Columbia. With regard to ammonoids, the facts in support of this new correlation are:

1) The occurrence of *Frankites sutherlandi* at site B, level SCAN 14 and 15 (Balini, in press).

2) The occurrence of *Daxatina* from the lower part of site A to the top of site B, and in level D10.

3) The occurrence of *Trachyceras* rather high in the succession (site F, level F1).

Ongoing investigations are focused in three directions:

a) To complete the study of the Trachyceratidae at site A and B in order to determine if *Daxatina* occurs together with *Trachyceras*. As shown in Figure 5, some ammonoids resemble the external morphology of *T. desatoyense* Johnston (Fig. 11E-F) from the top of the Lower Member to the top of Site B. The suture line of these specimens is unknown.

b) To test whether the F.O. of *Trachyceras* is recorded in the 2nd marker level or in the 1st marker level. The suture line of specimens from level D4 (=E14) is not known.

c) To study the beds overlying F1 in order to determine where the main faunal change occurs.

Given that in North America the Ladinian-Carnian boundary traditionally has been placed at the first occurrence of *Trachyceras* (Tozer, 1967; Silberling and Tozer, 1968; Tozer, 1981 and 1994), the identification of *Trachyceras s.s.* only from higher levels at South Canyon strongly suggests that the Ladinian-Carnian boundary should be moved from the ammonoid barren shallow water limestones of the Lower Member to the fossil rich limestones of the Middle Member. This relocation of the boundary improves the overall significance of the South Canyon succession since the Ladinian-Carnian boundary would not be influenced by a facies change. However, the practical difficulties in the separation of *Daxatina* from *Trachyceras* would suggest the re-evaluation of *Trachyceras* as a guide fossil for the base of the Carnian Stage. The final decision on the selection of the boundary marker event will depend on the possibility of having the support of additional marker events for identification and correlation. The experience with the South Canyon succession (Balini et al., 2007) demonstrates that for the definition of the base of the Carnian Stage, no single bio-chronostratigraphic tool prevails over the others for the power of resolution and correlatability.

ACKNOWLEDGMENTS

We are especially indebted to N.J. Silberling for providing accurate information on the position of the fossil localities and to H. Rieber and W. Weitschat for preliminary visits with JJ. L. Krystyn (Vienna University) very kindly provided information on South Canyon lithostratigraphy and specimens for comparison. The manuscript has been carefully reviewed by M. Gaetani (Milano University) and P. Mietto (Padova University). Their suggestions are greatly appreciated.

Since 2001 South Canyon has been visited several times by MB and JJ. In 2002 the sections at Sites A and B were sampled together with M.J. Orchard and C.A. McRoberts with the help of C. Larghi (Milano University), T. Beattie (Simon Fraser University, Vancouver) E. Hopkin (at that time at SUNY, Cortland), and V. Atudorei (University of New Mexico). Sites D and E were sampled in 2005 with the help of A. Nicora and P. Taiana (Milano University). Site F was investigated in October 2006.

This study is a contribution to IGCP 467 "Triassic Time and trans-Panthalassan Correlations" (M. J. Orchard). The 2006 field sampling was carried out within the framework of the field activity of the Museo di Paleontologia, Dipartimento di Scienze della Terra (Milano University).

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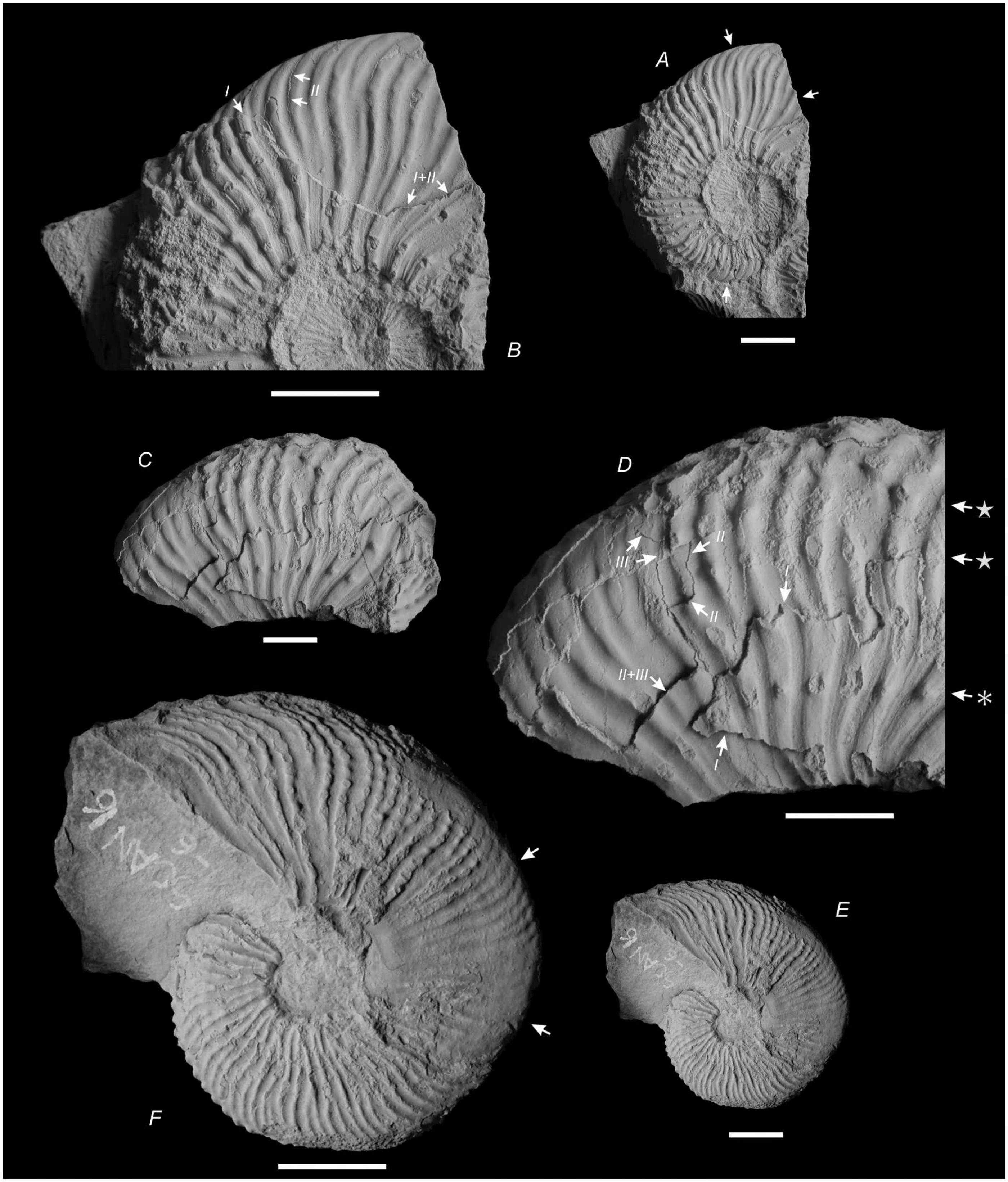

FIGURE 11. Trachyceratidae from sites B and D, showing some examples of development of preseptal layer. **A-B**, specimen D10-91. **A**, the arrows indicate the position of the internal mold. **B**, in this view two layers are visible. I: outer layer (?test), II: preseptal layer. **C-D**, specimen D10bis-77, body chamber. **C**, natural size. **D**, enlarged view showing multilayer structure. I: outer layer, II: intermediate layer, III: inner layer (preseptal layer). Asterisk marks the position of a row of nodes which are visible on both external and the intermediate layers. Stars indicate two rows of nodes, which are visible on the intermediate layer, but not on the internal mold. **E-F**, specimen SCAN16-6. **E**, natural size. **F**, enlarged view. Arrows indicate the part of the internal mold "smoothed" by the preseptal layer. Scale bar for all specimens is 1 cm.

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LOWER TRIASSIC MICROBIALITES VERSUS SKELETAL CARBONATES, A COMPETITION ON THE GONDWANA MARGIN

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As shown by Baud et al. (2005, 2007), a major crisis occurred in Phanerozoic carbonate systems during the end-Permian mass extinction that involved a wholescale change in oceanic geochemistry. The prolific upper Paleozoic skeletal carbonate factory was abruptly replaced by a non-skeletal carbonate factory (Baud, 1998). When preserved between the two carbonate systems, the boundary is marked by a post-extinction clay (boundary clay) of latest Permian age (*preparvus-meishanensis* conodont zone). Microbial communities affected sedimentation in a variety of normal marine areas (Baud et al., 1997).

On the Cimmerian margin and on the Gondwana margin, from Zagros through Taurus westward, a post-extinction calcimicrobial unit occurs above the extensive Permian skeletal carbonate platform exposed in the shallow, low energy post-extinction carbonate ramp with massive thrombolitic mounds and/or stromatolites. To the east, on the Gondwana margin in Oman and North India, the calcimicrobial unit is more discrete or absent as shown by the Wasit block (Krystyn et al., 2003), where the skeletal carbonate is entirely building the basal Triassic limestones. In the Salt Range (Pakistan), with deepening of depositional environment, the basal Triassic crinoid-brachiopod grainstones are progressively replaced by ammonoid-bivalve packstone-wackestone (Wignall and Hallam, 1993). For these authors, the matrix of the limestone beds in the Ceratite marls is made of disintegrated shells of the bivalve *Leptocondria minima*. A similar situation exists in Kashmir with deeper limestone deposits. There are no visible microbial textures seen or published in the Lower Triassic of Zanskar and the Spiti areas (Western Tethys Himalaya), but more research is needed.

In a Tethys Himalaya section of Central Nepal, Bassoullet and Colchen (1976) report a planar stromatolite bed of half a meter thickness in their "coupe 2" of Ganesh Himal (probable Dienerian age), between skeletal (bivalves-ammonoids) lime wackestone to packstone beds.

To the east, in the Tulong section of South Tibet, isolated stromatolite buildups (cm to dm) have grown on the top of ammonoid wackestone-packstone beds (Smithian age: H.Bucher, oral communication). In this section, the Spathian red ammonoid limestones show levels with stromatactis and thrombolitic texture, but the microbial activity seems incidental compared to the skeletal carbonate production (mainly ammonoids and bivalves).

In summary, in the southern latitudes of the Gondwana margin, in contrast to the low latitudes and equatorial domains, the environments of deposition are more favorable to the skeletal organisms, which are in competition with the microbial carbonate factory, but the result is a very low rate of deposition (condensed deposit).

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FLORAL AND PALEOENVIRONMENTAL CHANGES DURING THE END-TRIASSIC: NEW DATA FROM EUROPEAN KEY SECTIONS

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The Triassic-Jurassic boundary extinction event is still subject to many controversies. There were major changes during the end-Triassic in both the terrestrial and marine realm, but the cause, timing and pattern of the extinction is not clear yet. Palynology is a very useful biostratigraphic tool for land-sea correlation because events in terrestrial microfloral assemblages preserved in marine sediment successions can be integrated in a marine (bio)stratigraphic framework. Another application of palynology is the reconstruction of past changes in vegetation and climate. We present the results of a high resolution palynological study from two European Tr-J boundary key sections: the Hinteriss section in the Northern Calcareous Alps (Austria), and the St. Audrie's Bay section in the UK. The main objective is to document floral changes and infer palaeoenvironmental changes throughout the Late Triassic. In the Hinteriss section, the palynomorph assemblages (e.g., *Ovalipollis, Rhaetipollis*) still show a Rhaetian age for the lowermost part of the Kendlbach Formation (i.e., Schattwald Beds of the Tiefengraben Member). Based on palynological evidence, the Tr-J boundary may be drawn in the middle part of the Tiefengraben Member, where also the oldest Jurassic ammonite enters the record. In both the Tethys realm and St. Audrie's Bay, pollen assemblages below the initial negative carbon excursion show a vegetation dominated by conifers (e.g., *Cheirolepidiaceae*) and seed ferns. Just after the initial shift both sections show a distinct increase in fern spores and a decrease in the amount of pollen from *Cheirolepidiaceae*. It seems that this change in vegetation occurs earlier in St. Audrie's Bay. At the start of the main negative isotope shift (lower part of the Blue Lias Fm), the St. Audrie's Bay pollen record indicates a vegetation almost completely consisting of *Cheirolepidiaceae,* which persists throughout the section. The contemporaneous pollen record from the Alpine realm consists, in contrast, of continuously high amounts of fern spores, while *Cheirolepidiaceae* pollen occur at significantly lower abundances.

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SMITHIAN (EARLY TRIASSIC) AMMONOID SUCCESSIONS OF THE TETHYS: NEW PRELIMINARY RESULTS FROM TIBET, INDIA, PAKISTAN AND OMAN

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Following the end-Permian mass extinction, ammonoids were among the fastest clades to recover (Brayard et al., 2006), with at least two diversification phases during the Early Triassic. Diversification first peaked during the Smithian and was followed by a marked extinction phase at the end of this (sub-)stage. It was then followed by a second and massive evolutionary radiation during the Spathian. The well-documented, ammonoid-rich Smithian succession of NW Guangxi, South China is subdivided into three main faunas, i.e., the "*Flemingites rursiradiatus* beds", the "*Owenites koeneni* beds" and the "*Anasibirites multiformis* beds," in ascending order (Brayard and Bucher, subm.). Ongoing work on other Smithian Tethyan sections such as Tulong (Tibet), Spiti (India), Salt Range (Pakistan), and Oman (exotic blocks at Baid, Wadi Musjah and Jabal Safra) shows that these subdivisions have Tethyan-wide correlatives. Moreover, even finer subdivisions can be correlated throughout the studied basins (Fig. 1).

The beginning of the Smithian is characterized by beds with *Rohillites*, which occur in Guangxi, Spiti (Krystyn et al., 2007), the Salt Range and Oman. The subsequent "*Flemingites* beds" occur in Guangxi, Spiti, the Salt Range, and Oman and contain a highly diversified ammonoid fauna. In the Tulong section, ammonoids are not preserved in this interval, but this time interval is nevertheless represented by diagnostic conodont assemblages. The next overlying *"new prionitid A"* beds were found in Tulong and in the Salt Range. Associated with this new genus are *Aspenites acutus* and *Juvenites*. Their exact correlation with the NW Guangxi succession remains open.

The genus *Owenites* of middle Smithian age is relatively long-ranging and occurs in all studied localities except for the Salt Range. In NW Guangxi, the "*Owenites* beds" are further subdivided into the *Ussuria*, *Hanielites/Proharpoceras* and the *Inyoites/Pseudoceltites* horizons (Brayard and Bucher, subm.). These smaller subdivisions are partly found in the other studied sections. The lower part of the *Owenites* beds in Tulong, Spiti, the Salt Range and in Oman is represented by beds containing a new genus, provisionally called *"new prionitid B,"* as well as *Paranannites spathi* and *Owenites simplex*. These beds are more or less correlative to the *Ussuria* and *Hanielites/Proharpoceras* horizons from NW Guangxi. *Proharpoceras* was also found in an exotic block from Oman of presumably the same age (Brayard et al., in press). The next beds in the Salt Range and in Tulong are characterized by the occurrence of *"flemingitid A,"* which may possibly represent a new genus among Flemingitidae. Exact correlation of this fauna with the NW Guangxi succession remains open. The upper part of the "*Owenites* beds" is characterized by the association of *Inyoites*, *Pseudoceltites*, *Stephanites* and/or *Meekoceras* and is present at all studied localities.

The subsequent "*Anasibirites/Wasatchites* beds" also occur in all localities. However, in Tulong, only poorly preserved prionitids here referred to as ?*Wasatchites* were obtained. Therefore, the occurrence of this fauna in South Tibet still needs to be confirmed. The "*Anasibirites/Wasatchites* beds" mark the onset of the end-Smithian ammonoid extinction and are characterized by reduced diversity and a high degree of cosmopolitanism. The next overlying beds with *Glyptophiceras sinnatus* (Waagen) occur in the Salt Range, Kashmir and Spiti (*G. aequicostatus* (Diener) is here treated as a synonym of *G. sinnatus*) and probably also at Tulong, where they contain a new species of *Hedenstroemia*, called here *"Hedenstroemia A."* The uppermost Smithian beds contain *"Hedenstroemia A"* and various representatives of *Xenoceltites*. These beds were recognized in NW Guangxi, Tulong, Spiti and in the Salt Range. They correspond to the extinction peak at the very end of the Smithian.

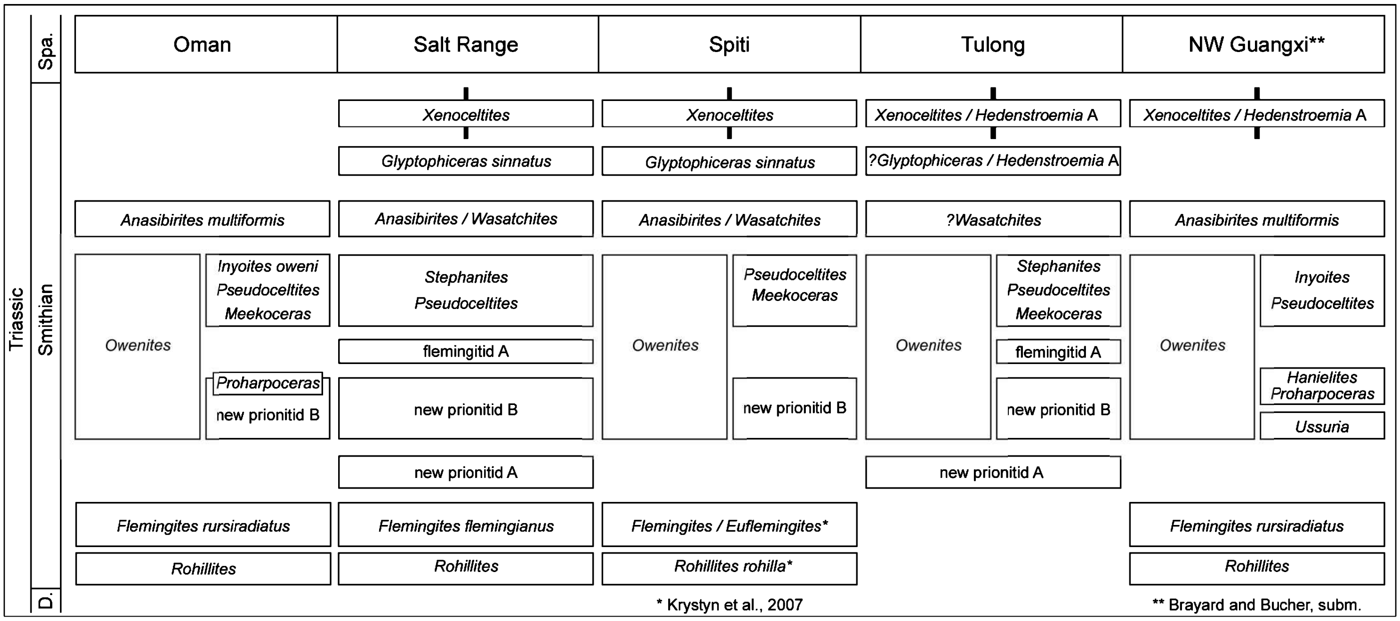

FIGURE 1. Correlation of Smithian Tethyan ammonoid successions.

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GLOBAL DISTRIBUTION OF RHAETIAN RADIOLARIAN FAUNAS AND THEIR CONTRIBUTION TO THE DEFINITION OF THE TRIASSIC-JURASSIC BOUNDARY

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This contribution presents a brief synopsis of past and newly studied areas where radiolarian faunas of Rhaetian age are adding to our global understanding of the end of the Triassic, and hence, the Triassic-Jurassic boundary.

Before the finding of complete successions of Rhaetian radiolarian faunas in the Sandilands Formation of Queen Charlotte Islands (QCI), British Columbia, Canada (Carter et al., 1989; Carter, 1990), only scattered records of the fauna were available from disparate regions of the world. These included: Cache Creek, British Columbia (Cordey et al., 1991), Oregon, USA (Yeh, 1989), Austria (Kozur & Mostler, 1981; Kozur 1984a,b); New Zealand (Spörli & Aita, 1988), Japan (Yao et al., 1980 a, b; Yao, 1982; Kishida and Sugano, 1982; Kishida and Hisada, 1986; Yoshida, 1986), China (Kojima & Mizutani, 1987; Kojima, 1989; Mizutani, Shao & Zhang, 1989), Tibet (Wang, Wang & Pei, 1990), the Philippines (Cheng, 1989; Yeh, 1990, 1992), Far East Russia (Bragin, 1986, 1990, 1991), and Oman (Carter, 1993). Following discoveries in QCI, Carter (1993) described many species and established Unitary Associations (UA) zonation for the *Proparvicingula moniliformis* Zone (assemblages 1 plus 2a-d; lower-middle Rhaetian) and the *Globolaxtorum tozeri* Zone (assemblage 3; upper Rhaetian). Since that time, Rhaetian faunas have been discovered in many other areas of the world (Table 1), new species have been described, some well known species have been confirmed to have a cosmopolitan distribution, and the faunas have proved very beneficial for age dating, particularly in areas where other age-diagnostic faunas are absent.

Newly studied areas where Rhaetian radiolarians have provided age dating or contributed to terrane analysis and/or the evolution of Tethys are briefly summarized below in the order they were reported:

The Philippines - Yeh & Cheng (1996) documented Rhaetian faunas from red chert on Busuanga Island. They described new species, reported the presence of other species described from QCI and Japan, and concluded the fauna was late early Rhaetian in age, closely resembling Rhaetian faunas from Central Japan.

Timor - Rose (1997) studied Late Triassic faunas from the River Meto sections of the Aitutu and Wai Luli formations in west Timor, finding comparison with taxa from Tethyan areas. Some Rhaetian taxa documented are cosmopolitan but others have stronger affinities with those in Japan and the Philippines.

Vancouver Island, B.C. - Mushroom Point, Kyuquot area, western coast of Vancouver Island - Carter (1997; internal report to GSC) reported lower Rhaetian faunas (lower part of the *Proparvicingula moniliformis* Zone). The faunas mirror QCI assemblages but also contain some species of lower latitude affinity similar to those of Baja California Sur (see below).

Japan – in a comprehensive study of Triassic and Lower Jurassic faunas of the Mino terrane, central Japan, Sugiyama (1997) documented the fauna, described new species and established 20 zones (TR 0-JR 0B). Rhaetian faunas were assigned to TR 8C: first occurrence (FO) Skirt F (possibly derived from *Haeckelicyrtium takemurai*) (late Norian to early Rhaetian) and TR 8D: FO *Haeckelicyrtium breviora* (early to late Rhaetian).

Turkey - Tekin (1999) studied Late Triassic radiolarians from the Antalyia Nappes, Central Taurides, Southern Turkey. Rhaetian faunas from the Dikmetas section, Cataltepe Nappe of the Antalyia Nappes were assigned to assemblages 2b-2c and 3 of Carter (1993). Later studies of the Hocaköy section of the Gökdere Formation, Alakirçay Nappe (Tekin, 2002), indicated that the radiolarians could be well correlated with Rhaetian faunas from the Mino terrane, central Japan (uppermost two Triassic zones of Sugiyama (1997)) and Queen Charlotte Islands (*Proparvicingula moniliformis* Zone).

Italy - Amodeo (1999) first recognized Rhaetian radiolarians in the Buccaglione Member of the Scisty Silicei Formation of the Lagonegro Basin, southern Italy. A number of species occurring in QCI were reported and the fauna was correlated with the *Proparvicingula moniliformis* Zone. Reggiani et al. (2005) found Rhaetian and Hettangian faunas in red shales and radiolarites of the Buccaglione Member of the Madonna del Sirino succession in the same area; and Bazzucchi et al. (2005) found early Rhaetian faunas correlative with the *Proparvicingula moniliformis* Zone, in the upper part of the Calcari con Selce Formation, Mt. Crocetta section, Pignola.

Tibet (Xizang, China) - Ziabrev et al. (2004) reported the occurrence of rare Rhaetian species in red chert from the Bainang Terrane, Yarlung-Tsangpo suture, southern Tibet. These faunas have helped record the long history of sedimentation of Tethyan strata in an intra-oceanic island arc subduction complex that was accreted to the Bainang terrane in the Cretaceous.

Queen Charlotte Islands - Central Japan - Carter & Hori (2005) established global correlation for Triassic-Jurassic boundary radiolarian faunas from QIC and Central Japan using identical Rhaetian and Hettangian species from these far disparate areas of Panthalassa.

China - Yeh & Yang (2006) described new species from the Nadanhada Terrane in NE China, and compared age to early Rhaetian species from QCI.

Hungary - Pálfy et al. (2007) discussed Triassic- Jurassic boundary radiolarians from the Csövár section, part of the Transdanubian range unit of the Alcapa terrane, Hungary. The Rhaetian assemblage was assigned to the *Globolaxtorum tozeri* Zone, containing the nominal taxon and other elements common to low latitude faunas of Tethys.

Nevada, USA - Orchard et al. (2007) reported radiolarians of *the Globolaxtorum tozeri* Zone in the Mount Hyatt and Muller Canyon members of the Gabbs Formation in the Ferguson Hill section at New York Canyon. The section is one of several proposed GSSP candidates for the base of the Jurassic System.

Baja California Sur – Whalen et al. (1998) first reported radiolarians and conodonts of Rhaetian age from the sandstone member of the San Hipólito Formation on the Vizcaino Peninsula. Orchard et al. (this volume) presented the detailed stratigraphy of inland and coastal radiolarian-bearing sequences and utilized radiolarian zonation from QCI to date the conodont succession. Long sequences of radiolarians in several sections are assigned to both the *Proparvicingula moniliformis* and *Globolaxtorum tozeri* zones. The radiolarians compare closely with Rhaetian faunas of the Sandilands Formation, QCI, but minor variation exists in the range of some species and other taxa occur that characterize low latitude regions of Tethys.

The updated information presented on Rhaetian radiolarian faunas (Table 1) emphasizes the cosmopolitan distribution of many species and the propensity for radiolarians to occur in different sedimentary facies, hence their usefulness for global correlation. This is significant in dating strata surrounding the Triassic-Jurassic boundary. In years past, little was known of Rhaetian radiolarian faunas but now they are known worldwide as evidenced by the data submitted in this paper. Hettangian faunas, although currently not as well known as Rhaetian ones, are,

TABLE 1. Distribution of radiolarian faunas in Rhaetian strata around the world. QCI, Queen Charlotte Islands, (Carter, 1993); BCS, Baja California Sur (Orchard et al., this volume; Carter, personal collections); NEV, Nevada, USA (Orchard et al., 2007); PHI, Philippines (Yeh, 1990, 1992, Yeh & Cheng, 1996); JAP, Japan (Yao et al., 1980 a,b; Yao, 1982; Sugiyama, 1997); CHI, China (Yang & Mizutani, 1991; Yeh & Yang, 2006); TIB, Tibet (Wang et al., 1989; Ziabrev et al., 2004); NZL, TIM, Timor (Rose, 1994); RUS, Far East Russia (Bragin, 1986, 1990, 1991); ITY, Italy (Amodeo, 1999; Reggiani et al., 2005; Bazzucchi et al., 2005); AUS, Austria (Kozur & Mostler, 1981; Kozur, 1984 a,b); HUN, Hungary (Pálfy et al., 2007); TUR, Turkey (Tekin, 1999, 2002), OMA, Oman (Carter, 1993).

Radiolarian species	QCI	BCS	NEV	PHI	JAP	CHI	TIB	TIM	RUS	ITL	AUS	HUN	TUR	OMA
Amuria sp. A sensu (Carter 1993)	X	X												
Artonius elizabethae Sugiyama					X			X					X	
Betraccium aff. *inornatum* Blome sensu Carter 1993	X	X		X	X					X				
Betraccium nodulum Carter	X	X												
Betraccium perilense Carter	X			X									X	
Bipedis acrostylus Bragin	X	X			X				X	X			X	
Bistarkum cylindratum Carter	X	X											X	
Canoptum triassicum Yao	X	X		X	X	X			X			X		
Canoptum aff. *unicum* Pessagn &Whalen sensu Carter 1993	X	X					cf						X	
Canoptum (= *Neocanoptum*) sp. A sensu Carter 1993	X	X												
Cantalum gratum Carter	X			X										
Cantalum sp. A sensu Carter 1993	X	X												
Canutus? *beehivensis* Carter	X	X												
Citriduma asteroides Carter	X	X		cf	X							X	X	
Citriduma sp. C sensu Carter 1993	X	X						cf		X				
Crucella flowerpotensis Carter	X	X												
Crucella? sp. A sensu Carter 1993	X	X												
Crucella sp. A sensu Yeh & Cheng 1996		X	X	X										
Deflandrecyrtium carterae Yeh & Cheng		X		X	X	X								
Deflandrecyrtium ithacanthum Sugiyama	X	X		X	X	X		X					X	
Deflandrecyrtium nobense Carter	X	X												
Deflandrecyrtium sp. A sensu Carter 1993	X	X		X										
Entactinosphaera? *amphilapes* Carter	X	X												
Entactinosphaera? *spinulata* Carter	X	X												
Eptingium amoenum Carter	X	X		X										
Eptingium onesimos Carter	X	X												
Eucyrtid gen. et sp. indet. sensu Carter 1993	X	X												X
Ferresium teekwoonense Carter	X	X												
Ferresium triquetrum Carter	X	X											X	
Ferresium sp. A sensu Carter 1993	X	X												
Ferresium sp. B sensu Carter 1993	X	X											X	
Fontinella clara Carter	X	X								X				
Fontinella habros Carter	X	X												
Fontinella inflata Carter	X	X								X				
Fontinella louisensis Carter	X	X		X						X				
Fontinella primitiva Carter	X	X								X				
Globolaxtorum hullae (Yeh & Cheng)	X	X		X	X					X			X	
Globolaxtorum tozeri Carter	X	X			X					X			X	X
Haeckelicyrtium breviora Sugiyama		X			X							?	X	
Haeckelicyrtium karcharos Carter	X	X		X	X				cf					
Haeckelicyrtium takemurai Yeh & Cheng		X		X	X	X							X	
Hagiastrum giganteum Carter & Hori	X	X			X									
Hagiastrum? *pacificum* Sugiyama	X	X		X	X	X				X				
Hagiastridae sp. B sensu Yeh & Cheng 1996		X		X										
Icrioma? *cistella* Carter	X	X											X	
Icrioma? sp. A sensu Carter 1993	X	X	?							X				
Kahlerosphaera sp. A sensu Carter 1993	X	X												
Kungalaria newcombi Dumitrica & Carter	X	X						X						
Laxtorum capitaneum Carter	X	X		cf								X	X	
Laxtorum aff. *kulense* Blome sensu Carter 1993	X	X		X										
Laxtorum perfectum Carter	X	X				X						X	X	

Table 1.(continued)

Radiolarian species	QCI	BCS	NEV	PHI	JAP	CHI	TIB	TIM	RUS	ITL	AUS	HUN	TUR	OMA
Laxtorum porterheadense Carter	X	X										X		
Livarella densiporata Kozur & Mostler	X	X		X	X	X		X		X	X		X	X
Livarella gifuensis Yoshida	X			X	X	X			X	X				X
Livarella longus Yoshida		X		X	X	X	X		X	X		X	X	X
Livarella valida Yoshida	X	X		X	X	X				X		X	X	X
Loupanus thompsoni Carter	X	X												
Mesosaturnalis acuminatus Carter	X	?												cf
Nabolella (=*Squinabolella*) aff. causia sensu Carter 1993	X	X								X			X	
Nabolella desrochersi (Carter)	X	X												
Nabolella? *trispinosa* (Carter)	X	X		?	X			X					X	
Nabolella? cf. *trispinosa* (Carter) sensu Yeh & Cheng 1996		X		X										
Nabolella sp. C sensu (Carter 1993)	X	X												
Natraglia spp.	X	X						X	X				X	
Octostella dihexacanthus (Carter)	X	X			X								X	
Pantanellium aff. *fosteri* Pessag& Blome sensu Carter 1993	X	X												
Pantanellium newkluense Carter	X	X		X	cf	X				X				
Paratriassoastrum crassum Carter	X	X	X		X	X								
Paratriassoastrum omegaense Carter	X	X								X			X	
Paratriassoastrum parvum Kozur & Mostler				X	X					X				
Paronaella pacofiense Carter	X	X		X	X		cf						X	
Parvibrachiale spp.		X			X									
Pentactinocarpus sevaticus Kozur & Mostler	X										X		X	
Poulpus sp. A sensu Yeh & Cheng 1996		X		X										
Praecitriduma apexensis Carter	X	X												
Praecitriduma canthofistula Carter	X	X											X	
Praecitriduma mostleri Kozur	X	X		X							X			
Proparvicingula moniliformis Carter	X	X		cf			?		X	X				
Psedacanthocircus troegeri Kozur & Mostler	X													X
Pseudohagiastrum monstruosum Pessagno	X	X						X						
Pseudohagiastrum? *tasuense* Carter	X	X												
Pseudohagiastrum sp. A sensu Carter 1993	X	X												
Pseudoheliodiscus beattiense (Carter)	X	X						X	cf					
Pseudoheliodiscus decilobum Carter	X			X										
Pseudoheliodiscus huxleyensis (Carter)	X	X		X					cf	cf				
Pseudoheliodiscus sandspitense (Blome)	X	X		X				X		X			X	cf
Pseudoheliodiscus sp. B sensu Carter 1993	X	X												
Pseudoheliodiscus sp. A sensu Yeh & Cheng 1996		X		X										
Serilla ellisensis (Carter)	X	X				X							X	
Serilla stalkungi (Carter)	X	X		X					X				X	
Serilla tledoensis (Carter)	X	X		X	X					X			X	
Serilla conclusum (Carter)	X	X			X									
Syringocapsa rhaetica Kozur& Mostler		X								X	X	X	X	
Tetraporobrachia composita Carter	X	X				X		X					X	
Tetraporobrachia sp. C sensu Carter 1993	X	X												
Tetraporobrachia sp. D sensu Carter 1993	X	X												
Tipperella spp. (= Spum indet. D sensu Carter 1993)	X	X											X	
Tricornicyrtium dikmetaensis Tekin		X		X	X								X	
Vegicyclia austriaca Kozur & Mostler	X	X			X						X		X	
Spumallaria indet. gen A, sp. A sensu Yeh 1992		X		X										
Spumellaria indet. gen et sp. indet. B sensu Carter 1993	X	X											X	

nevertheless, becoming more and more recognized and understood as time passes. More research in needed in this area to expand our global knowledge of Hettangian radiolarians.

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Lucas, S.G. and Spielmann, J.A., eds., 2007, The Global Triassic. New Mexico Museum of Natural History and Science Bulletin 41.

ECOLOGIC COLLAPSE OF BENTHIC COMMUNITIES FROM RESTRICTED PLATFORM TO RAMP DURING THE PERMIAN-TRIASSIC MASS EXTINCTION: CASE STUDIES OF THE MEISHAN AND HUANGZHISHAN SECTIONS, SOUTH CHINA

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Both the Huangzhishan and Meishan sections are geographically closely located, about 40 km apart in northwestern Zhejiang Province, South China, but were situated at a restricted platform and ramp settings, respectively, during the P/Tr transition. The P/Tr boundary beds exposed at these two sections can be correlated bed by bed in terms of refined conodont zones, benthic faunal assemblages and geochemical signals. However, the so-called Survival Fauna Beds are rather thick, about 3.5 m thick at Huangzhishan, in sharp contrast to their thin counterpart, about 24 cm, at Meishan, and thus provide a window into more details of benthic responses to the P/Tr crisis. Benthic communities in both niches underwent a significant decrease in the high level taxonomic groups and a distinct reduction in body sizes during the P/Tr extinction. However, the surviving platform communities are much more abundant and diverse than the ramp communities. The former are dominated by brachiopods and bivalves, and the latter by foraminiferans and brachiopods. Of these, most of the surviving platform brachiopods escaped the P/Tr disaster and continued to populate the same niches; whereas the surviving brachiopods on the ramp migrated from other habitats after the event. These survivors, however, became extinct about 1-2 million years after the end-Permian crisis, and the communities were replaced by the low-diversity, *Claraia-Ophiceras* communities in the earliest Triassic. In addition, the disaster taxon *Lingula* proliferated in the relatively shallow platform rather than the ramp habitats.

Lucas, S.G. and Spielmann, J.A., eds., 2007, The Global Triassic. New Mexico Museum of Natural History and Science Bulletin 41.

WHAT DO WE KNOW ABOUT THE MAGNETOSTRATIGRAPHY ACROSS THE TRIASSIC-JURASSIC BOUNDARY?

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INTRODUCTION

Rocks deposited across the Triassic-Jurassic boundary (TJB) are preserved in several areas, including eastern North America (Newark Supergroup), the United Kingdom (St. Audrie's Bay), Morocco (central High Atlas), Paris Basin (Montcornet), Turkey (Oyuklu), Argentina (Neuquen Basin), parts of the Colorado Plateau and adjacent areas of western North America (e.g., Moenave Formation). Despite considerable analysis of these sections, including but not limited to biostratigraphy, geochemistry, and magnetostratigraphy, correlations among these stratigraphic sections continue to generate questions about the definition of the TJB, timing of extinction events, widespread volcanism associated with the Central Atlantic Magmatic Province (CAMP), and the state of the geomagnetic field during this time period. Parts of the global polarity time scale (GPTS) are calibrated to marine magnetic anomalies recorded in oceanic crust, yet the oldest oceanic plates are too young to provide data to attempt to calibrate the latest Triassic to earliest Jurassic GPTS. Strata from terrestrial and marine basins reflect variations in depositional environments, sedimentation rates, and biological preservation, and thus complicate efforts at universal correlation of all TJB sections. We present a review and evaluation of published magnetostratigraphic records that include, but do not necessarily span, the time period between (about) the Norian/Rhaetian (NR) boundary to near the Hettangian/Sinemurian (HS) boundary and use this review as a framework by which to analyze new magnetostratigraphic data currently being obtained (L. Donohoo-Hurley, PhD dissertation in progress, 2007) from previously unsampled sections of the Moneave Formation located both on and off the Colorado Plateau in southwestern Utah, and northern Arizona. In this discussion, we adhere to the nomenclature of Opdyke and Channell (1996), where a polarity zone is a magnetostratigraphic polarity unit with duration between 10^6 and 10^7 Ma; the geochronologic (time) equivalent is a chron, and the chronostratigraphic equivalent is a chronozone. Similarly, for shorter duration (10^5 to 10^6 Ma) features, the terms polarity subzone, subchron, and subchronozone, respectively, apply.

THE TRIASSIC/JURASSIC BOUNDARY

One of the many factors hindering our understanding of the TJB relates to how the boundary is actually defined. In the Newark Basin, the TJB is inferred by vertebrate tracks and pollen preserved in the predominantly lacustrine rift basin sequence (Kent and Olsen, 1999; Whiteside 2007). Geochemical, biostratigraphic, magnetostratigraphic, and chemostratigraphic data from CAMP lava flows interbedded with sediments are used to define the TJB in Moroccan sediments (Marzoli et al., 2004; Knight et al., 2004). The transition from white, conodont-bearing limestones to overlying chert-rich rocks is used to define the TJB in typical Tethyan sections (Gallet et al., 2007). The TJB in the Neuquen Basin of Argentina preserves terrestrial sediments deposited in an inferred back arc basin that are conformably overlain by shallow marine transgressive deposits containing ammonoids indicative of a TJB age (Llanos and Riccardi, 2000). The early Mesozoic of the American Southwest is dominated by terrestrial sediments, and the TJB is defined by tetrapod tracks preserved in fluvial and lacustrine red-bed deposits (Lucas and Heckert, 2001; Molina-Garza et al., 2003; Lucas and Tanner, 2006 b; Lucas et al., 2006; Tanner and Lucas, 2006). Placement of the TJB in Jurassic marine sediments that overlie Upper Triassic nonmarine variegated silty clays and marls of the Paris Basin is constrained by ammonoids, bivalves, ostracodes, and pollen (Yang et al., 1996). The St. Audrie's Bay section, Somerset Coast, UK, consisting of limestones and shales, is a candidate Global Stratotype Section and Point for the base of the Hettangian Stage (i.e. TJB), as defined by lowest occurrence (LO) of the ammonoid *Psiloceras planorbis* (Hounslow et al., 2004). The LO of *Psiloceras planorbis* has been used as a working definition of the TJB in marine rocks since the early 1960's (Lucas et al., 2007) and is adhered to in this review, pending a formal definition of the GSSP for the base of the Jurassic System, now in progress

From a magnetostratigraphic perspective, strata deposited at the TJB and over the ~ 2 Ma time interval centered on the TJB (NR boundary to HS boundary) appear to be characterized by dominantly normal polarity chronozones to subchronozones (Fig. 1). The polarity character of these intervals, however, is not consistent from basin to basin. The Late Triassic to very earliest Jurassic polarity time scale of Kent and Olsen (1999) (KO99) documents Newark Supergroup sedimentary rocks of Rhaetian age to define mostly reverse polarity zones and subzones and normal polarity zones and subzones during the latest Rhaetian to early Hettangian, with a short, yet critical reverse polarity subzone (E23r of KO99) that is inferred to lie just below the TJB. The strata at St. Audrie's Bay define mostly normal polarity zones and subzones with one reverse polarity subzone in the latest Norian (SA5n.1r), and three reverse polarity subzones in the early Rhaetian (SA5n.2r, SA5n.3r, and SA5r) (Hounslow et al., 2004). A recent compilation of Tethyan sediments shows the latest Triassic to be dominated by normal polarity punctuated by one short reverse subzone in the late Norian (F-) and two reverse subchrons in the early Rhaetian (H-, J-) (Gallet et al., 2007). The Paris Basin section, which is largely in Lower Jurassic strata, yields, for the late Rhaetian and Hettangian, magnetic directions of dominantly normal polarity with one reverse subzone in the late Rhaetian, and four reverse subzones in the Hettangian (Yang et al., 1996). The High Atlas, Morocco section of basaltic lava flows reported by Marzoli et al. (2004), which is inferred to span the TJB, is entirely of normal polarity, with the exception of a single lava flow defining an inferred reverse subzone at or near the TJB (Marzoli et al., 2004; Knight et al., 2004). The magnetostratigraphic record of the Neuquen composite section of Argentina for the lower Hettangian is consistent with previous interpretations of a mostly normal polarity geomagnetic field, but by the middle Hettangian the overall character of the geomagnetic record changes to reverse polarity (Llanos and Riccardi, 2000). Although complicated by the possibility of several short-lived disconformities, uppermost Chinle Group and lowermost Glen Canyon Group strata from the American southwest yield mostly normal polarity zones and subzones across the Norian-Rhaetian boundary to the Hettangian-Sinemurian boundary with one reverse subzone defined by sediments from the lower Glen Canyon Group at Echo Cliffs (Molina-Garza et al., 2003; Hutny, 2006).

In particular for North America, but also for many other continents, a major change in plate motion may be essentially coincident with the TJB (Fig. 2). Although specific paleomagnetic directions alone clearly cannot be used to define the exact boundary, if the hypothesis of Gordon et al. (1984) is viable, the apparent polar wander path for North America, as well as other continents, is characterized by a major cusp (the J1 cusp for North America) between two small circle tracks of paleomagnetic poles, each with a very distinct Euler pole of rotation. For the American Southwest, for example, paleomagnetic data (of normal polarity) from rocks of latest Triassic age should track from north-northwest declina-

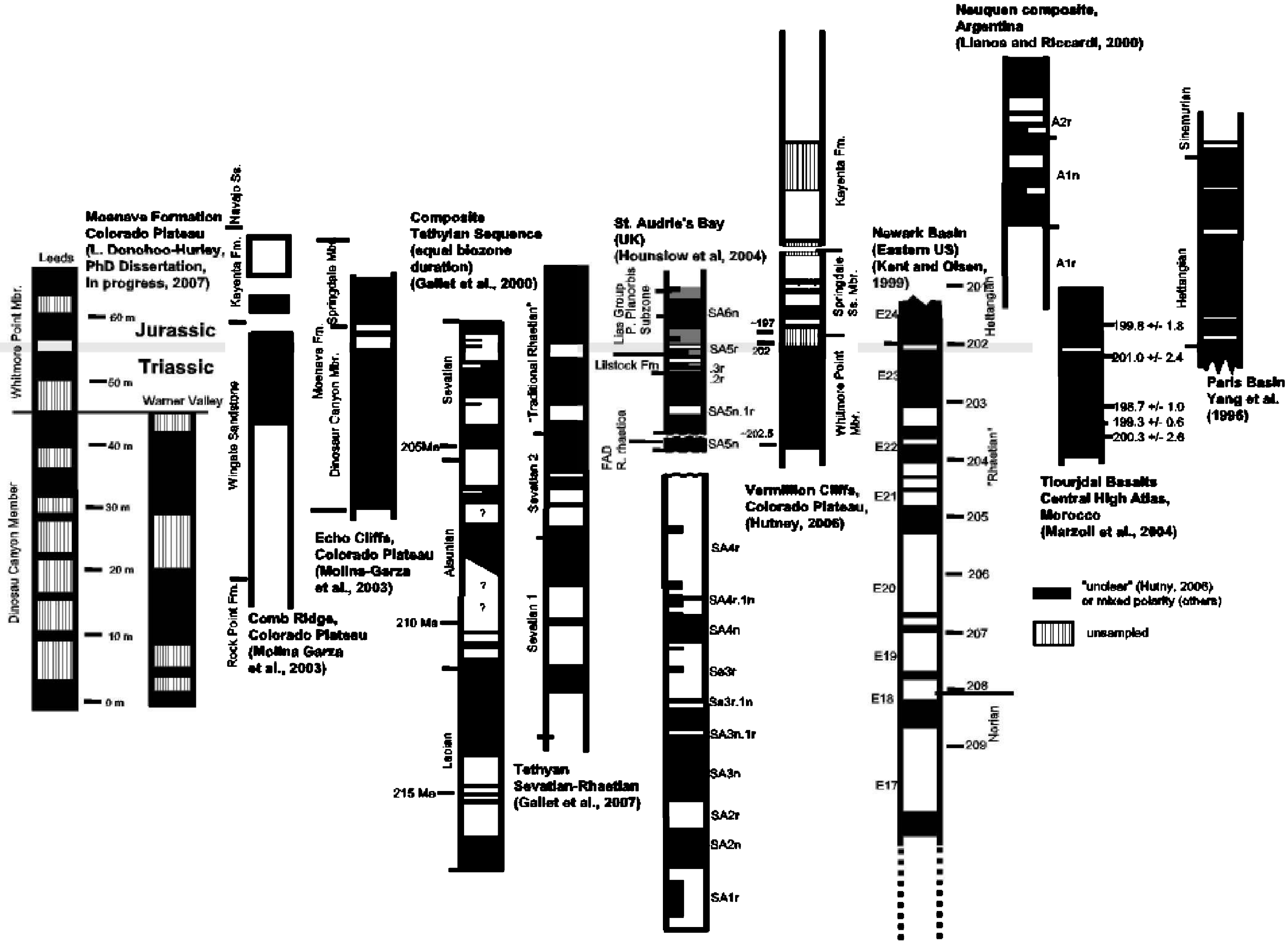

FIGURE 1. Compilation of magnetostratigraphic sections that span the Triassic-Jurassic boundary, see text for details.

tion to declinations east of north, while maintaining very shallow inclinations; rocks of Early Jurassic age should show the opposite behavior, with declinations tracking back to the north-northwest, and then ultimately steepening in inclination.

MAGNETOSTRATIGRAPHY

The use of red sediments in paleomagnetism (and in particular magnetostratigraphy) has been controversial because of uncertainties regarding the actual mode and timing of remanence acquisition (Collinson, 1974; Elston and Purucker, 1979; Larson et al., 1982; Ekstrand and Butler, 1989; Beck et al., 2003) as well as the likelihood that sedimentation in such sequences is far from continuous. Although the presence of normal and reverse polarity magnetizations that pass a paleomagnetic reversals test (e.g., McFadden and McElhinny, 1990) is often interpreted as supporting the preservation of a primary or at least near-primary magnetization, the time duration required for magnetization acquisition and associated diagenetic processes clearly can span two or more polarity intervals (Larson et al., 1982; Beck et al., 2003), and there are several well-documented cases of secondary yet dual-polarity magnetizations in sedimentary sequences (e.g., Geissman et al. , 1990). Utilization of intraformational fold tests, conglomerate fold tests, statistical analysis of virtual geomagnetic poles, and/or replication of bedding parallel magnetostratigraphy is needed to adequately clarify primary magnetization (Hagstrum, 1993; Beck et al, 2003).

The following discussion concentrates on a review of magnetostratigraphic records and their correlation with the proposed polarity time scale based on extensive work on Newark Supergroup sediments (KO99). Marzoli (2004) and Knight (2004) (MK04) propose, on the basis of biostratigraphic, geochemical, radiometric (Palfy et al., 2000, 2002), and magnetostratigraphic arguments, that the CAMP volcanism in the Moroccan section is synchronous with volcanism in the Newark and the onset of volcanism post-dates the TJB. An alternative correlation the MK04 magnetostratigraphy posits the Moroccan strata may be of Early Jurassic age, synchronous with poorly sampled Jurassic flows in the Newark Basin, and implies the onset of CAMP occurs later in Morocco than Newark (Whiteside et al., 2007). The preferred correlation of magnetostratigraphy from the St. Audrie's Bay, based on biostratigraphy, to the Newark polarity time scale correlates reversal SA5r (occurs below the LO of planorbis but only by a few stratigraphic meters) to E23r placing the TJB within the Newark CAMP basalt flows. Whiteside et al. (2007) argue that biostratigraphy and carbon isotope records support correlation of the St. Audrie's Bay section to poorly sampled Jurassic lava flows.

Molina-Garza et al. (2003) proposed magnetostratigraphic correlation of the reversal found in the upper Dinosaur Canyon Member of the Moenave Formation (description of Moenave Formation to follow) to E23r of K099. In the absence of biostratigraphic tie points it is possible (although not desirable) to correlate between magnetostratigraphic records by visual comparison. Dominantly normal polarity magnetization directions acquired from sediments preserved in the Paris Basin are visually correlated to the limited Hettangian part of the Newark time scale (Yang et al., 1996). Paleomagnetic data from the Planorbis Zone (basal strata) of the Neuquen section, Argentina, yields normal polarity data and has a reported age of latest lower Hettangian (Llanos and Riccardi,

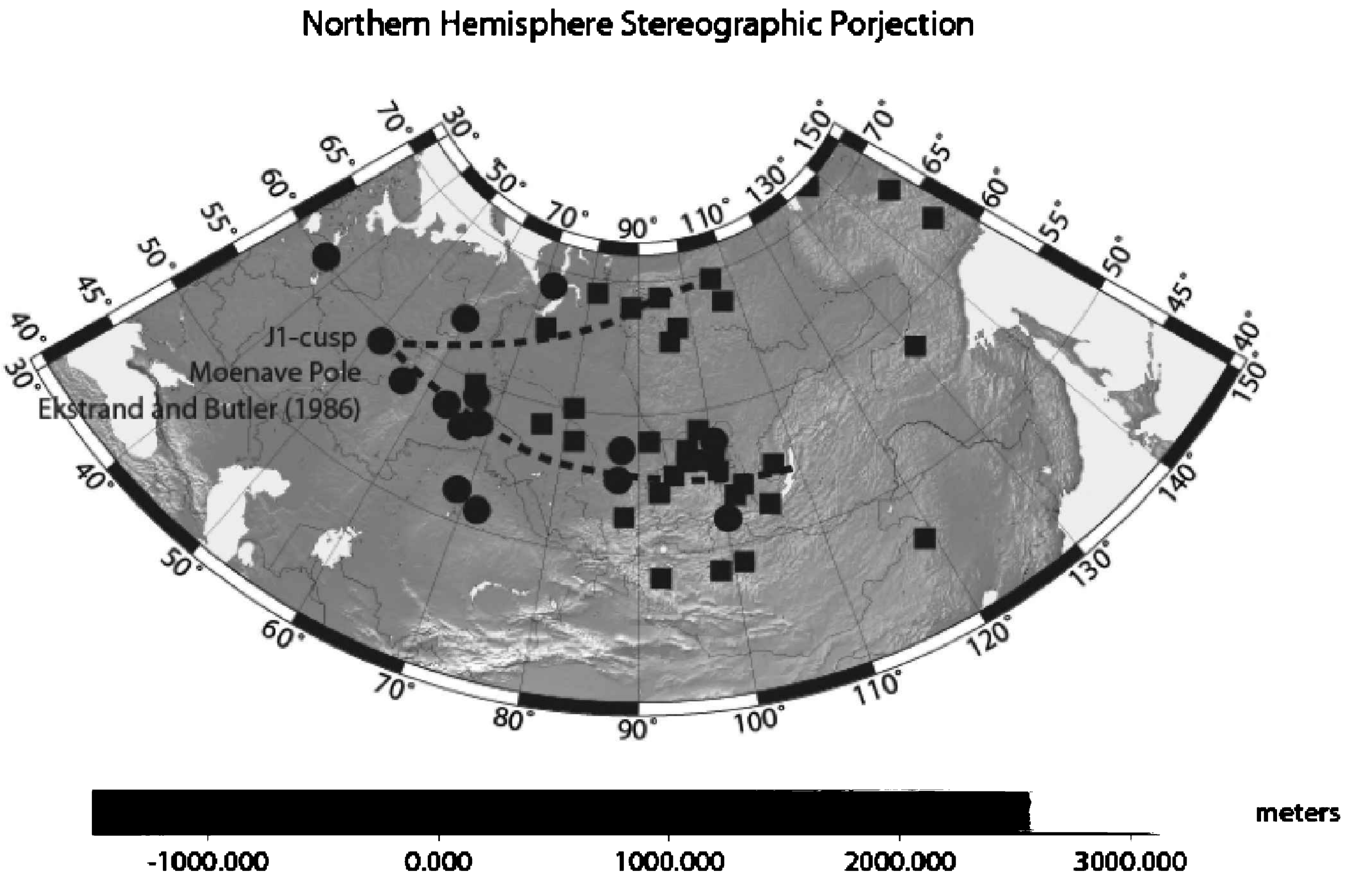

FIGURE 2. Part of northern hemisphere projection showing paleomagnetic poles (IAGA Global Paleomagnetic Database) based on the following search criteria: North America, ranging in age from 220 Ma to 180 Ma, primary remanence, and with demagnetization procedures including principle component analysis. Squares represent cratonic poles or poles calculated from rocks in eastern North America. Poles derived from rocks in the American Southwest are shown in circles. The approximate location of an apparent polar wander path constructed using the paleomagnetic Euler pole method of path construction as described in Gordon et al. (1984).

2000). The preservation potential for magnetic polarity reversals in the Tethyan basins is lower than in the Newark section because sedimentation rates were much higher in the Newark. However, magnetostratigraphic correlation of the Tethyan sediments to the Newark polarity time scale, together with the biostratigraphic arguments of Kozur and Weems (2005) and geochemical arguments of Pálfy et al. (2000, 2002), indicate that more reversals may be in preserved in the Turkish sections than in the Newark (Gallet et al., 2007). Gallet et al. (2007), therefore, propose that the Newark Supergroup is missing lower Rhaetian sediments and thus encompasses an early Rhaetian hiatus.

MOENAVE FORMATION

The Moenave Formation (siltstone and fine-grained sandstone) (Fig. 3) is the lowest stratigraphic unit of the Glen Canyon Group and is disconformably overlain by the Lower Jurassic Kayenta Formation (Harshbarger et al., 1957; Lucas and Heckert, 2001; Molina-Garza, 2003; Hutny, 2006). It is likely that strata of the Moenave Formation were deposited across the TJB (Lucas et al., 2006). In southern Utah and northwest Arizona, about 67 m of Dinosaur Canyon Member strata, the basal member of the Moenave Formation, consist of fluvial and eolian red-beds (Fig. 4). The Dinosaur Canyon Member interfingers with the Wingate Sandstone to the east (Wilson, 1967; Lucas and Heckert, 2001; Marzolf, 1994; Molina-Garza et al., 2003; Lucas and Tanner, 2004; Hutny, 2006; Tanner and Lucas, 2006; Lucas and Tanner, 2006a). The Whitmore Point Member conformably overlies the Dinosaur Canyon Member and consists of about 25 m of mostly lacustrine strata with minor intervals of hematitic to non-hematitic mudstone and limestone (Harshbarger et al., 1957; Irby 1995; Lucas and Heckert, 2001; Molina-Garza et al., 2006). The Springdale Sandstone has been previously described as an uppermost member of the Moenave Formation. This review accepts lithologic and stratigraphic arguments suggesting the Springdale Sandstone is a discrete, basal member of the Kayenta Formation (Marzolf, 1994; Lucas and Heckert, 2001; Tanner et al., 2002; Tanner and Lucas, 2006; Lucas and Tanner, 2006 a, b). The reader is referred to Tanner and Lucas (2006), Lucas and Tanner (2006 a, b), and Lucas et al., (2006) for a more detailed description of sedimentology, stratigraphy, biostratigraphy, and biochronology of the Moenave Formation. Uppermost Triassic and lowermost Jurassic red beds of the Moenave Formation were deposited on the craton margin, east of the evolving Cordilleran arc (Bazard and Butler, 1991). Principal features associated with post-Early Jurassic deformation in the American Southwest, which led to local tilting of these strata, include formation of Laramide (basement-involved) monoclines and normal faults of a range of geometries associated with formation of the Basin and Range Province and Rio Grande rift.

Previous paleomagnetic and magnetostratigraphic studies on the

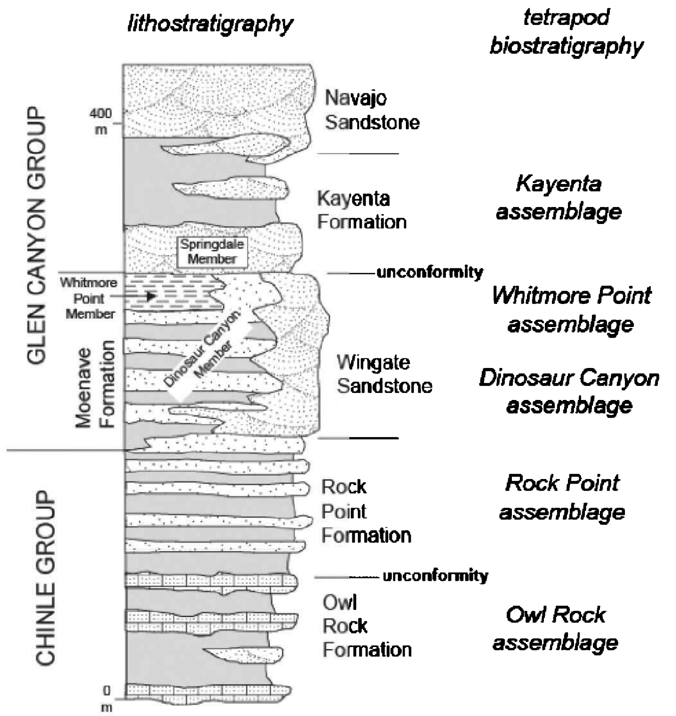

FIGURE 3. Stratigraphic representation of the Chinle and Glen Canyon Groups from Lucas and Tanner (2006). The Moenave Formation is comprised of the Dinosaur Canyon and Whitmore Point members but only the Dinosaur Canyon Member interfingers with the Wingate Sandstone to the east.

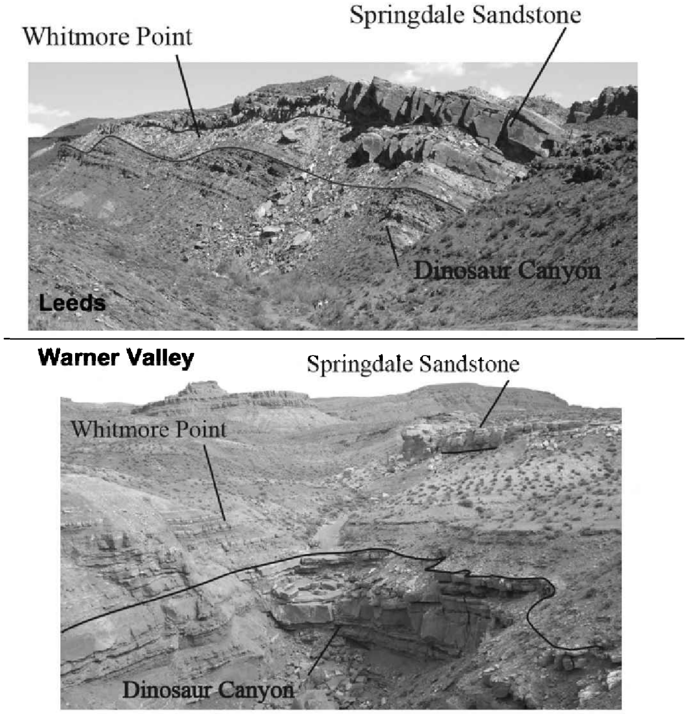

FIGURE 4. Field photographs of the Leeds (top) and Warner Valley (bottom) stratigraphic sections in the Moenave Formation.

Moenave Formation have been obtained from sections dominated by fluvial and eolian sediments that appear to record fewer polarity zones and subzones than rocks of equivalent age/time duration in northeastern North America (Ekstrand and Butler, 1989; Molina-Garza et al., 2003; Hutny, 2006) (Fig. 1). The work of Ekstrand and Butler (1986) was principally intended to provide an initial paleomagnetic pole for the formation and test the Gordon et al. (1984) hypothesis that the TJB was the time period of a major, sharp change (J1 cusp) in the apparent polar wander path for North America (Fig. 2). These workers described the geomagnetic field during Moenave deposition as dominantly normal polarity with four reverse polarity subzones in the upper two meters of the Whitmore Point Member.

Molina-Garza et al. (2003) sampled fluvial Moenave sections at the Echo Cliffs and Comb Ridge and obtained a considerably lower resolution polarity stratigraphy than the KO99 polarity record. At these two localities, the Dinosaur Canyon Member is the only component of the Moenave Formation, and two reverse polarity subzones were identified in the upper part of the Dinosaur Canyon Member. Additional polarity zones/subzones were assumed by Molina-Garza et al. (2003) to be defined in the (unsampled) less resistant mudstone and claystone intervals. Molina-Garza et al. (2003) placed the TJB in the lower of the two reverse polarity subzones in the upper part of the Dinosaur Canyon Member. In her Masters thesis, Hutny (2006) documents an exclusively normal polarity zone for the Whitmore Point Member of the Moenave Formation. The Springdale Sandstone Member of the Kayenta Formation, where sampled, is dominated by normal polarity near its base and reverse polarity in the middle and upper part. The Dinosaur Canyon Member was not sampled by Hutny (2006). Hutny (2006) concluded that the TJB was located near the contact between the Whitmore Point and Springdale Sandstone, in an “unsampled” part of the section.

Magnetostratigraphic data are being obtained from four previously unsampled sections (Leeds, Warner Valley, Washington Dome, and Fredonia) of the Moenave Formation (both Dinosaur Canyon Member and Whitmore Point Member) as well as, where possible, the Springdale Sandstone Member of the Kayenta Formation, in southwestern Utah and northwestern Arizona. Our goal is to obtain the highest resolution possible across latest Triassic to earliest Jurassic time in these rocks through replicate section sampling and testing of the internal consistency of the polarity record contained in these rocks. Our effort to prepare a composite magnetostratigraphy for this time period will strive to mitigate complexities associated with quasi-continuous deposition of sediment of the Moenave Formation and provide data to better interpret the morphology of the J1-cusp. The new polarity stratigraphy should be a far more robust record of the Late Triassic to Early Jurassic geomagnetic field for the American Southwest, thus ideally providing a comparable high-quality magnetostratigraphy to lacustrine sediments from northeast North America.

Initial work on sections collected at Leeds and Warner Valley (Fig. 4), north and south of St. George, Utah, respectively, yields interpretable demagnetization results showing the isolation of north-directed and shallow inclination magnetizations (in stratigraphic coordinates) (or antipodes) over a range of laboratory unblocking temperatures between about 500 and 670°C (Fig. 5) and over a relatively short range of time in chemical demagnetization. On the basis of their directions (Fig. 6), we tentatively assume that these magnetizations are early-acquired and can be used to define a magnetic polarity history for the Moenave Formation. The preliminary magnetostratigraphic results (Fig. 1) suggest that the Dinosaur Canyon Member is a single normal polarity chronozone, consistent with previous work on these rocks. One reverse polarity subzone is defined in the lower part of the Whitmore Point Member of the Leeds section and, tentatively, we correlate this subchron to that defined as E23r in the Newark composite record of KO99 and SA5r of the St. Audrie’s Bay section (Hounslow et al., 2004).

CONCLUSIONS

Paleomagnetic directions obtained to date from the Moenave Formation at two previously unsampled sections (Leeds and Warner Valley) yield dominantly normal polarity directions consistent with published

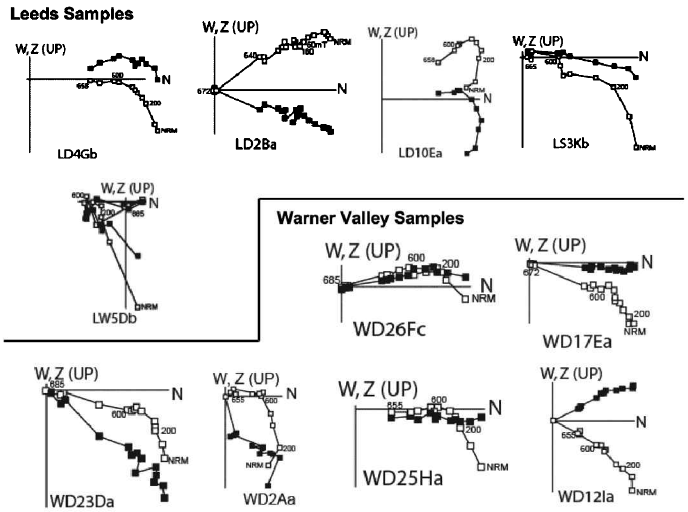

FIGURE 5. Orthogonal vector diagrams for Leeds and Warner Valley samples showing typical response to progressive thermal demagnetization and the isolation of a representative, typically north-seeking, shallow inclination characteristic remanent magnetization (ChRM) used to calculate site mean direction. Horizontal projection shown in black squares, and vertical projection is shown by open squares.

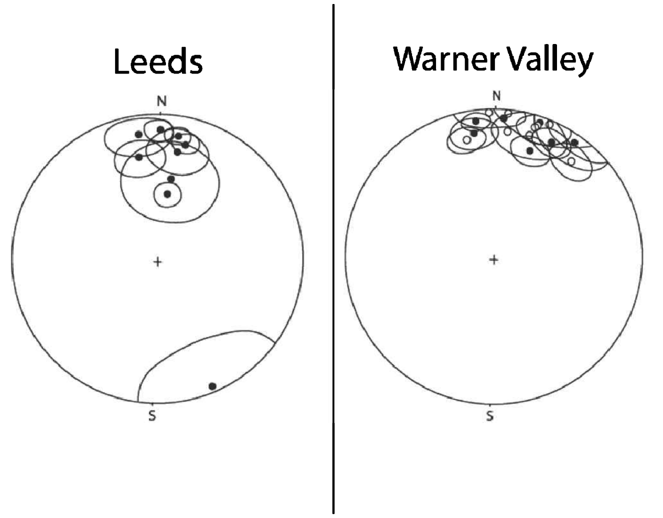

FIGURE 6. Preliminary paleomagnetic data from Moenave sections at Leeds and Warner Valley, as discussed in the text. Equal area projections of preliminary site (individual bed) mean directions. All site (bed) mean directions are based on at least seven independent samples, and those shown, with one exception, have a_{95} values less than 17°. The exception is one site at Leeds (LW5, a_{95} = 31.7°) tentatively defining the reverse subzone in the Whitmore Point Member.

magnetostratigraphic records of the latest Rhaetian including Comb Ridge and Echo Cliffs, Colorado Plateau (Molina-Garza et al., 2003), the most recent Tethyan composite section, Turkey (Gallet et al., 2007), St. Audie's Bay, UK (Hounslow et al., 2004), Vermillion Cliffs, Colorado Plateau (Hutny, 2006), Newark Basin, (Kent and Olsen, 1999), Neuquen composite section, Argentina (Llanos and Riccardi, 2000), the Central High Atlas, Morocco (Marzoli et al., 2004), and the Paris Basin section (Yang et al., 1996). One interval of reverse polarity is identified in the lower Whitmore Point (Leeds sections) and is inferred to correlate with the short polarity reversal E23r of KO99 and SA5r of the St. Audrie's Bay section. The differing interpretations of magnetostratigraphic correlation among basins illustrate a deficiency in our understanding of the geomagnetic field behavior from the Norian-Rhaetian boundary to the Hettangian-Sinemurian boundary. New high-quality paleomagnetic data from the Moenave Formation will aid in a better characterization of geomagnetic field behavior across the TJB.

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Lucas, S.G. and Spielmann, J.A., eds., 2007, The Global Triassic. New Mexico Museum of Natural History and Science Bulletin 41.

EARLY TRIASSIC TIMESCALE AND NEW U-PB AGES FROM SOUTH CHINA: FIRST CALIBRATION OF THE EARLY TRIASSIC CARBON CYCLE PERTURBATIONS

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Crucial for carbon cycle modeling and for the interpretation of carbon isotope shifts is a precise time framework based on the calibration of high-resolution ammonoid zones with high-precision radiometric ages. The outer platform, ammonoid- and conodont-rich, mixed carbonate-siliciclastic series of the Early Triassic Luolou Fm. (NW Guangxi, South China) contains a succession of volcanic ash layers. Among these, high precision U-Pb ages on zircons of two late Early Triassic (i.e., Spathian) ash layers were proposed by Ovtcharova et al. (2006). Taking a Permian-Triassic boundary age of 252.6 ± 0.2 Ma (Mundil et al., 2004), the recalculated uncertainties of these ages now indicate a minimal duration of 2.7 ± 0.7 My for the Spathian, thus confirming that it represents about half of the duration of the entire Early Triassic.

A new U-Pb age of 251.22 ± 0.20 Ma is proposed for an ash layer associated with the early Smithian "*Kashmirites densistriatus* beds" of the Luolou Fm. This new date, together with recalculated uncertainties of previous Spathian U-Pb ages (Ovtcharova et al., 2006) allow narrowing down of the absolute duration of the Griesbachian-Dienerian interval as well as the duration of the Smithian substage, which are estimated to be ca. 1.4 ± 0.4 My and to ca. 0.7 ± 0.6 My, respectively.

This new age model provides the fundamental basis for the calibration of a new high-resolution carbonate carbon isotope and ammonoid records of the Early Triassic Luolou Fm., which in turn are seen as essential for global correlations and for future carbon cycle modeling studies. This calibration indicates that the most significant and fastest Early Triassic carbon isotope perturbations occur between the early Smithian and the early Spathian, thus spanning a time interval of about 1 My.

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NEW BIOSTRATIGRAPHIC DATA AROUND THE CARNIAN/NORIAN BOUNDARY FROM THE PIZZO MONDELLO SECTION, SICANI MOUNTAINS, SICILY

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GEOLOGICAL SETTING

The Pizzo Mondello section is located in western Sicily (Sicani Mountains) and is one of the most continuous and well-preserved Upper Triassic hemipelagic successions of the Mediterranean domain. The Sicani Mountains are composed of pelagic sediments of Permian to Cenozoic age and derive from the Neogene deformation of the Sicanian domain, developed along the African margin (Catalano et al., 1991). The Pizzo Mondello tectonic unit, which includes the Pizzo Mondello section, consists of ca. 1200 m of hemipelagic carbonates, radiolarites and marls of Mesozoic to Cenozoic age. It overthrusts a thick allochthonous complex of Neogene clays and evaporites attributed to the Gela Nappe (Fig. 1) (Bellanca et al., 1993; Bellanca, 1995, and references therein).

The base of the Pizzo Mondello section is characterized by a few meters of marls and marly limestones of late Carnian age tentatively attributed to the Mufara Formation (Di Stefano and Gullo, 1997; Buratti and Carrillat, 2002). Above this unit, 430 m of evenly-bedded to nodular *Halobia*-bearing cherty calcilutites (Cherty Limestones Formation) follow. These are overlain by 20 meters of Lower to Middle Rhaetian calcilutites and marls (Portella Gebbia Formation), which are locally disconformably overlain by Jurassic sediments (Gullo, 1996). In this new study, we present biostratigraphic and sedimentological data from the Carnian-Norian boundary interval.

SEDIMENTOLOGY

The Cherty Limestones Fm at Pizzo Mondello was divided by Muttoni et al. (2001, 2004) into four lithostratigraphic parts:

1. The basal 3 m are characterized by calcilutites with rare chert nodules.
2. 143.5 m of dm-thick, well-bedded white calcilutites with black chert nodules, intercalated with cm-thick marl levels. The calcilutites contain abundant pelagic bivalves (halobids), foraminifers, radiolarians, sponge spicules, sparse ammonoids and ostracods (Gullo, 1996), as well as calcispheres and calcareous nannofossils (Bellanca et al., 1993; 1995).
3. 11.5 m of brecciated limestones, hereafter referred to as the “breccia” level.
4. The upper 267.5 m are dm- to cm-thick, well-bedded to nodular whitish calcilutites with chert nodules. Chert disappears at meter level 290 ca.

In this study. we analyzed the ca. 140 m of sediments belonging to the Cherty Limestones Fm, within Interval 2 of Muttoni et al. (2004), which includes the C/N boundary interval (Fig. 2). The high resolution of sedimentological analysis allowed the recognition of three facies:

Facies A: well-bedded, dm-thick, white calcilutites with black-brown cherty nodules concentrated in the interlayers. Calcilutite layers are composed mostly of micrite, with thin-shelled bivalves (halobids), radiolarians, ammonoids, foraminifers and calcispheres; bioturbation and laminations are rare. Bivalve coquinas also occur. The interlayers are composed of mm-thick brownish clays, which are rarely laminated.

Facies B: similar to facies A, but layers are nodular, up to 1 m thick, and characterized by stylolitic joints. Thin-shelled bivalves, calcispheres and coquinas are more abundant. Bioturbation and laminations are common.

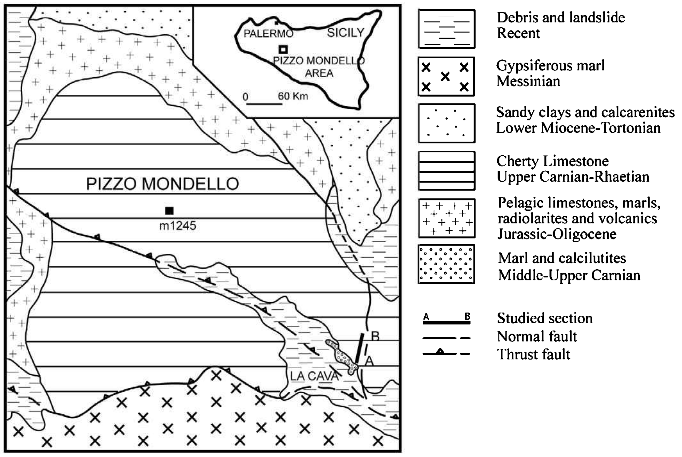

FIGURE 1. Geological setting of the Pizzo Mondello area, Sicani Mountains, Sicily (after Bellanca et al., 1993).

Facies C: calcilutite layers are even more nodular than in facies B but generally thinner (8-15 cm), and always laminated. Thin-shelled bivalves and calcispheres are extremely common. Silicified coquinas are very abundant. Cm- to dm-scale interlayers, composed of brown-black dolomitized clay-marls, are more common than in all other facies. This facies is rich in black chert, occurring in 5-7 cm thick beds.

Facies alternate in the studied interval following the scheme A-B-C-B-A (Fig. 3), with interval C centered at ca m 92.This facies alternation may represent a combination of oscillations in the carbonate sediment supply from surrounding carbonate platforms, varying dissolution rates at the sea-bottom, and different autochthonous carbonate productivity (e.g. ,benthic, thin-shelled bivalves or calcispheres, supposedly pelagic according to Bellanca et al., 1993, 1995).

BIOSTRATIGRAPHY

At present, Pizzo Mondello is one of the best pelagic-hemipelagic sections of Late Triassic age, and it has been recently proposed as the GSSP candidate for the base of the Norian base. During the last 10 years, several researchers have studied in detail the Pizzo Mondello section in order to better define the bio-, chemo- and magnetoevents around the boundary (e.g. Muttoni et al., 2001; Krystyn et al., 2002; Muttoni et al. 2004).

Recently (Autumn 2006), the lower part of this section corresponding to Interval 2 of Muttoni et al. (2004) has been sampled in detail (ca. each 1.5 m) for conodont analyses. Seventy-one new samples of limestones with the average weight of 8-9 kg have been collected and worked with standard techniques in order to extract conodonts (both platform and ramiforms) for biostratigraphical and geochemical analyses. Recovered conodonts were exceptionally abundant; they allowed us to recognize several taxa not yet described in this section such as, for instance, *Zieglericonus* sp. (samples NA 9, 31), *Misikella longidentata* (NA 9, 31) as well as plenty of ramiform elements (e.g. >700 in NA27). The Carnian/Norian boundary has not substantially modified compared

FIGURE 2. Panoramic view of the Pizzo Mondello section.

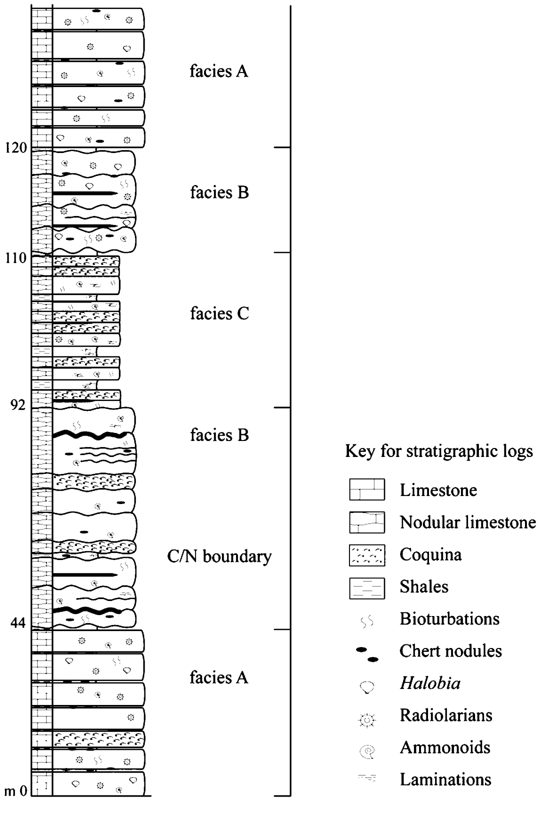

FIGURE 3. Schematic log of Pizzo Mondello section.

to the position presented by Nicora et al. (2006) at the ICOS Congress in Leicester (UK), even though the study on conodont biostratigraphy is still in progress and a possible change of the base of the Norian is not completely excluded. Furthermore, in the same interval many layers bearing bivalves belonging to the genus *Halobia* and ammonoids have been identified.

STABLE ISOTOPE STRATIGRAPHY, MAGNETOSTRATIGRAPHY AND THE AGE OF THE BOUNDARY INTERVAL

Burial diagenesis has been very weak at Pizzo Mondello, as demonstrated by the CAI (Conodont Alteration Index) value of 1 exhibited by conodonts throughout the section. This allowed the preservation of physical signals as the $\delta^{13}C$ values and a primary magnetization.

Muttoni et al. (2004) identified a positive shift of the $\delta^{13}C$ curve a few meters below the boundary interval. If this isotopic signal can be established as primary, e.g., identifying it in correlated sections, it could become an important marker for physical correlations.

A sequence of 27 magnetozones has been established at Pizzo Mondello, 12 of which are present in our section near the boundary interval (Muttoni et al., 2004). Krystyn et al. (2002) and later Muttoni et al. (2004) tentatively correlated this sequence of magnetozones with the astronomically-tuned magnetic polarity time scale in the Newark Basin (Kent and Olsen, 1999). We here follow the correlation of Muttoni et al. (2004). The oldest astronomically tuned point of the Newark Basin composite section is in the lower part of magnetozone E8r, dated at ca. 226 Ma (Kent and Olsen, 1999). Magnetozone E8r correlates with the highest part of our studied section at Pizzo Mondello (magnetozone PM6r), well above the boundary interval. Furin et al. (2006) provided a U/Pb zircon age for a Late Carnian ash-bed (i.e., below the boundary interval) deposited at 230.91 ± 0.33 Ma. The absolute age of the boundary interval is thus between 230.91 ± 0.33 and 226 Ma.

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Lucas, S.G. and Spielmann, J.A., eds., 2007, The Global Triassic. New Mexico Museum of Natural History and Science Bulletin 41.

A STUDY OF THE LOWER TRIASSIC CYCLOSTRATIGRAPHY IN THE WEST PINGDINGSHAN SECTION, CHAOHU, ANHUI PROVINCE

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As a GSSP (Global Stratotype Section and Point) candidate of the Induan-Olenekian boundary (Tong et al., 2003), the Lower Triassic of the West Pingdingshan Section has been extensively studied for biostratigraphy, carbon isotope stratigraphy, magnetostratigraphy and sedimentology (Tong et al., 2005). The Lower Triassic sequence is well defined by conodont and ammonoid zonations and is continuously exposed from the upper Changhsingian to the lower Olenekian at the section. Lithologically, the sequence appears to be a persistent rhythmic repetition of couplets composed of mudstone and limestone beds (Fig. 1). It is impossible not to notice the rhythmic bedding, and the consistency of bed thicknesses is characteristic of orbital forcing. Thus, the 44 m of strata from the uppermost Changhsingian to the lowermost Olenekian were carefully described and counted bed by bed in lithology and continuously sampled at intervals of 2 cm for magnetic susceptibility.

The cyclostratigraphic study of the Induan strata at the West Pingdingshan Section achieved the following results:

1. The bundles and bundle sets identified in lithology at the field outcrops are proved by the wavelet analysis of the magnetic susceptibility data, resulting in a 4-5:1 ratio between the cycles and subcycles. The spectral analysis of the magnetic susceptibility data shows that the first and second predominant cycles are 0.76 m and 3.41 m, respectively, coinciding with the lithologic and wavelet analyses. Thus, the cycles are believed to be a proxy of the orbital forcing Milankovitch cycles during the Triassic (Berger et al., 1994).

2. The Induan sequence at the West Pingdingshan section is composed of 12 cycles and 56 subcycles in lithology, and the same composition of cycles is presented by the magnetic susceptibility data according to wavelet analysis. The spectral analysis of the susceptibility data yields two predominant frequencies during the Induan, separate at 11.6 and 54.13. Provided these cycles reflect the Earth's orbital eccentricity and precession, the age-range of the Induan would be 0.983-1.171 Ma. Supposing the Permian-Triassic boundary has an age of 252.6 Ma (Mundil et al., 2004), the Induan-Olenekian boundary defined by the conodont *Neospathodus waageni* at the West Pingdingshan Section is around 251.5 Ma.

3. The application of the sedimentary accumulation mode (Schwarzacher, 2000) indicates that the tectonic setting and deposition were constant in Chaohu throughout the Induan, so that it is a perfect sequence for various stratigraphic studies.

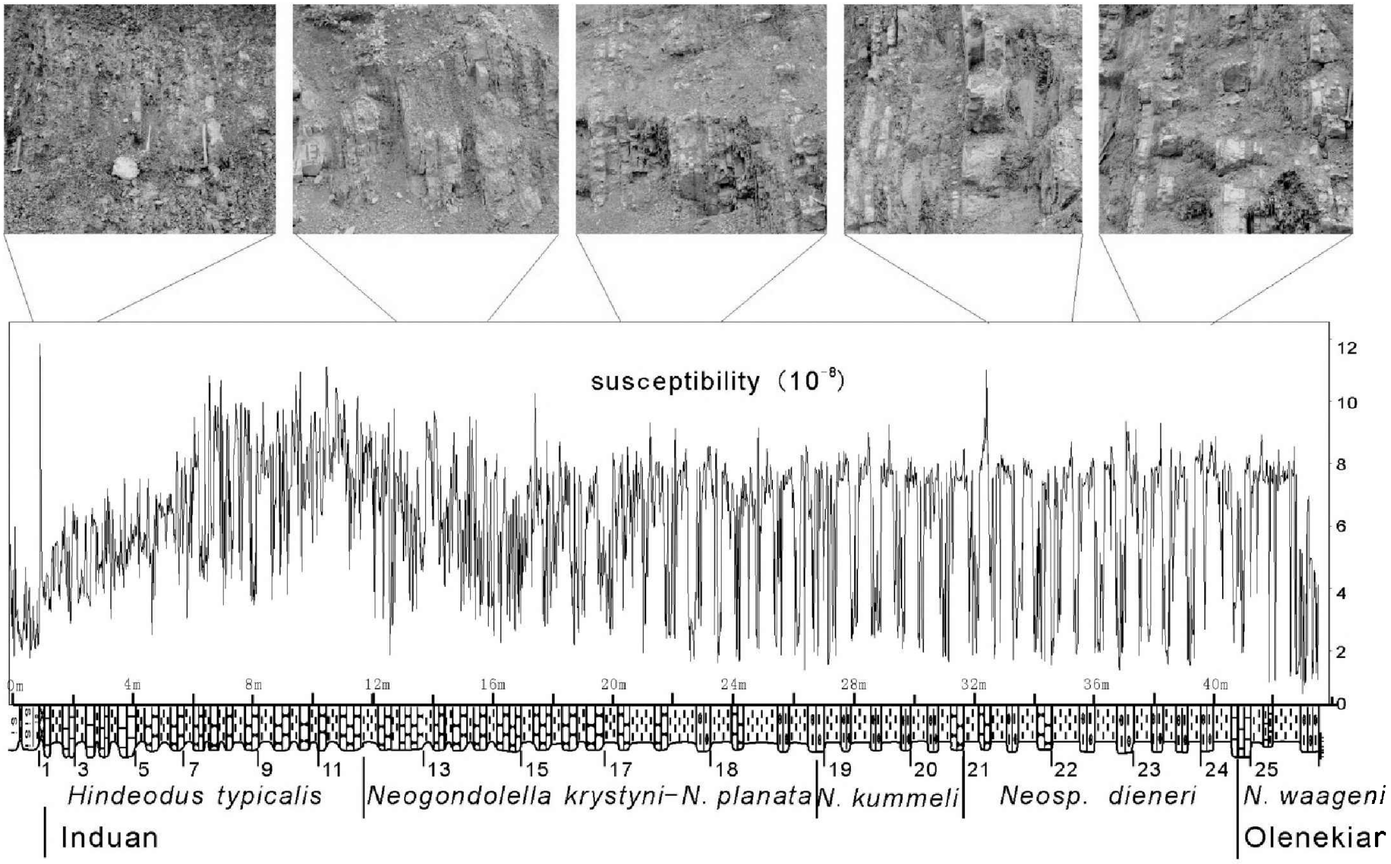

FIGURE 1. Lower Triassic cycles and stratigraphic sequence in the West Pingdingshan Section, Chaohu, Anhui Province, China

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Lucas, S.G. and Spielmann, J.A., eds., 2007, The Global Triassic. New Mexico Museum of Natural History and Science Bulletin 41.

DENTAL MORPHOLOGY OF THE HYBODONTOID SHARK *LONCHIDION HUMBLEI* MURRY FROM THE UPPER TRIASSIC CHINLE GROUP, USA

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Abstract—We describe the morphology and histological structure of the teeth of the hybodontoid shark *Lonchiodion humblei* from the Upper Triassic Chinle Group in Texas and New Mexico. The five morphotypes (symphyseal, mesial, anterolateral, lateral and posterior) previously applied to the teeth of other species of *Lonchidion* are applicable to *L. humblei*, which exhibits moderate heterodonty. The histological structure of the teeth also changes slightly posteriorly through the dentition. The function of the teeth of *L. humblei* was probably differentiated, from cutting in the symphyseal and mesial positions to crushing in the lateral and posterior ones.

INTRODUCTION

The Upper Triassic Chinle Group in the western United States is known primarily for its rich paleontological record, especially of petrified wood (e.g., Daugherty, 1941; Ash and Creber, 2000 and references therein) and tetrapod vertebrates (e.g., Long and Murry, 1995; Heckert and Lucas, 2002a). Less well-known, but still substantial, are the fish faunas of non-tetrapod vertebrates, including both freshwater sharks and diverse osteichthyans (reviewed by Huber et al., 1993; see also Johnson et al., 2002; Murry and Kirby, 2002; Milner et al., 2006).

Hybodontoid sharks are the most common non-xenacanth chondrichthyans in Chinle Group microvertebrate faunas (Murry, 1981, 1982, 1986, 1987, 1989a,b,c; Hunt and Lucas, 1993a; Kaye and Padian, 1994; Murry and Kirby, 2002; Heckert, 2004; Milner et al., 2006). Of these, the most common taxon is the lonchidiid *Lonchidion humblei* Murry, known from localities in Texas, Arizona, and New Mexico. The collections of the New Mexico Museum of Natural History and Science (NMMNH) include specimens from many of these localities, including *Lonchidion humblei* fossils from two localities near Kalgary, Texas, a locality near Ojo Huelos, New Mexico, and a locality from the Sloan Canyon Formation in northeastern New Mexico (Fig. 1). Other records of that species in the Chinle Group are from the *Placerias* quarry (Murry and Long, 1989), the "Dying Grounds" and "Crocodile Hill" localities (Murry and Long, 1989), Stinking Springs (Polcyn et al., 2002), and, possibly, the Otis Chalk *Trilophosaurus* quarry 1 (Murry, 1989). Figure 2 shows a generalized stratigraphic distribution of these localities.

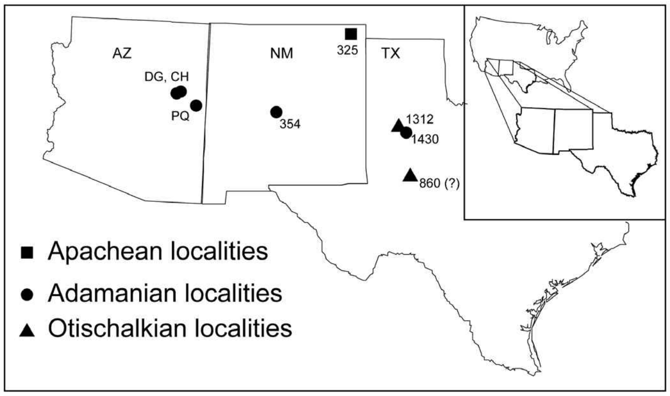

FIGURE 1. Geographic distribution of specimens of *Lissodus* from the American Southwest. Numbers refer to NMMNH localities (354 = Ojo Huelos, 324 = Sloan Canyon, 860 = *Trilophosaurus* quarry 1, 1312 = lower Kalgary, 1430 = upper Kalgary). Letters refer to other localities: CH = Crocodile Hill, DG = Dying Grounds, PQ = *Placerias* quarry.

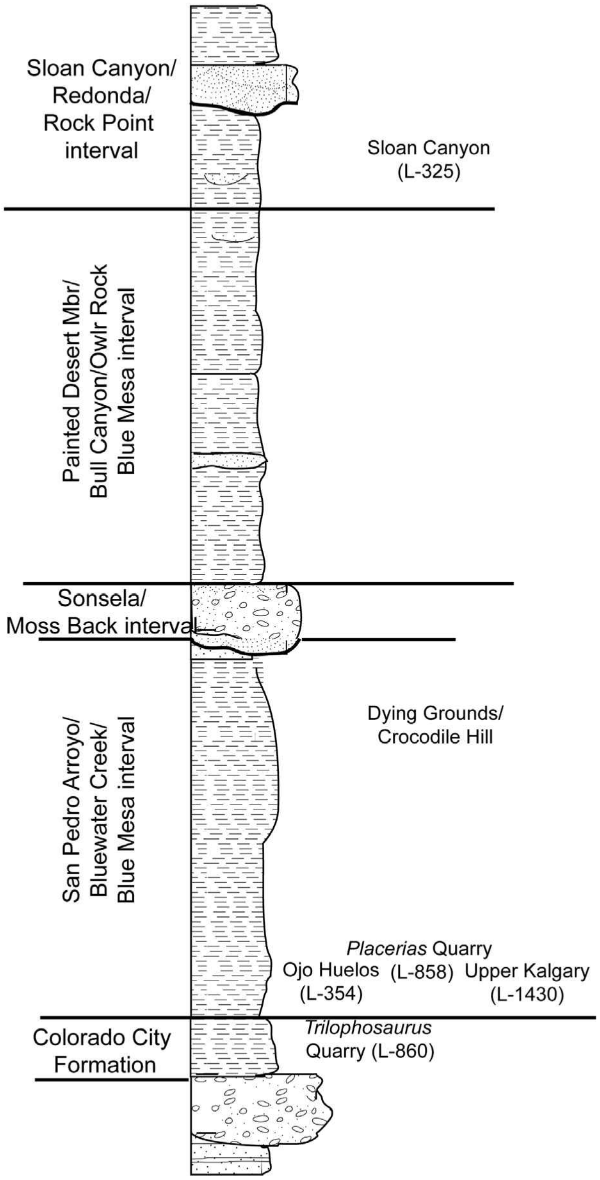

FIGURE 2. Generalized stratigraphic distribution of *Lonchidion* localities in Figure 1.

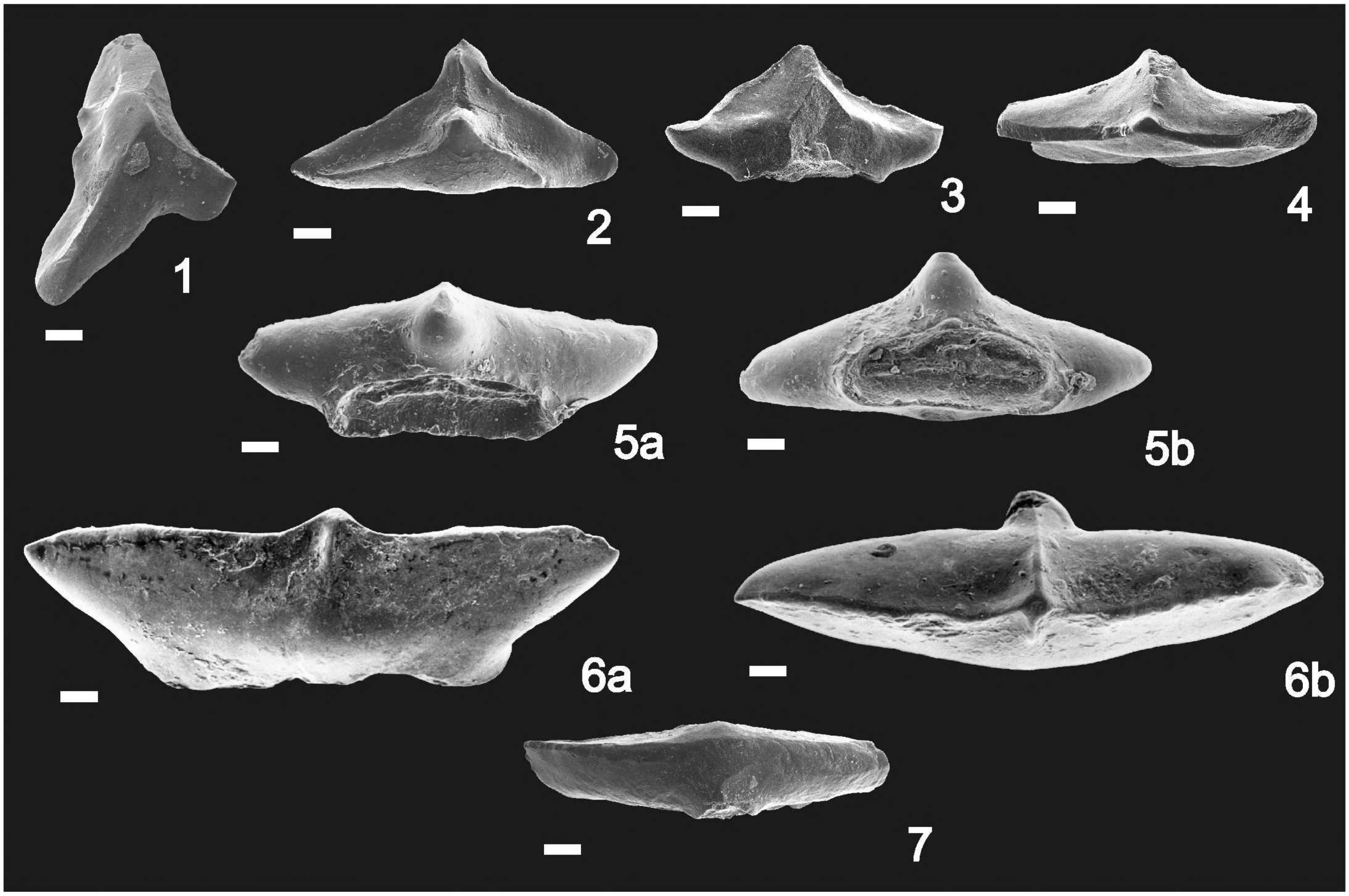

FIGURE 3. Scanning electron micrographs of tooth crowns of *Lonchidion humblei* Murry. **1**, probable symphyseal tooth with the living abrasion on the central cusp, in oblique lateral view; NMMNH P-31620, locality L-354. **2**, symphyseal tooth in occlusal view, NMMNH P-10086a, locality L-354. **3**, symphyseal or mesial tooth in labial view, NMMNH P-10086b, locality L-354. **4**, mesial or anterolateral tooth in occlusal view, NMMNH P-10086c, locality L-354. **5**, anterolateral tooth in **a,** labial view, and **b,** basal views, NMMNH P-26429a, locality L-01430. **6**, lateral tooth in **a,** lingual view, and **b,** occlusal views, NMMNH P-26429b, locality L-01430. **7**, posterior tooth in oblique occlusal view, NMMNH P-10086d, locality L-354. All scale bars = 100 microns.

STRATIGRAPHY AND AGE

The upper Kalgary microvertebrate locality is stratigraphically low in the Tecovas Formation of West Texas. This site is of Adamanian age, as the bulk of the Tecovas Formation, including sites in this area at this level, yields a typical Adamanian fauna of the phytosaur *Rutiodon* (=*Leptosuchus*) and the aetosaur *Stagonolepis* (see Heckert, 2004 for additional information).

The Adamanian Ojo Huelos Member represents a freshwater carbonate setting (Heckert and Lucas, 2002b), a depositional environment that is relatively rare in the Chinle (Tanner, 2003). The Ojo Huelos Member of the San Pedro Arroyo Formation is stratigraphically low in the Chinle Group (Lucas, 1991; Heckert and Lucas, 1997, 2002b). The localities sampled here range from approximately 2 to 8 m above the base of the "mottled strata," a pedogenically modified horizon that, with the Shinarump Formation, marks the base of the Chinle Group regionally (Lucas, 1993; Heckert and Lucas, 2003).

DESCRIPTION

The remains of *Lonchidion humblei* are represented by numerous isolated teeth and some fragments of fin spines (e.g., Murry, 1981; Heckert, 2004). Here we provide scanning electron microscope images (Fig. 3) and photographs of teeth immersed in aniseed oil (Fig. 4). Almost all of teeth lack the base, and the labial peg is not preserved in some teeth. However, the preservation of crown tissue is very good and allows us to study the structure when immersed in aniseed oil under the optical microscope.

Small teeth of *Lonchidion humblei* possess a smooth crown with a strong occlusal crest and a transverse ridge on the labial peg; they lack accessory cusps and vertical ridges. The crown comprises orthodentine covered by a considerably thick layer of enameloid. The narrow vascular canals pass into the lower part of the crown, along the base/crown junction. The dentine tubules run up from those canals to an enameloid layer. They are equally distributed over most of the crown and concentrated only in the crown shoulders. Such histological structure of the crown is similar to that described for the teeth of *Lonchidion breve* Patterson (1966). However, it differs from the internal structure of the teeth of *Lissodus angulatus* (Stensiö) documented by Błażejowski (2004) in the absence of osteodentine in the crown in any of the tooth morphotypes.

Duffin (2001) proposed five morphotypes depending on tooth position: symphyseal, mesial, anterolateral, lateral and posterior. Most morphotypes appear applicable to *Lonchidion humblei*, which exhibits moderate heterodonty. The variations of the crown are expressed in size and proportions, in the height of the central cusp, the length of the labial peg, the curvature of the occlusal crest, the direction of the crown shoulder, and in the degree of convexity in the lingual side. The articulated dentition is known in only two lonchidiid forms— *Lissodus africanus* (Broom) (Brough, 1935; Duffin, 1985; Rees and Underwood, 2002) and *Lissodus johnsonorum* Milner and Kirkland (2006).

We assigned the teeth studied here to potential positions based on

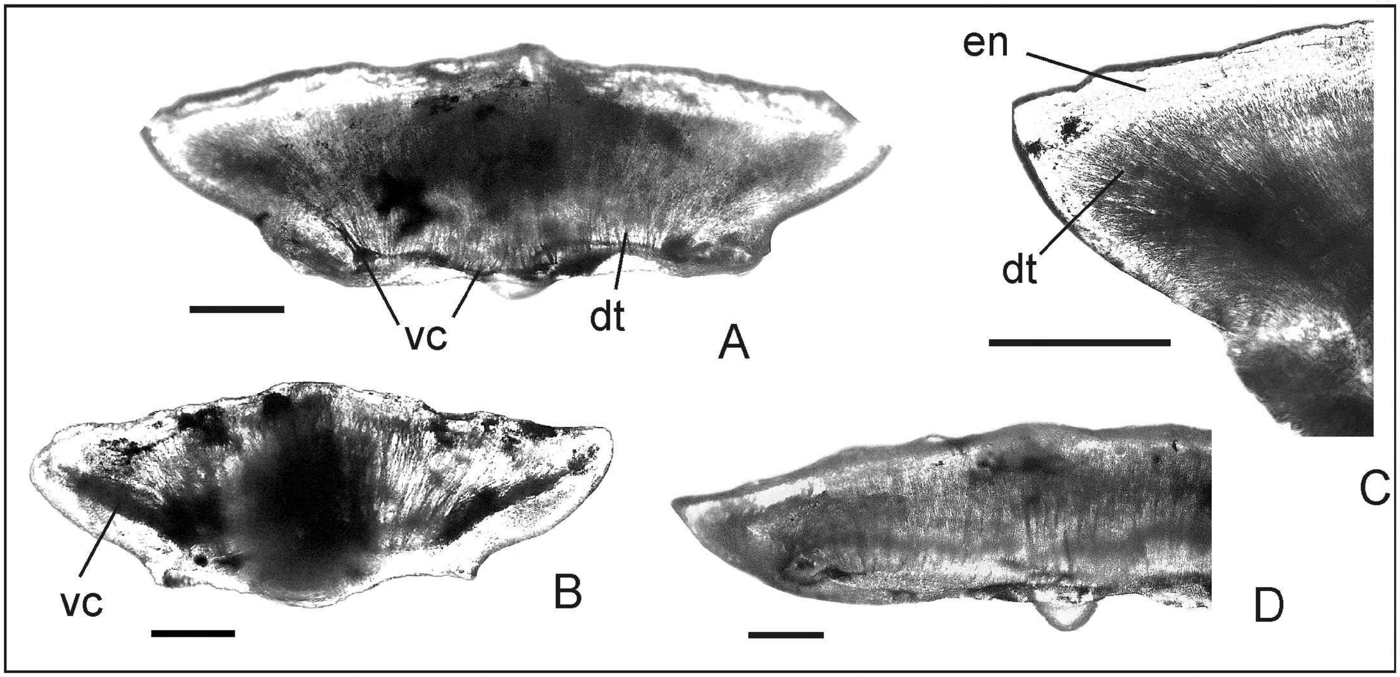

FIGURE 4. Internal structure of *Lonchidion humblei* crown immersed in aniseed oil, labial views.**A**, lateral tooth; **B**, mesial or anterolateral tooth, **C**, crown shoulder of lateral tooth, **D**, posterior tooth. Abbreviations: dt – dentine tubules, en - enameloid, vc – vascular cannals. All scale bars = 200 microns.

comparison to the reconstruction of the dentition of *Lissodus nodosus* (Seilacher) suggested by Duffin (1985) and Duffin's extrapolation of tooth arrangement for some lonchidiids (Duffin, 2001) with regard to complete dentitions. The teeth hypothesized to be symphyseal and mesial are characterized by moderate length and a high crown bearing a long labial peg, a well developed central cusp, and acute occlusal crest. Such crowns have a shape close to an equilateral triangle in occlusal view. The central cusp in some specimens is inclined labially. The teeth of the anterior dental position possess the narrow base/crown junction ("neck"). Extending distally from the symphyseal to posterior teeth the crowns become lower and more mesiodistally extended, a central cusp increases in that direction, the occlusal crest becomes smooth, and the labial peg shortens. The internal structure of the teeth changes slightly posteriorly through the dentition. The teeth of the anterior position contain the vascular canals running along the crown shoulders and a considerable concentration of dentine tubules in those parts of crown. The vascular canals are located only near the base/crown junction of the lateral and posterior teeth. The dentine tubules are more equally distributed in the crowns of such teeth. The enameloid layer is rather thickened posteriorly in the dentition.

The function of the teeth in the jaw was probably differentiated, from cutting in the symphyseal and mesial positions to crushing in the lateral and posterior ones. The traces of living abrasion in some specimens are observed on the central cusp of the anterior teeth and on the occlusal crests of lateral and posterior teeth.

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Susan Harris and Ken Kietzke originally picked specimens illustrated here from screenwash concentrate. The NMMNH Foundation funded A.I.'s visits to the collections.

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LATE TRIASSIC AETOSAUR BIOCHRONOLOGY REVISITED

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Abstract—Eleven years ago Lucas and Heckert (1996) proposed five biochrons based on aetosaur genus-level occurrences in the Upper Triassic Chinle Group of the southwestern U.S.A., another for *Stegomus* in the eastern U.S.A., and a Greenlandic-European *Aetosaurus* biochron. While some have embraced this biochronological framework, others have challenged it on taxonomic, stratigraphic, and evolutionary grounds, while additional discoveries have further modified the underlying taxonomic framework. Here, we take this opportunity to evaluate the past decade's progress in aetosaurian systematics and distribution to critically reevaluate the biochronological potential of aetosaurian taxa. No fewer than nine genera of aetosaurs provide biostratigraphic correlations within the Chinle Group, and five of these reliably correlate Chinle Group strata to other strata across Pangea. Thus, it is clear that aetosaurs remain robust biochronological tools for the subdivision of Late Triassic time.

INTRODUCTION

Lucas and Heckert (1996) documented five biochrons based on the occurrence of five aetosaur genera in the Upper Triassic Chinle Group of the southwestern U.S.A. Our current assessment of the aetosaurian record documents that at least 11 genera of aetosaurs are present in the Chinle Group: *Longosuchus*, *Coahomasuchus*, *Stagonolepis*, *Adamanasuchus*, *Desmatosuchus*, *Tecovasuchus*, *Paratypothorax*, *Typothorax*, *Rioarribasuchus*, *Aetosaurus*, and *Redondasuchus* (Fig. 1), a number based not only on our own work, but on the consensus of others (Heckert and Lucas, 1999, 2000; Lucas et al., 2002; Martz and Small, 2006; Parker, 2007). Of these, all but *Coahomasuchus* and *Adamanasuchus* are known from multiple localities, and therefore have biochronological utility. Most taxa are monospecific, with the exceptions of *Typothorax* (*T. antiquum*, *T. coccinarum)*, *Redondasuchus* (*R. reseri*, *R. rineharti)*, *Aetosaurus* (*A. ferratus*, *A. crassicauda*, *A. arcuatus)*, *Stagonolepis* (*S. robertsoni*, *S. wellesi)*, and possibly *Desmatosuchus* (*D. haplocerus*, *D. smalli)*. Additional taxa we do not consider valid include *Lucasuchus* (=*Longosuchus*) and *Acaenasuchus* (=*Desmatosuchus*), although, if proved valid, both have their own biostratigraphic utility as putative occurrences of each are restricted to narrow stratigraphic intervals (Fig. 1).

BIOCHRONOLOGY

Accordingly, it is now possible to recognize no fewer than nine genus-level aetosaur biochrons in the Chinle Group:

(1) *Longosuchus* (=*Lucasuchus*) biochron of Otischalkian age.

(2) *Stagonolepis* biochron of Adamanian (St. Johnsian) age.

(3) *Tecovasuchus* biochron, also of Adamanian (St. Johnsian) age.

(4) *Desmatosuchus* biochron of Adamanian-Revueltian (Barrancan) age.

(5) *Typothorax* biochron of Adamanian (Lamyan)-Revueltian age.

(6) *Paratypothorax* biochron of Adamanian (Lamyan)-Revueltian (possibly Apachean) age.

(7) *Aetosaurus* biochron of Revueltian-Apachean age.

(8) *Rioarribasuchus* biochron of Revueltian age.

(9) *Redondasuchus* biochron of Apachean age.

With the recognition of multiple species of *Desmatosuchus*, *Typothorax*, and *Aetosaurus,* several of these biochrons can be subdivided still further: *D. haplocerus* = Adamanian. *D. smalli* (if valid) = Revueltian (Barrancan). *T. antiquum* = Adamanian (Lamyan). *T. coccinarum* = Revueltian. *A. arcuatus* = Revueltian. *A. ferratus* = Revueltian-Apachean. The first appearance datum (FAD) of *T. antiquum* defines the Lamyan sub-lvf.

Importantly, the *Longosuchus*, *Stagonolepis*, *Paratypothorax*, and *Aetosaurus* biochrons can all be correlated with aetosaur occurrences outside the Chinle Group. Specifically, additional records of *Longosuchus*(=*Lucasuchus*) are known from the eastern U.S.A. and North Africa. *Stagonolepis* records include *S. robertsoni* from North America, Argentina, Brazil, and Scotland and *S. wellesi* and *S.* cf. *S. wellesi* from North and South America, respectively. *Stagonolepis* records we are not yet able to assign to species are known from Poland and

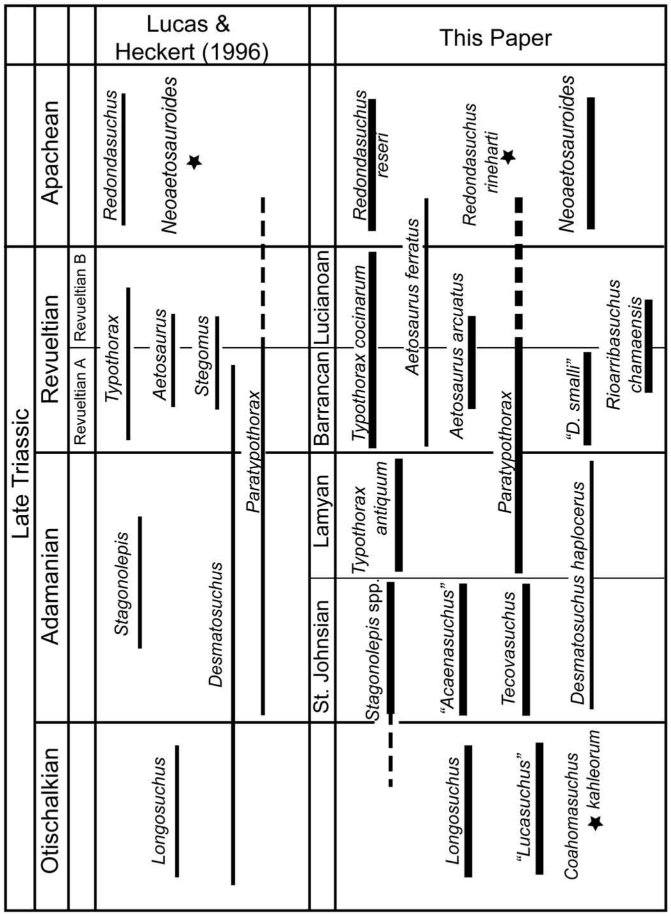

FIGURE 1. Revised biochronological hypothesis of Lucas and Heckert (1996) showing increased resolution provided by advances in aetosaurian taxonomy in the past decade. Taxa in quotation marks are those we do not recognize as valid, but whose occurrences are stratigraphically restricted. Taxa denoted with a star are (were) known from single occurrences.

Germany and appear to extend the *Stagonolepis* biochron into the Otischalkian. *Paratypothorax* is known from North America, Greenland, and Germany. *Aetosaurus arcuatus* is known from the eastern and southwestern U.S.A., and *A. ferratus* is known from Germany, Italy, and the southwestern U.S.A. There are records of aetosaurs from India, but published descriptions are inadequate to assign them to genus, but they resemble descriptions of *Longosuchus* and *Paratypothorax*.

CONCLUSIONS

This brief review demonstrates that aetosaurs remain a robust biochronologic tool for the subdivision of Late Triassic time. Since 1996, discoveries of both new taxa and new records of previously known taxa have modified the biochronological hypotheses of Lucas and Heckert (1996), but the net effect, seen in Figure 1, is a greatly improved biochronological framework that now recognizes not only the same major faunachrons, but also subdivisions of those faunachrons postulated by others (Hunt, 2001; Hunt et al., 2005). Consequently, the number of Chinle aetosaur biochrons based on genus-level taxonomy has grown from five to nine, and the precision of correlation, especially within previously long-ranging taxa such as *Paratypothorax* and *Desmatosuchus*, has improved with a better understanding of new- and previously poorly-known taxa such as *Tecovasuchus* and *Rioarribasuchus*.

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Lucas, S.G. and Spielmann, J.A., eds., 2007, The Global Triassic. New Mexico Museum of Natural History and Science Bulletin 41.

BIOSTRATIGRAPHIC UTILITY OF THE UPPER TRIASSIC AETOSAUR *TECOVASUCHUS* (ARCHOSAURIA:STAGONOLEPIDIDAE), AN INDEX TAXON OF ST. JOHNSIAN (ADAMANIAN:LATE CARNIAN) TIME

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Abstract—The recently recognized aetosaur *Tecovasuchus chatterjeei* Martz and Small occurs at several localities in lower Chinle Group strata across Texas, New Mexico, and Arizona. Based on lithostratigraphic correlation and other vertebrate occurrences, all *Tecovasuchus* occurrences are of Adamanian age. Indeed, all occurrences are consistent with assignment to the St. Johnsian sub-land vertebrate faunachron of the Adamanian. We therefore recognize *Tecovasuchus* as an index taxon of Adamanian (St. Johnsian) time, and demonstrate that aetosaur biostratigraphy and biochronology is now more robust and precise than it was a decade ago.

INTRODUCTION

Aetosaurs are a group of extinct, heavily armored archosaurian reptiles known from Upper Triassic sediments in North and South America, Greenland, Europe, North Africa, and India (Heckert and Lucas, 2000). The armor of aetosaurs consists of multiple columns of osteoderms—two on the dorsal surface (paramedian osteoderms), one each lateral to those osteoderms (lateral osteoderms), multiple columns of ventral osteoderms, and additional appendicular and, in some cases, gular, osteoderms. Due to the biases of preservation, these osteoderms are among the most commonly recovered fossils in many Upper Triassic deposits, and the first aetosaurs described by paleontologists were named on the basis of distinctive, yet largely isolated, osteoderms (e.g., Agassiz, 1844; Cope, 1877, 1892). More recently, Long and Ballew (1985) demonstrated that basing the alpha taxonomy of aetosaurs primarily on osteoderm morphology, originally borne out of the necessity of working with fragmentary fossils, is remarkably sound taxonomically, and showed how features of the paramedian and lateral armor facilitate ready discrimination of four genera of aetosaurs, some of which co-occur. Ensuing work has modified their hypothesis, but two decades' work on taxonomy naming new taxa (Hunt and Lucas, 1990, 1991; Long and Murry, 1995; Heckert and Lucas, 1999; Lucas et al., 2002; Zeigler et al., 2002; Parker, 2005a; Spielmann et al., 2006) and examining aetosaur phylogeny (Heckert et al., 1996; Heckert and Lucas, 1999, 2000; Parker, 2007) demonstrate that substantial taxonomic and phylogenetic signals reside in the morphology of aetosaur osteoderms, particularly the paramedian and lateral osteoderms. Combining this information with a detailed understanding of the stratigraphic distribution of aetosaur occurrences resulted in a robust biochronology based on aetosaurs (Lucas and Heckert, 1996; Heckert and Lucas, 2000), and indeed aetosaur biochronology underpins the best biochronology of Late Triassic time available in the nonmarine record (Lucas and Hunt, 1993; Lucas, 1998).

Recently, Martz and Small (2006) named a new aetosaur, *Tecovasuchus chatterjeei*, and referred some additional material to that taxon, but did not expound on its biostratigraphic and biochronological significance. Similarly, Parker (2003, 2005b, 2007) has indicated that *Tecovasuchus* is a valid taxon and can be identified based on isolated osteoderms. Here we demonstrate that *Tecovasuchus* is actually widely distributed across the Chinle Group of the southwestern United States (Fig. 1), but only occurs through a limited stratigraphic interval, and is therefore an index taxon of the St. Johnsian sub-faunachron of the Adamanian land-vertebrate faunachron (lvf) of Lucas and Hunt (1993; Lucas, 1998; Hunt et al., 2005).

Abbreviations: MNA = Museum of Northern Arizona, Flagstaff; NMMNH = New Mexico Museum of Natural History, Albuquerque; TTUP = Texas Tech Museum of Paleontology, Lubbock; UCMP = University of California, Berkeley; UMMP = University of Michigan Museum of Paleontology, Ann Arbor.

SYSTEMATIC PALEONTOLOGY

Stagonolepididae Lydekker, 1887

Paratypothoracini Parker, 2007

Tecovasuchus Martz and Small, 2006

"New Taxon": Lucas et al., 1995, fig. 2d-f, fig. 3d-f, p. 467
cf. *Paratypothorax* sp.: Lucas et al., 1995, fig. 2a-c, 3a-c, p. 467
Paratypothorax? Heckert, 1997, fig. 3f, p. 29
Paratypothorax-like aetosaur: Parker, 2005b, fig. 3, p. 39
Tecovasuchus chatterjeei Martz and Small, 2006, figs. 1-7, 8d, p. 308
Tecovasuchus: Parker, 2007, fig. 8i-j, p. 43

Amended diagnosis: Martz and Small (2006, p. 312) diagnosed *Tecovasuchus* as:

> An aetosaur with the following unique combination of characters: dorsal paramedian osteoderms very wide (width:length ratio approaching 4.0) as in *Typothorax coccinarum* and *Paratypothorax*; raised anterior bar on dorsal surface of dorsal paramedians as in most aetosaurs except *Desmatosuchus* and *Acaenosuchus* [sic]; dorsal boss on dorsal paramedians a low rounded keel at center of ossification as in *Aetosaurus ferratus*; ornamentation on dorsal paramedians consisting of both deep, rounded pits and shallower radiating grooves as in *Stagonolepis*; posterior edge of dorsal paramedians strongly thickened and beveled (autapomorphy); thick ventral strut on dorsal paramedians similar to that of *Typothorax*, *Redondasuchus*, and some specimens of *Paratypothorax*; at least some lateral osteoderms very similar to *Paratypothorax* in having short, curved, dorsoventrally compressed, and posteriorly excavated horn, and reduced tongue-shaped dorsal flange forming angle of about 45° with larger plate-like ventral flange.

We follow this diagnosis, but also consider that the strongly developed depth of the arcuate pattern on the lateral scutes and the extreme compression (narrow arch) of these osteoderms distinguish *Tecovasuchus* from *Paratypothorax*, whose lateral scutes have a similar pattern that is not as deeply textured (e.g., Lucas et al., 2006; fig. 6a).

Holotype: TTUP 545, a partial braincase and eight associated osteoderms of varying completeness from the "breaks of Sierrita de la Cruz creek," Oldham County, Texas (Martz and Small, 2006).

Referred specimens: TTUP 9222, left dorsal paramedian osteoderm from Cedar Hill West Texas; UMMP 7244, incomplete dorsal

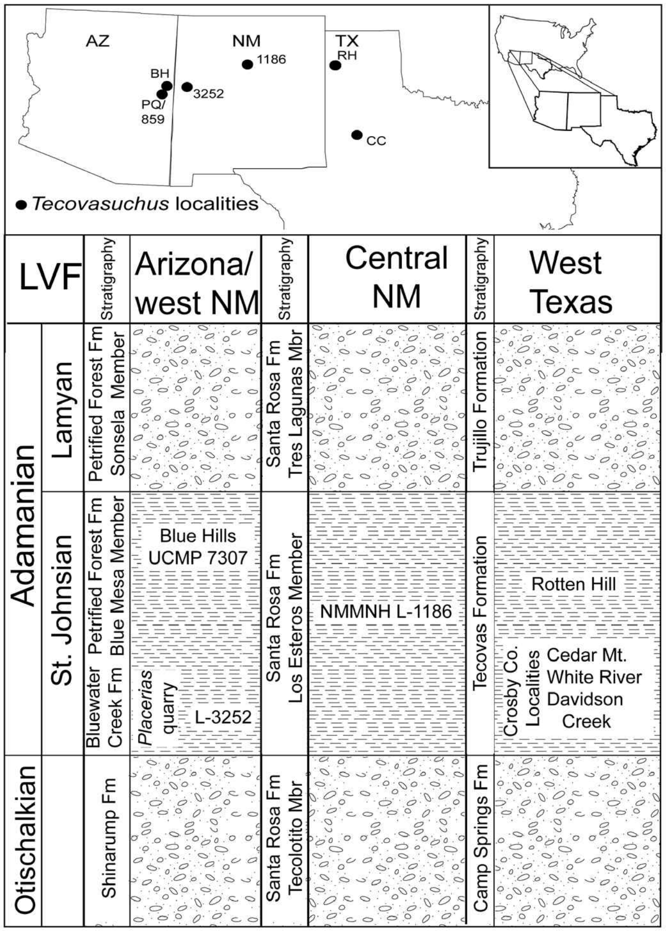

FIGURE 1. Geographic and stratigraphic distribution of *Tecovasuchus* occurrences in western North America. Abbreviations: BH = Blue Hills, CC = Crosby County, PQ = *Placerias* quarry (including the nearby Downs' quarry); RH = Rotten Hill.

paramedian scute from Davidson Creek, Texas; UMMP 8869, a nearly complete lateral osteoderm from Crosby County, Texas; UMMP 9600, a nearly complete dorsal paramedian osteoderm, also from Crosby County Texas (Fig. 2A-B); all previous specimens from the Tecovas Formation of West Texas. MNA 2898, an incomplete left lateral osteoderm (Fig. 2F-H), from the *Placerias* quarry (NMMNH locality 859), Upper Triassic Bluewater Creek Formation, Arizona; MNA 3202, several osteoderms, including incomplete right lateral and paramedian osteoderms illustrated by Parker (2005b, fig. 3.1-2, 3.5) from the Downs' quarry, Upper Triassic Bluewater Creek Formation, Arizona; NMMNH P-25641, an incomplete right? lateral osteoderm (Fig. 2C-E), left? lateral osteoderm (Fig. 3C) and two dorsal paramedian osteoderm fragments (Fig. 3D) from the Upper Triassic Los Esteros Member, Santa Rosa Formation (NMMNH locality 1186), New Mexico; NMMNH P-18305, an incomplete left lateral osteoderm (Fig. 3A) from the Upper Triassic Bluewater Creek Formation (NMMNH locality 3252), New Mexico.

All of the above specimens were either referred to *T. chatterjeei* by Martz and Small (2006) and/or Parker (2007) or, in the case of material we have added here (Figs. 2-3), clearly possess the distinctive features of *T. chatterjeei* as enumerated by Martz and Small (2006). In particular, lateral osteoderms we refer to *T. chatterjeei* have a posteriorly excavated horn that is short, curved, and dorsoventrally compressed (as is the osteoderm generally) with a ventral flange that possesses a distinctive pattern of arcuate, radial ridges and grooves and a reduced dorsal flange that extends from the ventral flange at an acute angle.

Specimens referred to *Tecovasuchus*? sp.: NMMNH P-18422, an osteoderm fragment from the Upper Triassic lower Bluewater Creek Formation (NMMNH locality 3252) (Fig. 3A), New Mexico; UCMP A269/126847, paramedian osteoderm fragment, A269/136744, incomplete right paramedian fragment, both from the *Placerias* quarry, lower Bluewater Creek Formation, east-central Arizona; UCMP 7307/27049, from the Blue Hills, Upper Triassic Blue Mesa Member, Petrified Forest Formation, east-central Arizona; TTUP 10079, incomplete carapace from L-7 Ranch, near Negro Hill, Upper Triassic Tecovas Formation of West Texas (this last assignment follows Martz and Small, 2006).

Material we refer to *Tecovasuchus*? sp. here and not previously referred by Martz and Small (2006) consists of fragments of osteoderms we are reasonably certain pertain to *Tecovasuchus* but which cannot be unambiguously referred to that taxon. In general, these are short, wide, osteoderms that are incomplete but appear to possess the attributes of *Tecovasuchus*.

We note here that Lehman and Chatterjee (2005, p. 345) used the generic name "*Tecovasuchus*," but from the context of their text it is clear that this is a *lapsus calami* referring to the possible ornithischian *Tecovasaurus murryi* Hunt and Lucas (1994), not *Tecovasuchus chatterjeei* Martz and Small (2006), which was then unnamed.

STRATIGRAPHIC DISTRIBUTION

Presently material of *Tecovasuchus* occurs in only three formations—the Tecovas Formation of West Texas (Martz and Small, 2006), the Los Esteros Member of the Santa Rosa Formation in central New Mexico (documented here), and the Bluewater Creek Formation of western New Mexico and eastern Arizona (Parker, 2005b). The holotype specimen is from the Tecovas Formation of West Texas in the northern Triassic outcrop belt in the vicinity of Sierrita de la Cruz Creek, an area that includes the famous "Rotten Hill" metoposaur assemblage (Long and Murry, 1995). Other Texan occurrences include the material collected by Case, given as "near [the] river crossing old Spur-Crosbyton road" on museum labels (Lucas et al., 1995, p. 467). Throughout West Texas, including the outcrops embracing these occurrences, the Tecovas Formation yields a tetrapod assemblage that includes the phytosaur *Rutiodon* (=*Leptosuchus*), the aetosaur *Stagonolepis wellesi*, and/or the enigmatic taxon *Colognathus*, all of which are index taxa of the Adamanian (St. Johnsian) lvf (e.g., Hunt et al., 2005; Heckert and Lucas, 2006).

The Los Esteros Member material was recovered from a ~20 m thick interval that includes three NMMNH localities (149, 1179, 1271) documented by Hunt and Lucas (1995) plus the locality noted here (NMMNH locality 1186). All four of these localities are east of Lamy, New Mexico (Hunt and Lucas, 1995, fig. 1; see also Lucas and Heckert, 1995, for a description of the Triassic stratigraphy in this area). The fauna from these localities includes the metoposaur *Buettneria*, the aetosaurs *Desmatosuchus*, *Typothorax* cf. *T. antiquum* and cf. *Stagonolepis*, and the problematic reptile *Colognathus* (Hunt and Lucas, 1995; Heckert, 2001). Although the aetosaurian records are fragmentary, the record of *Colognathus* from this locality (Heckert, 2001, identified as a possible procolophonid) is diagnostic of an Adamanian (St. Johnsian) age (Heckert and Lucas, 2006).

The *Placerias*-Downs' quarry complex in eastern Arizona is, taxonomically, the single richest vertebrate site known from the Chinle (e.g., Kaye and Padian, 1994; Long and Murry, 1995; Lucas et al., 1997). Lucas et al. (1997) demonstrated that the *Placerias* quarry occurs low in the Bluewater Creek Formation, just above the base of the Chinle Group locally, and that the nearby (<100 m) Downs' quarry occurs at a slightly higher (~1.5 m) level. Parker (2005) demonstrated that some specimens from the Downs' quarry previously attributed to *Stagonolepis wellesi* by Long and Ballew (1985) actually pertain to *Tecovasuchus*. Additionally, we note that the left lateral osteoderm MNA V2898 from the *Placerias* quarry itself (Fig. 2F-H) is a near perfect mirror image of the right lateral osteoderms of *Tecovasuchus* illustrated by Parker (2005b, fig. 3.1-4). We have also observed fragmentary paramedian osteoderms from the *Placerias* quarry in the UCMP collections (in particular UCMP

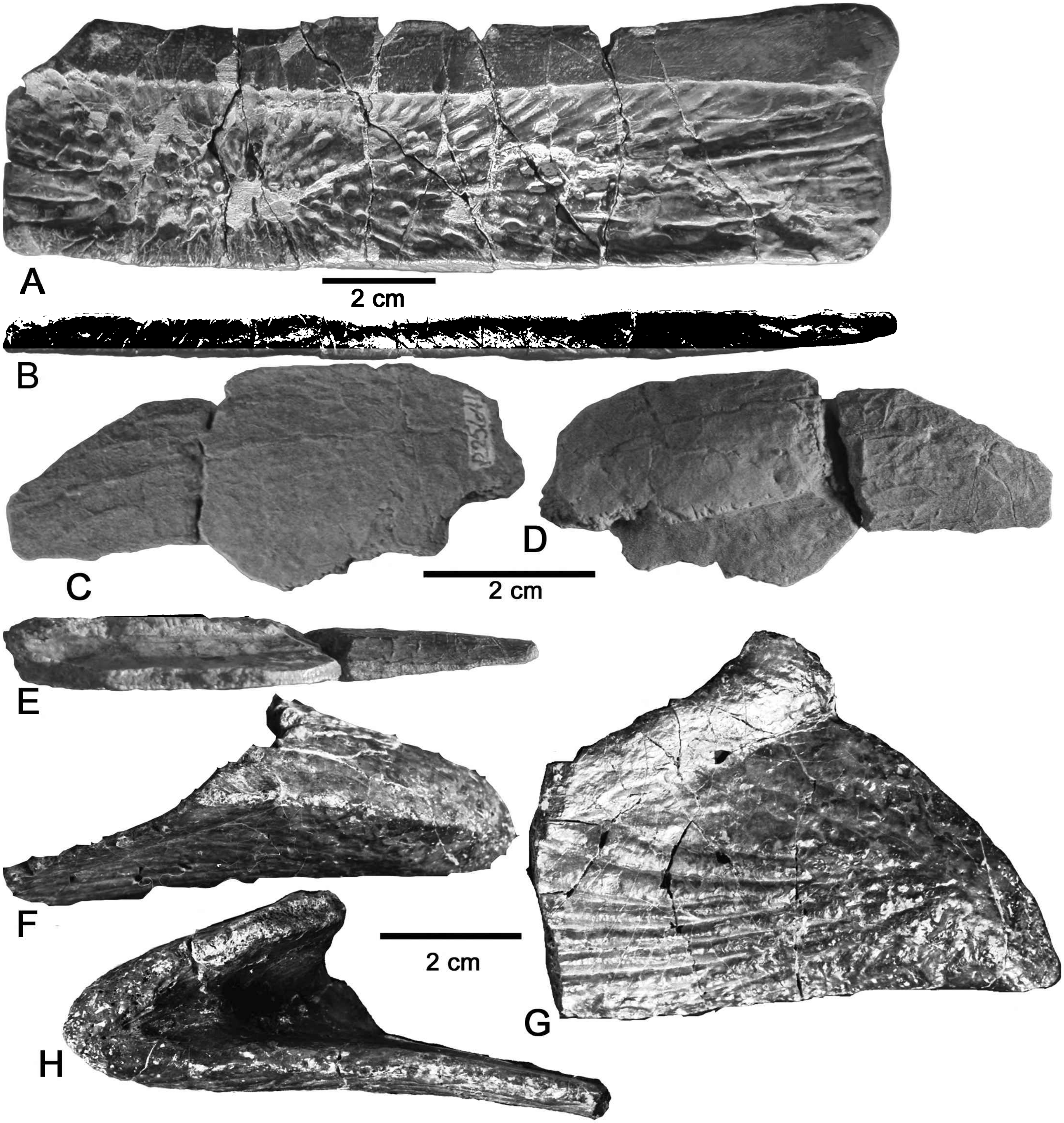

FIGURE 2. *Tecovasuchus chatterjeei*. **A**-**B**, UMMP 9600, right dorsal paramedian osteoderm in **A**, dorsal and **B**, posterior views. **C**-**E**, NMMNH P-25641, right? lateral osteoderm in **C**, ventral, **D**, dorsal and **E**, medial views; **F**-**H**, MNA V2898, left lateral osteoderm in **F**, anterior, **G**, ventral, and **H**, posterior views.

126847, a left, and 136744, a right, both from UCMP locality A269) that represent a wide-bodied aetosaur that we tentatively ascribe to *Tecovasuchus* sp. The *Placerias*-Downs' quarry horizon is nearly equivalent to the probable New Mexican occurrence of *Tecovasuchus* from the Bluewater Creek Formation originally documented as a possible *Paratypothorax* sp. specimen by Heckert (1997) and subsequently identified as *Tecovasuchus*? sp. by Parker (2005b) (Heckert and Lucas, 2002).

A single fragmentary specimen in the collections of the UCMP may represent an additional occurrence of *Tecovasuchus*. The specimen in question, UCMP 27049 from UCMP locality 7307, is from the Blue Hills in east-central Arizona. UCMP 7307 is one of C.L. Camp's classic collecting localities, and occurs low in the Blue Mesa Member of the Petrified Forest Formation (Fig. 1). This locality yields a typical Adamanian (St. Johnsian) fauna (e.g., Heckert and Lucas, 2003), so this fragmentary specimen does not change the biostratigraphic utility of *Tecovasuchus* at the faunachron-level, although it does indicate that it

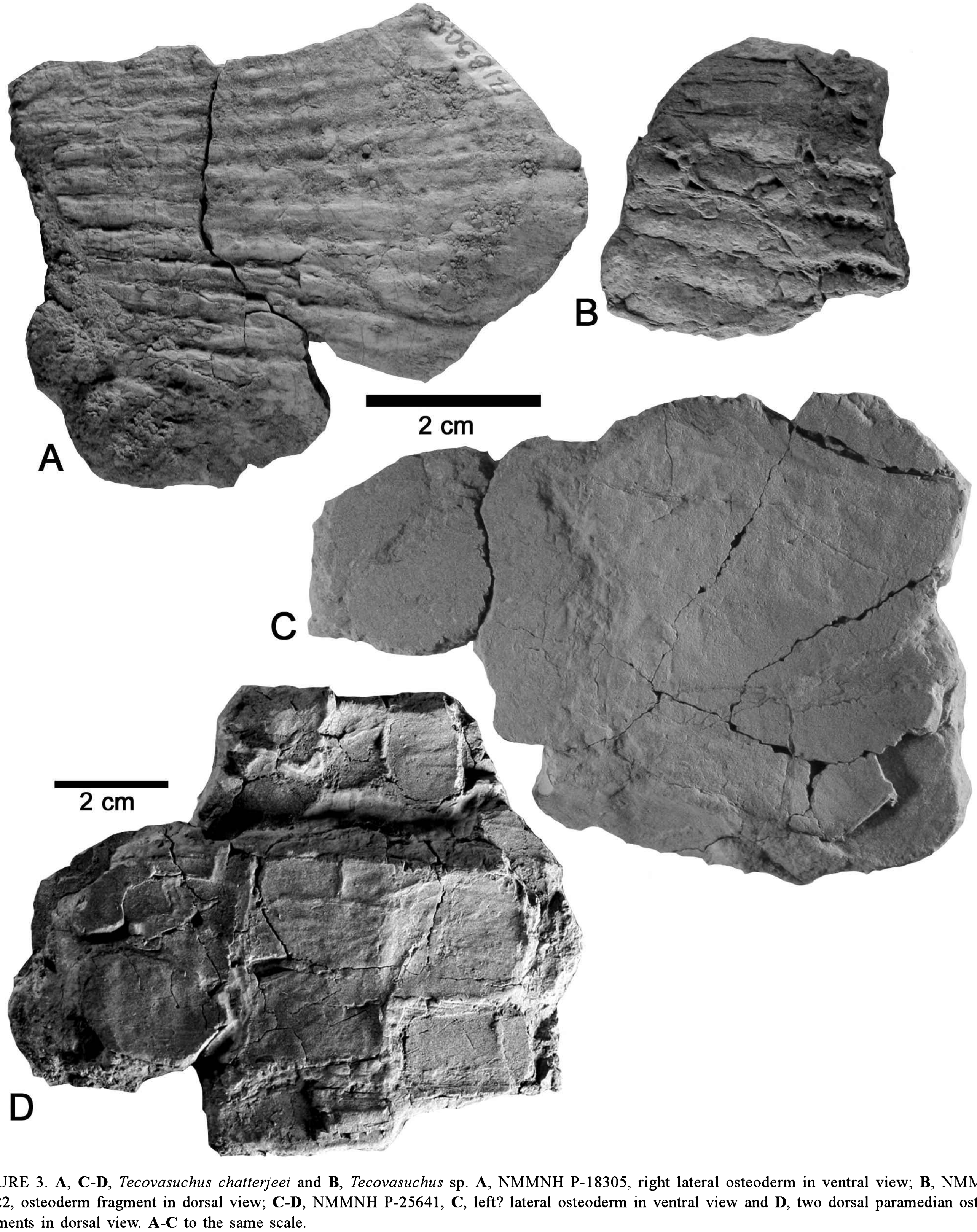

FIGURE 3. **A**, **C-D**, *Tecovasuchus chatterjeei* and **B**, *Tecovasuchus* sp. **A**, NMMNH P-18305, right lateral osteoderm in ventral view; **B**, NMMNH P-18422, osteoderm fragment in dorsal view; **C-D**, NMMNH P-25641, **C**, left? lateral osteoderm in ventral view and **D**, two dorsal paramedian osteoderm fragments in dorsal view. **A-C** to the same scale.

may occur through at least 60 m of section in eastern Arizona.

CORRELATION

Tecovasaurus occurrences are reliably correlated by a variety of lithostratigraphic and biostratigraphic techniques. The Tecovas Formation yields a single vertebrate fauna readily identified as Adamanian (St. Johnsian) in age, so all occurrences in West Texas are, within biostratigraphic resolution, the same age (Lucas and Hunt, 1993; Long and Murry, 1995). The Los Esteros Member of the Santa Rosa Formation is homotaxial to the Tecovas Formation and similarly represents an interval dominated by deposition of relatively fine-grained sediments overlying coarser-grained sediments (Tecolotito Member) representing infill of incised topography present at the onset of Chinle deposition (Lucas et al., 1994, 2001). The Bluewater Creek Formation is comprised of similar strata representing this same interval in western New Mexico and eastern Arizona (Heckert and Lucas, 2002).

DISCUSSION

Since its creation, the biochronology of Lucas and Hunt (1993; Lucas, 1998) has drawn diverse challenge and rebuke (e.g., Long and Murry, 1995; Lehman and Chatterjee, 2005; Parker, 2005b, 2007; Martz and Small, 2006, among others). Criticism of the aetosaur-based biochronology of Lucas and Heckert (1996) underpinning Lucas' (1998) revision of Lucas and Hunt's (1993) hypothesis has centered around the following arguments: (1) various aetosaurs identified as index taxa of different faunachrons actually co-occur; (2) aetosaur armor is not as readily identifiable as suggested by Lucas and Heckert (1996); and (3) new occurrences falsify the hypothesis. To be sure, additional information has changed some taxonomic assignments and otherwise altered our understanding of aetosaurian distribution in time and space. However, Figure 4 demonstrates that, instead of diminishing it, subsequent work has actually enhanced the biostratigraphic utility of aetosaurs. In particular, we note the following:

(1) Supposed co-occurrences of aetosaurian index taxa, specifically *Stagonolepis wellesi* and *Typothorax* are records of *Stagonolepis wellesi* and the recently described taxon *Typothorax antiquum* (Lucas et al., 2002) and are restricted to a narrow interval (< 10 m thick) in the Petrified Forest National Park (Hunt et al., 2005; Parker, 2005b; Parker and Irmis, 2005). This leaves *S. wellesi* and *T. coccinarum*, which never co-occur, as discrete index taxa of the Adamanian and Revueltian lvfs, respectively. Although some (e.g., Parker, 2005b, 2007) do not recognize *T. antiquum* as a distinct species of *Typothorax*, we maintain that we can readily discriminate specimens of *T. coccinarum* from *T. antiquum* Lucas et al. (2002).

(2) In spite of repeated criticism of the utility of isolated aetosaurian osteoderms (e.g., Martz and Small, 2006; Parker, 2007), some of which resorts to nearly *ad hominum* verbiage ("shoehorning" of Martz and Small, 2006, p. 308, for example), these same workers have repeatedly demonstrated that additional study of aetosaurs actually *enhances* the value of individual osteoderms. Indeed, these authors, by building upon the work of others (e.g., Long and Ballew, 1985; Long and Murry, 1995; Heckert and Lucas, 1999, 2000) and describing variation within a single carapace or quarry sample (Martz, 2002; Parker, 2003) have now extensively subdivided aetosaur carapaces at a much more anatomically precise level, effectively facilitating identification of more osteoderms not only to taxon, but to specific regions of the carapace (e.g., Martz, 2002; Parker, 2003, 2007; Martz and Small, 2006). We concur with their assessment that more and better fossils, specifically fossils documenting ontogenetic variation, will improve our understanding still further, but this is the nature of science, which by definition continues to seek improved resolution of our understanding of natural phenomena.

(3) In direct opposition to the assertion that new occurrences have falsified the biostratigraphy advocated by Lucas and Heckert (1996), Figure 4 demonstrates that new discoveries and improved taxonomic understanding have resulted in a substantial increase in the resolution of aetosaur ranges. One such example is the case of *Desmatosuchus*, once thought to range through much of the Upper Triassic section in western North America, but now restricted to a narrower stratigraphic interval, with the possibility that each of two species may subdivide that interval further. More germane to this paper, occurrences of *Paratypothorax* as understood in the 1990s are now known to pertain to at least two, and probably three, taxa, *Tecovasuchus*, *Paratypothorax*, and perhaps another taxon. The result is, as demonstrated here for *Tecovasuchus*, that records once tentatively referred to *Paratypothorax*, which had a long stratigraphic range, now are confidently assigned to two different taxa, each of which has a shorter stratigraphic range. Thus, where there was once a long "*Paratypothorax*" biochron, there are now shorter, discrete, and superposed *Tecovasuchus* and *Paratypothorax* biochrons (Fig. 4).

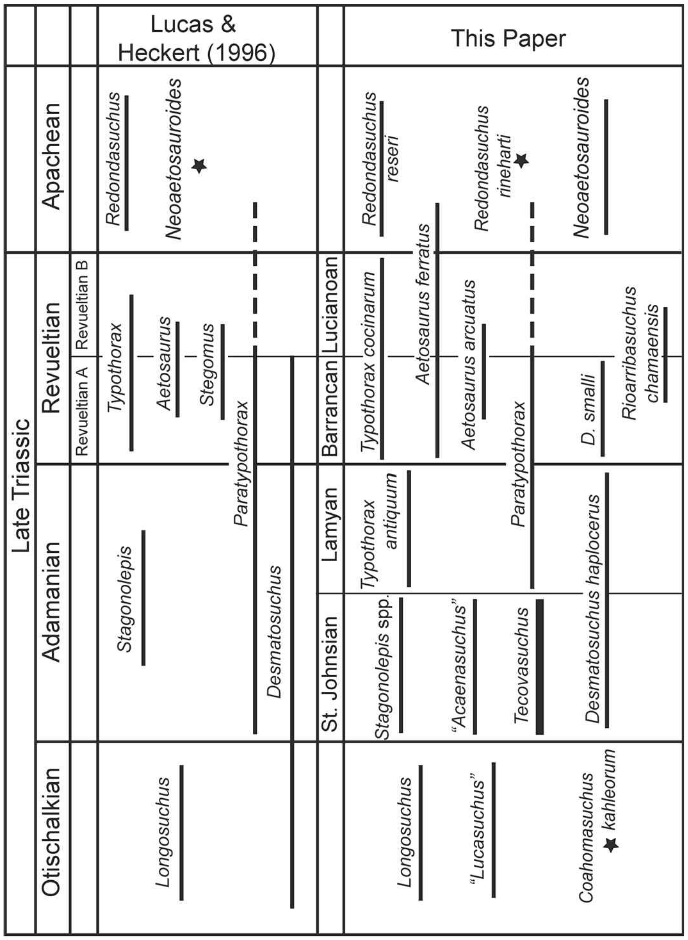

FIGURE 4. Revised biochronological hypothesis of Lucas and Heckert (1996) showing increased resolution provided by advances in aetosaurian taxonomy in the past decade. Taxa in quotation marks are those we do not recognize as valid, but whose occurrences are stratigraphically restricted. *Tecovasuchus* is highlighted with a particularly wide bar. Taxa denoted with a star are (were) known from single occurrences.

CONCLUSIONS

Figure 4 illustrates the biochronologic hypothesis advanced by Lucas and Heckert (1996) compared to our present understanding of aetosaur distribution, including the many new species described in the intervening decade. Comparison of the two hypotheses reveals numerous advances. In particular, Lucas and Heckert (1996) recognized six taxa that were biostratigraphically useful in that they were restricted to a single faunachron (*Longosuchus*, *Stagonolepis*, *Typothorax*, *Aetosaurus*, *Stegomus*, and *Redondasuchus*), and none were reliable index taxa of a sub-faunachron. Several taxa, in particular *Desmatosuchus* and *Paratypothorax*, had extensive stratigraphic ranges that hindered their utility as index taxa. With advances in our understanding of taxonomy and stratigraphic distribution, there are now at least 11, and perhaps 13, aetosaurs diagnostic of intervals of time at the faunachron- or sub-faunachron level (*Longosuchus*, *Stagonolepis*, *Tecovasuchus*, *Desmatosuchus haplocerus*, *Typothorax antiquum*, *T. coccinarum*, *A. arcuatus* (=*Stegomus*), *D. smalli*, *Rioarribasuchus*, *Redondasuchus*, and *Neoateosauroides*). We do not accept *Lucasuchus* or *Acaenasuchus* as valid taxa, but all supposed occurrences of either are restricted to strata of Otischalkian and Adamanian age, respectively. Almost all of these taxa, with the possible exception of *D. smalli*, are readily identified by isolated osteoderms and, in some cases, even by osteoderm fragments. Taxa Lucas and Heckert (1996) previously considered as long-ranging, such as *Desmatosuchus* and *Paratypothorax*, are now recognized as consisting of more than one taxon. Splitting *Paratypothorax* records into *Tecovasuchus* and *Paratypothorax* occurrences, and *Desmatosuchus* records into *D. haplocerus*, *D. smalli*, and *Rioarribasuchus* occurrences, results in greatly improved biostratigraphic resolution with these previously problematic taxa. In conclusion, aetosaurs remain robust biostratigraphic tools by which Upper Triassic strata can be correlated, both within basins and across continents.

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Lucas, S.G. and Spielmann, J.A., eds., 2007, The Global Triassic. New Mexico Museum of Natural History and Science Bulletin 41.

$\delta^{13}C$ ISOTOPE CURVE IN THE LOWER TRIASSIC FROM SHALLOW WATER CARBONATES IN JAPAN, PANTHALASSA REALM

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In the Jurassic accretionary wedges in Japan, exotic blocks that have been deposited in the Panthalassa Ocean have been incorporated. Most of the blocks are pelagic cherts; rarely, shallow water carbonates are present, too. We present a $\delta^{13}C$ study on the Lower Triassic of a shallow water carbonate succession that was deposited on a mid-ocean seamount in the Panthalassa Ocean, accreted in the Chichibu Belt, Japan. Two sections have been sampled at Kamura, central Kyushu Island. The carbon isotope curve shows depleted values across the Permian-Triassic boundary (PTB) followed by an increase to heavier values towards the Dienerian, culminating to a maximum of almost +4‰ V-PDB, before a steep drop. Lower values with an ascending trend follow in the Smithian, of which only a part is present. In the Spathian, isotopically depleted values continue and rise to enriched $\delta^{13}C$ values exceeding +3.5‰ near the Lower/Middle Triassic boundary. The observed trend of the stable carbon isotope curve from Japanese sediments mirrors the curve derived from sections in the Tethys (e.g., China, Italy, Iran). The results give proof that the derived curve represents a global trend, although some distinct features are absent due to erosion/gaps at the base and top of the Smithian. The profound variations of the carbon isotope curve now globally indicate severe changes in the Lower Triassic carbon cycle, which can be counted among the reasons for a delayed biotic recovery after the PTB. Large amounts of carbon were shifted between the carbon reservoirs, most probably between shallow and deep ocean waters, and /or ocean and sediment. Observed anoxia in the Panthalassa Ocean followed by overturn of the ocean water masses may have been the mechanism to quickly alter ecological conditions in the ocean leading to variable availability of nutrients, oxygen and isotope composition of the available carbon in the surface waters that was incorporated in the precipitated carbonate.

Lucas, S.G. and Spielmann, J.A., eds., 2007, The Global Triassic. New Mexico Museum of Natural History and Science Bulletin 41.

MULTISTRATIGRAPHIC CONSTRAINTS ON THE NW TETHYAN "CARNIAN CRISIS"

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Abstract—The "Carnian Crisis" is documented in basinal, shallow-marine and epicontinental northwestern Tethyan facies areas by, successively, (1) a demise of carbonate platforms and reefs in the Julian 1/IIc, (2) a major faunal and floral turnover in the Late Julian and (3) a significant extinction event affecting conodonts and ammonoids at the Julian/Tuvalian boundary. Based on the study of 19 successions from the NW Tethys, the presence of short-lived ammonoid and conodont taxa and the sudden absence of reef-derived debris in basinal and shallow-marine successions document a strict synchroneity in latest Julian 1 of a carbonate productivity crisis. $\delta^{18}O_{phos}$ values measured on conodont apatite display a major negative shift of 2.0 ‰ [V-SMOW] in the latest Julian 1 and Julian 2 indicating climate warming and a change in seawater salinity. This interpretation fits with changes in lithofacies and argues for humidification and enhanced freshwater runoff (sensu Simms and Ruffell, 1989), resulting in higher nutrient levels as the main factors of both reef disease and decline of nektonic biodiversity in late Early Carnian time.

INTRODUCTION

The Carnian stage is characterized by one of the most severe ecological crises of the Triassic, well recognized in many regions of the Tethys (e.g., S. Tethys: Hornung et al., in press a, and references therein). Carnian sediments have been studied intensively in the Northern Calcareous and the Southern Alps (NW Tethys; Fig. 1) where large carbonate platforms flourished at the beginning of the stage. The demise of these carbonate platforms marked a severe cut in Triassic reef development (Flügel, 2002) and has been well-dated by short-lived conodont and ammonoid taxa (*Metapolygnathus carnicus*; *Trachyceras* n. sp. 1) into the uppermost *aonoides* Zone representing the Julian 1/IIc (Fig. 2; see also Hornung and Brandner, 2005; Hornung et al., in press a, b). The platform demise was followed by a turnover of faunal and floral assemblages in marine and epicontinental environments (reef builders, bivalves, crinoids, bryozoans: Simms and Ruffell, 1989, 1990; Hallam, 1996; flora: Pott et al., 2006; tetrapods: Benton, 1991). Subsequently, a major extinction event affected many ammonoid and conodont taxa at the Julian-Tuvalian boundary (Krystyn, 1983, 1991; Rigo et al., in press).

The ultimate causes of the biotic crisis are still a matter of discussion, but have been often related to a drastic change to more humid climatic conditions. The onset of intensified siliciclastic input to wide parts of the epicontinental basins and marginal Tethyan environments (e.g., Enos et al., 1998; Geyer, 2002; Lehrmann et al. 2005; Hornung and Brandner, 2005; Rigo et al., in press; Hornung et al., in press b; Hornung, 2007, subm.) have been called the "Carnian-Pluvial Event" by Simms and Ruffell (1989).

In order to describe facies evolution during critical time slices of the Early and Late Carnian, we studied 19 sections within the main facies belts of the Alpine area (Figs. 1-2; Table 1). The main objective of this paper is to decipher the mode that led to a changed late Early Carnian climate and to develop a possible scenario of the "Carnian Crisis."

THE NW TETHYS DATABASE

The Sections

The sudden, basinwide change from carbonate to terrigeneous sedimentation is considered as a basin-to-platform-top timeline. From that we started to study low-energy, stratigraphically complete basinal successions by means of biochronostratigraphy and (micro)facies, and to correlate the results to shallow-marine environments. This method was used successfully by Reijmer and Everaas (1991) and Schlager et al. (1994), who demonstrated a close interaction between Triassic platforms and basins. The results of this part of the study are outlined in Figure 2, which summarizes the bio-, litho-, event-, and sequence-stratigraphy of major Alpine facies belts throughout the "Carnian Crisis."

The microproblematic ?algae *Tubiphytes* was one of the important Early Carnian reef builders (among corals and coralline sponges: Flügel, 2002). The sudden absence of reef-derived debris within eight Hallstatt- and Reifling Limestone sites was dated as the uppermost *aonoides* ammonoid Zone representing Julian 1/IIc. This date coincides with the onset of unbioturbated fine laminites (Göstling Member, Fig. 2: sites 6-8; "Ferchenbach Member," site 9) and thrombolite limestones ("ochre-coloured limestones," Fig. 2, site 1), in turn marking the standstill of the shallow water carbonate factories (Table 1). The dating of this first event within the basins was correlated with the Wetterstein carbonate platform-top in Julian 1/IIc, which suffered local emergence during a sea level lowstand (Fig. 2).

The onset of deposition of black shales with minor contents of carbonate and terrigenous silt (NCA: Reingraben Shales; Dolomites: Heiligkreuz Formation) that are overlain by silt- and sandstones ("Northern Alpine Raibl Beds") was dated as basal Julian 2 and Julian 2/II, respectively. Observation of similar sediments that cover locally emerged and karstified Wetterstein carbonate platforms proves common sedimentary gaps in the latest Julian 1/II and the Julian 2/I (Fig. 2: sites 11-12).

The ammonoid and conodont extinction event near the Julian-Tuvalian boundary (Krystyn, 1991; Rigo et al., in press) coincides wth both the end of the "Carnian Pluvial" interval and the prompt restart of carbonate production during the earliest Tuvalian (Fig. 2: sites, 1, 4-5; Fig. 4e).

Stable isotopes: $\delta^{18}O_{phos}$

Using the method of Wenzel et al. (2000), Joachimski and Buggisch (2002) and Joachimski et al. (2004, 2006), $\delta^{18}O_{phos}$ values were measured exclusively on neogondolellinine conodont apatite. From the late Ladinian (*regoledanus*-), late Early Carnian (*austriacum*-) and earliest Norian (*jandianus* ammonoid zone), they show an average $\delta^{18}O_{phos}$ ratio around 22.0 ‰ [V-SMOW], respectively. Around the Julian/Tuvalian boundary the $\delta^{18}O_{phos}$ trendline exhibits a negative excursion of 2.0 ‰, including

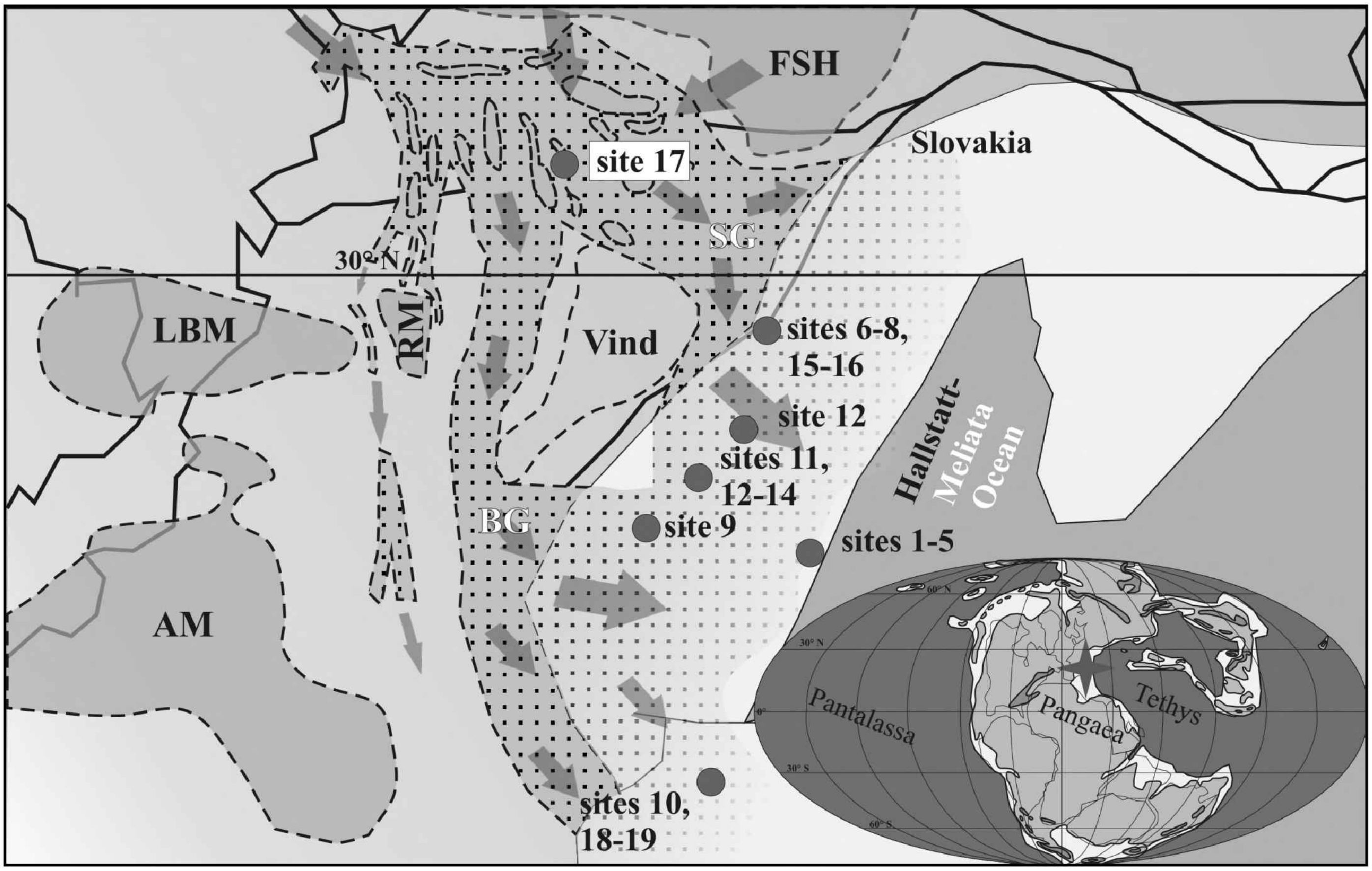

FIGURE 1. Palaeogeography in Julian 2 during deposition of the Schilfsandstein (modified after Kiessling et al., 2006 and Golonka, in press): 1 = "Dürrnberg standard section"; 2 = Rappoltstein; 3 = Draxllehen; 4 = Feuerkogel; 5 = Höllgraben; 6 = Lehen; 7 = Polzberg; 8 = Scheiblingsgraben; 9 = Wamberg succession; 10 = Tamarin; 11 = Wendelin gallery; 12 = Inzell-Weissbach; 13 = Bergangerl-Kartelleriöchl; 14 = Halleranger-Gschniergraben (Krainer, 1985); 15 = Lunz type locality (Verloop, 1908); 16 = Stiegengraben (Kristan-Tollmann and Hamidani, 1973); 17 = Schwanberg; 18 = Lavarella; 19 = Heiligkreuz. Abbreviations: li.lst. = limonitic limestones (Hallstatt Facies); b. = bioarenites (Pötschen Facies). Abbreviations: AM = Amoricanic Massif; FSH = Fennoscandian High; LBM = London-Brabant Massif; RM = Rheinic Massif; Vind = Vindelizic Landmass.

two plateaus in the earliest Tuvalian (20.5 ‰) and in the middle to early late Tuvalian (20.9 ‰). Conodonts from the Middle Norian (Lacian 2) generally show lower values (21.2 ‰) (Fig. 3). All values are listed in Table 2.

DISCUSSION

Earlier hypotheses argued that carbonate platforms can suffer death due to a "rapid regression-transgression couplet"' (e.g., Hallam and Wignall, 1999). This *"death by emergence and submergence-hypothesis"* was established by, for instance, Winterer (1998). However, this hypothesis was rejected because the growth potential of reefs always exceeds tectono-eustatic sea level rises (Schlager, 1999). Although the late Early Carnian successions in the Tethys document a significant sea level fall followed by a sea level rise (Brandner, 1984; Rüffer and Bechstädt, 1998; Hornung et al., in press a), we exclude the "death by emergence and submergence-theory" because it fails to explain why emerging reefs have not stepped towards the basins to more suitable water depths.

Reef disease as a consequence of rapidly enhanced siliciclastic input (Jerz, 1966; Schuler, 1968) can be clearly ruled out, as the reef demise was dated as Julian 1/IIc (uppermost aonoides Zone), and the climax of siliciclastic input reached the marginal Tethyan depositional area not before Julian 2/II (upper austriacum Zone). Following the updated Triassic time scale (Ogg, 2004; Furin et al., 2006), this equates to approximately 1 Ma.

If high-amplitude sea level fluctuations or enhanced siliciclastic influx were not responsible for initiating the "Carnian Crisis," we are in need of another factor that was efficient and fast enough to suppress the growth potential of reefs to keep pace with subsidence.

Isotope and Facies Evidence: Climatic Warming and Changes in Sea Water Salinity

For a reasonable calculation of Carnian sea water temperatures, we followed Hornung et al. (in press b), who assumed subtropical, open marine Triassic sea water values close to 0.25 ‰ (V-SMOW). This equates to the studies of Zachos et al. (1994), who suggested a correction factor for low tropical and subtropical latitudes, where evaporation exceeds precipitation. However, the interpretation of the oxygen isotope curve of Figure 3 and calculation of Carnian sea water temperatures based on conodont apatite (Kolodny et al., 1983) need additional knowledge about the life habitat of conodonts. Conservatively interpreted as exclusively benthonic forms in pelagic environments (e.g., Kozur, 1974), current studies argue that Carboniferous gondolellids, the Paleozoic ancestors of the Triassic neogondolellinins (Orchard, 2005), lived in surface waters and represent surface water temperatures (Joachimski et al., 2006). If gondolellids have not changed their live habitat substantially through time, the $\delta^{18}O_{phos}$ values of Upper Triassic neogondolellinins represent sea surface water signals.

Taking the above considerations into account, Longobardian 2-, Julian 1/I- and Lacian 1 paleotemperatures ranged between 12 and 16°C (Fig. 3). Julian 2 $\delta^{18}O_{phos}$ values translate to 19° C. Conodont isotope data close to the Julian/Tuvalian boundary and within the Tuvalian 1 are calculated from 22 to 25° C, whereas Tuvalian 2-3 $\delta^{18}O_{phos}$ values pro-

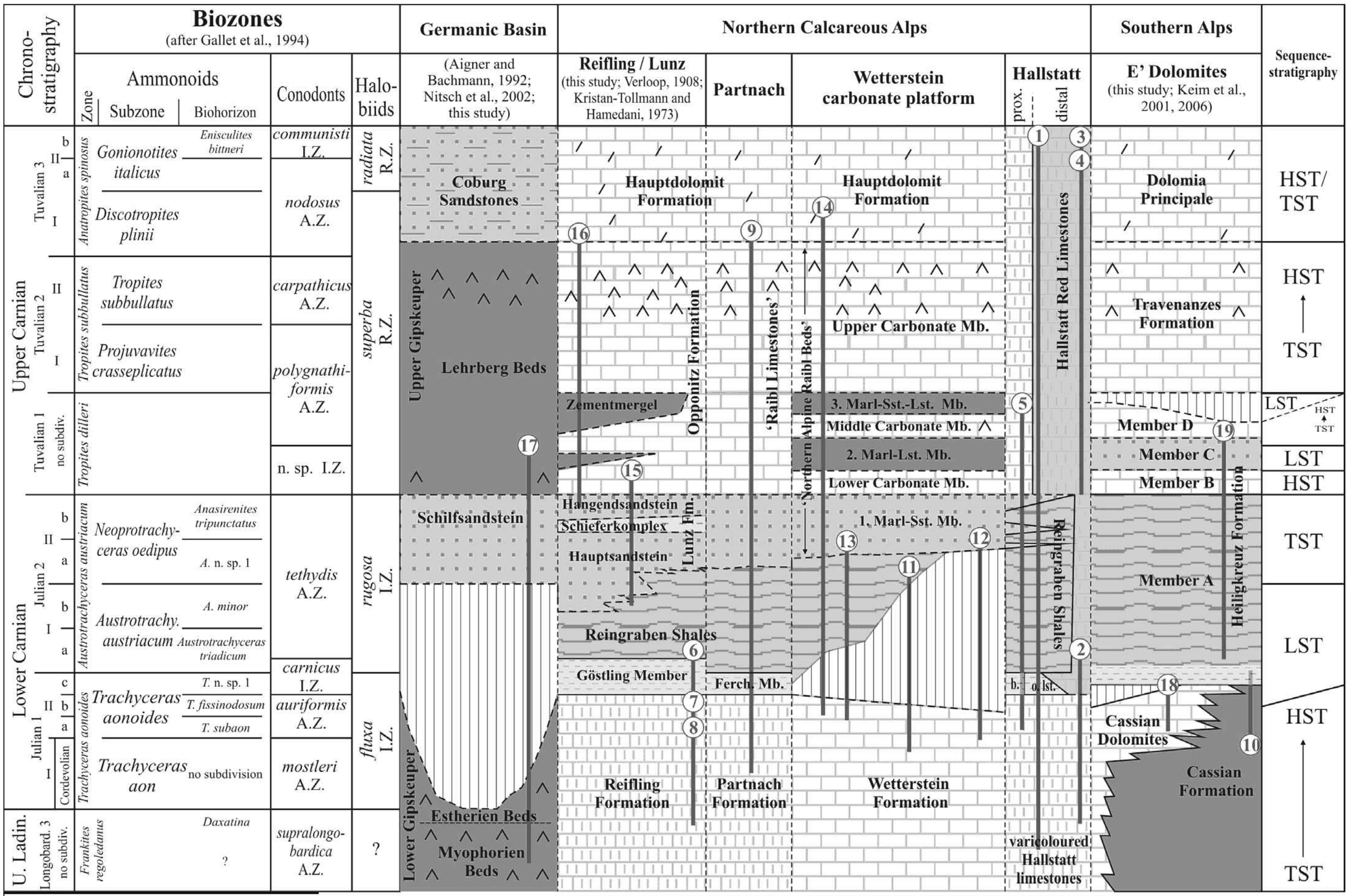

FIGURE 2. Proposed basin-platform-epicontinental correlation, including the studied sections in different facies zones: for the numbering of sites see Figure 1. Abbreviations: o. lst. = ochre-coloured limestones (Hallstatt Facies); b. = bioarenites (Pötschen Facies).

vide paleotemperatures around 21°C. Keeping in mind that the temperature tolerance of Carnian-Norian reef-builders probably was between 18 and 34°C (Kleypas et al., 1999), only the Julian 2 and Tuvalian conodonts document water temperatures that were suitable for reef development. However, no reefs are known from the NW Tethys in Julian 2 and only small patch reef-like mounds are known from Tuvalian 1 and 2. In contrast, extended reef belts developed in the Early Carnian and Early Norian (e.g., Flügel, 2002; Hornung and Brandner, 2005), when sea water temperatures derived from conodont apatite $\delta^{18}O$ have been calculated at their lowest (22.0-22.8 ‰: 12-16° C). This contradiction implies that temperature cannot be the sole factor for the recorded variation in $\delta^{18}O_{phos}$.

Changes in seawater salinity can shift the O-isotope curve to more positive or negative values (Fabricus et al., 1970): evaporation of surface-near sea water enriches surface water in ^{18}O, which might be interpreted as cooling. Enhanced input of freshwater otherwise enriches surface water in ^{16}O, resulting in lower $\delta^{18}O_{phos}$ ratios and may thus be interpreted as warmer surface water temperatures. Both, enhanced evaporation and freshwater influx should have left their imprint not only in the $\delta^{18}O_{phos}$ fractionation trend of conodont apatite, but also within the sedimentary (and thus climate) history of shallow marine and epicontinental series.

An arid phase is assumed for the Longobardian and Julian 1, where evaporites are abundant in the Germanic Basin (Fig. 4a; Fig. 2, site 17: Myophorien- and Estherien Beds; see Geyer, 2002). Evaporites are further known from the Arlberg Formation, an equivalent of the upper Wetterstein Formation situated in the western sectors of the NCA (Tollmann, 1976). Onset of decreasing $\delta^{18}O_{phos}$ values around the Julian 1 / Julian 2 boundary may indicate both climatic warming and/or enhanced fresh water input into the marginal NW Tethys and coincide with the aforementioned major reef demise in Julian 1/IIc. The accelerated decrease in $\delta^{18}O_{phos}$ in the uppermost Julian 2 may display climatic warming and progressive fresh water input (Fig. 3) in conjunction with the "Carnian Pluvial Event" of Simms and Ruffell (1989). Enhanced siliciclastic input becomes evident in many parts of the Germanic Basin (Fig. 2, site 17: Schilfsandstein), and by refill of pre-existing west-Tethyan intraplatform basinal troughs (Lunz Formation: Reifling Basin, see Figure 1, sites 6-8, 15; "Northern Alpine Reds Beds": Partnach Basin, see Figure 2, site 9; Heiligkreuz Formation, Member C: Heiligkreuz-Hospiz Basin, see Figure 2 and Keim et al., 2001). The accelerated decrease in $\delta^{18}O_{phos}$ during this relatively short interval of time renders it most likely that climatic warming together with enhanced fresh water input may have been lethal for many Early Carnian conodont and ammonoid species, giving way to a rapid overturn and diversification in the Early and Middle Tuvalian (Krystyn, 1991).

The two $\delta^{18}O_{phos}$-plateaus of the Tuvalian 1 and Tuvalian 2 (Fig. 3), respectively, represent a warm period, but under decreased humidity. Gypsum layers within the Lehrberg Beds (Fig. 2, site 17), anhydrites and rauhwackes within the "Northern Alpine Raibl Beds" (Fig. 2, sites 9, 12-14) and the Opponitz Formation (Fig. 2, site 16) record semi-arid conditions, repeated short humid pulses ("Middle and Upper Marl-Sandstone-Limestone Members" of the "Northern Alpine Raibl Beds,"

TABLE 1. List of main Triassic facies belts of the Alpine region.

Facies Domain	Facies Area	Site	Location (UTM Koordinates)	**Short interpretation**	References
Austroalpine Facies Domain	Hallstatt Basin	**Dürrnberg (1)** (Salzburg, Austria) Longobardian 2 - Lacian 2	WGS84, Zone 33; E 356297; N 5280587	Condensed, distal pelagic settings. The platform demise is indicated by absence of reef-derived debris (*Tubiphytes*) in ochre-coloured thrombolithe limestones and black Reingraben Shales (Julian 1/IIc). Restart of red limestones records prompt recreation of carbonate precipitation in the basal Tuvalian.	Hornung and Brandner, 2005; Hornung, 2006
		Rappoltstein (2) (S' Germany) ?Longob. 2-Julian 2/Ia	WGS84, Zone 33; E 355409; N 5283021	Distal, strongly condensed pelagic red limestone succession. The platform demise is indicated by absence of reef-derived derbis (*Tubiphytes*) and the presence of manganese-pyrite foraminifer buildups and hardgrounds in Julian 1/IIc.	Hornung et al., in press (b)
		Draxllehen (3) (S' Germany) Tuvalian 1/I - Lacian 2	WGS84, Zone 33; E 354772; N 5279684	Monotonous well-bedded pelagic red limestone succession in a graben-situation on 'Hallstatt deep swells' in the immediate aftermath of the 'Carnian Crisis'.	Hornung, unpubl. 2007; Hornung, subm. 2007
		Feuerkogel (4) (Styria, Austria) Longobardian 2 - Lacian 2	WGS84, Zone 33; E 414835; N 5271718	Strongly condensed pelagic red limestone succession. The platform demise is indicated by the presence of manganese-pyrite foraminifer buildups and hardgrounds.	Krystyn, 1973, 1980, 1991
		Höllgraben (5) (Upper Austria) Julian 1/IIa - Tuvalian 1	WGS84, Zone 33; E 386158; N 5265704	Proximal periplatform setting. The platform demise is indicated by absence of reef-derived debris (*Tubiphytes*) in unburrowed bioarenites in Julian 1/IIc overlain by black Reingraben Shales. Restart of grey limestones records prompt recreation of carbonate precipitation in the basal Tuvalian.	Schlager, 1967; Mandl, 1984; Hornung, subm. 2007
	Reifling intraplatform basin	**Lehen, Polzberg, Scheiblingsgraben (6-8)** (Lower Austria) Longobardian 2 - Julian 2	WGS84, Zone 33; E 501414; N 5297752 E 505606; N 5303652 E 477796; N 5279280	Intraplatform basinal setting. The platform demise is indicated by the absence of reef-derived debris (*Tubiphytes*) in unburrowed laminites (Göstling Member - alternation of fossil-poor mudstones and radiolarian grainstones) in Julian 1/IIc overlain by black Reingraben Shales.	Krystyn, 1991; Hornung, subm. 2007
	Partnach intraplatform basin	**'Wamberg' (9)** (S' Germany) Julian 1 - Tuvalian 3	WGS84, Zone 32N; E 667119; N 5262002	Intraplatform basinal setting. The platform demise is indicated by absence of reef-derived grains (*Tubiphytes*) in unburrowed laminites ('Ferchenbach Member' - alteration of fossil-poor mudstones and radiolarian grainstones) in Julian 1/IIc, overlain by black Reingraben Shales. Restart of grey limestones and rauhwackes records prompt recreation of carbonate precipitation in Tuvalian 1.	Hornung, subm. 2007
	Wetterstein Carbonate Platform	**Wendelin gallery (11)** (Tyrol, Austria) Julian 1/IIb - Julian 2/Ib	WGS84, Zone 32, E 637553; N 5242344	Subtidal to supratidal cyclic Wetterstein limestone succession. The platform demise is indicated by sharp insertion of Reingraben Shales documenting a stratigraphic hiatus (basal Julian 2/I).	Hornung, subm. 2007
		Inzell (12) (S' Germany) Julian 1/IIb - Julian 2/II	WGS84, Zone 33N; E 328577; N 5289349	Subtidal to intertidal succession. Platform demise is indicated by onset of dark marls of the 'Northern Alpine Raibl Beds' documenting a major stratigraphical hiatus (Julian 2/I).	Hornung, subm. 2007
		Bergangerl, Halleranger (13-14) (Tyrol, Austria) Julian 1/IIb - Lacian 1	WGS84, Zone 32N, E 687281; N 5244637 E 688489; N 5248395	Subtidal to intertidal succession. Platform demise is indicated by platform emersion, palaeokarst and amalgamation of pyrit-rich winnowed foraminifer sands, in turn overlain by dark Reingraben Shales. This part is suceeded by the ternary 'Northern Alpine Raibl Beds' documenting a cyclic marl- and limestone-dominated subtidal to intertidal succession, triggered by sealevel fluctuations (sensu Rüffer and Bechstädt, 1998).	Krainer, 1985; Hornung, subm. 2007
	Lunz Facies	**Lunz, Stiegengraben (15-16)** (Lower Austria) Julian 2/II - Tuvalian 3	WGS 84; Zone 33N, E 501552; N 5301702 E 498449, N 5296889	Subtidal deltaic to littoral-brackish environment (Lunz Formation) and complete refill of the Reifling intraplatform basin with fossil-rich Lunz Sandstones and Marls. Shallow-marine-hypersaline settings (Opponitz Formation).	Verloop, 1908; Kristan-Tollmann and Hamedani, 1973;
Southern Alps	Cassian intraplatform basin	**Tamarin (10)** (Belluno, N' Italy)	WGS84, Zone 33N, E 281624; N 5160502	Subtidal, periplatform calciturbiditic setting. The platform demise is indicated by a sandstone layer and the absence of reef-derived debris (*Tubiphytes*) in unburrowed bio-rudstones above (basalmost Julian 2).	Mastandrea, 1995 Hornung, subm. 2007
		Lavarella (18) (South Tyrol, N' Italy)	WGS84, Zone 32N, E 725635; N 5162353	Subtidal intraplatform basinal, shallowing upward setting. The platform termination can be noticed with a rapid cessation of reef growth overlain by thrombolithic mud mounds. The overlying succession is dominated by black shales (Heiligkreuz Formation 'Member A') overlain by oolithes ('Member B'), sandstones ('Member C') and lime- and dolostones ('Member D').	Keim et al., 2001
		Heiligkreuz (19) (South Tyrol, N' Italy)	WGS84, Zone 32N, E 725519; N 5167014		Keim et al., 2006
Germanic Basin	Epicontinental Keuper	**Schwanberg (17)** (S' Germany) Longobardian - Tuvalian 3	WGS84, Zone 32N; E 591831; N 5507625	Limnic-brackish, saline, partly sabkha-environment (Myophorien-, Estherien- and Lehrberg Beds), fluvial deposits (Schilfsandstein). Major sedimentary gap between Estherien Beds and Schilfsandstein Member (Julian 1/Ib - Julian 2/Ib)	Cramer, 1964; Geyer, 2002; Hornung, subm. 2007

Fig. 2) with slow aggradational growth of carbonate platforms. The significant increase in ^{18}O in the earliest Norian mirrors an arid interval with desert-like conditions in the Germanic Basin (Coburg Sandstone; see Geyer, 2002) and flourishing Tethyan carbonate platforms and reef belts (Hauptdolomite resp. Dachstein Facies).

Evidence by Facies Analysis: Ocean Nutrification and Anoxia

The ultimate reasons for a late Early Carnian warm and humid phase are still unclear but might have been triggered by intensified tectonics within the early Upper Triassic period (Golonka, in press): the breakup of Pangea, the Indosinian orogeny and the closure of the Palaeotethys were not only responsible for global sea level fluctuations as a consequence of accelerated rifting and higher intra-plate stress (Nikishin et al., 1996), but may have enhanced volcanic activity in the wider W Tethys. Extensive Carnian alkaline basalt flows are recorded from Turkey (Kara Dere lavas, Western Taurids and Antalya Nappes – Ricou et al., 1984; Huglu Tuffites, Central Taurids -Andrew and Robertson, 2002), Oman (Haybi resp. Umar volcanics – Searl and Graham, 1982), the Southern Appenines (Furin et al., 2006), Djebel Moro and Tibesti (Morocco), Levant (Middle East), and other Tethyan regions (Golonka and Bocharova, 2002, cum. lit.). It is possible that volcanic degassing contributed to the postulated Carnian humidification, as volcanic activity led to CO_2-emission and subsequent climatic warming.

Warming of the mega-monsoonal Triassic climate (e.g., Parrish, 1999) implies increased rainfall and river runoff (intensification of the hydrologic cycle, see Wortmann and Weissert, 2000). Southward fluvial discharge by braided river systems crossing nearly the complete Germanic Basin (ca. 250 km width and 1500 km length; estimated from Beutler and Szulc, 1999; Golonka, in press) may have led to sediment erosion in epicontinental environments, but also to a lowering of surface water salinity in the marginal NW Tethyan sea.

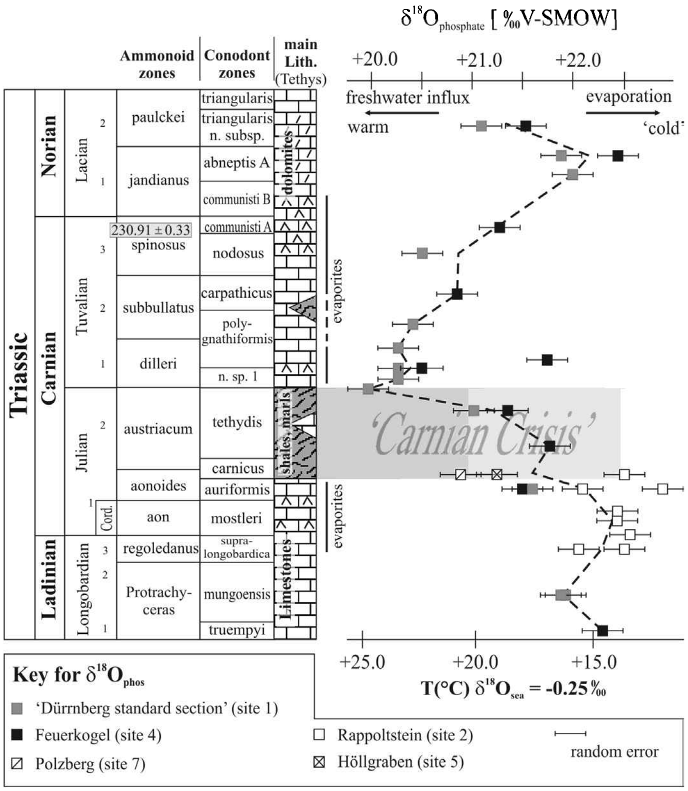

FIGURE 3. $\delta^{18}O_{phos}$ data obtained from conodont apatite of the biostratigraphically best-controlled conodont associations (radiometric age 230.91 ± 0.33 Ma, after Furin et al., 2006).

TABLE 2. Comparison of $\delta^{18}O_{phos}$ of Upper Ladinian to Lower Norian conodont taxa.

Sample	Conodont taxa	age	Unit/Location	$\delta^{18}O_{phos}$ [V-SMOW]
LO 8	Neogondolella (*Epigondolella*)	Lacian 2	Dürrnberg standard section'	**21.1**
F4/31	Neogondolella (*Epigondolella*)	Lacian 2	Feuerkogel	**21.6**
LO 7	Neogondolella (*Epigondolella*)	Lacian 1	Dürrnberg standard section'	**21.9**
70/50	Neogondolella (*Epigondolella*)	Lacian 1	Feuerkogel	**22.5**
LO 6	Neogondolella (*Epigondolella*)	Lacian 1	Dürrnberg standard section'	**22.0**
F4/V	Neogondolella (*Metapolygnathus*)	Tuvalian 3/II	Feuerkogel	**21.3**
T 13	Neogondolella (*Metapolygnathus*)	Tuvalian 3	Dürrnberg standard section'	**20.5**
F4/VII/1	Neogondolella (*Metapolygnathus*)	Tuvalian 2/II	Feuerkogel	**20.9**
TO6 - 09	Neogondolella (*Metapolygnathus*)	Tuvalian 2/I	Dürrnberg standard section'	**20.3**
To4	Neogondolella (*Metapolygnathus*)	Tuvalian 1	Dürrnberg standard section'	**20.3**
88/254	Neogondolella (*Metapolygnathus*)	Tuvalian 1	Feuerkogel	**20.5**
To3	Neogondolella (*Metapolygnathus*)	Tuvalian 1	Dürrnberg standard section'	**20.3**
To1	Neogondolella (*Metapolygnathus*)	Tuvalian 1	Dürrnberg standard section'	**20.0**
J 16	Neogondolella (*Gladigondolella* ; *Metapolygnathus*)	Julian 2/II	Dürrnberg standard section'	**21.0**
77/41	Neogondolella (*Gladigondolella* ; *Metapolygnathus*)	Julian 2/II	Feuerkogel	**21.4**
77/42	Neogondolella (*Gladigondolella* ; *Metapolygnathus*)	Julian 2/I	Feuerkogel	**21.8**
H 8	Neogondolella (*Gladigondolella* ; *Metapolygnathus*)	Julian 1/IIc	Höllgraben	**21.2**
GO 9	Neogondolella (*Gladigondolella* ; *Metapolygnathus*)	Julian 1/IIc	Polzberg	**20.8**
La	Neogondolella (*Gladigondolella* ; *Metapolygnathus*)	Julian 1/IIb	Dürrnberg standard section'	**21.6**
76/7	Neogondolella (*Gladigondolella* ; *Metapolygnathus*)	Julian 1/II	Feuerkogel	**21.5**
Rap 4	Neogondolella (*Gladigondolella* ; *Metapolygnathus*)	Julian 1/II	Rappoltstein / Berchtesgaden	**22.9**
P 5	Neogondolella (*Gladigondolella* ; *Metapolygnathus*)	Julian 1/I	Rappoltstein / Berchtesgaden	**22.1**
P 4	Neogondolella (*Gladigondolella* ; *Metapolygnathus*)	Julian 1/I	Rappoltstein / Berchtesgaden	**22.4**
Rap 3	Neogondolella (*Gladigondolella* ; *Metapolygnathus*)	Julian 1/I	Rappoltstein / Berchtesgaden	**22.4**
P 3	Neogondolella (*Gladigondolella* ; *Metapolygnathus*)	Julian 1/I	Rappoltstein / Berchtesgaden	**22.6**
Rap 2	Neogondolella (*Gladigondolella* ; *Metapolygnathus*)	Longobardian 3	Rappoltstein / Berchtesgaden	**22.5**
Rap 1	Neogondolella (*Gladigondolella* ; *Metapolygnathus*)	Longobardian 3	Rappoltstein / Berchtesgaden	**22.1**
Le 10	Neogondolella (*Gladigondolella* ; *Metapolygnathus*)	Longobardian 2	Lercheckweg / Berchtesgaden	**21.8**
Le 35	Neogondolella (*Gladigondolella* ; *Metapolygnathus*)	Longobardian 2	Lercheckweg / Berchtesgaden	**21.9**
79/2	Neogondolella (*Gladigondolella* ; *Metapolygnathus*)	Longobardian 1	Feuerkogel	**22.3**

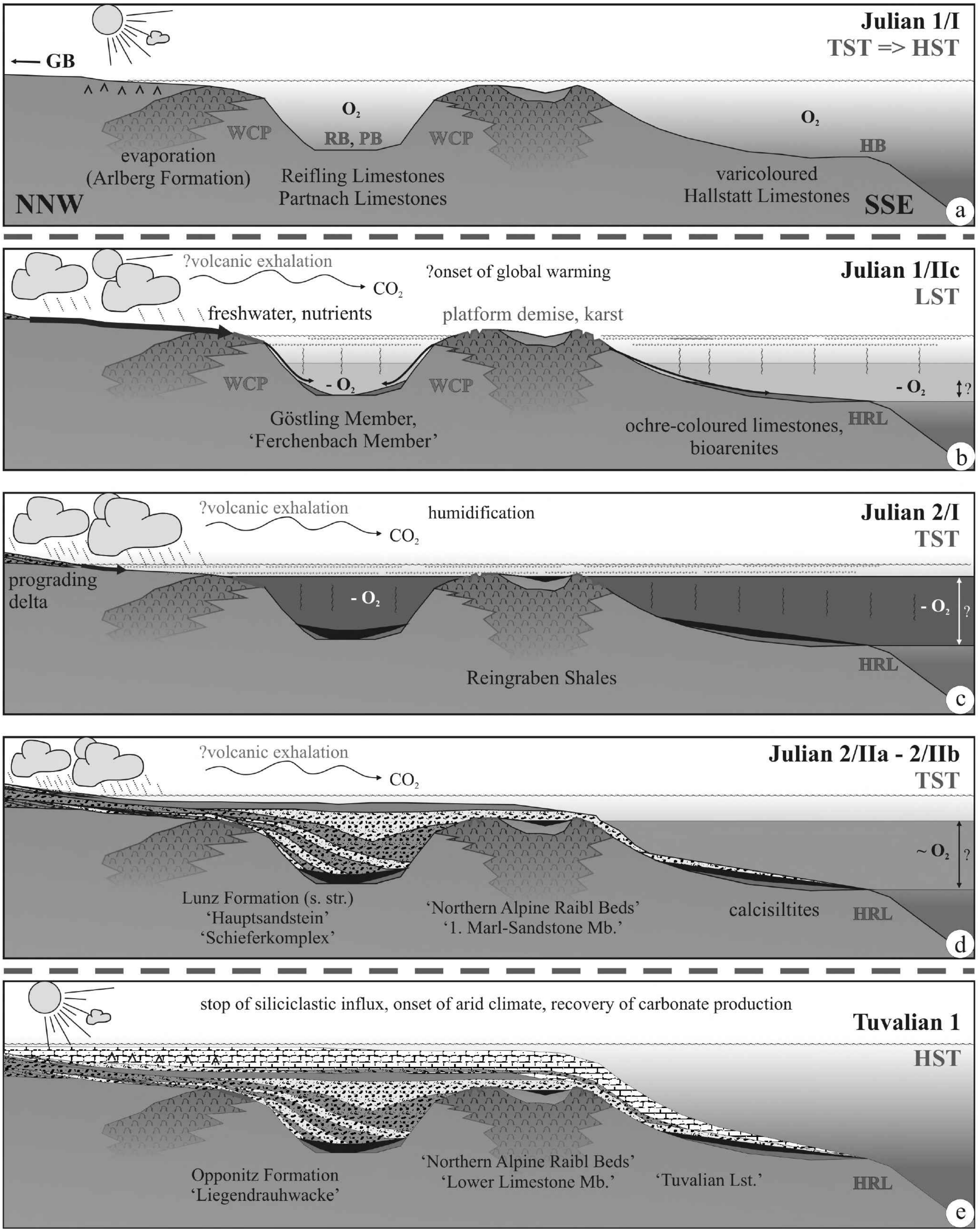

FIGURE 4. Schematic and exaggerated cross-section through shallow-marine NW Tethyan environments. **(a)** Pre-turnover situation in Longobardian and Julian 1. **(b)** Platform demise: sea level fall and onset of warming, humidification, freshwater influx caused nutrient excess and expansion of the O_2-minimum zone. **(c)** Expansion of the O_2-minimum zone to nearly the complete water column – deposition of black Reingraben Shales in basins and on carbonate platforms. **(d)** Siliciclastics reached the NW Tethys in Julian 2/II: deposition of "Lunz Formation s.str." and "Northern Alpine Raibl Beds". **(e)** Post-turnover situation showing a rapid recovery of carbonate production on a shallow-marine peneplain. Abbreviations: WCP = Wetterstein carbonate platform; RB = Reifling Basin; PB = Partnach Basin; HB = Hallstatt Basin; HRL = Hallstatt Red Limestones.

During Julian 1, a major portion of weathering products was retained in the large Germanic Basin, which eroded older sediments and produced a major stratigraphic gap encompassing the Middle and Upper Estherien Beds (Nitsch et al., 2002; Geyer, 2002). High rates of freshwater import lowered not only salinity in the marginal Tethys, but also led to enhanced nutrient concentrations (Fig. 4b). Nutrification of sea surface water could have had negative consequences for Upper Triassic shallow-marine coral reef-builders, which lived in assumed symbiosis with zooxanthellate algae (Stanley and Swart, 1995; Kiessling, 2002) and were numbered amongst the important Ladinian-Early Carnian reef builders (Flügel, 2002, Table 2; Kiessling, 2002, Fig. 16). Basically, nutrient excess has (and had) consequences for the zooxanthellate symbiont but, in particular, even major negative consequences for the rate of reproducibility of the coral host (Gautret et al., 1997). Coevally, elevated nutrient supply advanced growth of fixosessile microbial organisms and stimulated planktonic blooms, together leading led to an expulsion of coral reef builders (Hallock and Schlager, 1986; Sanders and Baron-Szabo, 2005). Concerning the late Early Carnian platform and reef demise, we have sedimentary evidences for a scenario suggested in Hallock (2005): starting from a climate warming causing nutrification and eutrophication, microbial overgrowth (thrombolite crusts in the uppermost varicolored Hallstatt Limestones and ochre-colored limestones, Fig. 2: site 1; see also Hornung and Brandner, 2005; thrombolite mud mounds in Keim et al., 2001, 2006; sites 18-19) and planktonic blooms (radiolarian and halobiid grainstones in the Göstling and "Ferchenbach" members, see Table 1 and Figure 2, sites 6-9) leading to reduced water transparency, destabilisation of coral symbiosis, completed by increasing bio-erosion and the decline of reef-building organisms and the loss of reef structures and habitats. The widespread standstill of carbonate production and the disappearance of reef-builders being the major carbonate producers in the Upper Triassic (e.g., Bellanca et al., 1995) prevented carbonate platforms not only from keeping pace with subsidence, but may have also been crucial for an oceanic $CaCO_3$ under-saturation and a rise of the CCD as suggested in Rigo et al. (in press).

Following Hallock (2005, and references therein), nutrification is also responsible for a high biological oxygen demand and the presence of anoxia in bottom waters. The presence of anoxia concomitant with abundant (pseudo)planktonic radiolarians and/or halobiids indicating the above-mentioned planktonic blooms is suggested in Hallstatt ochre-colored limestones (Fig. 2; site 1), bioarenites within the Pötschen-Facies (Fig. 2; site 2), the Göstling and "Ferchenbach" members (Fig. 2; sites 6-9), and the Heiligkreuz Formation, "Member A" (Fig. 2; site 10). The base of all these litho-units corresponds with the *carnicus* conodont interval zone (Julian 1/IIc-2/Ia).

Increased oxygen consumption and an O_2-minimum layer spreading over nearly the complete water column (Cenomanian-Turonian model of Turgeon and Brumsack, 2006) can be assumed during the deposition of the Reingraben Shales in Julian 2/I (Fig. 4c). Only minor parts of the Hallstatt Basin with condensed, manganese- and pyrite-bearing red limestones (Rappoltstein and Feuerkogel, sites 2-3) faced oxygenated conditions, most probably situated beneath the oxygen-minimum layer (Hornung et al., in press, b). Reingraben black shales, at first devoid of silt, subsequently overlain by shales with increasing silt- and sand contents, indicate, at first, the arrival of Germanic Basin-derived clayey suspensions, followed by epicontinental sediments from river systems that expanded towards the NW Tethys. The climax of siliciclastic downpour on Alpine facies belts in Julian 2/II, finally, led to the deposition of the "Lunz Formation" (Fig. 2; site 15), the "Northern Alpine Raibl Beds" (Fig. 2; sites 12-14) and the "Hallstatt calcisiltite intercalations" (Fig. 2: sites 1 and 5). This event marks a "Carnian Pluvial Event" sensu stricto (Fig. 4d), as it is used in Rigo et al. (in press). The original intention of Simms and Ruffell (1989) is here distinguished as the "Carnian Pluvial Event" sensu lato and encompasses the whole timespan of the "Carnian Crisis" (Julian 1/IIc to Julian 2/II).

The ammonoid and conodont extinction event at the Julian-Tuvalian boundary (Krystyn, 1991 and Rigo et al., in press) is also recorded in the "Dürrnberg" section (site 1) by Hornung and Brandner (2005). It could be linked to the climax of siliciclastic shedding in late Julian 2. How far these changed patterns triggered the evolution of nektonic biota, however, remains as speculation (stenohalinity vs. euryhalinity; stenothermy vs. eurythermy; Kozur, 1974).

CONCLUSIONS

1) High-resolution multistratigraphy points to a simultaneity of platform demise in the NW Tethys in Julian 1/IIc, and a duration of the "Carnian Crisis" up to the Julian / Tuvalian boundary (approximately 1 Ma). Several basin-to platform tie-in correlations, finally, led to compilation of a NW Tethys sequence-stratigraphic framework encompassing the Late Ladinian to the Early Norian.

2) Oxygen isotope data from conodont apatite display the first quantitative constrain on the "Carnian Pluvial Event" of Simms and Ruffell (1989), and probably represent a mixed signal of climate warming and changes in sea water salinity during Julian 2.

3) Climatic warming and humidification, and fresh water import in marginal marine NW Tethyan settings fit well with observed facies patterns in marine and epicontinental settings and lead us to suspect that ocean nutrification was the crucial and lethal factor that triggered and accompanied platform disease and extinction events of the "Carnian Crisis."

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Lucas, S.G. and Spielmann, J.A., eds., 2007, The Global Triassic. New Mexico Museum of Natural History and Science Bulletin 41.

INTERCALIBRATION OF BOREAL AND TETHYAN TIMESCALES: THE MAGNETO-BIOSTRATIGRAPHY OF THE BOTNEHEIA FORMATION (MIDDLE TRIASSIC), AND THE LATE EARLY TRIASSIC, SVALBARD (ARCTIC NORWAY)

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Understanding the timing and synchronicity of environmental and faunal changes at both low and high latitude successions in the Triassic can be improved by better inter-calibration of stratigraphic tools. This is all the more important for tools which potentially provide means for high resolution intersection correlation, such as those often required for defining the primary means of correlation in GSSP definitions. In this spirit an integrated biostratigraphic and magnetostratigraphic study of the latest Early Triassic to the upper parts of the Middle Triassic, at Milne Edwardsfjellet (central Spitsbergen), allows a detailed correlation of Boreal and Tethyan biostratigraphies. This is primarily achieved by linking the magnetostratigraphic patterns, from the new magnetostratigraphic data described here, to existing published magneto-biostratigraphy from Tethyan sections with conodont biostratigraphies (Muttoni et al., 1998, 2000, 2004; Nawrocki and Szulc, 2000).

The biostratigraphy from Milne Edwardsfjellet consists of ammonoid and palynomorph zonations, supported by conodonts, through some 234 m of succession in two adjacent sections. The sections range through the entire thickness of the Botneheia Formation and the Vendomdalen Member of the Vikinghøda Formation (Fig. 1). A fragmentary, but well established ammonoid zonation from the sections demonstrates relationships to more complete ammonoid zonations from sections in NE Asia and British Columbia (Dagys and Weitschat, 1993; Mørk et al; 1999). Recovery of sporadically distributed conodonts from the sections, allows confirmation of Late Spathian, Lower Anisian, the Anisian/Ladinian boundary and Late Ladinian intervals in the sections, confirming and supplementing the ammonoid age control. The palynology allows a zonation based on the definitions utilized by Hochuli et al. (1989) and Vigran et al. (1998) from Svalbard and the Barents Sea.

The resulting magnetostratigraphy consists of ten substantive normal-reverse polarity chrons (and a number of minor sub-magnetozones) defined by sampling at 150 stratigraphic levels. The magnetization is carried by magnetite and an unidentified magnetic sulphide, and is difficult to fully separate, using demagnetization, from a strong present-day like magnetization. Nevertheless, demagnetization of 292 specimens (2 to 3 from each horizon sampled) allows a robust magnetostratigraphy to be determined. The magneto-biostratigraphy from the Late Olenekian (Vendomdalen Member), is supplemented by data from Vikinghøgda (central Spitsbergen; Hounslow et al., unpubl. 2007), showing that this unit has substantial regional changes in sedimentation rate, particularly in the Early Spathian.

The synthesis demonstrates the succession at Milne Edwardsfjellet is complete across the Olenekian-Anisian boundary (Fig. 2), but an erosional disconformity occurs at the boundary of the Vikinghøgda and Botneheia formations at Vikinghøgda to the west. An expression of this unconformity at Milne Edwardsfjellet is reworked Permian palynomorphs at the correlative unconformity. The lowest parts of the Botneheia Formation contain the ammonoid *Karangatites evolutus* and the conodont *Chiosella timorensis* (Fig. 2), the latter a key marker for the base of the Anisian. The Early and Mid Anisian has a high sedimentation rate, comprising over half the ca. 140 m thickness of the Botneheia Formation, whereas the late Anisian and lower Ladinian is condensed into about 20 m. In the early Ladinian, the Boreal to Tethyan correlations are supplemented by ammonoid evolutionally changes which are closely associated with the definition of the Anisian–Ladinian boundary (Brack et al., 2005). In the Botneheia Formation, the latest Ladinian is probably absent due to erosional truncation below the overlying Tschermakfjellet Formation (Hounslow et al., in press), although the boundary beds in both formations, contain conodonts indicative of the Ladinian-Carnian boundary interval. The magnetostratigraphic correlation to Tethyan-based magneto-biostratigraphies allows greater detail, than hitherto available, for high to low-latitude correlation of ammonoid and palynological zonations (Fig. 2).

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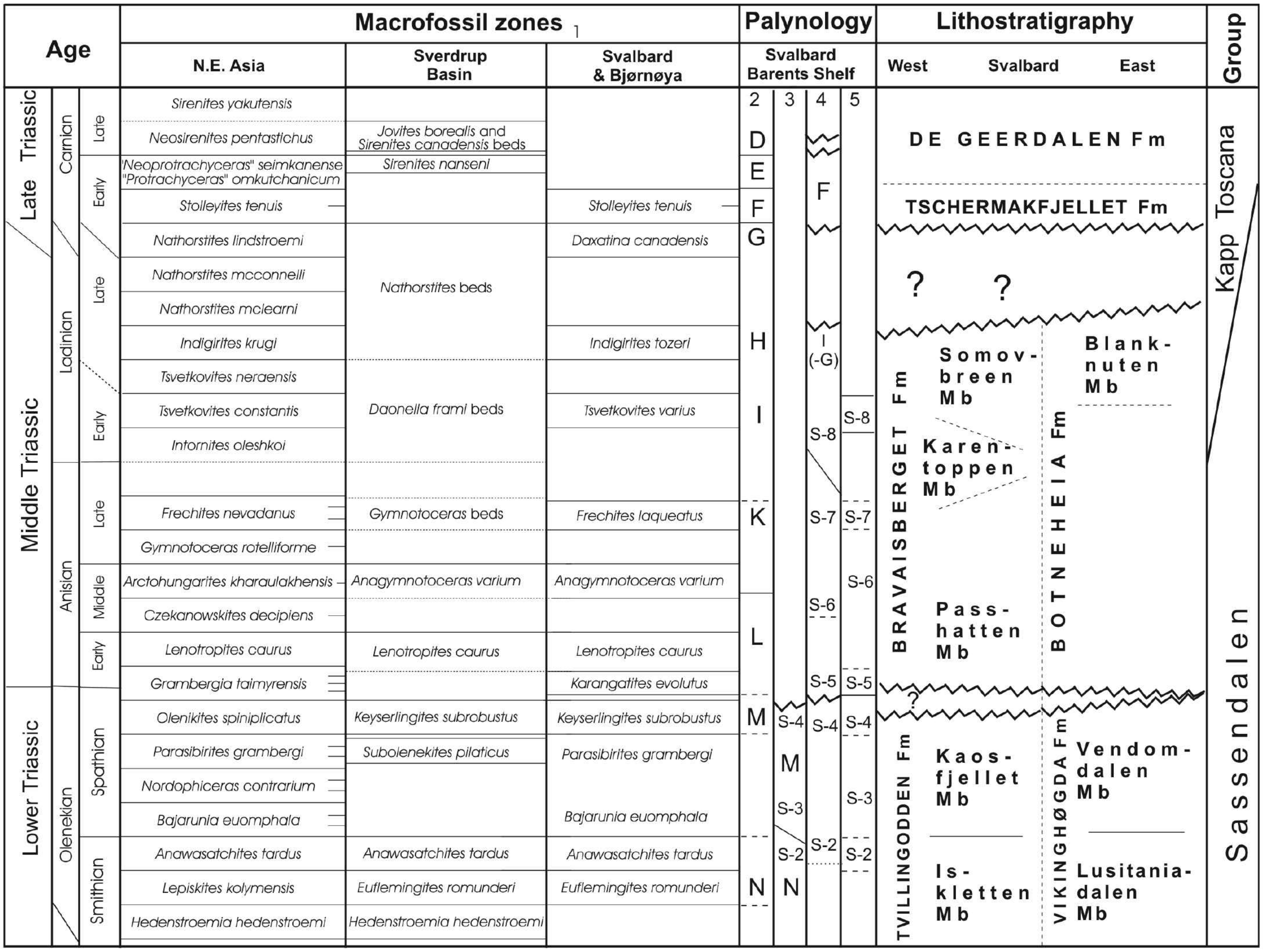

Solid lithostratigraphic boundaries are biostratigraphically dated; **Broken** lithostratigraphic boundaries are inferred

FIGURE 1. Lithostratigraphy and biostratigraphy of Svalbard and some parts of the Barents Sea (modified from Vigran et al., in press). 1. Ammonoid zones (Dagys and Weitschat, 1993; Dagys and Sobolev, 1995). 2-5 Palynological assemblages; 2. From Svalbard and the Barents Sea region (Hochuli et al., 1989). 3. Vikinghøgda Formation (Mørk et al (1999). 4. Milne Edwardsfjellet (this work) and Hounslow et al. (in press). 5. From The Svalis Dome area, western Barents Sea (Vigran et al. 1998).

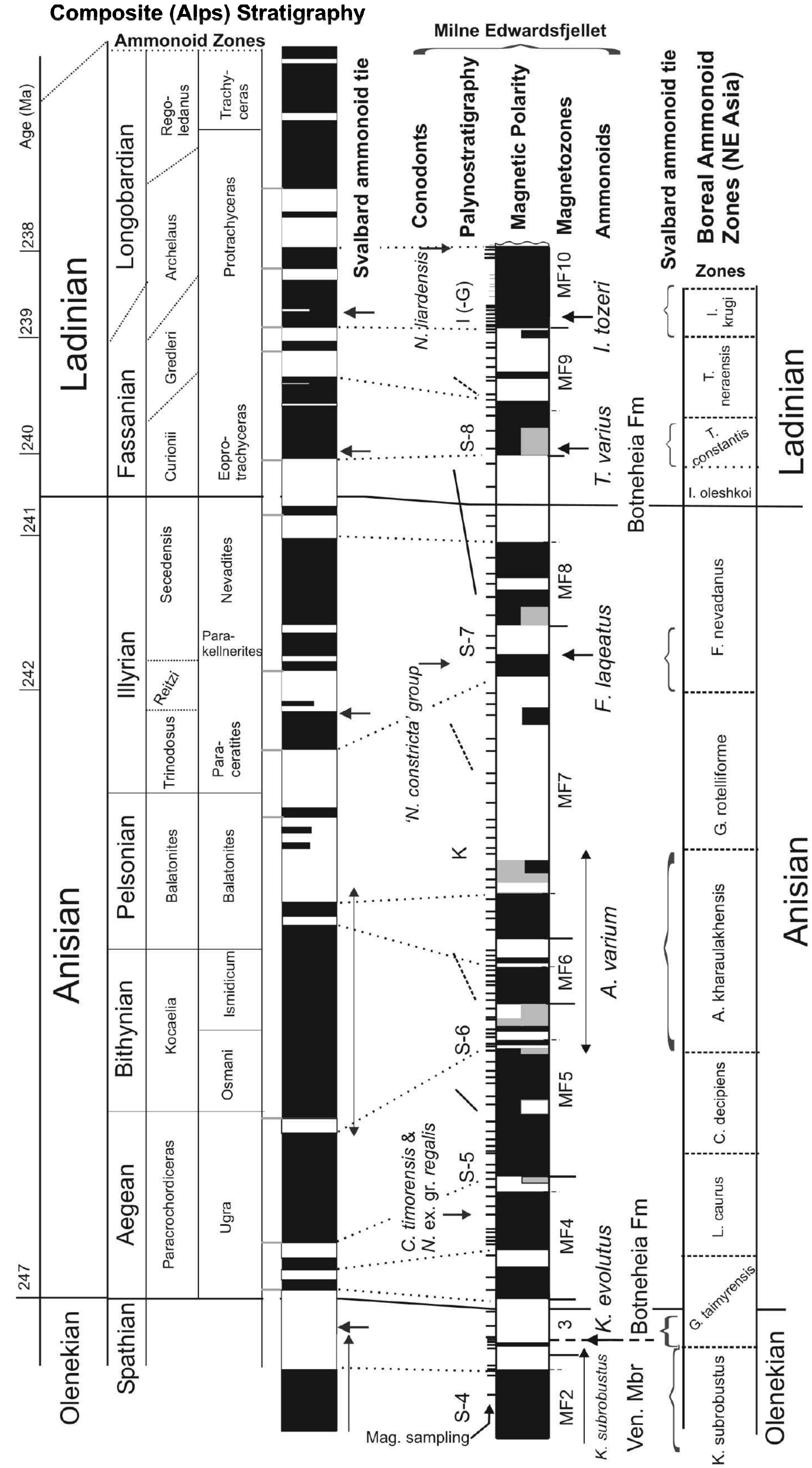

FIGURE 2. Correlation between the Boreal (NE Asia) ammonoid middle Triassic timescale and a composite Alpine ammonoid magneto-biostratigraphy (composite compiled from Muttoni et al., 1998; 2000, 2004; Nawrocki and Szulz, 2000). Radiometric ages from Muttoni et al. (2004), Brack et al. (2005). Palynostratigraphy zones of Hochuli et al. (1989) and Vigran et al. (1998). Dashed palyno-zone zone boundaries indicate uncertain bases (or top). Polarity-black=normal; white=reverse; grey=uncertain. The magnetostratigraphic column is not in depth scale, it has been stretched linearly over the Late Anisian and Early Ladinian boundary interval to match the Tethyan composite better.

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A NEW TETRAPOD ICHOGENUS FROM THE UPPER TRIASSIC OF NEW MEXICO, WITH NOTES ON THE ICHNOTAXONOMY OF *RHYNCHOSAUROIDES*

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Abstract—The Redonda Formation (Upper Triassic: late Norian/Rhaetian: Apachean) of the Chinle Group of east-central New Mexico yields a significant tetrapod ichnofauna. Some specimens previously referred to *Rhynchosauroides* represent a new ichnogenus named *Apachepus cottonorum* igen. et isp. nov. characterized by having a pedal print that is elongate with long, narrow digits, with digit V being very short and digits II-IV being subequal in length with a deep, rounded heel. The ichnogenus *Rhynchosauroides* is in need of taxonomic revision.

INTRODUCTION

The Redonda Formation is of broadly lacustrine origin and is widely exposed in northeastern New Mexico (Hester and Lucas, 2001). Indeed, the mesalands of eastern Quay County preserve an Upper Triassic lacustrine margin of the Redonda Formation that abutted the Frio uplift (Hunt and Lucas, 2001). Shoreline facies of the San Jon Creek Member of the Redonda Formation preserve an abundant tetrapod ichnofauna in this area (Fig. 1). Mesa Redonda yields an extensive ichnofauna that has been collected for three-quarters of a century and includes *Rhynchosauroides* isp., *Brachychirotherium eyermani*, *Grallator cursorius*, *Evazoum sirigui* and *Ameghinichnus* isp. (Hunt and Lucas, 1989; Hunt et al., 1989; Lockley et al., 2000; Lucas et al., 2001; Klein et al., 2006; Hunt and Lucas, 2007). Farther east, the Redonda is exposed along the margin of the Llano Estacado in Apache Canyon and at Red Peak where it yields *Rhynchosauroides* ispp., *Brachychirotherium* isp., *Grallator cursorius*, *Eosauropus* isp. and *Evazoum sirigui* (Hunt and Lucas, 1989; Hunt et al., 2000; Lucas et al., 2001; Lockley et al., 2006; Hunt and Lucas, 2007). The Redonda Formation also yields a significant body-fossil fauna in this area (Spielmann et al., 2006).

The majority of Redonda tracks derive from cliff-forming calcarenites of the San Jon Creek Member. Most tracks are medium-large in size (> 10 cm in length), and they are often relatively poorly-preserved. In Apache Canyon, the upper portion of the San Jon Creek Member is locally finer-grained and is relatively thinly-bedded (beds < 1 cm), as at NMMNH locality 6954. These strata yield a distinct morphology of track (e. g., Cotton et al., 1996) that we herein describe as a new ichnogenus. Previously, this new ichnotaxon has been referred to *Rhynchosauroides* isp. (e. g., Lucas et al., 2001, fig. 3A-B; Hunt and Lucas, 2007). MDM refers to Mesalands Dinosaur Museum, Tucumcari and NMMNH refers to New Mexico Museum of Natural History and Science, Albuquerque.

SYSTEMATIC PALEONTOLOGY

Apachepus, igen. nov.

New ichnotaxon: Cotton et al., 1996, p. 56.
Rhynchosauroides sp. Lucas et al., 2001, p. 178, fig. 3A-B.
Rhynchosauroides sp. Hunt and Lucas, 2007.

Type species: *Apachepus cottonorum* isp. nov.

Included species: Known only from the type ichnospecies.

Etymology: From Apache, for the name of the canyon from which the holotype derives, and from the Latin *pus,* for foot.

Distribution: Upper Triassic of New Mexico (late Norian/Rhaetian: Apachean).

Diagnosis: Tetrapod trackway that differs from other similar ichnotaxa (such as *Rhynchosauroides*) in having a pedal print that is elongate with long, narrow digits, with digit V being very short and digits II-IV being subequal in length with a deep, rounded heel.

Discussion: This ichnogenus is distinct from *Rhynchosauroides* in many features, including the lack of curvature of the digit impressions, the subequal length of digits II-IV and the small pace angulation.

Apachepus cottonorum isp. nov.

Holotype: MDM P-017, trackway consisting of three left pes prints, one right pes print and possible manus imprints (Figs. 3A-B, 4).

Etymology: For Bill and Jenny Cotton, who found the holotype of this ichnotaxon.

Type locality: NMMNH locality 6954, Quay County, New Mexico.

Type horizon: San Jon Creek Member of Redonda Formation (Late Triassic: late Norian/Rhaetian: Apachean), New Mexico.

Distribution: As for genus.

Referred specimens: MDM P-017, pedal print (Fig. 3A); other possible referred specimens are MDM P-015, pedal print (Fig. 3B) and MDM P-02, ?pedal print (Fig. 3C).

Diagnosis: As for ichnogenus.

Description: The holotype (MDM P-017) is a trackway consisting of three left pedal prints, one right pedal print and possible manual imprints (Figs. 3A-B, 4). Other tracks occur on this surface (Fig. 3A) and the obverse of the slab.

The trackway is approximately 170 mm wide. The pace angulation is about 45° and the stride is 80-99 mm.

Pedal prints are narrow and elongate with lengths of 56-60 mm and widths of 45-50 mm. The pes print has an elongate and deep heel imprint that is posteriorly rounded. On the posteromedial margin of each heel impression is an acutely-tipped ridge from 8 to 20 mm long.

The pes is pentadactyl but is often preserved as tetradactyl. Digit V is very short (typically 5-8 mm long) and oriented at an angle of about 45° to the long axis of the foot. Digits IV to I are narrow, straight and subequal in length (up to 35 mm). Anterolateral and anteromedial to the digit impressions there are small acute impressions (notably related to the right pes and to the anteriormost left pes) that may be subsequent imprints of the pedal digits.

There are no clear manual imprints. There are poorly defined impressions located anterolateral to the right pedal imprint and anteromedial to the first two pedal imprints that could represent fairly equant manual imprints with relatively short digits. Alternatively, the pes may have overstepped and manus – the first left pedal impression has a suggestion of a second overlapping medial heel imprint, which could have resulted from slippage or the overprint of a manual print.

Discussion: This ichnospecies is currently only known from the Redonda Formation of east-central New Mexico. The trackmaker is a small reptile with an elongate pes which is not represented in the body-fossil fauna of the Redonda Formation (Spielmann et al., 2006). The ichnofauna of the Redonda Formation represents a more terrestrial ecosystem than is sampled by the body-fossil fauna. This disparity is also very apparent in Early-Middle Triassic ichnofaunas of the *Chirotherium* ichnocoenosis of the *Batrachichnus* ichnofacies (Hunt and Lucas, 2006).

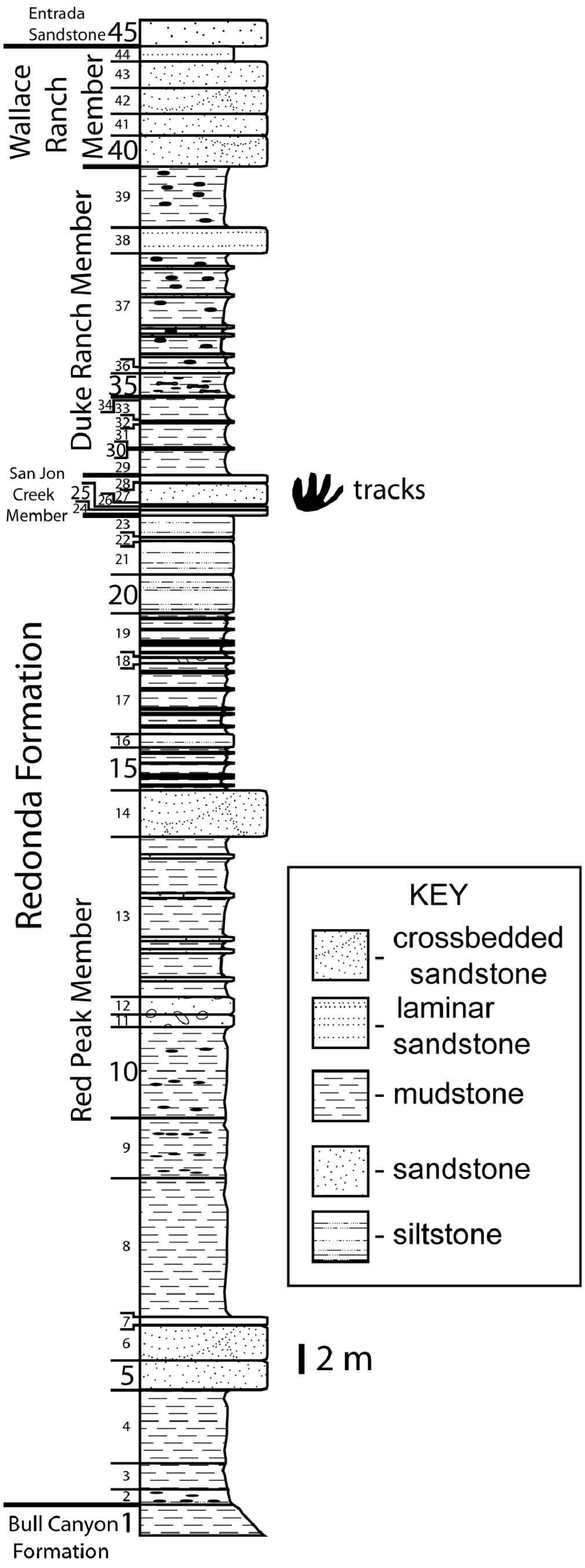

FIGURE 1. Stratigraphic column of the Redonda Formation in the Apache Canyon area (after Lucas et al., 2006) and the location of the track-producing horizon.

THE ICHNOTAXONOMY OF *RHYNCHOSAUROIDES* MAIDWELL, 1911

Rhynchosauroides has long been recognized as a form genus for Triassic lacertoid tracks (e.g., Baird, 1957, p. 498). Currently, there are a large number of named Triassic ichnospecies, and the ichnotaxon is in need of revision (Table 1). This ichnogenus also occurs in the Late Permian (e. g., Cassinis and Santi, 2005). Triassic records are limited to North and South America and to Europe (Haubold, 1984; Melchor and De Valais, 2006).

This ichnotaxon is usually attributed to Beasley in Maidwell (1911), with the type species *Rhynchosauroides rectipes*. However, Owen (1842) first referred to tracks of this morphology using the osteological binomen *Rhynchosaurus articeps*. Pohlig (1893) used the binomen *Protritonichnites sublacertoides* for Triassic lacertoid tracks, although he had previously used this ichnogenus to apply to Permian lacertoid tracks now assigned to *Dromopus*.

Pending a revision of all the ichnospecies of *Rhynchosauroides* we offer some taxonomic comments. Most species of *Rhynchosauroides* can easily be distinguished into two size classes with pedal lengths of the larger species being greater than 5 cm and the smaller usually less than 3 cm. The larger Triassic species include *R. moenkopiensis*, *R. schochardti*, *R. hyperbates*, *R. tirolicus* and *R. peabodyi* and are restricted to the Middle-Late Triassic. *R. majus* is probably a *nomen dubium*. Baird (1957, p. 494, fig. 9A) named *R. hyperbates* for a small number of specimens from the Brunswick Formation of New Jersey. Subsequently, exquisitely preserved specimens have been found of this ichnotaxon (e. g., Olsen, 1988, fig. 8-8), and this is the best known of the larger ichnospecies. *Rhynchosauroides* specimens demonstrate a wide range of extramorphological variation including overall size, relative position and orientation of manual and pedal imprints, divarication of digit impressions (particularly digit impression V) and curvature of digit impressions (Baird, 1964). In many trackways the pedal impressions are weakly imprinted or unrecognizable and drag marks extend the length of digit impressions (Baird, 1964). Based on this wide range of variation, it is likely that that many "ichnospecies" are actually synonymous, for example the large Middle Triassic taxa *R. tirolicus* Abel, 1926, *R. peabodyi* (Faber, 1958) and *R. moenkopiensis* Haubold, 1970 from Europe and North America. Avanzini and Renesto (2002) discussed the similarities between *R. tirolicus* and *R. peabodyi*, but considered them distinct, based principally on the morphology of the pedal digit impressions and the location of pedal impression V. These two characters are subject to extramorphological variation.

Characters of potential taxonomic importance include absolute size and the relative size of the manual imprint relative to the pedal (*R. rectipes* has a relatively small manual imprint and *R. hyperbates* has a relatively large one). In conclusion, there is a need for more ichnotaxonomic work on *Rhynchosauroides*. In general, Triassic lacertoid tracks have been much less studied than archosaur tracks.

ACKNOWLEDGMENTS

The collection of these specimens would not have been possible without the permission of the late Johnny Duke. Bill and Jenny Cotton collected the specimens describe herein. We thank Justin Spielmann for a helpful review.

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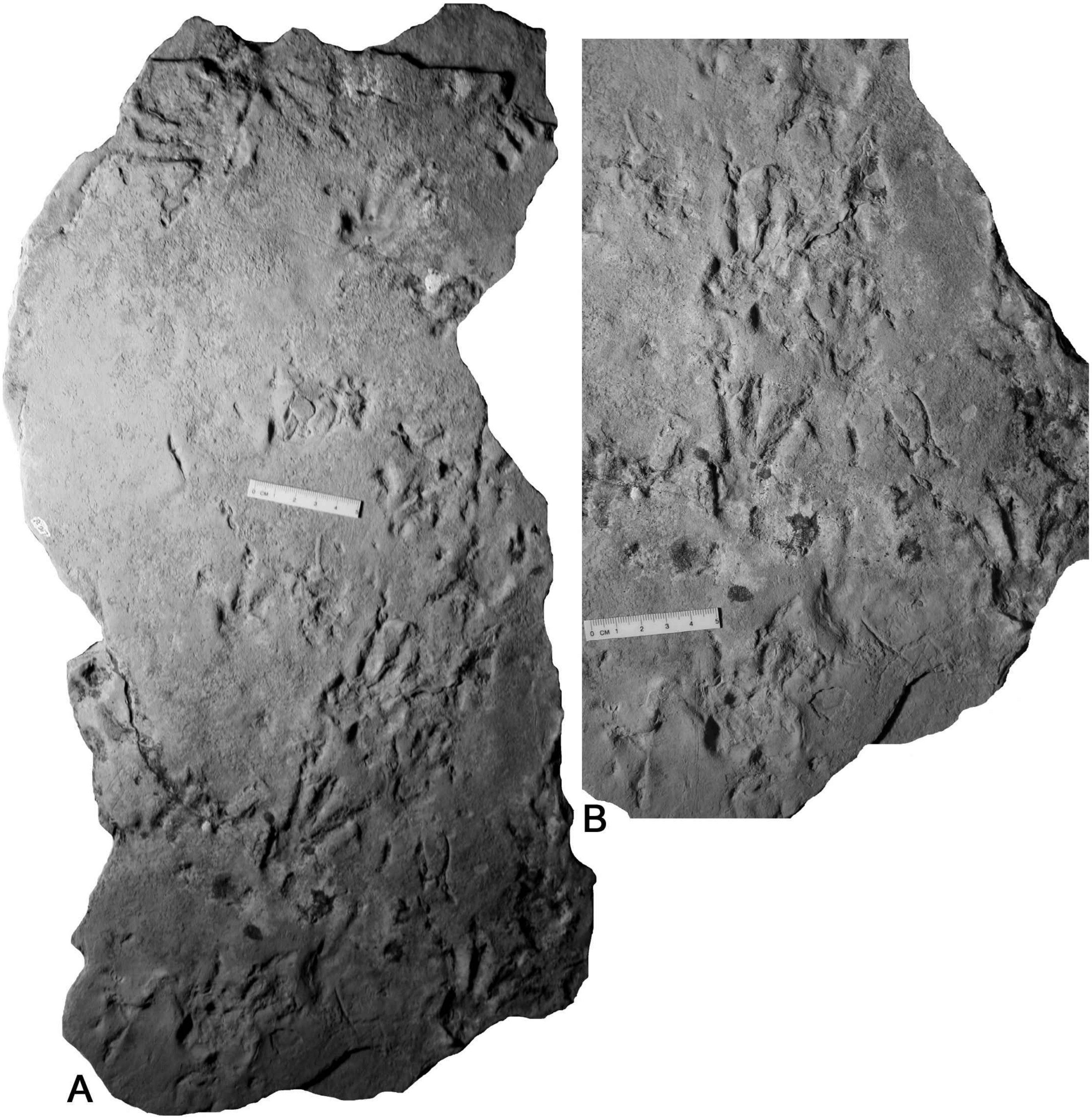

FIGURE 2. Holotype and topotype specimens of *Apachepus cottonorum* igen. et isp. nov. (MDM P-017). **A**, Overview of specimen. **B**, Close-up of holotype trackway.

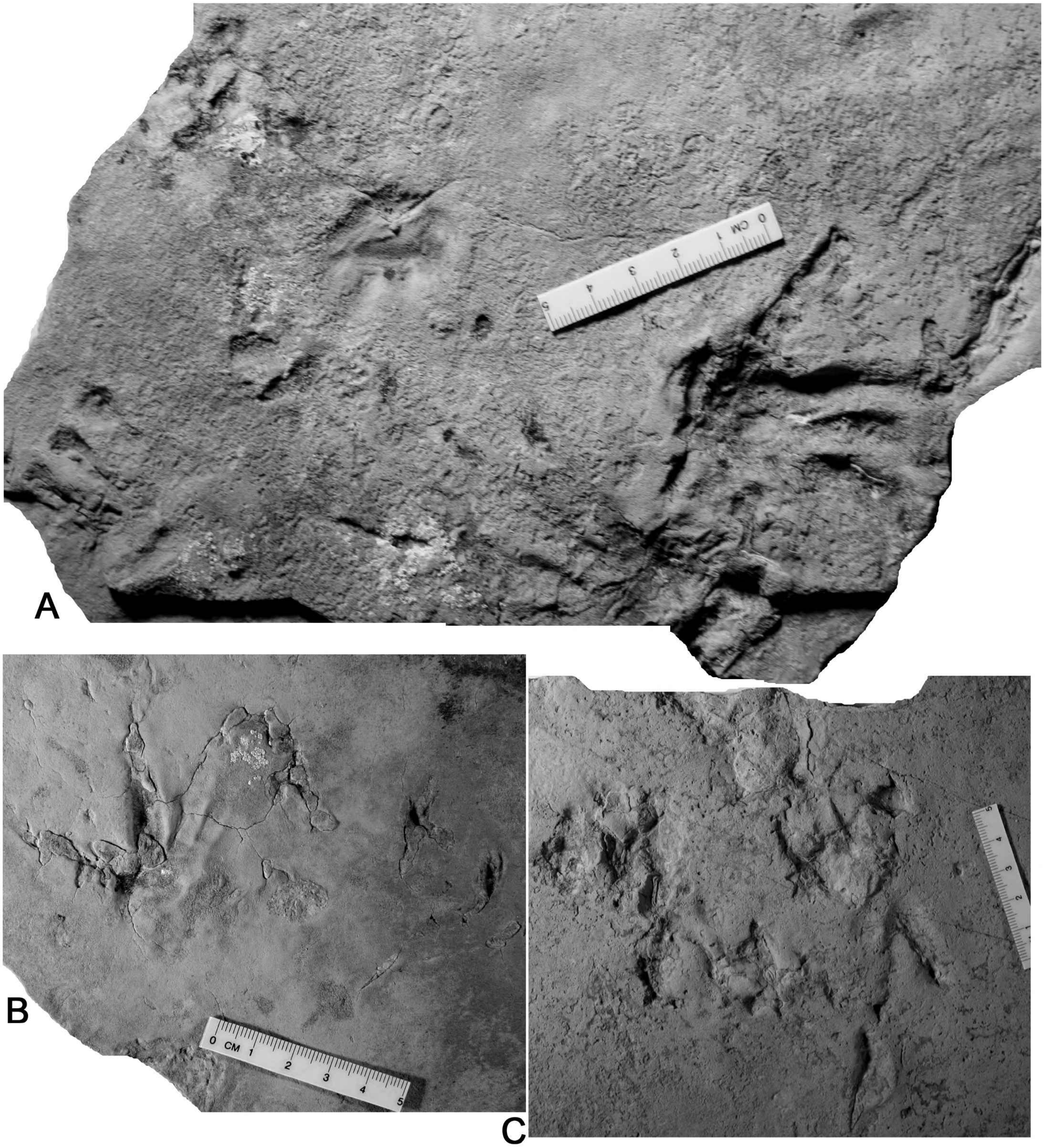

FIGURE 3. Topotype and possibly referred specimens of *Apachepus cottonorum* igen. et isp. nov. **A**, Topotype specimens of *Apachepus cottonorum* igen. et isp. nov. (MDM P-017). **B**, Possible specimen of *Apachepus cottonorum* igen. et isp. nov. (MDM P-015). **C**, Possible specimen of *Apachepus cottonorum* igen. et isp. nov. (MDM P-002).

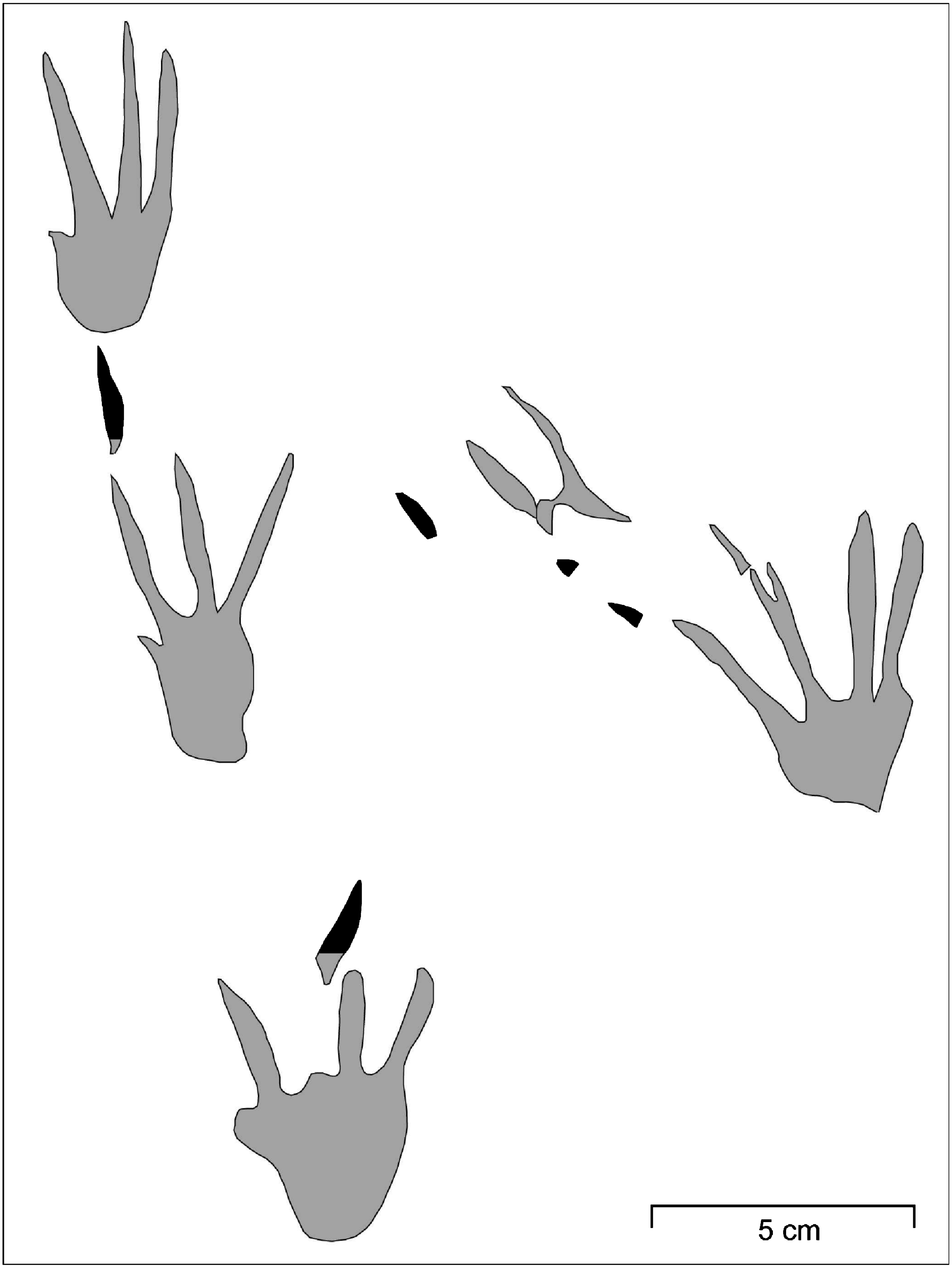

FIGURE 4. Interpretative drawing of the holotype trackway of *Apachepus cottonorum* igen. et isp. nov. (MDM P-017).

TABLE 1. Named Triassic species of *Rhynchosauroides*.

Rhynchosauroides (Rhynchosaurus) " articeps" (Owen, 1842)
Rhynchosauroides (Protritonichnites) sublacertoides (Pohlig, 1893)
Rhynchosauroides rectipes Maidwell, 1911
Rhynchosauroides membranipes Maidwell, 1911
Rhynchosauroides minutipes Maidwell, 1914
Rhynchosauroides (Ichnites) pisanus (Fucini, 1915)
Rhynchosauroides beasleyi Nopsca, 1923
Rhynchosauroides maidwelli Nopsca 1923
Rhynchosauroides tirolicus Abel, 1926
Rhynchosauroides (Aetosaripus) schlauersbachensis (Weiss, 1934)
Rhynchosauroides (Akropus) schochardti Rühle von Lilienstern, 1939
Rhynchosauroides (Akropus) langi Rühle von Lilienstern, 1939
Rhynchosauroides (Hamatopus) wilfeueri Rühle von Lilienstern, 1939
Rhynchosauroides (Rhynchocephalichnus) etruscus (Huene, 1941)
Rhynchosauroides (Eurichnus) jenseni (Lull, 1942)
Rhynchosauroides (Collettosaurus) palmatus (Lull, 1942)
Rhynchosauroides (Kintneria) brunswickii (Ryan and Willard, 1947)
Rhynchosauroides (Orthodactylus) howelli Bock, 1952
Rhynchosauroides (Rhynchocephalichnus) franconicus (Heller, 1956)
Rhynchosauroides hyperbates Baird, 1957
Rhynchosauroides (Chirotherium) peabodyi (Faber, 1958)
Rhynchosauroides bornemanni Haubold, 1966
Rhynchosauroides petri Demathieu, 1966
Rhynchosauroides pusillus Haubold, 1966
Rhynchosauroides majus Demathieu, 1967
Rhynchosauroides sphaerodactylus Demathieu, 1967
Rhynchosauroides haarmüblensis Holst et al., 1969
Rhynchosauroides moenkopiensis Haubold, 1970
Rhynchosauroides maximus Demathieu, 1974
Rhynchosauroides santanderensis Demathieu and de Omenaca 1977
Rhynchosauroides extraneus Demathieu and de Omenaca 1979
Rhynchosauroides simulans Demathieu and de Omenaca 1979

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THE TRIASSIC TETRAPOD TRACK RECORD: ICHNOFAUNAS, ICHNOFACIES AND BIOCHRONOLOGY

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Abstract—Triassic tetrapod tracks have long been studied, including classic ichnofaunas such as those of the lower Newark Supergroup of eastern North America and the Bundsandstein of central Europe. They are known from all seven continents and encompass five archetypal vertebrate ichnofacies for nonmarine environments (*Chelichnus, Grallator, Batrachichnus, Brontopodus, Characichnos),* all of which are present in the Triassic: (1) *Chelichnus* ichnofacies – *Brasilichnium* ichnocoenosis; (2) *Grallator* ichnofacies – *Grallator* ichnocoenosis; (3) *Batrachichnus* ichnofacies – *Chirotherium* and *Apatopus* ichnocoenoses; (4) *Brontopodus* ichnofacies – *Dicynodontipus*, *Therapsipus*, *Brachychirotherium* and *Evazoum* ichnocoenoses; and (5) *Characichnos* ichnofacies – unnamed ichnocoenosis. There are five temporal subdivisions of the Triassic that can be recognized based on tetrapod tracks: (1) earliest Triassic – dicynodont tracks; (2) Early-Middle Triassic (Olenekian-early Anisian) – chirothere- (archosaur-) dominated assemblage; (3) late Middle Triassic (late Anisian-Ladinian) – dinosauromorph assemblage; (4) early Late Triassic (Carnian-early Norian) – tridactyl dinosaur assemblage; and (5) late Norian-Rhaetian – sauropodomorph track assemblage.

INTRODUCTION

Triassic tetrapod tracks are among the longest studied and the best known tetrapod footprints and they include the classic ichnofaunas of the Chinle Group of the American Southwest, the lower Newark Supergroup of eastern North America and the Bundsandstein of central Europe (Hunt and Lucas, 2006b; Lucas, 2007). There is thus a very large database of Triassic tetrapod tracks, which are known from six continents (North America, South America, Europe, Asia, Australia, Antarctica: Fig. 1). Lucas (2006) recently provided a synthesis of the biochronology and biostratigraphy of these ichnofaunas, and Hunt and Lucas (2007b) reviewed the tetrapod ichnofacies of the Triassic. The purpose of this paper is to provide an overview of the Triassic track record — its extent, ichnofacies and biochronology.

TRIASSIC TETRAPOD TRACK RECORD

Introduction

The first Triassic tetrapod tracks were described by Sickler (1834, 1835) from the upper part of the Buntsandstein (Olenekian) near Hildburghausen (Thuringia, Germany). Subsequently, Kaup (1835a, b) named these tracks *Chirotherium barthii* and *Chirotherium sickleri*, which became the first published binomens of tetrapod tracks.

Triassic tetrapod tracks are now known from North America, South America, Europe, North Africa, Australia, Antarctica and South Africa (Fig. 1). The Triassic track record is archosaur- and synapsid-dominated and includes the oldest dinosaur tracks. The oldest footprints attributed to mammals are also of Late Triassic age, but they are rare (Sarjeant, 2000). The following review is principally based on Lucas (2007) and Hunt and Lucas (2006b).

Earliest Triassic

The oldest Triassic tetrapod tracks are dicynodont footprints from the Karoo basin in South Africa (Watson, 1960), the Fremouw Formation of Antarctica (MacDonald et al., 1991) and the Sydney basin in Australia (Retallack, 1996).

Early Triassic-early Middle Triassic

The best known Triassic footprint assemblage is of late Early to early Middle Triassic (Olenekian-Anisian) age and has a Euramerican distribution. This is a chirothere- (archosaur-) dominated assemblage that also persists during most of the Middle Triassic.

The first described tracks of this assemblage were from the upper part of the Buntsandstein (Solling Formation: Olenekian) (Sickler, 1834, 1835: Kaup, 1835a, b), but elsewhere in Germany, similar track assemblages occur in the uppermost Buntsandstein (Röt Formation: e.g., Willruth, 1917; Soergel, 1925; Rühle v. Lilienstern 1939; Schreiber, 1956; Krebs, 1966; Haubold 1971b; Demathieu and Leitz, 1982; Haderer et al., 1995; Ebel et al., 1998). The Röt yields a diversity of archosaur ichnogenera, including *Chirotherium*, *Isochirotherium*, *Synaptichnium*, *Brachychirotherium* and *Rotodactylus*. Equivalent ichnofaunas outside of Germany come from France (Provence, Massif Central, Alpes Maritimes) and the Vosges of the French-German-Belgian borderland (e.g., Charles, 1949; Demathieu and Durand, 1975; Demathieu and Leitz, 1982; Orzag-Sperberg, 1966; Demathieu, 1977, 1984). The Buntsandstein ichnofaunas have a demonstrated age range of late Olenekian through early Anisian (Nonesian-Perovkan: Lucas, 1998, 2007; Lucas and Schoch, 2002).

The Moenkopi Formation in Arizona and New Mexico has a very similar ichnofauna of early Anisian age. Most tracks can be assigned to *Chirotherium*, *Isochirotherium* and *Rotodactylus*, as well as the synapsid track *Therapsipus* (Peabody, 1948; Hunt et al., 1993b; Nesbitt and Angielczyk, 2002; Lucas et al., 2003). In Italy, there are *Rhynchosauroides* tracks in the Olenekian Werfen Formation (Mietto, 1986). Early Anisian rocks in Italy yield archosaur tracks referred to a variety of ichnogenera, including *Rhynchosauroides*, *Chirotherium*, *Brachychirotherium*, *Synaptichnium*, *Parasynaptichnium* and *Isochirotherium* (e.g., Abel, 1926; Mietto, 1987; Sirna et al., 1994; Avanzini et al., 2001; Avanzini and Lockley, 2002).

Late Middle Triassic

The Anisian interval of the Muschelkalk in Germany and the Netherlands yields tetrapod ichnofaunas in carbonate tidal flat facies that are dominated by the ichnogenera *Rhynchosauroides* and *Procolophonichnium*; chirothere tracks are much rarer (Demathieu and Oosterink, 1983, 1988; Diedrich, 1998, 2000, 2002a, b).

Marginal siliciclastic equivalents of the Muschelkalk in Germany and from the French Middle Triassic yield chirothere-dominated ichnofaunas into rocks as young as Ladinian, including the ichnogenera *Isochirotherium*, *Synaptichnium*, *Sphingopus*, *Brachychirotherium* and *Rotodactylus* (e.g., Demathieu, 1966, 1970, 1971; Demathieu and Gand, 1972, 1973; Courel and Demathieu, 1973, 1976; Gand, 1976, 1977,

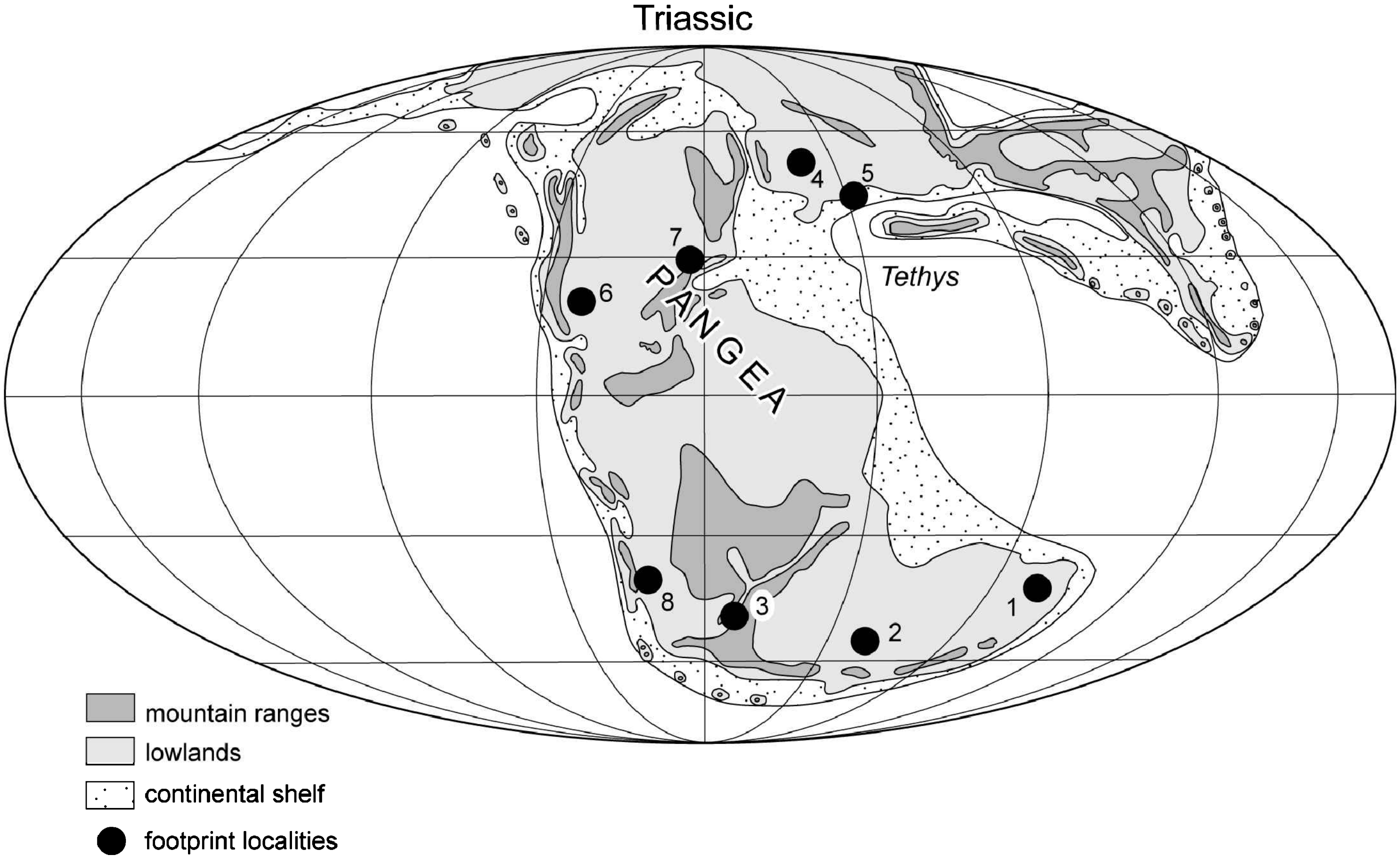

FIGURE 1. Distribution of principal Triassic tracksites on Triassic Pangea (from Lucas, 2007). Locations are: 1, Sydney basin, Australia; 2, Karoo basin, South Africa; 3, Antarctica; 4, western Europe, 5, Italy; 6, Chinle basin, western United States; 7, Newark basin, New Jersey-Pennsylvania; 8, Argentina. Base map after Wing and Sues (1992).

1978, 1980; Gand and Pellier, 1976; Gand et al., 1976). Middle Triassic red beds in Italy (Avanzini and Neri, 1998; Avanzini, 1999; 2002; Avanzini et al., 2001; Avanzini and Leonardi, 2002), Great Britain (Sarjeant, 1967, 1970, 1996; King and Benton, 1996) and Spain (Demathieu et al., 1978) also have a similar ichnofauna. In Argentina, chirothere tracks dominate the Lower and Middle Triassic records in San Juan, Mendoza and La Rioja provinces (e.g., Huene, 1931b; Rusconi, 1951, 1967).

Huene (1931a) named *Rigalites ischigualastianus* for tracks from the Middle Triassic (Berdyankian = Ladinian?) Los Rastros Formation in San Juan Province of Argentina. Melchor and DeValais (2006) also listed records of *Rigalites* from the Berdyankian Cerros de las Cabras and Ischichuca formations in Mendoza and La Rioja provinces. *Rigalites* is the trackway of a quadruped in which the pes is much larger than the manus, the pes nearly oversteps the manus and both manus and pes are pentadactyl (we regard the supposed tetradactyl pes of *Rigalites* as a result of extramorphological variation). The tracks are obviously chirothere, and the neotype illustrated by Melchor and De Valais (2006, text-fig. 7) is strikingly similar to some of the *Brachychirotherium* tracks illustrated by Klein et al. (2006). Therefore, we regard *Rigalites* as a junior synonym of *Brachychirotherium*.

In Middle Triassic assemblages, which are both Anisian and Ladinian (Perovkan-Berdyankian: Lucas, 1998) in age, the only biostratigraphic datum that can be used to distinguish them from the earlier chirothere assemblage is the Ladinian lowest occurrence of dinosaur or dinosaur-like (dinosauromorph) tracks (Lucas, 2007). These tracks are not simply extramorphological variants of chirothere tracks (Haubold, 1999; Haubold and Klein, 2000; Lucas, 2007). In Germany, tridactyl *Atreipus*- and *Grallator*-like tracks have their lowest occurrence in the Ladinian Benker Sandstein (Rehnelt, 1950, 1952, 1959, 1983; Weiss, 1976, 1981) and increase in abundance up section. Haubold and Klein (2000) identify these tracks as "*Parachirotherium-Atreipus-Grallator*" and conclude that they represent dinosauromorph track makers.

Late Triassic

The Late Triassic footprint record is distinct from older Triassic footprint assemblages in its near domination by *bona fide* dinosaur tracks. These are generally assigned to the ichnogenera *Grallator*, *Atreipus*, *Eosauropus* and *Evazoum* (Lockley et al., 2006). *Brachychirotherium* records begin earlier in the Triassic, but it is the most common and characteristic Late Triassic chirothere footprint ichnogenus.

Late Triassic tetrapod footprint assemblages dominated by these ichnogenera are known from the lower Stormberg Group (Molteno and lower Elliott formations and equivalents) of southern Africa (e.g., Ellenberger, 1970; Olsen and Galton, 1984; Raath et al., 1990; Raath, 1996), the upper Keuper in Germany and equivalent strata in Switzerland and Great Britain (e.g., Beurlen, 1950; Heller, 1952; Haubold, 1971b, 1984; Demathieu and Wiedmann, 1982; Olsen and Baird, 1986; Haderer, 1988, 1990, 1991; Lockley et al., 2006; Karl and Haubold, 1998, 2000; Lockley and Meyer, 2000; Gand et al., 2000), the Upper Triassic portion of the Newark Supergroup in eastern North America (e.g., Lull, 1953; Olsen and Baird, 1986; Silvestri and Szajna, 1993; Szajna and Silvestri, 1996; Olsen et al., 1998; Lucas and Sullivan, 2006) and the Chinle Group in the American Southwest (e.g., Baird, 1964; Conrad et al., 1987; Hunt et al., 1993a; Lockley and Hunt, 1995; Lockley et al., 2001; Lucas et al., 2001; Hunt and Lucas, 2006a; 2007a).

In Morocco, the Carnian interval of the Argana Group yields a similar footprint assemblage that includes *Rhynchosauroides*, *Brachychirotherium*, *Atreipus* and *Grallator*? (Biron and Dutuit, 1981). The South American Late Triassic footprint record is from Argentina (Brazilian records are doubtful: Leonardi, 1994). Prosauropod, small

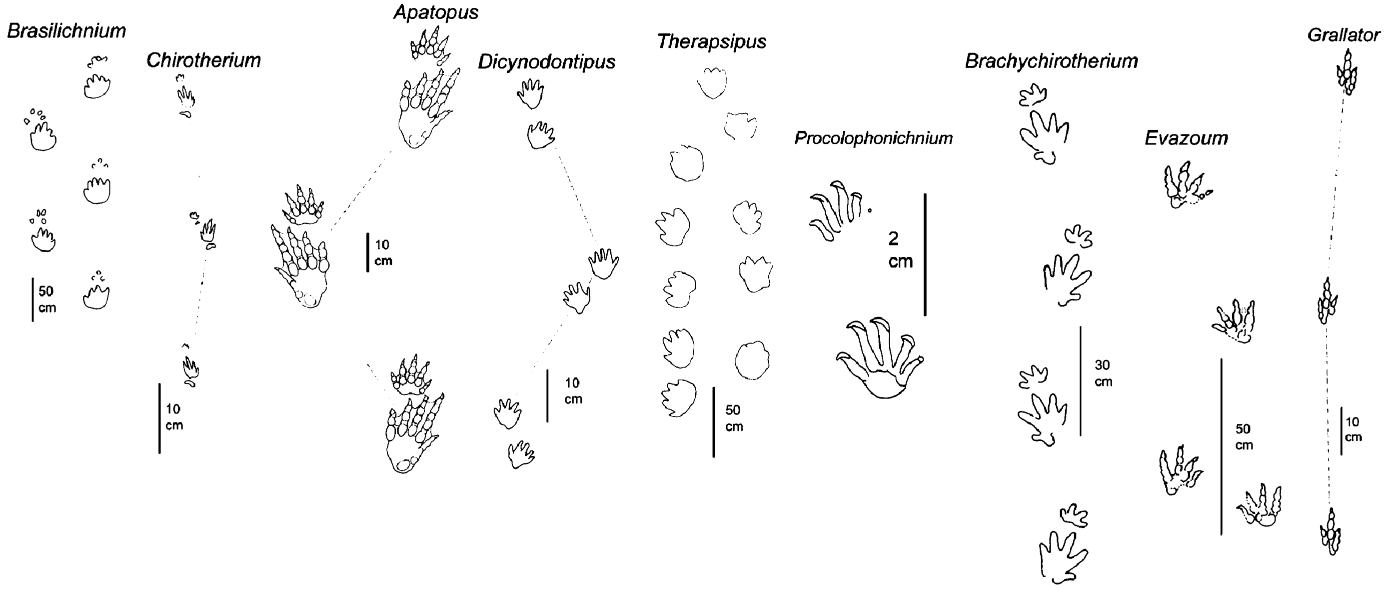

FIGURE 2. Representative tracks of the *Grallator*, *Brontopodus*, *Chelichnus*, *Batrachichnus* and *Characichnos* ichnofacies from the Triassic (after Lockley and Hunt, 1995; Haubold, 1984; Demathieu and Oosterink, 1983). *Brasilichnium* ichnocoenosis of the *Chelichnus* ichnofacies. *Chirotherium* and *Apatopus* ichnocoenoses of the *Batrachichnus* ichnofacies. *Dicynodontipus*, *Therapsipus*, *Procolophonichnium*, *Brachychirotherium* and *Evazoum* ichnocoenoses of the *Brontopodus* ichnofacies, and *Grallator* ichnocoenosis of the *Grallator* ichnofacies.

theropod, synapsid (both small cynodont and large dicynodont) and chirothere (*Brachychirotherium*) tracks are known from Upper Triassic strata in Río Negro, San Juan and La Rioja provinces (e.g., Casamiquela, 1964; Bonaparte, 1969; Arcucci et al., 1995, 2000; Marsicano and Barredo, 2000). Late Triassic theropod tracks are also known in Australia from the Sydney basin in New South Wales and the Callide basin in southeastern Queensland (e.g., Molnar, 1991; Thulborn, 1998).

TRIASSIC TETRAPOD ICHNOFACIES AND ICHNOCOENOSES

Introduction

Hunt and Lucas (2007b) provided a discussion of terminology relevant to the study of tetrapod ichnofacies. An ichnocoenosis can be defined as a trace fossil assemblage produced by a biological community that can be characterized by morphological criteria (independent of depositional environment or biological affinities) (e.g., Bromley, 1996; McIlroy, 2004; Hunt and Lucas, 2007). Seilacher (1964, p. 303) introduced the term ichnofacies for “general trace associations, or types of ichnocoenoses, representing certain facies with a long geologic range.” Subsequently, Hunt and Lucas (2007) defined five archetypal tetrapod ichnofacies for nonmarine environments: *Chelichnus*, *Grallator*, *Brontopodus*, *Batrachichnus* and *Characichnos* ichnofacies (Table 1). The following review is principally based on Hunt and Lucas (2006b, 2007).

Batrachichnus Ichnofacies

Hunt and Lucas (2007b) proposed the *Batrachichnus* ichnofacies for ichnofaunas in which the majority of tracks are of quadrupedal carnivores with a moderate-high diversity (four to eight ichnogenera). This ichnofacies represents tidal flat-fluvial plain environments from the Devonian to the Cretaceous. Hunt and Lucas (2006b, 2007) recognized two ichnocoenoses of this ichnofacies in the Triassic (Fig. 2; Table 1).

Hunt and Lucas (2007b) named the *Chirotherium* ichnocoenosis for the well-studied Early-Middle Triassic ichnofaunas of Europe and North America that are dominated by *Chirotherium* tracks (e.g., Peabody, 1948, Haubold, 1971a; Lucas et al., 2003) (Fig. 2). Other common ichnotaxa are *Rotodactylus*, *Rhynchosauroides*, *Isochirotherium* and *Synaptichnium*.

Hunt and Lucas (2006b) recognized a distinctive and pervasive ichnocoenosis throughout much of the Upper Triassic portion of the Newark Supergroup in eastern North America assigned to the *Apatopus* ichnocoenosis. Ichnofaunas of this ichnocoenosis lack *Evazoum* and *Eosauropus*, contain less than 50% *Brachychirotherium* and *Grallator* and are characterized by ichnotaxa that are rare or absent elsewhere, including *Apatopus* and *Gwyneddichnium*.

Brontopodus Ichnofacies

Hunt and Lucas (2007b) proposed the *Brontopodus* ichnofacies for medium diversity ichnofaunas in which the majority of tracks are of terrestrial herbivores with a small quantity (generally > 10%) of terrestrial carnivore tracks. This ichnofacies includes coastal plain-marine shoreline environments and some lacustrine shorelines, and it ranges from Late Permian to Recent in age. Hunt and Lucas (2006b) recognized four ichnocoenoses within this ichnofacies in the Triassic and herein we define a fifth (Fig. 2; Table 1).

The oldest ichnocoenosis within the *Brontopodus* ichnofacies occurs in the earliest Triassic (possibly restricted to the Induan) and is characterized by dicynodont footprints in southern Africa, Antarctica and Australia (Watson, 1960; MacDonald et al., 1991; Retallack, 1996). Hunt and Lucas (2006b) termed this the *Dicynodontipus* ichnocoenosis (Fig. 2).

The majority of Early Triassic to early Middle Triassic ichnofaunas represent the *Chirotherium* ichnocoenosis of the *Batrachichnus* ichnofacies. However, a small number of localities are dominated by therapsid tracks. Hunt and Lucas (2006b) termed this the *Therapsipus* ichnocoenosis for the therapsid ichnotaxon from the Moenkopi Formation of Arizona (Hunt et al., 1993b).

Herein, we recognize a new ichnocoenosis in the Anisian carbonate tidal flats of Germany and the Netherlands. This *Procolophonichnium* ichnocoenosis represents a temporal equivalent of the red-bed *Chirotherium* ichnocoenosis (Lucas, 2007). This ichnocoenosis is dominated by tracks of *Procolophonichnium* and *Rhynchosauroides* with only rare chirothere tracks (Demathieu and Oosterink, 1983, 1988; Diedrich, 1998, 2000, 2002a, b; Lucas, 2007).

TABLE 1. Archetypal tetrapod ichnofacies (Hunt and Lucas, 2007b) and representative ichnocoenoses of the Triassic.

Archetypal Tetrapod Ichnofacies	Predominant trace fossil types	Constituent Triassic ichnocoenoses	Inferred environment
Chelichnus	Low diversity ichnofaunas (less than 4 ichnogenera) of tetrapod tracks that have equant shape with subequal manual and pedal impressions and short digit impressions	*Brasilichnium* (Late Triassic-Early Jurassic: Lockley et al., 1994)	Eolian crossbeds
Batrachichnus	Majority of tracks are of quadrupedal carnivores; medium-high diversity (4-8 ichnogenera)	*Chirotherium* (Early-Middle Triassic: Hunt and Lucas, 2007); *Apatopus* (Late Triassic: Hunt and Lucas, 2006b)	Tidal flat-fluvial plain
Brontopodus	Majority of tracks are terrestrial herbivores with small quantity (generally > 10%) of terrestrial carnivore tracks; medium-high diversity (4-8 ichnogenera)	*Dicynodontipus* (Early Triassic: Hunt and Lucas, 2006b); *Therapsipus* (Middle Triassic: Hunt and Lucas, 2006b); *Procolophonichnium* (Middle Triassic: herein) *Brachychirotherium* (Late Triassic: Hunt and Lucas, 2006b); *Evazoum* (Late Triassic: Hunt and Lucas, 2006b)	Coastal plain, clastic or carbonate marine shoreline
Grallator	Medium-high diversity ichnofaunas (5-8 ichnogenera) with tracks (usually dominant) of tridactyl avian and non-avian theropods	*Grallator* (Late Triassic: Hunt and Lucas, 2007)	Lacustrine margin
Characichnos	Parallel scratch marks and fish swimming trails (*Undichna*)	unnamed	Shallow lacustrine/ aquatic

Hunt and Lucas (2007b) redefined Lockley's (2007) Late Triassic *Grallator-Brachychirotherium-Rhynchosauroides* ichnofacies as the *Grallator* ichnocoenosis of the *Grallator* ichnofacies. Further study of Late Triassic ichnofaunas by Hunt and Lucas (2006b) indicated that four individual ichnocoenoses can be discriminated within this plexus, and two of them can be assigned to the *Brontopodus* ichnofacies, and one each to the *Grallator* and *Batrachichnus* ichnofacies.

Hunt and Lucas (2006b) recognized the *Evazoum* ichnocoenosis for Late Triassic ichnofaunas that are numerically dominated by tracks of quadrupedal herbivores (e.g., Lockley and Hunt, 1995, fig. 3.25). The Redonda Formation of east-central New Mexico is typical of these ichnofaunas (Klein et al., 2006). The ichnogenus *Evazoum* also occurs in Wales and Lesotho and often co-occurs with *Eosauropus* (Lockley et al., 2006), in, for example, western North America, Lesotho and Wales (Lockley and Hunt, 1995; Lockley and Meyer, 2000). In Switzerland and Greenland, *Eosauropus* occurs without *Evazoum* (Lockley and Meyer, 2000). Hunt and Lucas (2006b) diagnosed the *Evazoum* ichnocoenosis as consisting of ichnofaunas in which more than 40% of the specimens represent *Evazoum* and/or *Eosauropus*.

Other Late Triassic ichnofaunas, dominated by the tracks of quadrupedal herbivores, are composed of more than 50% *Brachychirotherium* tracks (e.g., sites in the Chinle Group of western North America, including Shay Canyon in Utah and sites in Sloan Canyon in New Mexico). These tracksites typically have 0-10% *Evazoum* or *Eosauropus*. Hunt and Lucas (2006b) assigned these ichnofaunas to the *Brachychirotherium* ichnocoenosis (Fig. 2).

Grallator Ichnofacies

Hunt and Lucas (2007b) proposed the *Grallator* ichnofacies for medium to high diversity ichnofaunas (five to eight ichnogenera) dominated by tracks of tridactyl avian and non-avian theropods (usually dominant) or of other habitual bipeds. Tracks of bipedal and quadrupedal ornithischians, sauropods and herbivorous mammals are also locally common in this ichnofacies. This ichnofacies extends from the Late Triassic to the Recent and often characterizes lacustrine margin environments. We recognize four ichnocoenoses of the *Grallator* ichnofacies during the Triassic (Table 1).

As noted above, Hunt and Lucas (2007b) recognized a *Grallator* ichnocoenosis in the Late Triassic. There are many Late Triassic ichnofaunas in which the most abundant (> 50%) ichnogenus is *Grallator*. Notable ichnofaunas occur at the very top of the Chinle Group or in the overlying Wingate Sandstone in Colorado (Gaston et al., 2003; Lucas et al., 2006b); other prominent examples are in Wales, France, Germany, Italy, Switzerland and Greenland (Lockley and Meyer, 2000, figs. 4.4, 4.10, 4.14).

Hunt and Lucas (2006b) noted that there is potential to subdivide the *Grallator* ichnocenosis, and it clearly includes several sub-ichnocoenoses, e.g., on the Colorado Plateau, the upper and lower Wingate Sandstone have different sub-ichnocoenoses: a lower *Eosauropus* sub-ichnocoenosis includes *Brasilichnium*, *Brachychirotherium*, and *Eosauropus*, and an upper *Otozoum* sub-ichnocoenosis includes *Eubrontes*, *Batrachopus* and *Otozoum* (Lucas et al., 2006b).

Chelichnus Ichnofacies

Hunt and Lucas (2007b) proposed the *Chelichnus* ichnofacies for ichnofaunas that have a low diversity (fewer than five ichnogenera) of tetrapod tracks in which manus and pes tracks are equant in shape, of subequal size and have short digit impressions. This ichnofacies is recurrent on dune faces in eolian environments, and it extends from the Early Permian to the Early Jurassic.

Hunt and Lucas (2007b) redefined the *Brasilichnium* ichnofacies of Lockley et al. (1994) as an ichnocoenosis of this ichnofacies (Table 1; Fig. 2). *Brasilichnium* is abundant in the Early Jurassic Navajo Sandstone and coeval Aztec Sandstone in western North America (Utah, California, Colorado). The *Brasilichnium* ichnocoenosis is also locally present in the lower Wingate Sandstone in western Colorado (Schultz-Pittman et al., 1996; Hunt and Lucas, 2006b).

Characichnos Ichnofacies

Hunt and Lucas (2007b) proposed the *Characichnos* ichnofacies for medium diversity ichnofaunas in which the majority of tracks are tetrapod swimming traces (parallel scratch marks) and fish swimming trails (*Undichna*). This ichnofacies represents shallow lacustrine (and tidal) environments. Swimming traces are notable in various Triassic units in the western United States, including the Moenkopi Formation (Lower-Middle Triassic) and equivalent strata in Arizona, Utah, Wyoming and New Mexico (e.g., Peabody, 1948; Boyd and Loope, 1984; McAllister and Kirby, 1998; Schultz et al., 1994; Lucas et al., 2003; Mickleson et al., 2006a, b) and the Chinle Group (Upper Triassic) in Arizona and New Mexico (e.g., Hunt et al., 1993a; Hunt and Lucas, 2006b). There is no named ichnocoenosis of this ichnofacies in the Triassic.

Late Triassic Ichnoceonoses

There are thus five ichnocoenoses present in the Late Triassic: *Evazoum*, *Brachychirotherium* (*Brontopodus* ichnofacies), *Grallator* (*Grallator* ichnofacies), *Apatopus* (*Batrachichnus* ichnofacies) and *Brasilichnium* (*Chelichnus* ichnofacies). The *Apatopus* ichnocoenosis is geographically restricted to eastern North America (although *Apatopus* occurs at one locality in Utah: Foster et al., 2003) and probably environmentally controlled by the distribution of large rift lakes. The *Evazoum* ichnocoenosis is principally restricted to western North America, where it is replaced in the uppermost Chinle, Wingate and Sheep Pen formations (latest Triassic) by the *Grallator* ichnocoenosis. The Shay Canyon tracksite in Utah pertains to the *Brachychirotherium* ichnocoenosis and is stratigraphically low in the upper Chinle. It may represent a lateral equivalent of the *Evazoum* ichnoceonosis or it may be stratigraphically lower, which would suggest a temporal progression of ichnocoenoses from *Brachychirotherium* to *Evazoum* to *Grallator* (Hunt and Lucas, 2006b).

The ichnofaunas of the lower Chinle are poorly known but include *Brachychirotherium*, lack *Evazoum*, and several include *Barrancapus* (Hunt and Lucas, 2006a). These ichnofaunas may represent the *Brachychirotherium* ichnocoenosis (possibly a *Barrancapus* sub-ichnocoenosis). *Barrancapus* appears to be a potential index ichnotaxon of the Barrancan sub-lvf (land-vertebrate faunachron) of the Revueltian lvf. *Eosauropus* and *Evazoum* are index ichnotaxa of the Apachean lvf (Hunt and Lucas, 2006b).

TRIASSIC TETRAPOD TRACK BIOSTATIGRAPHY AND BIOCHRONOLOGY

Introduction

Lucas (2007) reviewed the Phanerozoic record of tetrapod tracks (Devonian-Neogene) and noted that three principal factors limit their use in biostratigraphy and biochronology (palichnostratigraphy): (1) invalid ichnotaxa based on extramorphological variants; (2) slow apparent evolutionary turnover rates; and (3) facies restrictions. The ichnotaxonomy of tetrapod footprints has generally been oversplit, largely due to a failure to appreciate extramorphological variation. Thus, many tetrapod footprint ichnogenera, and most ichnospecies, are useless "phantom" taxa that confound biostratigraphic correlation and biochronological subdivision. Tracks rarely allow identification of a genus or species known from the body fossil record. Indeed, almost all tetrapod footprint ichnogenera are equivalent to a body fossil-based family or a higher taxon (order, superorder, etc.). This means that ichnogenera necessarily have much longer temporal ranges and therefore slower apparent evolutionary turnover rates than do body fossil genera. Because of this, footprints cannot provide as refined a subdivision of geological time as do body fossils. The tetrapod footprint record is also much more facies controlled than the tetrapod body fossil record. The relatively narrow facies window for track preservation, and the fact that tracks are almost never transported, redeposited or reworked, limits the facies that can be correlated with any track-based biostratigraphy (Lucas, 2007).

Biostratigraphy and Biochronology

There is much literature on Triassic tetrapod footprint biostratigraphy, especially based on the European and North American records. The most comprehensive are the publications of Demathieu (e.g., 1977, 1982, 1984, 1994; Demathieu and Haubold, 1972, 1974), who established the presence of three different Triassic footprint assemblages in Europe that Lucas (2007) validated. These are the chirothere assemblage of Olenekian-early Anisian age (early-Middle Triassic), the dinosauromorph assemblage of late Anisian-Ladinian age (late Middle Triassic) and the dinosaur assemblage of Carnian-Rhaetian age (Late Triassic). Lucas (2007) suggested that a fourth footprint assemblage, based on earliest Triassic dicynodont footprints from Gondwana, may also be discernable.

Earliest Triassic

The dicynodont tracks from the South Africa, Antarctica and Australia (Watson, 1960; MacDonald et al., 1991; Retallack, 1996) may represent a distinct ichnofauna. Retallack (1996) attributed these tracks to the body-fossil genus *Lystrosaurus*, which defines a classic biochron of earliest Triassic (Induan) age (Lucas, 1998). However, these dicynodont tracks cannot be reasonable be attributed at the generic level so they cannot be used to support the *Lystrosaurus* biochron. There is a need for additional study of the latest Permian and earliest Triassic ichnofaunas. The most significant ichnofaunas of these ages are from South Africa.

Early-Middle Triassic

The late Early to early Middle Triassic (Olenekian-Anisian) is characterized by a chirothere- (archosaur-) dominated assemblage that also persists throughout most of the Middle Triassic. European evidence (especially France) suggests that the chirothere-dominated footprint assemblage continues in red-bed facies into rocks as young as Ladinian (Lucas, 2007). The chirothere-dominated ichnofauna includes the archosaur ichnogenera *Isochirotherium*, *Synaptichnium*, *Sphingopus*, *Chirotherium*, *Rotodactylus*, *Rhynchosauroides* and *Brachychirotherium*, as well as the synapsid track *Therapsipus* (e.g., Peabody, 1948; Hunt et al., 1993b; Nesbitt and Angielczyk, 2002; Lucas et al., 2003; Lucas, 2007).

Late Middle Triassic

Later Middle Triassic assemblages are both Anisian and Ladinian (Perovkan-Berdyankian: Lucas, 1998) in age. The only biostratigraphic datum to distinguish them from the earlier chirothere assemblage is the Ladinian lowest occurrence of dinosaur or dinosaur-like (dinosauromorph) tracks (Lucas, 2007). Apparent tridactyl, bipedal tracks have long been known from Middle Triassic strata in Europe and attributed to dinosaurs by various workers (see review by Demathieu, 1989). More recently, a more sophisticated analysis of this problem by Haubold (1999; Haubold and Klein, 2000) argues that there was a lengthy and complex evolutionary transition from the dinosauromorph foot/gait to the dinosaur foot/ gait well documented in the Triassic of the German section.

In Germany, track surfaces of the Benker Sandstein up to the Löwenstein Formation (Gipskeuper) and in the Lower Steinmergelkeuper have quadrupedal, chirotherian-like, pentadactyl pes imprints and trackways assigned to the ichnogenus *Parachirotherium* (Lucas, 2007). Tridactyl *Atreipus*- and *Grallator*- like tracks have their lowest occurrence in the Benker Sandstein (Rehnelt, 1950, 1952, 1959, 1983; Weiss, 1976, 1981) and increase in abundance up section. Haubold and Klein (2000) identify these tracks as "*Parachirotherium-Atreipus-Grallator*" and concluded that they represent dinosauromorph track makers.

Regardless of how these tracks are identified, the lowest occurrence of tridactyl dinosaur or dinosaur-like (dinosauromorph) tracks appears to be Ladinian and may form a valuable biostratigraphic datum. Lucas (2007) recognized the appearance of dinosauromorph tracks in the later Middle Triassic as marking a distinct footprint assemblage of this age.

Late Triassic

There have been attempts to identify two temporally successive Late Triassic footprint assemblages. Thus, Olsen (1980) identified three footprint assemblages in the Newark Supergroup of eastern North America, two of Late Triassic age and one of Early Jurassic age. More detailed stratigraphic data have shown that the two Late Triassic assemblages should be combined into one characterized primarily by *Brachychirotherium*, *Gwyneddichnium*, *Grallator*, *Atreipus* and *Rhynchosauroides* (Silvestri and Szajna, 1993; Szajna and Silvestri, 1996; Lucas and Huber, 2003; Lucas, 2007). Olsen and Huber (1998) raised the possibility that an older, distinctive footprint assemblage may be present near the base of the Newark Supergroup, but when extramorphological variation is considered, this assemblage consists of characteristic Late Triassic ichnotaxa, including *Apatopus*, *Grallator* and *Brachychirotherium*. Haubold (1986) followed Olsen's (1980) zonation, applying it to the European and South African records. However, current ichnotaxonomy and understanding of stratigraphic distribution makes it clear that only one Late Triassic footprint assemblage can be identified in these regions (Lucas and Hancox, 2001; Lucas and Huber, 2003).

Lockley (1993) and Lockley and Hunt (1994, 1995) also presented a similar zonation for the upper Chinle Group and the Glen Canyon Group in the western United States. They identified four successive zones, two of which are Late Triassic in age: (1) *Brachychirotherium* and small grallatorid zone of the upper Chinle Group (Rock Point sequence of Lucas, 1993); and (2) medium-size grallatorid assemblage of the Wingate Sandstone. However, subsequent collecting and stratigraphic data demonstrate that assemblages 1 and 2 are a single assemblage dominated by *Grallator* and *Brachychirotherium*, which Lucas et al. (2006a) termed the *Brachychirotherium* assemblage zone.

However, it is possible to discriminate two successive Late Triassic intervals based on ichnofaunas. The sauropodomorph traces *Evazoum* and *Eosauropus* first appear in the later Norian or Rhaetian. These ichnotaxa occur in the Late Triassic of western North America, Greenland, Switzerland and Lesotho (e.g., Lockley and Hunt, 1995; Lockley and Meyer, 2000; Lockley et al., 2006; Lucas et al., 2006a). Older Late Triassic ichnofaunas lack these ichnotaxa, and their appearance corresponds with the evolution of larger sauropodomorphs in the Norian. The Newark Supergroup is conspicuous among Upper Triassic units that yield significant tracks in lacking these sauropodomorph tracks. It is important to note that the extensive ichnofaunas of the Late Triassic-Early Jurassic Newark Supergroup represent a very narrow range of depositional environments, essentially lacustrine margins of rift basin lakes. These ichnofaunas are distinct from contemporary ichnofaunas in other significant ways, including the presence of *Apatopus* and the prevalence of *Atreipus*.

CONCLUSIONS

There are five subdivisions of the Triassic that can be recognized based on tetrapod tracks: (1) earliest Triassic – dicynodont tracks; (2) Early-Middle Triassic (Olenekian-early Anisian) - chirothere- (archosaur-) dominated assemblage; (3) late Middle Triassic (late Anisian-Ladinian) - dinosauromorph assemblage; (4) early Late Triassic (Carnian-early Norian) – tridactyl dinosaur assemblage; and (5) late Norian-Rhaetian - sauropodomorph track assemblage.

A global Triassic biochronology based on tetrapod body fossils recognizes eight biochronological units (Lucas, 1998). The Triassic tetrapod footprint record resolves to about five time intervals, so it has much less temporal resolution than the body fossil record (Lucas, 2007).

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A REVIEW OF VERTEBRATE COPROLITES OF THE TRIASSIC WITH DESCRIPTIONS OF NEW MESOZOIC ICHNOTAXA

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Abstract—Coprolites are the least studied and most under-sampled vertebrate trace fossils. They are very common in some Triassic localities. We recognize six new coprolite ichnotaxa: *Alococopros triassicus*, *A. indicus*, *Saurocopros bucklandi*, *Liassococopros hawkinsi*, *Malericopros matleyi* and *Falcatocopros oxfordensis*. The distribution of coprolite ichnotaxa is: Permian - *Hyronocopros amphipolar* and *Heteropolacopros texaniensis*; Early Triassic - *Hyronocopros amphipolar* and *Alococopros triassicus*; Middle Triassic - *Alococopros triassicus* and ?*Liassocopros* sp.; Late Triassic - *Heteropolacopros texaniensis*, *Alococopros triassicus*, *Dicynodontocopros maximus*, *Malericopros matleyi*, *Liassocopros hawkinsi* and S*aurocopros bucklandi*; Early Jurassic- *Liassocopros hawkinsi* and S*aurocoporos bucklandi*. We recognize the *Liassocopros* and *Heteropolacopros* coprolite ichnofacies.

INTRODUCTION

Coprolites are the least studied and most under-sampled vertebrate trace fossils. When we started extensively collecting Triassic vertebrate fossil assemblages in the early 1980s, we were struck by the prevalence of vertebrate coprolites at many localities but their virtual absence in museum collections. Other paleontologists noted that they didn't collect these coprolites or that they subsequently disposed of them rather than accession them. A similar lack of attention (or respect) befell human coprolites in archeological sites (Bryant and Dean, 2006). We have strived to sample vertebrate coprolites as assiduously as other fossils, and thus the New Mexico Museum of Natural History and Science now has the largest collection of Triassic vertebrate coprolites (Appendix).

There is an acme for vertebrate coprolites in Permian-Triassic redbeds (Hunt and Lucas, 2005b) with a worldwide distribution of Triassic assemblages (Fig. 1). Buckland (1829, p. 227), the founder of the study of coprolites (which we term paleoscatology), first described them in detail from the Rhaetian Westbury Formation of Great Britain (Buckland and Conybeare, 1822, p. 302, pl. 37 had earlier noted them but not recognized them as coprolites): "some similar substances which have long been known to exist at Westbury, Aust Passage, and Watchet, on the banks of the Severn, and which now also prove to be faecal balls of digested bone: they mostly occur in a thin bed of sandy micaeous lias, so full of bones and teeth and spines of reptiles and fishes, as to form a bony breccia known to geologists by the name of bone-bed, and occupying the lowest place at the bottom of the lias." Subsequently, much later in the twentieth century, there were several published studies of Triassic coprolites (e.g., Rusconi, 1947, 1949, Ochev, 1974; Jain, 1983). Recently, there have been more detailed studies of the ichnotaxonomy, ichnofacies and biostratigraphy of Triassic vertebrate coprolites (e.g., Lucas et al., 1985, Hunt et al., 1993, 1994, 1998; Northwood, 2005). However, these studies were very preliminary. The purpose of this paper is to provide a first review of Triassic coprolites and provide a stimulus for future work. In the course of this work, we recognized the need to describe several new coprolite ichnotaxa from the Triassic, Jurassic and Cretaceous.

Institutional abbreviations: BCM, Bristol City Museum and Art Gallery, Bristol; BMMNH, Natural History Museum (formerly British Museum of Natural History), London; GSI, Geological Survey of India, Calcutta; ISI, Indian Statistical Institute, Calcutta; MNA, Museum of Northern Arizona in Flagstaff; NMMNH, New Mexico Museum of Natural History and Science, Albuquerque; NMW, National Museum of Wales, Cardiff; UCMP, University of California Museum of Paleontology, Berkeley; UMMP, University of Michigan Museum of Paleontology, Ann Arbor; YPM PU, Princeton collection at the Yale Peabody Museum, New Haven.

SYSTEMATIC ICHNOLOGY

Introduction

Currently, there are only two named ichnogenera of Triassic coprolites. Hunt et al. (1998) named *Heteropolacopros texaniensis* for a heteropolar-coiled coprolite and *Dicynodontocopros maximus* for large coprolites presumed to have been produced by dicynodonts (Fig. 2).

In the course of our review of Triassic coprolites, we have noted the need to formalize a number of distinct ichnotaxa. These include a form that is currently only known from the Jurassic but that we expect to be present in the Triassic, and an ichnogenus that has two species, one of which is Cretaceous in age.

Alococopros igen. nov.

Type species: *Alococopros triassicus* isp. nov.

Included species: *A. triassicus* and *A. indicus*.

Etymology: From the Greek *alocos* for "furrowed" and *kopros* for "dung."

Distribution: Early Triassic–Late Cretaceous of Australia, India and North America.

Diagnosis: Differs from other copolite ichnogenera in often being arcuate in lateral view and sub-rounded in cross-section with regularly spaced, thin, longitudinal grooves.

Discussion: Specimens here ascribed to this distinctive ichnogenus were first described from the Upper Triassic of West Texas (Case, 1922, figs. 33C-D). It may be possible to distinguish between thinner, straighter forms (e.g., Northwood, 2005, fig. 2F) and broader, more arcuate forms (e.g., Case, 1922, figs. 33C-D).

Alococopros triassicus isp. nov.

Holotype: UMMP 7253 (partim), coprolite (Fig. 3A).

Type locality: Crosby County, Texas.

Type horizon: Tecovas Formation.

Etymology: Named for the Triassic Period, which yields all known specimens of this species.

Distribution: Early-Late Triassic of Australia, India and North America.

Referred specimens: UMMP 7253 (partim), coprolite (Fig. 3B).

Diagnosis: Differs from *A. indicus* in being less than one-fourth as long (typically 2 cm in length).

Discussion: This ichnospecies is currently only known from the Triassic. Northwood (2005) discussed the origin of these types of coprolites at length. Longitudinal intestinal rugae occur in both amphibians and reptiles, but Northwood (2005) argued that *Alococopros triassicus* (her "longitudinally striated coprolites") represent archosauromorphs, because: (1) this ichnotaxon first occurs in the Early Triassic; (2) some

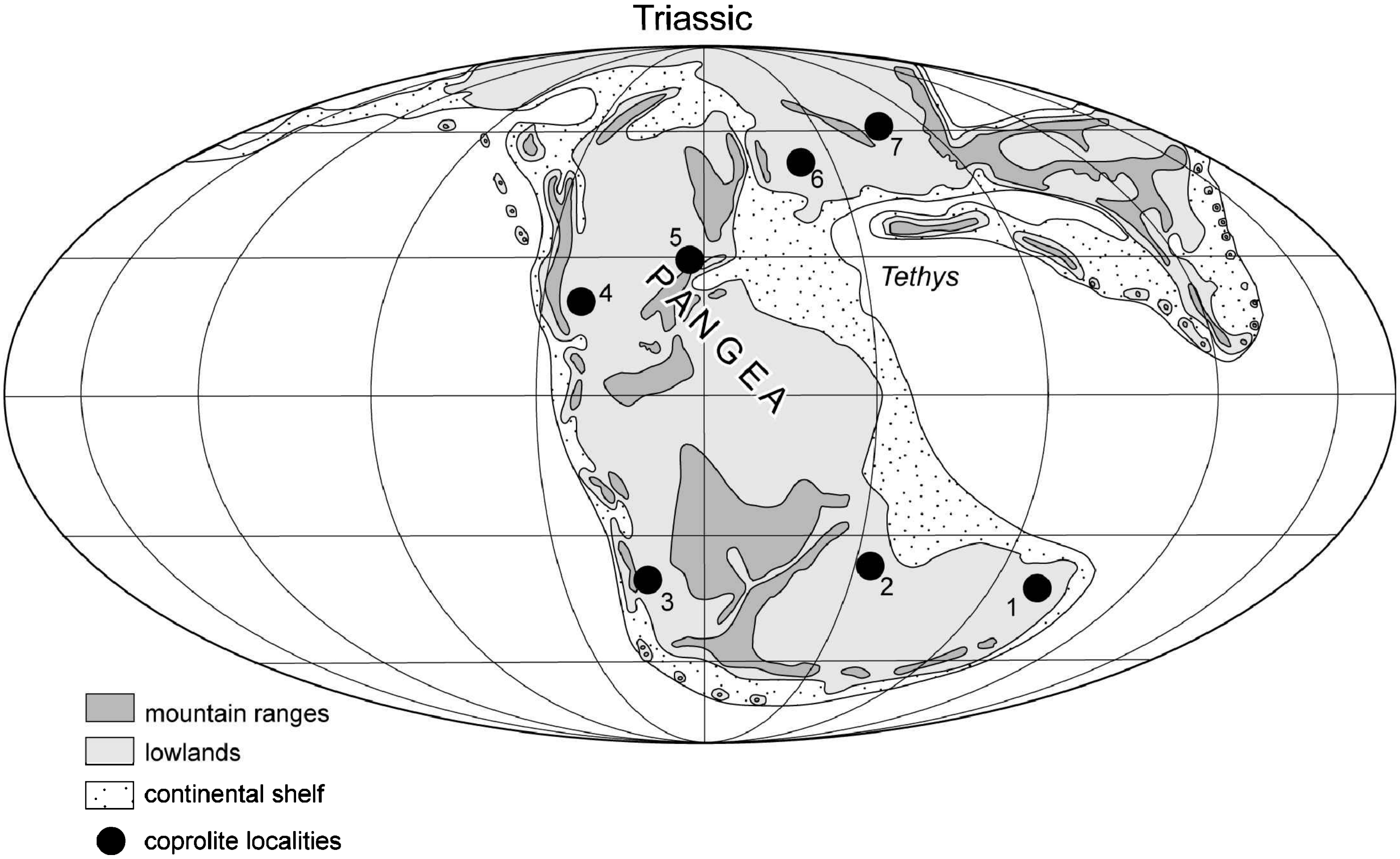

FIGURE 1. Distribution of principal Triassic coprolite-rich areas on Triassic Pangea. Locations are: 1, Queensland, Australia (Early Triassic); 2, Pranhita-Godavari basin, India (Middle-Late Triassic); 3, Mendoza region, Argentina (Middle Triassic); 4, Chinle and Moenkopi basins, United States (Early-Late Triassic); 5, Newark Supergroup basins, United States and Canada (Late Triassic); 6, United Kingdom and Germany (Middle-Late Triassic); 7, Kazakhstan and Russia (Middle Triassic). Base map after Wing and Sues (1992).

extant reptiles have longitudinal rugae; and (3) they resemble extant crocodile feces (Young, 1964). This is a reasonable hypothesis, since this ichnospecies is restricted to the Triassic, as are basal archosauromorphs.

Alococopros indicus isp. nov.

Holotype: BMNH, unnumbered Matley Collection, two sections of the same coprolite (Fig. 3C-D).

Type locality: North of Kadubana, India.

Type horizon: Lameta Formation.

Etymology: Named for the country of India from which the type specimens originate.

Distribution: Upper Cretaceous of India.

Referred specimens: Unnumbered coprolites, Matley Collection (Matley, 1939b, pls. 74, 75, figs. 1-4).

Diagnosis: Ichnospecies that differs from *A. triassicus* in being more than four times as long (typically 10 cm in length).

Discussion: This ichnospecies is currently only known from the Lameta Formation of India. This ichnospecies is considerably larger than *A. triassicus*.

Saurocopros igen. nov.

Type species: *Saurocopros bucklandi* isp. nov.

Included species: Known only from the type ichnospecies.

Etymology: From the Greek *sauros* for "reptile" and *kopros* for "dung" to honor Buckland's (1829, p. 227, caption for plate 28) use of the term "sauro-coprolites" for specimens of this ichnotaxon.

Distribution: Late Triassic-Late Cretaceous of Europe and North America.

Diagnosis: Microspiral heteropolar coprolite that differs from *Malericopros* in being tapered below the spiral demarcation and from *Heteropolacopros* in having a small number of wide spirals (typically 3) at the anterior end (compare Fig. 2A-I and Fig. 4).

Discussion: We name this ichnogenus with the full knowledge that this coprolite does not pertain to a reptile. Rather, we name it to honor William Buckland, who used the term "Sauro-coprolites" to refer to coprolites of this morphology from the lower Lias of Lyme Regis (e.g., Buckland, 1829, p. 227, pl. 28, figs. 6, 7, 9). These coprolites are abundant in the Lower Jurassic of England (e.g., Buckland, 1829; Hawkins, 1834, 1840). Hunt and Lucas (2005c) described large heteropolar coprolites from the Lower Permian of Texas. These specimens may pertain to *Saurocopros*.

Saurocopros bucklandi isp. nov.

Holotype: BMMNH R. 2102 (Fig. 4B: Hawkins, 1840, pl. 29).

Type locality: Lyme Regis, England.

Type horizon: Lower "Lias."

Etymology: Named for the Rev. William Buckland, who first described specimens of this ichnogenus.

Distribution: As for the ichnogenus.

Referred specimens: BMNH R. 41285 (Fig. 4A), BMNH R. 1402 (Fig. 4C-D) and other coprolites from the Lower Lias of Lyme Regis, England (Fig. 4E-G).

Diagnosis: As for the ichnogenus.

Discussion: For obvious reasons, it is only appropriate to name coprolites after scholars who have made contributions to paleoscatology and who would presumably consider the attribution an honor. Such is the case with William Buckland, who not only coined the term "coprolite" but who also founded and pursued the field of paleoscatology.

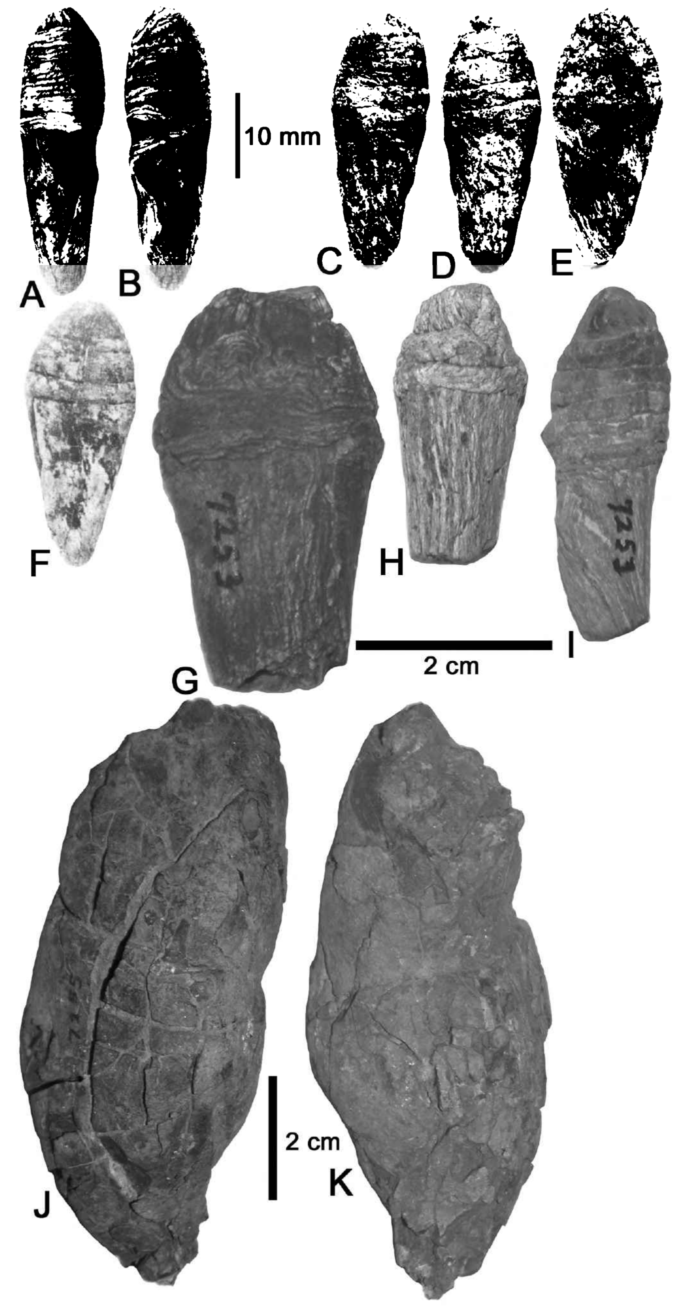

FIGURE 2. **A-B**, *Heteropolacopros texaniensis*, UMMP 7253 (partim), holotype, in lateral views from the Tecovas Formation, Crosby County, West Texas, USA. **C-D**, *Heteropolacopros texaniensis*, ISI P.58, in lateral views from the Maleri Formation, India. **E-F**, *Heteropolacopros texaniensis*, ISI P.51, in lateral views from the Maleri Formation, India. **G-I**, *Heteropolacopros texaniensis*, UMMP 7253 (partim), topotypes of *H. texaniensis* in lateral views from the Tecovas Formation, Crosby County, West Texas, USA. **J-K**, *Dicynodontocopros maximus*, UMMP 7255, holotype in lateral views from the Tecovas Formation, Crosby County, West Texas, USA. Note that Hunt et al. (1998, p. 228, 229) incorrectly listed the number of the holotype of *Dicynodontocopros maximus* as UMMP 7253 and UMMP 7285). **A-B**, after Hunt et al. (1998, fig. 2K-L); **C-F**, after Jain (1983, pl. 82, figs. 5-6, 10-11).

Liassocopros igen. nov.

Type species: *Liassocopros hawkinsi* isp. nov.

Included species: Known only from the type species.

Etymology: From the Liassic of England, which has yielded the first and most numerous specimens of this ichnogenus.

Distribution: Late Triassic-Late Cretaceous of Europe, India and North America.

Diagnosis: Coprolite that differs from most ichnotaxa in being heteropolar and that differs from *Heteropolacopros* and *Saurocopros* in being macrospiral (see definition below) in morphology.

Discussion: Neumayer (1904) introduced the terms "heteropolar" and "amphipolar" to describe the coiling of spiral coprolites, and these terms have been widely accepted (e.g., Williams, 1972; Duffin, 1979; Jain, 1983; Hunt et al., 1994, 1998). To provide a framework for description, we refer to the tightly coiled end of a heteropolar coprolite as anterior and the line of separation at the posterior end of the tightly-coiled segment as the spiral demarcation. The anterior portion (typically 30-40%) of heteropolar coprolites is tightly coiled, and the posterior fraction consists of one long coil with a wide lip (*sensu* Jain, 1983). Amphipolar coprolites (*sensu* Neumayer, 1904) exhibit an even distribution of coils (e.g., *Hyronocopros*: Hunt et al., 2005d, fig. 3).

Jain (1983) utilized the term "amphipolar" to refer to coprolites that have multiple spirals that extend for more than 50% of the length of the coprolite (e.g., Jain, 1983, fig. 2B) but that do not extend the whole length, so they are not truly amphipolar (*sensu* Neumayer, 1904). These coprolites are often reminiscent of trochospiral gastropods in overall morphology (e.g., Fig. 5A) and are, technically as well as etymologically, heteropolar in form. We introduce here the terms "microspiral" for the more typical heteropolar coprolites such as *Heteropolacopros* in which the markedly spiral portion constitutes less than 50% of the overall length, and "macrospiral" for the forms described by Jain (1983) in which the tightly spiral portion of the coprolite constitutes 50% or more of its length (Fig. 6). As with microspiral heteropolar coprolites, the largest diameter of the macrospiral *Liassocopros* is at the posterior end of the tightly coiled fraction of the coprolite. *Liassocopros* is broader relative to its height than are other heteropolar coprolites.

These coprolites are abundant in the Lower Jurassic of England (e.g., Buckland, 1829; Hawkins, 1834). The first coprolite described from North America derives from the Upper Cretaceous of New Jersey and probably also represents this ichnotaxon (DeKay, 1830, pl. 3, fig. 6).

Liassocopros hawkinsi isp. nov.

Holotype: BMNH R. 2107, coprolite (Fig. 5D-E).

Type locality: Lyme Regis, England.

Type horizon: Lower Lias.

Etymology: Named for Thomas Hawkins, who described specimens attributed here to this ichnogenus in 1834.

Distribution: As for the ichnogenus.

Referred specimens: Coprolites from the Lower Lias of Lyme Regis, England (Fig. 5A-C: Buckland, 1829, pl. 28, figs. 4, 7, pl. 29, fig. 1).

Diagnosis: As for genus.

Discussion: Hawkins (1834, pls. 27-28; 1840, pls. 29-30) illustrated a number of coprolites from the Lower Lias of Lyme Regis that, in 1840, were still listed as "in the Author's Collections, not yet transferred to the British Museum" (Hawkins, 1840, unnumbered page – list of plates). These specimens, which were collected by Mary Anning, were subsequently "transferred," and several are illustrated herein, including the holotype of *Liassocopros hawkinsi* (compare Fig. 5D and Hawkins, 1834, pl. 28; 1840, pl. 30) and a referred specimen of *Saurocopros bucklandi* (compare Fig. 4A and Hawkins, 1834, pl. 27; 1840, pl. 29 – note that the image is reversed in Hawkins' plates and that the specimen has lost part of its posterior extremity during the last 167 years!).

It is possible that two forms may be distinguishable within this ichnospecies. One form is trochospiral with an acute anterior tip (Fig. 5A) and the other has much more rounded anterior and posterior extremities (Fig. 5D).

Malericopros igen. nov.

Type species: *Malericopros matleyi* isp. nov.

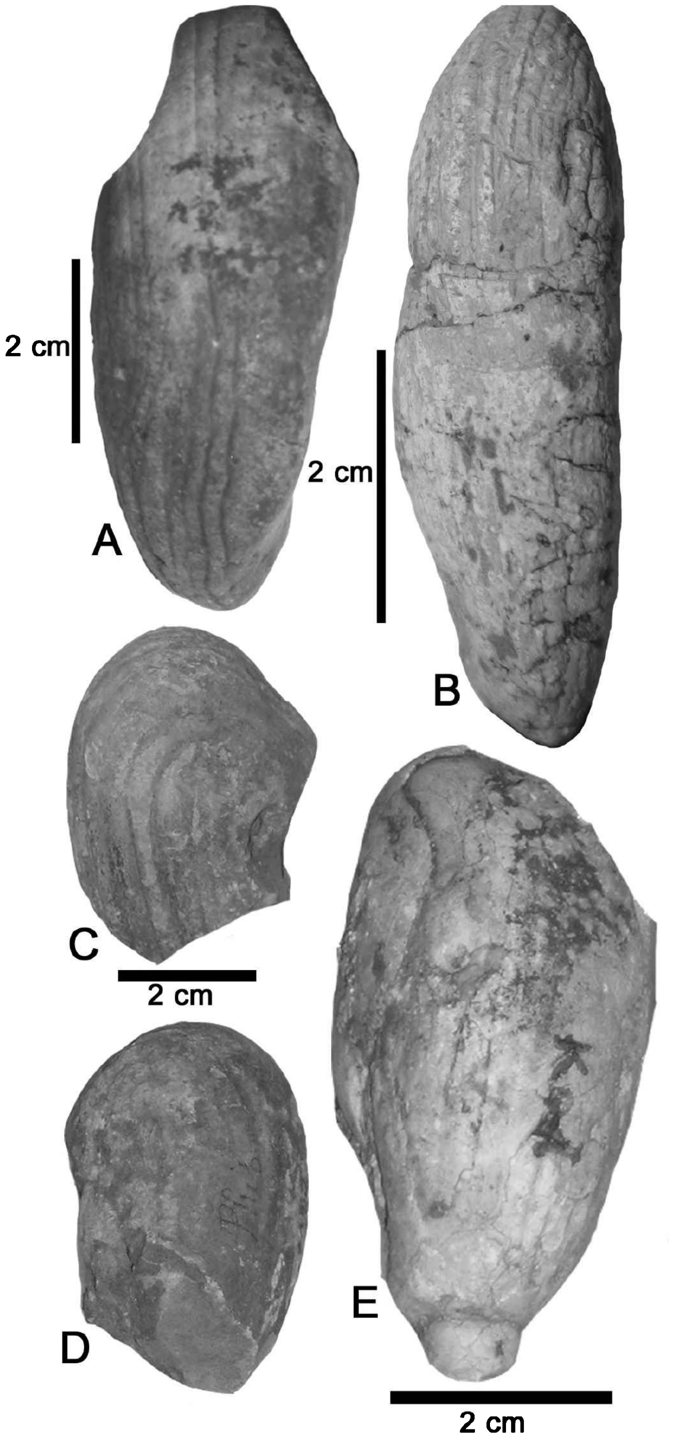

FIGURE 3. **A-B**, *Alococopros triassicus* igen. et isp. nov., UMMP 7253 (partim), in lateral views, from the Tecovas Formation, Crosby County, West Texas, USA. **C-E**, *Alococopros indicus* igen. et isp. nov., BMNH unnumbered (Matley collection), in lateral views from the Lameta Formation, India.

Included species: Known only from the type species.

Etymology: From the Maleri Formation, which yielded the holotype of the ichnogenus, and the Greek *kopros* for "dung."

Distribution: Late Triassic of India.

Diagnosis: Microspiral heteropolar coprolite that differs from *Saurocopros* and *Heteropolacopros* in that the maximum diameter is posterior to the spiral demarcation.

Discussion: In all other heteropolar coprolites (*Heteropolacopros*, *Saurocopros*, *Liassocopros*) the maximum diameter is near the posterior end of the tightly-coiled portion of the coprolite, and the portion of the coprolite posterior to the spiral demarcation tapers in lateral view.

Malericopros matleyi isp. nov.

Holotype: GSI K.42/419 (Fig. 5F; Matley, 1939a, pl. 33, fig. 1; Jain, 1983, pl. 82, fig. 9).

Type locality: Near Maleri, India.

Type horizon: ?Lower Maleri Formation (upper Carnian).

Etymology: Named for C. A. Matley, who first described Indian Triassic and Cretaceous coprolites in detail.

Distribution: As for the ichnogenus.

Referred specimens: ISI P.71 (Jain, 1983, pl. 81, fig. 10).

Diagnosis: As for the ichnogenus.

Discussion: Currently, this ichnospecies is only known from the Upper Cretaceous of India.

Falcatocopros igen. nov.

Type species: *Falcatocopros oxfordensis* isp. nov.

Included species: Known only from the type species.

Etymology: From the Latin *falcatus* for "crescent," referring to the thin, curved shape of this coprolite, and the Greek *kopros,* for "dung."

Distribution: Early-Late Jurassic of England.

Diagnosis: Differs from other coprolite ichnogenera in being long, narrow and arcuate in lateral view, rounded to sub-rounded in cross section with a width that gradually decreases from one end to the other.

Discussion: This ichnogenus is currently only documented from the Jurassic, but it may be present in Rhaetian ichnofaunas.

Falcatocopros oxfordensis isp. nov.

Holotype: BMNH R. 2094, coprolite (Fig. 5H).

Type locality: Near Peterborough, England.

Type horizon: Oxford Clay.

Etymology: Named for the Oxford Clay, which yielded the holotype.

Distribution: As for the ichnogenus.

Referred specimens: BMMNH R 2110, coprolite, Lower Lias, Lyme Regis, England (Fig. 5G; Hawkins, 1834, pl. 35; 1840, pl. 30).

Diagnosis: As for the ichnogenus.

Discussion: This highly distinctive ichnospecies is uncommon, probably, at least in part, the result of a taphonomic artifact related to its slender morphology.

TRIASSIC VERTEBRATE BIOCHRONOLOGY

Lucas and co-workers (Lucas and Hunt, 1993; Lucas, 1997, 1998, 1999; Lucas and Hancox, 2001; Lucas and Huber, 2003) have developed a global biochronological scheme for Triassic tetrapods. This scheme involves the definition of eight land-vertebrate faunachrons (lvfs) to encompass Triassic time. Subsequently, Lucas and others (Lucas, 1997, 1998; Hunt, 2001; Hunt et al., 2005a; Lucas et al., 2007) further refined this biochronology. In the following review of Triassic coprolites, we utilize this biochronology wherever possible.

TRIASSIC VERTEBRATE COPROLITE RECORD

Early Triassic

Northwood (1997, 2005) published the most thorough study of a Triassic coprolite ichnofauna, describing specimens from the Arcadia Formation in Queensland, northeastern Australia. Northwood (2005) recognized three main forms of coprolites (although obviously did not utilize the ichnotaxa erected herein): (1) amphipolar coprolites assignable to *Hyronocopros amphipola* (Hunt et al., 2005c); (2) longitudinally-striated coprolites representing *Alococopros triassicus*; and (3) indeterminate coprolites. *Hyronocopros amphipola* and *Alococopros triassicus*

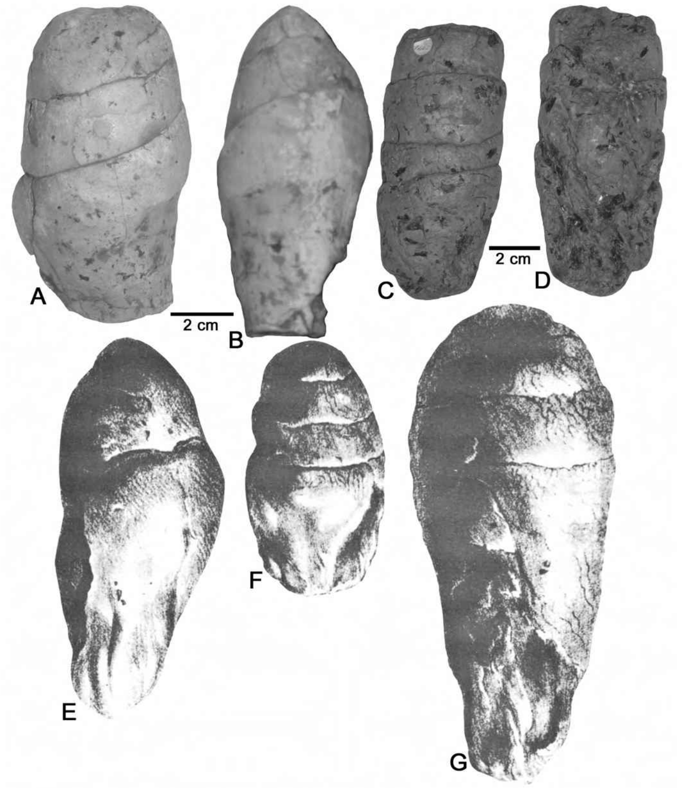

FIGURE 4. **A**-**G**, *Saurocopros bucklandi* igen. et isp. nov. from the Lower “Lias” of southwestern England. **A,** BMNH R 41285 from Charmouth in lateral view. **B,** BMNH R 2102, holotype of *Saurocopros bucklandi* igen. et isp. nov. from Lyme Regis. **C**-**D**, BMNH R 1402, one specimen in lateral view from Lyme Regis. Note the abundant inclusions and that one side is abraded. **E**-**G**, Specimens from the Buckland collection, presumably at the University of Oxford, three specimens in lateral view from Lyme Regis. **E**-**G**, after Buckland, 1829, pl. 28, figs.6, 7, 9, specimens rotated 180° from original publication, are to the same scale and **G**, is 10.7 cm long. **A**-**D**, Specimens collected by Mary Anning.

constitute less than 25% of the sample. She also noted that some of the broken coprolites may represent a heteropolar form based on the large number of whorls in cross section. The Acadia coprolites commonly contain inclusions (over 50%)that include two kinds of cyanobacteria, macrofloral specimens and rare invertebrate specimens (e.g., conchostracan valves, impressions of an insect wing, an insect head segment), scales, teeth, tooth plates and bones of actinopterygian and dipnoan fish and fragmentary amphibians (Northwood, 2005). Dipnoan remains were relatively more common in *Alococopros* specimens (Northwood, 2005).

Benz (1980) reported coprolites from the Moqui Member of the Moenkopi Formation in northern Arizona. However, Benz (1980) included the lower portion of the superjacent Holbrook Member (Middle Triassic) within the Moqui and there none of the coprolites that she described are actually from the Lower Triassic.

Middle Triassic

Ochev (1974) described coprolites from four Middle Triassic localities, one in Kazakhstan and three in Russia: (1) Mollo-Khara-Bala-Kantemir (Kazakhstan); (2) Karagachka; (3) Donguz I; and (4) Bukobay V. Ochev (1974) discriminated three types of coprolites that he compared with those described from the Upper Triassic of West Texas by Case (1922). The most easily identified are longitudinally striated forms assignable to *Alococopros triassicus* (Ochev, 1974, fig. 1e-f). These coprolites are described as being quite common.

Ochev (1974, fig. 1d) compares spirally-coiled specimens to those illustrated by Case (1922, fig. 33A-B) assigned to *Heteropolacopros texaniensis* by Hunt et al. (1998). However, the one specimen that is illustrated appears to be amphipolar in form, rather than heteropolar as described (Ochev, 1974, fig. 1d). These coprolites are noted as less common. The third form of coprolite is described as large (2-10 cm long), with a smooth surface and containing possible plant impressions. The only illustration of this type of coprolite is a cross section (Ochev, 1974, fig. 1c). Ochev (1974) compares this large form with specimens that Case collected and briefly described, but did not illustrate, some of which represent *Dicynodontocopros maximus* (Hunt et al., 1998, fig. 2A-B). Ochev (1974) listed the occurrence of his three types of coprolites as: (1) Mollo-Khara-Bala-Kantemir – all three forms; (2) Karagachka - *Alococopros triassicus* and small specimens of the large morphotype; and (3) Donguz I and Bukobay – spiral and large forms.

Rusconi (1947, figs. 1-4; 1949, figs. 2-6) described Triassic and Permian coprolites from the Mendoza area in Argentina. The large Triassic sample is dominated by spiral forms (e.g., Rusconi, 1949, figs. 2-4) but also includes small, cylindrical forms (Rusconi, 1949, fig. 5) and large, wide amorphous forms (Rusconi, 1949, fig. 6). The large forms are up to 120 mm in length and 58 mm in width. They are comparable in size to *Dicynodontocopros* but differ in having more rounded terminations and a more regular width. It is possible that these differences are taphonomic in origin.

The spiral coprolites appear to be dominantly heteropolar (e.g., Rusconi, 1949, fig. 4, first two coprolites in first row) although a few may be amphipolar (e.g., Rusconi, 1949, fig. 2, bottom left). They are relatively short and wide compared to the holotype of *Heteropolacopros* (Hunt et al., 1998, fig. 2K-L). The heteropolar coprolites are apparently mainly macrospiral. Some spiral forms include ganoid scales, possibly referable to the holostean fish *Pholidophorus*. We tentatively assign some of these coprolites to *Liassocopros* (e.g., Rusconi, 1949, fig, 2, center right) based on their macrospiral structure and width:length ratios.

Benz (1980) reported coprolites from the Holbrook Member of the Moenkopi Formation at Radar Mesa in northern Arizona. Benz (1980, pl. 7) illustrated some indeterminate coprolites and noted that coprolites were locally abundant. Many contain temnospondyl bones, including intercentra (Morales, 1987). Coprolites are present at other Moenkopi localities, but they have not been described. We, for example, have observed coprolites at several localities near the town of Holbrook. There is an unstudied coprolite collection at the MNA.

Fraas (1891) reported that spiral coprolites are common in the German Muschelkalk, and he attributed them to sharks. The Muschelkalk ranges in age from Anisian to Ladinian.

In India, the Yerrapilli Formation (early Middle Triassic) yields spherical, ovoid and elliptical coprolites (Chatterjee, 1967; Jain, 1983). These specimens are covered by desiccation cracks and differ in morphology from those from the Late Triassic of India (Jain, 1983).

Late Triassic

The majority of Triassic vertebrate coprolites in museum collections and mentioned or described in the literature are from the Late Triassic. Vertebrate coprolites are common and locally abundant in strata of the Upper Triassic Chinle Group of Lucas (1993) in western North America (Hunt and Lucas, 1989, 1993a, b; Murry, 1989; Murry and Long, 1989; Heckert et al., 2005; Hunt et al., 1998, 2005c).

The Newark Supergroup of eastern North America ranges in age from Middle Triassic-Early Jurassic. There has been more study of the vertebrate trace fossils of this stratigraphic unit, almost exclusively tracks, than any other over the last 150 years (Hitchcock, 1858; Lull, 1953; Olsen, 1988; Olsen et al., 1998). However, the coprolites of the Newark have been virtually ignored. The few references to coprolites in published works suggest that they are most common in the Carnian and Jurassic portions of the Newark (Olsen, 1988; Olsen et al., 1989, 2003, 2005a,b; Olsen and Flynn, 1989; Olsen and Huber, 1998; Olsen and Rainforth, 2002; Gilfillian and Olsen, 2000).

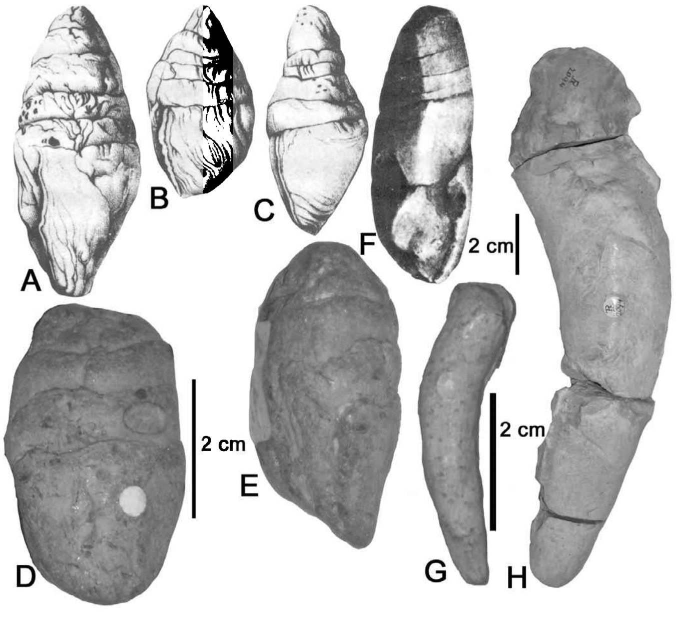

FIGURE 5. **A-E**, *Liassocopros hawkinsi* igen. et isp. nov. from the Lower "Lias" of Lyme Regis, England. **A-C**, Three specimens in the Buckland collection, presumably at the University of Oxford, in lateral view. **D-E**, BMNH R 2107, holotype of *Liassocopros hawkinsi* igen. et isp. nov., in lateral views. **F**, *Malericopros matleyi* igen. et isp. nov., GSI K. 42/419, holotype in lateral view, from the ?lower Maleri Formation, near Maleri, India. **G-H**, *Falcatocopros oxfordensis* igen. et isp. nov. from the Jurassic of England. **G,** BMNH R 2110, from the Lower "Lias" of Lyme Regis, in lateral view. **H,** BMNH R 2094 (Leeds collection), holotype of *Falcatocopros oxfordensis* igen. et isp. nov., from the Oxford Clay at Peterborough, in lateral view. **A-C**, after Buckland (1841, v. 2, pl. 15, p. 27-29); **F**, after Jain (1983, pl. 82, fig. 9).

Carnian

Vertebrate coprolites are common and locally abundant in the upper Carnian strata of the Upper Triassic Chinle Group of Lucas (1993) in western North America. The oldest coprolites are from the Otischalkian of West Texas. Elder (1978, 1987) described coprolites from the Colorado City Formation near Midland, noting that they are particularly abundant at Otis Chalk quarries 1 and 2. Elder (1978) explicitly discriminated the same three morphologies as Case (1922), notably heterospiral forms representing *Heteropolacopros texaniensis* (Elder, 1978, pl. 14, fig. 1a), longitudinally-striated forms assignable here to *Alococopros triassicus* (Elder, 1978, pl. 14, fig. 1b) and a third variable and indeterminate form (Elder, 1978, pl. 14, figs. 1c-d). The indeterminate forms, at least as illustrated, do not represent *Dicynodontocopros*. The NMMNH collection includes indeterminate coprolites from the Popo Agie Formation of Wyoming (Hunt et al., 1998).

Outcrops of younger Carnian (Adamanian) Chinle strata are much more widespread. Lipman and McLees (1940) described a new species of bacteria, *Thiobacillus coproliticus*, from a coprolite from Arizona, but did not describe the coprolite that yielded it. Case (1922) recognized three coprolite forms from the Tecovas Formation of West Texas that include the holotype and referred specimens of *Heteropolacopros texaniensis* (Case, 1922, fig. 33A-B; Hunt et al., 1998, fig. 2C-L). Case (1922, fig. 33C-D) also described specimens now referable to *Alococopros triassicus*. Coprolites of the third category described by Case (1922, p. 83) are large (5-18 cm long), smooth surfaced and lack vertebrate inclusions. One of these specimens in the UMMP collection is the holotype of *Dicynodontocopros maximus* (Hunt et al., 1998, fig. 2A-B). Other specimens in the collection are smaller and lack a distinct morphology.

Hunt et al. (1998) described *Dicynodontocopros maximus* from the Bluewater Creek Formation at the *Placerias* quarry near St. Johns, Arizona. Coprolites are locally abundant in the *Placerias* quarry (e.g., Camp and Welles, 1956; Kaye and Padian, 1994). Hunt et al. (1998) also noted that *Heteropolacopros texaniensis* occurs in the Blue Mesa Member of northeastern Arizona at Petrified Forest National Park (Hunt and Santucci, 1994). Coprolites, some of which contain fish scales, teeth and plant debris, are common in the Blue Mesa Member at the "Dying Grounds" locality in Petrified Forest National Park (e.g., Murry and Long, 1989; Heckert, 2001, 2004). Undescribed coprolites occur in the Blue Mesa and Painted Desert members of the Petrified Forest Formation at Petrified Forest National Park. Wahl et al. (1998) described evidence of coprophagy in the Blue Mesa Member of Petrified Forest National Park.

Ash (1978a, b) described a large number of coprolites from a lacustrine mudstone unit in the Bluewater Creek Formation in western New Mexico that he subsequently donated to the NMMNH. Ash (1978a) recognized three main forms: cylindrical, cigar-shaped with tapered ends (rare), and spiral. The spiral coprolites are microspiral and heteropolar; some clearly represent *Heteropolacopros texaniensis* (e.g., Ash, 1978a, fig. 2h) and at least one specimen represents *Alococopros triassicus* (Ash, 1978a, fig. 2g). Weber and Lawler (1978) analyzed the lipid content of a sample of these coprolites. Other localities in the Bluewater Creek Formation yield abundant coprolites (Heckert and Lucas, 2003).

Other Adamanian coprolites in New Mexico are known from the Los Esteros Member of the Santa Rosa Formation, Garita Creek Formation, lower Petrified Forest Formation and Salitral Formation (Hunt and Lucas, 1988, 1990, 1993; Hunt et al., 1989). Parrish (1999) reported abundant coprolites from the Monitor Butte Formation in southern Utah.

There are a few references to coprolites in the Carnian portion of the Newark Supergroup. Olsen (1988) noted abundant coprolites in the Cumnock Formation. The Lockatong Formation yields coprolites from several localities (Olsen et al., 1989; Olsen and Flynn, 1989; Olsen and Rainforth, 2002; Jenkins in Häntzschel et al., 1968; YPM PU specimens). Olsen and Huber (1998, table 1) noted coprolites in the Pekin Formation in North Carolina.

Burmeister et al. (2006, fig. 6) described coprolites from the Isalo "Group" (Isalo II beds) of Madagascar. These coprolites are 10-60 mm in length and nonspiral. About 5% of the coprolites contain fish bones and scales.

Carnian/Norian

Oldham (1859, pl. 15, figs. 11-12) first described coprolites from the Maleri Formation of India. The Maleri Formation is known to span the Carnian/Norian boundary and to contain both late Carnian and early-middle Norian faunas (Bandyopadhyay and Sengupta, 2006). Most fossils appear to derive from the upper Carnian portion of the Maleri Formation, but we are not certain of the exact age of any of the Maleri coprolites described by Oldham or many subsequent workers.

King (1881, p. 271-272) noted that, in the Maleri, the "commonest remains are coprolites which lie about the fields in large numbers, of all sizes and shapes, from the short cylindrical forms with tapering ends and spiral foldings up to large flat rudely discoid coils." Aiyengar (1937, p. 104) mentioned that "coprolites are abundant about a mile W.S.W. of Maleri" and he later reported (in Matley, 1939a, p. 531) that these coprolites are found in red clays in association with *Ceratodus* and two large reptile vertebrae "which have been described by F. von Huene as a new species of reptile" and so these coprolites thus presumably derive from the lower Maleri (Huene, 1940). Aiyengar (in Matley, 1939a) also notes that another locality about a mile southwest of Maleri yielded large reptile bones from a calcareous sandstone and lacked coprolites. Matley (1939a) described coprolites first described by Oldham (1859) and one that is inferred to have been collected by Aiyengar from the lower Maleri. Matley (1939a, pl. 33) described these coprolites as fusiform and spiral in structure and varying in length from 55 to about 80 mm long. These coprolites include the holotype of *Malericopros matleyi* (Matley, 1939a, pl. 33, figs.1a-b), possible specimens of *Heteropolacopros texaniensis*

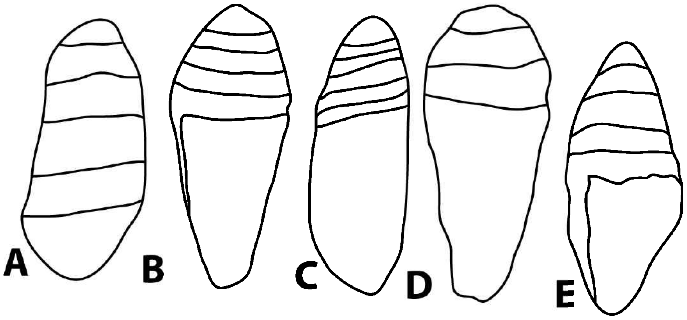

FIGURE 6. Principal morphotypes of amphipolar (**A**), microspiral heteropolar (**B-D**) and macrospiral heteropolar (**E**) coprolites. **A**, *Hyronocopros*. **B**, *Heteropolacopros*. **C**, *Malericopros*. **D**, *Saurocopros*. **E**, *Liassocopros*. Not to scale.

(Matley, 1939a, pl. 33, figs. 4), probable specimens of *Liassocopros hawkinsi* (Matley, 1939a, pl. 33, figs. 5a), a possible specimen of *Saurocopros bucklandi* (Matley, 1939a, pl. 33, fig. 8) and apparently amphipolar forms (Matley, 1939a, pl. 33, fig. 3).

Sohn and Chatterjee (1979) described ostracodes from coprolites from the lower Maleri Formation. These coprolites are described as a distinct type from near Achlapur village. They are large, with lengths from 7 to 10 cm and widths from 50 to 80 mm. Sohn and Chatterjee (pl. 1, fig. 4-5) only illustrated a fragment of the end of one coprolite. These coprolites were found near some rhynchosaur bones, so they are clearly from the lower (upper Carnian) portion of the Maleri.

Jain (1983) described a sample of coprolites from the lower Maleri Formation that are heteropolar, amphipolar and non-spiral. Some of these specimens pertain to *Heteropolacopros texaniensis* (Jain, 1983, pl. 82, figs. 1-6, 10-11), *Malericopros matleyi* (Jain, 1983, pl. 82, fig. 9) and *Liassocopros hawkinsi* (Jain, 1983, pl. 81, figs. 5, 10). Other fragmentary spiral coprolites are heteropolar (e.g., Jain, 1983, pl. 81, figs. 6, 8, 11-14) and possibly amphipolar (e.g., Jain, 1983, pl. 81, fig. 16).

Buckland (1841, p. 13) noted that "Professor Jaeger has recently discovered many Coprolites [sic] in the alum slate of Gaildorf [sic] in Wirtemberg [sic]; a formation which he considers to be in the lower region of that part of the new red sandstone formation which in Germany is called Keuper." The classic "Keuper," like the Maleri, is of both late Carnian and Norian age. Fraas (1891) reported common spiral coprolites from the "Keuper," which he attributed to sharks. Major European museum collections do not include "Keuper" coprolites (e.g., Natural History Museum, London and Museum für Naturkunde, Stuttgart).

DeBlieux et al. (2006, figs. 9A-C) illustrated numerous coprolites from the Petrified Forest Formation of Zion National Park in southern Utah. These specimens could be of either Carnian or Norian age.

Norian

The Bull Canyon Formation of east-central New Mexico yields large coprofaunas. Lucas et al. (1985) described three morphologies of coprolites: (1) longitudinally furrowed specimens that represent *Alococopros triassicus* (Lucas et al., 1985, fig. 7M-R); (2) small, rod-like to oval morphology (> 90% of sample) (Lucas et al., 1985, fig. 7A-L); and (3) large, irregularly shaped forms with numerous inclusions (fish scales, bone fragments) (Lucas et al., 1985, fig. 7S-U). This sample (NMMNH locality 110) is from the younger Lucianoan sub-lvf of the Revueltian. The NMMNH also contains a large sample from the older Barrancan time interval (NMMNH locality 1) and numerous isolated specimens from various Barrancan loaclities.

Coprolites are present at other Revueltian Chinle localities in New Mexico, including the upper Petrified Forest Formation in the San Ysidro area (Hunt and Lucas, 1990) and Chama Basin (Hunt and Lucas, 1993), Trujillo Formation (Hunt, 1991) and Correo Sandstone Member of Petrified Forest Formation at Mesa Gigante and the Hagan Basin (Hunt and Lucas, 1993b).

In Arizona, Revueltian coprolites occur in the Painted Desert Member of the Petrified Forest Formation at Petrified Forest National Park (Hunt and Santucci, 1994). Coprolites are also common in the Owl Rock Formation at Ward Terrace (Kirby, 1989).

Late Norian/Rhaetian

Coprolites are locally common in Apachean strata of the Chinle Group, notably in New Mexico and Utah. Hunt et al. (1993) noted that coprolites were common in the Bell Springs Formation in northeastern Utah. Coprolites occur on the main track bed at the Shay Canyon tracksite (Rock Point Formation) in southeastern Utah (Lockley, 1986; Lockley and Hunt, 1995, fig. 3.8).

In New Mexico, coprolites are locally abundant in the Redonda Formation of east-central New Mexico. The largest concentration is at the Gregory quarry (NMMNH locality 485) in Apache Canyon. This large sample lacks *Heteropolacopros texaniensis* and *Alococopros triassicus*.

One of the most interesting occurrences of coprolites in the Triassic occurs at the *Coelophysis* quarry in north-central New Mexico. Coprolites occur associated with skeletons of *Coelophysis* (Rinehart et al., 2005a,b). These coprolites occur in the vicinity of the cloaca in more than one skeleton and include bones assignable to *Coelophysis*, which indicates cannibalism in this early dinosaur (Rinehart et al., 2005a, b *contra* Nesbitt et al., 2006).

Rhaetian

Buckland (1829) first recognized coprolites from the Rhaetian Westbury Formation (Penarth Group) of England (Swift and Duffin, 1999). Coprolites are common in the bone beds of the Westbury Formation (Buckland, 1829; Duffin, 1979; Storrs, 1994; Martill, 1999; Swift and Duffin, 1999). Duffin (1979; Swift and Duffin, 1999) recognized four broad morphological types of coprolites. However, two of these categories included both amphipolar and heteropolar forms, which we regard as fundamentally distinct morphologies representative of different ichnotaxa (e.g., Hunt et al., 1998, 2005c). Therefore, we recognize six categories:

1. Large (up to 80 mm), usually brown, often tapered with well-defined amphipolar structure. Undigested vertebrate remains include fish scales (often tangential or normal to spiral folds) and crustacean remains (*Tropifer laevis*, possible isopods). Discrete food "boli" are discernable in thin section. Swift and Duffin (1999) interpreted these specimens to represent sharks, possibly myriacanthid holocephalans and palaeoniscid chondrostreans (coprolites with vertebrate inclusions) or dipnoans (coprolites with arthropod inclusions).
2. Large (up to 80 mm), usually brown, often tapered with well-defined heteropolar structure. Swift and Duffin (1999, fig. 32A) described coprolites of this general form as amphipolar, but the specimen that they illustrate is clearly heteropolar in morphology. Undigested vertebrate remains include fish scales (often tangential or normal to spiral folds) and crustacean remains (*Tropifer laevis*, possible isopods). Discrete food "boli" are discernable in thin section. Swift and Duffin (1999) interpreted these specimens to represent sharks, possibly myriacanthid holocephalans and palaeoniscid chondrostreans (coprolites with vertebrate inclusions) or dipnoans (coprolites with arthropod inclusions).
3. Elongate (~30 mm long) with amphipolar coiling and no visible vertebrate and invertebrate inclusions (Swift and Duffin, 1999, fig. 32B). Swift and Duffin (1999) attributed these coprolites to *Ceratodus* or myriacanthid holocephalans.
4. Elongate (~30 mm long) with heteropolar coiling and no visible vertebrate and invertebrate inclusions. Swift and Duffin (1999) attributed these coprolites to *Ceratodus* or myriacanthid holocephalans.
5. Small (maximum 30 mm long), capsule-shaped, lacking spiral form or inclusions. They are often black and shiny due to polishing and abrasion during post-fossilization transport. These coprolites are usually homogeneous in thin section with disseminated pyrite (Swift and Duffin, 1999, fig. 32C).

6. Small (up to 30 mm long) flattened, shiny forms. They include undigested scales and teeth, but no internal spiraling (Swift and Duffin, 1999, fig. 32D). Swift and Duffin (1999) attributed these coprolites possibly to small reptiles. Duffin (1979) notes that types 5 and 6 are by far the most common.

Some Type 2 (notation above, not that of Duffin or Swift and Duffin) coprolites pertain to *Liassocopros hawkinsi* (BCM 4891; Duffin, 1979, pl. 21, fig. 1; Swift and Duffin, 1999, fig. 32A). Some specimens of Type 4 may represent *Saurocopros bucklandi* (NMW G2066; Duffin, 1979, pl. 21, fig. 3; Swift and Duffin, 1999, fig. 32B).

Coprolites also occur in other Rhaetic bone beds in western Europe although none have been described.

TRIASSIC COPROLITE BIOSTRATIGRAPHY

Coprolites are potentially of biochronological utility (e.g., Hunt, 1992; Hunt et al., 1998, 2005a). Trace fossils generally represent higher level taxonomic groups of body fossils. Thus, track ichnogenera are commonly only equivalent to the "family" level of body fossils (Lucas, 2007). Coprolites probably represent, in most cases, even higher level taxonomic levels ("order" or above). However, the stratigraphic distribution of coprolites obviously mirrors the stratigraphic ranges of the animals that produced them. Also, given also that some localities/stratigraphic units produce numerous coprolites and no body fossils, there is a potential to utilize coprolites in biochronology. We can presently recognize the following ranges for ichnotaxa that are present in the Triassic:

Permian: *Hyronocopros amphipolar*, *Heteropolacopros texaniensis*

Early Triassic: *Hyronocopros amphipolar*, *Alococopros triassicus*.

Middle Triassic: *Alococopros triassicus*, *?Liassocopros* isp.

Late Triassic: *Heteropolacopros texaniensis*, *Alococopros triassicus*.

Dicynodontocopros maximus, *Malericopros matleyi*, *Liassocopros hawkinsi*, *Saurocopros bucklandi*.

Early Jurassic: *Liassocopros hawkinsi*, *Saurocopros bucklandi*.

Alococopros triassicus is a good index fossil for the Triassic because it is easily identifiable, widespread and relatively common. The characteristic Early Permian *Hyronocopros amphipolar* also appears to be restricted to the Early Triassic. Even though certain Middle Triassic specimens could represent this ichnotaxon, it is certainly absent in the Late Triassic.

Dicynodontocopros maximus and Malericopros matleyi are both restricted to the Late Triassic (upper Carnian), but their distribution is limited. The ubiquitous Early Jurassic *Liassocopros hawkinsi* and *Saurocopros bucklandi* have their first appearance in the Late Triassic. *Heteropolacopros texaniensis* is not currently known from strata younger than Carnian.

There appears to be a change in coprofaunas near the end of the Norian. Apachean (upper Norian/Rhaetian) and Rhaetian assemblages lack the long-ranging *Alococopros triassicus* and/or include good examples of the characteristic Jurassic *Liassocopros hawkinsi* and *Saurocopros bucklandi*. This change is apparent in both the nonmarine Chinle Group and the mixed marine and nonmarine Westbury Formation.

TRIASSIC COPROLITES AND ICHNOFACIES

Hunt et al. (1994, 1998) recognized "coprofacies" in the Upper Triassic of western North America. Hunt and Lucas (2007) noted that these should be referred to as ichnocoenoses because of their relatively limited distribution in space and time.

Hunt et al. (1994, 1998) distinguished three ichnocoenoses: (1) *Dicynodontocopros* ichnocoenosis, in which coprolites occur in gray to black mudstones that formed in alternating wet and dry conditions, including periods of standing water, and are associated with aquatic vertebrate microfossils; (2) *Heteropolacopros* ichnocoenosis, which occurs in fluvial redbeds; and (3) ovoid, structureless coprolite ichnocoenosis, which occurs in highly carbonaceous strata that formed in ponds. There is a third obvious Triassic ichnocoenosis that yields significant specimens of spiral coprolites, notably *Liassocopros hawkinsi*, and occurs in shallow marine strata, with the exemplar being the Westbury Formation.

Are any of these ichnocoenoses pervasive enough, spatially and temporally, to be considered to be ichnofacies? Arguably, at least two represent widely distributed ichnofacies. The *Liassocopros* ichnofacies is characterized by a prevalence of spiraled coprolites that occur in shallow marine strata. This ichnofacies is represented at least in the Pennsylvanian (Zangerl and Richardson, 1963), Early Permian (Williams, 1972) and Early Jurassic (Buckland, 1829) as well as the Upper Triassic.

The *Heteropolacopros* ichnofacies is characterized by the presence of microspiral heteropolar coprolites that occur in fluvial redbeds. This ichnofacies occurs at least from the Early Permian (Hunt et al., 2005b, c) until the Late Triassic.

It seems reasonable that a *Dicynodontocopros* ichnofacies, which contains large herbivore coprolites, might characterize swampy environments and that an ichnofacies, which we could term the *Alococopros* ichnofacies, should characterize ponds. However, we do not have the data to support these hypotheses.

PROSPECTUS FOR FUTURE WORK

In the last few years we have made a concerted effort to describe and document Permo-Triassic coprolites (e.g., Hunt et al., 1994, 1998, 2005a, b, c; Hunt and Lucas, 2005a, b, c). This work is based on the extensive samples that we have collected and the very limited collections in other museums. We have four basic purposes in these works:

1. To raise awareness of the general abundance of the vertebrate coprolite fossil record and its potential importance.
2. To demonstrate that distinct morphologies can be discriminated, described and of utility.
3. To illustrate that vertebrate coprolites have importance in biochronology.
4. To suggest that coprolites have utility in ichnofacies studies.

Despite these lofty goals, we realize that vertebrate coprolites have been grossly undersampled and that paleoscatology is in a protean stage. We hope that other workers will be inspired to collect and describe more vertebrate coprolites and to further this still nascent sub-discipline of paleontology.

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APPENDIX

List of Triassic coprolite specimens in the Geoscience Collection of the New Mexico Museum of Natural History and Science, Albuquerque.

Specimen	Description	Period	Age	Formation	Member
3024	trace fossil-(3) coprolites	Triassic	Carnian	Santa Rosa Fm	Los Esteros Mbr
3660	trace fossil-(9) coprolites	Triassic	Carnian	Bluewater Creek Fm	Upper Mbr
3682	trace fossil-(1) coprolite	Triassic	Carnian	Garita Creek Fm	
3683	trace fossil-(1) coprolite	Triassic	Carnian	Garita Creek Fm	
3684	trace fossil-(1) coprolite	Triassic	Carnian	Garita Creek Fm	
3685	trace fossil-(24) coprolites	Triassic	Carnian	Garita Creek Fm	
3686	trace fossil-(1) coprolite	Triassic	Carnian	Garita Creek Fm	
3687	trace fossil-(5) coprolites	Triassic	Carnian	Garita Creek Fm	
4101	trace fossil-(1) coprolite	Triassic	Norian	Bull Canyon Fm	
4111	trace fossil-(42) coprolites	Triassic	Norian	Bull Canyon Fm	
4122	trace fossil-(2) coprolites	Triassic	Norian	Bull Canyon Fm	
4147	trace fossil-(2) coprolites	Triassic	Norian	Bull Canyon Fm	
4165	trace fossil-(1) coprolite	Triassic	Norian	Bull Canyon Fm	
4181	trace fossil-(1) coprolite	Triassic	Norian	Bull Canyon Fm	
4190	trace fossil-(58) coprolites	Triassic	Norian	Bull Canyon Fm	
4197	trace fossil-(83) coprolites	Triassic	Norian	Bull Canyon Fm	
4199	trace fossil-(1) coprolite	Triassic	Norian	Bull Canyon Fm	
4202	trace fossil-(3) coprolites	Triassic	Norian	Bull Canyon Fm	
4209	trace fossil-(14) coprolites	Triassic	Norian	Bull Canyon Fm	
4223	trace fossil-(15) coprolites	Triassic	Norian	Bull Canyon Fm	
4227	trace fossil-(104) coprolites	Triassic	Norian	Bull Canyon Fm	
4234	trace fossil-(125) coprolites	Triassic	Norian	Bull Canyon Fm	
4240	trace fossil-(3) coprolites	Triassic	Norian	Bull Canyon Fm	
4245	trace fossil-(2) coprolites	Triassic	Norian	Bull Canyon Fm	
4249	trace fossil-(31) coprolites	Triassic	Norian	Bull Canyon Fm	

Specimen	Description	Period	Age	Formation	Member
4252	trace fossil- (57) coprolites	Triassic	Norian	Bull Canyon Fm	
4263	trace fossil- (1) coprolite	Triassic	Norian	Bull Canyon Fm	
4265	trace fossil- (1) coprolite	Triassic	Norian	Bull Canyon Fm	
4270	trace fossil- (1) coprolite	Triassic	Norian	Bull Canyon Fm	
4272	trace fossil- (2) coprolites	Triassic	Norian	Bull Canyon Fm	
4292	trace fossil- (104) coprolites	Triassic	Norian	Bull Canyon Fm	
4294	trace fossil- (1) coprolite	Triassic	Norian	Bull Canyon Fm	
4302	trace fossil- coprolites	Triassic	Norian	Bull Canyon Fm	
4328	trace fossil- (9) coprolites	Triassic	Norian	Bull Canyon Fm	
4332	trace fossil- (4) coprolites	Triassic	Norian	Bull Canyon Fm	
4359	trace fossil- (1) coprolite	Triassic	Norian	Bull Canyon Fm	
4364	trace fossil- (17) coprolites	Triassic	Norian	Bull Canyon Fm	
4366	trace fossil- (5) coprolites	Triassic	Norian	Bull Canyon Fm	
4370	trace fossil- (1) coprolite	Triassic	Norian	Bull Canyon Fm	
4379	trace fossil- (1) coprolite	Triassic	Norian	Bull Canyon Fm	
4381	trace fossil- (2) coprolites	Triassic	Norian	Bull Canyon Fm	
4384	trace fossil- (1) coprolite	Triassic	Norian	Bull Canyon Fm	
4385	trace fossil- (1) coprolite	Triassic	Norian	Bull Canyon Fm	
4386	trace fossil- (1) coprolite	Triassic	Norian	Bull Canyon Fm	
4393	trace fossil- (1) coprolite	Triassic	Norian	Bull Canyon Fm	
4405	trace fossil- (23) coprolites	Triassic	Norian	Bull Canyon Fm	
4406	trace fossil- (1) coprolite	Triassic	Carnian	Santa Rosa Fm	Los Esteros Mbr
4412	trace fossil- (197) coprolites	Triassic	Norian	Bull Canyon Fm	
4414	trace fossil- (1) coprolite	Triassic	Carnian	Santa Rosa Fm	Los Esteros Mbr
4417	trace fossil- (1) coprolite	Triassic	Norian	Bull Canyon Fm	
4425	trace fossil- (6) coprolites	Triassic	Norian	Bull Canyon Fm	
4435	trace fossil- (1) coprolite	Triassic	Norian	Bull Canyon Fm	
4436	trace fossil- (1) coprolite (see remarks)	Triassic	Norian	Bull Canyon Fm	
4437	trace fossil- (1) coprolite	Triassic	Norian	Bull Canyon Fm	
4438	trace fossil- (1) coprolite	Triassic	Norian	Bull Canyon Fm	
4444	trace fossil- (5) coprolites	Triassic	Norian	Bull Canyon Fm	
4449	trace fossil- (2) coprolites	Triassic	Norian	Bull Canyon Fm	
4460	trace fossil- (2) coprolites	Triassic	Norian	Bull Canyon Fm	
4481	trace fossil- (5) coprolites	Triassic	Norian	Bull Canyon Fm	
4489	trace fossil- (1) coprolite	Triassic	Norian	Bull Canyon Fm	
4490	trace fossil- (9) coprolites	Triassic	Norian	Bull Canyon Fm	
4496	trace fossil- (2) coprolites	Triassic	Norian	Bull Canyon Fm	
4512	trace fossil- (1) coprolite	Triassic	Norian	Bull Canyon Fm	
4520	trace fossil- (1) coprolite	Triassic	Norian	Bull Canyon Fm	
4522	trace fossil- (1) coprolite	Triassic	Norian	Bull Canyon Fm	
4534	trace fossil- (2) coprolites	Triassic	Carnian	Santa Rosa Fm	Los Esteros Mbr
4536	trace fossil- (7) coprolites	Triassic	Norian	Bull Canyon Fm	
4542	trace fossil- (1) coprolite	Triassic	Norian	Bull Canyon Fm	
4552	trace fossil- (14) coprolites	Triassic	Norian	Bull Canyon Fm	
4557	trace fossil- (10) coprolites	Triassic	Norian	Bull Canyon Fm	

Specimen	Description	Period	Age	Formation	Member
4560	trace fossil- (31) coprolites	Triassic	Norian	Bull Canyon Fm	
4568	trace fossil- (8) coprolites	Triassic	Norian	Bull Canyon Fm	
4583	trace fossil- (1) coprolite	Triassic	Norian	Bull Canyon Fm	
4591	trace fossil- (21) coprolites	Triassic	Norian	Bull Canyon Fm	
4592	trace fossil- (100+) coprolites	Triassic	Norian	Bull Canyon Fm	
4597	trace fossil- (1) coprolite	Triassic	Norian	Bull Canyon Fm	
4599	trace fossil- (5) coprolites	Triassic	Norian	Bull Canyon Fm	
4614	trace fossil- (1) coprolite	Triassic	Norian	Bull Canyon Fm	
4721	trace fossil- (3) coprolites	Triassic	Norian	Bull Canyon Fm	
4723	trace fossil- (1) coprolite	Triassic	Norian	Bull Canyon Fm	
4727	trace fossil- (1) coprolite	Triassic	Norian	Bull Canyon Fm	
4737	trace fossil- (3) coprolites	Triassic	Rhaetian	Redonda Fm	
4740	trace fossil- (1) coprolite	Triassic	Carnian	Petrified Forest Fm	
4750	trace fossil- (1) coprolite	Triassic	Norian	Bull Canyon Fm	
4803	trace fossil- (1) coprolite	Triassic	Norian	Bull Canyon Fm	
4867	trace fossil- (1) coprolite?	Triassic	Norian	Bull Canyon Fm	
4918	trace fossil- (1) coprolite	Triassic	Norian	Bull Canyon Fm	
4925	trace fossil- (3) coprolites	Triassic	Norian	Bull Canyon Fm	
4933	trace fossil- (1) coprolites	Triassic	Norian	Bull Canyon Fm	
4936	trace fossil- (9) coprolites	Triassic	Norian	Bull Canyon Fm	
4939	trace fossil- (7) coprolites	Triassic	Norian	Bull Canyon Fm	
4947	trace fossil- (17) coprolites	Triassic	Norian	Bull Canyon Fm	

Specimen	Description	Period	Age	Formation	Member
4962	trace fossil- (4) coprolites	Triassic	Carnian	Garita Creek Fm	
7116	(26) coprolites	Triassic	Rhaetian	Redonda Fm	
7135	trace fossil- (1) coprolite	Triassic	Carnian	Petrified Forest Fm	Blue Mesa Mbr
11031	trace fossil- (9) coprolites	Triassic	Carnian	Petrified Forest Fm	
11034	trace fossil- (3) coprolites	Triassic	Carnian	Petrified Forest Fm	
11035	trace fossil- (10) coprolites	Triassic	Carnian	Poleo Fm	
11041	trace fossil- (2) coprolites	Triassic	Carnian	Petrified Forest Fm	Mesa Montosa Mbr
11043	trace fossil- (1) coprolite	Triassic	Carnian	Salitral Fm	
11046	trace fossil- (2) coprolites	Triassic	Carnian	Petrified Forest Fm	
11050	trace fossil- (1) coprolite	Triassic	Norian	Petrified Forest Fm	Mesa Montosa Mbr
14389	trace fossil- (1) coprolite	Triassic	Norian	Petrified Forest Fm	Painted Desert Mbr
14397	trace fossil- (5) coprolites	Triassic	Norian	Petrified Forest Fm	
16538	trace fossil- (2) coprolites	Triassic	Norian	Bull Canyon Fm	
16539	trace fossil- (1) coprolite	Triassic	Norian	Bull Canyon Fm	
16540	trace fossil- (13) coprolites	Triassic	Norian	Bull Canyon Fm	
16541	trace fossil- (25) coprolites	Triassic	Norian	Bull Canyon Fm	
16542	trace fossil- (8) coprolites	Triassic	Norian	Bull Canyon Fm	
16544	trace fossil- (1000+) coprolites	Triassic	Norian	Bull Canyon Fm	
16554	trace fossil- (4) coprolites in concretions	Triassic	Norian	Bull Canyon Fm	
16615	trace fossil- (2) coprolites	Triassic	Norian	Bull Canyon Fm	
16616	trace fossil- (3) coprolites	Triassic	Norian	Bull Canyon Fm	
16617	trace fossil- (9) coprolites	Triassic	Norian	Bull Canyon Fm	

Specimen	Description	Period	Age	Formation	Member
16631	trace fossil-(6) coprolites	Triassic	Norian	Bull Canyon Fm	
16633	trace fossil-(5) coprolites	Triassic	Norian	Bull Canyon Fm	
16721	trace fossil-(2) coprolites	Triassic	Norian	Petrified Forest Fm	Painted Desert Mbr
16814	trace fossil-(75) coprolites	Triassic	Norian	Bull Canyon Fm	
16824	trace fossil-(1) coprolite	Triassic	Norian	Bull Canyon Fm	
16835	trace fossil-(1) coprolite	Triassic	Norian	Bull Canyon Fm	
16842	trace fossil-(1) coprolite	Triassic	Norian	Bull Canyon Fm	
16855	trace fossil-(2) coprolites	Triassic	Norian	Bull Canyon Fm	
16866	trace fossil-(11) coprolites	Triassic	Norian	Bull Canyon Fm	
16883	trace fossil-(1) coprolite	Triassic	Norian	Bull Canyon Fm	
16899	trace fossil-(2) coprolites	Triassic	Norian	Bull Canyon Fm	
16905	trace fossil-(1) coprolite	Triassic	Norian	Bull Canyon Fm	
16994	trace fossil-(6) coprolites	Triassic	Rhaetian	Redonda Fm	
17003	trace fossil-(37) coprolites	Triassic	Rhaetian	Redonda Fm	
17034	trace fossil-(198) coprolites	Triassic	Rhaetian	Redonda Fm	
17041	trace fossil-(2) coprolites	Triassic	Rhaetian	Redonda Fm	
17049	trace fossil-(10) coprolites	Triassic	Rhaetian	Redonda Fm	
17078	trace fossil-(6) coprolites	Triassic	Rhaetian	Redonda Fm	
17119	trace fossil-(4) coprolites	Triassic	Norian	Bull Canyon Fm	
17122	trace fossil-(1) coprolite	Triassic	Norian	Bull Canyon Fm	
17144	trace fossil-(25) coprolites	Triassic	Norian	Bull Canyon Fm	
17146	trace fossil-(4) coprolites	Triassic	Norian	Bull Canyon Fm	

Specimen	Description	Period	Age	Formation	Member
17159	trace fossil-(3) coprolites	Triassic	Norian	Bull Canyon Fm	
17169	trace fossil-(3) coprolites	Triassic	Norian	Bull Canyon Fm	
17189	trace fossil-(4) coprolites	Triassic	Norian	Bull Canyon Fm	
17200	trace fossil-(2) coprolites	Triassic	Norian	Bull Canyon Fm	
17201	trace fossil-(1) coprolite	Triassic	Norian	Bull Canyon Fm	
17202	trace fossil-(5) coprolite fragments	Triassic	Norian	Bull Canyon Fm	
17205	trace fossil-(13) coprolites	Triassic	Norian	Bull Canyon Fm	
17240	trace fossil-(2) coprolites	Triassic	Norian	Bull Canyon Fm	
17246	trace fossil-(2) coprolites	Triassic	Norian	Bull Canyon Fm	
17276	trace fossil-(1) coprolite	Triassic	Norian	Bull Canyon Fm	
17293	trace fossil-(1) coprolite	Triassic	Norian	Bull Canyon Fm	
17304	trace fossil-(17) coprolites	Triassic	Norian	Bull Canyon Fm	
17336	trace fossil-(107) coprolites	Triassic	Norian	Bull Canyon Fm	
17339	trace fossil-(2) coprolites	Triassic	Norian	Bull Canyon Fm	
17347	trace fossil-(13) coprolites	Triassic	Norian	Bull Canyon Fm	
17364	trace fossil-(22) coprolites	Triassic	Norian	Bull Canyon Fm	
17389	trace fossil-(1) coprolites	Triassic	Norian	Bull Canyon Fm	
17406	trace fossil-(1) coprolite	Triassic	Norian	Trujillo Fm	
17442	trace fossil-(192) coprolites	Triassic	Norian	Bull Canyon Fm	
17446	trace fossil-(9) coprolites	Triassic	Norian	Bull Canyon Fm	
17449	trace fossil-(1) coprolite	Triassic	Norian	Bull Canyon Fm	
17465	trace fossil-(2) coprolites	Triassic	Norian	Bull Canyon Fm	

Specimen	Description	Period	Age	Formation	Member
17478	trace fossil-(12) coprolites	Triassic	Norian	Bull Canyon Fm	
17495	trace fossil-(1) coprolite	Triassic	Norian	Bull Canyon Fm	
17514	trace fossil-(1) coprolite	Triassic	Carnian	Garita Creek Fm	
17541	trace fossil-(54) coprolites	Triassic	Carnian	Garita Creek Fm	
17544	trace fossil-(19) coprolites	Triassic	Carnian	Garita Creek Fm	
17545	trace fossil-(9) coprolites	Triassic	Carnian	Garita Creek Fm	
17555	trace fossil-(1) coprolite	Triassic	Carnian	Garita Creek Fm	
17557	trace fossil-(6) coprolites	Triassic	Carnian	Garita Creek Fm	
17559	trace fossil-(5) coprolites	Triassic	Carnian	Garita Creek Fm	
17560	trace fossil-(3) coprolites	Triassic	Carnian	Garita Creek Fm	
17561	trace fossil-(6) coprolites	Triassic	Carnian	Garita Creek Fm	
17565	trace fossil-(1) coprolite	Triassic	Carnian	Garita Creek Fm	
17575	trace fossil-(1) coprolite	Triassic	Carnian	Garita Creek Fm	
17576	trace fossil-(1) coprolite	Triassic	Carnian	Garita Creek Fm	
17577	trace fossil-(1) coprolite	Triassic	Carnian	Garita Creek Fm	
17578	trace fossil-(1) coprolite	Triassic	Carnian	Garita Creek Fm	
17580	trace fossil-(2) coprolites	Triassic	Carnian	Garita Creek Fm	
17585	trace fossil-(1) coprolite	Triassic	Carnian	Garita Creek Fm	
17600	trace fossil-(1) coprolite	Triassic	Norian	Trujillo Fm	
17606	trace fossil-(7) coprolites	Triassic	Carnian	Garita Creek Fm	
17609	trace fossil-(1) coprolite	Triassic	Carnian	Garita Creek Fm	
17613	trace fossil-(1) coprolite	Triassic	Carnian	Garita Creek Fm	

Specimen	Description	Period	Age	Formation	Member
17618	trace fossil-(91) coprolites	Triassic	Carnian	Garita Creek Fm	
17636	trace fossil-(53) coprolites	Triassic	Carnian	Dockum Fm	Colorado City Mbr
17644	trace fossil-(74) coprolites	Triassic	Carnian	Petrified Forest Fm	Painted Desert/Correo
17645	trace fossil-(15) coprolites	Triassic	Carnian	Petrified Forest Fm	Painted Desert/Correo
17650	trace fossil-(12) coprolites	Triassic	Carnian	Petrified Forest	Painted Desert/Correo
17657	trace fossil-(3) coprolites	Triassic	Carnian	Petrified Forest	Painted Desert/Correo
17667	trace fossil-(9) coprolites	Triassic	Carnian	Petrified Forest	Painted Desert/Correo
17670	trace fossil-(101) coprolites	Triassic	Carnian	Petrified Forest	Painted Desert/Correo
17700	trace fossil-coprolites in (2) matrix slabs	Triassic	Rhaetian	Sloan Canyon Fm	
17735	trace fossil-(6) coprolites	Triassic	Anisian	Moenkopi Fm	Anton Chico Mbr
17741	trace fossil-(2) coprolites	Triassic	Carnian	Bluewater Creek Fm	
17758	trace fossil-(1) coprolite	Triassic	Carnian	Bluewater Creek Fm	Upper Mbr
17759	trace fossil-(1) coprolite	Triassic	Carnian	Petrified Forest Fm	
17789	trace fossil-(91) coprolites & fragments	Triassic	Carnian	Popo Agie Fm	
17848	trace fossil-(1) coprolite	Triassic	Carnian	Bluewater Creek Fm	Lower
17861	trace fossil-(1) coprolite	Triassic	Carnian	Garita Creek Fm	
17885	trace fossil-(11) coprolites	Triassic	Carnian	Garita Creek Fm	
17889	trace fossil-(3) coprolites	Triassic	Carnian	Santa Rosa Fm	Los Esteros Mbr
17908	trace fossil-(1) coprolite	Triassic	Carnian	Santa Rosa Fm	Los Esteros Mbr
17915	trace fossil-(2) coprolites	Triassic	Carnian	Santa Rosa Fm	Los Esteros Mbr
17942	trace fossil-(17) coprolites	Triassic	Carnian	Santa Rosa Fm	Los Esteros Mbr
17950	trace fossil-(4) coprolites	Triassic	Carnian	Santa Rosa Fm	Los Esteros Mbr

Specimen	Description	Period	Age	Formation	Member
17963	trace fossil-(2) coprolites	Triassic	Carnian	Santa Rosa Fm	Los Esteros Mbr
18071	trace fossil-(9) coprolites	Triassic	Carnian	Santa Rosa Fm	Los Esteros Mbr
18097	trace fossil-(2) coprolites	Triassic	Carnian	Santa Rosa Fm	Los Esteros Mbr
18104	trace fossil-(7) coprolites	Triassic	Carnian	Santa Rosa Fm	Los Esteros Mbr
18115	trace fossil-(8) coprolites	Triassic	Carnian	Santa Rosa Fm	Los Esteros Mbr
18127	trace fossil-(1) coprolite	Triassic	Carnian	Santa Rosa Fm	Los Esteros Mbr
18164	trace fossil-(3) coprolites	Triassic	Carnian	Santa Rosa Fm	Los Esteros Mbr
18180	trace fossil-coprolites	Triassic	Carnian	Garita Creek Fm	
18184	trace fossil-(1) coprolite	Triassic	Norian	Bull Canyon Fm	
18282	trace fossil-(6) coprolites	Triassic	Carnian	Bluewater Creek Fm	Lower mbr
18294	trace fossil-(59) coprolites	Triassic	Carnian	Bluewater Creek Fm	McGaffey Mbr?
18301	trace fossil-(2) coprolites	Triassic	Carnian	Bluewater Creek Fm	"Lower Mbr"
18319	trace fossil-(2) coprolites	Triassic	Carnian	Bluewater Creek Fm	"Lower Mbr"
18341	trace fossil-(95) coprolites	Triassic	Carnian	Bluewater Creek Fm	McGaffey Mbr?
18385	trace fossil-(1) coprolite	Triassic	Carnian	Bluewater Creek Fm	
18395	trace fossil-(13) coprolites	Triassic	Carnian	Bluewater Creek Fm	
18423	trace fossil-(1) coprolite	Triassic	Carnian	Bluewater Creek Fm	Lower
18436	trace fossil-(1) coprolite	Triassic	Carnian	Bluewater Creek Fm	"Lower Mbr"
18454	trace fossil-(5) coprolites	Triassic	Carnian	Bluewater Creek Fm	McGaffey Mbr?
18461	trace fossil-(8) coprolites	Triassic	Carnian	Bluewater Creek Fm	
18478	trace fossil-(1) coprolite	Triassic	Carnian	Bluewater Creek Fm	Lower mbr
18482	trace fossil-(1) coprolite	Triassic	Carnian	Bluewater Ck Fm	lower

Specimen	Description	Period	Age	Formation	Member
18486	trace fossil-numerous coprolites	Triassic	Carnian	Petrified Forest Fm	Blue Mesa Mbr
18487	trace fossil-(16) striated coprolites	Triassic	Carnian	Petrified Forest Fm	Blue Mesa Mbr
18488	trace fossil-(2) small striated coprolites	Triassic	Carnian	Petrified Forest Fm	Blue Mesa Mbr
18493	trace fossil-(12) coprolites	Triassic	Carnian	Bluewater Creek Fm	
18495	trace fossil-(12) coprolites	Triassic	Carnian	Bluewater Creek Fm	Lower
20293	trace fossil-(2) coprolites	Triassic	Anisian	Moenkopi Fm	Anton Chico Mbr
20303	trace fossil-(24) coprolites	Triassic	Anisian	Moenkopi Fm	Anton Chico Mbr
22092	trace fossil-(7) coprolites	Triassic	Rhaetian	Redonda Fm	
22100	trace fossil-(29) coprolite fragments	Triassic	Norian	Bull Canyon Fm	
22365	trace fossil-(14) coprolites	Triassic	Carnian	Petrified Forest Fm	
22406	trace fossil-(1) coprolite	Triassic	Carnian	Santa Rosa Fm	Los Esteros Mbr
22474	trace fossil-(2) coprolites	Triassic	Carnian	Bluewater Creek Fm	lower
25639	trace fossil-(14) coprolites	Triassic	Norian	Trujillo Fm	
25640	trace fossil-(14) coprolites	Triassic	Norian	Bull Canyon Fm	
25681	trace fossil-(61) coprolites	Triassic	Rhaetian	Redonda Fm	
25682	trace fossil-(1) coprolite	Triassic	Carnian	Bluewater Creek Fm	lower
25683	trace fossil-(1) coprolite (2 pieces)	Triassic	Carnian	Bluewater Creek Fm	lower
25684	trace fossil-(1) coprolite	Triassic	Carnian	Bluewater Creek Fm	lower
25685	trace fossil-(1) coprolite	Triassic	Carnian	Bluewater Creek Fm	lower
25686	trace fossil-(1) coprolite	Triassic	Carnian	Bluewater Creek Fm	lower
25687	trace fossil-(1) coprolite	Triassic	Carnian	Bluewater Creek Fm	lower
25688	trace fossil-(1) coprolite	Triassic	Carnian	Bluewater Creek Fm	lower

Specimen	Description	Period	Age	Formation	Member
25689	trace fossil-(1) coprolite	Triassic	Carnian	Bluewater Creek Fm	lower
25690	trace fossil-(1) coprolite	Triassic	Carnian	Bluewater Creek Fm	lower
25691	trace fossil-(1) coprolite	Triassic	Carnian	Bluewater Creek Fm	lower
25692	trace fossil-(1) coprolite	Triassic	Carnian	Bluewater Creek Fm	lower
25693	trace fossil-(1) coprolite	Triassic	Carnian	Bluewater Creek Fm	lower
25694	trace fossil-(1) coprolite-flattened	Triassic	Carnian	Bluewater Creek Fm	lower
25695	trace fossil-(1) coprolite-flattened	Triassic	Carnian	Bluewater Creek Fm	lower
25696	trace fossil-(1) coprolite-flattened	Triassic	Carnian	Bluewater Creek Fm	lower
25697	trace fossil-(1) coprolite-flattened	Triassic	Carnian	Bluewater Creek Fm	lower
25698	trace fossil-(1) coprolite-flattened	Triassic	Carnian	Bluewater Creek Fm	lower
25699	trace fossil-(1) coprolite-flattened	Triassic	Carnian	Bluewater Creek Fm	lower
25700	trace fossil-(1) coprolite-wrinkled?	Triassic	Carnian	Bluewater Creek Fm	lower
25701	trace fossil-(1) coprolite-spirally grooved	Triassic	Carnian	Bluewater Creek Fm	lower
25702	trace fossil-(1) coprolite-spirally grooved	Triassic	Carnian	Bluewater Creek Fm	lower
25703	trace fossil-(1) coprolite-spirally grooved	Triassic	Carnian	Bluewater Creek Fm	lower
25704	trace fossil-(1) coprolite-longitudinally grooved	Triassic	Carnian	Bluewater Creek Fm	lower
25705	trace fossil-(1) coprolite-transversely grooved	Triassic	Carnian	Bluewater Creek Fm	lower
25706	trace fossil-(1) coprolite-spirally grooved	Triassic	Carnian	Bluewater Creek Fm	lower
25707	trace fossil-(1) coprolite-wrinkled?	Triassic	Carnian	Bluewater Creek Fm	lower
25708	trace fossil-(1) coprolite-spirally grooved	Triassic	Carnian	Bluewater Creek Fm	lower
25709	trace fossil-(1) coprolite-spirally grooved	Triassic	Carnian	Bluewater Creek Fm	lower
25710	trace fossil-(1) coprolite	Triassic	Carnian	Bluewater Creek Fm	lower
25711	trace fossil-(1) coprolite	Triassic	Carnian	Bluewater Creek Fm	lower
25712	trace fossil-(1) coprolite	Triassic	Carnian	Bluewater Creek Fm	lower
25713	trace fossil-(1) coprolite	Triassic	Carnian	Bluewater Creek Fm	lower
25714	trace fossil-(1) coprolite	Triassic	Carnian	Bluewater Creek Fm	lower
25715	trace fossil-(1) coprolite	Triassic	Carnian	Bluewater Creek Fm	lower
25716	trace fossil-(1) coprolite	Triassic	Carnian	Bluewater Creek Fm	lower
25717	trace fossil-(1) coprolite	Triassic	Carnian	Bluewater Creek Fm	lower
25718	trace fossil-(1) coprolite	Triassic	Carnian	Bluewater Creek Fm	lower
25719	trace fossil-(1) coprolite	Triassic	Carnian	Bluewater Creek Fm	lower
25720	trace fossil-(1) coprolite	Triassic	Carnian	Bluewater Creek Fm	lower
25721	trace fossil-(1) coprolite	Triassic	Carnian	Bluewater Creek Fm	lower
25722	trace fossil-(1) coprolite	Triassic	Carnian	Bluewater Creek Fm	lower
25723	trace fossil-(1) coprolite	Triassic	Carnian	Bluewater Creek Fm	lower
25724	trace fossil-(1) coprolite	Triassic	Carnian	Bluewater Creek Fm	lower
25725	trace fossil-(1) coprolite	Triassic	Carnian	Bluewater Creek Fm	lower

Specimen	Description	Period	Age	Formation	Member
25706	trace fossil-(1) coprolite-spirally grooved	Triassic	Carnian	Bluewater Creek Fm	lower
25707	trace fossil-(1) coprolite-wrinkled?	Triassic	Carnian	Bluewater Creek Fm	lower
25708	trace fossil-(1) coprolite-spirally grooved	Triassic	Carnian	Bluewater Creek Fm	lower
25709	trace fossil-(1) coprolite-spirally grooved	Triassic	Carnian	Bluewater Creek Fm	lower
25710	trace fossil-(1) coprolite	Triassic	Carnian	Bluewater Creek Fm	lower
25711	trace fossil-(1) coprolite	Triassic	Carnian	Bluewater Creek Fm	lower
25712	trace fossil-(1) coprolite	Triassic	Carnian	Bluewater Creek Fm	lower
25713	trace fossil-(1) coprolite	Triassic	Carnian	Bluewater Creek Fm	lower
25714	trace fossil-(1) coprolite	Triassic	Carnian	Bluewater Creek Fm	lower
25715	trace fossil-(1) coprolite	Triassic	Carnian	Bluewater Creek Fm	lower
25716	trace fossil-(1) coprolite	Triassic	Carnian	Bluewater Creek Fm	lower
25717	trace fossil-(1) coprolite	Triassic	Carnian	Bluewater Creek Fm	lower
25718	trace fossil-(1) coprolite	Triassic	Carnian	Bluewater Creek Fm	lower
25719	trace fossil-(1) coprolite	Triassic	Carnian	Bluewater Creek Fm	lower
25720	trace fossil-(1) coprolite	Triassic	Carnian	Bluewater Creek Fm	lower
25721	trace fossil-(1) coprolite	Triassic	Carnian	Bluewater Creek Fm	lower
25722	trace fossil-(1) coprolite	Triassic	Carnian	Bluewater Creek Fm	lower
25723	trace fossil-(1) coprolite	Triassic	Carnian	Bluewater Creek Fm	lower
25724	trace fossil-(1) coprolite	Triassic	Carnian	Bluewater Creek Fm	lower
25725	trace fossil-(1) coprolite	Triassic	Carnian	Bluewater Creek Fm	lower

Specimen	Description	Period	Age	Formation	Member
28183	(numerous) coprolites (3 of 3 boxes)	Triassic	Norian	Bull Canyon Fm	
28184	(numerous) coprolites (2 of 3 boxes)	Triassic	Norian	Bull Canyon Fm	
28185	(numerous) coprolites (1 of 3 boxes)	Triassic	Norian	Bull Canyon Fm	
28309	(2) coprolites	Triassic	Late Carnian	Salitral Fm	Youngsville Mbr
29185	(numerous) coprolites	Triassic	Carnian	Petrified Forest Fm	Blue Mesa Mbr
29338	(2) coprolites	Triassic	Carnian	Dockum Fm	Upper Tecovas Mbr
29399	coprolites (49)	Triassic	Carnian	Dockum Fm	Colorado City Mbr
29404	(4) coprolites	Triassic	Carnian	Dockum Fm	Colorado City Mbr
29701	(9) coprolites	Triassic	Anisian	Moenkopi Fm	Anton Chico Mbr
29711	(10) coprolites	Triassic	Anisian	Moenkopi Fm	Anton Chico Mbr
29952	(2) coprolites	Triassic	Norian-Early	Dockum Fm	Trujillo Mbr
30789	(2) coprolites	Triassic	Carnian	Tecovas Fm	
30828	(1) coprolite	Triassic	Carnian	Tecovas Fm	
31617	Miscellaneous burrows or coprolites	Triassic	Carnian	San Pedro Arroyo Fm	Ojo Huelos Mbr
34003	(1) coprolites	Triassic	Carnian	Dockum Fm	Colorado City Mbr
34055	(1) coprolite	Triassic	Carnian	Dockum Fm	Colorado City Mbr
34080	(6) coprolites	Triassic	Carnian	Tecovas Fm	
34181	(7) coprolites	Triassic	Carnian	Tecovas Fm	
34243	(2) coprolites	Triassic	Carnian	Tecovas Fm	
34462	(6) small coprolites	Triassic	Carnian	Bluewater Creek Fm	Lower mbr
34525	(5) coprolites	Triassic	Carnian	Bluewater Creek Fm	Lower mbr
35432	(1) coprolite	Triassic	Rhaetian	Redonda Fm	
35822	(6) coprolites	Triassic	Norian	Bull Canyon	(lower)
35964	(1) tiny coprolite(?)	Triassic	Norian	Petrified Forest Fm	Painted Desert Mbr

Specimen	Description	Period	Age	Formation	Member
36201	(12) coprolites and coprolite fragments	Triassic	Norian	Petrified Forest Fm	Painted Desert Mbr
36202	(1) long bone and associated coprolite	Triassic	Norian	Petrified Forest Fm	Painted Desert Mbr
36217	(1) coprolite	Triassic	Norian?	San Pedro Arroyo Fm	upper
36238	(24) coprolites	Triassic	Carnian	Dockum Fm	Tecovas Mbr
37401	(5) coprolites	Triassic	Carnian	Popo Agie Fm	Lyons Valley Mbr
37409	(1) coprolite	Triassic	Carnian	Popo Agie Fm	Lyons Valley Mbr
37425	(1) coprolite	Triassic	Carnian	Popo Agie Fm	Lyons Valley Mbr
37445	(1) coprolite	Triassic	Carnian	Popo Agie Fm	Lyons Valley Mbr
37448	(1) coprolite	Triassic	Rhaetian	Redonda Fm	
38613	(20) coprolites	Triassic	Anisian	Moenkopi Fm	Anton Chico Mbr
38614	(24) coprolites	Triassic	Anisian	Moenkopi Fm	Anton Chico Mbr
38735	(8) coprolites	Triassic	Anisian	Moenkopi Fm	Anton Chico Mbr
38737	(~31) coprolites & coprolite fragments	Triassic	Anisian	Moenkopi Fm	Anton Chico Mbr
38739	(2) coprolites	Triassic	Anisian	Moenkopi Fm	Anton Chico Mbr
38754	(10) coprolites	Triassic	Anisian	Moenkopi Fm	Anton Chico Mbr
39216	(1) coprolite fragment	Triassic	Carnian	Salitral Fm	Youngsville Mbr
39222	(1) coprolite in (4) fragments	Triassic	Carnian	Salitral Fm	Youngsville Mbr
39226	(1) coprolite	Triassic	Carnian	Salitral Fm	Youngsville Mbr
39241	(2) coprolites	Triassic	Carnian	Salitral Fm	Youngsville Mbr
39293	(9) coprolites	Triassic	Rhaetian	Redonda Fm	
39296	(3) coprolites	Triassic	Rhaetian	Redonda Fm	
39638	(2) coprolites	Triassic	Norian	Petrified Forest Fm	Mesa Montosa Mbr

Specimen	Description	Period	Age	Formation	Member
39645	(1) coprolite	Triassic	Norian	Petrified Forest Fm	Mesa Montosa Mbr
39650	(2) coprolites	Triassic	Norian	Petrified Forest Fm	Mesa Montosa Mbr
40142	(10) coprolites	Triassic	Carnian	Dockum Gm	Colorado City Mbr
40502	(2) coprolites	Triassic	Rhaetian	Redonda Fm	
40658	(numerous) coprolites	Triassic	Rhaetian	Redonda Fm	
41308	(1) coprolite	Triassic	Norian	Rock Point Fm	
41331	(4) coprolites	Triassic	Norian	Bull Canyon Fm	
41769	(3) coprolites	Triassic		Petrified Forest Fm	Sonsela Mbr
41777	(3) coprolites	Triassic	Carnian	Bluewater Creek Fm?	
41840	(3) coprolites(?)	Triassic	Norian	Petrified Forest Fm	Painted Desert Mbr
41841	(1) coprolite fragment	Triassic	Norian	Petrified Forest Fm	Painted Desert Mbr
42280	(27) coprolites & coprolite fragments	Triassic	Carnian	Dockum Fm	Colorado City Mbr
42282	(1) coprolite	Triassic	Carnian	Tecovas Fm	
42705	(1) coprolite w/fish scales	Triassic	Norian	Bull Canyon Fm	
42708	(1) coprolite	Triassic	Carnian	Bluewater Creek Fm	Lower
43194	(1) coprolite	Triassic	Norian	Petrified Forest Fm	Painted Desert Mbr
43317	(several) coprolites	Triassic	Rhaetian	Redonda Fm	
43865	(2) coprolites	Triassic	Carnian	Petrified Forest Fm	Blue Mesa Mbr
43866	(1) coprolite	Triassic	Carnian	Petrified Forest Fm	Blue Mesa Mbr
43867	(1) striated coprolite	Triassic	Carnian	Petrified Forest Fm	Blue Mesa Mbr
43868	(1) short coprolite	Triassic	Carnian	Petrified Forest Fm	Blue Mesa Mbr
43869	(2) coprolites	Triassic	Carnian	Petrified Forest Fm	Blue Mesa Mbr
43870	(1) coprolite	Triassic	Carnian	Petrified Forest Fm	Blue Mesa Mbr
43871	(1) coprolite	Triassic	Carnian	Petrified Forest Fm	Blue Mesa Mbr

Specimen	Description	Period	Age	Formation	Member
43872	(2) coprolites	Triassic	Carnian	Petrified Forest Fm	Blue Mesa Mbr
43873	(numerous) small coprolites	Triassic	Carnian	Petrified Forest Fm	Blue Mesa Mbr
43874	(numerous) moderately small coprolites	Triassic	Carnian	Petrified Forest Fm	Blue Mesa Mbr
43934	(1) coprolite	Triassic	Carnian	Petrified Forest Fm	Blue Mesa Mbr
43953	(2) coprolite pieces	Triassic	Carnian	Petrified Forest Fm	Blue Mesa Mbr
43954	(1) large coprolite	Triassic	Carnian	Petrified Forest Fm	Blue Mesa Mbr
43965	(1) large coprolite in (3) cross-sectional pieces	Triassic	Carnian	Petrified Forest Fm	Blue Mesa Mbr
43968	(4) coprolites	Triassic	Carnian	Petrified Forest Fm	Blue Mesa Mbr
44083	(numerous) coprolites	Triassic	Rhaetian	Redonda Fm	
44096	(numerous) coprolites	Triassic	Norian	Bull Canyon Fm	
44103	(1) large coprolite	Triassic	Norian	Bull Canyon Fm	
44104	(3) small coprolites	Triassic	Norian	Bull Canyon Fm	
44114	(2) coprolites	Triassic	Norian	Bull Canyon Fm	
44559	(1) tiny coprolite	Triassic	Norian	Petrified Forest Fm	Painted Desert Mbr
44560	(1) tooth in (?)coprolite	Triassic	Norian	Petrified Forest Fm	Painted Desert Mbr
44658	(2) coprolite fragments	Triassic	Norian	Petrified Forest Fm	Mesa Montosa Mbr
44664	(3) coprolites	Triassic	Norian	Petrified Forest Fm	Mesa Montosa Mbr
44678	(2) coprolites	Triassic	Norian	Petrified Forest Fm	Mesa Montosa Mbr
44695	(2) coprolites	Triassic	Norian	Petrified Forest Fm	Mesa Montosa Mbr
44751	(1) coprolite(?)	Triassic	Carnian	Dockum Fm	Colorado City Mbr
44752	(1) coprolite	Triassic	Carnian	Dockum Fm	Colorado City Mbr
44753	(8+) coprolites in vial	Triassic	Carnian	Dockum Fm	Colorado City Mbr
44801	(1) partial proximal caudal series w/coprolites	Triassic	Norian	Rock Point Fm	
44815	(10) coprolites	Triassic	Norian	Petrified Forest Fm	Mesa Montosa Mbr
44967	(1) coprolite w/scales or bone fragments	Triassic	Carnian	Dockum Fm	Colorado City Mbr
44968	(1) coprolite w/scales or bone fragments	Triassic	Carnian	Dockum Fm	Colorado City Mbr
45053	(1) tiny coprolite	Triassic	Carnian	Petrified Forest Fm	Blue Mesa Mbr
45557	(1) twinned coprolite	Triassic	Norian	Bull Canyon Fm	
45564	(numerous) coprolites	Triassic	Norian	Bull Canyon Fm	
45570	(1) coprolite	Triassic	Carnian	Bluewater Creek Fm	lower
45571	(1) coprolite	Triassic	Carnian	Bluewater Creek Fm	lower
45572	(1) coprolite	Triassic	Carnian	Bluewater Creek Fm	lower
45573	(1) large coprolite in 2 pc (nice cross-section)	Triassic	Carnian	Bluewater Creek Fm	lower
45964	(1) coprolite w/fish scales	Triassic	Rhaetian	Redonda Fm	
45965	(1) coprolite w/fish scales	Triassic	Rhaetian	Redonda Fm	
45966	(1) coprolite w/abundant fish scales	Triassic	Rhaetian	Redonda Fm	
45967	(several) coprolites	Triassic	Rhaetian	Redonda Fm	
46111	(2) tiny coprolites	Triassic	Carnian	Petrified Forest Fm	Blue Mesa Mbr
46112	(2) bags small coprolites	Triassic	Carnian	Petrified Forest Fm	Blue Mesa Mbr
51868	(12) coprolites	Triassic	Carnian	Petrified Forest Fm	Blue Mesa Mbr

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TRIASSIC MARINE FISHES FROM SIBERIA, RUSSIA

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Triassic fishes are poorly known from Siberia, Russia. A few actinopterygians are mentioned from some regions of Siberia, frequently from the freshwater deposits. The first chondrichthyan and actinopterygian microremains were discovered from the marine deposits of four regions of Central Siberia - Verkhoyan'e and Northern Siberia: Taimyr Peninsula, Kotelniy Island (New Siberian Archipelago) and Omolon.

The Central Siberia locality of Triassic fishes is situated on the left bank of the Barayi River (tributary of Aldan River), Lena River Basin, Western Verkhoyan'e, Sakha (Yakutia) Republic (Fig. 1). The fish microremains occur there in the section of the Monom Formation, Olenekian, Lower Triassic. The deposits are dark gray mudstones and siltstones with intercalations of green-gray sandstones and light gray limestones yielding ammonoids, bivalves and the conodont *Neogondolella buurensis* Dagys. The fishes are represented by isolated teeth and scale fragments of actinopterygians, and various scales of neoselachian and hybodontoid chondrichthyans resembling *Fragilicorona*, *Duplisuggestus* and *Gracilisuggestus* types described by Johns et al. (1997).

The fish microremains were found in the Lower Triassic Pribrezhnaya Formation (Olenekian) and the Middle Triassic Morzhovaya Formation (Anisian) of the Cape of Tsvetkov and Chernokhrebetnaya River, eastern part of Taimyr Peninsula, Krasnoyarsk Area (Kray). The vertebrate-bearing part of the formations includes dark gray siltstones and mudstones with ammonoids, nautiloids, bivalves and conodonts. The latter belong to *Neogondolella* cf. *N. altera* Klets, *Xaniognathus* sp. and *Neogondolella jubata* Sweet in the Pribrezhnaya Formation; to *Chiosella* sp. nov. in the lower part and *Neogondolella mombergensis* (Tatge) and *Neogondolella constricta* (Mosher et Clark) in the upper part of the Morzhovaya Formation. The fish assemblages contain the teeth and scales of actinopterygians (colobodontid and redfieldiid), as well chondrichthyan teeth of a new *Synechodus* that are similar to *S. streitzi* Delsate, Duffin and Weis (2002), and numerous chondrichthyan scales of *Proprigalea* and the above mentioned types.

The vertebrates are recorded in the Lower Triassic Tuor-Yuryakh Formation (Olenekian) of the Tikhaya River, Kotelniy Island, New Siberian Archipelago, Sakha (Yakutia) Republic. The formation encompasses the rhythmic interbedding of dark gray clays and gray bioclastic limestones containing ammonoids, bivalves and conodonts such as *Neospathodus waageni* Sweet, *Scythogondolella mosheri* (Kozur et Mostler), *Sc. milleri* (Müller), *Neogondolella composita* Dagys, *N. buurensis* Dagys, *N. jakutensis* Dagys and *N. altera* Klets. The fish microremains are represented by the teeth and scale fragments of actinopterygians, chondrichthyans scales of *Fragilicorona* and *Gracilisuggestus* types, as well as a *Synechodus* tooth resembling the teeth of *S. enniskilleni* Duffin and Ward (1993).

The Middle Triassic fishes are found in the Left Kedon Formation (Lower Anisian) of the Dzhugadzhak River, Kolyma River Basin, Omolon Massif, Magadan District. The deposits are dark gray bituminous limestones and siltstones with ammonoids, bivalves and the conodonts *Neospathodus waageni* Sweet, *Scythogondolella mosheri* (Kozur

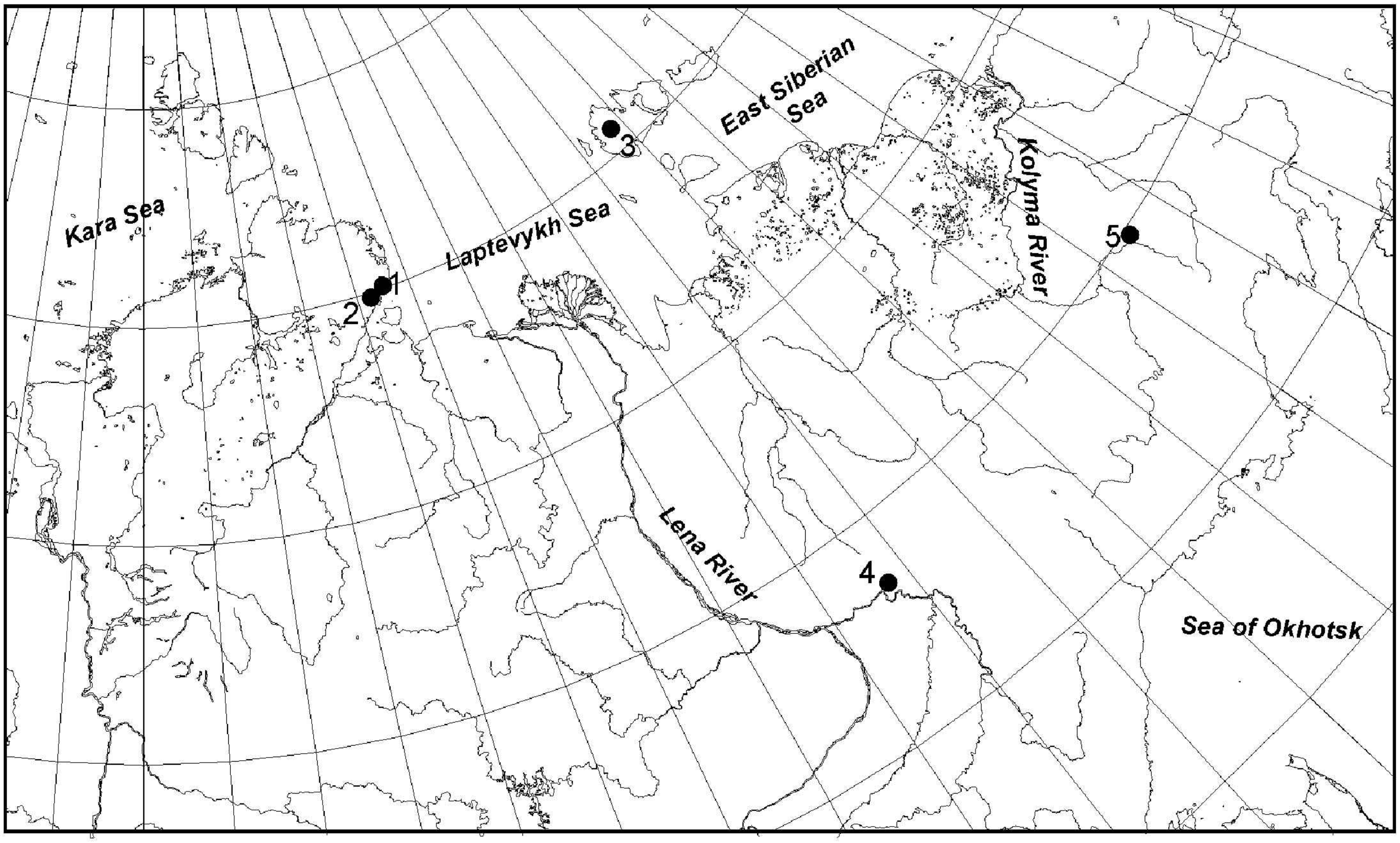

FIGURE 1. Map of Siberia, Russia, highlighting Triassic marine fish localities.

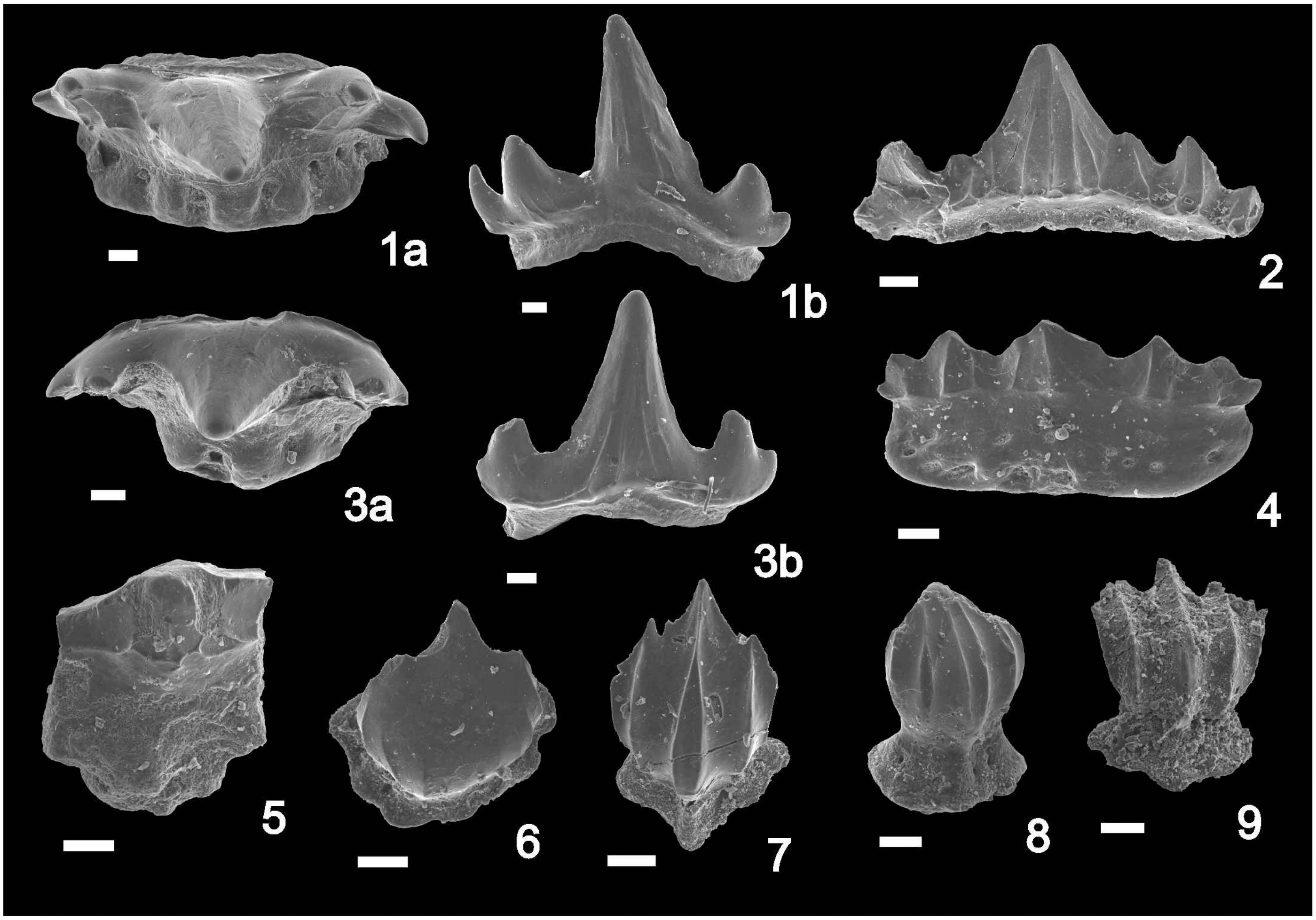

FIGURE 2. **1**, **3**, **4**, *Synechodus* sp. nov. **1**, anterior tooth, MP SPU 41-1 in **a**, occlusal and **b**, labial views; Morzhovaya Formation, Anisian, Middle Triassic; Cap of Tsvetkov, Taimyr Peninsula. **3**, anterior tooth, MP SPU 41-2 in **a**, occlusal and **b**, labial views; Morzhovaya Formation, Anisian, Middle Triassic; Cap of Tsvetkov, Taimyr Peninsula. **4**, lateral tooth, MP SPU 41-3 in lingual view; Pribrezhnaya Formation, Olenekian, Lower Triassic; Cap of Tsvetkov, Taimyr Peninsula. **2**, **5**, *Synechodus* sp. **2**, lateral tooth, MP SPU 41-4 in labial view; Tuor-Yuryakh Formation, Olenekian, Lower Triassic; Tikhaya River, Kotelniy Island. **5**, tooth fragment, MP SPU 41-5 in occlusal view; Pribrezhnaya Formation, Olenekian, Lower Triassic; Cap of Tsvetkov, Taimyr Peninsula. **6-9**, Chondrichthyan scales; Monom Formation, Olenekian, Lower Triassic; Barayi River, Lena River Basin, Western Verkhoyan'e; **6**, *Fragilicorona* scale type, MP SPU 41-6 in crown view. **7**, *Fragilicorona* scale type, MP SPU 41-7 in anterior crown view. **8**, *Duplisuggestus* scale type, MP SPU 41-8 in anterior view. **9**, *Duplisuggestus* scale type, MP SPU 41-9 in anterior view. All scale bars = 100 im.

et Mostler), *Sc. milleri* (Müller), *Neogondolella composita* Dagys, *N. buurensis* Dagys, *N. jakutensis* Dagys, *N. altera* Klets. The fish remains are actinopterygian teeth and various chondrichthyan scales of *Fragilicorona*, *Proprigalea* and *Gracilisuggestus* types.

The diverse assemblages of marine fishes (Fig. 2) are reported for the Boreal area of Siberia for the first time.

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TRIASSIC-JURASSIC BOUNDARY ON THE SOUTHERN MARGIN OF TETHYS: IMPLICATIONS OF FACIES, TECTONICS AND VOLCANISM

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Abstract—The facies changes, tectonics and magmatism across the Triassic–Jurassic boundary in the southern Tethyan margin have been studied in Egypt, Sudan, Jordan and Saudi Arabia. In Saudi Arabia and Jordan an unconformable contact is recognized between the Upper Triassic and Lower Jurassic rocks. This unconformity surface is marked by the truncation of the fluvial clastics of the uppermost Triassic before and during the deposition of the lowermost Jurassic carbonate, recording a regression-transgression pulse. In Egypt and Sudan, there is substantial ambiguity in the position of the Triassic-Jurassic contact, because Middle and Upper Triassic rocks are not present and the Lower Triassic rocks are overlain directly by Lower and Middle Jurassic rocks. This unconformity may have resulted from the east-west tectonics and possibly volcanic activity that took place during this period (Late Triassic-Early Jurassic). Numerous tectonic processes were active during the time represented by this unconformity, most of which were east-west uplifts that dominated in Egypt, following which the Upper Triassic rocks were eroded or not deposited. In the Arabian Basin, east-west tectonics (in the south) and northeast-directed tectonics (in the north) caused intermittent erosion of the Upper Triassic facies. Magmatism that was active at the end of the Triassic generated hydrothermal iron deposits within the fluvial sandstones and triggered volcanic eruptions in the south and some northern parts of Egypt.

INTRODUCTION

One of the five largest extinction events of the Phanerozoic, (Sepkoski, 1996; Hallam and Wignall, 1997; Hallam, 2002), the Triassic–Jurassic boundary has been studied by different authors in different localities all over the world. For example, the stratigraphy of the Triassic-Jurassic boundary in Europe has been well-studied in southern Sweden and northwest of Poland (Bertelson, 1978), in the Northern Calcareous Alps of Austria (Satterley et al., 1994) and in England (Hallam, 1990, 1995). Pronounced facies changes across the Triassic-Jurassic boundary have been studied in Nevada, USA (Hallam and Wignall, 2000), in southern Tibet (Hallam et al., 2000) and in Hungary (Haas and Tardt-Filacz, 2004).

Hallam and Wignall (1999) mentioned that the contact between the Triassic and Jurassic in Africa and Asia is generally poorly known because of a paucity or absence of marine successions across the boundary. The present study presents good evidence for the unconformable relationship between the fluvial and fluvio-marine facies of the uppermost Triassic and lowermost Jurassic on the shelf area in Egypt and Sudan (northeast Africa), Jordan, and Saudi Arabia (southwest Asia) (Fig. 1). However, the recognition of the Triassic-Jurassic boundary in Sudan is difficult because the facies around the boundary are represented by coarse clastics. Well-exposed sections and subsurface data in other studied localities provide a good opportunity to contribute a better understanding about the facies changes, tectonics, and volcanism across the Triassic-Jurassic contact.

The Triassic rocks in Egypt were studied in the subsurface in the Western Desert, while the exposed Triassic-Jurassic rocks are measured in Northern Galala (north Eastern Desert) and in western and central Sinai (Fig. 1). On the Arabian Peninsula, the Triassic–Jurassic rocks were examined east of the Dead Sea rift at Jordan and Al Mustawi area (Al Qasim Province), Saudi Arabia (Fig. 1).

The aim of this study is to explain the facies architecture across the Triassic-Jurassic boundary in Egypt, Sudan, Jordan and in Saudi Arabia and to clarify the nature of the contact at the Triassic–Jurassic boundary. Also, this study aims to determine the factors responsible for the unconformable contact and major gap between the two systems.

UPPER TRIASSIC STRATA

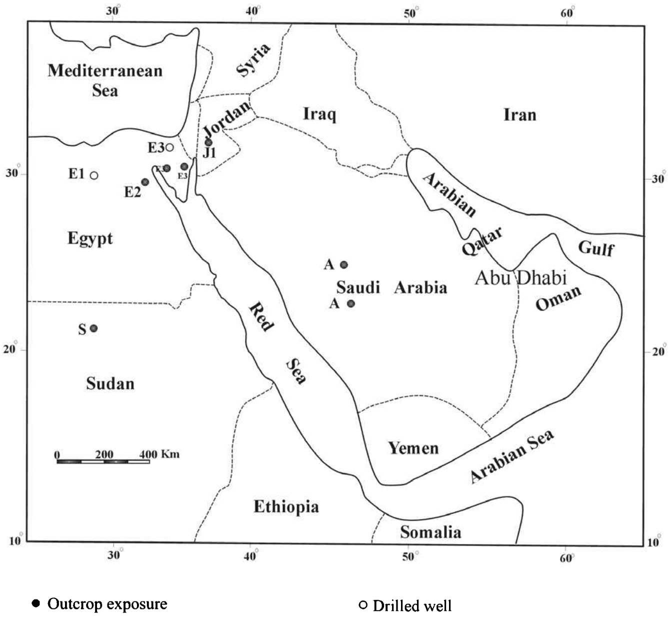

FIGURE 1. Location map showing the studied sections of the Triassic-Jurassic rocks in Sudan, Egypt, Jordan and Saudi Arabia.

In Saudi Arabia, the Upper Triassic rock unit termed the Rukhman Formation (Khalifa, 1992) is exposed in the Al Mustawi area, northeast of Al Qasim Province (north of latitude 25° 30′ N (Fig. 2). It is equivalent to the Minjur Sandstone that appears south of latitude 25° 30′ (Powers et al., 1966). This formation is studied in the surface and in the subsurface. In the exposed sections, the formation consists of kaolinitic claystone with interbeds of siltstones and sandstones at the top (Fig. 2). The kaolinitic claystones are usually creamy white red–buff in color, and massive. The siltstones are yellow to white in color enclosing lenticular beds of reddish siltstones. The sequence is capped by siliceous quartzarenitic sandstone. Within the above succession, there are vertical ironstone dikes distributed throughout the sequences that also appear in underground tunnels. These iron bands are repeated vertically through the rocks; the vertical extent of individual dikes ranges from 50 cm to 1 m, with an average width of a few decimeters (Fig. 2). Where exposed at the ground surface, the iron ore appears as weathered nodules; in some

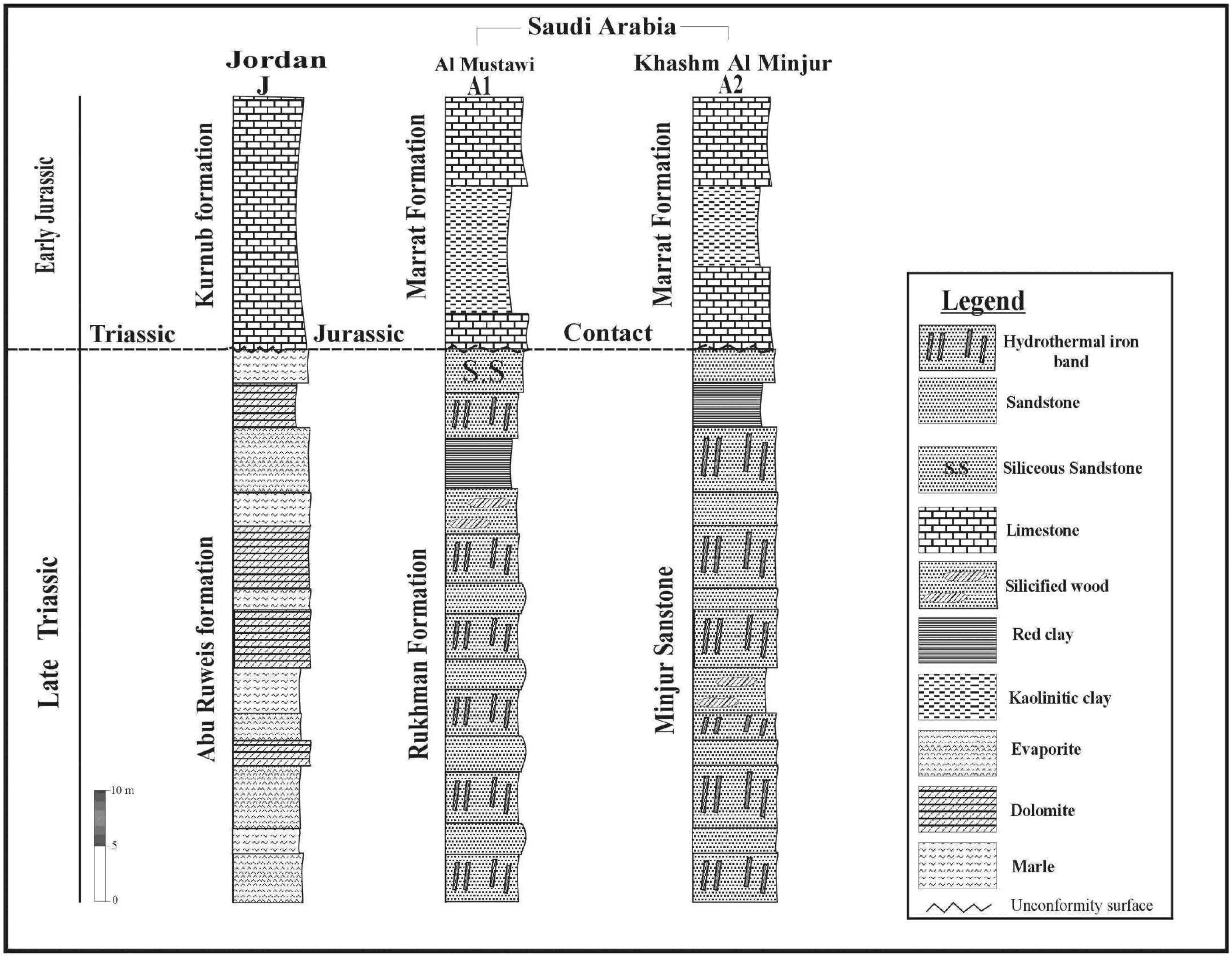

FIGURE 2. Lithostratigraphic correlation of the Triassic-Jurassic rocks in Jordan and Saudi Arabia.

places there is a hexagonal staining coloration within the siltstones. The formation measures about 220 m in thickness at its type locality (Gabal Ar Rukhman).

The Minjur Sandstone is coeval to the Rukhman Formation and occurs at Khashm al Minjur (Lat.23° 30′ N) and consists of about 290 m of sandstone with a small amount of conglomerate and shale. The sandstones are coarse-grained, pebbly, white tan to brown, and cross-bedded. Lenses of conglomeratic sandstone occur at several levels in the sequence (Fig. 2). The shale is usually thin bedded, and reddish purple with green intercalations in the sequences. No fossils were recorded except for the presence of fossil plants in the form of crude stem impressions, tree trunks and silicified wood. The age of the Rukhman Formation/Minjur Sandstone is based on palynology; Powers et al. (1966) found pollen grains in the Minjur Sandstone recovered from bore holes. The lower part of the Minjur contains pollen grains such as *Sulcatisporitus interpositus* Leschik and *Pityosporites ruttneri* Klaus. These fossils indicate a Late Triassic age.

The Triassic formations in the Arabian Peninsula are, from base to top, the Sudair, Jilh and Minjur formations. The Sudair Formation consists of brick-red and green shale (Triassic red beds) whereas the other two formations are represented by sandstones. These shales and sandstones thin northeastward and are replaced in the subsurface by a shallow marine limestone known as the Khail and Gulailah formations. The Triassic strata are truncated by a regional unconformity known as the pre-Toarcian erosional unconformity.

In Jordan, the Upper Triassic rock was formerly named the Gypsum Formation (Basha, 1981), but in a revised lithostratigraphic classification by Bandel and Khoury (1981), the Upper Triassic rocks (Carnian) were renamed the Abu Ruweis Formation (Fig. 2). This formation is exposed between the confluence of Wadi Huni and Wadi Abu Ruweis, from which the formation received its name. The formation measures about 200 m thick and consists of alternating layers of clays, shale, dolostone and anhydrite. Its base is defined by the first appearance of a thick bed of anhydrite and its top by the first appearance of Jurassic sediments (Bandel and Khuory, 1981). The facies association of the Abu Ruweis Formation indicates deposition took place in a tidal zone or sabkha. In the area of Suweilih, sediments of the Abu Ruweis Formation were largely eroded before the deposition of the Lower Jurassic Kurnub limestone.

In Egypt, Upper Triassic rocks are not present at the surface or in the subsurface. The only Triassic formations that occur belong to the Lower Triassic. These are recorded in the subsurface in the northern Western Desert (Anges-1, Yakou-1), where they are represented by the Eghi Group (Dahi and Shahin, 1992) or Ras Qattara Formation and consist of reddish sandstones and silty clays (Fig. 3). The Ras Qattara Formation is encountered in wells, and has an average thickness of about 200 m. It consists of coarse-grained reddish-buff sandstones to sandy-siltstone. On the surface, the only Triassic rock unit known is the Qiseib

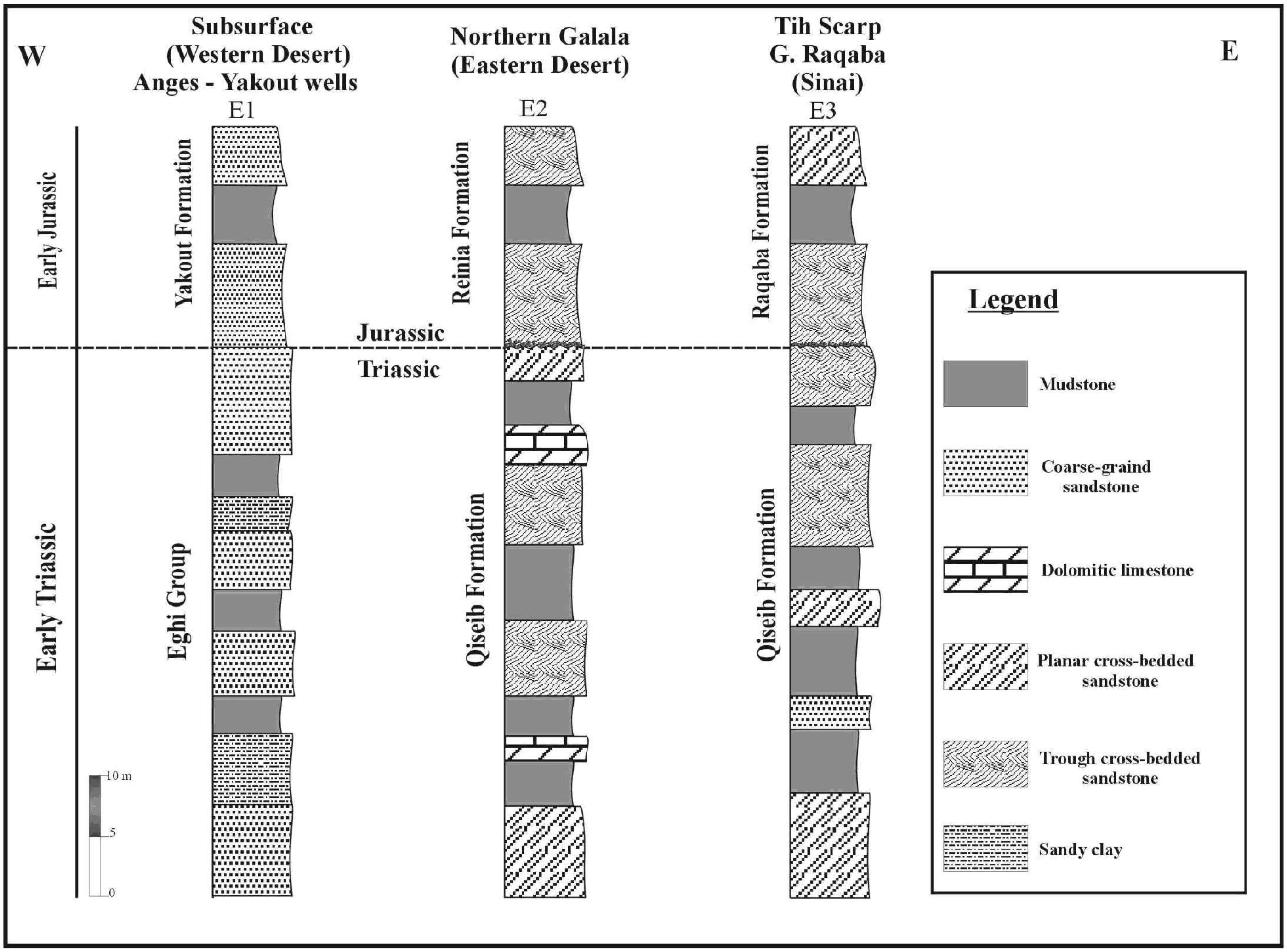

FIGURE 3. Lithostratigraphic correlation of the Triassic-Jurassic rocks in Egypt.

Formation (Abdallah, et al., 1963), which dates to the Permo-Triassic to Triassic. Its type section lies at Wadi Qiseib at the eastern side of the Northern Galala plateau (Lat.29° 24′ 20¨, Long. 32° 28′ 45¨). The formation consists of two members; the lower one is made up of intercalated sandstones, siltstones and red clays and is assigned a Late Permian age. The upper member, which has been dated to Late Triassic (Abdallah et al., 1963), consists of intercalated sandstone, siltstone and in the upper part a few thin beds of dolostone (Fig. 3). The Qiseib Formation measures about 43 m at its type locality. In western Sinai, the Qiseib Formation was recorded in the foothill of Gabal Raqaba in the Tih escarpment (Fig.3; Lat. 92° 1′ 40¨, Long.33° 40′ 00¨) (El Barkooky, 1986). The stratigraphic position of the Qiseib Formation varies at different localities along this escarpment. At Gabal Raqaba, the formation unconformably overlies the Carboniferous Abu Thora Formation and is overlain unconformably by the Lower Jurassic Raqaba Formation. In Wadi Budra, volcanics separate the basal part of the Qiseib Formation and the top of Abu Thora Formation. In this locality, the Qiseib Formation consists of interbeds of multi-colored sandstone and mudstone. The sandstones are reddish brown, cross-bedded, fining-upward, medium to coarse-grained with quartz granules at the base of each bed. The mudstones are brown, reddish, thin laminated to massive, with few mud cracks. Both the sandstones and mudstones show fining-upward cycles that characterize the fluvial environments. Each cycle begins with sandstone, capped by mudstone. In eastern Sinai, the Qiseib Formation wedges out laterally until at Gabal Dhalal the formation is absent, and the lower Cretaceous Malha Formation unconformably overlies the Lower Paleozoic Naqus Formation. In general, there is no record of Upper Triassic rocks in the Egyptian territory of northern Sinai.

The Qiseib Formation is generally barren of fauna. However, some badly preserved fossils, e.g. *Nucula sp.; Hornesia sp. Leda sp.* and *Naticopsis sp.*, have been identified from the uppermost carbonate bed above the red beds. These fossils indicate Muschelkalk (Middle Triassic) affinity (Abdallah et al., 1963), although according to Abdallah et al. (1963) the Qiseib Formation is dated as Permo-Triassic because it overlies the Upper Carboniferous rocks without unconformity and underlies the Muschelkalk carbonates. Druckman et al. (1970) and Weissbord (1976) rejected the Permian age of Qiseib Formation and attributed an Early to Middle Triassic age for this formation. It is noteworthy that the lithologies of the Qiseib Formation (reddish color of both sandstones and claystones) are closely similar to the Sudair Shale in Saudi Arabia and in many Gulf countries e.g., Oman, Qatar, and United Arab Emirates, which definitely are of Early Triassic age (Powers et al., 1966). Additionally, the upper carbonate beds are closely similar to the Middle Triassic Jilh Formation that appears in the Al Qasim Provinces, Saudi Arabia. Therefore, the Qiseib Formation is attributed herein to be of Early-Middle Triassic affinity.

LOWER JURASSIC STRATA

In Saudi Arabia, Lower Jurassic rocks are represented by the Marrat Formation that has been formally defined and described by Powers et al. (1966) and Powers (1968) who also informally defined lower, middle, and upper units of the formation. The Marrat Formation unconformably overlies the Upper Triassic Rukhman/Minjur formations. Discontinuous exposures of the Marrat Formation can be traced from Khashm Mawan (Lat.22° 50′ N) to Taysyah plateau (Lat.28° 03′ N) a distance of more than 650 km (Powers et al., 1966). This formation comprises three members, soft red shale in the middle bracketed by resistant limestones (Fig. 2). The lower limestone member is well exposed in the Sharabith escarpment west of Nafud ath Thuwayrat. The middle shale members show maximum thicknesses between Shaqra and Khashm adh Dhibi, and wedge out northwards and southwards from these localities. It consists of red to buff shales and interbeds of reddish brown siltstones. This facies is dominant from Khashm adh Dhibi in the north up to Khashm Jufayr in the south. North and south of the above localities, the shaley facies of this member changes gradually to sandstone with some conglomerate, especially near the base of the member. The upper limestone member is exposed from Nafud ath Thuwayrat in the north to Khashm adh Dhibi in the south. South of the latter locality the limestone is replaced by claystone and sandstone. The lower member of the Marrat Formation has yielded *Bouleiceras nitescens* Thevenin, *B. arabicum* Arkell, *B. elegans* Arkell. These fossils are considered of Lower Toarcian age (Powers et al., 1966). In Jordan, the Lower Jurassic rocks are known by the term Kurnub limestone.

In northern Sudan and southern Egypt, the Triassic-Jurassic boundary is difficult to discern and is thought to occur within the Lakia Formation (Fig.4). This formation ranges in age from Permian to Early Jurassic and extends over a large area northwest of Sudan (Wycisk, 1990). The formation was studied by Wycisk (1984, 1987). The Lakia Formation consists of a succession made up of texturally and mineralogically immature arkosic fluvial sandstones with conglomerate of varying depositional facies (Wycisk, 1990). These alluvial clastic sediments were deposited by fluvial processes in grabens and display various facies within the alluvial paleoenvironments. The alluvial architecture varies according to paleogeographic setting and to sediment supply, which were in turn controlled by tectonics during the Permo-Triassic to Early Jurassic (Wycisk, 1990). The cyclic sequences within the formation differ from east to west. In the south of Gebel Kissu, the Lakia Formation shows coarsening-upward cycles, while in the area of Lakia Arbain and south-eastwards the formation exhibits entirely fining-upward cycles. In general the paleocurrent direction of the cross-bedded sandstones indicates a southwest to westward paleodrainage system towards the Kufra. In northern Egypt, the marine Jurassic facies were recognized in the subsurface (northern Western Desert) at the Anges-1 and Yakout-1 wells (Fig. 3). The formation was named the Yakout Formation and is dated as Early Jurassic (Paleoservices, 1988). This formation is made up of shale and claystone, deposited under dominantly fluvio-lacustrine conditions with frequent periods of oxidations and subaerial exposure (Paleoservices, 1988). At Khashm El Galala and at Ras Abd areas on the western side of the Gulf of Suez, these rocks were divided into two rock units; the lower is the Bajocian Rieina Formation (Hassanein, 1970) and the upper is the Bathonian-Oxfordian Ras El Abd Formation (Abd El Shafi, 1980, 1988). The Rieina Formation is exposed at Khashm El Galala and has a thickness of about 55 m. Its basal part is unexposed, while its upper part conformably underlies the Ras El Abd Formation. This formation comprises compact massive to slightly cross-bedded sandstones intercalated with silty claystone. The sandstone facies is pale white to yellow, sometimes varicolored, coarse grained with some pebbles and granules towards the base. Both the sandstone and siltstone show vertical fining-upward cycles that may indicate fluvial facies (El Younsy, 2001).

In the Sinai, the Early Jurassic strata are named the Raqaba or Temmariya formations (El Barkooky, 1986; Barakat et al., 1986) and consist of clastic rocks extending from Wadi El Hammur in the west to Gabal Gunna in the east, on the foothills of the Tih escarpments. This formation shows an unconformable contact with the underlying Lower-Middle Triassic Qiseib Formation. The contact is placed between the reddish to brown claystone and siltstone of the uppermost Qiseib Formation and the massive sandstones of the lowermost Raqaba Formation (Fig. 3). The thickness ranges from 350 to 250 m and it tapers to the west and to the east, where it is truncated completely at Gabal Dhalal, east of Gabal Gunna. The formation consists of trough cross-bedded sandstone with interbeds of mudstones. The sandstones are usually pale yellow, medium to coarse-grained and they are massive to trough cross-bedded and channelized. The mudstones are mostly red, and violet to dark brown, and they wedge out laterally. The sandstones and mudstone are arranged vertically in fining-upward cycles that characterize the fluvial environment of deposition.

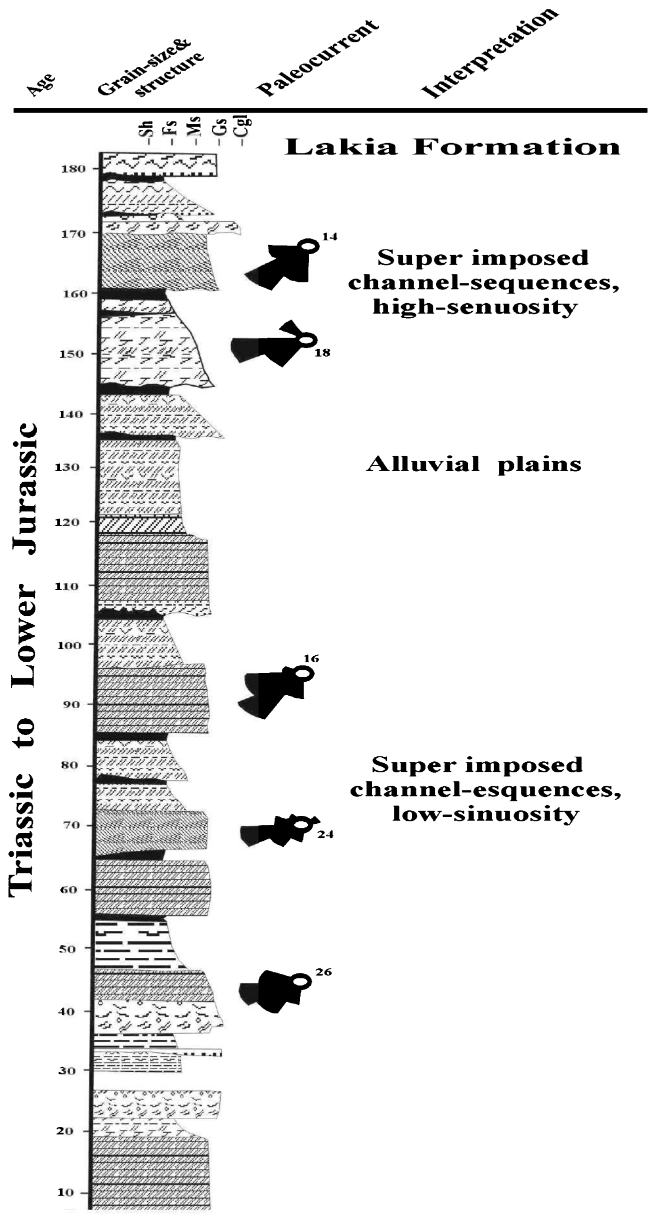

FIGURE 4. Lithological column of the Triassic-Jurassic rocks in southwest Egypt and northwest Sudan.

THE CONTACT BETWEEN THE TRIASSIC AND JURASSIC SYSTEMS

The contact between the uppermost Triassic Minjur/Rukhman formations and the overlying Lower Jurassic Marrat Formation is well demonstrated at Al Mustawi area, northeast of Al Qasim Province. The contact is placed between the quartzitic sandstone of the uppermost Rukhman Formation and the olive gray vuggy dolostone and oolitic limestone of the lowermost Marrat Formation. However, the contact in

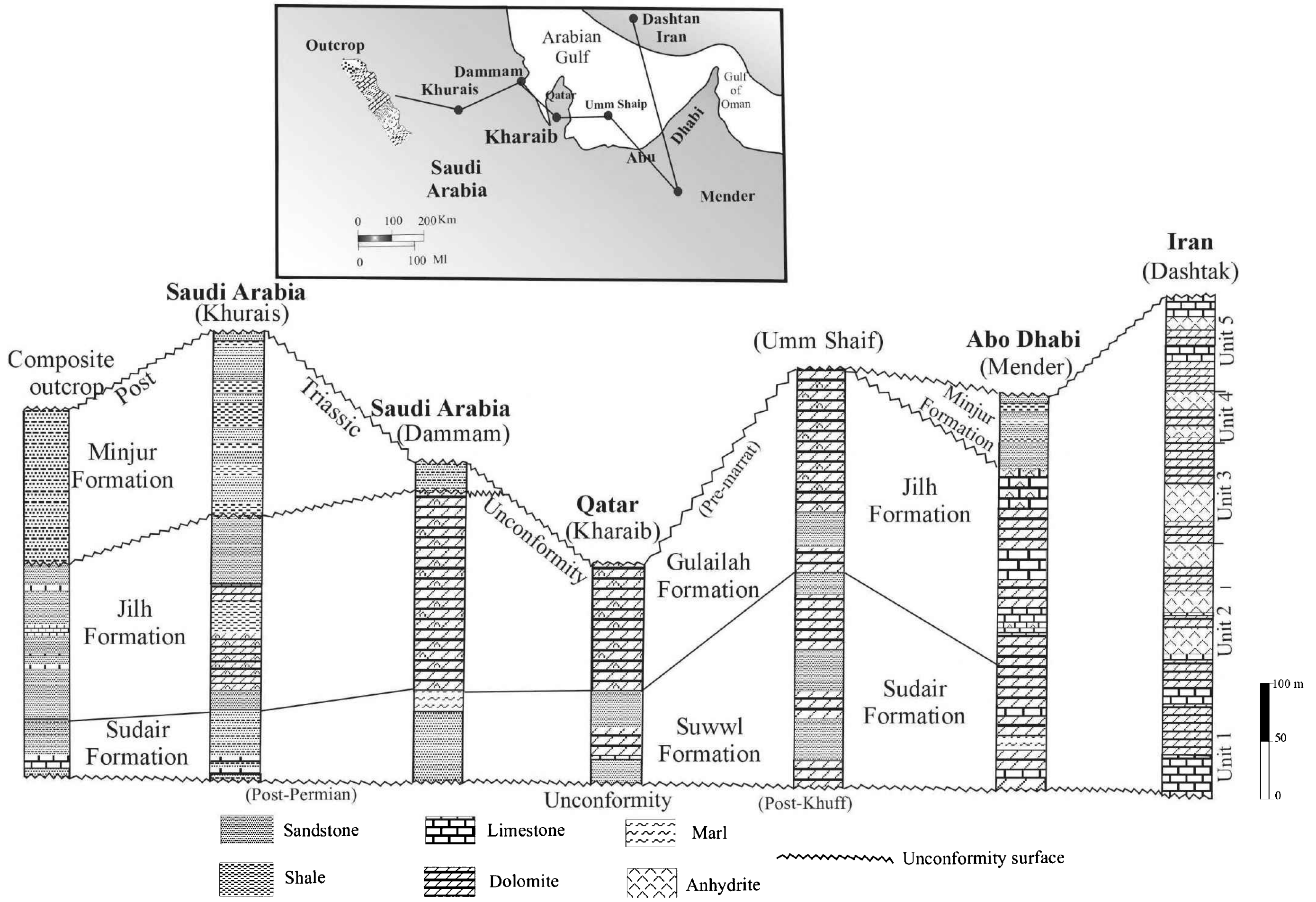

FIGURE 5. Lithostratigraphic correlation of the Middle-Upper Triassic rocks in Saudi Arabia, Qatar, Abu Dhabi and Iran, showing the unconformable relationship between the Upper Triassic-Lower Jurassic rocks.

the northern area of outcrop, the boundary between the Minjur Sandstone and the Marrat is placed at the contact of gray friable, cross-bedded sandstone of the Minjur Sandstone below and the tan-brown limestone above. In fact, there is some evidence that the Triassic rocks were entirely removed at least over the southern half of the Rub al Khali basin and much of the coastal province as well (Powers et al., 1966). So far as known, the passage from Triassic to Jurassic is everywhere represented either by an unconformity or by non-marine sedimentation. For example, in the areas around the margins of the Arabian Shield, marine rocks dated as Jurassic are separated from undoubtedly Triassic or older units by nonfossiliferous sandstones that are tentatively assigned to the Early Jurassic (Powers et al., 1966) (Fig. 5). The lower part of the Marrat Formation shows an unconformable contact with the underlying Triassic rocks that is evident through the general beveling of underlying strata and absence of lower middle Liassic stages (Powers et al., 1966). In Jordan, the Triassic-Jurassic boundary is also unconformable due to the erosion of the uppermost Abu Ruweis Formation at several localities

In Egypt, the Triassic-Jurassic contact is always unconformable and there is a substantial gap between the Qiseib Formation (Early Triassic) and the Lower-Middle Jurassic in all studied localities. For example, there is a gap between the Lower Triassic Qiseib Formation and the Middle Jurassic Rieina Formation at Khashm El Galala (North Eastern Desert). In Sinai, the same large gap occurs between the lower Triassic Qiseib Formation and the Middle Jurassic Raqaba Formation. Moreover, in the subsurface in the northern Western Desert, the Eghi Group or Qattara Formation shows an unconformable relation with the Jurassic Yakout Formation. This suggests that the Upper Triassic rocks are not present in Egypt and were either not deposited or have been truncated (Fig. 6).

LATE TRIASSIC-EARLY JURASSIC STRUCTURAL FRAMEWORK

During the Carboniferous, the African plate at its eastern parts (Libya and Egypt) was uplifted over a large area. Marine transgression subsequently remained north of Egypt or reached it only marginally. Most of Egypt and eastern Libya became an east-west trending structural high and underwent erosion until the Early Jurassic (Klitzsch and Squyres, 1990). The collision of northeast Africa with the northern continents initiated the east-north-east trending structures by re-opening of pre-existing zones of structural weakness which had been more or less inactive since Precambrian time (Schandelmeier et al., 1987). This collision caused initiation of rising magma which in turn caused the arch or domal uplift in the Gabal El Uweinat and in the Aswan area. This ultimately gave rise to the east-west uplift structures that dominated during the Permian, Triassic and Early Jurassic time (Fig. 7).

Toward the end of the Paleozoic, the whole area from directly east of Gabal El Uweinat to Aswan formed a regional high from which the Paleozoic rocks together with some Precambrian basement were eroded. The removed material was transported mainly southwards. South of this uplift, the basement is covered by a 150-200 kilometer wide stretch of Permo-Triassic to Early Jurassic sediments of fluvio-continental origin that were deposited by a southwest to southeastward depositional re-

Age		Egypt			Jordan	Saudi Arabia
Jurassic	Middle	North Galala	West Sinai	East Sinai		
		Riena Fm.	El Raqaba Fm.			
	Early				Kurnub Fm.	Marrat Formation
Triassic	Late				Abu Runeise Fm.	Rukhman Formation
					Um Tina Fm.	
					Iraq al Amir Fm.	Adgham Fm.
	Middle				Mukheiris Fm.	Jilh Fm.
					Hisban Fm.	
					Ain Musa Fm.	
					Dardor Fm.	
	Early	Qiseib Fm.			Main Fm.	Sudair Shale

FIGURE 6. General correlation of the Triassic-Jurassic contact in Egypt, Jordan and Saudi Arabia. Notice that Middle-Upper Triassic rocks are missing across all of Egyptian territory.

gime (Klitzsch, 1984). The uplift was accompanied by extensive faults, striking more or less east-west. Accompanying these faults were magmatic intrusions, such as the alkalic rhyolites of Gabal Musab al Balgum, which date to about 216 ± 5 Ma (Schandelmeier and Darbyshire, 1984).

Regional instability began during the Late Triassic and terminated the stable shelf condition which had persisted on the northern Arabian platform throughout the Paleozoic and into the Middle Triassic (Sadooni and Alsharhan, 2004). Extension and rifting during the Triassic–Jurassic occurred in the suture zone between the Arabian Basin and Iranian Basin. This gave rise to the development of the Zagros Mountain (Fig. 7). At the same time extension and rifting created rift basins within the greater Arabian Basin, which extends in a northeast-southwest to east–west direction parallel to the Tethyan zone (Fig. 7). The indication of Triassic–Jurassic rifting can be deduced from the nature of the cyclic sequences of the Lower Jurassic Marrat Formation. In this formation the cycles are submergence cycles (Khalifa, 1996) beginning with sandy limestone (sandy wackestone /packstones) at the base, capped by deeper marly lime mudstone at the top. Such cycles suggest widening or extension accompanying submergence.

In the Gulf States, partial erosion of the Upper Triassic formations resulted from a drop in relative sea level, caused either by a eustatic fall in sea level, or by an uplift of the shield and the activation of the regional Qatar arch extending to south Fars (Fig. 5). Powers (1968) and Murris (1980) suggestion that most of the cratonic Arabian Peninsula was still tectonically active is supported by data from offshore Abu Dhabi (Fig. 5). During the Late Triassic, tectonic activity caused a major transgression across the Arabian foreland and Iran, and produced the major Rhaetic unconformity throughout the Middle East (Stocklin, 1968; Alsharhan and Kendall, 1986). Extension occurred during the Triassic and Early Jurassic (Tethyan rifting), with a subsequent extensional period lasting from Early Jurassic to Early Cretaceous (Neocomian) and a clearly defined subsidence episode occurring in all basins (Brunet and Cloetingh, 2003).

TRIASSIC-JURASSIC IGNEOUS ACTIVITY

The magmatism and volcanism during rifting at the Triassic-Jurassic transition are clearly observed in the Al Mutawi area (northeast Al Qasim Province) Saudi Arabia. This is well represented by such magmatic effects as volcanic dikes, hydrothermal solution and iron oxide emplacement in the Upper Triassic Rukhman Formation and the Minjur Sandstone (Fig. 2). In this formation the claystones and sandstones were intruded by hydrothermal solutions that were enriched with iron oxides. The formation also contains calcite geodes, and deposits of quartz, fluorite and barite. The iron oxides occur within the Rukhman Formation as vertically oriented pipes that became apparent during construction work on the Burydah-Riyadh highway. These were also encountered in all water wells drilled in this area (Fig. 2). The iron oxides also appear as granules at several horizons through the vertical sequence in the Rukhman Formation. Additionally, it is observed that iron oxide staining occurs on the tops of the sandy siltstones of the Rukhman Formation where it is expressed as a polygonal network covering an area of about 100-200 square meters. Such ferruginous deposits were precipitated vertically along fissures and cracks that originally connected to deep-seated faults. The volcanic dikes are usually associated with the iron oxides and range in width from 20 to 30 cm and an average length of 60 cm. Some of these appear on the surface of outcrops forming black patches. These may have been emplaced before the earliest phase of Jurassic sedimentation.

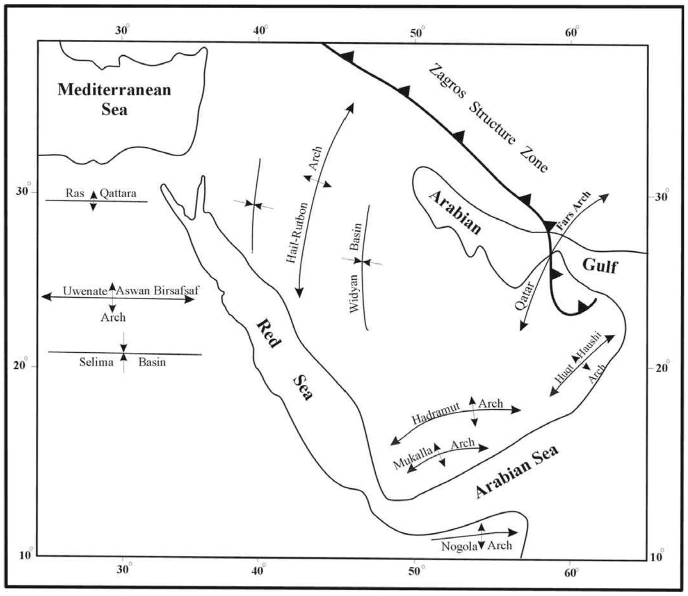

FIGURE 7. Structural elements dominant in northeast Africa and Arabia during the Triassic-Jurassic transition.

In Egypt, at the Gabal Uweinat-Bir Safsaf uplift, subaerial alkaline magmatism occurred long after the Carboniferous collision, from the end of the Permo-Triassic up to the Early Jurassic (Schandelmeier et al., 1987). During this time, formation of domal structures, which had occurred since the Carboniferous, continued for more than 50 Ma, driven by heat flow under the uplift. Extrusion of alkaline volcanics and generation of graben and horsts structures accompanied rifting. The change from alkaline to more theoleiitic continental volcanism that commonly occurs in widening rift systems is not recorded in the Gebel Uweinat–Bir Sasaf uplift system (Giret and Lameyre, 1985). The alkaline volcanics at Gabal Uweinat were dated by Klerkx and Rundel (1976) using K/Ar to yield 235±5 Ma. Also, age dating of the trachytic-phonolithic rocks from Gabal Kamel using K/Ar yields 233± 9 Ma and 240± 7 Ma respectively (Franz et al., 1987). In addition, dating the alkali- rhyolitic rocks north of the Bir Safsaf complex using Rb/Sr yielded 216± 5 Ma (Schandelmeier and Darbyshire,1984). In the Late Permian/Early Triassic the area between Gabal Uweinat and Bir Safsaf, south Western Desert was uplifted along zones of pre-existing crustal weakness. These reactivated fractures gave way to the intrusion of basaltic dikes around 235 Ma as well as rhyolitic subvolcanics around 216 Ma (Schandelmeier and Darbyshire, 1984). A group of K/Ar ages falling in the range of 230 ± 15 Ma was reported from northwest Sudan. During this period the massifs of Zarqat Naam, Bir Um Hebal and Gabal Silaia were emplaced (Meneisy, 1990). In Sinai, a major unconformity between the dominantly clastic Upper Carboniferous and Triassic deposits was encountered in several wells indicating a major unconformity in the Late Paleozoic or Permo-Triassic (Meneisy, 1986). The grano-syenite masses of Gabal Silaia and Gabal Zarqat Naam fall along major transform fault that runs nearly N 60 E, while the Bir Um Hebal complex is located along parallel transform fault south of the above mentioned localities. In central Sinai, the presence of a basaltic sheet below the Qiseib Formation indicates Permo-Triassic magmatic events. However, Weissbrod (1969) regarded the basalt that occurs in other localities as a sill of Late Triassic to Early Jurassic age. The relative age of this sill is about 178±12 Ma, based on K/Ar analysis.

The above data indicate frequent igneous activity during the Middle to Late Triassic (240–216 Ma) followed by a major gap, as the next age is 178 Ma. This suggests a major unconformity between the end of Triassic and the beginning of Jurassic in Egypt and Sudan as found in several other countries.

DISCUSSION

The boundary between the Late Triassic and Early Jurassic periods represents a major event in the Mesozoic Era, during which extinction, diastrophism, structures crisis, radical facies changes, and volcanic eruptions occurred. The causes of widespread extinction during the Late Triassic/Early Jurassic have long been based on the assumption that extinction at the system boundary was sudden and synchronous in both the terrestrial and marine environments. Indeed many paleontologists have long described the end Triassic extinction as one of the five largest extinction in the Earth history and attributed it to catastrophic cause such as bolide impact and widespread volcanism, although this view is now being modified (Lucas and Tanner, 2004; Tanner and Kyte, 2005; Stanley, 2005; Vuks, 2005).

The Triassic-Jurassic boundary in northeast Africa (Egypt and Sudan) is difficult to study, since there is major gap between the Triassic and Jurassic strata over Egyptian territory. This resulted from the epiorogenic movement that took place from the advent of the Early Triassic to the earliest Cretaceous in the southern and middle parts of Egypt (maybe the Laramide Movements) and the Mediterranean Movement (east-west) in the northern parts. The studied localities (northeast Africa and Arabian plate) present two good examples of these Triassic-Jurassic events. The first one occurs in Egypt (northeast Africa) due to the structural uplift dominating during this event, where diastrophic ruptures and volcanism took place. In this area the there are no records of the exposed Upper Triassic rocks, either in the Western or Eastern Deserts or on the Sinai Peninsula (Fig. 6). Triassic and Jurassic facies in southern Egypt from latitude 22° N to latitude 29° N are not recorded, and were most probably not deposited. The Triassic shoreline appears to have been located at the eastern side of the northern Galala (Lat. 30° N). This may be due to the east-west tectonic movement concurrent with the Triassic period (Hussein and Abd Dallah, 2001). The structural crisis in northeast Africa was a result of the collision of northeast Africa with the northern continents causing the east-north-east trending structures by re-opening of pre-existing zones of structural weakness which had been more or less inactive since Precambrian time (Schandelmeier et al., 1987). This shear zone gave rise to melting of the upper mantle and a part of the lower crust and in turn formed rising magma expressed as lava flows. North of these localities at northern Sinai, where the Middle Triassic facies occur at Arief el Naqa, however, the Upper Triassic facies were not recognized in this area.

The second case occurs in the Arabian plate (Saudi Arabia, Qatar, Oman and Iraq), where there is discontinuous sedimentation between Upper Triassic and Lower Jurassic sediments. The discontinuity shows evidence for the sudden lowering in sea level, depositing fluvial to continental sediments represented by the Upper Triassic Rukhman Formation in the northern Saudi Arabia and Minjur Sandstones in the south parts of Saudi Arabia (Figs.2, 6) The presence of the volcanic eruptions between the Permo-Triassic Qiseib Formation and the Jurassic rocks in western Sinai (Um Bogma area) suggests the widening and extension of the basins in the transitional period between the Paleo- and new Tethys. The volcanics are dated to 225 Ma, which confirms a Middle/Late Triassic age. This interpretation contradicts the opinion of Sahrief (1982, 1983) who mentioned that the Early Triassic facies were deposited during widespread regressive conditions.

The presence of siliceous sandstone at the top of the Rukhman Formation is a good indicator of the subaerial exposure between the Late Triassic and Early Jurassic periods, referring to the fact that this type of sandstone is considered a diagenetic quartzarenite that formed due to intensive subaerial weathering for an extended period of time, perhaps several million years. This phenomenon was studied by Khalifa (2006), who considered that this could be used for recognition of sequence boundaries, rather than using unconformity surfaces.

The sea level changes across the Triassic–Jurassic boundary are represented by a "regression-transgression couplet" (Hallam and Wignall, 1999). For example, in classic sections in and around New York Canyon in Nevada the regression is marked by a late Rhaetian siltstone facies separating Hettangian-Sinemurian limestones (Hallam and Wignall, 1999). Also, in northern Bavaria, fluviatile Hettangian sediments occur in marine channels cut into Rhaetian sandstones and are overlain by the marine Hettangian. A major world wide regression has long been advocated and considered one of the main causes of the significant biotic changes that mark the Triassic-Jurassic boundary (Krystin et al., 2005). Hallam (1990) has argued that there was a fast regression followed by transgression couplet in the Northern Calcareous Alps and elsewhere, with a maximum sea level fall of 50 m (Hallam and Wignall, 1997). The same situation can be observed in the Triassic-Jurassic contact in Saudi Arabia. In the Upper Triassic Rukhman/Minjur formations the sea level reaches the minimum level during which the uppermost sandstone bed was altered diagenetically concurrent with the subaerial exposure that formed the siliceous quartzarenite (Khalifa, 2006). This was followed by the transgression during Early Jurassic during which the carbonate rocks of the basal Marrat Formation were deposited. The relationship between sea level changes and mass extinctions was discussed by Hallam and Wignall (1999). They showed that nearly all-mass extinctions are associated with rapid, probably global sea level fluctuations of which regressive-transgressive couplets are the most common. Thus the end of Triassic extinction is more obviously associated with regression than the subsequent transgression and is well conformable with the theory of Newell (1967). Also, during the Late Triassic, there was decrease in the subsidence rate or a decrease in the sedimentation rate near the end of the Triassic (Satterley, 1996). An increase in subsidence rate at this time is preferred because rift-related subsidence peaked in the Early Jurassic (Garrison and Fischer, 1969; Bernoulli and Jenkyns, 1974). Similar arguments apply to the facies changes at the Triassic/Jurassic boundary and to the red wackestone beds in the Steinernes Meer section (Satterely, 1996). Thus, in the Rhaetian, stepped (fault-controlled) subsidence related to rift activity at the future Tethyan passive margins seems to have partially controlled deposition. This is entirely in agreement with deposition within this area of active Late Triassic extensional tectonics. The presence of red beds in the middle member of the Lower Jurassic Marrat Formation may also indicate a sudden deepening event. The sudden occurrence of this red color may reflect extension and spreading of the southern Tethys basin. This is consistent with the iron and manganese staining in the wackestone facies in the Lower Jurassic in the Hallstatt Basin, Austria (Satterely, 1996).

The paleogeographic distribution of the Upper Triassic rocks in the studied localities indicates that at the end of Triassic period Egypt was land above sea level. This may have accompanied the West-East domal structure in the north Western Desert (parallel to Ras Qattara uplift) and in the south Western Desert, where volcanic eruptions are recorded (Gabal Uweinat-Bir Safsaf-Aswan uplift) and all over the Sinai

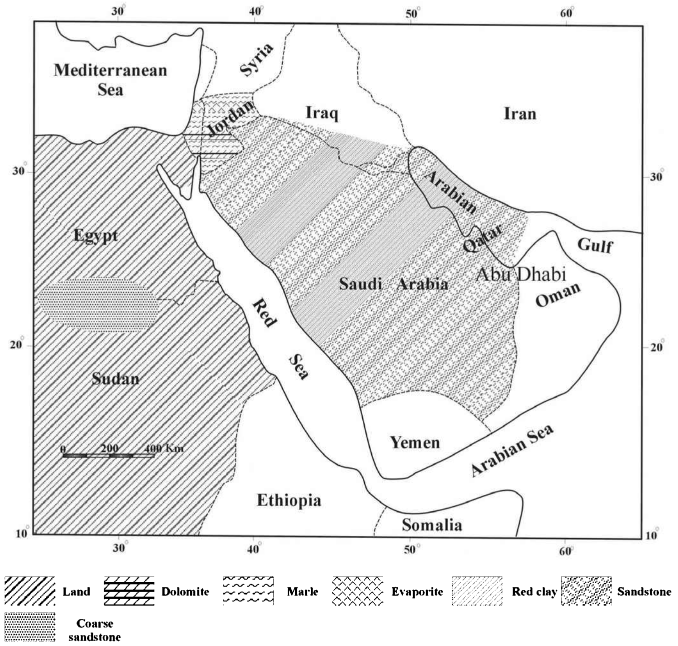

FIGURE 8. Paleogeographic distribution of Upper Triassic rocks in northeast Africa and Arabia.

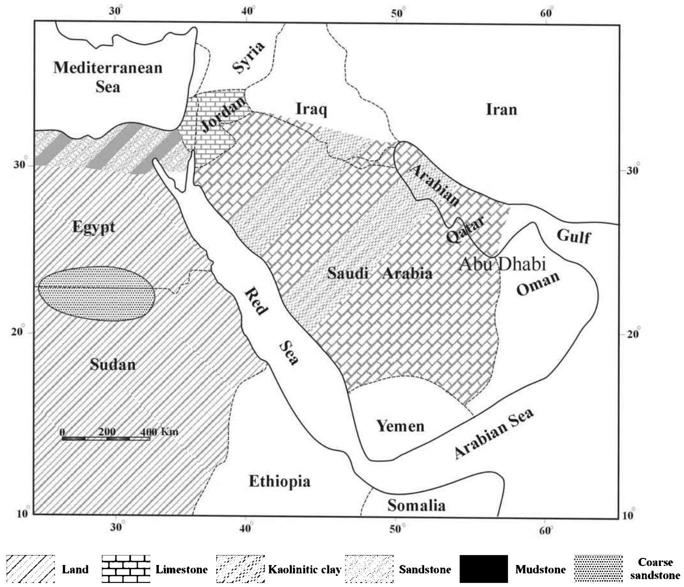

FIGURE 9. Paleogeographic distribution of the Lower Jurassic rocks in northeast Africa and Arabia.

Peninsula (Fig. 8). The paleoshoreline was located at 30° N (modern latitude), extending from Jordan southeastward parallel to the Arabian Shield, forming the western margin of the Arabian Basin. Depth increased east and northeastward, covering Jordan, Saudi Arabia and the other adjacent countries (Fig. 8). The shoreline facies have a wide geographic distribution across Saudi Arabia, Oman, Qatar, Abu Dhabi, and Iraq. Most of the fluvial facies are sandstones and kaolinitic claystone similar to facies of the Rukhman and the coeval Minjur Sandstone. East and northeastward the fluvial facies intertongue with the coastal marine facies represented by fine-grained syngenetic dolostone, intercalated with evaporites and sandy clays as found in the Upper Triassic Abu Ruweis Formation in Jordan. The facies deepen northeastwards, grading to marine shelf limestone and dolostones covering most of Iran (Fig. 8). During the Lower Jurassic period, the sea transgressed and overlapped the costal marine and fluvial facies of the Upper Triassic and extended southwards to (modern) latitude 28°-29° N. Most of northern Egypt was covered by clastic facies of fluvial to fluvio-marine environments as found in the subsurface in the Western Desert (Yakout Formation) and in the northern Galala (Reinia Formation) and in central–western Sinai (El Raqaba and Temmariya formations) (Fig. 9). Continued sedimentation and deepening to the north and northeastwards resulted in the deposition of shelf limestones enriched with fossils covering most of the Arabian Basin (Saudi Arabia, Jordan, Iraq, Iran, Qatar, and Oman) (Fig. 9).

CONCLUSIONS

The facies across the Triassic-Jurassic boundary were studied in southern Tethys (Egypt, Jordan and Saudi Arabia). In Saudi Arabia, the Upper Triassic Rukhman/Minjur formations are mainly clastics and are unconformably overlain by the Lower Jurassic Marrat Formation at Al Qasim Province. Such a contact represents a regression-transgression couplet. In Egypt the east-west movement gave rise to tectonic uplift preventing the deposition of the Triassic and Jurassic sediments. Northward of 30ºN (modern latitude), the Lower Triassic Qiseib Formation represents the only rock unit of Triassic age, and it is unconformably overlain by the Lower Jurassic Raqaba Formation. That Upper Triassic rocks were not recorded in Egypt demonstrates that a large gap or hiatus exists between the Triassic and Jurassic. During this hiatus volcanic eruption took place in the southern Western Desert and hydrothermal iron ores formed in the Upper Triassic rocks in Saudi Arabia.

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ARCHOSAUR FOOTPRINTS – POTENTIAL FOR BIOCHRONOLOGY OF TRIASSIC CONTINENTAL SEQUENCES

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Abstract—Historically, footprint-bearing localities in eastern and western North America and southern Thuringia and northern Bavaria have played pivotal roles in Triassic archosaur footprint research. In a nearly complete sequence of formations and footprint-horizons in the Moenkopi Group (U.S.A.), Newark Supergroup (U.S.A. and Canada), and Buntsandstein, Muschelkalk, and Keuper groups (Olenekian to Norian-Rhaetian) of central Europe, the principal morphs of archosaur footprints are represented by *Rotodactylus*, *Synaptichnium*, *Isochirotherium*, *Brachychirotherium*, *Chirotherium*, *Sphingopus*, *Parachirotherium*, *Atreipus*, and *Grallator*. Additionally, the temporal and, in principal, the evolutionary "root" is documented by *Protochirotherium* from the early Olenekian of Hessen. Of utmost significance is the evolutionary succession from *Chirotherium* to *Grallator*. Therein, the development of two key features seen in the origin and early evolution of dinosaurs – tridactyl foot-morphology and the bipedal gait – is documented between the Olenekian and Norian. The stratigraphic distribution of these forms and their potential for biochronology yields a biochronological sequence we sketch out as follows: For the Triassic we discriminate six successive biochrons (I-VI). Each biochron is marked by an index taxon (in bold), a characteristic footprint assemblage, and its stratigraphic distribution. I. *Protochirotherium* (*Synaptichnium*), Late Induan-Olenekian. II. *Chirotherium*, *Rotodactylus*, *Isochirotherium*, *Synaptichnium* ("*Brachychirotherium*"), Late Olenekian-Anisian. III. *Sphingopus–Atreipus–Grallator, Rotodactylus*, *Isochirotherium*, *Synaptichnium* ("*Brachychirotherium*"), Late Anisian-Ladinian. IV. *Parachirotherium–Atreipus–Grallator*, *Synaptichnium* ("*Brachychirotherium*"), Late Ladinian. V. *Atreipus–Grallator*, *Brachychirotherium*, Carnian-Norian. VI. *Grallator–Eubrontes*, *Brachychirotherium*, Norian-Rhaetian.

In addition to their biostratigraphic utility, the succession of ichnotaxa and ichno-assemblages also reflects evolutionary developments in foot morphology and in the locomotor apparatus of the Archosauria, a progression thus far incompletely documented by the body fossil record. As a consequence of their limited temporal ranges, and their intercontinental distributions in large quantities, the principal archosaurian ichnotaxa open up additional and innovative possibilities for the biochronology of continental sequences.

INTRODUCTION AND BACKGROUND

The scientific history of Triassic tetrapod tracks begins with the description and binominal naming of the famous footprints and trackways of *Chirotherium barthii* and *C. sickleri* from the Buntsandstein near Hildburghausen in Thuringia, Germany by Sickler (1834) and Kaup (1835). These momentous events were followed, beginning in 1836, by documentation of the extensive discoveries in the "New Red Sandstone" (now the Newark Supergroup) of Connecticut and Massachusetts by E. Hitchcock with the descriptions of important ichnotaxa like *Eubrontes* and *Grallator* (Hitchcock, 1845, 1858). The next phase of significance commenced in the middle of the twentieth century with the study of the Early-Middle Triassic tetrapod ichnofauna of the Moenkopi Formation of Arizona by F.E. Peabody. In his pioneering monograph, Peabody (1948) demonstrated for the first time the intercontinental distribution of *Chirotherium*, with identical ichnospecies (*C. barthii* and *C. sickleri* [= *C. minus*]) present in both the Moenkopi Formation and the Solling Formation of southern Thuringia. *Rotodactylus* constitutes another remarkable tetrapod ichnotaxon from Arizona described by Peabody that was subsequently recognized preserved in association with *C. barthii* and *C. sicklerii* in several strata in the Buntsandstein near Hildburghausen, further supporting the correlation between the two units. Building on the results of Peabody (1948, 1955a, 1956), Haubold (1967, 1971a, b), in his studies of the track assemblages in the Buntsandstein, further substantiated the intercontinental distribution of *Rotodactylus*.

In the following decades, the anatomical interpretations of *Chirotherium*, *Rotodactylus*, *Eubrontes*, *Grallator*, and other classical Triassic ichnotaxa were shown to parallel the evolutionary sequence of Triassic archosaurs documented by an increasing quantity of skeletal evidence. It was J. Walther (1917) who first proposed a dinosaur-like producer based on the footprint morphology and trackway pattern of *Chirotherium*. Soergel (1925) likened the *C. barthii* track maker to *Euparkeria*, a taxon whose phylogenetic position is presently recognized as close to the base of the hypothesized crown-group Archosauria (Gauthier, 1986; Sereno, 1991). This corresponds well with the geological age and the morphology of *C. barthii*. Based on these data, and following the excellent reconstruction of *Euparkeria* presented by Paul (2002), the *Chirotherium* track maker was reconstructed and displayed in a life-size bronze-sculpture in the *Chirotherium* Monument that was inaugurated in 2004 in the market-place of Hildburghausen, close to the type locality of *Chirotherium barthii* (Haubold, 2006).

The most common and popular interpretation of *Chirotherium barthii* and *C. sickleri* as tracks of various members of the Crurotarsi is not followed here. To the contrary, the Olenekian to early Anisian age of *Chirotherium*: (1) supports a more general interpretation in the sense stated above, and (2) the morphology of the pes imprints of both *C. barthii* and *C. sickleri* include and presage the tridactyl pattern of the later dinosaurs, and of theropods in particular. Support for this interpretation is further substantiated by the development of the two key-features in the evolution of dinosaurs: tridactyly and bipedality, both of which are reflected in a stratigraphic succession of footprint morphs and trackways from *Chirotherium*, *Sphingopus*, *Parachirotherium* and *Atreipus* through *Grallator* and *Eubrontes* (Haubold and Klein, 2000, 2002). For *Synaptichnium* and *"Brachychirotherium,"* as well as

Isochirotherium in the Middle Triassic and *Brachychirotherium* (*sensu stricto*) in the Upper Triassic, a general affinity with the Crurotarsi appears to be realistic. However, this cannot be demonstrated convincingly as is usually supposed, and there is no evidence for any synapomorphies of the group in these footprints.The correlation of footprint morphs, beginning in the Lower Triassic with *Protochirotherium*, with the archosaurian evolutionary "grades" seems to be well substantiated, in particular by the extraordinarily fine preservation of the latter described by Fichter and Kunz (2004) from the Detfurth Formation of the Middle Buntsandstein of Hessen.

The *Rotodactylus* track maker has been interpreted as a member of the Lagosuchia resp. Dinosauromorpha (Haubold, 1967, 1999; Haubold and Klein, 2002), a conclusion supported by correspondence of the tracks with skeletal anatomy. Of importance is the geological age of the tracks compared to their proposed skeletal correlates: *Rotodactylus* and *Chirotherium*, as well as *Isochirotherium* and *Synaptichnium* ("*Brachychirotherium*"), occur as early as the Olenekian-Anisian transition, and prove a diversity that has to be younger than the hypothetical stage of Archosauria, i.e., the beginning of the differentiation of this crown-group.

Early-Late Triassic archosaur tracks come from sequences with multiple horizons in localities as far removed today as southern Thuringia and northern Bavaria on one side and Arizona, Connecticut and Massachusetts on the other. In tandem, they play key roles in the biochronological documentation of the evolution of archosaurian foot morphology and locomotion by fossil imprints and tracks. On both continents, sequences with known track horizons range from the Olenekian to the Norian-Rhaetian (Fig. 1). Through intensive research, important correlative locations have been discovered in other regions of Germany, Switzerland, France, Great Britain, Italy and Poland. In North America, the number of occurrences in the Triassic of the Newark Supergroup, for example in Pennsylvania, and in the Chinle Group of Colorado, New Mexico, Utah, Arizona and Texas have increased. Triassic archosaur tracks are known from Lesotho in southern Africa (Molteno and Lower Elliot formations), South America (Argentina), and southern China (Guanling Formation of the Guizhou Province [Lü et al., 2004]).

The large number of ichnogenera with archosaurian affinities that have been described so far– roughly 50, even excluding *Chirotherium*, *Rotodactylus*, *Eubrontes* and *Grallator* – is a further indication that the record is truly extensive. Besides *Chirotherium* itself, the following ichnogenera are considered chirotherian: *Brachychirotherium* Beurlen, 1950, *Isochirotherium* Haubold, 1971, *Parachirotherium* Kuhn, 1958, *Protochirotherium* Fichter and Kunz, 2004, *Parasynaptichnium* Mietto, 1987, *Sphingopus* Demathieu, 1966, and *Synaptichnium* Nopcsa, 1923. Furthermore we consider as archosaur tracks forms that have been described under the following names: *Aetosauripus* Weiss, 1934, *Agialopous* Branson and Mehl, 1932, *Agrestipus* Weems, 1987, *Anchisauripus* Lull, 1904, *Atreipus* Olsen and Baird, 1986, *Banisterobates* Fraser and Olsen, 1996, *Batrachopus* Hitchcock, 1845, *Brontozoum* Hitchcock, 1847, *Coelurosaurichnus* v. Huene, 1941, *Dahutherium* Montenat, 1968, *Dinosaurichnium* Rehnelt, 1950, *Eubrontes* Hitchcock, 1845, *Evazoum* Nicosia and Loi, 2003, *Gigandipus* Hitchcock, 1856, *Grallator* Hitchcock,

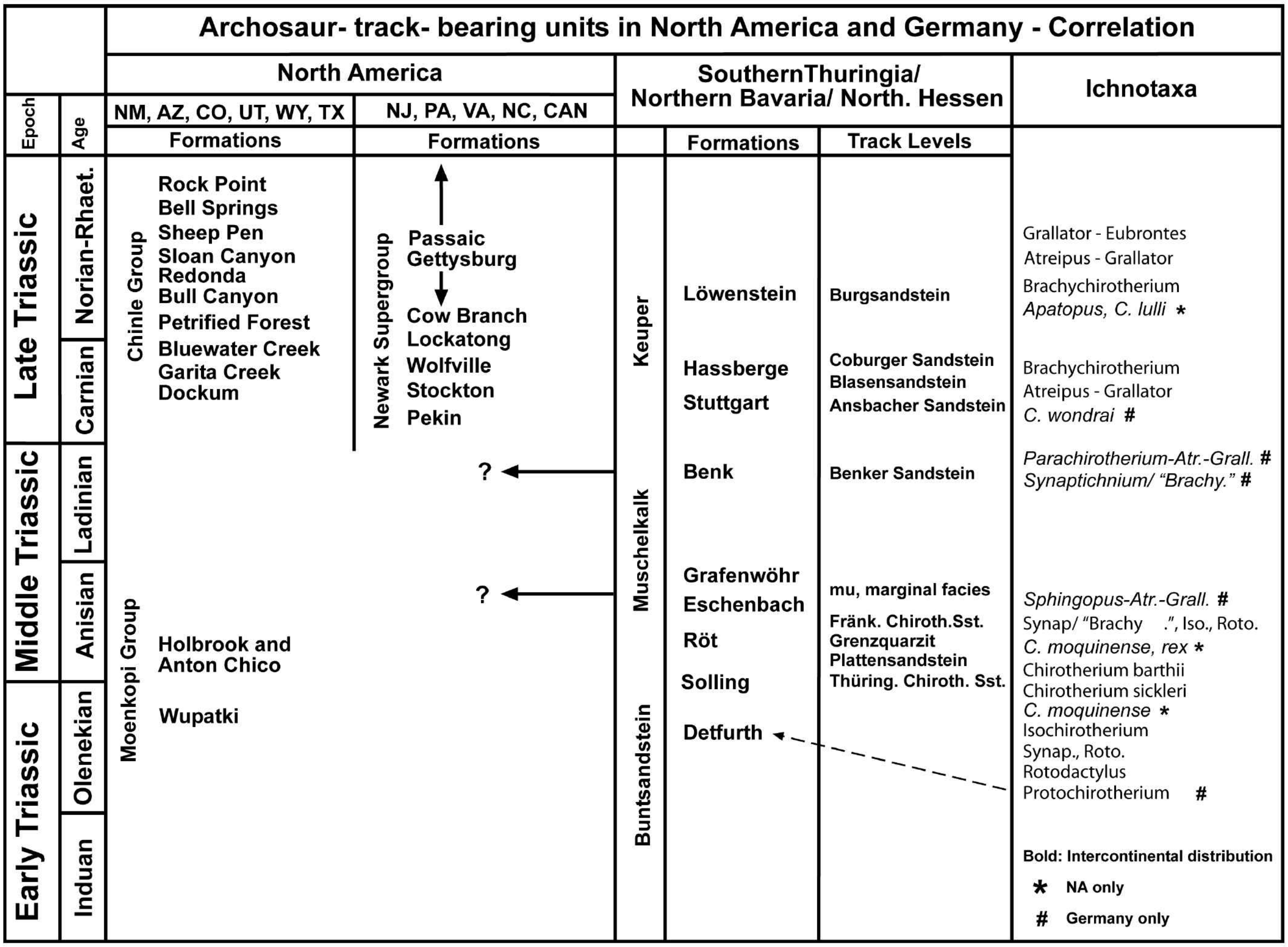

FIGURE 1. Archosaur footprint horizons and track-bearing formations in North America and southern Thuringia/northern Bavaria (Germany). In nearly complete sequences, the intercontinental distributions of characteristic ichnotaxa are used for correlation. Notice conformity of the assemblages at the corresponding levels and differences due to the gap in the North American record between the late Anisian and late Ladinian.

1858, *Gregaripus* Weems, 1987, *Otozoum* Hitchcock, 1847, *Pachysaurichnium* Demathieu and Weidmann, 1982, *Prorotodactylus* Ptaszynski, 2000, *Rigalites* v. Huene, 1931, *Swinnertonichnus*, Sarjeant, 1967 and *Thecodontichnus* v. Huene, 1941. These ichnotaxa pertain to specimens from different parts of the Triassic and their alphabetical listing above does not indicate an evaluation of their validity. A special taxonomic situation surrounds the tracks from the Upper Triassic of Lesotho for which Ellenberger (1972) introduced a wide variety of names like *Anatrisauropus*, *Bosiutrisauropus*, *Deuterosauropodopus*, *Deuterotrisauropus*, *Paratetrasauropus*, *Paratrisauropus*, *Pentasauropus*, *Prototrisauropus*, *Pseudotetrasauropus*, *Pseudotrisauropus*, *Psilotrisauropus*, *Qemetrisauropus*, *Sauropodopus*, *Seakatrisauropus*, *Tetrasauropus*, and *Trisauropodiscus*. Comparisons of these with ichnotaxa described from elsewhere, and consensus on synonymies, are still in progress; most of his ichnotaxa have not been recognized outside Lesotho and are generally perceived (even in the absence of detailed analyses) as junior synonyms of other, better-known ichnotaxa.

Even larger is the number of ichnospecies that have been established within the aforementioned ichnogenera. For *Chirotherium* alone, the authors counted 50 species names; for all chirotherians, in nearly any combination within the ichnogenera, there are at least 75 ichnospecies. Altogether, about 50 ichnogenera and about 180 ichnospecies have been ascribed to Triassic archosaurs. The status of many ichnotaxa is doubtful; in many cases, they are demonstrably synonyms of well-established taxa. However, this synonymy is evaluated differently, depending on the material and the describing author. Some authors have erected ichnotaxa while ignoring extramorphology, a phenomenon that was recognized as having a misleading influence on tetrapod ichnotaxonomy as long ago as Peabody (1948). For many of the named ichnotaxa, synonymy remains open, and such forms must be considered phantom taxa (*sensu* Haubold, 1996).

Following the very precise guidelines established by Peabody (1955a), ichnospecies and ichnogenera cannot be definitively attributed to a species or genus that is based on body fossils. Body fossil genera are nearly equivalent to ichnospecies. So, the lowest level to which a Triassic archosaur track can be differentiated corresponds with an osteological genus. Consequently, the number of named ichnotaxa cited above would imply a correlative number of osteological ichnogenera. This seems unrealistic – the presently documented ichnological archosaur diversity in the Triassic must be reduced substantially to a smaller number of ichnogenera and ichnospecies.

TRIASSIC ARCHOSAUR FOOTPRINTS – THE EVIDENCE

Early Early Triassic

Tetrapod footprints from this interval come from the Labyrinthodontidae Beds (late Induan) of Wióry (Poland) and from the Dethfurt and Hardegsen formations (early Olenekian) of northern Hessen, Germany (Demathieu and Haubold, 1982; Fuglewicz et al., 1990; Ptaszynski, 2000; Fichter and Kunz, 2004). Essential components of these assemblages are *Synaptichnium* (Fig. 2A-B) and *Protochirotherium*, including the type species of the latter, *P. wolfhagense* Fichter and Kunz, 2004 (Figs. 2C, 3A-B). The status of *Synaptichnium* and the relationship to *Protochirotherium* is uncertain (see also below). From the locality in Poland, *Brachychirotherium* and *Isochirotherium* were described by Fuglewicz et al. (1990) and Ptaszynski (2000). However, the features exhibited by these specimens, particularly the digit proportions (long pedal digit IV), differ from those listed in the diagnoses for these taxa (Beurlen, 1950; Haubold, 1971b; Karl and Haubold, 1998). We therefore refer this material to *Protochirotherium* (Fig. 2D-E). *Synaptichnium* and *Protochirotherium* indicate a primitive archosaur foot morphology typified by long pedal digits IV and V.

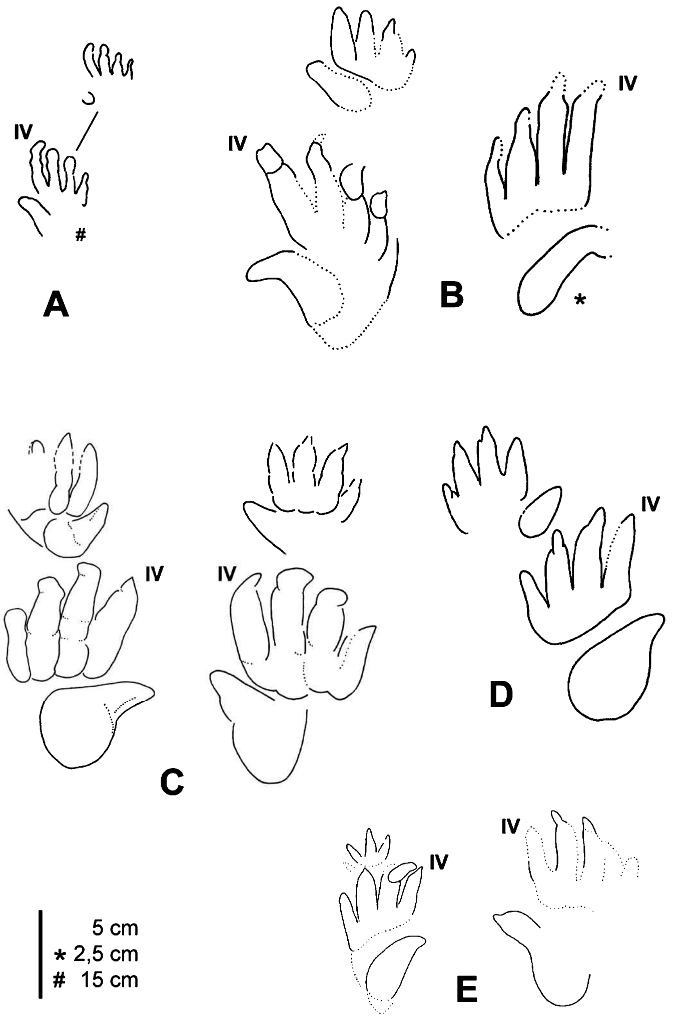

FIGURE 2. Characteristic archosaur footprints from the early Early Triassic. **A, B,** *Synaptichnium*, Hardegsen Fm., Hessen and Labyrinthodontidae beds, Wiòry, Poland. **C,** *Protochirotherium wolfhagense* Fichter and Kunz, 2004, Detfurth Fm., Hessen (holotype at right). **D, E,** *Protochirotherium* (*Brachychirotherium* and *Isochirotherium* after Ptaszynski, 2000 and Fuglewicz et al., 1990), Labyrinthodontidae beds, Wiòry. Notice digit proportions and long digits IV and V in the pes. **A** after Demathieu and Haubold (1982); **B, D, E** after Ptaszynski (2000) and Fuglewicz et al. (1990).

Late Early Triassic and Middle Triassic

Beginning in the late Olenekian, there is evidence of a broad spectrum of archosaur tracks in the global record, exemplified by *Rotodactylus*, *Synaptichnium*, *Isochirotherium* and *Chirotherium*, reflecting different evolutionary developments in foot morphology and a biological diversity not thus far documented by the skeletal record. From strata in the "Thüringischer Chirotheriensandstein" (late Olenekian-Anisian) of southern Thuringia, dense concentrations of pentadactyl pes and manus impressions of *Rotodactylus* are known (Fig. 4A-C; Haubold, 1967, 1971a, b, 1999). A characteristic feature of *Rotodactylus* is the dominance of digit group II-IV and the extreme posterior position of a small punctiform mark that constitutes the impression of digit V. The digit proportions are I<II<III<IV. Trackways preserve evidence of long strides and a primary, lateral overstep of the manus by the pes, though respective values of overstepping and stride length show high variability. The data indicate cursorial trackmakers that, with our present knowledge, must be attributable to dinosauromorphs comparable in "grade" to lagosuchians

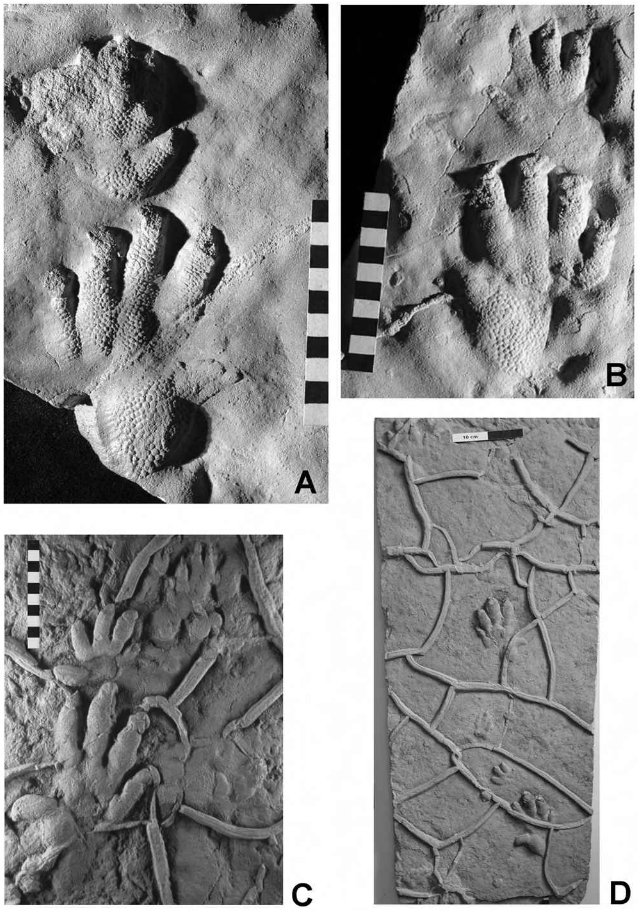

FIGURE 3. **A, B,** *Protochirotherium wolfhagense* Fichter and Kunz, 2004 pes and manus imprints with preserved skin impressions (holotype at right) from the Detfurth Fm. (Olenekian) of Hessen, Germany. **C, D,** *Chirotherium barthii* and *C. sickleri* from the type surface in the Thüringischer Chirotheriensandstein, Olenekian-Anisian of southern Thuringia (Germany). **C,** *C. barthii* (center), *C. sickleri* (upper right) and small "*Brachychirotherium*" (lower right). **D,** Trackways of *C. barthii* and *C. sickleri.* Notice differences in digit proportions, particularly the long pedal digit IV in *C. sickleri* compared with *C. barthii.* **A, B,** from casts in the Institute for Geological Sciences, Martin-Luther-University Halle-Wittenberg (original material in the Provincial Museum Wolfhagen, Hessen); **C, D,** from Haubold (2006).

(Haubold, 1999). *Rotodactylus* was first described from material from the Moenkopi Group of Arizona by Peabody, 1948 (see above). Additional important evidence comes from the Middle Triassic of France (Demathieu and Gand, 1973).

Synaptichnium continues from the Early into the Middle Triassic. This ichnogenus retains an overall conservative foot structure and long digits IV and V. (Fig. 5A-E). Such footprints are recorded on surfaces in the Moenkopi Group of Arizona (Peabody, 1948) and the Middle Triassic of England, France, Italy and Germany (Demathieu, 1970; Tresise and Sarjeant, 1997; Avanzini, 2000; Klein and Haubold, 2004). The ichnotaxonomic situation in *Synaptichnium* is complicated by the following circumstances: (1) no type has been fixed thus far (see Nopsca 1923, Haubold, 1971b), (2) *Synaptichnium* in the early Early Triassic can possibly be synonymized with *Protochirotherium* (see above), and (3) footprints described under *Synaptichnium* from the late Early – Middle Triassic show a transition to *"Brachychirotherium"* in different extramorphological variations, (Klein and Haubold, 2004; see below). The ichnotaxon is presently under revision by the authors. A primary component of the assemblages in Germany and France are footprint morphs that have been referred to *Brachychirotherium* (Haubold, 1971b). However, in the revision of the type material from the Keuper (Karl and

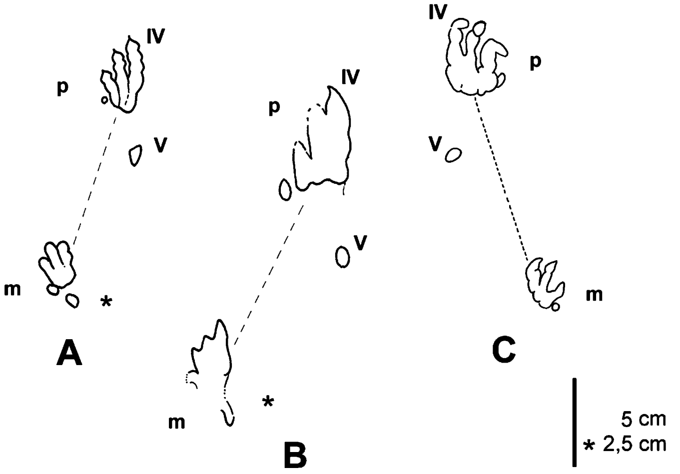

FIGURE 4. Tracks of *Rotodactylus* from late Early and Middle Triassic. **A,** *Rotodactylus matthesi*, Thüringischer Chirotheriensandstein, southern Thuringia. **B,** *Rotodactylus cursorius*, Moenkopi Group, Arizona. **C,** *Rotodactylus lucasi*, Anisian-Ladinian, Massif Central, France. Notice posterior position of digit V and overstepped manus. After Peabody (1948), Haubold (1967), and Gand (1976).

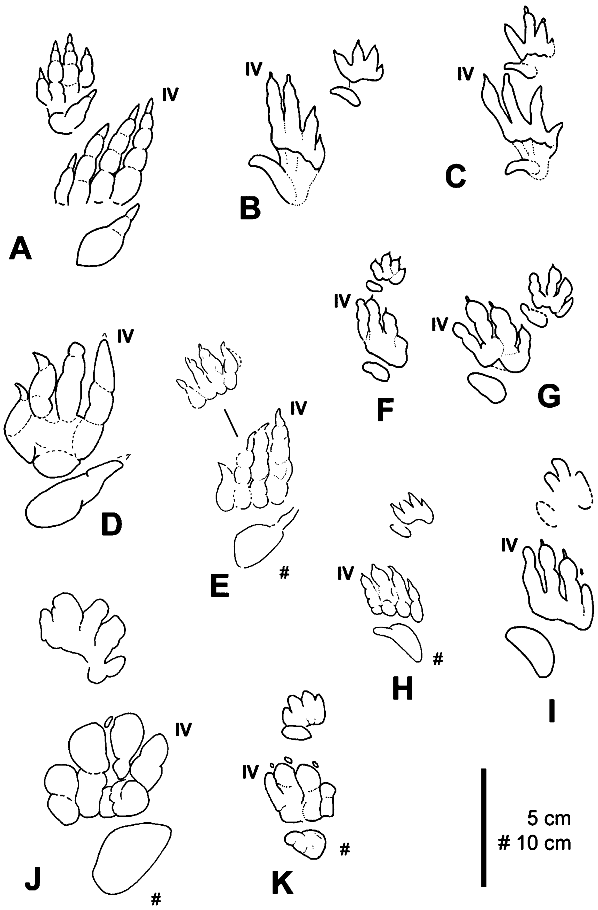

FIGURE 5. **A-E,** *Synaptichnium* and **H-K,** "*Brachychirotherium*" from the late Early and Middle Triassic, from **A,** Great Britain; **B, C,** Moenkopi Group, Arizona; **D, J, K,** Anisian-Ladinian, Massif Central, France; **E,** Eschenbach Fm., northern Bavaria; **F, G,** Thüringischer Chirotheriensandstein, southern Thuringia; and **H, I,** Röt Fm., northern Bavaria. Notice conservative pes morphology with long digits IV and V. After Peabody (1948), Haubold (1971b, 1984), and Klein and Haubold (2004).

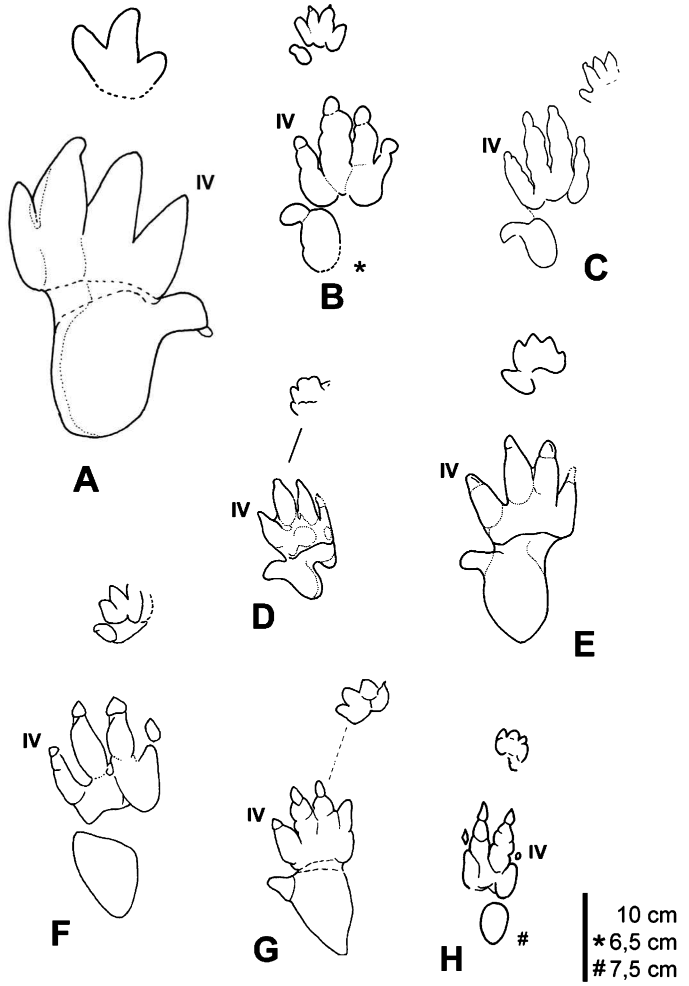

FIGURE 6. *Isochirotherium* from the late Early and Middle Triassic, from **A, B,** Thüringischer Chirotheriensandstein, southern Thuringia; **C,** Cheshire, Great Britain; **D, E,** Moenkopi Group, Arizona; and **F-H,** Anisian-Ladinian, Massif Central, France. Important are the digit proportions in the pes, with digits II and III longest, in some cases II>III. The manus is extremely small compared to the pes. After Peabody (1948), Demathieu (1970), Haubold (1971b) and Courel and Demathieu (1976).

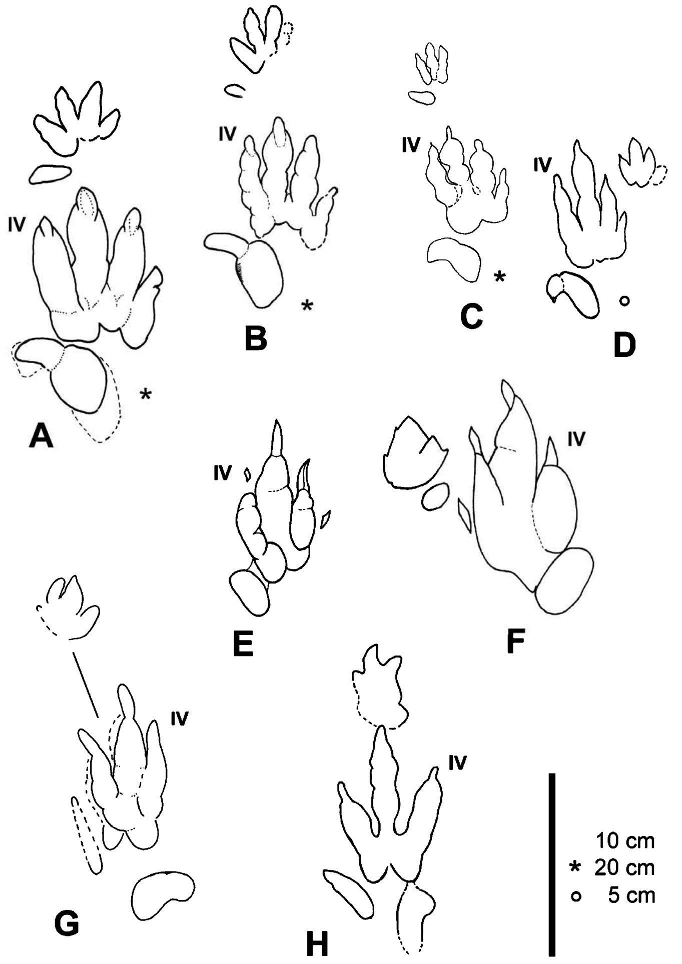

FIGURE 7. Pentadactyl tracks from the late Early and Middle Triassic showing the initial stages of a trend toward tridactyly via reduction of digit V and a posterior shift of digit I. **A, B,** *Chirotherium barthii*, type surface of the Thüringischer Chirotheriensandstein, Hildburghausen. **C, D,** *C. sickleri*, Thüringischer Chirotheriensandstein. **E, F,** *Sphingopus ferox*, Anisian/Ladinian, Massif Central, France. **G, H,** *Sphingopus* isp. and *Parachirotherium postchirotherioides*, Eschenbach–Benk fms., northern Bavaria. After Demathieu (1966, 1970), Haubold (1971a, b), and Haubold and Klein (2000).

Haubold, 1998, 2000), their relationship to Late Triassic *Brachychirotherium* turned out to be problematic. Consequently, the so-called "brachychirotherians" of the Middle Triassic are referred to here as "*Brachychirotherium*" (Fig. 5F-K). They are demonstrably extramorphological variants of *Synaptichnium* (Klein and Haubold, 2004), though they form a characteristic and striking group of track morphs particularly in the late Middle Triassic (Demathieu, 1970; Demathieu and Gand, 1973; Courel and Demathieu, 1976; Demathieu and Demathieu, 2004).

Isochirotherium (Fig. 6A-H), the type species of which is *Isochirotherium soergeli* from surfaces of the "Thüringischer Chirotheriensandstein" (Fig. 6B), exhibits a striking dominance of II and III in the digit proportions of the pes (II > III in part) and an extremely small manus impression compared to that of the foot (Haubold, 1971b). This track type can be interpreted as an evolutionary trend toward a tridactyl foot pattern comprised of digits I, II, III rather than the II, III, IV pattern displayed by *Grallator*, for example. The tracks are also present in the Moenkopi Group of Arizona and the Middle Triassic of Great Britain, France and Italy (Peabody, 1948; Courel and Demathieu, 1976; Gand, 1979; Tresise and Sarjeant, 1997; Avanzini and Lockley, 2002).

In *Chirotherium*, particularly in the type species *C. barthii*, the initial stages of the development of the tridactyl dinosaurian foot are indicated by the posteriorly shifted pedal digit I and the dominance of digits II-IV (Figs. 3C-D, 7A-B; Haubold and Klein, 2002). *Chirotherium* manus impressions display a distinctive (dinosaurian) reduction of digits IV and V. Compared to *C. barthii*, the smaller *C. sickleri* appears to be more conservative in its retention of a long pedal digit IV (Figs. 3C-D, 7C-D). *C. barthii* footprints are one of the best documented Triassic archosaur tracks, including specimens from the classic Buntsandstein locality (Olenekian-Anisian) of Hildburghausen (Haubold 1971a, 2006) and abundant material from corresponding stratigraphic levels in England (Tresise and Sarjeant, 1997), Arizona (Peabody, 1948), France (Demathieu, 1984), Spain (Calderon, 1897), Scotland (Clark et al., 2002), Argentina (Peabody, 1955b) and China (Lü et al., 2004).

Between the late Anisian and late Ladinian, additional tracks with a principally pentadactyl imprint morphology similar to *C. barthii* can be recognized in *Sphingopus* and *Parachirotherium*. (Fig. 7E-H). The dominance of the main digit-group II-IV, with III being longest, is a striking feature, as is the posteriorly-shifted digit I, following the trend established by *C. barthii.* The type species, *S. ferox* (Fig. 7E-F), was first described by Demathieu (1966) from the Middle Triassic of the eastern margin of the Massif Central (France). Subsequently, *Sphingopus* has been documented in strata of similar age from the western margin of the Bohemian Massive in northern Bavaria (Haubold and Klein, 2002; Fig. 7G). *Parachirotherium postchirotherioides* is known from the Benker Sandstein (Middle Keuper, Late Ladinian) of northern Bavaria (Rehnelt, 1950; Kuhn, 1958; Haubold and Klein 2000; Fig. 7H). *Sphingopus* and *Parachirotherium* possess small manus imprints.

The oldest truly tridactyl pes imprints are late Anisian in age. They occur alongside pentadactyl *Sphingopus* and *Parachirotherium* tracks, often in trackways demonstrating that the track maker was capable of adopting a facultatively bipedal gait. They have been described under the names *Coelurosaurichnus* and *Anchisauripus* (Rehnelt, 1950; Weiss 1976; Demathieu, 1989; Gand and Demathieu, 2005; Gand et al., 2005), and they can be referred to *Atreipus-Grallator* (Figs. 8A-D). Especially in *Parachirotherium*, the transition from a pentadactyl quadruped to a tridactyl biped is documented in single trackways (Haubold and Klein, 2000).

Late Triassic

In this time interval, assemblages with archosaur tracks are characterized by the following taxa and imprint forms:

Brachychirotherium (Fig. 9A-E), beginning in the Carnian, with the type species *Brachychirotherium hassfurtense* (Fig. 9A) plus *B. thuringiacum* (Fig. 9B-C) from surfaces of the Coburger- and Blasensandstein of northern Bavaria and southern Thuringia (Beurlen, 1950, Karl and Haubold, 1998, 2000), this ichnogenus occurs in North America up to the Triassic-Jurassic boundary (Baird, 1957, Silvestri and Szajna, 1993; Silvestri and Olsen, 1989; Szajna and Silvestri, 1996; Szajna and Hartline, 2003; Olsen et al., 2002; Fig. 9D-E). *Brachychirotherium* is characterized by a broad, pentadactyl pes imprint with short, blunt digits and tiny claws. The fifth digit, represented only by an oval basal pad, occupies a posterolateral position. The manus exhibits a similar morphology.

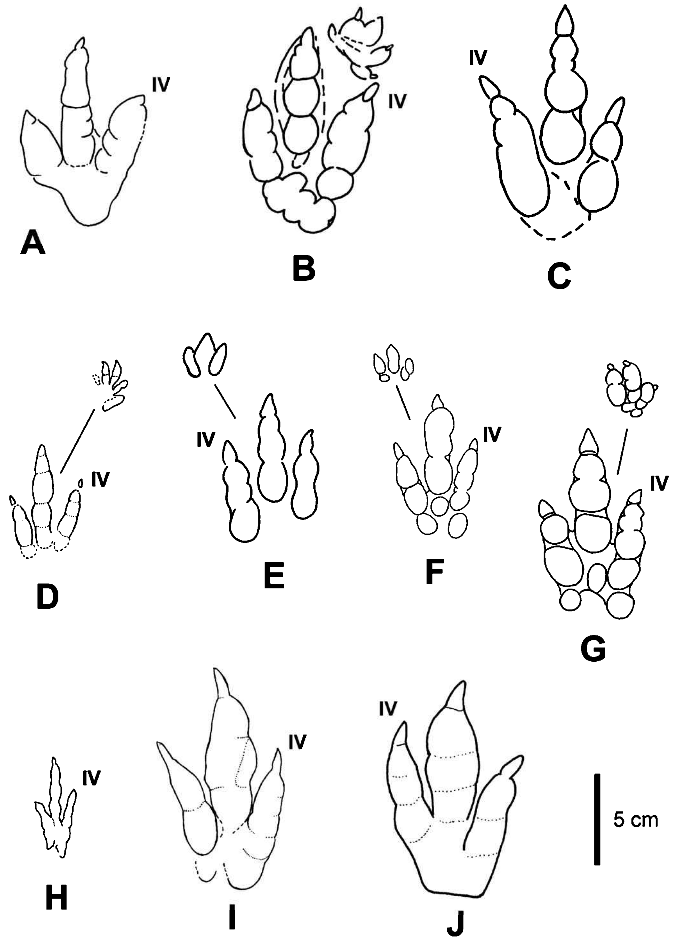

FIGURE 8. Tridactyl tracks *Atreipus–Grallator* (“*Coelurosaurichnus*,” “*Anchisauripus*”) from the Middle and Late Triassic with occasional impressions of the manus, reflecting a tendency toward bipedalism, from **A-C**, Anisian-Ladinian, Massif Central, France; **D**, Upper Ladinian, Benker Sandstein, northern Bavaria; **E**, Carnian, Massif Central, France; **F**, Carnian, Ansbacher Sandstein, northern Bavaria; **G**, Norian, Newark Supergroup; and **H-J**, Upper Carnian, Coburger Sandstein, northern Bavaria. After Haubold (1971b), Olsen and Baird (1986), Courel and Demathieu (2000), Haubold and Klein (2000), and Gand and Demathieu (2005).

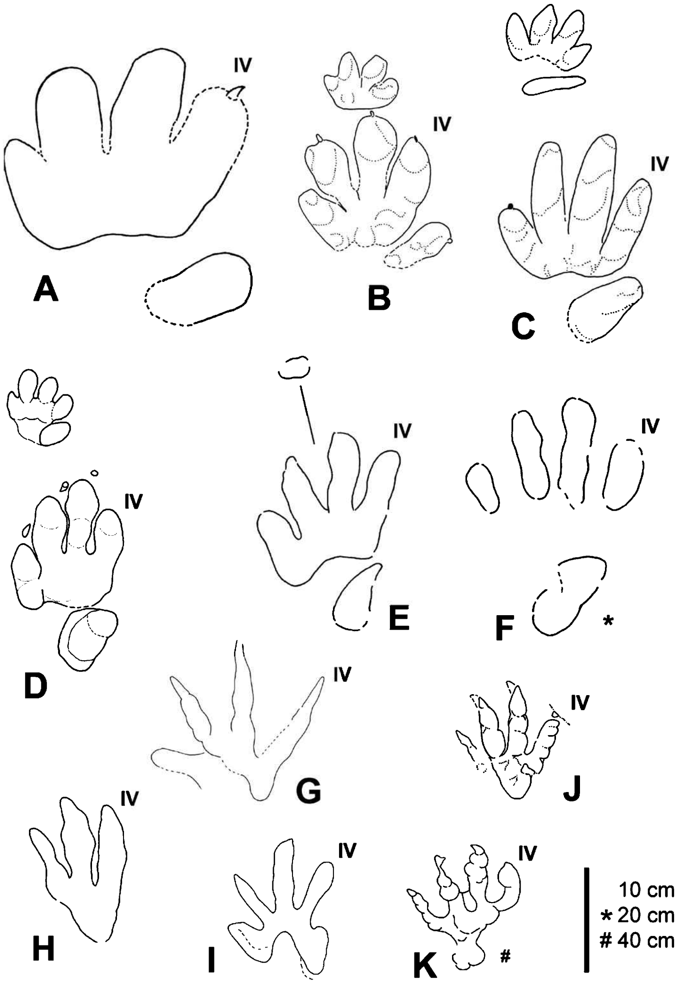

FIGURE 9. *Brachychirotherium*. **A,** *Brachychirotherium hassfurtense* (type species), Late Carnian, Coburger Sandstein. **B, C,** *B. thuringiacum*, Late Carnian, Coburger Sandstein and Blasensandstein, northern Bavaria. **D,** *B. parvum*, Passaic Fm., New Jersey. **E,** *B.* sp., Passaic Fm., Pennsylvania. **F-K,** Extramorphological variations of *Brachychirotherium* (“*Pseudotetrasauropus*,” “*Evazoum*,” “*Otozoum*”), from **F,** Norian, Lower Elliot Fm., South Africa; **G-I,** Norian, Redonda Fm. New Mexico; **J,** Carnian, Italy; and **K,** Norian, France. After Baird (1957), Karl and Haubold (1998), Gand et al. (2000), Nicosia and Loi (2003), and Klein et al. (2006).

Imprint forms that have been described under *Pseudotetrasauropus*, *Evazoum* or *Otozoum* from the Carnian-Norian of South Africa, North America, Italy and France (Ellenberger, 1970, 1972; Gand et al., 2000; Lockley et al., 2000, 2006; Lucas et al., 2001; Nicosia and Loi, 2003; Fig. 9F-K) are, in most cases, extramorphological variants of *Brachychirotherium* that appear different because their manufacture was controlled by differing conditions of the substrate and, possibly, variable gaits (see Klein et al., 2006 for details).

Atreipus, *Grallator*, and *Eubrontes* (type species *Atreipus*

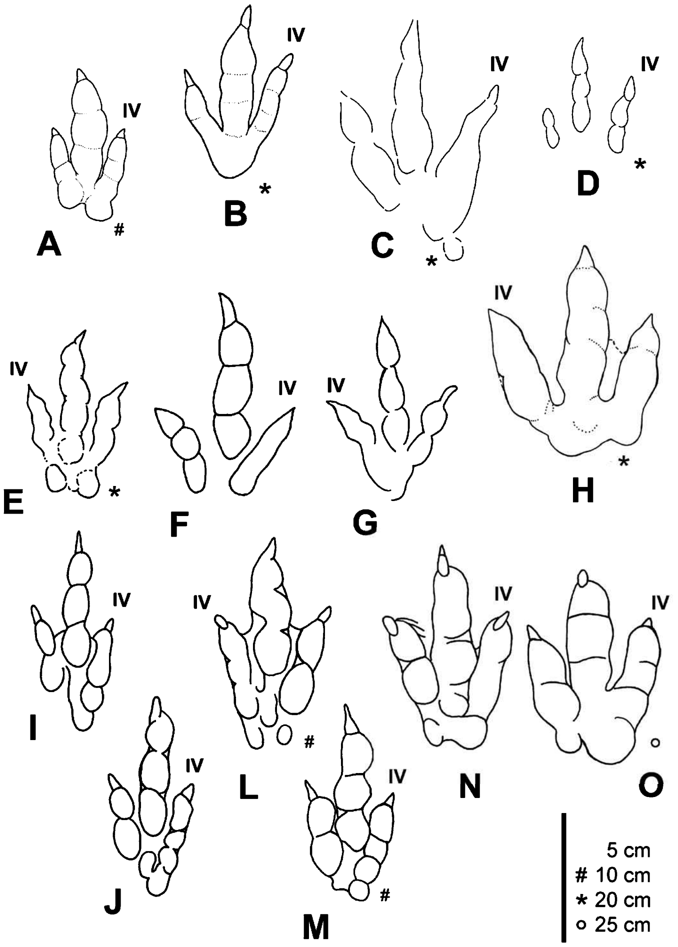

FIGURE 10. *Grallator–Eubrontes.* Tridactyl bipedal tracks from the Norian to Early Jurassic; from **A,** Norian, Wales, Great Britain; **B,** ?Rhaetian-Early Jurassic, northern Bavaria; **C,** Lower Elliot Fm., South Africa; **D,** Norian, southern France; **E-G,** Norian, Chinle Group, Utah, New Mexico, Colorado; **H,** Rhaetian, Sweden; and **I-O,** Lower Jurassic Newark Supergroup, (**I, J,** *Grallator*; **L, M,** *Anchisauripus*; and **N, O,** *Eubrontes*). After Haubold (1971b), Gierlinski and Ahlberg (1994), Lockley and Hunt (1995), Olsen et al., (1998), Hunt et al. (2000), Gaston et al. (2003), and Gand and Demathieu (2005).

milfordensis from the Passaic Formation, and *Grallator parallelus* and *Eubrontes giganteus* from the Lower Jurassic part of the Newark Supergroup [Hitchcock, 1836, 1845, 1947, 1858; Bock, 1952; Olsen and Baird, 1986; Silvestri and Olsen, 1989; Silvestri and Szajna, 1993; Szajna and Silvestri, 1996; Olsen et al., 2002; Szajna and Hartline, 2003]) are tridactyl, mesaxonic pes imprints of different sizes (Figs. 8E-J, 10) that are widely distributed between the Carnian and Early Jurassic, with occurrences in Germany, Great Britain, Switzerland, France, Sweden, Greenland, and the Lower Elliot Formation of South Africa (Ellenberger, 1970, 1972, 1974; Furrer, 1993; Gierlinski and Ahlberg, 1994; Jenkins et al., 1994; Lockley et al., 1996; Gatesy et al., 1999; Haubold and Klein, 2000, 2002; Gand et al., 2000, 2003; Milàn et al., 2004). Occasionally manus imprints are associated with older trackways (e.g., *Atreipus*). From the late Norian, for example in the Redonda Formation of New Mexico, only bipedal *Grallator* and *Eubrontes* are present, though in the Newark Supergroup *Atreipus* still occurs in the Rhaetian.

INTERPRETATION – THE BIOCHRONOLOGICAL POTENTIAL

From the preceding overview, it is obvious that the vertical (stratigraphic) distribution of some archosaurian ichnotaxa and form groups in the global record demarcate distinct biostratigraphic units that themselves occur in distinct, limited chronostratigraphic intervals. Hence, an attempt is made to establish the following archosaur footprint-based biochronological concept for the Triassic.

Protochirotherium (*Synaptichnium*) is characteristic of the Induan-late Olenekian interval. *Protochirotherium*, temporally as well as morphologically, matches the hypothetical morphology of a basal archosaur and is the basis for later evolutionary developments and form groups. Its position marks the beginning of the biochronological succession. Between the late Olenekian (at which time *Protochirotherium* disappears) and the late Ladinian, further biochronological potential is offered by *Rotodactylus*, *Isochirotherium*, *Synaptichnium* and "*Brachychirotherium*". Their stratigraphic distributions essentially span the Middle Triassic. The stratigraphic upper limits of *Rotodactylus* and *Isochirotherium* are early Ladinian. *Brachychirotherium* (*sensu stricto*) spans the Upper Triassic, from the Carnian to the Triassic-Jurassic boundary.

The greatest biochronological potential lies in coupling the stratigraphic succession of the tracks with the functional evolutionary stages in the development of the tridactyl foot morphology and bipedal gait of dinosaurs that they delineate. They can be followed in an evolutionary succession between the late Olenekian and Early Jurassic, documenting morphological and behavioral changes, including trackways made by individuals shifting from quadrupedal to facultative bipedal locomotion. This transition is ichnotaxonomically delineated via the following sequence: *Chirotherium – Sphingopus – Parachirotherium – Atreipus – Grallator*. The stratigraphic ranges of these five ichnotaxa correspond with the Olenekian-Anisian, Anisian-Ladinian, Ladinian, Carnian-Norian and Norian-Rhaetian, respectively. The range of the pentadactyl forms in this succession is limited to pre-Carnian strata; after that time, the tracks are tridactyl.

An alternative, as well as a supplement and clarification of earlier biochronological concepts, is offered here. Attempts to tie ichnostratigraphy and correlation of sequences have been made by Haubold (1969, 1971b, 1984, 1986), Demathieu and Haubold (1972, 1974), Olsen (1980, 1983), Lockley and Hunt (1993, 1995), and Lucas (2003). Further contributions to this topic can be found in Ellenberger (1970, 1972, 1974), Demathieu (1984), Olsen and Galton (1984), Olsen and Baird (1986), Silvestri and Olsen (1989), Silvestri and Szajna (1993), Lockley et al. (1996), Szajna and Silvestri (1996), Avanzini et al. (2001), Lucas and Hancox (2001), Olsen et al. (2002), Szajna and Hartline (2003), Lucas and Huber (2003), Lucas and Tanner (2004), Gand et al. (2003), Lucas and Sullivan (2006), and Lucas et al. (2006a, b). Evident in all of these studies are different approaches of the respective authors to the fundamental problem of the non-uniform assignment and naming of tracks, particularly the differing methods of evaluating and dealing with extramorphological phenomena, specifically substrate-controlled features in track morphology (see above). As a consequence, different stratigraphic ranges of taxa have been stated and conclusions reached by the different authors. The concept presented here is based on principal form groups and the evolutionary developments they represent. By this reduction to the documentation of essential "lines," the temporal distribution pattern becomes apparent and offers possibilities for biochronological classification of the Triassic by archosaur footprints.

RESULTS

After analysis of the global record of archosaur tracks from the Triassic, a biochronological succession of six biochronological units (biochrons) is derived from the stratigraphic distribution of several characteristic forms and assemblages. Each unit represents a certain time span, the beginning of which is marked by the first appearance datum (FAD) of an index taxon. In the following, the principal index ichnotaxon is marked in bold. The units are:

I. *Protochirotherium* (*Synaptichnium*): FAD: Late Induan. Distribution: Late Induan-Olenekian.

II. *Chirotherium*, *Rotodactylus*, *Isochirotherium*, *Synaptichnium*

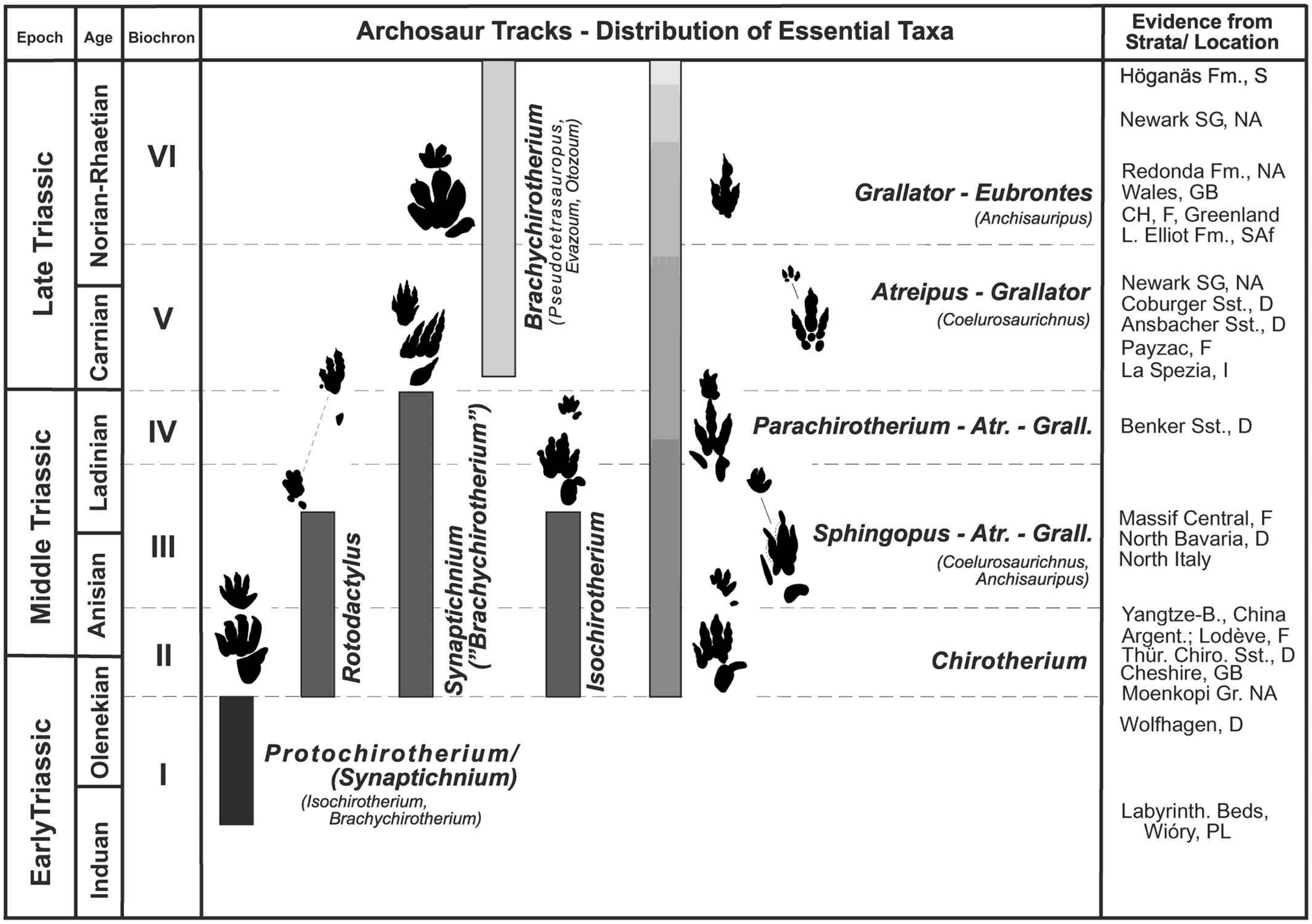

FIGURE 11. Stratigraphic distribution of characteristic archosaur tracks in the Triassic in biochrons I-VI and source track-bearing units and locations. Common synonyms and extramorphological variants that have been treated as distinct ichnotaxa to date are indicated in brackets. The track-bearing strata and locations are listed according to their stratigraphic positions. Notice evolutionary sequence and different stages in the development from pentadactyl to tridactyl pes morphology and of bipedality in *Chirotherium* through *Eubrontes* between the late Olenekian and Norian-Rhaetian. After Haubold (1971b), Olsen and Baird (1986), Karl and Haubold (1998), and Haubold and Klein (2000).

("*Brachychirotherium*"): FAD: late Olenekian. Distribution: Late Olenekian-Anisian.

III. *Sphingopus* – *Atreipus* – *Grallator*, *Rotodactylus*, *Isochirotherium*, *Synaptichnium* ("*Brachychirotherium*"): FAD: Late Anisian. Distribution: Late Anisian-Ladinian.

IV. *Parachirotherium* – *Atreipus* – *Grallator*, *Synaptichnium* ("*Brachychirotherium*"): FAD: Late Ladinian. Distribution: Late Ladinian.

V. *Atreipus*-*Grallator*, *Brachychirotherium*: FAD: Carnian. Distribution: Carnian-Norian.

VI. *Grallator*-*Eubrontes*, *Brachychirotherium*: FAD: Norian. Distribution: Norian-Rhaetian.

Most of the taxa that have been described and named can now be referred to one of these biochrons. In Figure 11, the different evolutionary sequences and biochrons are plotted. The composition of the ichnotaxonomic groupings and track sequences is based on the following ichnotaxa:

1. *Protochirotherium*. Late Induan-late Olenekian. Type species: *P. wolfhagense* Fichter and. Kunz, 2004.

2. *Rotodactylus*. Late Olenekian-early Ladinian. Type species: *R. cursorius* Peabody, 1948.

3. *Synaptichnium*. Late Induan-late Ladinian. Type species: *S. pseudosuchoides* Nopcsa, 1923.

4. "*Brachychirotherium*." Late Olenekian-Late Ladinian. Tracks described under *Brachychirotherium* but with a doubtful relation to Upper Triassic forms (see Karl and Haubold, 1998; Klein and Haubold, 2004).

5. *Brachychirotherium*. Carnian-Rhaetian. Type species: *B. hassfurtense* (Beurlen 1950); see also Karl and Haubold, 1998, 2000).

6. *Isochirotherium*. Late Olenekian-early Ladinian. Type species: *I. soergeli* (Haubold 1967); see also Haubold, 1971b.

7. *Chirotherium*. Late Olenekian-early Anisian. Type species: *C. barthii* Kaup, 1835.

8. *Sphingopus*. Late Anisian-early Ladinian. Type species: *Sphingopus ferox* Demathieu, 1966.

9. *Parachirotherium*. Late Ladinian. Type species: *P. postchirotherioides* (Rehnelt 1950); see also Kuhn, 1958.

10. *Atreipus*. Carnian-Norian. Type species: *A. milfordensis* (Bock 1952); see also Olsen and Baird, 1986.

11. *Grallator*. Norian-Early Jurassic. Type species: *Grallator parallelus* (Hitchcock 1847); see also Hitchcock, 1858.

12. *Eubrontes*. Norian-Early Jurassic. Type species: *E. giganteus* (Hitchcock 1836); see also Hitchcock, 1845.

CONCLUSIONS

The stratigraphic distribution of the principal morphs of archosaur tracks reflects different phylogenetic trajectories of the locomotor apparatus and foot morphology of archosaurs through the Triassic. Several functional evolutionary track sequences can be differentiated, each composed of characteristic taxa and form groups that characterize a certain time span. Beginning with early forms like *Protochirotherium* and *Synaptichnium* and through *Isochirotherium*, *Rotodactylus*, and *Brachychirotherium*, the evolution of the plesiomorphic tridactyl dinosaurian foot morphology and bipedality is documented in tracks from *Chirotherium* to *Eubrontes*. The sequence offers a biochronological potential that has not been considered so far. The stratigraphic distribution pattern is summarized in six units (biochrons I-VI). Although the quantity and quality of anatomical signals preserved in footprints is limited, some archosaur tracks give insight in the evolutionary context of their producers. This information, in tandem with their distinct stratigraphic distributions, makes Triassic archosaur footprints valuable for biochronology, especially in continental sequences where skeletal evidence is rare or missing. Furthermore, they often appear in dense concentrations and are geographically widespread. This potential can be used and augmented in the future through global prospecting of regions and sequences that have not been examined so far. The recent discovery of *Chirotherium barthii* in the Middle Triassic of the Yangtze basin of southern China (Lü et al., 2004) is just such a positive indication of the potential to utilize the track record of Triassic archosaurs.

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THE PROBLEM OF TRIASSIC GONDOLELLID CONODONT SYSTEMATICS (CONODONTOPHORIDA, CONODONTA)

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Abstract—We discuss the problems of systematics of Triassic gondolellid conodontophorids. The basic trends in development of morphological characters are shown.

INTRODUCTION

The taxonomy of gondolellid elements is one of the problems in the study of conodontophorids. Their morphological similarity originally led researchers to a conclusion about Carboniferous, Permian and Triassic pectiniform elements belonging to a uniform *Gondolella* Stauffer & Plummer, 1932. N. Bender and D. Stoppel for the first time established that the Triassic forms refered to *Gondolella mombergensis* Tatge actually differ from the Paleozoic species of *Gondolella* by a more rounded basal cavity and more extended lanceolate form of platform. Therefore, it is most logical that all Middle and Late Triassic gondolellid elements be consolidated in the new genus *Neogondolella* (type species *Gondolella mombergensis* Tatge), which appeared at the base of the Middle Triassic from spathognathodiform elements (Bender and Stoppel, 1965). Then, contrary to the initial value of the genus, all Early Triassic, Permian, and also unsculptured smooth Carboniferous elements began to be referred to *Neogondolella*, understanding it in a broad sense (s. l. = sensu lato), and only sculptured Upper Carboniferous conodontophorids were considered as *Gondolella* (type species *Gondolella elegantula* Stauffer & Plummer 1932) in a narrow sense (s. str. = sensu strictiore) (Ziegler, 1973). Further research indicates morphological distinctions and phylomorphogenetic connections between genera of gondolellid conodontophorids (Mosher, 1968b; Hayashi, 1968; Budurov, 1976; Buriy, 1989; Kozur, 1989; Orchard, 1991; Buryi, 1996). However, the conventional systematics does not exist now. H. Kozur, considering the taxonomy of Permian and Triassic gondolelloid conodontophorids in detail, considered that *Neogondolella* Bender & Stoppel had evolved from platform-less *Neospathodus* Mosher through the transitional forms of *Chiosella* Kozur from the end of the Olenekian Stage to the beginning of the Anisian Stage and that *Neogondolella* is the basic group of the Middle to the beginning of the Late Triassic (Kozur, 1989). It is necessary to note that the author made these conclusions based on research on of the Tethyan region.

Recently, the geography of locations of the Triassic conodontophorids has been considerably expanded due to new finds in areas of the Russian Arctic (Dagys, 1984; Konstantinov etc., 1997; Klets, 2000; Klets and Yadrenkin, 2001; Klets and Kopylova, 2006). The locations of the Olenekian forms in the up-stream of the Lena River, on Kotelny island (Novosibirsk islands), and in the basin of the Dzhugadzhak River (Omolon massif) has been established. It was documented by many specimens that have allowed specification of the stratigraphic distribution of *Neogondolella*. Research has shown that in northern lalitudes in the Early Olelnekian endemic *Neogondolella buurensis, N. composita, N. jakutensis, N. taimyrensis, N. sibirica*, having characteristics of *Neogondolella* in the form of the basal cavity and in platform microstructure (honey comb structure) were widely distributed (Dagys, 1984, tab. I, figs. 8-12; tab. II, figs. 1-16; tab. III, figs. 1-2; tab. V, figs. 4; tab. XI, figs. 1-4; tab. XII, figs. 1-2; tab. IV, figs. 1-8; Fig. 1). Therefore, specimens of *Neogondolella buurensis* from A. A. Dagys' collection had been referred by Kozur (1989, pl. 15, fig. 6-7) to *Paragondolella sweeti*, perhaps, wrongly. Records of Early Olenekian neogondolells (*Neogondolella elongata* Sweet) are known also in British Columbia, Western Pakistan, India and Svalbard (Sweet, 1970; Mosher, 1973; Goel, 1977; Dagys and Korchinskaya, 1989). Therefore, most probably, the genus *Neogondolella* had evolved from *Neospathodus* already by the beginning of the Early Olenekian and was widely distributed in southern and northern lalitudes (Fig. 1).

The study of conodontophorids in the north of Middle Siberia, the Northeast and the Far East of Russia, and also the analysis of numerous references shows that gondolellids are a rather conservative group, in spite of high enough rates of transformations of platform and blade-like elements. This feature of the group extremely complicates establishment of genera. It also originally formed the basis for their reference to one genus, *Gondolella* Stauffeã & Plummer 1932. There are some trends established during research on the evolution of the Triassic forms where both irreversible and reversible morphological changes are recognized. As the research shows, a character on the upper or lower side of an element taken separately is a poor indicator of closely related genera. In connection with the reversibility of many morphological characters in evolutionary trends, according to separately taken characters, for example the structure of a platform, Early Triassic *Neogondolella* are similar to Middle Triassic *Paragondolella* and Late Triassic *Norigondolella* (Fig. 1). The structure of the basal cavity of platform-less Early Triassic *Neospathodus* is rather like the structure of the basal cavity of Anisian *Nicoraella* and Rhaetian *Misikella*. Therefore, for diagnoses of genera it is necessary to take into consideration the structure of both sides. For more correct and reliable evolutionary constructions, all morphological changes are tracked on adult ontogenetic stages. In establishing genera, we use as a basis the morphological terminology developed by I. Barskov with colleagues (Barskov et al., 1975; Barskov, 1985).

BASIC TRENDS IN DEVELOPMENT OF MORPHOLOGICAL CHARACTERS

Platform

During certain times, the platform of gondolellids was evolving from platform-less conodonts, for example: *Neospathodus*→*Pseudogondolella*→*Paragondolella*, *Neospathodus*→*Chiosella*, *Neospathodus* → *Neogondolella*. Also, the platform could disappear completely: *Clarkina* →*Neospathodus*, *Mockina*→*Parvigondolella*, *Neogondolella* → *Celsigondolella*. There was no similar trend in the occurrence and (or) disappearance of the platform in the evolutionary line *Neospathodus*→*Nicoraella*→*Mosherella*→*Misikella*.

Sculpture of Platform

The sculpture consists of nodes, grooves and ribs developed only on the platform of gondolellids. Sculptured conodontophorids such as *Scythogondolella* and *Icriospathodus* appeared for the first time in the Triassic during the Olenekian Stage. Strongly- sculptured gondolellids arose in the Ladinian (*Budurovignathus* and *Pseudofurnishius*) and became very widely distributed in the Late Carnian-Norian (*Metapolygnathus*→*Epigondolella*→*Mockina*).

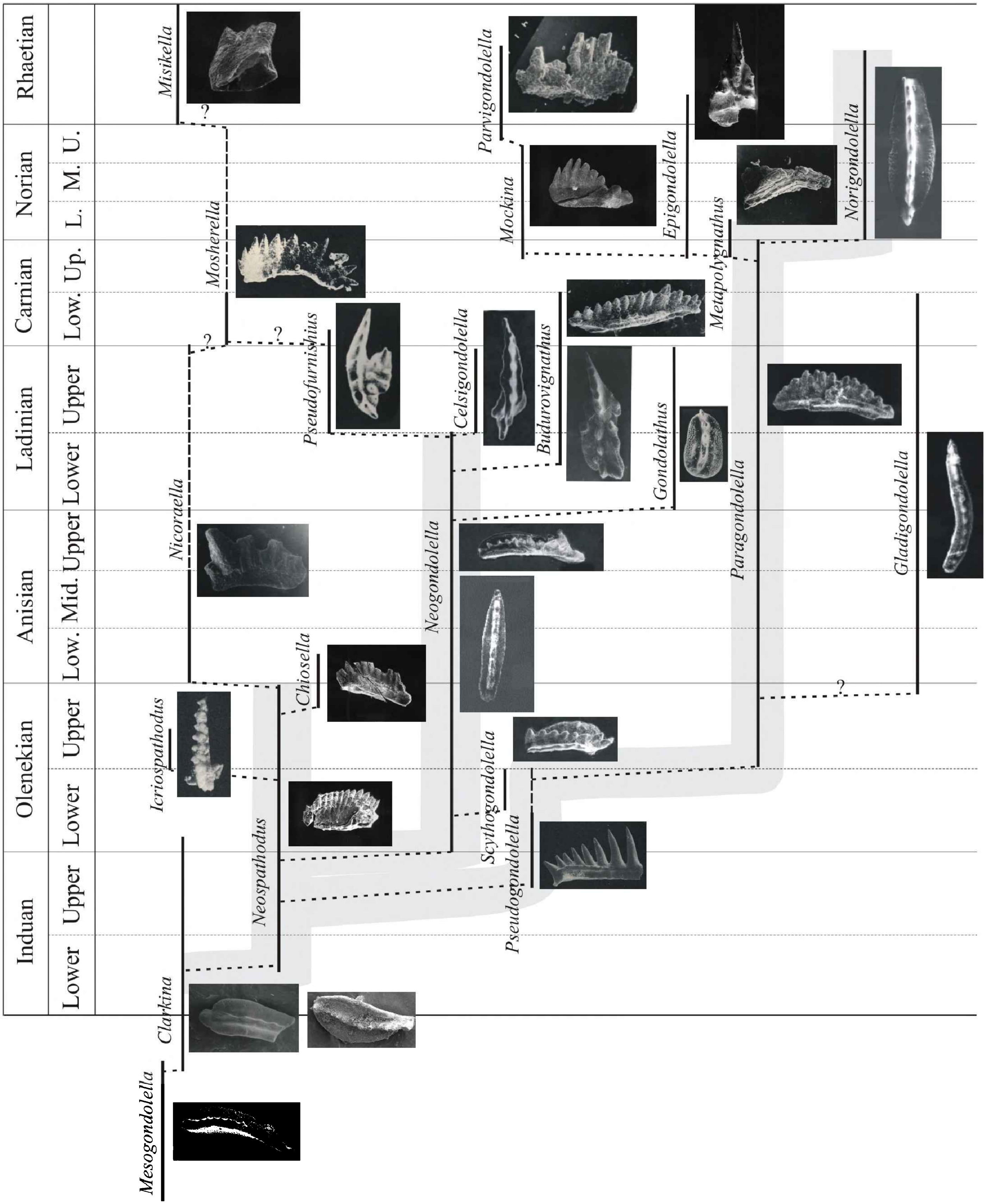

FIGURE 1. Scheme of phylomorphogenesis of Triassic conodontophorids.

Carina

The main similarity of gondolellid conodontophorids is in the carina, but in some cases, being combined with other characters, its development can be used to establish genera. In spite of variety of carina morphology even within a species, it is possible to identify three basic types:

1. Anterior denticles are the highest. Denticles in the posterior part of a carina are also high. Denticles in the middle part of an element are the lowest and frequently merged. This type of carina is most typical of *Neogondolella* and *Norigondolella*.
2. All denticles are high and equal or nearly equal in height. This type is especially shown in elements with a reduced or completely missing platform—*Chiosella, Parvigondolella*—but can be characteristic of platform-bearing *Scythogondolella* and some *Neogondolella*.
3. Denticles in the anterior part of a carina are very high, merged almost along all of the height and are also compressed from the sides. Denticles are gradually reduced in the direction of the posterior edge and become more rounded. This type is well shown in *Paragondolella* and its descendants *Metapolygnathus→Epigondolella→Mockina*. It is also characteristic of some species of *Budurovignathus*.

Free Blade

A free blade is well advanced only in conodonts in which the platform occupies one-half of the length of the element. It is well shown in *Clarkina* (Induan- the beginning of the Olenekian), then again it is observed in *Budurovignathus* (Ladinian–bottom of Carnian) and *Paragondolella→Metapolygnathus→Epigondolella→Mockina* (top of Carnian-Norian to bottom of Rhaetian). *Neogondolella*, *Pseudogondolella* and some species of *Paragondolella*, as well as *Norigondolella*, are tear-shaped and extended in length, but different on width and have a platform with missing or advancing, very poorly free blade (all till 1-2/10 of the length of the conodonts).

Keel

An important morphological character is the keel—a longitudinal axial eminence on the upper surface of conodonts. Trends in the change of its morphological features are connected to trends in the development of a platform and presence of a free blade. The structure of the lower surface changes in platform-less elements in the lines *Neospathodus→Chiosella* and *Neospathodus→Nicoraella→Mosherella→Misikella*. In an anterior direction, the basal cavity of all genera is narrowed (different genera have various degrees of narrowing) and the deepening always has a V-shaped form.

The form of the keel of platform-bearing conodonts not having a free blade (or in which the blade is poorly advanced) is a convertible character. In the line *Pseudogondolella→Paragondolella→Norigondolella* Induan conodonts with a poorly advanced platform have a V-shaped keel, younger *Paragondolella* has a straight lower surface, and Norian *Norigondolella* has a V-shaped keel again. The similar trends (transition from V-shaped keel to straight) are traced in the lines *Neospathodus →Neogondolella→Budurovignathus*, *Neospathodus →Neogondolella→Pseudofurnishius*, and *Pseudogondolella→Paragondolella→Gladigondolella*.

In the Late Triassic conodonts *Metapolygnathus →Epigondolella→ Mockina →Parvigondolella* with a well advanced free blade, the form of keel varies in the opposite direction from almost straight up to V-shaped.

Thus, for the establishment of genera of gondolellids it is important to use all characters, as during evolution morphological features have changed in parallel and were not independent from each other. Probably, some changes could be connected functional morphologically.

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BIVALVE ASSEMBLAGES IN NORTH VIETNAM AND SOUTH CHINA FOLLOWING THE END-PERMIAN CRISIS

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INTRODUCTION

Carbonate ramps, isolated carbonate platforms and surrounding marginal basin deposits are widely distributed throughout the Yangtze Block, South China (e.g., Zhang et al., 1997; Yin et al., 2001; Lehrmann et al., 2001, 2003) and extend into North Vietnam (Dang, 1998a; Nguyen et al., 2004). Within these deposits, the uppermost Permian to Lower Triassic Yinkeng Formation yields abundant well–preserved marine fossils that are important for studies of paleontology, stratigraphy, and paleobiogeography (e.g., Yang et al., 1995; Yin et al., 1996; Zhang et al., 1997; Jin et al., 2000), consequently, the Meishan section, in Zhejiang Province, South China, has been designated as the Global Stratotype Section and Point (GSSP) of the Permian–Triassic boundary section (Yin et al., 2001). Recently, abundant Upper Permian to Lower Triassic fossils have been found in the lower parts of the Yinkeng Formation in the Huangzishan area, Zhejiang Province (Chen and Komatsu, 2001; Komatsu et al., 2006).

Furthermore, Dang (1998a), Nguyen et al. (2004) and Dang and Nguyen (2005) reported that these Lower Triassic deposits are widely exposed in Vietnam. The Lower Triassic Hong Ngai and Song Hien Formations crop out over large parts of Ha Giang Province, North Vietnam (Fig. 1). In the Hong Ngai Formation, the Early Triassic conodont *Hindeodus parvus* and bivalve *Claraia wangi* have been reported from the Nhi Tao section, Cao Bang Province (Nguyen et al., 2004), and abundant Lower Triassic bivalves have been discovered at the Hong Ngai section, Ha Giang Province (Dang, 1998b).

Despite the large number of studies that have examined these fossils, little is known of the paleoecology and taphonomy, and, in particular, the habitats of bivalve fossils and bivalve assemblages in these areas following the end–Permian extinction event. Moreover, in North Vietnam, the Lower Triassic bivalve biostratigraphy has yet to be reported in detail, even though these bivalves are important in terms of international correlations.

In the present study, we investigated the fossil compositions and habitats of Lower Triassic Induan bivalve assemblages from the Yinkeng Formation in the Meishan and Huangzishan areas, South China and from the Hong Ngai Formation in North Vietnam. We report on poorly diversified Lower Triassic bivalve assemblages for each of the observed depositional environments and reconstruct the habitats of the Lower Triassic bivalves following the end–Permian mass extinction event.

GEOLOGIC SETTING AND BIVALVE FOSSIL ASSEMBLAGES

China Sites

The Upper Permian to Lower Triassic Yinkeng Formation is widely distributed throughout the Yangtze Block, South China, and conformably overlies Permian carbonate platform deposits (Liao, 1984; Yin et al., 2001). In the Meishan section (GSSP), Zhejiang Province, the basal part of this formation consists mainly of alternating beds of limestone and mudstone, intercalated with the P–T boundary.

The Yinkeng Formation consists of dark gray and light green mudstone, marl, limestone, dolomite and tuff. The lower part of the Yinkeng Formation is dominated by mudstone and marl that contain abundant bivalves, ammonoids and brachiopods (Sheng et al., 1984; Yin et al., 2001). The Griesbachian bivalve *Claraia wangi* occurs in abundant monospecific concentrated shell beds.

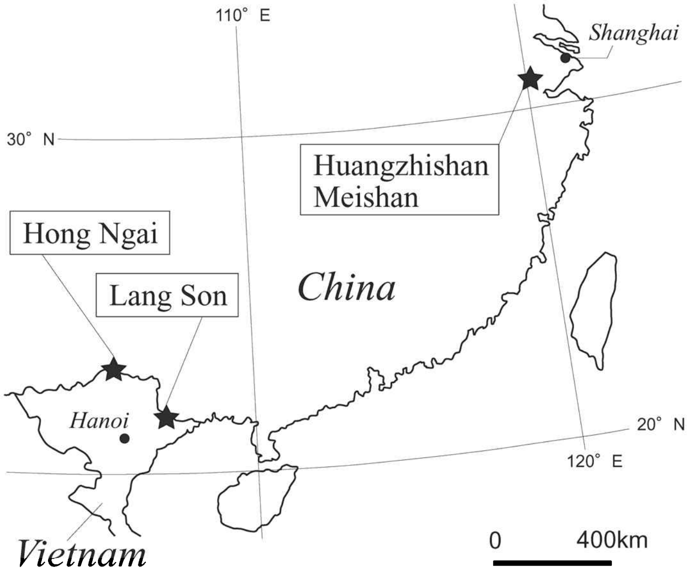

FIGURE 1. Study area.

In the Huangzishan area, about 40 km southeast of Meishan, the basal and lower parts of the Yinkeng Formation consist mainly of calcareous gray mudstone, marl and limestone. Several species of bivalves and brachiopods are commonly found in calcareous mudstone beds (Chen and Komatsu, 2001). The fossil compositions of this area are different from those of the Meishan area. Chen and Komatsu (2001) reported Lower Triassic bivalves, *Towapteria scythica*, *Claraia wangi*, *Pteria ussurica variabilis Eumorphotis* sp. (=*Eumorphotis teilhardi*) and *Promyalina* sp., from calcareous mudstone in the lower part of this formation.

The basal and lower parts of the Yinkeng Formation at Meishan are dominated by hemi–pelagic and pelagic mudstone that represents a basin environment; the mudstone overlies a Permian carbonate ramp platform (Zhang et al., 1997; Lehrmann et al., 2003; Komatsu et al., 2006). The calcareous deposits of the Huangzishan area accumulated in a deep ramp platform (Komatsu et al., 2006).

The *Claraia wangi* assemblage is found in the basin mudstone, and is composed of abundant *Claraia wangi* and rare *Claraia longyanensis* at the Meishan section. *Claraia wangi* is occasionally preserved as articulated shells. In the Huangzishan area, the *Eumorphotis teilhardi*–*Towapteria scythica* assemblage consists of epifaunal bivalves such as disarticulated valves of *Eumorphotis teilhardi*, *Towapteria scythica*, *Pteria ussurica variabilis*, and *Promyalina* sp. *Eumorphotis teilhardi* and *Towapteria scythica* account for about 50–80% of the assemblage.

Vietnam Sites

The Lower Triassic Hong Ngai Formation, which crops out over large parts of Ha Giang Province, North Vietnam, was investigated in detail by Dang (1998a) and Dang and Nguyen (2005). The formation is divided into three parts: a lowermost part dominated by fossiliferous calcareous shale, a lower part that consists of fossiliferous bedded limestone intercalated with oolitic beds and an upper part consisting of limestone and dolomite. The lowermost and lower parts yield abundant molluscan fossils such as *Claraia wangi, Claraia griesbachi, Claraia concentrica, Claraia stachei, Claraia yunnanensis, Claraia hunanica, Claraia aurita, "Claraia" phobangensis, Eumorphotis inaequicostata, E. multiformis*, *Pteria ussurica* (bivalves), *Glyptophiceras* sp. (ammonoid), and gastropods (Dang, 1998a, b). In particular, the basal calcareous shale yields *Claraia wangi, Glyptophiceras* sp., and *Lingula* sp. at the Hong Ngai type section, and *Eumorphotis multiformis*, *Claraia* sp., and *Hindeodus parvus* (conodont) at the Nhi Tao section, Cao Bang Province (Nguyen et al., 2004). These Triassic deposits unconformably or disconformably overlie the upper part of the Upper Permian Dong Dang Formation.

At the Hong Ngai type section, the depositional environments of the lowermost and lower parts of the Hong Ngai Formation are interpreted to represent shallow and deep carbonate ramp environments (Komatsu et al., 2006). The lowermost part is characterized by cross–stratification and hummocky cross-stratification (HCS). The lower part is composed of wavy-bedded limestone intercalated with oolitic limestone beds is interpreted to represent a shallow carbonate ramp located above the fair-weather wave base (Komatsu, et al., 2006).

In the lowermost and lower parts of the Hong Ngai Formation, the *Eumorphotis teilhardi–Towapteria scythica* assemblage is found in the deep ramp platform, and contains articulated shells of *Eumorphotis teilhardi*, *Towapteria scythica* and *Claraia wangi*, and disarticulated shells of *Pteria ussurica ussurica*, and *Promyalina* sp. *Eumorphotis teilhardi* and *Towapteria scythica* account for about 50–75% of the assemblage. The composition of this assemblage is similar to that of the *Eumorphotis teilhardi–Towapteria scythica* assemblage from South China, although *Claraia wangi* is commonly found in the assemblage in Vietnam. In the

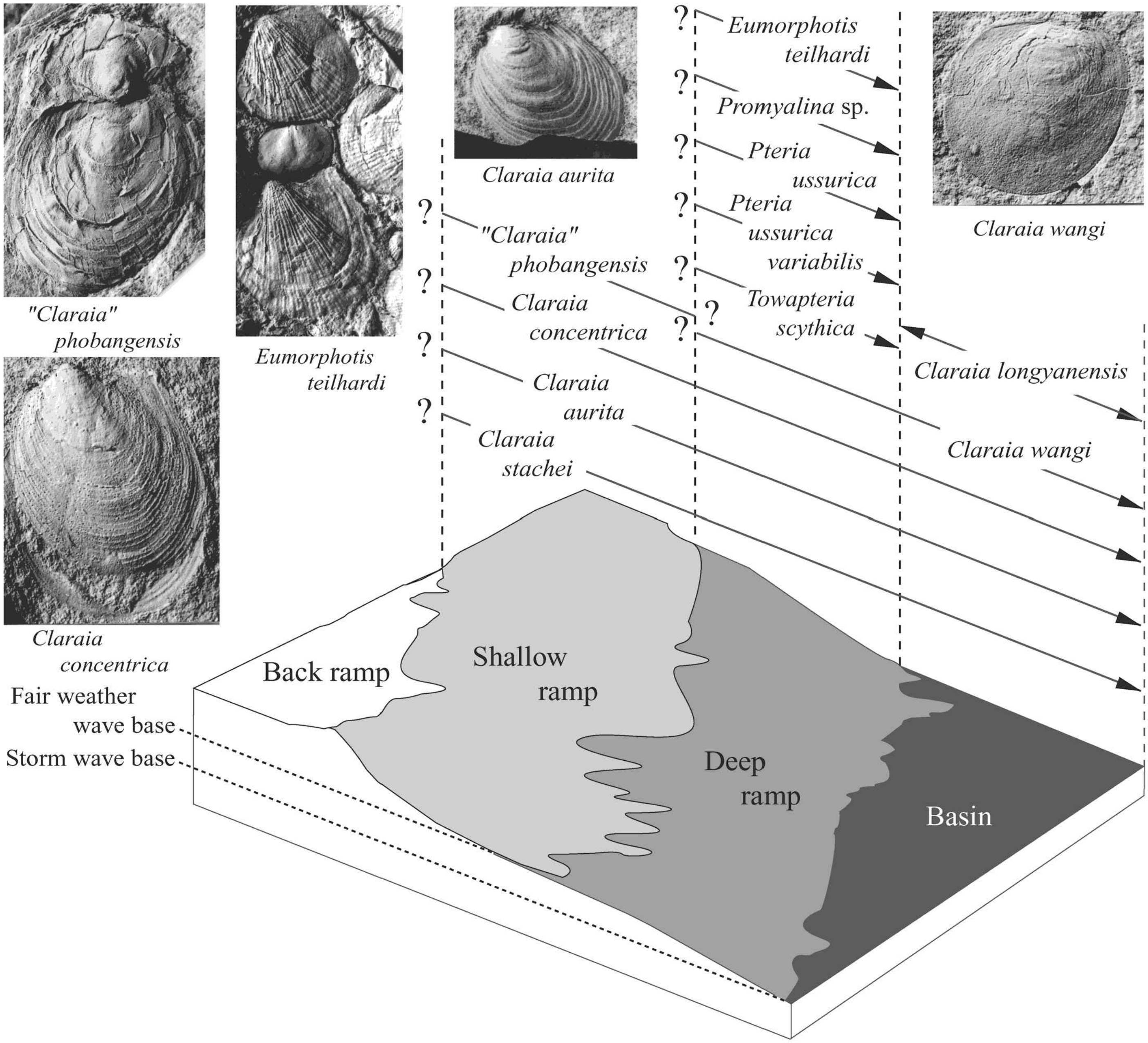

FIGURE 2. Reconstructed habitats of the Lower Triassic bivalves in the Yinkeng Formation, South China and the Hong Ngai and Lang Son formations, North Vietnam.

lower part of the formation, the *Claraia wangi* assemblage is found in the deep ramp carbonates, and is characterized by typical monospecific compositions. Disarticulated valves are abundant, but articulated valves in butterfly position are also commonly found.

In the upper parts of the Hong Ngai Formation, shallow ramp deposits yield the *Claraia stachei–"Claraia" phobangensis* assemblage. The assemblage consists of epifaunal elements such as *Claraia concentrica, Claraia stachei, Claraia aurita, "Claraia" phobangensis, Eumorphotis multiformis* and *Pteria ussurica*. *Claraia stachei* and *"Claraia" phobangensis* account for over 70% of the assemblage. *Claraia concentrica* is also abundant. Closed and open articulated valves are commonly found. These shells are well preserved. Detailed ornamentation, such as radial and concentric ribs, is preserved.

DISCUSSION AND CONCLUSION

These shells were generally transported by currents; they show allochthonous and parautochthonous modes of occurrence. Most of the bivalves are preserved as disarticulated valves in shell concentrations, representing typical allochthonous occurrences; however, parautochthonous modes of occurrence are common in certain horizons (Fig. 2).

In the *Claraia wangi* assemblage, paper shells such as *Claraia wangi* and *Claraia longyanensis* are occasionally preserved as closed and open articulated valves in certain beds. The shells are well preserved, although they are extremely thin and fragile. Accordingly, *Claraia wangi* assemblages consist of parautochthonous elements in certain horizons. This monospecific bivalve assemblage is found in deep carbonate ramp environments, above the storm–wave base, in North Vietnam and surrounding basin environments in South China. It is likely that the habitat of *Claraia wangi* was widely distributed within Lower Triassic shallow to deep–sea environments.

In the Huangzishan area, shells such as *Eumorphotis teilhardi, Towapteria scythica* and *Pteria ussurica variabilis* are preserved as disarticulated valves and fragments that accumulated on the basal erosion surfaces of bedding planes. Accordingly, the *Eumorphotis teilhardi–Towapteria scythica* assemblage probably consists of allochthonous elements. Besides, in the Hong Ngai Formation, the *Eumorphotis teilhardi–Towapteria scythica* assemblage is well preserved in deep carbonate ramp deposits. There are no signs of abrasion or breakage, even though the valves are thin and fragile, and articulated valves are occasionally found. Accordingly, these shells probably accumulated within or close to their habitats, suggesting that the *Eumorphotis teilhardi–Towapteria scythica* assemblage is parautochthonous. It is likely that *Eumorphotis teilhardi, Towapteria scythica, Pteria ussurica ussurica* and *Pteria ussurica variabilis* inhabited shallow marine environments that were influenced by wave currents and storm events below the fair–weather wave base.

In shallow ramp deposits, the *Claraia stachei–"Claraia" phobangensis* assemblage mainly consists of parautochthonous elements. *Claraia concentrica, Claraia stachei, Claraia aurita, "Claraia" phobangensis, Eumorphotis multiformis* and *Pteria ussurica ussurica* probably inhabited shallow seas above the fair-weather wave base. Komatsu and Dang (in press) report parautochthonous *Claraia concentrica, Claraia aurita* and *Claraia intermedia multistriata* from lower shoreface deposits in the Pa Khom Formation, Song Da Basin and the Lang Son Formation, An Chau Basin, North Vietnam, that contain wave–ripple laminations and HCS. Furthermore, in the Lang Son Formation, hemipelagic mudstone yields abundant *Claraia concentrica* and *Claraia aurita*, and well–preserved articulated valves are commonly found. Therefore, *Claraia concentrica* and *Claraia aurita* inhabited a wide range of habitats from shallow marine environments above the fair–weather wave base to basin environments.

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UPPER TRIASSIC CONCHOSTRACAN BIOSTRATIGRAPHY OF THE CONTINENTAL RIFT BASINS OF EASTERN NORTH AMERICA: ITS IMPORTANCE FOR CORRELATING NEWARK SUPERGROUP EVENTS WITH THE GERMANIC BASIN AND THE INTERNATIONAL GEOLOGIC TIME SCALE

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Abstract—A preliminary conchostracan zonation is established here for the Upper Triassic-lowermost Jurassic strata of the Newark Supergroup. This zonation is the prototype for an Upper Triassic conchostracan standard zonation for the entire northern hemisphere. The number of zones within this interval is about fifteen, averaging 2 to 3 million years in length, though the precise number will not be known until several key index species are described or revised and our understanding of the range of several other key species is improved. Most of the zones can be correlated closely with conchostracan zones of the Germanic Basin, which have been correlated closely with the international marine geologic time scale. Ultimately, the correlation of the Newark Supergroup with the Germanic Triassic and the international geologic time scale will be greatly improved. Progress to date includes: 1) Sedimentation in the Newark Supergroup began in the early Cordevolian, very close to the base of the Carnian (and Upper Triassic). 2) The basal, dominantly paludal to lacustrine Cordevolian sediments of the Newark Supergroup are separated by a regional unconformity from overlying upper Julian strata that represent fluvial deposits formed during the Middle Carnian Pluvial Event, just as in the Germanic Basin. 3) The Adamanian (Conewagian) Land Vertebrate Faunachron (LVF) is everywhere Tuvalian. 4) Confirmation of the Tuvalian age of the Adamanian LVF shows that magnetostratigraphic correlations of the Newark Supergroup with the Tethys region are incorrect. 5) In the Newark Supergroup, the base of the Hettangian does not lie slightly below the oldest of the Central Atlantic Magmatic Province (CAMP) volcanic flows as previously assumed, but rather within or near the second lava flow of the CAMP sequence. 6) The location of the Triassic – Jurassic boundary near the middle of the vast plateau basalt flows formed by the CAMP volcanic episode indicates that the biotic crisis across the Triassic-Jurassic boundary was intimately linked to the CAMP events.

INTRODUCTION

Investigation of Triassic conchostracans began in the 19th century in the Germanic Basin of Germany (von Zieten, 1833; Beyrich, 1857; Giebel, 1857; Sandberg, 1871;Weiss, 1875), in France (Voltz, 1835), in Great Britain (Jones, 1862, 1890, 1891), and in the Newark Supergroup of the eastern United States (Emmons, 1856, 1857, 1863; Lea,1856; Jones, 1890, 1891). After this initial flurry of research, a long interval followed in all of these regions during which only a few new Triassic conchostracans were described. These rare contributions were by Picard (1911), Schmidt (1928), Defretin (1950), and Defretin-Lefranc (1963) for the Germanic Basin, and Bock (1946) and Raymond (1946) for the Newark Supergroup. A modern description of Upper Triassic conchostracans of the Newark Supergroup was given by Bock (1953a), who also published a brief taxonomic revision that replaced the generic name *Howellites* Bock, 1953 with *Howellisaura* Bock, 1953 because of homonymy (Bock, 1953b). After Bock's work, the study of Newark Supergroup conchostracans and their taxonomy languished until the work of Kozur and Weems (2005, 2006), who described the upper Alaunian to lower Hettangian conchostracans of the Culpeper and Newark basins and established the first conchostracan zonation for that time interval. Other authors since 1953 occasionally have noted occurrences of conchostracans in the Newark Supergroup, but they either did not attempt any taxonomic designations or else used "wastebasket" names (e.g., *Cyzicus* sp.) to describe them. In a few cases small photographs were shown, with insufficient magnification for accurate taxonomic determination, or else drawings were presented (e.g., Gore, 1986; Olsen, 1988).

In the Germanic Basin, modern work on Triassic conchostracans began with Reible (1959, 1962) and Warth (1969). Since that time, a number of papers concerning Triassic conchostracans have been published (e.g., Alexandrowicz and Slupczynski, 1971; Gall, 1971; Kozur, 1979, 1980, 1982, 1983; Kozur and Seidel 1981, 1983a, b). The taxonomy of Lower Triassic and lower Anisian conchostracans was revised, and an uppermost Permian to lower Anisian conchostracan biostratigraphy was established (Kozur and Seidel, 1983a, b; Kozur, 1993b, 1999) and correlated with the palaeomagnetic succession, carbon isotope excursions, and Milankovitch cyclicity (Bachmann and Kozur, 2004; Korte and Kozur, 2005). In contrast, very little work has been done on the taxonomy of Upper Triassic conchostracans since Reible (1962) and Warth (1969). With the exception of two new genera, two new species, and one new subspecies established from the Carnian of the Germanic Basin (Kozur, 1982; Geyer, 1987; Olempska, 2004), Upper Triassic conchostracans have been only mentioned, illustrated (e.g., Hopf and Martens, 1992; Reimann and Schmidt-Kaler, 2002), or described in open nomenclature (Seegis, 1997). Because taxonomic investigations of Upper Triassic conchostracans in the Germanic Basin have been inadequate, the majority of Upper Triassic conchostracan species from that region either are undescribed or in need of major revision. The Germanic Basin and the Newark Supergroup of eastern North America have nearly the same Upper Triassic conchostracan species and succession, but the majority of species in the Newark also are undescribed or in need of major revision.

In contrast, comprehensive taxonomic work on Upper Triassic and Liassic conchostracans has been undertaken in Asia (e.g., Mansuy, 1912a, b; Chi, 1931; Kobayashi, 1951, 1955, 1973, 1975; Chen, 1974, 1982; Chang et al., 1976; Chen and Shen, 1980, 1985; Liu, 1982; Shen, 1985; Li and Shen, 1995). Many of these species also are found in the Germanic Basin and in the Newark Supergroup. Upper Triassic conchostracans found in South America, however, do not represent taxa found in China, the Newark Supergroup, or the Germanic Basin (e.g., Katoo, 1971; Herbst and Ferrando, 1985; Gallego, 1992a, b, 2001a,b,c; Gallego et al., 2004), though some taxa (e.g., *Anyuanestheria* = *Menucoestheria*) are the same at the generic level.

Some Triassic conchostracans have been described from terrestrial rocks intercalated with marine deposits in the Tethys region or from brackish areas within the Tethys (Vadász, 1952; Nagy, 1959, 1960, 1968; Kozur, 1987, 1999; Tintori, 1990; Tintori and Brambilla, 1991; Kozur and Mock, 1993). These have been extremely important for correlating continental deposits with the well established marine geologic time scale (Kozur, 1999; Kozur and Mock, 1993).

A comprehensive revision of the Upper Triassic conchostracans of the Germanic Basin is in preparation by H.W. Kozur and K.-P. Kelber. Unfortunately, the Upper Triassic sequence in the Germanic Basin has numerous time gaps, often of unknown duration, as well as thick sequences of strata formed in environments unsuitable for conchostracans (e.g., the hypersaline gypsum-bearing beds of the Grabfeld and Weser formations). Thus, the much more complete Carnian to Hettangian continental sequence of the Newark Supergroup is here chosen to establish an Upper Triassic standard conchostracan zonation for the Northern Hemisphere. The first results of these studies are presented in the present paper. Taxonomic results are presented only where they are necessary to support our biostratigraphic evaluation.

Our biostratigraphic results allow us to reach several important conclusions. First, the age of the oldest known rocks in the Newark Supergroup of the eastern United States finally can be established with certainty. Second, the controversy can be resolved as to whether the biostratigraphic boundary between the Adamanian (Conewagian) Land Vertebrate Fauna (LVF) and the Revueltian (Neshanician) LVF corresponds to the Carnian-Norian boundary, or whether the Carnian-Norian boundary lies within the early Adamanian LVF (or even earlier in the middle Sanfordian LVF) as indicated by correlation of Newark palaeomagnetic reversal patterns. Third, it is now possible to establish the precise age of the Central Atlantic Magmatic Province (CAMP) volcanics within the upper Newark Supergroup.

INVESTIGATED SECTIONS

Basins and subbasins of the Newark Supergroup are shown in Figure 1. The stratigraphic sections within investigated basins are shown in Figures 2-4, and locality data are given in Table 1. Most of the investigated material was collected by the authors, but some additional material from museums and other collections is included. This includes the type material of Lea (1856) and Bock (1946, 1953a) curated by the Academy of Natural Sciences, Philadelphia (ANSP), material from the collections of the North Carolina Museum of Natural Sciences (NCMNS), the New Mexico Museum of Natural History (NMMNH), and the Yale Peabody Museum (YPM). For specimens borrowed from these institutions, we have attempted to determine their exact collection localities and their stratigraphic position within the present-day lithostratigraphic framework. In a few cases, available locality data provided a degree of precision less than what we would have liked. With two exceptions, discussed later, samples that we collected were relatively easy to assign to lithostratigraphic units. Stratigraphic horizons can be seen in Figures 2-4, and the level of reliability of locality data is indicated in Table 1.

For comparison, we have investigated Upper Triassic conchostracans from the Keuper in Germany (Bavaria and Baden-Württemberg), Poland, and England from our own collections, as well as material from a number of colleagues: Dr. M. Hounslow (Lancaster, UK) for upper Rhaetian material of England; Dr. Grzegorz Niedzwiedzki and Dr. Tomasz Sulej (both Warsaw) for material from the middle Tuvalian Krasiejów locality in southwestern Poland; the Naturkundemuseum in Stuttgart (Germany) for material from the Keuper of Baden-Württemberg; and the Geological Institute of the Würzburg University for material from their collection (the holotype of *Laxitextella multireticulata*).

RESULTS AND ANALYSES

Systematics

Taxonomic revision of the Upper Triassic conchostracans of the Newark Supergroup will be published in several forthcoming papers. In the present paper, mostly illustrations of relevant conchostracan taxa, their ranges, and occasional short remarks concerning their taxonomy are presented. Three new species, namesakes for the Tuvalian conchostracan biozones, are described in the Appendix at the end of this paper. Families are listed below in alphabetical order.

Family Bulbilimnadiidae Kozur & Weems, 2005
Genus *Bulbilimnadia* Shen, 1976

Type species: *Bulbilimnadia bullata* Shen, 1976

Bulbilimnadia froelichi Kozur & Weems, 2005
(Pl. 9, Figs. 13, 15, 16)

2005 *Bulbilimnadia froelichi* nov. sp. – Kozur & Weems, p. 31, Pl. 4, Figs. 12, 14-16; Pl. 5, Figs. 1-4, 6

Occurrence: Upper Waterfall Formation, Hettangian, Culpeper Basin.

Bulbilimnadia sheni Kozur & Weems, 2005
(Pl. 9, Figs. 6, 7, 10, 11, 14)

2005 *Bulbilimnadia sheni* n. sp. – Kozur and Weems, p. 30-31, Pl. 4, Figs. 8-11, 13

Occurrence: Lower Waterfall Formation, lower Hettangian, Culpeper Basin; middle East Berlin Formation, lower Hettangian, Hartford Basin.

Family Euestheriidae Defretin, 1965
Genus *Euestheria* Depéret & Mazeran, 1912

Type species: *Posidonia minuta* (von Zieten, 1833)

Synonym: *Howellisaura* Bock, 1953b (for *Howellites* Bock, 1953a)

Remarks: Representatives of this genus often have been assigned to the recent genus *Cyzicus* Audouin, 1837 and its junior synonym *Isaura* Joly, 1841, but also partly to *Palaeestheria* Barnard, 1929, which has a Lower Cretaceous type species (*Estheria anomala* Jones, 1901). Warth (1990) rejected the use of *Euestheria* because, in his opinion, it was based on an incorrectly determined type species, the Lower Permian "*Estheria minuta* d'Autun," which does not even belong in *Euestheria*. The name *Estheria minuta* was erroneously assigned by Depéret and Mazeran (1912) to lowermost Permian (or uppermost Carboniferous) conchostracans (*Pseudestheria* Raymond, 1946). They wrote that, if their assignment of these forms to the Triassic *E. minuta* proved to be correct, then *E. minuta* first appeared in the Early Permian. This indicates that they were well aware that the typical *E. minuta* are found in the Triassic. They also discussed that the Upper Triassic species "*Estheria*" *laxitexta* should not be united with *Euestheria minuta*, because in their opinion these were two different species (and we concur). Thus, *Euestheria* was clearly defined, with the Triassic species *E. minuta* (von Zieten) designated as its type species. The systematic position of *Palaeestheria* Barnard, 1929, emend. Raymond, 1946 is not clear because the systematic position of its Lower Cretaceous type species, *Estheria anomala* Jones, 1901, is not clear. Species of *Euestheria* (including the type species *E. minuta*) should not be assigned to *Palaeestheria* as was done in Warth (1969, 1990) because, even if the two genera prove to be synonymous, *Palaeestheria* Barnard, 1929 still would be the junior synonym of *Euestheria* Depéret and Mazeran, 1912. The recent generic name *Cyzicus* likewise is an inappropriate name for Triassic conchostracans.

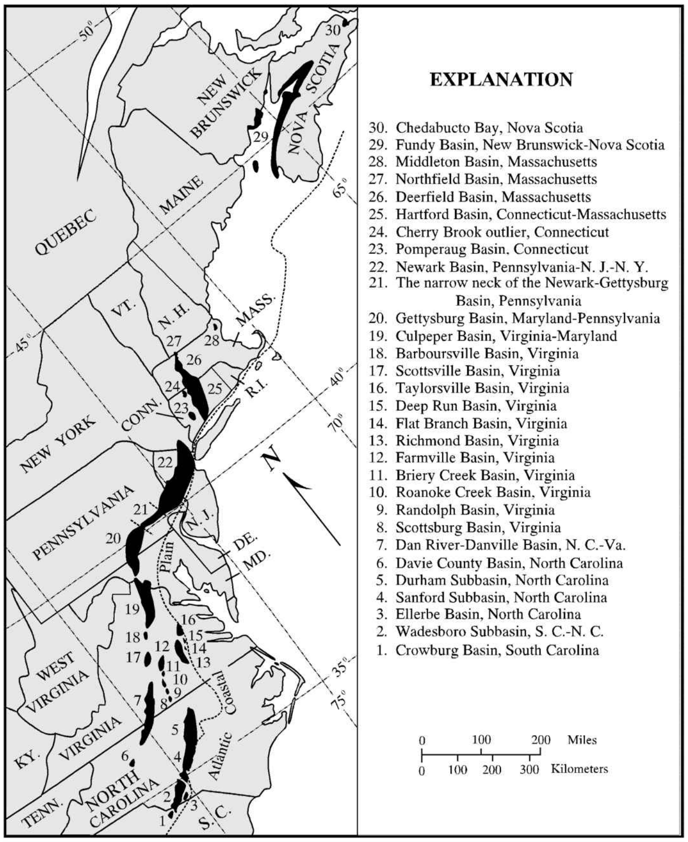

FIGURE 1. Upper Triassic continental rift basins in eastern North America (after Luttrell, 1989).

The genus *Howellisaura* Bock, 1953b has been used to encompass a number of species that belong in several different genera, but the type species (*Howellites princetonensis* Bock, 1953a) clearly is a large *Euestheria*.

Euestheria brodieana (Jones, 1862)
(Pl. 9, Figs. 1-5, 8, 9, 12)

1862 *Estheria minuta* var. *brodieana* Jones, pp. 66-78, Pl. 2, Figs. 8-15
1955 *Euestheria minuta brodieana* – Kobayashi, p. 98
2005 *Euestheria brodieana* (Jones) – Kozur & Weems, p. 27, Pl. 3, Fig. 8, Pl. 4, Figs. 1-7

Occurrence: England (upper Rhaetian and basal Liassic ?); northern Germany (upper part of lower Rhaetian), southern Germany (upper Rhaetian); Argiles de Levallois of France (upper Rhaetian); Midland Formation of Culpeper Basin (upper Rhaetian), lower Waterfall Formation of Culpeper Basin (lower Hettangian).

Euestheria buravasi Kobayashi, 1975
(Pl. 5, figs. 2, 3)

1975 *Euestheria buravasi* Kobayashi, sp. nov.–Kobayashi, p. 80-81, Pl. 7, Figs. 8, 9

Remarks: The upper Tuvalian *Euestheria princetonensis* (Bock, 1953), which is the forerunner of *E. buravasi*, differs from *E. buravasi* in that it has an ovoid outline, an anterior margin that is distinctly higher than the posterior margin, and an anteroventral margin that is not so distinctly oblique.

Occurrence: Nam Pha Formation of Khorat Group at Nam Phrom Dam, northwest Khorat Plateau, Thailand (lower Norian); Triangle Brick Quarry, "lithofacies association II" of Hoffman and Gallagher (1989) (equivalent to the lower Sanford Formation), Durham Subbasin of Deep River Basin (lowermost Norian).

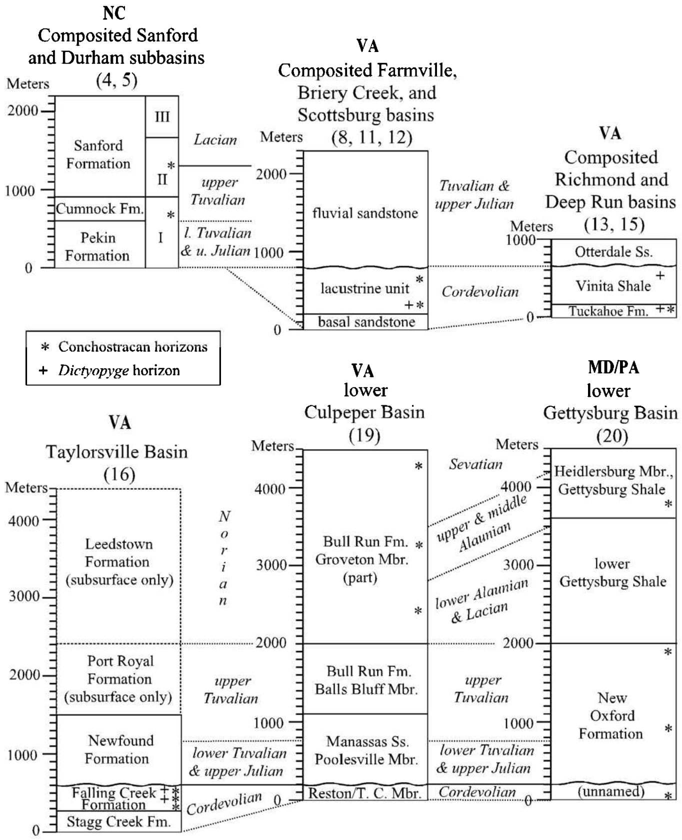

FIGURE 2. Correlation chart and conchostracan sites of the Sanford and Durham Subbasins of the Deep River Basin (NC), Farmville, Briery Creek, Scottsburg, Richmond, Deep Run, Taylorsville, lower sequence of Culpeper basins (all VA) and lower sequence of Gettysburg Basin (MD/PA).

Euestheria hausmanni (Schmidt, 1938)
(Pl. 4, Figs. 2, 3)

1938 *Estheria hausmanni* Berger –Schmidt, p. 46, Fig. 861a

Remarks: *E. hausmanni* is very similar to *E. ovata* (Lea), but it is distinguished by a distinctly oblique anteroventral margin, whereas *E. ovata* has its entire anterior margin rather highly rounded. The posterior margin is high and broadly rounded in both species, and the growth bands are uniformly closely spaced without a broad zone of very narrow growth bands concentrated in the outer part of the shell.

There is a possibility that *E. hausmanni* is the junior synonym of *E. pennsylvanica* (Wanner). To determine this, it will be necessary to investigate the type material of the latter species (repository not given in the description) or to re-sample the type locality if the type material cannot be located. It is impossible to tell from the illustrated material whether *E. pennsylvanica* is a synonym of *E. ovata* (Lea), as assumed by Bock (1953a), or whether it is synonymous with *E. hausmanni*, because the illustrated material does not show whether the anterior margin of *E. pennsylvanica* (which is somewhat distorted) is high and broadly rounded as in *E. ovata* or whether the anteroventral margin is distinctly oblique as in *E. hausmanni*.

Occurrence: Cumnock Formation in the Sanford Subbasin of the Deep River Basin, lower third of the Lockatong Formation in the Newark Basin, upper New Oxford Formation in the Gettysburg Basin, all upper Tuvalian (within the late Adamanian LVF); Coburg Sandstein of southern Germany (upper Tuvalian).

Euestheria sp. cf. *E. hausmanni* (Schmidt, 1938)
(Pl. 5, Fig. 4)

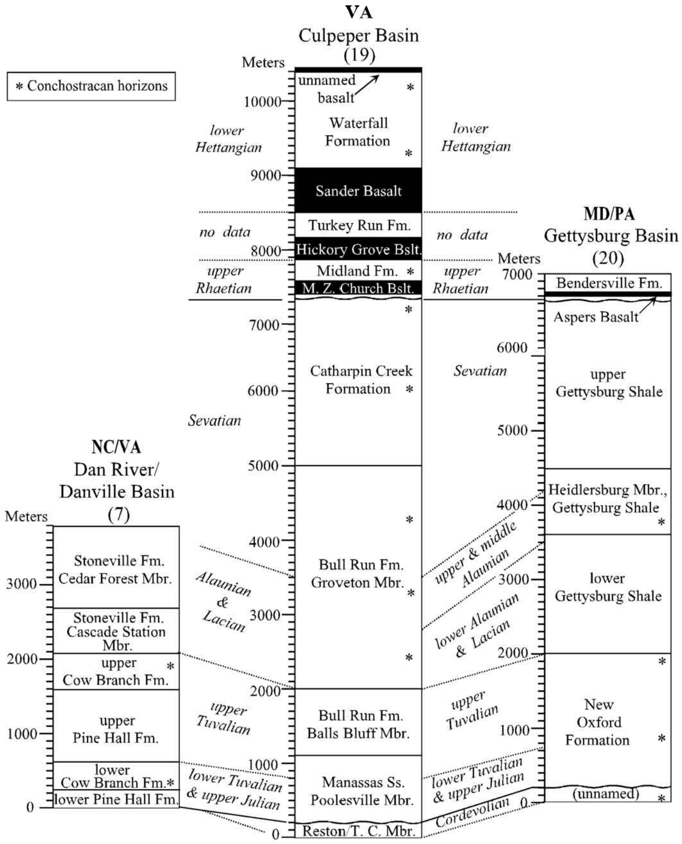

FIGURE 3. Correlation chart and conchostracan sites of the Dan River/Danville Basin (NC/VA), Culpeper Basin (VA), and Gettysburg Basin (MD/PA).

Remarks: This form is distinguished from *E. hausmanni* by possessing fewer growth bands, which are rather wide in the outer part. Anterior and posterior margins are broadly rounded, and the anteroventral margin is only slightly oblique.

Occurrence: Triangle Brick Quarry, "lithofacies association II" of Hoffman and Gallagher (1989) (equivalent to the lower Sanford Formation), in the Durham Subbasin of the Deep River Basin (lowermost Norian); lower "Untere Bunte Steinmergel" (lowermost Arnstadt Formation) of Thuringia, Germany, Lacian (lower Norian).

Euestheria minuta (von Zieten, 1833)
(Pl. 1, Figs. 2, 5; Pl. 3, Figs. 3, 5)

1833 *Posidonia minuta* von Alberti – von Zieten, p. 72, Pl. 5, Fig. 5
1862 *Estheria minuta,* Alberti sp., pars – Jones, pp. 42-57, Pl. 1, Figs. 28, 29
1912 *Estheria* (*Euestheria*) *minuta* Alberti – Depéret & Mazeran, pp. 169-173, referring to the subgenus *Euestheria* on page 173
1955 *Euestheria minuta* (von Zieten) – Kobayashi, pp. 54, 97, 131

Remarks: *E. minuta* is a long-ranging species that is common and dominant throughout the entire upper Ladinian, but also ranges up into the Cordevolian. When a Ladinian age can be excluded by the presence of other taxa with ranges that begin after the Ladinian, its presence indicates an age no younger than early Carnian (Cordevolian). *Isaura midlothianensis* Bock, 1953 may be a junior synonym of *E. minuta*, but this remains uncertain because only the umbonal region is preserved in *I. midlothianensis*.

Occurrence: Throughout the entire Northern Hemisphere. In the Newark Supergroup, it occurs only in the oldest (Cordevolian) beds: lacustrine unit of the Briery Creek and Farmville basins, Tuckahoe Formation of the Deep Run and Richmond basins, Falling Creek Formation of the Taylorsville Basin.

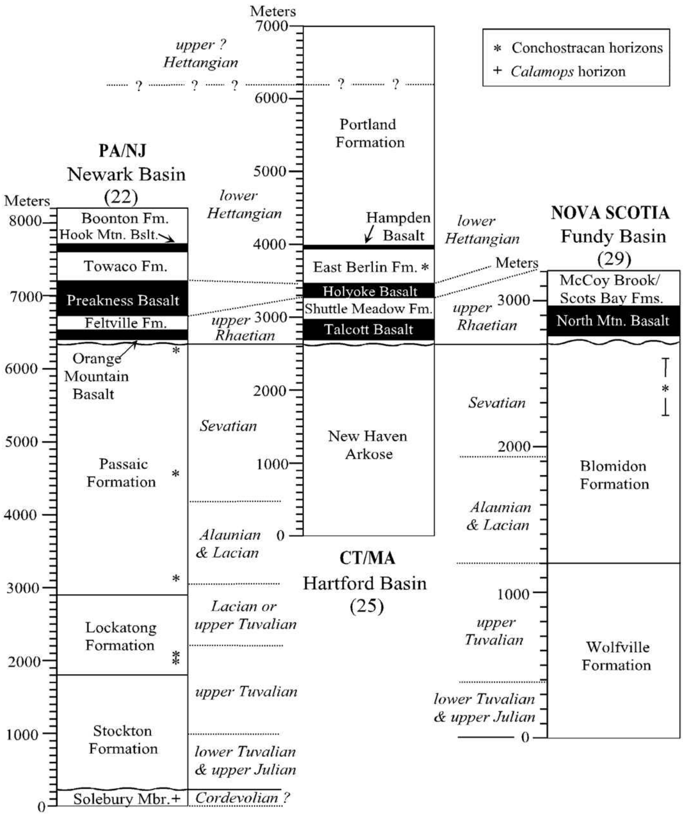

FIGURE 4. Correlation chart and conchostracan sites of the Newark Basin (PA/NJ), Hartford Basin (CT/MA), and Fundy Basin (Nova Scotia).

Euestheria ovata (Lea, 1856)
(Pl. 5, Fig. 1)

1856 *Posidonia ovata* Lea – Lea, p. 78

Remarks: This species was adequately described by Bock (1953a) from the type material of Lea (1856) and other material. For description and synonymy list, see Bock (1953a). The holotype is re-figured in the present paper (Pl. 5, Fig. 1). No definitive synonymy list can be given yet because some type material of other described species from the Newark Supergroup is in need of restudy. This is especially important for "*Estheria*" *pennsylvanica* Wanner, 1926, which is listed by Bock as a junior synonym of *E. ovata*. However, the material illustrated by Wanner does not show if the anterior margin is high and broadly rounded (as is typical for *E. ovata*) or whether the anteroventral margin is strongly oblique (as is typical for *E. hausmanni*). The type material of Wanner (1926) may be lost, so the type strata may need to be resampled.

Euestheria princetonensis (Bock, 1953)
(Pl. 4, Figs. 4-6)

1953a *Howellites princetonensis* Bock, n. sp. – Bock, pp. 71, 72, Pl. 13, Figs. 1-3
1953a *Howellites berryi* Bock, n. sp. – Bock, p. 72, Pl. 13, Fig. 4
1953b *Howellisaura princetonensis* – Bock, p. 759

Remarks: This species was adequately described by Bock (1953a). The very minor differences between it and *Howellisaura berryi* (Bock, 1953) (e.g., a somewhat higher posterior margin) are within the range of intraspecific variability for *H. princetonensis*. *H. princetonensis* conforms to the definition of the genus *Euestheria*, to which it is assigned

TABLE 1. Investigated conchostracan localities in the Newark Supergroup

Locality	New Age	Old Age	Unit and Horizon	Latitude	Longitude	Other Data
Sanford Subbasin of Deep River Basin						
Pomona Pipe Co., pit near Gulf	upper Julian to lower Tuvalian	upper Carnian	Pekin Fm., near middle of unit	35.5694 N	79.2976 W	Goldston Quad Chatham Co., NC
Bethany Church	upper Tuvalian	upper Carnian	Cumnock Fm., about 80 m above base	35.5584 N	79.2921 W	Goldston Quad Chatham Co., NC
Deep River coal basin (ANSP 31194)	upper Tuvalian	upper Carnian	Cumnock Fm., between 100-200 m above base	vague locality	vague locality	Goldston Quad ? Chatham Co., NC
Durham Subbasin of Deep River Basin						
Triangle Brick Quarry, NMMNH and NC museums	basal Norian, near Tuvalian-Lacian boundary	lower Norian	"Lithofacies Association II" of Hoffman and Gallagher, 1989	35.8694 N	78.8960 W	Green Level Quad Durham Co., NC
Dan River / Danville Basin						
U.S. 220 road cut N of Dan River	upper Julian to lower Tuvalian	Carnian	lower Cow Branch Fm., about 10 m above base	36.3875 N	79.9411 W	Mayodan Quad Rockingham Co., NC
Solite Quarry	upper Tuvalian	Carnian	upper Cow Branch Fm., about 100 m below top ?	36.5412 N	79.6698 W	Northeast Eden Quad Rockingham Co., NC
Briery Creek Basin						
Worthy Property * (YPM 34659 and YPM 220198)	lower Cordevolian	Carnian	lacustrine unit, about 100 m above base	37.2190 N	78.4445 W	Hampden Sydney Quad Prince Edward Co., VA
Flournoy's coal pit * (YPM 34664)	lower Cordevolian	Carnian	lacustrine unit, about 100 m above base	37.1949 N	78.4754 W	Hampden Sydney Quad Prince Edward Co., VA
Farmville Basin						
Little Willis River *	Cordevolian	Carnian	lacustrine unit, about about 450 m above base	37.4115 N	78.3939 W	Willis Mountain Quad Cumberland Co., VA
Richmond Basin						
Midlothian coal mine spoil (ANSP 31497)	lower Cordevolian	Carnian	upper Tuckahoe Fm., about 150 m above base	37.5029 N	77.6402 W	Midlothian Quad Chesterfield Co., VA
Winterpock * (ANSP 31497)	lower Cordevolian	Carnian	upper Tuckahoe Fm., about 150 m above base	37.3459 N	77.7204 W	Winterpock Quad Chesterfield Co., VA

here. As *H. princetonensis* is the type species of *Howellisaura*, *Howellisaura* becomes a junior synonym of *Euestheria*. Other species that have been assigned to *Howellisaura* in the past, however, belong to genera other than *Euestheria*.

Euestheria winterpockensis (Bock, 1953)
(Pl. 1, Figs. 1, 4)

1953 *Howellites winterpockensis* Bock, n. sp. –Bock , p. 73, Pl. 12, Figs. 7, 8

1987 *Cyzicus* (*Euestheria*) *minutus multicostatus* n. subsp. – Geyer, pp. 288, 289, Abb. 7, Figs. 1-15

Remarks: *E. winterpockensis* is a small species that is characterized by its numerous, very narrow growth bands across the entire carapace. Typically, 20-30 growth bands are present, but the number can range from 19 to 46. Specimens with 19 or 20 growth lines overlap slightly with the forerunner species *E. minuta*, which has 10-20 growth bands, but specimens with 19 or 20 growth lines are very rare. The type material from the Tuckahoe Formation at Winterpock, Richmond Basin includes both *E. minuta* and *E. winterpockensis*. Bock (1953a) distinguished an alpha-form (male) and a beta-form (female). He assigned specimens with 19 growth bands to the alpha-form and specimens with 21 growth bands to the beta-form. His beta-form lies above the narrow zone of overlap, so this form can be readily distinguished from *E. minuta*. As *E. multicostata* Geyer has the same features as *E. winterpockensis*, it is a junior synonym of that species.

E. winterpockensis is very characteristic of the Cordevolian. In the lower Cordevolian, small forms occur that typically are 1.8 to 3.3 mm long but rarely range up to 4 mm. Toward the upper Cordevolian, specimens become larger on average and mostly fall within the upper part of the size range just given or even slightly larger. These forms, illustrated on Plate 3, Figure 4, here are regarded as *Euestheria* sp. cf. *E. winterpockensis* (Bock).

Occurrences: Lower Estherienschichten of the upper Grabfeld Formation in Germany (lower Cordevolian); Tuckahoe Formation in the Richmond and Deep Run basins (lower Cordevolian); lower Falling Creek Formation in the Taylorsville Basin (lower Cordevolian). Within the upper Falling Creek Formation, mainly *E.* sp. cf. *E. winterpockensis* is present.

FAMILY SHIPINGIIDAE KOZUR & WEEMS, 2005
Genus *Anyuanestheria* Zhang & Chen, 1976

Type species: *Anyuanestheria subquadrata* Zhang & Chen, 1976

Synonym: *Menucoestheria* Gallego & Covacevich, 1998

Remarks: Most characteristic for *Anyuanestheria* are weak and irregular radial lirae on the outer growth bands and reticulation on the inner growth bands. The reticulation may be totally replaced by radial

TABLE 1. (Continued)

Deep Run Basin						
Three Chopt Road fish locality	lower Cordevolian	Carnian	upper Tuckahoe Fm. about 150 m above base	37.6351 N	77.5816 W	Glen Allen Quad Henrico Co., VA
Taylorsville Basin						
Stagg Creek, older level	lower Cordevolian	Ladinian to Carnian	lower Falling Creek Fm., 40 m above base	37.7831 N	77.5450 W	Hanover Academy Quad Hanover County, VA
Stagg Creek, younger level	lower Cordevolian	Ladinian to Carnian	lower Falling Creek Fm., 44 m above base	37.7833 N	77.5450 W	Hanover Academy Quad Hanover County, VA
Little River site, W of C & O RR bridge	lower Cordevolian	Ladinian to Carnian	middle Falling Creek Fm., about 155 m above base	37.8225 N	77.4285 W	Ashland Quad Hanover County, VA
Falling Creek, N of Ashland	Cordevolian	Ladinian to Carnian	upper Falling Creek Fm., exact position unknown	37.7882 N	77.4855 W	Ashland Quad Hanover County, VA
Culpeper Basin						
Carriage Ford	upper Lacian to lower Alaunian	Norian	Groveton Mbr., Bull Run Fm. 350 m above base	38.6420 N	77.5928 W	Nokesville Quad Fauquier County, VA
I-66 at VA Route 234, NW corner	upper Alaunian	Norian	Groveton Mbr., Bull Run Fm.,1,250 m above base	38.8014 N	77.5264 W	Gainesville Quad Prince William County, VA
Groveton Cemetery, Bull Run Battlefield	lower Sevatian	Rhaetian	Groveton Mbr., Bull Run Fm., 2,100 m above base	38.8136 N	77.5460 W	Gainesville Quad Prince William County, VA
Cedar Run	Sevatian	Rhaetian	Catharpin Creek Fm., 1,050 m above base	38.6530 N	77.6768 W	Catlett Quad Fauquier County, VA
Haymarket	upper Sevatian	Rhaetian	Catharpin Creek Fm., 100 m below top and 2,350 m above base	38.8481 N	77.6352 W	Thoroughfare Gap Quad Prince William County, VA
Killian Property	upper Rhaetian	Liassic	Midland Fm., 150 m above base	38.7551 N	77.6597 W	Thoroughfare Gap Quad Prince William County, VA
Avalon Farm	lower Hettangian	Liassic	lower Waterfall Fm. about 300 m above base	38.7734 N	77.6963 W	Thoroughfare Gap Quad Prince William County, VA
McDonald site on I-66 (YPM 202438 and YPM 202439)	lower Hettangian	Liassic	lower Waterfall Fm. about 300 m above base	38.8219 N	77.6855 W	Thoroughfare Gap Quad Prince William County, VA; assigned to Turkey Run Fm. by McDonald
Catletts Branch	lower Hettangian	Liassic	upper Waterfall Fm. about 300 m above base	38.8234N	77.6998 W	Thoroughfare Gap Quad Prince William County, VA

lirae, very indistinct, or not present at all. *Menucoestheria* has the same morphological features. *Anyanestheria* evolved in the late Cordevolian from small *Euestheria*. The oldest known examples of upper Cordevolian *Anyuanestheria*, *A. fimbriata* (Warth, 1969) and an unnamed species, are very small, mostly being less than 3 mm long. Upper Julian forms, such as *Anyuanestheria* n. sp. A from the Schilfsandstein Formation and the lower Cow Branch Formation, are much larger (5-7 mm). In the Tuvalian, small to medium-sized forms again occur (3-5 mm). The Jurassic form *Eosestheria* Shen, 1976 differs from *Anyuanestheria* in its much larger carapace (generally greater than 12 mm and reaching up to 28 mm) and the presence of radial lirae that are much more pronounced.

Anyuanestheria n. sp. A
(Pl. 4, Fig. 1)

Remarks: *Anyuanestheria* n. sp. A is much larger than other Triassic *Anyuanestheria*, and the radial lirae are more pronounced. It is a transitional form to *Eosestheria* Shen, but has not yet achieved the size of the latter genus.

Occurrence: Middle Schilfsandstein of Germany, lower Cow Branch Formation of the Dan River/Danville Basin (upper Julian).

Genus *Laxitextella* Kozur, 1982

Type species: *Estheria laxitexta* Sandberger, 1871

Laxitextella sp. cf. *L. laxitexta* (Sandberger, 1871)
(Pl. 3, Fig. 6)

1871 *Estheria laxitexta* –Sandberger, p. 48
1946 *Euestheria laxitexta* (Jones) –Raymond, p. 242
1962 *Isaura laxitexta* (Jones 1890) – Reible, pp. 210-212, Text-Fig. 15, Pl. 8, Figs. 3-6
1969 *Palaeestheria laxitexta* (Jones) – Warth, pp. 137-138, Text-Fig. 7, Pl. 3, Fig. 5
1982 *Laxitextella laxitexta* (Sandberger, 1871) – Kozur, p. 378-379

Remarks: Typical *Laxitextella laxitexta* occur in the upper Cordevolian middle gray Estherienschichten of the upper Grabfeld Formation in Germany. In the upper Julian Schilfsandstein to middle Tuvalian Lehrberg Beds, most specimens have a reticulation in which the polygons are elongated parallel to the growth bands. In the middle Tuvalian, however, the reticulations sometimes have irregularly arranged polygons that are not elongated parallel to the growth bands, as in typical *L. laxitexta*. Statistical studies on approximately 1000 excellently preserved specimens from upper Cordevolian, upper Julian and middle Tuvalian localities are in progress to determine whether or not the upper Julian and middle Tuvalian forms are separate taxa. For the moment, the forms with elongated polygons parallel to the growth lines are regarded as *L.* sp. cf. *L. laxitexta*. Specimens of this type from the Newark

TABLE 1. (Continued)

Gettysburg Basin						
Hanover Street, SE of town of New Oxford	lower Cordevolian	Carnian	unnamed unit below New Oxford Fm., about 10 m above base	39.8450 N	77.0340 W	McSherrystown Quad Adams Co., PA
Fulton site on Beaver Branch	lower part of upper Tuvalian	Carnian	middle New Oxford Fm.	39.6355 N	77.3347 W	Emmitsburg Quad Frederick Co., MD
Little Conewago Creek mine spoil	upper Tuvalian	Carnian	upper New Oxford Fm.	40.0703 N	76.7353 W	York Haven Quad York Co., PA
U.S. 15 SSE of Heidlersburg	middle Alaunian	Norian	lower Heidlersburg Mbr., about 200 m above base	39.9393 N	77.1432 W	Biglersville Quad Adams Co., PA
Newark Basin						
Gwynedd * (ANSP 16849)	upper Tuvalian	upper Carnian or lower Norian	Lockatong Fm., within lower 150 m ?	40.1438 N	75.5129 W	Phoenixville Quad Chester Co., PA
Eureka Quarry * (ANSP 16847-48, 65528, 65530)	upper Tuvalian	upper Carnian or lower Norian	Lockatong Fm., level unknown	40.2602 N	75.1815 W	Doylestown Quad Montgomery Co., PA
Princeton Library	upper Tuvalian	upper Carnian or lower Norian	Lockatong Fm., about 200 m above base	40.3497 N	74.6578 W	Princeton Quad Mercer Co., NJ
Granton Quarry (ANSP 31192)	upper Tuvalian	upper Carnian or lower Norian	Lockatong Fm., about 300 m above base	40.8447 N	73.9839 W	Central Park Quad Bergen Co., NJ
Milford	Lacian or lower Alaunian	Norian	Passaic Fm., about 300 m above base	40.5725 N	75.1123 W	Frenchtown Quad Hunterdon Co., NJ
150 m east of Cornet localities GHT 1 & 3	Sevatian	Rhaetian	Passaic Fm., 1,750 m from top	40.3185 N	75.7850 W	Birdsboro Quad Berks Co., PA
14 Constitution Avenue, Exeter	upper Sevatian	Rhaetian	Passaic Fm., 25 m from top	40.3134 N	75.8435 W	Birdsboro Quad Berks Co., PA
Hartford Basin						
North Branford	lower Hettangian	Liassic	middle East Berlin Fm., about 80 m below top	41.3356 N	72.7686 W	Branford Quad New Haven Co., CT
Westfield fish bed along Miner Brook	lower Hettangian	Liassic	middle East Berlin Fm., 82 m below top	41.5918 N	72.7006 W	Middletown Quad Middlesex Co., CT
Fundy Basin						
Blomidon Cliff * (YPM 34664)	Sevatian	Norian	upper Blomidon Fm.	45.2455 N	64.3654 W	NTS 021 H01 Kings Co., Nova Scotia

* latitude and longitude somewhat uncertain, estimated from accession card data

Supergroup, the first evidence for the *L. laxitexta* group outside the Germanic Basin and England, occur at the Fulton site in the Gettysburg Basin together with *Eosolimnadiopsis* ? n. sp. The latter species also is found at the Krasiejów locality in southwestern Poland along with the reptiles *Paleorhinus* and *Stagonolepis*, whose co-occurrence indicates the early Adamanian LVF. The strata at the Krasiejów locality are the same age as the middle Tuvalian Lehrberg Beds in southwestern Germany, so the Fulton also is middle Tuvalian.

Occurrence: Middle Schilfsandstein of the Germanic Basin (upper Julian) up to the Lehrberg Beds of southern Germany (middle Tuvalian); contemporaneous beds of the Krasiejów locality in southwestern Poland (middle Tuvalian); middle New Oxford Formation in the Gettysburg Basin (middle Tuvalian, equivalent to the Lehrberg Beds and the Krasiejów locality).

Laxitextella multireticulata (Reible, 1962)

(Pl. 1, Fig. 3, 6; Pl. 2, Figs. 1-5; Pl. 3, Fig. 1)

1962 *Isaura laxitexta multireticulata* n. subsp. –Reible, pp. 12-213, Text-Fig. 17; Pl. 9, Fig. 3
1969 *Palaeestheria multireticulata* (Reible) – Warth, p. 138, Text-Fig. 7
1993 *Laxitextella multireticulata* (Reible) – Kozur & Mock, p. 265

Remarks: This oldest species of *Laxitextella* has a reticulation with very small polygons. They often are arranged in radial or oblique stripes (Pl. 1, Figs. 3, 4) or they are slightly elongated parallel to the growth bands. In advanced forms, the typical small polygons are present in some parts of the carapace (Pl. 2, Fig. 4c), but in other parts the polygons are bigger (Pl. 2, Fig. 4b) and in a size range between those of typical *L. multireticulata* and those of *L. laxitexta*, the index species of the overlying zone. These advanced forms are transitional between the two species, but closer to *L. multireticulata*.

Occurrence: Lower variegated Estherienschichten of the upper Grabfeld Formation of the Germanic Basin (lower Cordevolian); western part of the Southern Alps (lower Cordevolian); equivalents of the *Daxatina canadiensis - Frankites sutherlandi* Zone, lowermost Dunscombe Mudstone of western England (Cordevolian); lacustrine unit in the Briery Creek Basin (lower Cordevolian); lower Falling Creek Formation in the Taylorsville Basin (lower Cordevolian); lower part of unnamed unit below the New Oxford Formation in the Gettysburg Basin (lower Cordevolian).

Genus *Redondestheria* Kozur, Weems & Lucas, 2005

Type species: *Redondestheria novomexicoensis* Kozur, Weems & Lucas, 2005

Redondestheria grovetonensis Kozur & Weems, 2005

(Pl. 7, Figs. 1, 2)

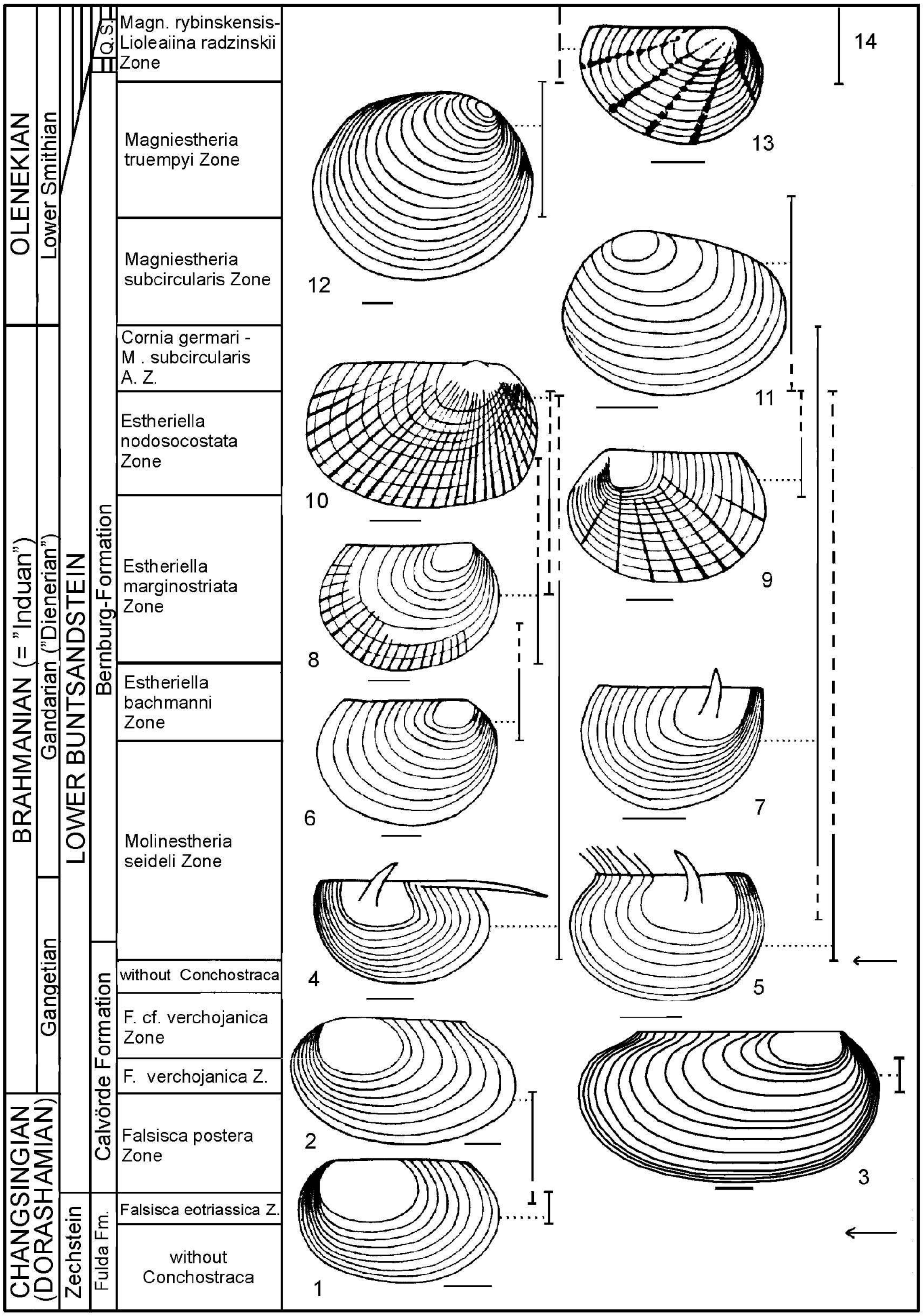

FIGURE 5. Conchostracan zonation of the Lower Buntsandstein of the Germanic Basin (standard conchostracan zonation for the upper Changhsingian to lower Smithian of the Boreal realm, low and median latitudes of Northern Hemisphere, northern and central Gondwana). Modified from Kozur (1993b). The ranges of the index species and some selected other species are shown. For *Magniestheria rybinskensis*, only the range below the Volpriehausen Formation is shown (for illustration see Fig. 6). Scale = 1 mm. Arrows show time of conchostracan immigration into the Germanic Basin after facies-controlled conchostracan-free intervals (sabkha deposits) throughout the entire Germanic Basin. Q.S.= Quickborn Sandstein. 1 = *Falsisca eotriassica* Kozur & Seidel; 2 = *Falsisca postera* Kozur & Seidel; 3 = *Falsisca verchojanica* (Novozhilov); 4: *Molinestheria seideli* Kozur; 5 = *Vertexia tauricornis* Ljutkevich; 6 = *Estheriella bachmanni* Kozur & Hauschke; 7 = *Cornia germari* (Beyrich); 8 = *Estheriella marginostriata* Kozur; 9 = *Estheriella nodosocostata* (Giebel); 10 = *Estheriella costata* Weiss; 11 = *Magniestheria ? subcircularis* (Chernyshev); 12 = *Magniestheria truempyi* Kozur & Seidel; 13 = *Lioleaiina radzinskii* Kozur & Seidel; 14 = *Magniestheria rybinskensis* (Novozhilov).

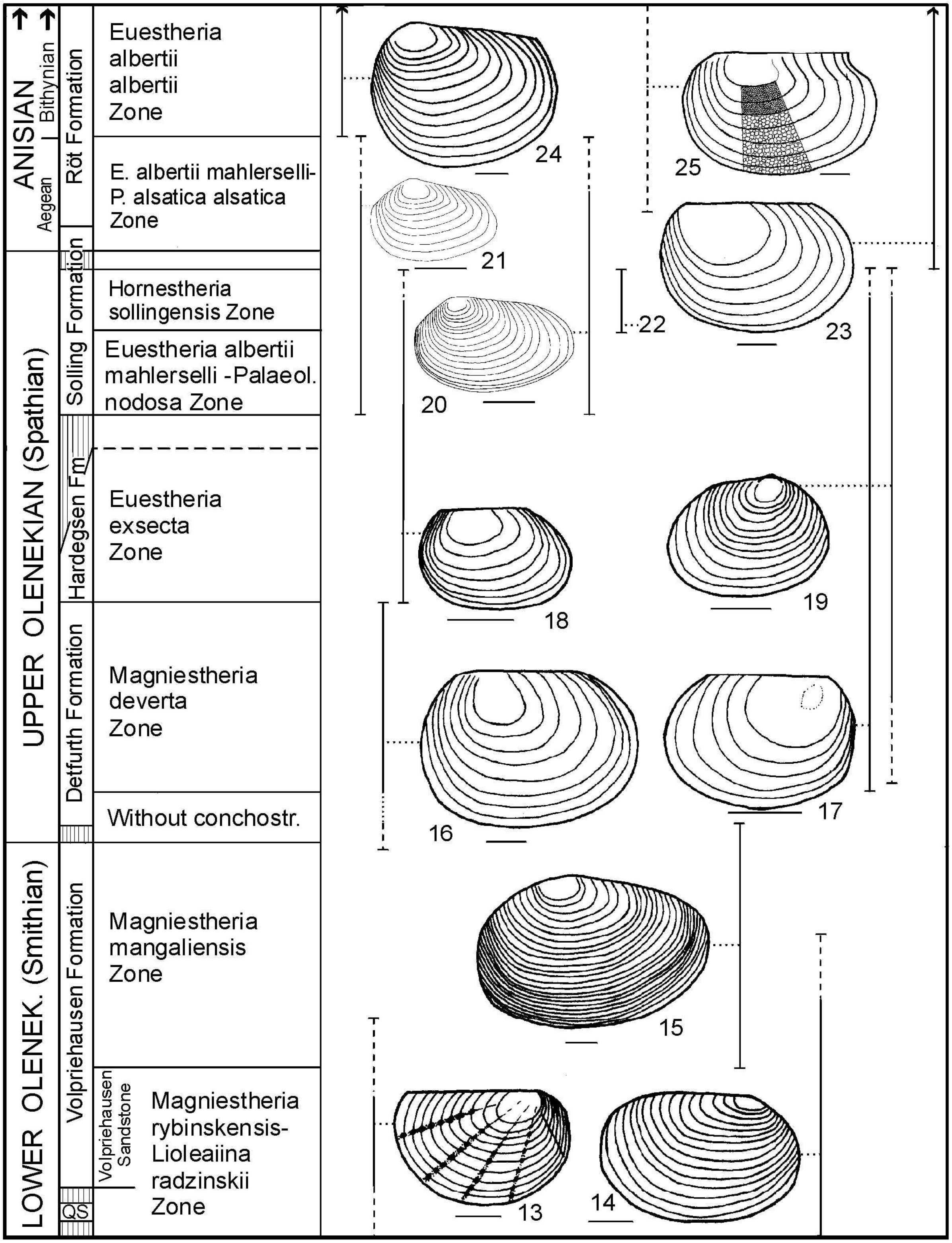

FIGURE 6. Conchostracan zonation of the Middle (Volpriehausen and Solling formations) and Upper Buntsandstein (Röt Formation) in the Germanic Basin. This standard conchostracan zonation applies to the Olenekian to lower Anisian of Eurasia and also the upper Spathian and lower Anisian of North and (partly) South America. The ranges of the index species (except *Hornestheria sollingensis* Kozur & Lepper n. gen. n. sp.) and of some selected species are shown. Scale = 1 mm. QS = Quickborn-Sandstone. 13 = *Lioleaiina radzinskii* Kozur & Seidel; 14 = *Magniestheria rybinskensis* (Novozhilov); 15 = *Magniestheria mangaliensis* (Jones); 16 = *Magniestheria deverta* (Novozhilov); 17 = *Palaeolimnadia alsatica detfurthensis* Kozur & Seidel; 18 = *Palaeolimnadia nodosa* (Novozhilov); 19 = *Euestheria exsecta* (Novozhilov); 20 = *Euestheria albertii mahlerselli* Kozur & Lepper n. subsp., slender morphotype; 21 = *Euestheria albertii mahlerselli* Kozur & Lepper n. subsp., stout morphotype; 22 = *Hornestheria sollingensis* Kozur & Lepper n. sp., for space problems only the range is shown; 23 = *Palaeolimnadia alsatica alsatica* Reible; 24 = *Euestheria albertii albertii* (Voltz); 25 = *Dictyonatella dictyonata* (Reible).

2005 *Redondestheria grovetonensis* Kozur & Weems n. sp.- Kozur and Weems, p. 30, Pl. 1, Figs. 3-7; Pl. 2, Figs. 1, 2

Occurrence: Common in the upper Groveton Member of the Bull Run Formation in the Culpeper Basin (lower Sevatian); rare in the lower Redonda Formation of New Mexico (Sevatian), where it co-occurs with *R. novomexicoensis* (Pl. 7, Figs. 4-6; Pl. 8, Fig. 8).

Genus *Shipingia* Shen, 1976

Type species: *Shipingia hebaozhaiensis* Shen, 1976

Shipingia hebaozhaiensis Shen, 1976

(Pl. 6, Figs. 1-7)

1976 *Shipingia hebaozhaiensis* Shen (sp. nov.) - Chang et al., p. 145, Pl. 32, Figs. 1-5

Remarks: Warth (1969) illustrated, under the name *Palaeestheria dorsorecta* (Reible), a large *Shipingia* from the Stubensandstein without specifying from which part of the Stubensandstein it came. Kozur and Weems (2005) referred this specimen to *S. olseni*. The microsculpture was not clearly recognizable in the illustration by Warth (1969), however, and restudy of the specimen in the Naturkundemuseum in Stuttgart, Germany, has shown that it actually is a large *S. hebaozhaiensis* (refigured on Pl. 6, Figs. 1, 2) with a distinct microsculpture and reticulations that are arranged in subvertical lines as is typical for *S. hebaozhaiensis*. According to Dr. Günter Schweigert (Stuttgart), the locality where this material was found (Gaiseiche in Stuttgart) is in Stubensandstein 2.

Occurrence: China (middle Norian = Alaunian); middle Arnstadt Formation of northern Germany and Thuringia (Alaunian); upper Stubensandstein 2 of southern Germany (upper Alaunian); middle Groveton Member of Bull Run Formation in Culpeper Basin (upper Alaunian); Heidlersburg Member of middle Gettysburg Shale Formation in Gettysburg Basin (middle Alaunian).

Shipingia olseni Kozur & Weems, 2005

(Pl. 6, Fig. 8, Pl. 7, Figs. 3, 7-11, Pl. 8, Figs. 1-7)

2005 *Shipingia olseni* Kozur & Weems n. sp. – Kozur and Weems, pp. 28-29, Pl. 1, Fig. 2; Pl. 2, Figs. 7-11; Pl. 3, Figs. 1-7

Occurrence: Stubensandstein 3 of southern Germany (Sevatian); middle Groveton Member of the Bull Run Formation in the Culpeper Basin (rare and very primitive forms) (upper Alaunian); upper Groveton Member of the Bull Run Formation and the Catharpin Creek Formation in the Culpeper Basin (very common, mostly monospecific faunas) (Sevatian); middle and upper Passaic Formation in the Newark Basin (Sevatian); upper Blomidon Formation in the Fundy Basin, Canada (Sevatian).

PREVIOUS CONCHOSTRACAN BIOSTRATIGRAPHIC WORK IN THE TRIASSIC

Upon completion of a comprehensive taxonomic revision of Lower Triassic and lower Anisian conchostracans, a very detailed conchostracan zonation was established and later refined for the Germanic Buntsandstein (Figs. 5, 6) (Kozur and Seidel, 1983a,b; Kozur, 1993b, 1999; Bachmann and Kozur, 2004; Kozur and Bachmann, 2005; Kozur and Weems, 2006). This zonation is just as detailed as the ammonoid and conodont zonations in the age-equivalent marine realm. To estimate the duration of conchostracan zones from the uppermost Permian to the lower Anisian, these zones were correlated with Milankovitch cyclicity (Kozur and Bachmann, 2003, 2005, 2006; Bachmann and Kozur, 2004). Milankovitch cycles are best recognized in continental lake deposits, which also are the favoured habitat of conchostracans, so a conchostracan zonation has exceptional potential for being accurately correlated with Milankovitch cycles. Best known are the Milankovitch cycles in the Calvörde and Bernburg formations (showing both ~ 20,000 year precession cycles and ~ 100,000 year short eccentricity cycles), which formed from continuous deposition in a lake that occupied the center of the basin for an interval of 2.2 million years (Bachmann and Kozur, 2004). These deposits are rich in conchostracans, except for the middle and upper Calvörde Formation where sabkha deposits are present that yield few or no conchostracans. Throughout the lowest three short eccentricity cycles of the Calvörde Formation, and throughout the entire Bernburg Formation, the conchostracan zonation is accurately established. Nine conchostracan zones (and the beginning of a tenth zone) can be observed within these two intervals. As measured by the Milankovitch cycle patterns, most of the conchostracan zones in these intervals are between 100,000 and 200,000 years long. The longest zone is 360,000 years, while the shortest zones are only 30,000 to 50,000 years (Fig. 7). For most fossil groups, the extraordinarily short duration of the conchostracan zones in the uppermost Changhsingian to lower Smithian interval might be ascribed in part to recovery effects during and after the biotic crisis across the Permian-Triassic boundary. Conchostracans were exceptionally unaffected by the biotic crisis around the PTB, however, so this seems unlikely. The interval from the base of the Smithian Volpriehausen Formation up to the top of the Bithynian (~ 5 myrs duration according to Bachmann and Kozur, 2004) has eight conchostracan zones, which indicates an average duration for each zone of about 600,000 years. These zones have a much longer duration than the conchostracan zones from the uppermost Changhsingian to the lower Smithian, but even so these zones still have short duration.

All Buntsandstein (uppermost Changhsingian to lower Bithynian) conchostracan zones are closely correlated with the marine time scale. This is possible because in some cases brackish water intercalations containing conchostracans have been found between ammonoid-bearing and/or conodont-bearing beds, and in other cases because conchostracans have been found in very shallow-water marine environments, such as in the widespread Lower Triassic Werfen facies. There, especially in marginal parts of the depositional basin, single bedding planes with conchostracans or brackish conchostracan-bearing intervals up to a few centimetres or metres in thickness are intercalated with beds that contain marine bivalves and conodonts (Kozur and Mock, 1993). Most of the conchostracan zones of the uppermost Changhsingian to Bithynian interval have been correlated with the marine scale within the Tethys, mainly in the Werfen Beds of Hungary (Kozur and Mock, 1993; Kozur 1999) but also partly in the Spathian of the Bolshoe Bogdo area (Astrachan steppe, southern Russia, where marine, ammonoid-bearing and conodont-bearing beds are intercalated with brackish and fresh water layers that contain ostracods, charophytes, and conchostracans), and in the Boreal realm of northern and north-eastern Siberia (Kozur, 1999). The Aegean and Bithynian conchostracan zones have been directly correlated within the Germanic Basin, where in the Röt Formation bivalve-bearing (and partly even ammonoid-bearing) marine beds interfinger with brackish conchostracan-bearing deposits. In the Mecsek Mountains (Hungary), rich Bithynian conchostracan faunas occur in brackish strata that contain marine bivalves and conchostracans. For a long time, the very short (but very distinctive) *Magniestheria truempyi* Zone could not be correlated directly with the marine scale, even though its lower Smithian character was obvious from its conchostracan fauna. This shortcoming was finally corrected when Shen et al. (2002) found the *M. truempyi* Zone in Madagascar immediately below lower Smithian beds that contained the ammonoid *Flemingites*.

Lower Triassic conchostracan zones have an extraordinarily wide regional distribution. Some zones can be traced from strata in Greenland (with marine intercalations) to strata in northeastern and northern Siberia (with ammonoid-bearing intercalations), and then to strata in the Germanic Basin, the Russian Platform, northern China, the inner Tethys in the Werfen Beds of the Alps and Hungary, all the way to the Gondwana sequences of northern India, western, central, and eastern Africa, and Madagascar. For these widely distributed conchostracan guide forms, the conchostracan zonation of the Buntsandstein in the Germanic Basin serves as a standard for the entire northern hemisphere, both in high and low latitudes, and even in parts of Gondwana during the uppermost Permian to lower Anisian interval.

The reasons for this extraordinarily wide distribution of conchostracan species, across climatic boundaries from the Boreal realm through low latitude areas all the way to large parts of Gondwana, are connected to the life cycle of conchostracans. They prefer temporary ponds and lakes where there is little competition from other faunal elements, but they also can live in large and deep lakes such as the lakes within rift basins. When a pond or small lake dries out, the drought-resistant (and also partly freeze-resistant) eggs can survive for a very long time, transported by wind across long distances like sporomorphs of similar size and weight. Even though these eggs may spend several months outside of water (often under very low winter temperatures), they still can hatch if conditions become favourable for them, such as when they fall into a lake or temporary pond, a brackish estuarine area, or when a dry seasonal pond again fills with water. Within only a few months, they can become mature enough to produce the next generation of eggs. By this strategy, conchostracans break through climatic barriers, colonizing water bodies all the way from widely scattered temporary fresh-water ponds in dry climatic zones at low latitudes to small lakes in high latitudes that are frozen in the winter but are ice-free in the summer. For these same reasons, modern carp ponds usually contain an abundance of conchostracans. In late autumn, the water in these ponds is drained so that they are dry for the entire winter under freezing conditions that may range down to -20°C or lower. Despite this, in the Spring when the carp-ponds are flooded, they soon regain an abundant fauna of conchostracans. In contrast, other crustaceans such as ostracods need to be reintroduced, often by birds, but generally only after the carp ponds already are teeming with conchostracans.

The Lower Triassic conchostracan zonation has been closely correlated with the palaeomagnetic zonation (Kozur and Bachmann, 2003, 2005, 2006; Bachmann and Kozur, 2004; Korte and Kozur, 2005; Kozur, 2006). Palaeomagnetic correlations in continental red beds are especially well-documented, and conchostracans are very common in redbed sequences that include lake deposits, such as the Buntsandstein. The Lower Buntsandstein of Germany includes numerous limestones in its lake deposits, some with both conchostracans and the ostracod *Darwinula*, which indicates a fresh water origin for these limestones. Korte and Kozur (2005) established that these fresh water limestones exhibit the same carbon isotope excursions as marine limestones, including the negative excursion at the Permian-Triassic boundary (PTB) and the positive excursion close to the base of the Olenekian.

As can be seen in Figure 7, the biostratigraphic PTB in the Germanic Basin, as established by conchostracan correlations, matches perfectly with the PTB as indicated by the carbon isotope negative excursion. It also is consistent with the palaeomagnetic correlation, though this is not very precise at this horizon because the PTB lies within the lower third of a quite long normal interval. Similarly, the biostratigraphic base of the Olenekian is placed at the base of the *Magniestheria subcircularis* Zone, which is at the base of eccentricity cycle 10 within the Bernburg Formation (Figs. 5 and 7). Within the marine carbon isotope sequence, a distinct positive shift occurs close to the base of the Olenekian in Spiti (Atudorei, 1999). There are no data from cycles 9 and 10 of the Bernburg Formation in the Germanic Basin, but the basal part of cycle 11 lies right at the upper boundary of a positive shift. From this position, it can be inferred that the maximum of the positive shift was slightly lower, within cycle 10. The values in cycle 8 are well before the positive shift. Thus, at the base of the Olenekian, the conchostracan-based biostratigraphic boundary (level B in Fig. 7) also coincides with the boundary that can be drawn by stable isotope investigations, and the biostratigraphic correlation actually is more precise. The Olenekian boundary (level A in Fig. 7), as determined by magnetostratigraphic correlation, lies somewhat below the biostratigraphic conchostracan-based boundary, within a typical Brahmanian conchostracan fauna.

Kozur and Weems (2005, 2006) established a conchostracan zonation for the upper Alaunian through lower Hettangian portion of the Newark Supergroup that includes six zones. A seventh zone occurs in the lower Rhaetian of the Germanic Basin, which is missing within a gap in the Newark Supergroup record. According to the Milankovitch cyclicity pattern presented by Kent and Olsen (2000), and allowing for a 5 million year long Rhaetian Stage that largely is missing within the Newark Supergroup gap, the time interval represented by the seven conchostracan zones encompasses about 16 Ma, which in turn indicates an average duration of 2.3 million years per zone within this interval. This is a much longer duration of conchostracan zones than found in the Lower Triassic, but this same pattern of longer biostratigraphic zones also occurs in other stratigraphically important fossil groups. For example, the average duration of conchostracan zones within the Sevatian and Rhaetian is exactly as long as the average duration of conodont zones (4 conodont zones, 4 conchostracan zones). Similarly, from the base of the Sevatian up through the lower Hettangian there are 7 ammonoid zones and 6 conchostracan zones, so the conchostracan zones are only slightly longer on average than the ammonoid zones in this interval. Thus, the ammonoid and conodont zonations also show a pattern of longer zones during the Upper Triassic when compared to Lower Triassic zones.

THE MARINE UPPER TRIASSIC BIOSTRATIGRAPHIC ZONATION, ITS CORRELATION TO NUMERIC AGE DATES, AND PROBLEMS WITH RHAETIAN PALYNOSTRATIGRAPHIC CORRELATIONS

The established marine geologic time scale, with its ammonoid and conodont zonations, is shown in Figure 8. There have been only a few changes in this marine scale since the work of Kozur (2003), Kozur and Bachmann (2003, 2004), and Bachmann and Kozur (2004). The base of the Carnian has been placed by Broglio Loriga et al. (1998) at the base of the *Daxatina canadiensis* (*-Frankites sutherlandi*) Zone, which lies in bed SW 4 in the GSSP candidate section of Stuores Wiesen (Prati di Stuores) in the Dolomites; we follow this proposal. At this boundary, distinct changes in all fossil groups can be observed. The conodont *Paragondolella noah* (Hayashi) appears at this level. Numerous Upper Triassic radiolarians also first appear at this level in radiolarian-bearing facies, such as saturnalids and numerous nassellarian taxa, as well as the bivalve *Halobia*. Close to the base of the *D. canadiensis* (*-Frankites sutherlandi*) Zone at the GSSP candidate site, a distinct change also occurs in sporomorphs. About 3.7 m above the base of this zone (which encompasses a total thickness of almost 150 m) *Patinasporites densus* Leschik, *Vallasporites ignacii* Leschick, and several other species appear, and their first appearances are important for correlation with the Germanic Triassic and other continental sequences. The conchostracan species *Laxitextella multireticulata* (Reible) also first appears close to the base of the Carnian. Therefore, this boundary can be recognized both in marine and continental sequences.

We follow the original three-fold subdivision of the Carnian by Mojsisovics et al. (1895) and recognize (from oldest to youngest) Cordevolian, Julian, and Tuvalian substages. The Cordevolian is readily distinguished from the Julian by the fact that a number of Ladinian and Carnian taxa co-occur in nearly all fossil groups. For this reason, the Cordevolian often was assigned to the Ladinian. For example: among conodonts, the Carnian taxon *Paragondolella noah* is present but the Ladinian taxon *Budurovignathus* persists along with it throughout this interval; among bivalves, the Upper Triassic genus *Halobia* appears but species of the Middle Triassic genus *Daonella* persist; among radiolarians, the Upper Triassic and younger saturnalids appear and are common, but the Ladinian advanced Oertlispongidae persist. The same pattern can be observed in continental conchostracan faunas. The upper Ladinian *Euestheria minuta* (von Zieten) persists and is still common in the Cordevolian, but the Carnian genus *Laxitextella* appears and is wide-

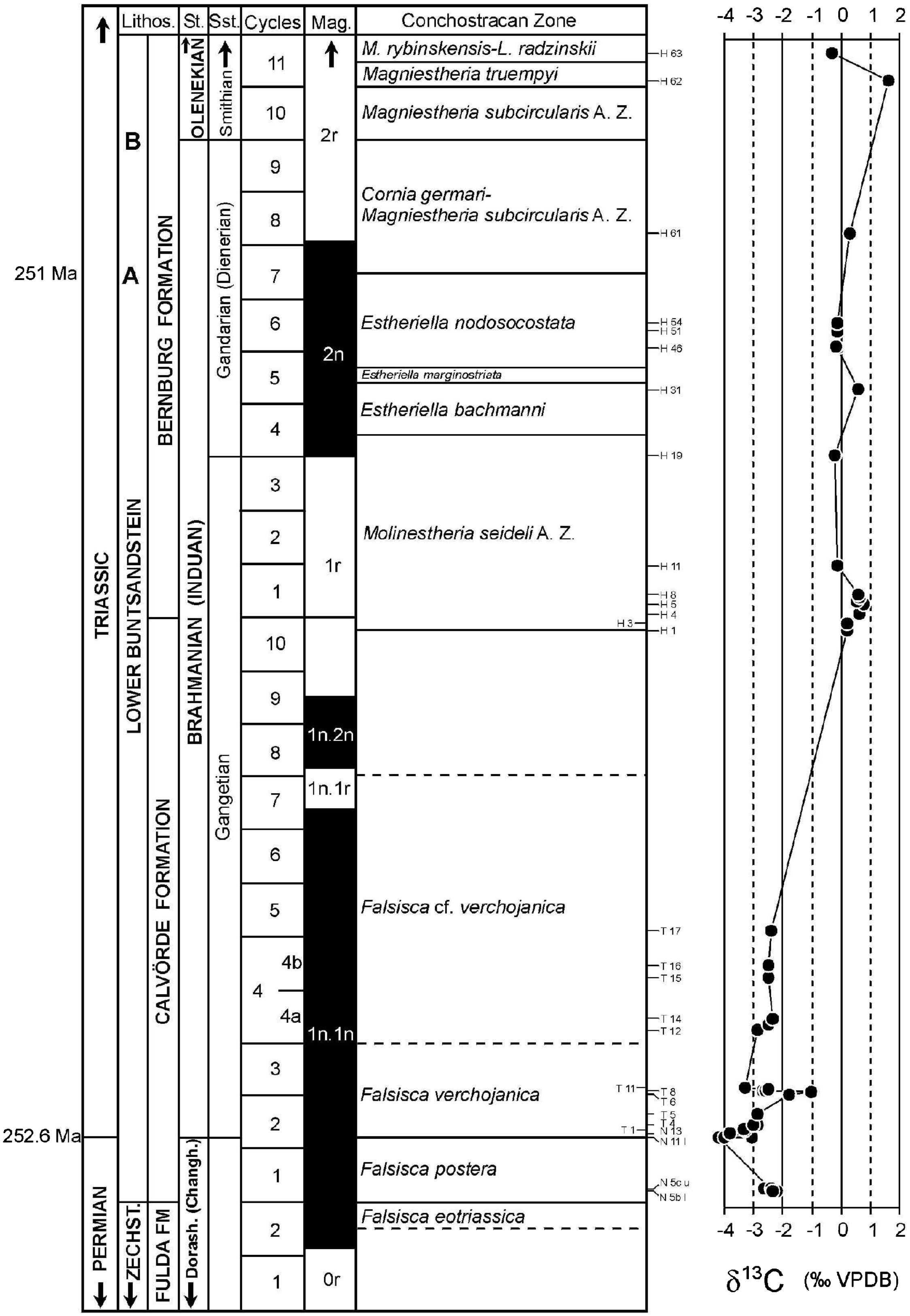

FIGURE 7. Correlation of the uppermost Permian to lower Smithian conchostracan zonation with the palaeomagnetic zones of Szurlies (2001), renumbered by Bachmann and Kozur (2004). The short eccentricity Milankovitch cycles are after Bachmann and Kozur (2004), and the carbon isotope record is from lake limestones after Korte and Kozur (2005) and modified after Kozur (2006). The biostratigraphic lower boundary of the Olenekian (B) at the base of the *M. subcircularis* A. Zone (at the base of cycle 10 of the Bernburg Formation) marks the biggest conchostracan turnover in the Triassic. According to the carbon isotope record, the Olenekian base must be at a positive shift above cycle 8 and below cycle 11, in agreement with the biostratigraphic boundary. According to the palaeomagnetic correlation with Chaohu in South China (A), the Olenekian base lies deeper within the Gandarian conchostracan fauna.

spread as well. Krystyn (1974) united the Cordevolian and Julian into a "Julian sensu lato," but later Krystyn (1978 and in all of his subsequent papers) subdivided this Julian s.l. back again into Julian I and Julian II. He used Cordevolian beside Julian I in Hornung et al. (2007) and in personal discussions has not rejected using the name Cordevolian.

The base of the Norian is defined by the FAD of *Epigondolella quadrata* Orchard, the only conodont event around the Carnian-Norian boundary that can be traced both throughout the Tethys and in North America. The base of the Rhaetian is defined by the FAD of the conodont *Misikella posthernsteini* (Kozur & Mock) in the Tethys and in western Panthalassa (Kozur, 1996). This boundary coincides with the base of the ammonoid *Cochloceras suessi* Zone, which can be correlated with the base of the ammonoid *Paracochloceras amoenum* Zone and the base of the conodont *Orchardella mosheri* Zone in North America (Kozur, 1996). This last boundary for the base of the Rhaetian in North America was earlier proposed by Orchard and Tozer (1997). Similarly, the base of the Rhaetian radiolarian *Propavicingula moniliformis* Zone (Carter, 1993) lies at this level.

In contrast, the FOD's of "Rhaetian" sporomorphs lie at different stratigraphic levels, depending on paleolatitude. Nearly all Rhaetian guide forms appear in the Germanic Basin and the Northern Alps (paleolatitudes 20-35^0 N) before the marine-defined Rhaetian in high northern latitudes. As shown by Schulz and Heunisch (2005), this tendency can be demonstrated even within the belt of the Germanic Basin and Northern Alps. Some species such as *Triancoraesporites ancorae* (Reinhardt) Schulz and *Zebasporites laevigatus* Schulz, which first appear in the lower Rhaetian in the northern Germanic Basin of Germany and Poland, do not appear until the upper Rhaetian in the southern Germanic Basin of Southern Germany and in the Northern Alps. This trend also can be traced backward toward northern high latitudes, where *T. ancorae* appears in the Arctic Archipelago as early as the middle Norian (Fisher, 1979). In the very high northern paleolatitudes in northern Middle Siberia, typical "Rhaetian" guide forms (such as *Limbosporites lundbladii* Nilsson, *Rhaetipollis germanicus* Schulz, *Triancoraesporites reticulatus* Schulz, *Zebrasporites laevigatus* Schulz, *Cingulizonates rhaeticus* (Reinhardt) Schulz, and *Semiretisporis gothae* Reinhardt) appear as far down in the section as the lower Carnian (Ilyina and Egorov, 2006). If we follow the trend southward toward the Triassic paleoequator, we find that from 0-15^0 N paleolatitude, in the Upper Triassic-Liassic rift basins of eastern North America, no "Rhaetian guide forms" occur (Fig. 9). This explains why, even in such comprehensive palynological reports as those of Cornet (1977, 1993), no Rhaetian guide forms ever were found. What were assumed to be proxy Rhaetian palynofloras are, in reality, upper Norian palynofloras (Kozur and Weems, 2005, 2006), and the real (upper) Rhaetian Newark Supergroup time interval was assigned to the Liassic because it lacked all Rhaetian (but also Liassic) sporomorph guide forms.

In addition to the problems discussed above concerning the correct correlation between the established Upper Triassic marine geologic time scale and Rhaetian palynostratigraphy, there also are problems with some of the numeric ages that have been applied to the Upper Triassic (Fig. 8). In the work of Kozur (2003), Kozur and Bachmann (2003, 2005, 2006), and Bachmann and Kozur (2004), two fixed radiometric points were assumed to be reliable: the base of the Carnian at 237 Ma and the top of the Rhaetian at 199.6 Ma. The numeric age for the base of the Carnian remains reasonably accurate. Both Mundil et al. (1996) in the Southern Alps and Pálfy et al. (2003) in the Balaton Highland have dated beds at ~ 238 Ma that lie one ammonoid Zone (~ 1 myrs) below the base of the Carnian. From this the base of the Carnian can be placed at 237 Ma, and this value will continue to be used.

Determining the age of the base of the Liassic is much more complicated, however. Pálfy et al. (2000) derived a 199.6±0.4 Ma multi-grain zircon U-Pb age from tuffs within a biostratigraphically well-dated marine uppermost Rhaetian sequence in a T/J boundary section in the Queen Charlotte Islands, Canada. This value currently is being used in all papers dealing with the numeric age of the T/J boundary (e.g., Channell et al., 2003; Kozur, 2003; Bachmann and Kozur, 2004; Gradstein et al., 2004; Menning et al., 2006). Older ages for this boundary, around 201-202 Ma from the continental Newark Supergroup, presently are out of favor.

Unfortunately, multi-grain zircon U-Pb analyses are prone to slight lead (Pb) loss, and this can result in ages that are slightly younger than the true ages. For example, apparent ages from the Middle Triassic of the Balaton Highland in Hungary (Pálfy et al., 2003) are nearly all somewhat younger than ages derived from contemporaneous beds in the Southern Alps that were dated by single-grain zircon U-Pb analyses (Brack et al., 2005, Mundil 1996, Mundil et al., 1996). Therefore, the accuracy of numeric ages determined in Pálfy et al. (2000) needs to be reconsidered in view of published, slightly older radiometric ages obtained from the CAMP volcanics of the Newark Supergroup and the new biostratigraphic age determination for the timing of the basal CAMP lava flows (Kozur and Weems, 2005, 2006). The numeric ages determined in Pálfy et al. (2000) also seem to contradict some previously and recently determined numeric ages from the Hettangian.

Dunning and Hodych (1990) determined that the age of the Palisades Sill is 200.9 ± 1 Ma and the age of the Gettysburg Sill is 201.3 ± 1 Ma. These ages are close to a 202 ± 1 Ma U-Pb zircon age reported for the Palisades Sill by Kent and Olsen (2002). Both sills are high-Ti quartz-normative tholeites. Dunning and Hodych (1990) stated that the Palisades Sill directly fed "some of the lowermost flows" (i.e., the Palisades Sill fed the Orange Mountain Basalt). However, there was a second pulse of intrusion that produced high-Fe quartz-normative tholeite before the Palisades Sill completely cooled. The date for the Palisades Sill came from the second pulse and not the first, and it is not clear whether the second pulse is co-magmatic with a later phase of the first lava flow or whether it is co-magmatic with the second lava flow. It seems probable, however, that this second pulse of intrusion belongs to a later phase of the first lava flow event. This ambiguity is reflected in the different correlations that have been proposed. Kent and Olsen (2000) concluded that the Palisades Sill of the Newark Basin probably is co-magmatic with the (second) Preakness Basalt (which was extruded very close to the Triassic-Jurassic boundary according to the results of Kozur and Weems, 2005, 2006, and the present paper), while Pálfy et al. (2002) favored the view that the Palisades Sill fed the lowermost Orange Mountain Basalt lava flow. Hodych and Dunning (1992) have dated the North Mountain Basalt at 201.7± 1.4/-1.1 Ma (2 σ SD), which averages to 202 ± 1 Ma. The North Mountain Basalt of the Fundy Basin (Canada) is correlated with the lowest lava flow in the Newark Basin (Orange Mountain Basalt).

Pálfy et al. (1999) have obtained age dates of 200.8±2.8/-2.7 Ma from middle Hettangian tuffs from Puale Bay, Alaska. Their data from the middle Hettangian clearly suggest a somewhat older age, >201 Ma, for the base of the Jurassic. Such an age for the base of the Jurassic fits well with most of the previous data derived from the CAMP volcanics within the Newark Supergroup.

Pálfy and Mundil (2006) also have derived radiometric ages from several important stratigraphic levels within the lowermost Jurassic by applying pretreatment of thermal annealing and chemical abrasion to single zircon crystals. Their technique yielded an age of 200.6 ± 0.3 Ma for the volcanic ash layer in the ammonoid-bearing middle Hettangian marine sediments at Puale Bay, Alaska. This value again suggests a likely age for the basal Jurassic of >201 Ma. Further dating effort is needed to re- analyze other critically important volcanic ash layers from the T/J boundary interval, and also from the upper Rhaetian basal lava flow of the CAMP volcanics in the Newark Supergroup. Recently, a single-crystal $^{206}Pb/^{238}U$ age of 201.3 ± 0.3 Ma has been reported from the North Mountain Basalt of the Fundy Basin in Nova Scotia, Canada (Schoene et al., 2006). If this value is correct, as well as the correlation of the North Mountain basalt with the upper Rhaetian lower lava flows of the CAMP volcanics in the Newark and Culpeper basins, then the base of the Jurassic should not be much older than 201 Ma. On the other hand, Pálfy and Mundil (2006) have reported a preliminary $^{206}Pb/^{238}U$ age of 198.0 ± 0.6 Ma from a volcanic tuff layer within lower Sinemurian sediments in the Mecsek Mountains, Hungary (single zircon investigation with a pretreatment of thermal annealing and chemical abrasion). From this value, the age of the Hettangian-Sinemurian boundary can be estimated to be between 199 and 198 Ma. Taking into consideration a middle Hettangian age date of about 200.6 Ma, an age > 201 Ma would be expected for the T/J boundary as assumed by Pálfy and Mundil (2006). Based on all recent latest Rhaetian and Hettangian radiometric data, the age of the base of the Jurassic probably lies between 201 and 201.5 Ma, and this value is used in the present paper.

In Kozur (2003), Kozur and Bachmann (2003, 2005, 2006), and Bachmann and Kozur (2004) the Milankovitch cycles (from the assumed base of the Liassic given in Kent and Olsen (2000) and other papers) were counted downward to the assumed base of the Norian. However, the conchostracan data presented by Kozur and Weems (2005, 2006, and present paper) have shown that the top of the Rhaetian as used by Kent and Olsen (2000) actually is somewhat below the top of the Norian. Thus, the duration of the Rhaetian becomes much more difficult to estimate. We assume that the globally recognized short, but pronounced, drop in $\delta^{13}C$ is related to the onset of CAMP volcanism in the upper part of the upper Rhaetian. Korte and others have correlated in detail the negative peak in $\delta^{13}C$ values with the conodont zonation in the Csõvár quarry section in Hungary (Korte et al., in prep.). Opposite to this quarry, at the base of the Várhegy, Pálfy et al. (2001) investigated the carbon isotope trends. Kozur and Mock (1991) studied the Várhegy section about 10 years earlier, but found it to have far fewer conodonts than the quarry section. Additionally, the Várhegy section showed strong sedimentological complications. For these reasons, Korte and Kozur decided that this section was unsuitable for a very detailed correlation of the uppermost Rhaetian negative excursion in $\delta^{13}C$, and they chose instead to use the quarry section for their detailed conodont studies. The quarry section is where Kozur and Mostler (1973) earlier had recognized that these beds are not Carnian, as then generally accepted, but rather upper Rhaetian. The presence of Jurassic strata (and the first known lower Hettangian conodonts) was not confirmed at Csõvár until the work of Kozur (1993c). The upper Rhaetian negative spike is located 0.6 m below the top of the upper Rhaetian *Misikella ultima* Zone, which lies less than a quarter of the way through the upper Rhaetian section downward from the base of the Hettangian (as determined by the FAD of Hettangian radiolarians).

If we correlate the upper Rhaetian negative spike with the onset of CAMP volcanism, this implies that only about a quarter of the upper Rhaetian is represented in the Newark Supergroup, which begins immediately above an unconformity and about one precession cycle (~ 20,000 years) below the first lava flow. Such a correlation is supported by the new palaeomagnetic data of Gallet et al. (2007), who have shown a distinct reversed zone somewhat below the middle of the upper Rhaetian. As this zone is missing within the Newark stratigraphic gap, as well as all lower parts of the Rhaetian and uppermost Norian (see below), the part of the Rhaetian represented by the interval from the base of the CAMP volcanism to the second lava flow can only correspond to the upper part of the upper Rhaetian.

Kent and Olsen (2000) have indicated that, based on Milankovitch cycles, the duration of volcanism from the base of the first lava flow upward to the Preakness Basalt is about 0.5 million years. If this estimate is correct, this implies a duration for the entire upper Rhaetian of about 2 million years. This in turn indicates a duration for the entire Rhaetian of about 4.5 to 5 myrs. Taking into consideration that the base of the Liassic is about 201-201.5 Ma, the Rhaetian therefore probably began at about 206 Ma, a value which was estimated previously in Bachmann and Kozur (2004).

As shown by Kozur and Weems (2005, 2006), what previously was considered to be the Rhaetian-Hettangian boundary in the Newark Basin actually is a stratigraphic gap that separates upper Norian beds from upper Rhaetian beds. Channell et al. (2003) established that the Norian-Rhaetian boundary, as defined by the FAD of *Cochloceras*/*Paracochloceras* and *Misikella posthernsteini*, lies within a pronounced reversed palaeomagnetic interval. The upper part of this interval lies within the lower Rhaetian as defined above, and the lower part comprises the *Misikella hernsteini-Parvigondolella andrusovi* Zone of the uppermost Norian. According to Kent & Olsen (2000), below the Newark stratigraphic gap there is a long normal interval of about one million year's duration. For this reason Kozur & Weems (2005) concluded that the stratigraphic gap between the upper Norian and upper Rhaetian not only includes a large part of the Rhaetian, but also the uppermost Norian *M. hernsteini-P. andrusovi* Zone (an interval of about one million years).

Gallet et al. (2007) recently have published for the first time a complete Rhaetian magnetostratigraphic scale for the marine Tethyan realm. Unfortunately, they used what they call a "traditional Rhaetian," which more accurately could be called "Rhaetian traditionally used by Krystyn." The base of this "Rhaetian" lies well within the lower Rhaetian, and Gallet et al. (2007) acknowledge that the FAD of *Cochloceras* (which is the Rhaetian base used, e.g., by Carter, 1993, Kozur, 1996, Orchard and Tozer, 1997, Channell et al., 2003, Muttoni et al., 2004, Ogg, 2004, Krystyn & Kuerschner, 2005) has officially been chosen as a proxy for a future internationally agreed Norian-Rhaetian boundary. The Rhaetian palaeomagnetic scale presented by Gallet et al. (2007) includes a predominantly reversed interval during the lower part of the lower Rhaetian (assigned to the Sevatian 2 by Gallet et al., 2007) that includes two short normal intervals. This is followed by a predominantly normal interval for the remainder of the Rhaetian that includes two short but prominent reversed zones, one in the upper part of the lower Rhaetian ("H-") and the other somewhat below the middle part of the upper Rhaetian ("J-"). This pattern for the middle and upper Rhaetian also has been documented at St. Audrie's Bay (Hounslow et al., 2004), where the "H-" reversed horizon in the upper part of the lower Rhaetian corresponds to SA 5n.1r and the "J-" reversed horizon within the upper Rhaetian corresponds to SA 5n.2r.

Gallet et al. (2007) also have presented a correlation of their Rhaetian palaeomagnetic scale with the Newark Basin. As the reversed horizons "H-" and "J-" are missing in the Newark Basin, this part defines a minimum duration for the Rhaetian stratigraphic gap (upper part of lower Rhaetian to middle part of upper Rhaetian). Thus, Gallet et al. (2007) have confirmed the gap recognized by the conchostracan succession in the Newark Supergroup. However, as they used only palaeomagnetic correlation without including biostratigraphic results in the Newark Basin, they were left with two options for the time at which the stratigraphic gap began. Option 1, which they favored, put the beginning of the gap within their long normal zone G +, well within the lower Rhaetian. This would require that, below the gap, there is still a long lower Rhaetian interval represented in the Newark Basin. So long as lower Rhaetian conchostracans were unknown, this option could be neither confirmed nor rejected by biostratigraphic data. However, we now have abundant lower Rhaetian conchostracans that are well dated in the Germanic Basin. They are different from the upper Rhaetian *E. brodieana* fauna, and also basically different from the upper Norian *Shipingia olseni* fauna. As this fauna is missing in the Newark Basin, we now can reject option 1. Option 2 of Gallet et al. (2007) included the entire "Sevatian 2" (= lower half of lower Rhaetian plus uppermost Norian *Misikella hernsteini-Parvigondolella andrusovi* Zone) within the Newark Basin stratigraphic gap. This option places the beginning of the gap close to the top of a long normal interval within the upper Sevatian, which explains both the presence of a long normal interval immediately below the gap and the presence of only upper Norian conchostracans of the *S. olseni* Zone nearly up to the gap. Therefore, their Option 2 corresponds to the view of Kozur & Weems (2005), which now is supported additionally by our lower Rhaetian conchostracan studies within the Germanic Basin. This means that the Milankovitch cycles of Kent &

Olsen (2000) within the Passaic Formation should be counted downward from the top of the Norian (just below the base of the first lava flow) to the Carnian-Norian boundary, not from 202 Ma as in Kent and Olsen (2000) or 200 Ma as in Channell et al. (2003), Gallet et al. (2003, 2007), and Muttoni et al. (2004), but from 207 Ma because 206 Ma is the base of the Rhaetian and about one million years of the uppermost Norian is missing within the gap.

In the Newark basin, the highest occurrence of Carnian vertebrates (Conewagian = Adamanian Land Vertebrate Fauna or LVF) is in the lower third of the Lockatong Formation. Conchostracans also occur in this level (Bock, 1953a; our collections) that represent the *Euestheria ovata-E. princetonensis* Zone of late Tuvalian age. The oldest known Newark basin Norian vertebrates (Neshanician = "Revueltian A" LVF) occur in the Warford Member (Member D) of the lower Passaic Formation (Huber et al., 1993b; Lucas et al., 1998), the same level from which we have obtained the oldest known conchostracans from the Passaic Formation. There are no age diagnostic vertebrates known from the intervening upper two-thirds of the Lockatong Formation or the basal Passaic Formation below its Warford Member, and we have not yet sampled for conchostracans within this interval. Thus, for now the age of this interval could be late Carnian (late Tuvalian), early Norian (early Lacian), or a combination of both. If we count the Milankovitch cycles presented by Kent and Olsen (2000) downward from 207 Ma (see above) to the base of the Warford Member (first unequivocal occurrence of Norian vertebrates), we derive a basal age for the Norian of 223 Ma. If we count down to the top of the lower third of the Lockatong Formation (uppermost unequivocal occurrence of late Tuvalian vertebrates), we derive a basal age for the Norian of 226 Ma. The age of the Carnian-Norian boundary therefore lies somewhere between 223 Ma and 226 Ma. This entire range of values is compatible with the data of Gehrels et al. (1987), who dated rhyolites from the basal Norian of southeastern Alaska at 225 ± 3 Ma (i.e., somewhere between 222 Ma and 228 Ma). An age of 230.91 ± 0.33 Ma (Fig. 8), derived from tuffs within the lower *Carnepigondolella zoae* Zone of middle Tuvalian age (Furin et al., 2006), tends to support an age of 225 Ma or a value very close to it for the base of the Norian. An age of 225-226 Ma for the base of the Norian corresponds reasonably well with an age of 226 Ma for the base of the Norian derived by Channell et al. (2003) and Bachmann and Kozur (2004), who at that time defined the base of the Norian as one conodont zone lower than the boundary we use in the present paper. Gallet et al. (2003) favored a basal Norian age of 227 Ma, Muttoni et al. (2004) favored an age of 227 to 228 Ma (at the lower end of the error range for the basal Norian data of Gehrels et al., 1987), and Gallet et al. (2007) favored 229 Ma for the base of the Norian, (somewhat below the lower end of the error range for the basal Norian data of Gehrels et al., 1987).

PRELIMINARY CARNIAN TO LOWER HETTANGIAN CONCHOSTRACAN ZONATION OF THE GERMANIC BASIN AND THE NEWARK SUPERGROUP AND ITS CORRELATION WITH THE INTERNATIONAL SCALE

A preliminary Carnian to lower Hettangian conchostracan zonation is given here for both the Germanic Basin and the Newark Supergroup, because nearly the same conchostracans and conchostracan succession are present in both regions. In some intervals, both in the Germanic Basin and in the Newark Supergroup, conchostracan taxonomic work remains unfinished or is yet to be done. For these intervals, taxa in open nomenclature (or no taxa) are listed. To avoid creating *nomina nuda*, the three submitted (but as yet unpublished) Tuvalian index species for the Germanic Basin Upper Triassic conchostracan zonation are briefly described in the present paper within an appendix, and they are illustrated on Plates 10 and 11. These are: *Eosolimnadiopsis gallegoi* Kozur n. sp. (index species for the lower Tuvalian), *Laxitextella seegisi* Kozur n. sp. (index species for the middle Tuvalian) and *Laxitextella freybergi* Kelber & Kozur n. sp. (index species for the upper Tuvalian). The lower Tuvalian interval has not yet been confirmed in the Newark Supergroup. We anticipate that it is present, for example, in the lower New Oxford Formation of the Gettysburg Basin, because we have found middle Tuvalian conchostracans in the middle part of the New Oxford Formation at the Fulton site. The presence of equivalents of the middle Tuvalian *Laxitextella seegisi* Zone can be confirmed in the Newark Supergroup at the Fulton site because two of the three guide forms for this zone are known from there. We have not yet found the third guide form, *Laxitextella seegisi* Kozur, but so far we only have a small sample of about 40 specimens from the Fulton site. This sample consists of the other two guide forms for that zone (*Eosolimnadiopsis* ? n. sp. and *Laxitextella* sp. cf. *L. laxitexta*), so the third form may well show up with more collecting. The upper Tuvalian index form for the Germanic Basin, *Laxitextella freybergi* Kelber & Kozur n. sp., is from the *Laxitextella* facies that formed in temporary ponds and temporary shallow-water lakes. Our upper Tuvalian conchostracan faunas from the Newark Supergroup, in contrast, are largely different because they represent persistent deep water lake faunas (e.g., the fauna from "Lake Lockatong"). Fortunately a common guide form for the *Laxitextella freybergi* Zone, *Euestheria hausmanni* (Schmidt), occurs in the temporary pond and small shallow-water lake environments of the Germanic Basin and also in the deep water lakes of the Newark Supergroup.

Some remarks will be made below about the specific correlation of conchostracan zones with the currently accepted international marine time scale and its numeric ages, which has been discussed above in more general terms.

Laxitextella multireticulata Zone

Definition: Occurrence of *Laxitextella multireticulata* (Reible) without *L. laxitexta* (Sandberger).

Lower Boundary: FAD of *L. multireticulata* and *Euestheria winterpockensis* (Bock).

Upper Boundary: FAD of *L. laxitexta*.

Important species: *Laxitextella multireticulata*, *Euestheria minuta* (von Zieten), *E. winterpockensis* (Bock).

Remarks: When *L. multireticulata* is absent, this zone can be recognized by the association of *E. minuta* with *E. winterpockensis*, which is quite different from any other conchostracan association within the Newark Supergroup. Toward the top of the zone, *E. winterpockensis* becomes larger (close to the upper size range of type *E. winterpockensis* or even a little larger = *E.* sp. cf. *E. winterpockensis*). In the lower *L. multireticulata* Zone, only typical specimens of the index species occur with a reticulation composed exclusively of very small polygons, which sometimes may be arranged in irregular vertical or oblique stripes. Some of these polygons also may be elongated parallel to the growth lines. In the upper part of this zone, in addition to typical forms, there also occur specimens that have some parts of the carapace covered with reticulations that are larger than normal and other parts covered with reticulations that are as small as in the type material. These younger *L. multireticulata* are probably transitional forms to *L. laxitexta*. The upper part of the *L. multireticulata* Zone is not recognized in the Germanic Basin, because there the *L. multireticulata* Zone and the *L. laxitexta* Zone are separated by an interval with soil horizons that have produced no conchostracans.

At nearly all localities in the Newark Supergroup where the *L. multireticulata* Zone is found, these beds also produce the fish *Dictyopyge*. Only in the unnamed unit below the New Oxford Formation in the Gettysburg Basin has *Dictyopyge* not been found so far, but this may be due to a lack of intensive collecting there.

Occurrence: This zone occurs with the same species in the lower variegated Estherienschichten of the upper Grabfeld Formation in the Germanic Basin, and in the lowermost strata of the Newark Supergroup. There, it occurs in an unnamed unit below the New Oxford Formation in the Gettysburg Basin, MD/PA, in the Falling Creek Formation in the Taylorsville Basin, VA, in the Tuckahoe Formation in the Deep Run and

Ma		Stage/Substage		Ammonoid Zone/Subzone Standard		Conodont Zone/Subzone		
						Tethys/Western Pacific		North America
201 to 201.5	UPPER TRIASSIC	RHAETIAN	Upper Rhaetian	Chor. marshi	Choristoceras marshi	Misikella ultima		Norigondolella sp.
					Chor. ammonitiforme	Misikella posthernsteini	Misikella koessenensis	Misikella posthernsteini
			Lower Rhaetian	"Ch." haueri	Vandaites stuerzenbaumi			Orchardella mosheri
					"Choristoceras" haueri		Misikella hernsteini-Misikella posthernsteini	
				Cochloceras suessi				
206		NORIAN	Sevatian	Sagenites reticulatus		M. hernsteini-P. andrusovi		Mockina bidentata
				Sagenites quinquepunctatus		Mockina bidentata	Subzone 2	
				Halorites macer			Subzone 1	Mockina ? serrulata
			Alaunian	Mesohimavatites columbianus		Mockina postera		Mockina postera
								Orchardella elongata
						Mockina ? spiculata		Mockina ? spiculata
				Cyrtopleurites bicrenatus		M. medionorica		Orchardella multidentata
			Lacian	Juvavites magnus		Epigondolella triangularis-Norigondolella hallstattensis		Epigondolella triangularis
				Malayites paulckei				
						Epigondolella rigoi		
225 ± 3				Stikinoceras kerri		Epigondolella quadrata		Epigondolella quadrata
223 to 226		CARNIAN	Tuvalian			E. orchardi-N. navicula	M. prim.	M. primitius M. comm.
				Klamathites macrolobatus		Carnepigondolella pseudodiebeli		Orchardella ? n. sp. – "Metapolyg. communisti"
230.91 ±0.33				Tropites welleri		Carnepigondolella zoae		Carnepigondolella zoae
						Paragondolella carpathica		Carnepigondolella lindae
				Tropites dilleri		P. postinclinata-P. noah		Paragondolella polygnathiformis
			Julian	Austrotrachyceras austriacum		Gladigondolella tethydis-Paragondolella polygnathiformis		
				Trachyceras aonoides				
			Cordevolian	Trachyceras aon		Budurovignathus diebeli-Paragondolella polygnathiformis		
237				D. canadensis-F. sutherlandi				

FIGURE 8. The marine Upper Triassic time scale (with ammonoid and conodont zonation) used for correlating conchostracan zones. Modified after Kozur (2003) and Bachmann and Kozur (2004).

Richmond basins, VA, and in the lacustrine unit in the Farmville, Briery Creek, and Scottsburg basins, VA.

Age: In the Germanic Basin, the FAD of *L. multireticulata* coincides with the FAD of *Patinasporites densus*. Slightly higher is the FAD of *Vallasporites ignacii*. In the Carnian GSSP candidate section at Stuores Wiesen, these two species begin immediately above the base of the Carnian as defined by the base of the *Daxatina* cf. *canadiensis* Zone (Broglio Loriga et al., 1998). The beginning of this sporomorph association in the Germanic Basin, close to the base of the Estherienschichten of the upper Grabfeld Formation, also defines the base of the Carnian (Schulz and Heunisch, 2005). The correlation of this association with the base of the Carnian in the Germanic Basin was first recognized by Hauschke and Heunisch (1989). In the western part of the Southern Alps, *L. multireticulata* occurs close to the Ladinian-Carnian boundary along with another undescribed species of *Laxitextella* (Tintori, 1990; Tintori and Brambilla, 1991; Kozur and Mock, 1993).

In the late Cordevolian, the *Anyuanestheria fimbriata-Laxitextella laxitexta* Zone begins. Thus, the *L. multireticulata* Zone includes only the early Cordevolian, and the presence of this fauna for the first time proves that sedimentation in the Upper Triassic rift basins of the eastern United States began either at or very shortly after the beginning of the Late Triassic.

Anyuanestheria fimbriata-Laxitextella laxitexta Zone

Definition: Occurrence of *Anyuanestheria fimbriata* (Warth) and/or *Laxitexella laxitexta* (Sandberger).

Lower boundary: First appearance of *Laxitextella laxitexta*.

Upper boundary: Disappearance of *Anyuanestheria fimbriata*.

Important species: *Anyuanestheria fimbriata* (Warth), *Anyuanestheria* n. sp., *Laxitextella laxitexta*.

Remarks: In the lower part of this zone, only *Laxitextella laxitexta* occurs along with some rare indeterminate small specimens of *Euestheria*. A small *Anyuanestheria* n. sp. that is much less abundant than *L. laxitexta* first appears slightly higher, then in the middle and upper part of the

	Low latitudes		High latitudes
	0-15^{0}N	20-35^{0}N	
	Newark	Germanic Basin, Northern Alps	Arctic Canada, Siberia
		Schulz and Heunisch, 2005	Fisher, 1979; Ilyina and Egorov, 2006
Rhaetian		***Limbosporites lundbladii*** xx ***Rhaetipollis germanicus*** xx *Cornutisporites seebergensis* *Perinosporites thuringiacus* *Polipodiisporites polymicroforatus* ***Triancoraesporites ancorae*** U.R. x ***Triancorasporites reticulatus*** xx ***Cingulizonates rhaeticus*** U.R. xx ***Zebrasporites laevigatus*** *xx* ***Semiretisporis gothae*** U.R. xx	*Limbosporites lundbladii* *Rhaetipollis germanicus* *Cingulizonates rhaeticus* *Triancorasporites reticulatus* *Zebrasporites laevigatus* *Semiretisporis gothae*
Norian			*Limbosporites lundbladii* *Rhaetipollis germanicus* *Cingulizonates rhaeticus* *Triancorasporites reticulatus* *Zebrasporites laevigatus* *Semiretisporis gothae*
Carnian			*Limbosporites lundbladii* *Rhaetipollis germanicus* *Cingulizonates rhaeticus* *Triancorasporites reticulatus* *Zebrasporites laevigatus* *Semiretisporis gothae*

FIGURE 9. Migration of Rhaetian sporomorph guide forms of the Germanic basin and Alps (20-35° N) from the Carnian and Norian of high latitudes. None of these forms reached the eastern North American Upper Triassic rift basins (0-15° N). Bold: Rhaetian species of the Germanic Basin and the Alps which began in high latitudes during the Carnian (xx) or during the middle Norian (x). U.R.: Species, which appear in southern Germany and in the Alps during the upper Rhaetian, in northern Germany and Poland during the lower Rhaetian.

zone the similarly small *Anyuanestheria fimbriata* comes to dominate the assemblage.

The upper boundary of this zone is difficult to define, because in the Germanic Basin it is followed by an interval barren of conchostracans that is particularly rich in pedogenic beds. A stratigraphic gap then follows. Above the gap, *Anyuanestheria fimbriata* is no longer present. There it is replaced by a large *Anyuanestheria* n. sp. A that has some similarity to the Jurassic genus *Eosestheria* Chen. *Laxitextella* sp. cf. *L. laxitexta* persists up to the middle Tuvalian, but probably it represents a separate species. Other forms, similar to *L. laxitexta*, also persist upward to the middle Tuvalian.

Occurrence: The *Anyanestheria fimbriata-Laxitextella laxitexta* Zone is known only from the Germanic Basin and England. It has not been found yet within the Newark Supergroup.

Age: Late Cordevolian.

Anyuanestheria n. sp. A – *Laxitexella* sp. cf. *L. laxitexta* Zone

Definition: Co-occurrence of the large *Anyuanestheria* n. sp. A and *Laxitextella* sp. cf. *L. laxitexta* (Sandberger).

Lower boundary: FAD of *Anyuanestheria* n. sp. A and *Laxitextella* sp. cf. *L. laxitexta*

Upper boundary: Disappearance of *Anyuanestheria* n. sp. A

Important species: *Anyuanstheria* n. sp. A, *Laxitextella* sp. cf. *L. laxitexta*, *Palaeolimnadia schwanbergensis* Reible.

Remarks: In thin basal lacustrine deposits of the Schilfsandstein Formation of the Germanic Basin, an indeterminate fauna composed mostly of small *Euestheria* occurs. This fauna is abruptly replaced upward by *Laxitextella* sp. cf. *L. laxitexta*, which has large polygons in its coarse reticulation that are elongated parallel to the growth lines. This species ranges up to the middle Tuvalian. In the middle Schilfsandstein Formation, there is an abundant conchostracan fauna that includes *Laxitextella* sp. cf. *L. laxitexta*, the large *Anyuanestheria* n. sp. A, and *Palaeolimnadia schwanbergensis*. *Anyuanestheria* n. sp. A is especially characteristic of (and restricted to) this short interval. This strong faunal turnover is related to the so-called Reingraben Event (Schlager and Schöllnberger, 1974), also called the Raible Event or the Carnian pluvial event (Simms and Ruffell, 1989). In the Germanic Basin, this event is characterized by the development of a huge fluvial system; in the Tethys, it is characterized by a widespread influx of clastic sediments (the Raible Beds, Lunz Beds, Reingraben Beds of the Alps and Carpathians, and equivalent beds in the central and eastern Tethys). This event reflects an interaction of tectonic unrest, connected with the beginning of the collision of the Cimmerian microcontinent with splinters of Eurasia (Stampfli and Kozur, 2006), with a period of wet climate that, in the Germanic Basin, interrupted the dry climates typical of the preceding Longobardian and Cordevolian substages (Lower Gypsum Keuper = Grabfeld Formation) and the dry climates of the subsequent Tuvalian substage (Upper Gypsum Keuper = Weser Formation) (Kozur, 1972). The sudden appearance of large *Anyuanestheria* in the upper Julian Schilfsandstein Formation probably reflects this climatic change because, by the Tuvalian, small *Anyuanestheria* again predominate as in the Cordevolian and only a few medium-sized forms co-occur.

Occurrence: Middle Schilfsandstein Formation of the Germanic Basin; lower Cow Branch Formation of the Dan River/Danville Basin, NC/VA. In the latter case, these strata have been assigned to the *Anyuanestheria* n.sp. A Zone only because of the occurrence of *Anyuanestheria* n. sp. A; so far *Laxitextella* sp. cf. *L. laxitexta* has not been found. The apparent absence of the latter species, however, may be illusory because the poor preservation of the conchostracans known from the lower Cow Branch Formation may have precluded seeing microsculpture (such as reticulation), which is rarely preserved at this site.

Age: The Schilfsandstein Formation begins with a brief brackish-marine ingression into the Germanic Basin after an intra-Carnian stratigraphic gap, especially in the northern part of the basin which has euryhaline marine ostracods of late Julian age, such as *Simeonella alpina* Bunza & Kozur. These thin brackish-water sediments are overlain by fluvial sandstones, as well as siltstones and shales. In the southwestern Germanic Basin, the Schilfsandstein Formation is overlain by a hypersaline marine horizon with Tuvalian bivalves (Dolomie de Beaumont Horizon) and conchostracans of the *Eosolimnadiopsis gallegoi* Zone. Thus, the *Anyuanestheria* n. sp. A – *Laxitextella* sp. cf. *L. laxitexta* Zone in the Germanic Schilfsandstein Formation clearly is of late Julian age. This age also can be assumed for the *Anyuanestheria* n. sp. A Zone of the lower Cow Branch Formation in the Newark Supergroup, because *Anyuanestheria* n. sp. A. is restricted to the late Julian in the Germanic Basin.

Eosolimnadiopsis gallegoi Zone

Definition: Range Zone of *Eosolimnadiopsis gallegoi* Kozur n. sp.

Lower boundary: First appearance of *Eosolimnadiopsis gallegoi* Kozur n. sp.

Upper boundary: Disappearance of *Eosolimnadiopsis gallegoi* Kozur n. sp.

Important species: *Eosolimnadiopsis gallegoi* Kozur, *Anyuanestheria* n. sp. C Kozur, *Laxitextella* n. sp. C Kozur.

Remarks: The timing of the first appearance of *Eosolimnadiopsis* Chen, 1976 is very curious. At this horizon in the Tethyan deep water sediments, the first Jurassic-type radiolarian genera appear, such as *Protunuma* Ichikawa & Yao. Seemingly, the base of the Tuvalian was a time of evolutionary radiation for a number of different fossil groups. For conodonts, however, it was a time of extinction and renewed radiation did not begin until later.

Occurrence: Only known from the Germanic Basin, where it occurs in the basal Rote Wand of the Weser Formation (base of the Upper Gypsum Keuper) of southern Germany, and the equivalent Dolomie de Beaumont Horizon in eastern France. The absence of equivalents of this zone in the Newark Supergroup potentially reflects the fact that we have not yet sampled this lower Tuvalian stratigraphic interval. We expect it to be present, for example in the lower New Oxford Formation below the middle Tuvalian Fulton site.

Age: The Dolomie de Beaumont Horizon of Eastern France marks a marine ingression into the southwestern Germanic Basin. The marine dolomites contain the bivalve *Costatoria vestita* (von Alberti). Intercalated brackish marls and brackish to freshwater facies equivalent to the Dolomie de Beaumont yield conchostracans typical of the *Eosolimnadiopsis gallegoi* Zone. According to Prof. Renato Posenato, Ferrara, (pers. comm.) this species occurs in latest Julian and earliest Tuvalian strata, and his specimens (sampled in situ) came from near the supposed Julian/Tuvalian boundary. Thus, this horizon can be assigned to the earliest Tuvalian.

Laxitextella seegisi Zone

Definition: Occurrence of *Laxitextella seegisi* Kozur n. sp.

Lower boundary: First appearance of *Laxitextella seegisi* Kozur n. sp.

Upper boundary: Disappearance of *Laxitextella seegisi* Kozur n. sp. and *L.* sp. cf. *L. laxitexta* (Sandberger).

Important species: *Anyuanestheria bocki* (Olempska), *Krasiestheria parvula* Olempska, *Eosolimnadiopsis* ? n. sp., *Laxitextella* sp. cf. *L. laxitexta* (Sandberger), *Laxitextella seegisi* Kozur n. sp..

Remarks: *Anyuanestheria bocki* (Olempska) and *Krasiestheria parvula* Olempska so far have been found only in the Krasiejów locality in Opole Silesia, southwestern Poland. The occurrence of *Laxitextella* sp. cf. *L. laxitexta* and *Laxitextella seegisi* Kozur n. sp. (= *Laxitextella* sp. A of Olempska, 2004), which also are common in the Lehrberg Beds of southwestern Germany, indicates that both horizons are the same age. Especially interesting is the occurrence of *Eosolimnadiopsis* ? n. sp. at the Krasiejów locality (Pl. 11, Fig. 3), because this species also occurs at the Fulton site in the New Oxford Formation in the Gettysburg Basin (MD/PA) (see below). The vertebrates from Krasiejów indicate that they belong to the early Adamanian LVF. According to Dr. Sulej, Warsaw, (pers. comm.) the following vertebrates have been found: *Metoposaurus diagnosticus krasiejowensis* Sulej, *Cyclotosaurus intermedius* Sulej & Majer, *Teratosaurus silesiacus* Sulej, *Stagonolepis* sp., *Paleorhinus* sp., and *Silesaurus opolensis* Dzik. The occurrence of *Teratosaurus* at a Tuvalian locality initially seems surprising, because this genus was described originally from the Norian of southern Germany. However, according to Dr. Sulej (pers. comm.), the Krasiejów *Teratosaurus silesiacus* clearly is more primitive than the southern German species *T. suevicus*.

Occurrence: Lehrberg Beds of southwestern Germany (Seegis, 1997); Krasiejów locality in Opole Silesia, southwestern Poland (Olempska, 2004).

Age: Middle Tuvalian. The Lehrberg Beds typically have a brackish to fresh water fauna, but in the deeper parts of the Germanic Basin there also is a fauna from a slightly hypersaline environment that includes *Reubenella* sp. Among euryhaline marine ostracods that also can live in brackish environments, Seegis (1997) mentioned and illustrated what he called *Simeonella alpina* (Bunza & Kozur). However, all of his specimens represent a new species that clearly can be distinguished from the upper Julian *Simeonella alpina*. This new species also occurs in middle Tuvalian beds in Hungary, which thereby indicates a middle Tuvalian age for the *Laxitextella seegisi* Zone.

Eosolimnadiopsis ? n. sp. – *Laxitextella* sp. cf. *L. laxitexta* Zone

Definition: Co-occurrence of *Eosolimnadiopsis* ? n. sp. and *Laxitextella* sp. cf. *L. laxitexta* (Sandberger).

Lower boundary: First occurrence of *Eosolimnadiopsis* ? n. sp.

Upper boundary: Last occurrence of *Laxitextella* sp. cf. *L. laxitexta*.

Important species: *Eosolimnadiopsis* ? n. sp. with a long, quite straight dorsal margin and distinct posterodorsal corner, *Laxitextella* sp. cf. *L. laxitexta*, *Euestheria* sp. (medium to large forms).

Remarks: The *Eosolimnadiopsis ?* n. sp.– *Laxitextella* sp. cf. *L. laxitexta* Zone corresponds to the *Laxitextella seegisi* Zone of the Germanic Basin. *Laxitextella seegisi* Kozur n. sp. so far has not been found in the Newark Supergroup, but we have not yet been able to obtain abundant material from this interval (only about 40 conchostracan specimens) so its absence is not definitive.

Occurrence: Fulton site in the middle New Oxford Formation(?) in the Gettysburg Basin, MD/PA.

Age: In the Germanic Basin, *Eosolimnadiopsis* ? n. sp. is restricted to the middle Tuvalian *Laxitextella seegisi* Zone and the youngest occurrence of *L.* sp. cf. *L. laxitexta* in the Germanic Basin is in this zone. Thus, a middle Tuvalian age is indicated for the *Eosolimnadiopsis* ? n. sp. - *L.* sp. cf. *L. laxitexta* Zone, corresponding to the *Laxitextella seegisi* Zone (Lehrberg Beds of southwestern Germany and the Krasiejów locality in southwestern Poland).

Euestheria ovata – Euestheria princetonensis Zone

Definition: Occurrence of *Euestheria ovata (*Lea) and *Euestheria princetonensis* (Bock).

Lower boundary: First appearance of *Euestheria hausmanni* (Schmidt), *E. ovata* (Lea), and *E. princetonensis* (Bock).

Upper boundary: First appearance of *Euestheria buravasi* Koayashi and *Euestheria* n. sp. aff. *E. hausmanni.*

Important species: *Euestheria hausmanni* (Schmidt), *E. ovata* (Lea), and *E. princetonensis* (Bock).

Remarks: This zone is characterized by mass occurrences of large species of *Euestheria*. Although *E. ovata* and *E. princetonensis* occur within the same stratigraphic interval, they do not co-occur. *E. ovata* and *E. hausmanni* may occur together, but often only one or the other species is present.

Occurrence: Upper Stockton (?) and lower third of Lockatong formations in the Newark Basin, PA/NJ; New Oxford Formation in the Gettysburg Basin, MD/PA; Cumnock Formation in the Sanford Subbasin of the Deep River Basin, NC; upper Cow Branch Formation in the Dan River/Danville Basin, NC/VA.

Age: All occurrences are within the middle to late Adamanian LVF of late Tuvalian age. This age is also supported by the occurrence of *E. hausmanni*, which occurs in the Germanic Basin in the upper Tuvalian *Laxitextella freybergi* Zone of the Coburg Sandstein.

Laxitextella freybergi Zone

Definition: Range of *Laxitextella freybergi* Kelber & Kozur n. sp. and *Euestheria hausmanni* (Schmidt).

Lower boundary: First appearance of *Laxitextella freybergi* Kelber & Kozur and *E. hausmanni.*

Upper boundary: Disappearance of *Laxitextella freybergi* Kelber & Kozur.

Important species: *Laxitextella freybergi* Kelber & Kozur n. sp., *Laxitextella dorsorecta* (Reible) emend., *Euestheria hausmanni* (Schmidt), and new species of *Euestheria* and *Anyuanestheria*.

Remarks: The *Laxitextella freybergi* Zone has a diverse conchostracan fauna. Most of the species are new species which will be described in Kelber and Kozur (in prep.). The occurrence of *E. hausmanni* indicates that the *Laxitextella freybergi* Zone of the Germanic Basin has an age similar to that of the *E. ovata – E. princetonensis* Zone within the Newark Supergroup. As *E. ovata* and *E. princetonensis* have not been found in the Germanic Basin, and as *Laxitextella freybergi* Kelber & Kozur has not been found in the Newark Supergroup, these zones cannot be merged. These zones could represent slightly different time intervals within the late Tuvalian, but alternatively the *E. ovata - E. princetonensis* Zone might represent a paleoequatorial fauna while the *Laxitextella freybergi* Zone might represent a fauna restricted to the vicinity of the Late Triassic Tropic of Cancer.

Occurrence: The Coburg Sandstein of the Germanic Basin.

Age: The advanced *Laxitextella* species, transitional to *Shipingia*, indicate a late Tuvalian age for the Coburg Sandstein. According to Schulz and Heunisch (2005) and Heunisch (2005), the overlying Mainhardt Formation also contains Tuvalian sporomorphs. Thus, the Coburg Sandstein lies in the upper, but not the uppermost part of the Tuvalian *Enzonalesporites vigens-Spiritisporites spirabilis* Phase (van den Bergh, 1987). This means that the Coburg Sandstein is late, but not latest Tuvalian in age (see also Bachmann and Kozur, 2004).

Euestheria buravasi –Euestheria n. sp. Zone

Definition: Occurrence of *Euestheria buravasi* Kobayashi and *Euestheria* n. sp. aff. *E. hausmanni* (Schmidt).

Lower boundary: Appearance of *Euestheria buravasi* and *Euestheria* n. sp. aff. *E. hausmanni.*

Upper boundary: Appearance of *Shipingia* of the *Shipingia* ? *mansuyi* (Kobayashi) group.

Important species: *Euestheria buravasi*, *Euestheria* n. sp. aff. *E. hausmanni*, *Euestheria bunopasi* (Kobayashi), *Anyuanestheria* ? n. sp. A.

Remarks: This zone is represented by the extraordinarily abundant conchostracan fauna of the Triangle Brick Quarry in the Durham Subbasin (Deep River Basin). It is strongly dominated by *Euestheria buravasi*; all other species are subordinate. Particularly interesting among these subordinate species is *Euestheria* n. sp. aff. *E. hausmanni*, which is also present in the Germanic Basin. The latter species also is very similar to *Asmussia symmetrica* Kobayashi, which differs somewhat in that it seems to have a central umbonal area. This distinction, however, may be the result of postmortem deformation. *A. symmetrica* also is similar to, but not identical to, *E. hausmanni*.

Occurrence: Triangle Brick Quarry in the Durham Subbasin of the Deep River Basin (NC), ("lithofacies Association II," equivalent to lower Sanford Formation in the adjacent Sanford Subbasin). A seemingly contemporaneous fauna is known from the lower Steinmergelkeuper of Thuringia, where *Euestheria* n. sp. aff. *E. hausmanni* is present. *E. buravasi* has not been reported from this poorly studied fauna, but a conchostracan specimen illustrated by Hopf and Martens (1992) from the lower Steinmergelkeuper (lower Arnstadt Formation) of Thuringia, Germany belongs to *Euestheria bunopasi* (Kobayashi), which co-occurs with *E. buravasi* in Thailand.

Age: *Euestheria buravasi* was originally described from the early Norian of Thailand (Kobayashi, 1975). An earliest Norian age also is indicated by vertebrates from the Triangle Brick Quarry. *Aetosaurus arcuatus* (Marsh) in particular indicates an age no older than Norian (Lucas et al., 1998), but the co-occurrence of a dicynodont at this quarry is unique because dicynodonts have not been reported elsewhere from the Norian (Sues et al., 2001). Thus, this particular tetrapod assemblage indicates an age very close to the Carnian- Norian boundary.

Interval with Small *Shipingia* and Large *Euestheria*

Remarks: Both in the Newark Supergroup (e.g., in the lower Groveton Member of the Bull Run Formation in the Culpeper Basin, Virginia) and in the Germanic Basin (upper part of the lower Steinmergelkeuper = upper part of the lower Arnstadt Formation), there is an abundant conchostracan fauna that has not been investigated adequately. It consists of big *Euestheria* species, some *Shipingia* similar to *Shipingia* ? *mansuyi* (Kobayashi, 1955), and *Laxitextella dorsorecta* (Reible, 1962), the latter a transitional form between *Laxitextella* and *Shipingia*. This fauna is younger than both the early Norian *Euestheria buravasi – Euestheria* n. sp. (aff. *E. hausmanni*) Zone of the Newark Supergroup and the *Euestheria* n. sp. aff. *E. hausmanni* fauna from the Germanic Basin, but it is older than the middle Norian *Shipingia hebaozhaiensis* fauna found in both areas. Therefore its age is late Lacian to early Alaunian. We have not been able yet to study this fauna in the detail that it deserves but, even at our present level of knowledge, it is obvious that the fauna within this Norian interval represents at least one conchostracan zone separable from the ones above and below. This fauna includes several new species that can be described only after we are able to revise "*Estheria*" *pennsylvanica* Wanner, 1926. We have not been successful so far in locating the type material of this species, and Bock (1953a) apparently did not get to see it either.

Shipingia hebaozhaiensis Zone

Definition: Range Zone of *Shipingia hebaozhaiensis* Shen.

Lower Boundary: FAD of *S. hebaozhaiensis*.

Upper Boundary: LAD of *S. hebaozhaiensis*.

Important species: Most localities yield monospecific faunas of *S. hebaozhaiensis* (except in the lower part of the zone), though occasionally undescribed species of *Euestheria* also occur.

Remarks: When Kozur and Weems (2005) established the *S. hebaozhaiensis* Zone in the Newark Supergroup, only its uppermost part was known. At that time this zone was not known from the Germanic Basin, though it was well represented in China. In the Newark Supergroup, the upper *S. hebaozhaiensis* zone is characterized by large forms of the species, most with well developed microsculpture, and very rarely the earliest very primitive *S. olseni* also occur. Re-study of the material published by Warth (1969) shows that the upper *S. hebaozhaiensis* Zone also is present in Germany (upper Stubensandstein 2 of Württemberg, southwestern Germany, upper Alaunian). There, the upper *S. hebaozhaiensis* Zone also is characterized by large specimens of *S. hebaozhaiensis* that have distinct microsculpture (Pl. 6, Figs. 1, 2).

Recently, we have found conchostracans in the Newark Supergroup that come from the middle part of the *S. hebaozhaiensis* Zone (the Heidlersburg Member of the Gettysburg Shale in the Gettysburg Basin, MD/PA). In this interval, the adult forms are moderately large and the microsculpture is indistinct or absent. We also have found conchostracans of this age in the Germanic Basin, likewise consisting only of moderately large *S. hebaozhaiensis*. Additionally, we have found in the Germanic Basin conchostracans from the lower *S. hebaozhaiensis* Zone, where the index species is even smaller and the microsculpture is missing or barely discernable. Throughout most of the *S. hebaozhaiensis* Zone, the index species either dominates or constitutes a monospecific fauna. *Euestheria* is fairly common in the lower *S. hebaozhaiensis* Zone, but never as numerous as *S. hebaozhaiensis*.

Occurrence: Middle Groveton Member of the Bull Run Formation in the Culpeper Basin (VA), Alaunian; Heidlersburg Member of the Gettysburg Shale in the Gettysburg Basin (MD/PA), Alaunian; middle Arnstadt Formation (middle Steinmergelkeuper) of northern Germany, Alaunian; Stubensandstein 2 of Württemberg (southwestern Germany), Alaunian; Morocco (material provided by Dr. Paul E. Olsen, Columbia University), upper Alaunian; China, middle Norian (Alaunian).

Age: All occurrences of the *S. hebaozhaiensis* Zone in the Newark Supergroup, the Germanic Basin, in Morocco, and China are Alaunian (middle Norian).

Redondestheria grovetonensis Zone

Definition: Range zone of *Redondestheria grovetonensis* Kozur & Weems.

Lower boundary: FAD of *Redondestheria grovetonensis*.

Upper boundary: LAD of the genus *Redondestheria*.

Important species: *Redondestheria grovetonensis*, *R. novomexicoensis* Kozur, Weems & Lucas (only in the upper part of the zone), *Shipingia olseni* Kozur & Weems.

Remarks: The *R. grovetonensis* Zone has not been found outside of North America. In North America, it is found in the Newark Supergroup and in New Mexico. This zone may be missing in the Germanic Basin, either due to the discontinuous conchostracan record there (because of gaps and often unsuitable preservational facies) or because so few investigations have been undertaken within this stratigraphic interval.

Occurrence: Lower Redonda Formation of New Mexico (lower Apachean LVF), Sevatian; upper Groveton Member of the Bull Run Formation at the Groveton locality, Culpeper Basin, VA, lower Sevatian.

Age: The occurrence of the *R. grovetonensis* Zone above the middle Norian *S. hebaozhaiensis* Zone and below the Sevatian *S. olseni* Zone in the Newark Supergroup indicates an early Sevatian age, because the uppermost *S. hebaozhaiensis* Zone belongs to the late Alaunian.

Shipingia olseni Zone

Definition: Occurrence of *S. olseni* Kozur & Weems in the absence of *S. hebaozhaiensis* and *Redondestheria*.

Lower boundary: LAD of *Redondestheria* and the beginning of an often monospecific *S. olseni* fauna.

Upper boundary: LAD of *S. olseni*.

Important species: Mostly a monospecific *S. olseni* fauna occurs. Rarely, small Norian *Euestheria* are present (also known from China and Southeast Asia) that are not well studied yet in the Newark Supergroup.

Remarks: The large form *S. olseni* is the dominant species up to the uppermost Sevatian. The lower Rhaetian is missing in the Newark Supergroup due to a stratigraphic gap, but it is present in the Germanic Basin. There, a totally different fauna occurs which includes several small species of *Anyuanestheria* ?, among them *Anyuanestheria* ? n. sp.

Occurrence: Uppermost Catharpin Creek Formation (Haymarket locality), middle Catharpin Creek Formation (Cedar Run locality), both in the Culpeper Basin (VA); Constitution Avenue section (Exeter, PA), in the uppermost 21-28 m of the Passaic Formation (according to measurements by Fowell and Olsen, 1993), Boyertown Road section, middle Passaic Formation, both in the Newark Basin (PA/NJ); upper Blomidon Formation in the Fundy Basin, (Nova Scotia, Canada); Stubensandstein 3 except for its basal part, Württemberg (SW Germany).

Age: All occurrences of the *S. olseni* Zone have a Sevatian age, and this species occurs up to the top of the Sevatian. No *Shipingia olseni* have been found anywhere in the Rhaetian.

Anyuanestheria ? n. sp. Zone

Definition: Range of *Anyuanestheria* ? n. sp.

Lower boundary: Disappearance of the large *Shipingia olseni* Kozur & Weems, appearance of the small *Anyuanestheria* ? n. sp. and other *Anyuanestheria* ? species.

Upper boundary: Disappearance of *Anyuanestheria* ? n. sp.; above this, nearly monospecific faunas of *Euestheria brodieana* occur.

Important species: *Anyuanestheria* ? n. sp. (Pl. 5, Fig. 5) and other new *Anyuanestheria* ? species. In the upper part of this zone, *Euestheria brodieana* (Jones) becomes steadily more abundant and ultimately dominates the fauna. Taxonomic studies of the lower Rhaetian faunas are not finished, so it is not yet certain if these species, which have radial lirae, can be properly assigned to *Anyuanestheria*. There are some differences in the arrangement of the radial lirae, compared to the small Carnian species of *Anyuanestheria*, but it is not yet clear whether this represents a species or genus level of difference.

Remarks: The base of the Olenekian and the base of the Rhaetian mark the two most sweeping turnovers in conchostracan faunas within the uppermost Permian to lowermost Jurassic (upper Changhsingian to lower Hettangian) interval.

Occurrence: Lower Exter Formation (Postera Sandstone), northern Germany, lower Rhaetian; southwestern Poland, lower Rhaetian.

Age: The Postera Sandstone contains early Rhaetian sporomorphs and is overlain by marine middle Rhaetian. Thus, the early Rhaetian age of this fauna in northern Germany is well documented.

Euestheria brodieana Zone

Definition: Range of *E. brodieana* (Jones), in the absence of both the lower Rhaetian form *Anyuanestheria* ? n. sp. and the basal Hettangian index forms such as *Bulbilimnadia sheni* Kozur & Weems and Liassic *Palaeolimnadia* and *Euestheria* species.

Lower boundary: Disappearance of *Anyuanestheria* ? n. sp. and other *Anyuanestheria* species. Beginning of the monospecific *E. brodieana* faunas.

Upper Boundary: First appearance of Liassic species, such as

Bulbilimnadia sheni Kozur & Weems, Liassic *Palaeolimnadia*, and often subcircular *Euestheria* which are known mainly from China.

Important species: Both in the Germanic Basin and in the Newark Supergroup, the *E. brodieana* Zone consists of monospecific *E. brodieana* conchostracan faunas.

Occurrence: Upper Rhaetian of England, Germany, and France (Argiles de Levallois); uppermost part of lower Rhaetian Postera Sandstone; upper Rhaetian Midland Formation of the Culpeper Basin.

Age: In Europe, all published occurrences of the *E. brodieana* fauna have been in upper or uppermost Rhaetian strata. Recently, *E. brodieana* has shown up in a phylomorphogenetic lineage within the upper part of the lower Rhaetian Postera Sandstone. This earliest known occurrence is with *Anyuanestheria* ? n. sp., so this fauna is assigned to the upper *Anyuanestheria* ? n. sp. Zone. In the uppermost part of the Postera Sandstone, somewhat below the marine middle Rhaetian, *E. brodieana* totally replaces the rest of the fauna of the *Anyuanestheria* ? n. sp. Zone. Thus, the full range of the *E. brodieana* Zone is latest early Rhaetian through late Rhaetian.

Bulbilimnadia sheni Zone

Definition: Co-occurrence of *Bulbilimnadia sheni* Kozur & Weems and other Liassic conchostracans with *Euestheria brodieana* (Jones).

Lower Boundary: FAD of *B. sheni*.

Upper boundary: LAD of the Rhaetian holdover species *E. brodieana*.

Important species: *Euestheria brodieana* (Jones) (dominant) along with earliest Jurassic conchostracans, especially *Bulbilimnadia sheni* but also very rarely *Palaeolimnadia* sp. cf. *P. longmenshanensis* Shen, and *P.* sp. cf. *P. semicircularis* Shen.

Remarks: Liassic conchostracans are well known from China (summarized in Chang et al., 1976), but they are known from strata somewhat younger than the earliest Hettangian. The Rhaetian form *Euestheria brodieana* is still common in the *B. sheni* Zone but, unlike in the underlying *E. brodieana* Zone, it is accompanied by earliest Liassic forms such as *B. sheni*. This indicates that the Rhaetian-Hettangian transition occurs in the Newark Supergroup without any stratigraphic gap.

Occurrence: Lower Waterfall Formation in the Culpeper Basin (VA), lower Hettangian; middle East Berlin Formation in the Hartford Basin (CT/MA), basal Hettangian.

Age: Early Jurassic, earliest Hettangian.

Bulbilimnadia froelichi Zone

Definition: Range Zone of *B. froelichi* Kozur & Weems.

Lower boundary: LAD of *Euestheria brodieana* (Jones), FAD of *B. froelichi* Kozur & Weems.

Upper boundary: LAD of *B. froelichi*.

Important species: *Bulbilimnadia froelichi* Kozur & Weems, *Palaeolimnadia baitianbaesis* Chen.

Remarks: The fauna of this zone consists almost exclusively of *B. froelichi*, but this may be because we have sampled this faunal horizon at a single locality. Except for *B. froelichi*, only a very few *Palaeolimnadia* sp. cf. *P. baitianbaensis* Chen are known from this locality. Rhaetian holdovers (e.g., *E. brodieana*) are absent.

Occurrence: Upper Waterfall Formation of the Culpeper Basin.

Age: Early Jurassic, late early Hettangian.

CORRELATION OF LITHOSTRATIGRAPHIC UNITS IN THE NEWARK SUPERGROUP WITH THE CONCHOSTRACAN ZONATION AND THE INTERNATIONAL MARINE GEOLOGIC TIME SCALE

Lithostratigraphic Units

A comprehensive bibliography of much of the earlier Newark Supergroup literature can be found in Margolis et al. (1986), and stratigraphic nomenclature for the Newark Supergroup has been summarized thoroughly by Luttrell (1989) including history of units, age of units, and location of type sections or areas. Since the summary of Luttrell, the only regional studies that have been conducted are by Weems and Olsen (1997) and Faill (2003). Stratigraphic nomenclature used by Luttrell (1989), as slightly modified by Weems and Olsen (1997), is followed here. The stratigraphy of basins that have produced conchostracans is briefly summarized below. Numbers refer to basin number designations used in Figures 1-4.

Sanford and Durham Subbasins of the Deep River Basin (4, 5)

The first major work on the Deep River Basin was done by Emmons (1856), who did not erect a formal stratigraphy for units within any of its constituent subbasins. Campbell and Kimball (1923) subsequently established names for units within the Sanford Subbasin, and these were mapped in considerable detail by Reinemund (1955). The units recognized were (from oldest to youngest) the Pekin Formation, the Cumnock Formation, and the Sanford Formation. The Pekin and Sanford formations are lithologically similar redbed formations, but they are readily separated in the Sanford Subbasin by the intervening Cumnock Formation which contains abundant brown, tan, grey, green, and black shales and coals that formed in paludal to lacustrine depositional environments. This is the interval from which Bock (1953a, b) described *Howellisaura berryi* (Bock). Unfortunately, the Cumnock lithology only can be traced into the southernmost Durham Subbasin. Therefore, the central and northern depositional sequences in that subbasin are not so readily divided because they mostly are redbeds from bottom to top. Hoffman and Gallagher (1989) divided the stratigraphic sequence in the Durham Subbasin into three successive lithofacies associations, of which their "lithofacies association I" corresponds rather closely to the combined stratigraphic interval of the Pekin and Cumnock formations. Their "lithofacies association II" corresponds to the lower part of the Sanford Formation. This interval, exposed in the Triangle Brick Quarry pit, has produced the highest known occurrences of (red) lacustrine strata in either subbasin and the highest occurrences so far of conchostracans in either subbasin. Their "lithofacies association III" corresponds to the upper part of the Sanford Formation (Lucas et al., 1998).

Dan River/Danville Basin (7)

Early reconnaissance mapping suggested that there were two different basins in this area, but subsequent detailed mapping demonstrated that only a single elongate basin is present. The location of this basin, astride the North Carolina – Virginia border, resulted in the erection of two different stratigraphies for the constituent strata. Meyertons (1963), working in the northern Danville (Virginia) end of the basin, recognized a basal Dry Fork Formation that generally is overlain by, but partly intertongues with, a Leaksville Formation, which in turn is overlain disconformably by a Cedar Forest Formation. Within the Leaksville, Meyertons additionally recognized two intertonguing members: the Cow Branch Member and the Cascade Station Member. Thayer (1970), mapping in the southern Dan River (North Carolina) end of the basin, erected a distinctly different stratigraphy. Thayer named his basal coarse and mostly fluvial unit the Pine Hall Formation, which is overlain gradationally by his finer and mostly lacustrine Cow Branch Formation, which in turn is overlain by, and partly intertongues with, his Stoneville Formation. Aspects of both stratigraphies have been adopted here (Fig. 3). Conchostracans have been found so far only in the Cow Branch lithology, but at two distinctly different stratigraphic levels.

Scottsburg, Briery Creek, and Farmville basins (8, 11, 12)

No formal lithologic names have been erected for the strata in any of the basins that lie along the trend of the Farmville Basin. Two basins (Randolph and Roanoke Creek) have not yielded any lacustrine strata so far, but the other three have paludal to lacustrine strata that contain fish

(*Dictyopyge* in the Scottsburg Basin) and conchostracans (in the Briery Creek and Farmville basins). These basins probably represent remnants of the "keel" of a once continuous and much more extensive basin along this trend. The most completely preserved stratigraphic section is in the Farmville Basin, which has a basal sandstone unit, an intermediate paludal/lacustrine unit that contains conchostracans, and a disconformably overlying fluvial to fanglomerate unit. This sequence is very reminiscent of the stratigraphy found in the Richmond and Taylorsville basins. Detailed mapping has been published only for the northern part of the Farmville Basin (Marr, 1980).

Richmond and Deep Run basins (13, 15)

The Deep Run Basin is a small, shallow eastern structural outlier of the Richmond Basin. It is separated from the main basin by only a few miles and has a stratigraphy identical to the basal part of the main basin (Shaler and Woodworth, 1899). The stratigraphy of the Richmond Basin was established by Shaler and Woodworth (1899) and has been revised since by Cornet and Olsen (1990). The interpretation of Cornet and Olsen (1990) is complex and based in large part on interpretation of seismic lines. In the absence of any surface control, we choose to largely follow the original stratigraphy of Shaler and Woodworth (1899), in which the basal unit of the basin is the Tuckahoe Formation ("Tuckahoe Group" in Shaler and Woodworth, 1899; reduced to Tuckahoe Formation by Cornet and Olsen, 1990), the middle unit is the Vinita Shale, and the upper unit is the Otterdale Sandstone. In this stratigraphy, the productive coal beds constitute the upper member of the Tuckahoe Formation. The coal bed interval is the horizon from which Bock (1953a,b) described *Isaura midlothianensis* and *Howellisaura winterpockensis*.

Taylorsville Basin (16)

The stratigraphy of the exposed Taylorsville Basin was described and mapped by Weems (1980, 1981, 1986). LeTourneau (2003) revised the stratigraphy of Weems and added several new formations for higher subsurface stratigraphic units that previously had been unavailable for study. Most of LeTourneau's revisions of the stratigraphy of Weems are here rejected, because his revisions are based on a number of assumptions that cannot be verified in the field. Specifically, the basal strata of LeTourneau's (2003) stratigraphic column (his South Anna Formation and Deer Creek Member of his Falling Creek Formation) nowhere can be shown to underlie the Stagg Creek and Falling Creek members of Weems (1980), who considered LeTourneau's basal strata simply to be direct lateral correlatives of his Stagg Creek and Falling Creek members. The sole justification for making a distinction between these two otherwise identical and adjacent sequences is that, according to LeTourneau, his Deer Creek Member represents a deeper water environment than the Falling Creek Member of Weems (1980). The type section of the Deer Creek member lies adjacent to the western border fault and is pervasively slickensided and sheared. Therefore, it is difficult to determine what water depths it represents because many of its features either are the result of tectonic shearing or have been destroyed by this shearing. Thus, the simpler interpretation of Weems (1980) is used here for the exposed units of the Taylorsville Basin. Some other changes advocated by LeTourneau (2003) are adopted, namely raising the Falling Creek and Newfound units from member to formational status, and the naming of younger subsurface formations. Additionally, the Stagg Creek Member is raised to formational status to conform to the new formational status of the Falling Creek and Newfound formations. The only unit in the Taylorsville Basin that so far has yielded conchostracans is the paludal to lacustrine Falling Creek Formation. The conformably underlying Stagg Creek Formation and the disconformably overlying Newfound Formation formed in fluvial depositional environments.

Culpeper Basin (19)

The stratigraphy of the Culpeper Basin has gone through a number of iterations. Roberts (1928) recognized a basal Manassas Sandstone overlain by a Bull Run Shale, but he did not describe the higher portions of the stratigraphic column. Lindholm (1979) provided the first inclusive stratigraphic compilation and applied stratigraphic names to the entire column. His work subsequently was revised and partially duplicated by Lee and Froelich (1989). The best aspects of both stratigraphies were synthesized by Weems and Olsen (1997), and this stratigraphy is used here (Figs. 2 and 3). The basal unit of the basin is the Manassas Sandstone (consisting of a lower Reston Conglomerate Member and an upper Poolesville Sandstone Member), which is overlain by the Bull Run Formation (consisting of a lower Balls Bluff Siltstone Member and an upper Groveton Member). The Bull Run is overlain by the Catharpin Creek Formation, which in turn is overlain by the Mount Zion Church Basalt. Above this first basalt is the Midland Formation, which is overlain by the Hickory Grove Basalt, the Turkey Run Formation, the Sander Basalt, and the Waterfall Formation. The Manassas Formation and Balls Bluff Member of the Bull Run Formation are fluvial sandstones and siltstones, respectively, that so far have yielded no conchostracans. All higher sedimentary formations include horizons with abundant conchostracans except for the Turkey Run. A rich conchostracan fauna, allegedly from the Turkey Run Formation, is listed among the Yale Peabody Museum collections. However, comparison of the exact collecting locality with the map published later by Lee and Froelich (1989) indicates that the collecting site is in the Waterfall Formation and not in the Turkey Run Formation. Dr. Oscar Gallego, Corrientes (Argentina), currently has this collection under study, but he graciously has shared with us his determinations of this conchostracan material and also its state of preservation. The fauna has a Rhaetian-Hettangian transitional character, with the first Liassic newcomers (especially *Bulbilimnadia sheni*) dominating Rhaetian holdovers (*E. brodieana*) exactly as in the lower Waterfall Formation. Such transitional faunas generally change fast, as exemplified in the immediately overlying upper Waterfall Formation where *E. brodieana* is gone and the fauna is strongly dominated by the Liassic newcomer *Bulbilimnadia froelichi*. For this reason, it seems unlikely that a Turkey Run fauna would be so very similar in its complexion to the lower Waterfall Formation fauna. Additionally, the preservation of the YPM material is identical to that seen in the lower Waterfall Formation, in that a white carbonate crust is present on many specimens. For all of these reasons, it seems clear that the YPM material, originally thought to be from the Turkey Run Formation, instead is from the lower Waterfall Formation.

Gettysburg Basin (20)

The stratigraphy of the southern Pennsylvania Gettysburg Basin was defined by Stose and Bascom (1929), and this stratigraphy later was extended into the Maryland part of the basin by Jonas and Stose (1938). These authors recognized two formations, a basal, predominantly fluvial New Oxford Formation and an overlying, predominantly lacustrine Gettysburg Shale. Within the Gettysburg Shale, they also distinguished a very sandstone-rich Heidlersburg Member. Cornet (1977) recognized two thin units at the very top of the Gettysburg, a basalt which he informally called the Aspers Basalt and sedimentary strata above it. These were formalized by Weems and Olsen (1997) as the Aspers Basalt and the Bendersville Formation. Based on our conchostracan studies, it is now clear that the basal sequence of the New Oxford Formation is distinctly older than overlying strata and separated from them by a disconformity. For this reason, these strata are shown here as an unnamed unit below the New Oxford Formation. A few horizons within the Gettysburg basin have yielded abundant conchostracans, and it seems likely that many more are to be found. The two conchostracan horizons within the New Oxford Formation have proven exceptionally difficult to place stratigraphically. The Fulton site, in Maryland well to the southwest of the type area of the New Oxford and Gettysburg formations, lies beyond several structural anomalies and is not readily correlated to the type New Oxford-Gettysburg area. Jonas and Stose (1938) mapped this horizon as the basal part of the Gettysburg Formation, and its lacustrine character would seem to make it a typical Gettysburg sequence, but we assign it to the New Oxford Formation because it appears to contain a middle Tuvalian conchostracan fauna (recognizing, however, that this has to be confirmed by further sampling to get more and better preserved material). Unless future finds lower the basal age of the Gettysburg Shale considerably, which seems unlikely, it is only possible to assign this particular lacustrine sequence to a lacustrine lense within the New Oxford. Similarly, the stratigraphic horizon of a locality along Little Conewago Creek is subject to interpretation. The geologic map of York County (Stose and Jonas, 1939) shows this locality to be near the middle of the New Oxford outcrop belt, and this was used by Cornet (1977) to estimate a relatively low horizon for this locality. However, Wanner (1926) estimated that this locality is nearly 2000 meters above the base of the New Oxford Formation, estimating strata thickness from an average regional 20° dip in this area. Stose and Jonas (1939) show a major fault north of this area within the New Oxford strike belt, seemingly with its west side up, so the New Oxford Formation may be largely repeated within this area. Thus, the horizon calculated by Wanner is probably close to correct, and this locality is probably near the top of the New Oxford Formation (or even in the basal Gettysburg Shale) and not near the middle of the New Oxford. In either case, its uppermost Tuvalian conchostracans place it higher in the stratigraphic section than the Fulton site with its middle Tuvalian conchostracans.

Newark basin (22)

The strata of the New Jersey portion of the Newark basin were divided into three formations by Kummel (1897), and these units were later carried over into Pennsylvania by Bascom et al. (1909). In ascending order, these units were a predominantly fluvial Stockton Formation, a lacustrine Lockatong Formation, and a predominantly redbed Brunswick Formation. The black shales, siltstones, and occasional black limestones of the Lockatong Formation document the most spatially and temporally persistent lake unit known within the entire Newark Supergroup. The Brunswick Formation included the bulk of the stratigraphic column of the Newark basin, and this interval later was divided into seven formations by Olsen (1980) who abandoned the name "Brunswick." The interval represented by the former Brunswick Formation now is occupied by (in ascending order) the Passaic Formation, the Orange Mountain Basalt, the Feltville Formation, the Preakness Basalt, the Towaco Formation, the Hook Mountain Basalt, and the Boonton Formation. Conchostracans occur at many levels in this basin, and much work remains to be done on the details of its conchostracan biostratigraphy.

Hartford Basin (25)

Krynine (1950) applied the first formal stratigraphy to the sediments of the Hartford basin. In ascending order, he recognized a predominantly fluvial New Haven Arkose, a Meriden Formation that consisted of interbedded lava flows and fluvial to lacustrine strata, and a Portland Formation that is predominantly lacustrine in its lower part but fluvial toward its top. Rodgers et al. (1959) named the lava flows as members of the Meriden, and called them (in ascending order) the Talcott Lava Member, the Holyoke Lava Member, and the Hampden Lava Member. Lehman (1959) slightly modified these names and additionally named the sedimentary packages between them as formations. In ascending order these were the Talcott Basalt, the Shuttle Meadow Formation, the Holyoke Basalt, the East Berlin Formation, and the Hampden Basalt. The name Meriden was abandoned, but since has been revived as a group name by Weems and Olsen (1997). Fossils are rare in the New Haven Arkose, but skeletal remains of *Rutiodon* and *Stegomus* (*Aetosaurus*) clearly indicate a late Carnian to Norian age (Lull, 1953). Overlying units are much more fossiliferous. To date, the only conchostracan horizon available to us for study is in the middle of the East Berlin Formation, but other horizons have been reported (McDonald, 1996).

Fundy basin (29)

Powers (1916) named strata in the Fundy basin (in ascending order) the Annapolis Formation (consisting of a lower Wolfville Sandstone member and an upper Blomidon Shale member), the North Mountain Basalt, and the Scots Bay Formation. Later, Klein (1962) abandoned the name Annapolis Formation and raised the Wolfville and Blomidon to formational rank. Beds immediately beneath the Wolfville Formation, called the Lower Economy beds, have been ascribed a Middle Triassic age (Baird and Olsen, 1983); these are not considered here to be part of the Newark Supergroup. Baird and Olsen (1983) discussed a vertebrate fauna from the middle of the Wolfville Formation, which they assigned to the Carnian, and a vertebrate fauna from the upper Wolfville that they assigned to the Carnian-Norian. Conchostracans from high in the Blomidon Formation demonstrate that the upper part of that unit is upper Norian (Sevatian). No conchostracan data is available yet from the highest (Scots Bay) strata above the North Mountain Basalt, but interbasin correlations suggest that these strata probably are late Rhaetian in age. The age range of Triassic strata in the Fundy basin seems to be approximately as long as the age range of Triassic strata in the other Newark Supergroup basins, but the thicknesses of the Fundy strata are only about half the thicknesses documented elsewhere. This suggests that the rate of deposition in the Fundy Basin during the Upper Triassic was much slower than it was in the other basins of the Newark Supergroup.

Previous Correlations with the International Geologic Time Sscale

The total age range for the Newark Supergroup, as estimated by various authors over the past 164 years, is shown in Figure 11. This historical review clearly shows that there has been long standing uncertainty as to the true total age range of the rocks that we now call the Newark Supergroup. Within the Newark Supergroup, the correct age assignments of the various formations, members, and biostratigraphic zones generally have been even less certain. Among the various studies undertaken to place ages on specific units and intervals, four categories can be distinguished.

The first category includes studies that have provided undisputed, precise and correct age assignments. Only a few results fall into this category. One is the Lacian-Alaunian (to early Sevatian ?) age range of the Neshanician (Revueltian) land-vertebrate faunachron (LVF), based on occurrences of *Aetosaurus* in well dated sequences of the Germanic Basin and Alps, including upper Alaunian marine beds of the Alps (Wild, 1989; beds correlated with the international marine scale by Jadoul et al., 1994 and Roghi et al., 1995). A second interval with undisputed and correct age assignment is the sequence of sediments and volcanic flows and ashes above the second lava flow. These were assigned to the Jurassic (Cornet, 1977), and conchostracans have confirmed this age assignment for the lower part of that sequence (specifically to the lowermost and lower Hettangian).

A second category of previous age assignments are those that have been undisputed but, even so, were wrong. The upper Passaic Formation and time equivalents in other rift basins always have been assigned by palynologists to the Rhaetian, despite the fact that they do not contain a single Rhaetian guide form, and by vertebrate paleontologists also without evidence from any Rhaetian guide form (if such guide forms actually exist). The conchostracan studies by Kozur and Weems (2005, 2006) have shown that all of this "Rhaetian" section below the previously alleged Rhaetian-Hettangian boundary actually belongs within the upper Norian (Sevatian). This interval is characterized by the occurrence of large *Shipingia olseni*, which also occur in the upper Norian of the Germanic Basin. At the time of Kozur and Weems (2005), we did not have a well dated lower Rhaetian conchostracan fauna for comparison, so it remained theoretically possible at that time that the *S. olseni* faunal zone might range upward as high as the lower part of the lower Rhaetian, because the co-occurring pollen species *Patinasporites densus* did not disappear until around the middle of the lower Rhaetian. Since our paper, an abundant and well dated lower Rhaetian conchostracan fauna has been found in the Germanic Basin in beds that contain many Rhaetian sporomorphs but also lie below marine middle Rhaetian strata. This rich conchostracan association is distinctly different from the upper Norian *S. olseni* Zone, with its large *S. olseni*, and contains only small conchostracans such as *Anyuanestheria* ? n. sp. and related forms. Higher in this section, *Euestheria brodieana* becomes more and more abundant. This demonstrates that the Norian-Rhaetian boundary is a point of major faunal turnover for conchostracans, comparable with the faunal turnover at the base of the Olenekian (mid-Lower Triassic). Curiously, there is no significant faunal turnover among conchostracans either at the Permian-Triassic boundary or at the Triassic-Jurassic boundary. Conchostracans at these two global extinction boundaries show neither a drop in diversity nor any very distinct change in the faunal composition. In contrast, the Norian-Rhaetian boundary is readily recognizable through conchostracan studies, because this was a significant crisis in their history.

Also in this second category belongs the Liassic age assumed for the lowermost lava flow of the CAMP volcanic sequence and the strata immediately overlying it. This age assignment has been undisputed, despite the fact that radiometric data indicated a Rhaetian age (see above) and that there really were no paleontological data to support this. The sediments above the first lava flow do not contain any Liassic guide forms among the sporomorphs, and the same is true for vertebrates and tetrapod footprints. The sudden appearance of the large tetrapod track ichnogenus *Eubrontes* has been used as evidence for a Liassic age of the entire CAMP basalt sequence within the Newark Supergroup (e.g., Olsen et al. 2002a,b) but, as shown by Lucas (2003) and Tanner et al. (2004), *Eubrontes* first appears in the uppermost Triassic; this is to be expected considering the animals that have been suggested as the trackmaker for this ichnotaxon (Lucas, 2003; Weems, 2003, 2006; Tanner et al., 2004). Thus, assignment of the onset of CAMP volcanism to the Liassic has neither paleontologic, palynologic, nor radiometric support. Kozur and Weems (2005, 2006) found a very abundant upper Rhaetian conchostracan fauna above the first lava flow in the Midland Formation of the Culpeper Basin (VA), and from this they were able for the first time to provide positive paleontological evidence for the late Rhaetian age of the lowermost lava flow of the CAMP volcanic event in the upper Newark Supergroup. In this case, even though the correlation of this stratigraphic interval from the Newark Supergroup to the international geologic time scale was undisputed, the correlation still was incorrect.

In a third category are correlations of Newark Supergroup lithologic units or biozones with the international scale that have been disputed, and one of the proposed correlations has proven to be correct. The most significant example of this category is the age of the Adamanian (Conewagian) Land Vertebrate Fauna (LVF). For quite some time it was universally accepted that this LVF belonged in the late Carnian, but then palaeomagnetic correlations led to a quite different age assignment (Channell et al., 2003; Gallet et al., 2003; Muttoni et al., 2004). According to these palaeomagnetic correlations, the late Adamanian LVF (Channell et al., 2003; Muttoni et al., 2004) or even the late Sanfordian and entire Adamanian LVF (Gallet et al., 2003) were Norian. Our conchostracan studies clearly show that the palaeomagnetic correlations are incorrect (see below): the Adamanian (Conewagian) LVF is entirely late Carnian (Tuvalian) in age.

A fourth category consists of previous correlations that have been disputed, yet none of the disputants was entirely right. The best example involves the *Dictyopyge*-bearing beds of the Richmond and Taylorsville basins (Falling Creek Formation in the Taylorsville Basin, Tuckahoe Formation and Vinita Shale in the Richmond Basin). Cornet and Olsen (1990) assigned these beds to the lower and middle Carnian; Huber et al. (1993a) assigned them to the Middle Triassic because of the primitive character of *Dictyopyge* and the cynodont-dominated tetrapod fauna; Huber et al. (1993b) wrote that a "Ladinian-Carnian (undivided) age range [for these beds] is as precise as can be achieved at present;" Lucas and Huber (1993) assigned these beds tentatively to the upper Carnian. The true age of these beds is early Carnian (early to perhaps early late Cordevolian), and their age is important for establishing when sedimentation began in the Triassic rift basins of eastern North America.

Biostratigraphic Assignment of Lithostratigraphic Units

The age of the stratigraphic units in the major basins of the Newark Supergroup are shown in Figures 2-4, and their age is also mentioned under the conchostracan zones. In this section, three important correlations are discussed: 1) the age of the oldest beds of the Newark Supergroup in eastern North America, which establishes when sedimentation began in the Triassic rift basins of eastern North America, 2) the age of the Conewagian (Adamanian) LVF, which is strongly disputed between vertebrate specialists of the Lucas group and palaeomagnetic specialists who have made correlations between well dated Tethyan marine sections and the Newark Supergroup, and 3) the age of the Central Atlantic Magmatic Province (CAMP) volcanics.

Timing of the Onset of Sedimentation in the Rift Basins of Eastern North America

As mentioned above, the age of the oldest rocks in the Newark Supergroup has been strongly disputed, and none of the correlations attempted up until now has been both detailed and correct. We now can say that the oldest units in the Newark Supergroup include lacustrine deposits that contain a rich conchostracan fauna of early Cordevolian age (*Laxitextella multireticulata* Zone). In the Germanic Basin, the base of this zone also can be correlated by the FAD of *Patinasporites densus, Vallasporites ignacii*, and other sporomorphs to the base of the Carnian (see under *L. multireticulata* Zone and under remarks concerning the international marine scale). *L. multireticulata* also occurs in Cordevolian beds close to the Ladinian-Carnian boundary in the westernmost Southern Alps. Thus, sedimentation in the rift basins of the eastern United States began at or soon after the beginning of the Carnian. This lower Cordevolian conchostracan fauna has been found in an unnamed formation below the New Oxford Formation in the Gettysburg Basin (MD/PA), in the Falling Creek Formation in the Taylorsville Basin (VA), in the Tuckahoe Formation in the Richmond and Deep Run basins, and in a lacustrine unit below fluvial sandstones in the Farmville and Briery Creek basins. The lower part of the *L. multireticulata* Zone is represented, as well as the upper part that also contains advanced forms of *L. multireticulata*. Both parts of this zone belong to the lower Cordevolian. Except for the unnamed unit below the New Oxford Formation, all these lacustrine beds also are characterized by a fish fauna that includes *Dictyopyge* (see Fig. 2). All of these Cordevolian basal Newark Supergroup units are separated by a stratigraphic gap from overlying beds, which consist predominantly of thick sandstone sequences deposited by rivers. The oldest conchostracans associated with these fluvial beds are of late Julian age and correlate with the Schilfsandstein Formation of the Germanic Basin.

The age of the Adamanian (Conewagian) Land Vertebrate Faunal Zone - Biostratigraphy versus Palaeomagnetic Correlations

Although we are biostratigraphers, we did not enter this study with a bias in favor of biostratigraphic correlations over palaeomagnetic correlations. Kozur was a co-author of the Channell et al. (2003) palaeomagnetic paper and was content at the time with affirming a Norian age for the upper Stockton and entire Lockatong formations, which belong within the late Adamanian (Conewagian) Land Vertebrate Faunal Zone (LVF). Thus, we undertook our conchostracan studies around the Carnian - Norian boundary without any strong preconceptions about the question discussed here.

The Conewagian LVF was established in outcrops along the Little

Conewago Creek in the middle New Oxford Formation of the Gettysburg Basin (MD/PA) by Huber et al. (1993). In the same volume, the contemporaneous Adamanian LVF was established in the Chinle Group of Arizona by Lucas and Hunt (1993). Important guide forms and index fossils for the Adamanian (Conewagian) are: *Scaphonyx*, *Rutiodon*, *Stagonolepis*, *Leptosuchus*, and *Smilosuchus* (Lucas, 1998). In the early Adamanian, *Palaeorhinus* also is present. The latter genus also is known from marine Tuvalian strata in Austria (Hunt and Lucas, 1991 [referring to von Huene, 1939]; Lucas, 1998), so the early Adamanian is undoubtedly late Carnian in age. For the late Adamanian, however, direct correlation with marine strata by vertebrates so far is impossible.

Channell et al. (2003) published a palaeomagnetic correlation of the Newark Supergroup that relied upon the carefully dated section at Silická Brezová in Slovakia as a standard. Previously published data by Gallet et al. (2000, and earlier papers) and Muttoni et al. (2001) also were used for comparison. Some of the data from this study already had been published in abstracts (2001, 2002), and Channell presented all of the results in a congress held in Nice (Nizza) in April of 2002, when the paper by Channell et al. (2003) already was in press. The main conclusion was that the base of the Norian lies not in the lower Passaic, as previously thought, but rather much lower in the middle of the Stockton Formation. By this correlation, only the early Adamanian (= early Conewagian) remained Tuvalian, and the late Adamanian was assigned to the Lacian (early Norian).

Gallet et al. (2000) had stated earlier that "a convincing correlation [of the Tethyan palaeomagnetic data] with the polarity data from the Newark Basin is still lacking." The Newark palaeomagnetic data to which they referred were those published in several papers by Kent and Olsen (for references see Kent and Olsen, 2000). Probably this statement is correct. Yet, contrary to this claim, Gallet and most of his previous coauthors shortly thereafter published that the base of the Norian lay within the middle of the Stockton Formation (Krystyn et al., 2002). This was asserted in the complete absence of any new palaeomagnetic data that they presented in this paper from either the Tethys or the Newark Basin (beyond the data published in Gallet et al., 2000) and without any first hand knowledge of the biostratigraphy of the Newark Supergroup. Their conclusion was exactly the same as that which was published shortly thereafter by Channell et al. (2003) but presented orally earlier by Channell in Nice (April, 2002). Krystyn et al. (2002) did not cite the presentation by Channell, but it is noteworthy that the manuscript of their paper was not put into press until one month after the presentation of Channell. In retrospect, it seems obvious that the only thing that could have changed their minds as to the accuracy of palaeomagnetic correlations within the Newark Supergroup was Channell's presentation. Krystyn and Gallet (2002) even wrote: "Based on our data elsewhere, the magnetostratigraphy [of Sliciká Brezová] is predicted as follow: Reversed polarity between 1 m and 3 m, normal polarity from 3 m to approximately 6 m". Their "predictions" of the reversals falls within centimeters of the actual reversals, except that they had reversed and normal polarities exactly backward. Anyone who has done magnetostratigraphy knows that "predictions" that match reversals in perfect detail are impossible unless the data are known already. One reviewer held up publication of the paper by Channell et al. (2003) for a considerable length of time while the paper by Krystyn et al. (2002) was submitted to a journal that published rapidly. This resulted in the paper by Krystyn et al. (2002) being published near the end of 2002, while the paper by Channell et al. (actually submitted earlier) was not published until early 2003.

Gallet et al. (2003) subsequently published a distorted correlation within the Upper Triassic. They placed the base of the Norian in the middle of the Sanfordian LVF, which in reality is in the middle of the Carnian. Had they been correct, then even the Schilfsandstein of the Germanic Basin would have been Norian. Equally skewed were the numeric ages that they presented for the Upper Triassic. Their Norian ranged from 227-202 Ma, which meant that (with its 25 million year-long duration) their Norian comprised *almost half* of the entire Triassic System. This would constitute a subsystem rather than only a stage. Their placement of the base of the Rhaetian at 202 Ma left only 0.5 to 1 million years for the duration of the entire Rhaetian (applying the new numeric ages from the Upper Triassic, see discussion of numeric ages), and their Norian became 2.5 times longer than their Carnian, which was only 10 million years long. If, for example, one uses the thickness of the radiolarites from Panthalassa as a relative time scale, because they probably accumulated at a nearly constant rate, it is evident that the Norian is somewhat longer than the Carnian, but far less so than 2.5 times.

Muttoni et al. (2004), the third group to publish data comparing strata of the Newark Supergroup with the Tethyan palaeomagnetic scale, chose to correlate the Newark Supergroup with the palaeomagnetic scale at Pizzo Mondello, a well dated Tuvalian to lower Rhaetian section in western Sicily. This group of authors consisted of magnetostratigraphic experts in the Newark Basin and Tethys and also of experts in Tethyan and Newark Basin biostratigraphy, a seemingly ideal combination of scientists for such a study. Their results were very similar to those of Channell et al. (2003) in that their Norian was 17 million years long (compared to19 million years long in Channell et al., 2003) and their base of the Norian in the Newark Basin also lay below the middle of the Adamanian (Conewagian) LVF. This quite independent confirmation of the data in Channell et al. (2003), by outstanding experts in magnetostratigraphy and biostratigraphy both in the Tethys and in the Newark Basin (Muttoni, Kent, Olsen), seemed to firmly establish the location of the base of the Norian in the Newark Supergroup. Yet despite this, our investigation of conchostracan faunas, at localities in North America and in Europe that clearly fall within the Adamanian (Conewagian) LVF interval, leads us to a different conclusion.

Our results show that all early Adamanian LVF localities contain conchostracan faunas that are no younger than middle Tuvalian, and late Adamanian LVF localities contain only late Tuvalian conchostracan faunas. From a Dockum Group locality at Kalgary in West Texas, Kozur has observed well preserved conchostracans that belong to a *Laxitexella* fauna of the *L. laxitexta* group, which we will study further after this congress. Significantly, *Laxitextella* of the *L. laxitexta* group range in Europe no higher than middle Tuvalian (Lehrberg Beds of southwestern Germany; Krasiejów in southwestern Poland). The vertebrates at this Dockum site, which include *Rutiodon*, indicate an early Adamanian LVF age (Spencer Lucas, pers. comm.). Similarly, we have been able to investigate conchostracans from two localities within the type Conewagian within the New Oxford Formation in the Gettysburg Basin (MD/PA). One locality is the Fulton site from the middle New Oxford Formation. It contains a key conchostracan fauna for correlating with the Germanic Basin, consisting of *Eosolimnadiopsis gallegoi* Kozur n. sp. and *Laxitextella* sp. cf. *L. laxitexta* (Sandberger). The same two species occur in the Krasiejów locality in southwestern Poland, where they occur together with a rich vertebrate fauna (see under *Laxitextella seegisi* Zone) that contains both *Stagonolepis* and *Paleorhinus*, undoubtedly an early Adamanian fauna. The Krasiejów conchostracan fauna in turn can be correlated closely with the conchostracan fauna from the Lehrberg Beds, first described by Seegis (1997). New observations of this fauna, deposited in the Naturkundemuseum Stuttgart, have shown that it consists of *Laxitextella seegisi* and *L.* sp. cf. *L. laxitexta*, both of which occur at the Krasiejów locality. From the Lehrberg Beds, Seegis (1997) reported *Simeonella alpina* Bunza & Kozur, but his ostracod material on reexamination proves to represent a new species that also is present in the middle Tuvalian of Hungary. A middle Tuvalian age also is indicated by the position of the Lehrberg Beds within the middle of the Tuvalian interval of the Germanic Basin. Thus, the type Conewagian LVF in the New Oxford Formation ranges down at least to the middle of the Tuvalian.

Our second locality appears to be in the uppermost New Oxford Formation and therefore should be late or latest Adamanian (Conewagian). The conchostracan fauna from this locality consists mainly of *Euestheria hausmanni* (Schmidt) which is also common in the Coburg Sandstein (upper Hassberge Formation) of the Germanic Basin and which is upper, but not uppermost Tuvalian (see under *Laxitextella freybergi* Zone). The lower third of the Lockatong Formation, which belongs within the late Adamanian (late Conewagian) LVF, also contains abundant conchostracan faunas. The type material from museum collections consists mainly of *Euestheria ovata* (Lea) and *E. princetonensis* (Bock), as well as some indeterminable conchostracans ("*Estheriellites*") that are not Norian types. Our most abundant personal collections from within this interval are from the Black Rock railway tunnel at the northern edge of Phoenixville (PA), close to the type locality of *E. ovata*. There we found a very abundant fauna that mainly consists of *E. ovata*, but *E. hausmanni* is also present. This fauna also indicates a late, but not latest Tuvalian age (see above). The upper Tuvalian species *E. hausmanni* also is known from the Adamanian (Conewagian) Cumnock Formation.

Thus, all outcrops referable to the Adamanian (Conewagian) LVF, from which we also have been able to obtain conchostracan faunas, only can be assigned to the middle and late Tuvalian. Norian conchostracan faunas occur nowhere in this interval. The oldest known Norian conchostracan fauna from the Newark Supergroup is the one collected from the Triangle Brick Quarry, where the co-occurrence of *Aetosaurus arcuatus* (Marsh) (Lucas et al., 1998) and a dicynodont indicates that the strata represent the most basal part of the Norian (Sues et al., 2001). Even here, only conchostracans typical of the Lacian *Euestheria buravasi* - *Euestheria* n. sp. aff. *E. hausmanni* Zone are present and no forms from the Tuvalian have been found.

These conchostracan faunas show that all palaeomagnetic correlations so far made between the Newark Supergroup and the Tethys region are wrong. This certainly is the case for the Sevatian beds of the upper Passaic Formation (previously assumed to be Rhaetian) that lie below the formerly assumed Triassic-Jurassic boundary. Part of the problem may be that, until very recently, only a very bad and incomplete palaeomagnetic record had been obtained from biostratigraphically well dated marine Rhaetian sections. Fortunately, a complete marine Rhaetian magnetostratigraphy now is available in Gallet et al. (2007). Around the Carnian-Norian boundary, however, many sections have been investigated in the Tethys by different groups (e.g. Gallet et al., 2000, 2003; Muttoni et al., 2001, 2004; Channell et al., 2003). Obviously, when very distinct palaeomagnetic markers like the Illawarra reversal are missing or remain undetected, accurate palaeomagnetic correlations can be made only in the context of robust biostratigraphic and other correlations. Only then can palaeomagnetic studies yield important detailed data to fine-tune correlations in intervals where fossils are rare or biostratigraphic dating is in dispute. A good example of this is the uppermost, very short reversed interval in the Permian (of about 110,000 years duration according to Milankovich cyclicity) that lies below a longer normal interval that straddles the Permian-Triassic boundary (Fig. 7). Where the biostratigraphic Permian-Triassic boundary is known, this short interval becomes extremely helpful for making correlations that are more detailed than any biostratigraphic correlation alone can achieve, either in marine or continental sequences (Kozur, 2007). This very detailed correlation showed that there was a single, brief interval of time, slightly below the PTB, during which there was an influx of cold water faunas into the Tethyan sequence of Iran. This influx of cold water was precisely at the time that an exceptionally strong eruption of the Siberian Trap occurred. That eruption produced distinctive tuffs, found in strata as far west as the vicinity of Moscow, and the same level in the Germanic Basin contains numerous microsphaerules of volcanic origin. Caution is warranted when palaeomagnetic correlations contradict previous biostratigraphic correlations on a major scale, such as when palaeomagnetic studies end up reassigning the entire late Adamanian LVF (Channell et al., 2003, Muttoni et al., 2004), or even the late Sanfordian LVF and the entire Adamanian LVF, to the Norian (Gallet et al., 2003).

A degree of compromise between the currently assumed biostratigraphic base of the Norian and the palaeomagnetic base of the Norian, based on correlations, may come from the fact that the biostratigraphically lowest confirmed Norian in the Newark Basin is near the base of the Warford Member of the lower Passaic Formation where the oldest known *Aetosaurus* has been found. The youngest known late Tuvalian Adamanian faunas, however, are known from considerably farther down section at the top of the lower third of the Lockatong Formation. The interval in between, where we have not yet sampled for conchostracans, could be either upper Tuvalian or lower Lacian. As discussed above in the section on Upper Triassic numeric ages, if the base of the Norian is placed immediately below the base of the first Norian vertebrate fauna in the Warford Member of the lower Passaic Formation, then the basal age of the Norian would be 223 Ma. If, instead, the base of the Norian is placed immediately above the youngest known late Tuvalian Adamanian vertebrates around the top of the lower third of the Lockatong Formation, then the basal age of the Norian would be 226 My. This latter value effectively agrees with the 226 Ma age for the base of the Norian given in Channell et al. (2003) and Bachmann and Kozur (2004).

AGE OF THE CENTRAL ATLANTIC MAGMATIC PROVINCE (CAMP) BASALTS IN THE NEWARK SUPERGROUP

A very surprising result of the conchostracan studies by Kozur and Weems (2005, 2006) was the discovery that the lower lava flow of the CAMP volcanics in the Newark Supergroup is late Rhaetian in age, because the Liassic age of all lava flows was never previously questioned (even though not supported by radiometric or biostratigraphic data). The upper Rhaetian conchostracan fauna of the Midland Formation, between the first and second lava flows in the Culpeper Basin (VA), demonstrated the late Rhaetian age of the first lava flow. Similarly, the occurrence of lower Hettangian conchostracans in the basal Waterfall Formation above the third lava flow demonstrated that the strata above the third lava flow are Jurassic. Left open, however, is the age of the second and third lava flow and the age of the strata between them. Recently, we have been able to establish that the lower Hettangian *Bulbilimnadia sheni* Zone also is found in the middle of the East Berlin Formation of the Hartford Basin (CT/MA). This formation lies between the second and the third lava flow in that basin. Assuming that the basal three lava flows in the two basins are correlative, which now seems likely, the lower Hettangian age of the third lava flow would seem to be established. The second lava flow, however, lies between underlying sediments with an upper Rhaetian conchostracan fauna and overlying sediments with a lowermost Hettangian conchostracan fauna. Thus, the Rhaetian-Hettangian boundary probably lies in or near the second lava flow (i.e., the Hickory Grove Basalt in the Culpeper basin, the Preakness Basalt in the Newark Basin, and the Holyoke Basalt in the Hartford Basin).

The evidence for a late Rhaetian age of the lower lava flow of the CAMP volcanics within the Newark Supergroup, as well as the position of the Triassic/Jurassic boundary around the second lava flow, are of great importance for explaining the biotic crisis around the Triassic/Jurassic boundary. In Morocco, the CAMP volcanism also began in the late Rhaetian (Marzoli et al., 2004) and continued past the Triassic-Jurassic boundary, which therefore also lies within the effusion interval of the huge CAMP plateau basalts. This precise correlation implies that these eruptions were the direct cause of the biotic crisis around the Triassic-Jurassic boundary. A nearly identical pattern occurred during the Permian-Triassic biotic crisis, when there was a precise coincidence between the time of maximum extinction and the strongest eruptions of the Siberian Trap plateau basalts, which also co-occurred with strong explosive volcanic activity in South China (Kozur, 1998a,b, 2007).

Correlation of the Newark Supergroup with the Germanic Basin

The correlation of the Newark Supergroup with the Germanic Basin by conchostracans is relatively simple, because the same species and the same conchostracan succession are present in both areas. The correlation of conchostracan zones between these areas is shown in Fig.

Stage	Substage	Germanic Basin	Units of Germanic Basin	Newark Supergroup	Units of Newark Supergroup	Other occurrences
Hettang.	Lower	No conchostracans, marine		*Bulbilimnadia froelichi*	Upper Waterfall Fm.	
				Bulbilimnadia sheni	Lower Waterfall Fm., East Berlin Fm.	
Rhaetian	Upper	*Euestheria brodieana*	Upper Exter Fm.	*Euestheria brodieana*	Midland Fm.	England
	Lower	*Anyuanestheria* ? n. sp.	Postera Sandstein	gap		
Norian	Sevatian	*Shipingia olseni*	Stubensandstein 3	*Shipingia olseni*	Upper Blomidon Fm., upper Passaic Fm., Catharpin Creek Fm., upper Groveton Mbr.	
				Redondestheria grovetonensis		
	Alaunian	*Shipingia hebaozhaensis*	Stubensandstein 2, middle Steinmergelkeuper	*Shipingia hebaozhaensis*	Heidlersburg Mbr., Middle Groveton Mbr.	China
		small *Shipingia* and large *Euestheria*	lower middle and upper lower Steinmergelkeuper	small *Shipingia* and large *Euestheria*	Lower Passaic Fm., lower Groveton Mbr.	
	Lacian	*Euestheria* n. sp.	Stubensandstein 1, lower Steinmergelkeuper	*Euestheria buravasi*-*Euestheria* n. sp.	Lower Sanford Fm.	Thailand
Carnian	Tuvalian	*Laxitextella freybergi* n. sp.	Coburg Sandstein	*Euestheria ovata*–*E. princetonensis*	Lower Lockatong Fm., upper Cow Branch Fm., Cumnock Fm.	
		Laxitextella seegisi n. sp.	Lehrberg Beds	*Eosolimnadiopsis* ? n. sp.-*Laxitextella* cf. *laxitexta*	Fulton site, middle New Oxford Fm.	Krasiejów, Poland
		Eosolimnadiopsis gallegoi n. sp.	basal Rote Wand, Dolomie de Beaumont horizon			
	Julian	*Anyuanestheria* n. sp. A-*Laxitextella* cf. *laxitexta*	middle Schilfsandstein Fm.	*Anyuanestheria* n. sp. A	lower Cow Branch	
		gap	gap	gap	gap	
	Cordevolian	*Anyuanestheria fimbriata*- *Laxitextella laxitexta*	middle Estherienschichten of upper Grabfeld Fm.			England
		Laxitextella multireticulata	lower Estherienschichten of upper Grabfeld Fm.	*Laxitextella multireticulata*	pre-New Oxford Fm. unit, Falling Creek Fm, Vinita Sh., Tuckahoe Fm., lacustrine unit of Farmville and Briery Creek basins	England, Southern Alps, Italy

FIGURE 10. Upper Triassic to lower Hettangian conchostracan zonation of the Germanic Basin and the Newark Supergroup, and its correlation with the marine scale. Except for the gap below the Middle Carnian Pluvial event, the numerous gaps in the Keuper of the in Germanic Basin are not shown. For their position and estimated duration, see Bachmann and Kozur (2004); the very long gap shown between the Carnian and Norian, encompassing the entire lower Norian, is probably much shorter and includes only the latest Tuvalian or/and earliest Norian interval in the basin center.

10 and discussed in the section on conchostracan zones. Only a few additional remarks are necessary.

The *Laxitextella multireticulata* Zone is present in both areas and includes the same species. Only the lower *L. multireticulata* Zone is present in Germany, but in the Newark Basin both the lower and upper *L. multireticulata* Zone are present. However, this difference is because the interval of the upper *L. multireticulata* Zone, characterized by advanced *L. multireticulata* that sometimes are transitional to *L. laxitexta* (Sandberger), is occupied in the Germanic Basin by the upper part of the lower *Estheria* Beds of the upper Grabfeld Formation, where layers with soil horizons occur and conchostracans have not yet been found.

The subsequent *Anyuanestheria fimbriata-Laxitextella laxitexta* Zone has not been found so far in the Newark Supergroup, though it possibly may be represented by the beds that include large *Euestheria winterpockensis* but so far no *Laxitextella* (e.g. upper Falling Creek Formation and contemporaneous levels). Additional sampling within this general interval obviously is needed. It also remains possible that the *A. fimbriata-L. laxitexta* Zone is missing everywhere in the Newark Supergroup within the stratigraphic gap between the Cordevolian and the upper Julian.

Above the Cordevolian beds there is a stratigraphic gap in the Newark Supergroup, because the next younger sediments in the Newark Supergroup can be assigned to the upper Julian. It is very interesting that, in the Newark Supergroup, the strata above this gap are fluvial sediments that were deposited by rivers running, at least in the Taylorsville Basin, from northeast to southwest. All of these features are identical to the depositional setting at that time in the Germanic Basin. Above the Cordevolian, there is a distinct intra-Carnian gap followed by the fluvial Schilfsandstein (upper Julian), which was deposited by rivers running from northeast to southwest. The Schilfsandstein of the Germanic Basin represents a humid climatic phase between earlier arid climates (represented by the Lower Gypsum Keuper, Grabfeld Formation) and later ones (represented by the Upper Gypsum Keuper, Weser Formation).

This climatic event, first recognized by Kozur (1972), later was named the Middle Carnian Pluvial Event (Simms and Ruffell, 1989). This event also is recognizable in the Tethys, where it is characterized by a carbonate productivity crisis that included the demise of carbonate platforms and an enhanced siliciclastic input (the Reingraben Event of Schlager and Schöllnberger, 1974, or the Raibl Event). In the Tethys, this event coincides with the closure of the Palaeotethys (Stampfli and Kozur, 2006), and this tectonic event may have been what triggered such profound climatic changes. In the Tethys, where both a tectonic and climatic event occurred, it is more appropriate to use the term Reingraben Event. Possible causes are summarized in Hornung et al. (2007) and in Rigo et al. (2007). In continental basins, like the Germanic Basin and the rift basins of eastern North America, the event is mainly characterized by a humid climatic phase. There the term Middle Carnian Pluvial Event is more suitable.

Probably these events are directly related to each other. Strong

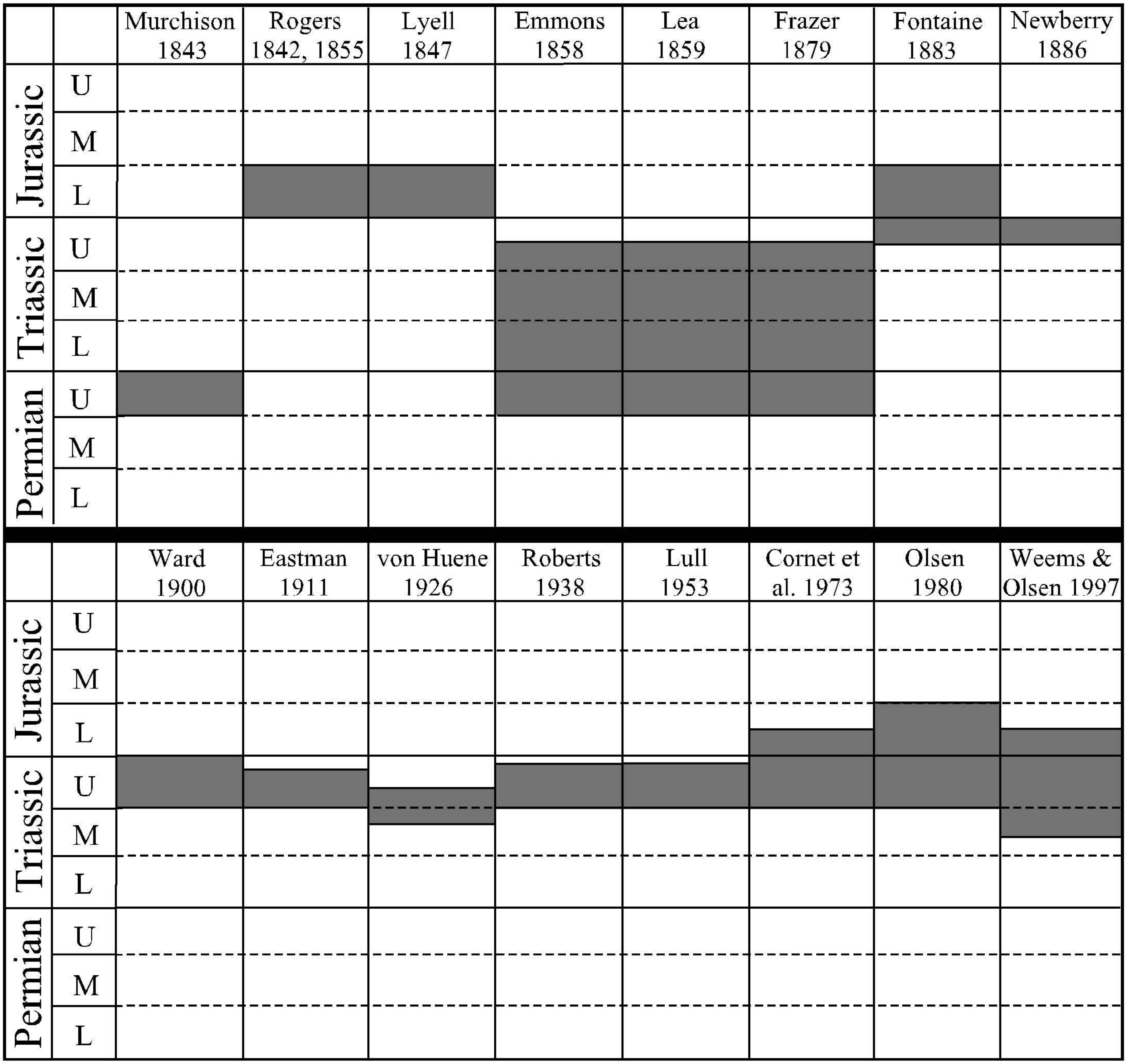

FIGURE 11. Different age assignments given to the Newark Supergroup over the past 164 years. Publications listed in Kozur and Weems (2005)

palaeogeographic changes in the Tethys, related to the closure of the Palaeotethys and the opening of the Pindos-Huðlu Ocean, in the western Tethys breached a feature called the Apulian-Tauride High that, during Ladinian and early Carnian time, had separated the equatorial Neotethys from the vast oceanic and shelf areas north of the High. When the Apulian-Tauride High was breached at the beginning of the Reingraben Event (Kozur, 2000, Kozur & Stampfli, 2006), this allowed warm oceanic currents from the equatorial western Neotethys to penetrate the vast western Tethyan areas north of the High. This may have caused a drastic temperature rise, resulting in a megamonsoonal regime in the surrounding western Tethys, especially to its north and northwest. The megamonsoonal regime in these areas greatly increased precipitation, which led to a huge influx of fresh water and siliciclastic sediments into the western Tethys, resulted in clastic sedimentation across the former carbonate platform, and produced a carbonate productivity crisis. Well preserved land plant remains are common in parts of these clastic beds, e.g. the famous floras from the Lunz Beds. Brackish water ostracods, among them the upper Julian guide form *Simeonella alpina* Bunza & Kozur, also are common in the Lunz and Raible beds (Bunza & Kozur, 1971), in the clastic upper Julian intra-Tethyan beds of Hungary, and in the basal Schilfsandstein of the northern Germanic Basin (Wienholz & Kozur, 1970; Kozur, 1975). Conchostracans also occur in these beds in the Western Carpathians and the Alps.

Within the Newark Supergroup, the climate was never really dry during this time interval because this region lay within the Triassic wet equatorial belt. Even so, the fluvial input within this interval is quite exceptional. It is possible that many of the big rivers that brought the sediments of the Schilfsandstein into the Germanic Basin, as well as many of the rivers feeding into the Newark Supergroup basins, had a common origin in western Scandinavia and Laurentia-Greenland along the rift shoulders of the major rift system that lay between Fennosarmatia and Laurentia-Greenland. Alternatively, it is also possible that these large rivers originated in the northern Urals. As pointed out by Otto and Bailey (1995) and Torsvik and Andersen (2002), compressional tectonics occurred during the Late Triassic between the Kara Block and Baltica. This compression probably raised the northernmost Ural Mountains and Novaya Zemlya into a major barrier to mega-monsoonal winds blowing from the Tethys during the Middle Carnian Pluvial Event (much like the present-day Himalayas), which would have induced heavy seasonal rainfall. In this model, rivers from the northern Urals would have crossed the lowland of Fennosarmatia and then linked to the Schilfsandstein rivers in the Germanic Basin. In the case of the Newark Supergroup, the rivers would have passed through the Faeroe and Rockall Trough rift grabens, the Fundy Graben, and other rift basins in eastern North America along what is now a NE-SW direction of flow but in the Late Triassic was an E-W direction of flow (Ziegler, 1988). Either model (river origin from the western Scandinavian rift shoulders or river origin from a strongly elevated area in the northern Ural Mountains) would explain the presence of mica flakes in the Schilfsandstein sediments that yield Early Devonian and Carnian ages.

Within the Tethys, the beginning and duration of the Reingraben Event has been tightly constrained by Horning et al. (2007). It started in the uppermost *Trachyceras aonoides* Zone and lasted throughout the *Austrotrachyceras austriacum* Zone into the lowermost Tuvalian. The age of the Middle Carnian Pluvial Event in the Germanic Basin Schilfsandstein has the same duration, beginning in the late Julian and ending in the earliest Tuvalian close to the Julian-Tuvalian boundary (Bachmann and Kozur, 2004). Conchostracan faunas now show that, within the Newark Supergroup basins, this event had the same duration.

The *Eosolimnadiopsis gallegoi* Zone of the lower Tuvalian has not been found so far within the Newark Supergroup, but this seems to be a sampling effect. A very important correlation level is the *Eosolimnadiopsis* ? n. sp. – *Laxitextella* sp. cf. *L. laxitexta* Zone, found at the middle Tuvalian Fulton site, which can be closely correlated by conchostracans with the *Laxitextella seegisi* Zone of the Lehrberg Beds in southwestern Germany and the Krasiejów locality in southwestern Poland. Early Adamanian LVF vertebrates at the latter locality confirm this correlation. In the upper Tuvalian, correlation is possible but it is not so tightly constrained as in the middle Tuvalian. The *Euestheria ovata* - E. *princetonensis* Zone of the Newark Supergroup and the *Laxitextella freybergi* Zone of the Coburg Sandstein in the Germanic Basin both have *Euestheria hausmanni*, which indicates a late Tuvalian age for both zones. Most probably these zones represent slightly different levels within the upper Tuvalian.

Very important for the Germanic Basin would be a definitive correlation of the *Euestheria buravasi-Euestheria* n. sp. Zone of the Newark Supergroup with the *Euestheria* n. sp. fauna of the lower Steinmergelkeuper in the Germanic Basin, but this interval still needs much more study in the Germanic Basin. A collection of several hundred well preserved conchostracans from this interval was made by Kozur from borehole cores from northern Germany. Unfortunately, these cores, stored at the Freiberg Mining University, later were destroyed by water penetrating into the storage room, and no equally abundant and well preserved faunas have been found since. Even so, a similar though less well preserved fauna may be present within the lower Steinmergelkeuper in western Thuringia. The lower Steinmergelkeuper was assigned to the lower Norian by Kozur (1972, 1975, 1993a), but since then it has been assumed that a large stratigraphic gap exists that encompasses the entire lower Norian. This view later was accepted by Bachmann and Kozur (2004), even though the lowermost Steinmergelkeuper belongs neither to the middle Norian *Shipingia hebaozhaiensis* Zone nor to the underlying upper Lacian – early Alaunian faunas with small *Shipingia* and large *Euestheria*. The amount of time possibly missing between the early Norian (Lacian) *Euestheria* n. sp. Zone and the horizon with small *Shipingia* and large *Euestheria* of late Lacian to early Alaunian age is not yet adequately documented within the Germanic Basin. Therefore, it is not clear yet whether the lowermost Steinmergelkeuper is lower Lacian or instead belongs to the upper Lacian-early Alaunian interval. It is probable, however, that the lower Lacian is present in the lower Steinmergelkeuper because *Euestheria* n. sp. aff. *E. hausmanni* occurs both in the clearly lowermost Lacian *Euestheria buravasi- Euestheria* n. sp. Zone at the Triangle Brick quarry in the Durham Subbasin of North Carolina and in the lowermost Steinmergelkeuper of the Germanic Basin. The upper range of *Euestheria* n. sp. is not yet known, but certainly it is not as high as the Alaunian (middle Norian). An early Norian age for the lower Steinmergelkeuper would mean that the duration of the Early Cimmerian unconformity in the Germanic Basin has been greatly overestimated, and that a much shorter stratigraphic interval is missing that includes only the uppermost Tuvalian and/or lower Lacian. This problem will be solved only by more collecting in the lower Steinmergelkeuper and in the lower Stubensandstein.

The interval with small *Shipingia* and large *Euestheria* is present both in the Germanic Basin and in the Newark Supergroup, but it has not yet been adequately investigated. Its age (late Lacian to early Alaunian) is known only from the age of the underlying and overlying conchostracan zones in the Newark Supergroup, which are well dated.

The subsequent *Shipingia hebaozhaiensis* Zone is a key interval for international correlation, because it is recognizable all the way from China, through the Germanic Basin, to Morocco and eastern North America. In contrast, the overlying *Redondestheria grovetonensis* Zone is known so far only from the lower Sevatian of North America (Newark Supergroup and New Mexico). The lower Sevatian part of the Germanic Triassic remains poorly studied, however, so this zone may yet be found there.

The overlying *Shipingia olseni* Zone is widespread in the Sevatian of the Newark Supergroup, where it occurs up to the formerly assumed Rhaetian/Hettangian boundary (in reality the Sevatian/upper Rhaetian boundary encompassing a significant stratigraphic gap). In the Germanic Basin, the upper part of this zone has been identified in the Stubensandstein 3, but the lowermost part of this zone so far has not been found.

The lower Rhaetian *Anyuanestheria* ? n. sp. Zone of the Germanic Basin is not present in the Newark Supergroup, but this is because this interval lies within the significant unconformity that separates the upper Sevatian from the upper Rhaetian. In contrast, the *Euestheria brodieana* Zone is present in the Newark Supergroup, and it defines the upper Rhaetian both there and in the Germanic Basin. Its age is well known because it can be correlated directly with marine, partly conodont-bearing beds in England that contain *Misikella posthernsteini* Kozur & Mock and *Zieglericonus rhaeticus* Kozur & Mock. In Germany, this zone lies above the marine middle Rhaetian. *Euestheria brodieana* first appears in the Germanic Basin in the uppermost part of the lower Rhaetian, but in the lower Rhaetian it is not found as monospecific faunas of *E. brodieana* such as are characteristic of the upper Rhaetian.

The two lower Hettangian conchostracan zones of the Newark Basin have not been identified in the Germanic Basin, because large parts of the Germanic Basin were marine at that time and the continental lower Liassic of the eastern Germanic Basin has not been investigated yet for conchostracans.

DISCUSSION AND CONCLUSIONS

A preliminary conchostracan zonation for the Upper Triassic and lowermost Jurassic strata of the Newark Supergroup is established here, which will become the basis for an Upper Triassic and lowermost Jurassic conchostracan standard zonation for the Northern Hemisphere during this stratigraphic interval. The number of zones will not increase much with future investigations (we anticipate a total of 14-15 zones within this interval), but several key index species still need to be described or revised, and our understanding of the precise stratigraphic range of several species needs to be improved. Most of the zones can be readily correlated with conchostracan zones of the Germanic Basin, which in turn generally are correlated firmly with the international marine geologic time scale. This will produce a greatly improved correlation of the Newark Supergroup both with the Germanic Triassic and with the international geologic time scale. Our most important stratigraphic results to date are:

(1) Sedimentation in the Newark Supergroup began in the early Cordevolian, at or very close to the beginning of the Carnian (= beginning of the Late Triassic).

(2) As in the Germanic Basin, the lacustrine Cordevolian strata of the Newark Supergroup are followed by a stratigraphic gap, above which the strata represent fluvial beds (mostly sandstones) that were deposited in rivers that generally ran from northeast to southwest. The same can be observed in the contemporaneous Schilfsandstein of the Germanic Basin, which also formed above an unconformity that separates it from Cordevolian strata, and in northern Germany and adjacent Poland where fluvial strata formed above a thin interval of brackish sediments that were deposited during a marine ingression into the Germanic Basin above the gap. The Schilfsandstein also was deposited by large rivers that flowed from northeast to southwest. The largely fluvial Schilfsandstein, and contemporaneous fluvial sediments above the stratigraphic gap in the Newark Supergroup, formed during the Middle Carnian Pluvial Event. Most of the source-rivers in both areas may have headed along the uplifted shoulders of the major Faroe rift zone, at the western margin of Scandinavia and the eastern margin of Laurentia-Greenland. Alternatively, at least for the rivers flowing into the Germanic Basin, a source area in the uplifted northern Ural Mountains, by way of the Fennosarmatia (Baltica) lowlands, also is possible. A strong uplift of the northernmost Ural Mountains and Novya Zemlya in the Late Triassic, caused by compressional tectonics due to collision of the Kara Block with Baltica, would have blocked mega-monsoonal winds from the Tethys and induced very large amounts of rainfall during the monsoon season.

(3) The Adamanian (Conewagian) LVF is everywhere Tuvalian. In the early Adamanian LVF of the Conewagian type area, middle Tuvalian conchostracans have been found that can be correlated closely with the *Laxitextella* n. sp. A Zone of the Lehrberg Beds of southwestern Germany and the Krasiejów locality in southwestern Poland. The late Adamanian interval has yielded conchostracans of the *Euestheria ovata – Euestheria princetonensis* Zone, which includes *Euestheria hausmanni* (Schmidt) that occurs in the upper Tuvalian interval of the Germanic Basin. Confirmation of the Tuvalian age of the Adamanian LVF shows that the magnetostratigraphic correlations of the Newark Supergroup proposed by Krystyn et al. (2002), Channell et al. (2003), Gallet et al. (2003), and Muttoni et al. (2004) are wrong. Channell et al. (2003) and Muttoni et al. (2004) placed the Norian boundary within the early Adamanian LVF, and Gallet et al. (2003) assigned the entire Adamanian LVF and even the late Sanfordian LVF to the Norian. The correlation of the Rhaetian with the Sevatian part of the upper Passaic Formation also was wrong in all magnetostratigraphic correlations.

(4) In the Newark Supergroup, the base of the Hettangian does not lie slightly below the oldest of the CAMP volcanic flows as generally has been assumed, but rather within or near the second lava flow of the CAMP sequence. The first lava flow of the Culpeper Basin lies below beds (Midland Formation) that contain the fauna of the upper Rhaetian *Euestheria brodieana* Zone (Kozur and Weems, 2005, 2006). The middle part of the East Berlin Formation in the Hartford Basin, which lies between the second and third lava flow, contains lowermost Hettangian conchostracans of the *Bulbilimnadia sheni* Zone. Therefore, the Triassic –Jurassic boundary lies near the middle of the huge plateau basalts of the CAMP volcanic event. This indicates that the biotic crisis around the Triassic-Jurassic boundary was triggered directly by the massive CAMP volcanic eruptions, and also probably indirectly by the eruptions triggering strong climatic changes which in turn strongly and adversely influenced the biota.

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SUPPLEMENTARY DATA FOR TABLE 1

In most cases, specimens are ones collected by the authors. Where material was borrowed from museum collections, the museum numbers or names are included in the table and/or mentioned here. ANSP 31194: type material of *Howellites berryi* Bock, 1953, synonym of *Euestheria princetonensis* (Bock, 1953). ANSP 31497: type material of *Isaura midlothianensis* Bock, 1953 = *Euestheria* sp. indet. ANSP 31197: type material of *Howellites winterpockensis* Bock, 1953 = *Euestheria winterpockensis* (Bock, 1953). ANSP 16849: type material of *Posidonia ovata* Lea, 1856 = *Euestheria ovata* (Lea, 1856). ANSP 16847, 65530: type material of "*Estheriella circularis*" Bock, 1946. ANSP 16848, 65528: type material of "*Estheriellites elliptoideus*" (Bock, 1953). ANSP 31192: Type material of *Howellites princetonensis* Bock, 1953a emended into *Howellisaura princetonensis* (Bock, 1953 b) = *Euestheria princetonensis* (Bock, 1953). YPM 34619: specimen from the Pomona Pipe Company Pit.

APPENDIX 1 – DESCRIPTION OF THE INDEX SPECIES FOR THE TUVALIAN CONCHOSTRACAN ZONATION OF THE GERMANIC BASIN

As requested by two reviewers of our paper, we describe here the index species of the three Tuvalian conchostracan zones of the Germanic Basin. This is to prevent creation of *nomina nuda* in the text and in Figure 10 of our paper. A more extended and thorough description of these new species will come in two future papers (one submitted and one in preparation). The appropriate author names for these species are given in the description here.

Genus *Eosolimnadiopsis* Chen, 1976

Type species: *Eosolimnadiopsis shambeienis* Chen, 1976

Eosolimnadiopsis gallegoi Kozur n. sp.
(Pl. 10, figs. 2-4)

Derivation of name: In honor of Dr. Oscar Gallego, Corrientes, Argentina for his very important contributions to our knowledge of the Paleozoic and Mesozoic Conchostraca of Argentina, South America.

Holotype: the specimen illustrated on Pl. 10, Figs. 2a-c

Type locality: Temporary outcrop at the new building of the Waldorf school, Stuttgart, Haussmannstrasse 44, Germany.

Horizon: 2-3 m above the base of the Rote Wand (lowermost Weser Formation), *Eosolimnadiopsis gallegoi* Zone, lower Tuvalian.

Material: More than 30 specimens from the type locality and from laterally equivalent beds of the Dolomie de Beaumont, eastern France. Holotype and majority of the material deposited in the Naturkundemuseum Stuttgart, Germany.

Diagnosis: Small conchostracans with straight dorsal margin and a very pronounced posterodorsal corner. The 23-30 growth bands are narrow and close to the posterior half of the recurved dorsal margin (Pl. 10, Fig. 2c). Particularly in elongated specimens, the dorsal recurvature of the growth lines cannot be recognized (not present?). The anterodorsal umbo is distinctly convex in undeformed specimens and slightly overreaches the dorsal margin. the free umbonal area is very small. In the marginal growth bands distinct radial lirae are present. In well preserved specimens, it can be seen that they consist of narrow lines of very closely spaced, tiny pustules. Toward the inner growth bands, the microsculpture becomes indistinct and the radial lirae change into an indistinct fine reticulation.

Measurements: length = 3.3 - 4.5 mm; height = 2.5 – 3 mm

Occurrence: Lowermost Rote Wand (lowermost Upper Gypsum Keuper, lowermost Weser Formation) of early Tuvalian age in southern Germany and contemporaneous lateral equivalents of the Dolomie de Beaumont in eastern France.

Remarks: *Eosolimnadiopsis* ? n. sp. (Pl. 11, Fig. 3), from the middle Tuvalian *Laxitextella seegisi* Zone of the Krasiejów locality in southwestern Poland and the Fulton site of the middle New Oxford Formation in the Gettysburg Basin, has the same outline and size, but so far the posterodorsal recurvature of the growth lines has not been observed (however, this is also sometimes not seen in *E. gallegoi*). In the Krasiejów material, the microsculpture is very indistinct. In the Fulton site material, so far only the reticulation on the inner growth bands has been observed because no well preserved specimens with preserved outer growth bands have been found yet. Therefore the assignment of *Eosolimnadioposis* ? n. sp. to this genus is not yet fully confirmed.

Genus *Laxitextella* Kozur, 1982

Type species: *Estheria laxitexta* Sandberger, 1871

Laxitextella freybergi Kelber & Kozur n. sp.
(Pl. 10, Figure 1)

Derivation of name: In honor of Prof. Bruno von Freyberg, for his outstanding contributions to the knowledge of the Keuper in southern Germany.

Holotype: The specimen on Pl. 10. Figs. 1a,b.

Type locality: Former Hahn quarry, SE of Eltmann, Franconia (Bavaria), southern Germany.

Horizon: Coburg Sandstein, upper Hassberge Formation, 0.15-0.30 cm above the basal sandstone (basal "Werkstein"), *Laxitextella freybergi* zone, upper Tuvalian.

Material: More then 50 specimens, collection Kelber, Geological Institute Würzburg.

Diagnosis: Large conchostracans with straight dorsal margin but without dorsal corners. Anterior margin only slightly rounded. Anteroventral margin somewhat oblique, ventral margin strongly rounded, posterior margin broadly rounded. The umbo is located anteroventrally and only slightly overreaches the dorsal margin. the free umbonal area is small. the sparse 10-13 growth bands are very broad and have a coarse reticulation with 6-10 polygons across one growth band. The polygons have an irregular outline (pentagonal, hexagonal, polygonal, roundish, or elongated and irregularly oval).

Measurements: length = 6.7–8 mm; height = 4.7 – 5.8, rarely to 7.2 mm (may be enlarged due to deformation).

Occurrence: Coburg Sandstein (upper Hassberge Formation), southern Germany.

Remarks: *Laxitextella freybergi* Kelber & Kozur n. sp. is the youngest representative of the *Laxitexella laxitexta* group and a perfect transitional form between *Laxitextella* and *Shipingia*, being almost perfectly intermediate in its morphology between these two genera. As early *Shipingia* evolved from *Laxitextella* that possessed a rather indistinct reticulation with small polygons (*Laxitextella dorsorecta* group), it is preferrable to assign *L. freybergi* to *Laxitextella* rather than to *Shipingia*. The earlier *Laxitextella* of the *L. laxitexta* group, such as *L. laxitexta* (Sandberger) and *L. seegisi* Kozur n. sp., have much more numerous and narrower growth bands. Especially in *L. laxitexta*, the strongly convex umbo greatly overreaches the dorsal margin.

Laxitexella seegisi Kozur n. sp.
(Pl. 11, Figs. 1, 2, 4)

Derivation of name: In honor of Dr. Dieter Seegis, Schorndorf, Germany, for his outstanding work on the fauna of the Lehrberg Beds in southern Germany.

Holotype: the specimen on Pl. 11, Figs. 1a, b.

Type locality: Creek W Ramshalden-Buoch/Württemberg, S "Salzbuckel," southern Germany (see Seegis, 1997, locality 329).

Horizon: Lehrberg Beds (upper Lehrberg Bank), middle Tuvalian *L. seegisi* Zone.

Material: More than 100 specimens from the Lehrberg Beds (southern Germany) and the Krasiejów locality (southwestern Poland). Holotype and illustrated specimens deposited in the Naturkundemuseum Stuttgart, Germany.

Diagnosis: The large carapace, in undeformed and three-dimensionally preserved specimens, is strongly convex, especially in the umbonal area where it overreaches the dorsal margin along the anterior third of the carapace. The straight to slightly convex part of the dorsal margin is short. the anterodorsal part is relatively short and somewhat oblique; the posterodorsal part is long and oblique. the anterior margin is most strongly rounded considerably above its mid-height, and the long anteroventral part is distinctly oblique. The ventral margin is convex with the strongest convexity about in its mid-length. The posterior margin is broadly rounded with the strongest convexity about in the mid-height. The numerous (18-24) growth bands are narrow, but widest in the middle part of the carapace. The free umbonal area is very small. The reticulation is moderately coarse, with 6-10 polygons present across the broadest growth lines. The polygons are of different shapes and sizes, but mostly roundish or oval.

Measurements: length = 7.0 - 8.6 mm; height = 4.9 - 5.4 mm

Occurrence: Lehrberg Beds of southern Germany and Krasiejów locality in southwestern Poland, both middle Tuvalian.

Remarks: *Laxitextella seegisi* Kozur n. sp. belongs to the *Laxitextella laxitexta* group. *L. laxitexta* (Sandberger) has larger polygons, however, with 2-5 polygons across one growth band. the umbonal area in *Laxitextella seegisi* Kozur n. sp. strongly overreaches the dorsal margin. *Laxitextella seegisi* Kozur n. sp. differs from *Laxitextella freybergi* Kozur n. sp. in that the latter species has much broader and fewer growth bands and a coarser reticulation.

EXPLANATION OF PLATES

Abbreviations used:
ANSP = Collection of Academy of Natural Sciences, Philadelphia
YPM = Collection of the Yale Peabody Museum, New Haven
NMMNH = Collection of New Mexico Museum of Natural History, Albuquerque

PLATE 1

Scale = 1mm

Figure 1: *Euestheria winterpockensis* (Bock, 1953), male, upper Tuckahoe Formation, about 150 m above the base, lower Cordevolian, Three Chopt Road fish locality, Deep Run Basin.

Figure 2: *Euestheria minuta* (von Zieten, 1833), female, from same rock specimen and bedding surface that contains the type material of *Euestheria winterpockensis*, upper Tuckahoe Formation, about 150 m above the base, lower Cordevolian, Richmond Basin, ANSP 31197.

Figures 3, 6: *Laxitextella multireticulata* (Reible, 1962), lower Falling Creek Formation, 40 m above the base, lower Cordevolian *L. multireticulata* Zone, Stagg Creek older level, Taylorsville Basin; 3a: Total view, 3b: detail of the same specimen, with small reticulation, partly longitudinally arranged; Figure 6: detail of another specimen, with small reticulation, partly longitudinally or obliquely arranged.

Figure 4: *Euestheria winterpockensis* (Bock, 1953), female, lower Falling Creek Formation, 44 m above the base, lower Cordevolian *L. multireticulata* Zone, Stagg Creek younger level, Taylorsville Basin.

Figure 5: *Euestheria minuta* (von Zieten, 1833), female, lower Falling Creek Formation, 44 m above the base, lower Cordevolian *L. multireticulata* Zone, Stagg Creek younger level, Taylorsville Basin.

PLATE 2

Scale = 1 mm, scale + 0.3 = 0.3 mm

Figures 1, 3: *Laxitextella multireticulata* (Reible, 1962), unnamed lacustrine unit, about 100 m above the base, lower Cordevolian *L. multirecticulata* Zone, Worthy property, Briery Creek Basin, YPM 220198.

Figure 2: *Laxitextella multireticulata* (Reible, 1962), lower Falling Creek Formation,40 m above the base, lower Cordevolian *L. multireticulata* Zone, Stagg Creek older level, Taylorsville Basin.

Figures 4, 5: *Laxitextella multireticulata* (Reible, 1962), advanced form, transitional to *L. laxitexta* (Sandberger, 1871), lower Falling Creek Formation, 44 m above the base, lower Cordevolian *L. multireticulata* Zone, Stagg Creek younger level, Taylorsville Basin; 4a: total view, 4b: reticulation on the outer growth bands in the middle part of the ventral margin, size of the reticulation between that of typical *L. multireticulata* and that of primitive *L. laxitexta*, 4c: same specimen, reticulation on the outer growth bands at the posterior margin, fine reticulation as typical for *L. multireticulata*, slightly elongated frames parallel to the growth lines; Figure 5: typical fine reticulation.

PLATE 3

Scale = 1 mm

Figures 1, 2: *Laxitextella multireticulata* (Reible, 1962), unnamed unit below New Oxford Formation, about 10 m above the base, lower Cordevolian *L. multireticulata* Zone, Hanover Street, SE of Town of New Oxford, Gettysburg Basin.

Figure 3: *Euestheria minuta* (von Zieten, 1833), male, upper part of lacustrine unit, Cordevolian, little Willis river, Farmville Basin, YPM 34647.

Figure 4: *Euestheria* sp. cf. *L. winterpockensis* (Bock, 1953), female, form around the upper size boundary for the species, ? upper Falling Creek Formation, exact position unknown, Cordevolian, Falling Creek, north of town of Ashland, Taylorsville Basin.

Figure 5: *Euestheria minuta* (von Zieten, 1833), female, large specimen with preserved strong convexity, ? upper Falling Creek Formation, exact position unknown, Cordevolian, Falling Creek, north of town of Ashland,

Taylorsville Basin.

Figure 6: *Laxitextella* sp. cf. *L. laxitexta* (Sandberger, 1871), middle New Oxford Formation (?), middle Tuvalian *Eosolimnadiopsis* ? n. sp.-*Laxitextella* sp. cf. *L. laxitexta* Zone, Fulton site on Beaver Branch south of Emmitsburg, Maryland, Gettysburg Basin, a) total view, b) detail with large reticulation.

PLATE 4

Scale = 1 mm

Figure 1: *Anyuanestheria* n. sp., Lower Cow Branch Formation, about 10 m above the base, upper Julian (middle Carnian), U.S. 220 road cut on north side of Dan River, Dan River/Danville Basin, a) total view, b) detail with radial lirae on the outer growth lines which changes into radially arranged reticulation on the inner growth lines.

Figures 2, 3: *Euestheria hausmanni* (Schmidt, 1938) emend. Reible (1962), female/female, Cumnock Formation, about 80 m above the base, upper Tuvalian, Bethany Church, Sanford Subbasin of Deep River Basin.

Figure 4: *Euestheria princetonensis* (Bock, 1953), holotype, Lockatong Formation, about 300 m above the base, upper Tuvalian, Granton Quarry, Newark Basin, ANSP 31192.

Figures 5, 6: *Euestheria princetonensis* (Bock, 1953), holotype and paratype of *Howellites* (=*Howellisaura*) *berryi* Bock, 1953, from a single bedding surface in a core from the Deep River coal basin, Cumnock Formation, upper Tuvalian, according to Bock (1953) 10-50 feet above the Cumnock coal which is between 100-200 m above the base Cumnock Fm., Sanford Subbasin of Deep River Basin, ANSP 31194; Figure 5: paratype, female, overprinted by a shell from a male; Figure 6: male, holotype.

PLATE 5

Scale =1 mm

Figure 1: *Euestheria ovata (*Lea, 1856), Lea's type specimen, the holotype is the left specimen (female), Lockatong Formation within the lower 150 m ?, upper Tuvalian, Gwynedd, Newark Basin, ANSP 16849.

Figures 2, 3: *Euestheria buravasi* kobayashi, 1975, "Lithofacies Association II" of Hoffman and Gallagher (1989), level corresponding to lower Sanford Formation in the Sanford Subbasin, basal Norian, Triangle Brick Quarry, Durham Subbasin of Deep River Basin, NMMNH material; Figure 2: female; Figure 3: male.

Figure 4: *Euestheria* sp. cf. *E. hausmanni* (Schmidt, 1938) emend. Reible (1962), female, with fewer and wider growth bands than in typical *E. hausmanni*, outline very similar to the female of *E. buravasi*, but without the more or less broad outer zone of very narrow growth bands, "Lithofacies Association II" of Hoffman and Gallagher (1989), level corresponding to lower Sanford Formation in the Sanford Subbasin, basal Norian, Triangle Brick Quarry, Durham Subbasin of Deep River Basin, material of North Carolina Museum of Natural Sciences.

Figure 5: *Anyuanestheria* ? n. sp., male, narrow outer zone with very dense growth lines with indistinct radial lirae, visible in the anterioventral area, "Lithofacies Association II" of Hoffman and Gallagher (1989), level corresponding to lower Sanford Formation in the Sanford Subbasin, basal Norian, Triangle Brick Quarry, Durham Subbasin of Deep River Basin, material of North Carolina Museum of Natural Sciences.

PLATE 6

Scale = 1 mm, scale + 0.1 = 0.1 mm

Figures 1, 2: *Shipingia hebaozhaiensis* Shen, female, large morphotype, upper Stubensandstein 2, upper Alaunian (upper middle Norian), upper *S. hebaozhaiensis* Zone, Gaiseiche in Stuttgart, Baden-Württemberg, Germany, material of the Naturkundemuseum Stuttgart, no. 21 258; Figure 1: reticulation radially arranged; Figure 2: detail of the microsculpture of another specimen on the same sample and same surface, reticulation arranged in irregular vertical stripes.

Figures 3-6: *Shipingia hebaozhaiensis* Shen, female, medium-sized morphotype, Heidlersburg Member of Gettysburg Shale, middle Alaunian (middle middle Norian), middle part of *S. hebaozhaiensis* Zone, U.S. Rt. 15 SSE of Heidlersburg, Gettysburg Basin; Fig 3: adult specimen, male; Figures 4-6: juvenile to subadult specimens, Figures 4, 5: male/male, Figure 6: two specimens on one piece, female/female.

Figure 7: *Shipingia hebaozhaiensis* Shen, female, large morphotype, middle Groveton Member of Bull Run Fm., upper part of middle Norian *S. hebaozhaiensis* Zone, section at intersection of I-66 with VA Route 234, Culpeper basin.

Figure 8: *Shipingia olseni* Kozur & Weems, 2005, male,middle Groveton Member of Bull Run Fm., upper part of middle Norian *S. hebaozhaiensis* Zone, section at intersection of I-66 with VA Route 234, Culpeper Basin; a) total view, b) detail with microsculpture, reticulation arranged parallel or somewhat oblique to the growth lines.

PLATE 7

Scale = 1 mm, scale + 0.3 = 0.3 mm

Figures 1-2: *Redondestheria grovetonensis* Kozur & Weems, 2005, female/female, upper Groveton Member of the Bull Run Fm., lower Sevatian *R. grovetonensis* Zone, road cut near Groveton Cemetery, Culpeper basin.; Figure 1: holotype; Figure 2: the elevation above the sinus is a piece of rock on the shell.

Figure 3: *Shipingia olseni* Kozur & Weems, 2005, female, upper Blomidon Formation, Sevatian *S. olseni* Zone, Fundy Basin (Canada), Blomidon Cliff, YPM 34664.

Figures 4-6: *Redondestheria novomexicoensis* Kozur, Weems & Lucas, 2005, siltstone within the lower Redonda Formation, early Apachean LVF, *R. grovetonensis* Zone, Sevatian, about 0.5 m thick bed at Revuelto Creek, 75 meters south of the north quadrangle border, and 94 meters northeast of the "o" in the label for "Revuelto Creek" on the Apache Canyon, New Mexico, 7.5-minute USGS quadrangle map (latitude 34.9995 N, longitude 103.4076 W); Figure 4: holotype, shell around the sinus wall-like and elevated; Figure 5: deformed tube-like elevation at the anterior margin; a) total view, b) detail with microsulpture; Figure 6: tube-like, anteriorly and terminally open elevation around the sinus at the anterior margin.

Figures 7, 10, 11: *Shipingia olseni* Kozur & Weems, 2005, upper Passaic Fm., *S. olseni* Zone, Sevatian, section at the Boyertown Road (Pennsylvania State Road 562), Newark Basin; Figure 7: female; Figure 10: microsculpture; Figure 11: microsculpture of another specimen.

Figures 8, 9: *Shipingia olseni* Kozur & Weems, 2005, uppermost Passaic Formation, uppermost horizon of the *Patinasporites densus* palynoflora, uppermost *S. olseni* Zone, upper Sevatian, Exeter section, Newark Basin; Figure 8: female; a) total view, b) detail with microsculpture; Figure 9: female, holotype.

PLATE 8

Scale = 1 mm

Figures 1, 5: *Shipingia olseni* Kozur & Weems, 2005, detail of the growth lines with microsculpture of two different specimens, upper Passaic Fm., *S. olseni* Zone, Sevatian, section at the Boyertown Road (Pennsylvania State Road 562), Newark basin.

Figures 2-4, 6: *Shipingia olseni* Kozur & Weems, 2005, Catharpin Creek Fm., *S. olseni* Zone, Sevatian, Cedar Run section, Culpeper basin; Figures 2-4: female/female; Figure 6: male.

Figure 7: *Shipingia olseni* Kozur & Weems, 2005, Catharpin Creek Fm., *S. olseni* Zone, upper Sevatian, Haymarket locality, Culpeper basin.

Figure 8: *Redondestheria novomexicoensis* Kozur, Weems & Lucas, 2005, dorsal view, anterior margin to the right. At the left valve the incision at the anterior margin and the elevations around this íncision are readily visible. Siltstone within the lower Redonda Formation, Lower Apachean LVF, upper *R. grovetonensis* Zone, Sevatian, about 0.5 m thick bed at Revuelto Creek, 75 m south of the north quadrangle border, and 94 m northeast of the "o" in the label for "Revuelto Creek" on the Apache Canyon, New Mexico, 7.5 minute USGS quadrangle map (latitude 3.9995N, longitude 103.4076W.

PLATE 9

Scale = 1 mm

Figures 1-5: *Euestheria brodieana* (Jones), Midland Fm., *E. brodieana* Zone, upper Rhaetian, Killian property, Culpeper Basin.

Figures 6, 7, 11, 14: *Bulbilimnadia sheni* Kozur & Weems, 2005, lower Waterfall Fm., *B. sheni* Zone, lower Hettangian, Avalon Farm, Culpeper basin; Figure 6: late juvenile specimen; Figure 7: juvenile specimen with only 2 growth lines; Figure 11: adult specimen, holotype; Figure 14: adult specimen.

Figures 8, 9, 12: *Euestheria brodieana* (Jones), lowermost Waterfall Fm., *B. sheni* Zone, lower Hettangian, Avalon Farm, Culpeper basin.

Figure 10: *Bulbilimnadia sheni* Kozur & Weems, 2005, very poorly preserved specimen, but small high elevation on the free umbonal surface is readily visible, middle East Berlin Fm., 82 m below top, lower Hettangian, Miner Brook (Westfield fish bed), Hartford Basin.

Figures 13, 15, 16: *Bulbilimnadia froelichi* Kozur & Weems, 2005, upper Waterfall Fm., *B. froelichi* Zone, Hettangian, Catletts Branch, Culpeper Basin; Figure 13: late juvenile specimen; Figure 16: holotype.

PLATE 10 (SEE APPENDIX)

Figure 1: *Laxitextella freybergi* Kelber & Kozur n. sp., holotype, Coburg Sandstein, upper Hassberge Formation, 0.15-0.30 cm above the basal sandstone (basal "Werkstein"), *Laxitextella freybergi* zone, upper Tuvalian, former Hahn quarry, southeast of Eltmann, Franconia (Bavaria), southern Germany; a) total view, b) detail with very large reticulation pattern visible (pentagonal, hexagonal, irregularly polygonal, and rarely roundish).

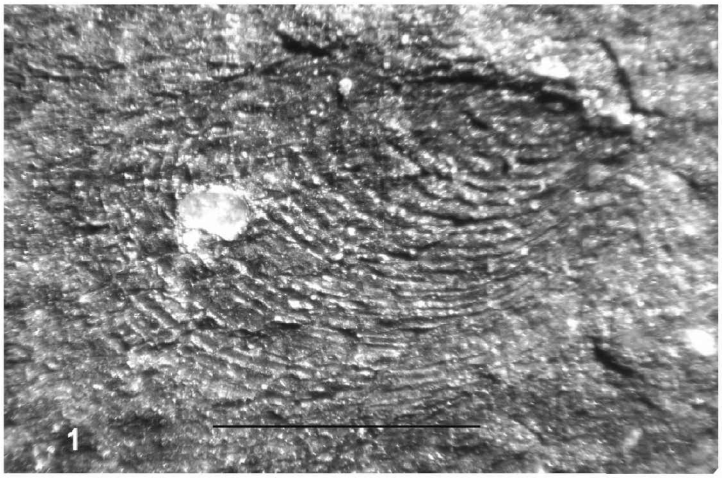
Figures 2-4: *Eosolimnadiopsis gallegoi* Kozur n. sp., 2-3 m above the base of the Rote Wand (lowermost Weser Formation), *Eosolimnadiopsis gallegoi* Zone, lower Tuvalian, temporary outcrop at the new building of the Waldorf school, Stuttgart, Haussmannstrasse 44, Germany; Fig. 2: holotype, a) total view, b) detail of the outer ventral part, radial lirae clearly visible, partly changing to very fine reticulation (especially toward the inner growth bands), c) detail of posterodorsal region, distinct posterodorsal corner with back-curvature of the growth lines visible; Fig. 3: an exemplar, total view, umbonal area not totally flattened; Fig. 4: detail of the microsculpture along the posterior margin of another exemplar, showing irregular radial lirae that partly change into a fine reticulation toward the inner growth bands.

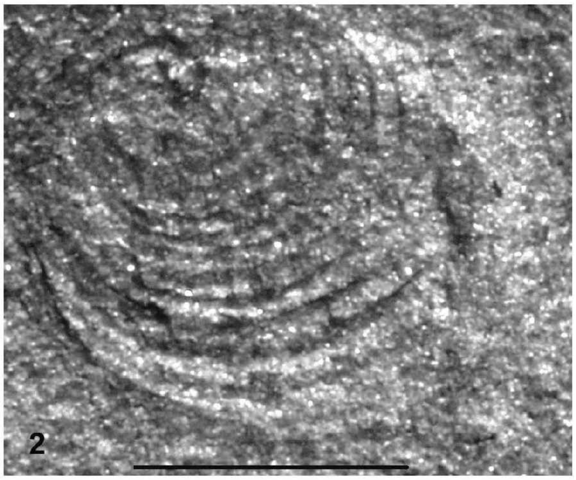
PLATE 11 (SEE APPENDIX)

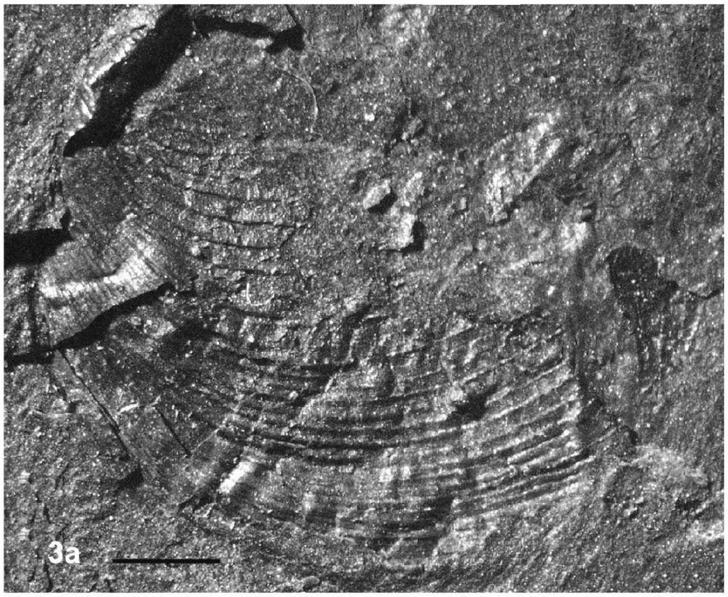
Figures 1, 2, 4: *Laxitextella seegisi* Kozur n. sp., Lehrberg Beds (upper Lehrberg Bank) of the middle part of the Upper Gypsum Keuper (Weser Formation), *Laxitextella seegisi* Zone, middle Tuvalian; Figs. 1, 4: Creek W Ramshalden-Buoch/Württemberg, S "Salzbuckel," southern Germany (see Seegis, 1997, locality 329); Fig. 1: holotype, a) total view, b) detail of the reticulation of the growth bands, 6-7 polygons above each other on the broadest growth bands; Fig. 4: detail of the reticulation in another exemplar, 7-10 polygons above each other on the broadest growth bands; Fig. 2: strongly convex, three-dimensionally preserved, unflattened specimen, the strongly convex umbonal area somewhat overreaches the dorsal margin, Lehrberg Beds, (upper Lehrberg Bank), *L. seegisi* Zone, middle Tuvalian, former marl pit southeast of Stetten/Württemberg, S "7 Linden" (see Seegis, 1997, locality 374), southern Germany.

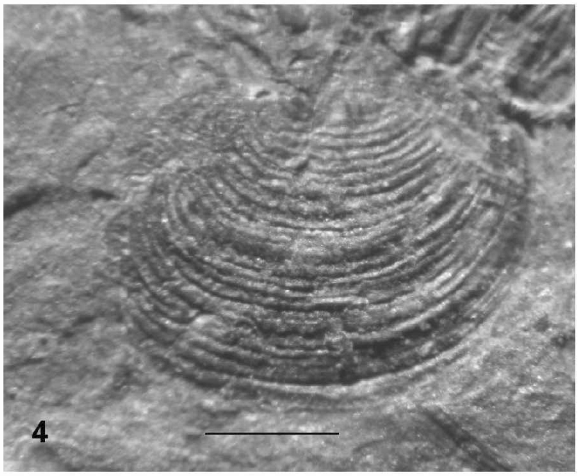
Figures 3: *Eosolimnadiopsis* ? n. sp., *Laxitextella seegisi* Zone, middle Tuvalian, Krasiejów locality, southwestern Poland, lower Adamanian LVF with *Stagonolepis* and *Palaeorhinus*. The outline is typical for *Eosolimnadiopsis* Chen, 1976. Especially characteristic is the very straight dorsal margin with a distinct posterodorsal corner. A back curvature of the growth bands close to the dorsal margin cannot be observed, however, and the microsculpture of radial lirae is very indistinct or not present so assignment to *Eosolimnadiopsis* is not yet certain. SEM picture sent by Dr. Tomasz Sulej (Warsaw), to whom we are very grateful.

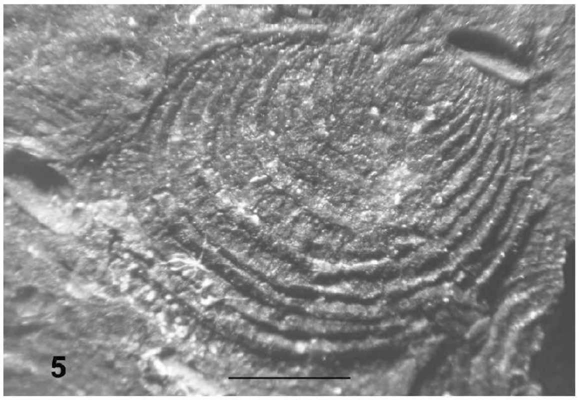
PLATE 1

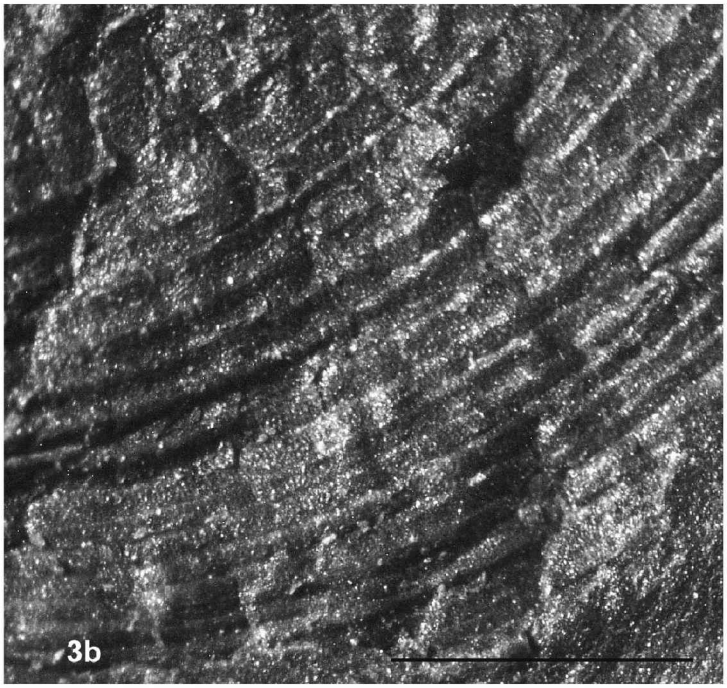


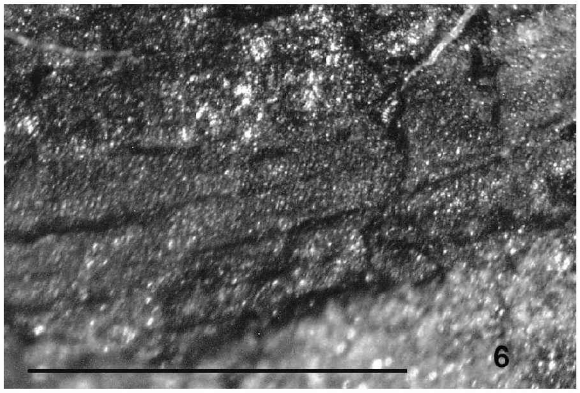












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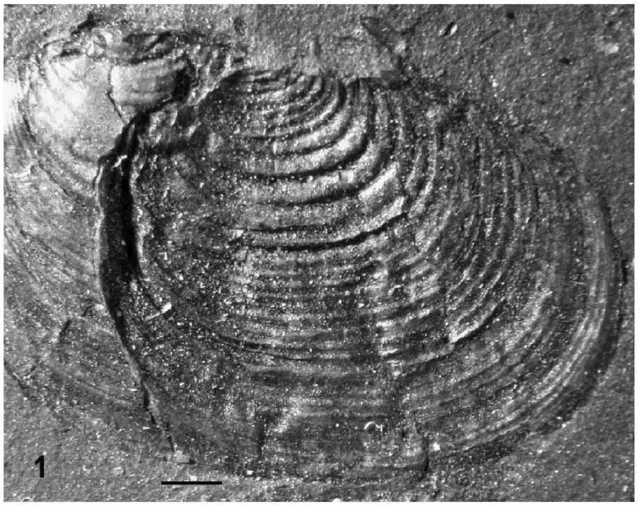

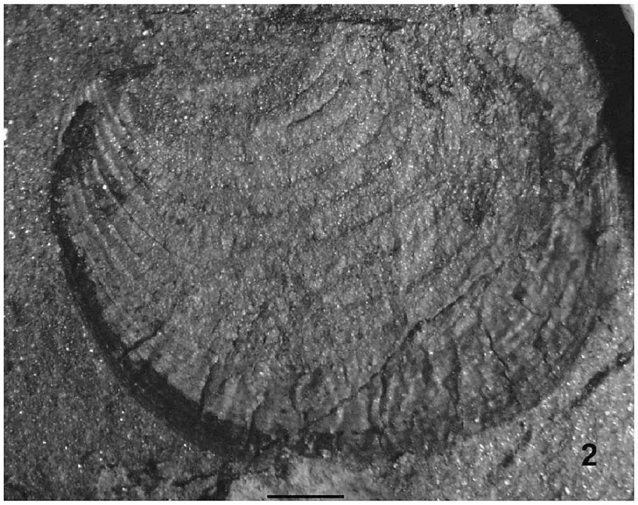

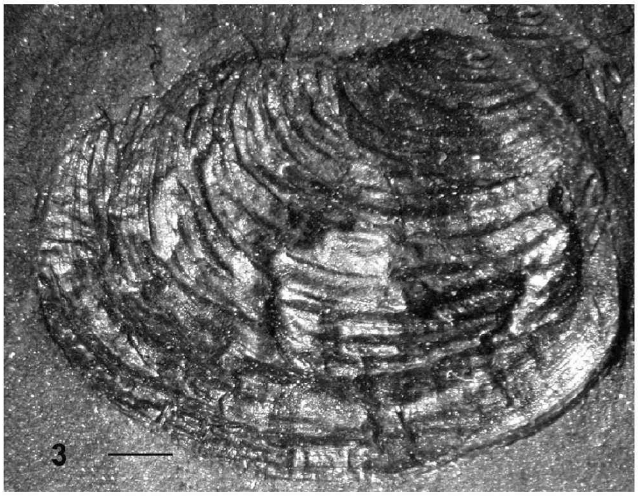

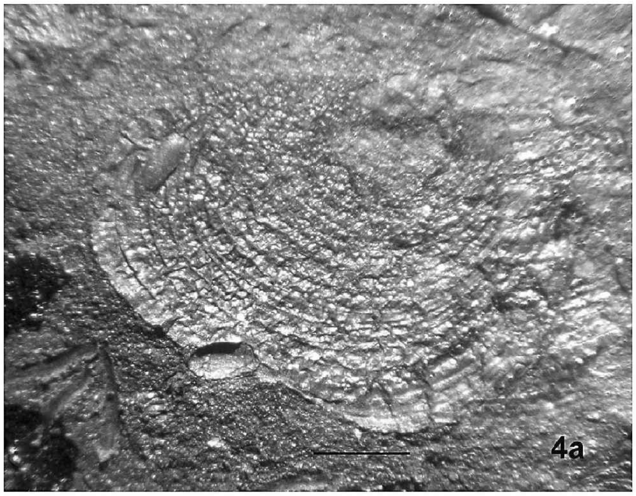

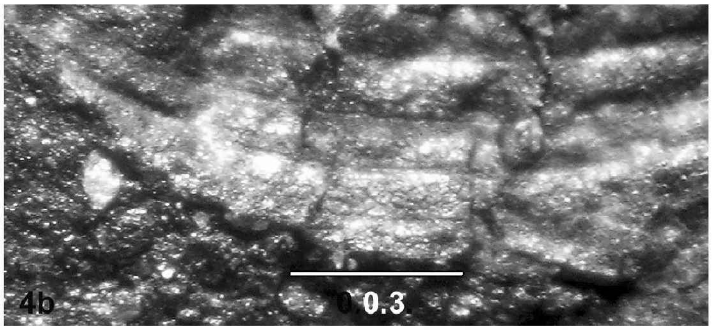

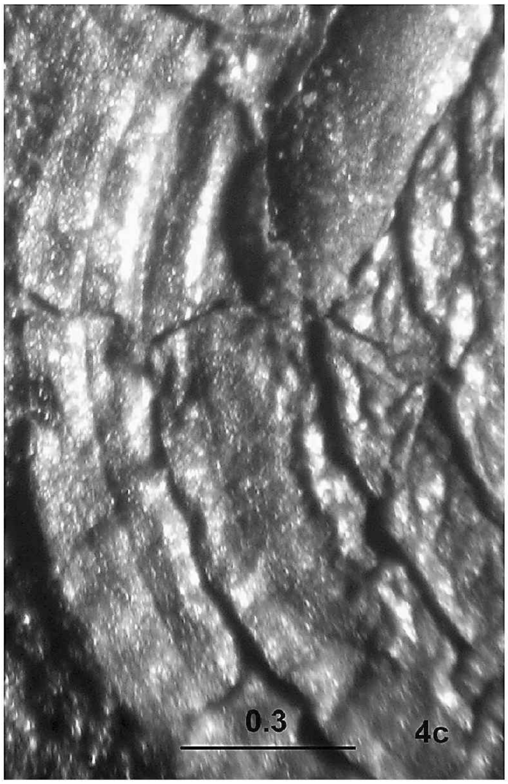

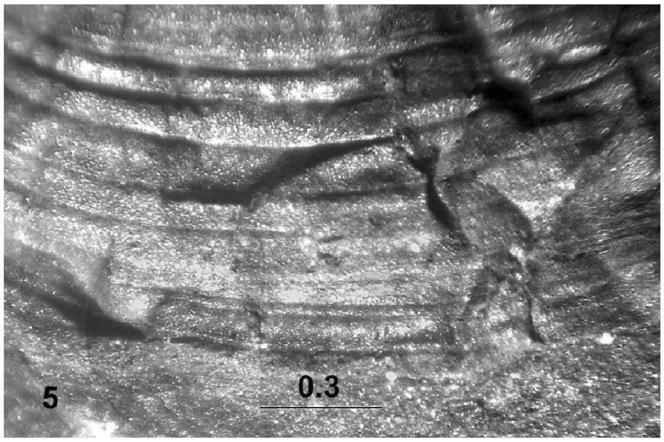

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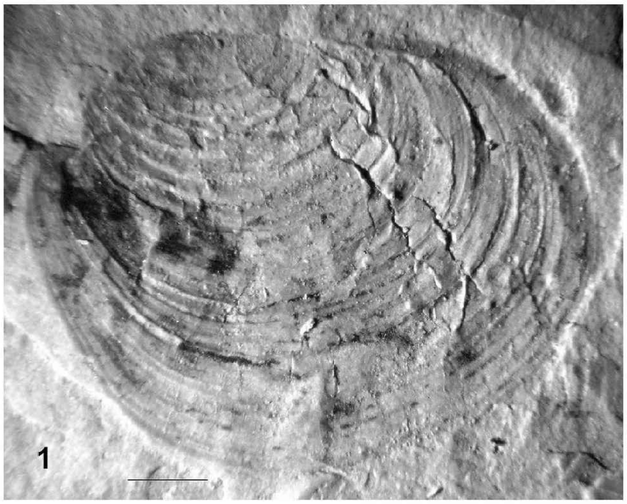
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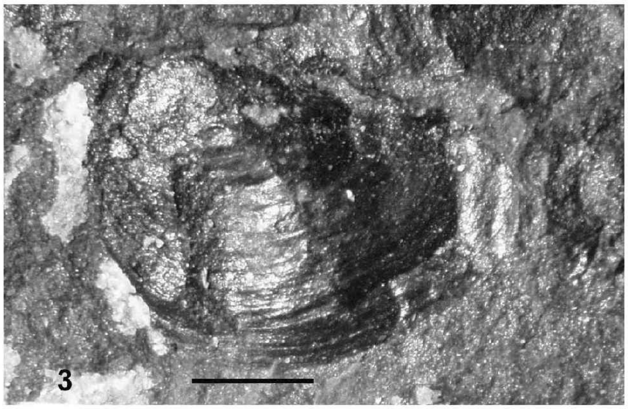
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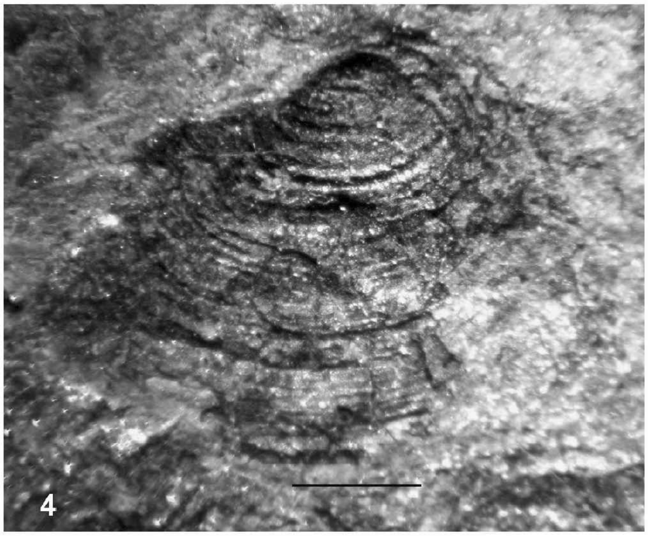
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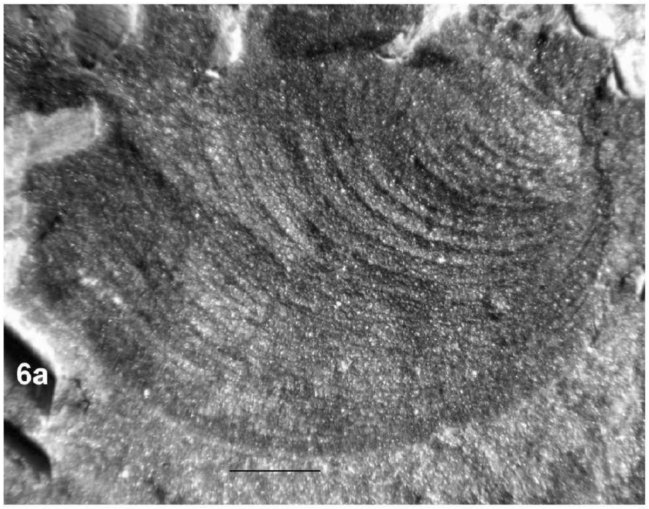
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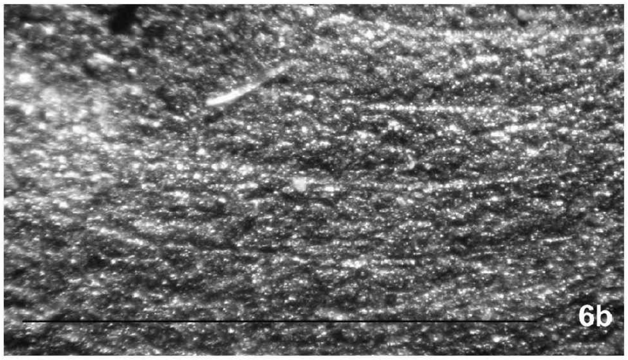
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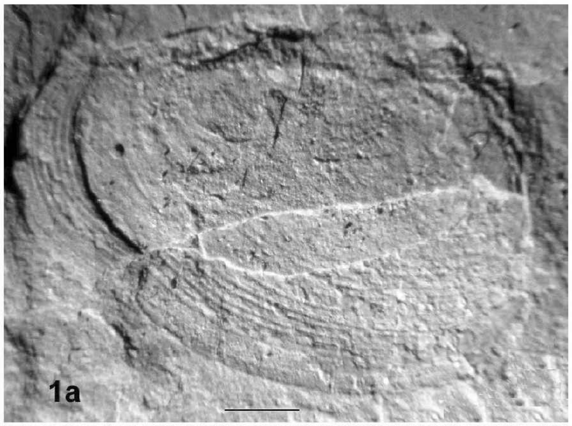

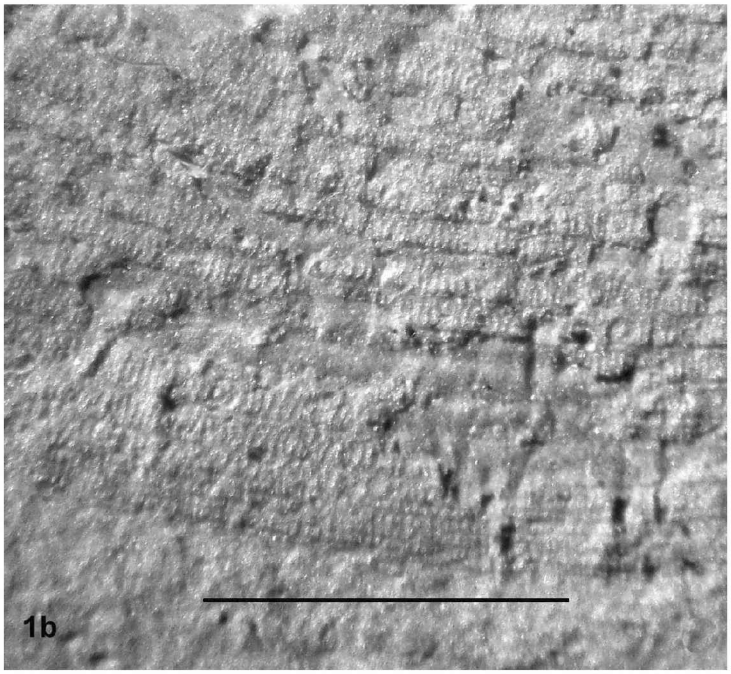

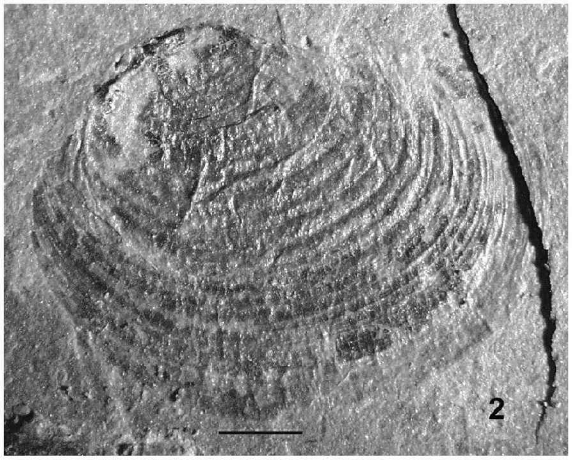

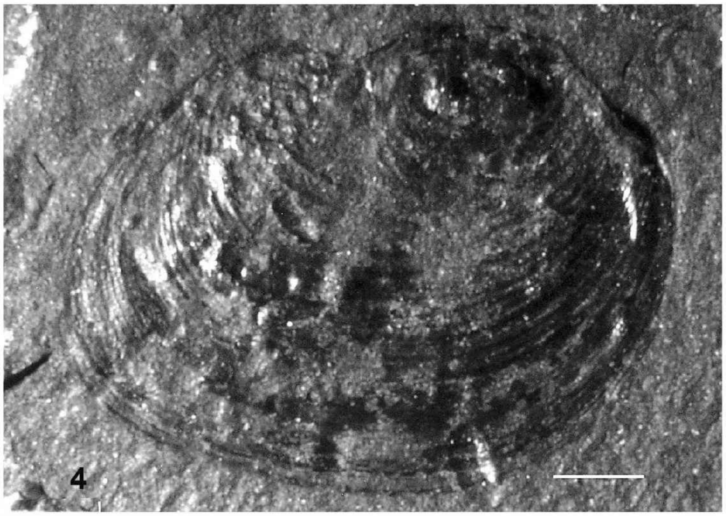

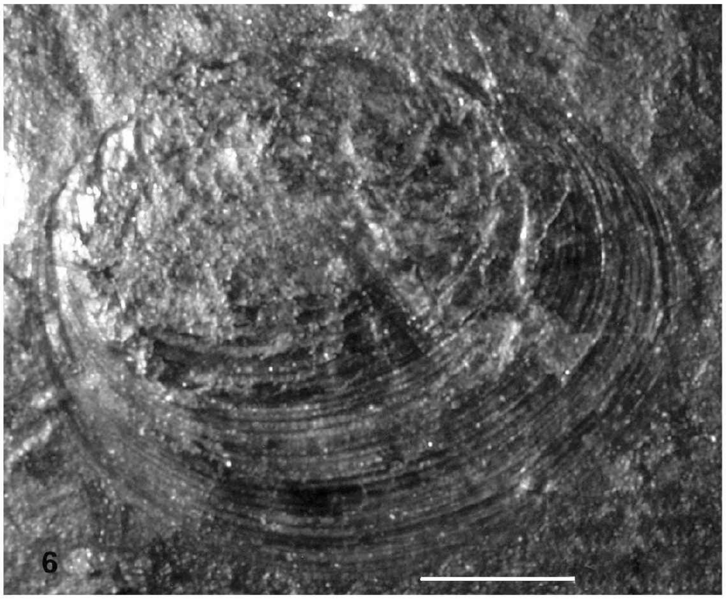

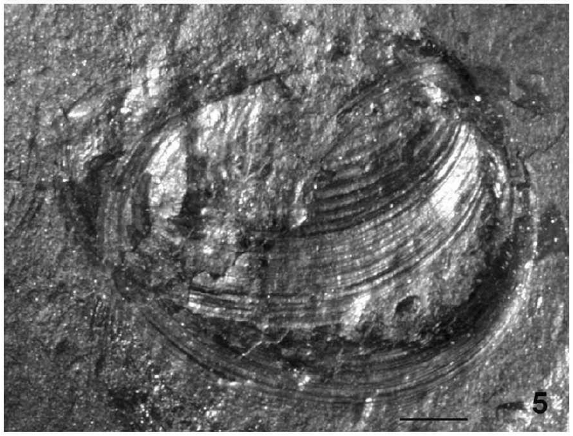

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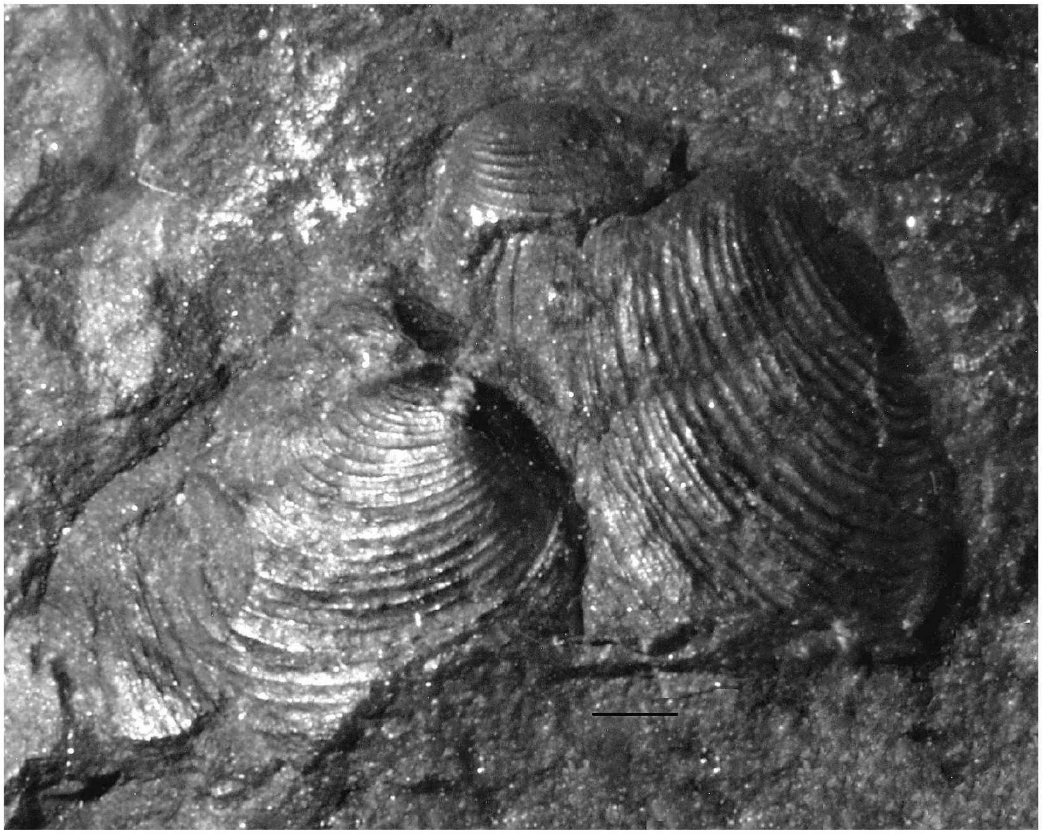
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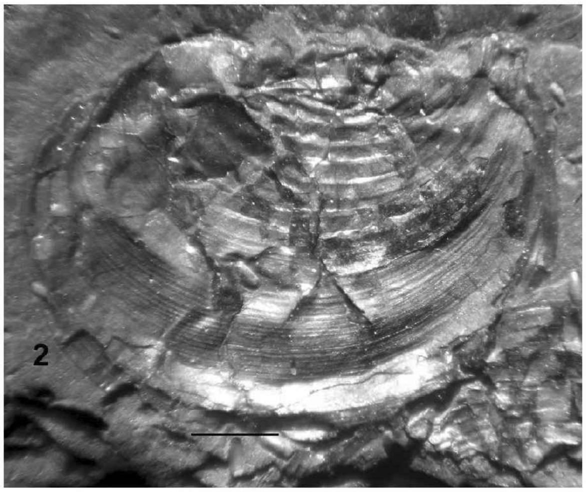
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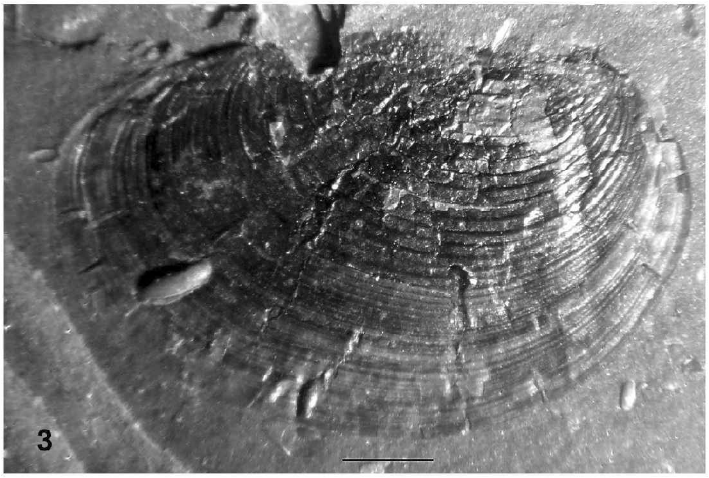
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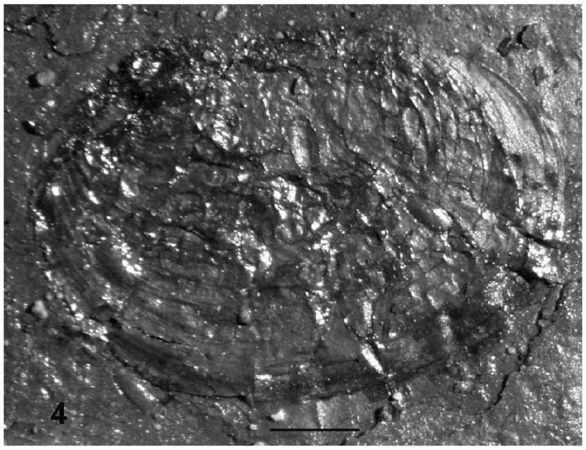
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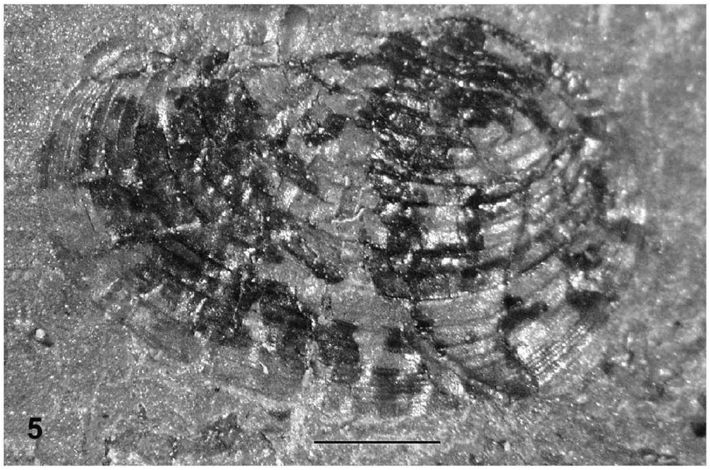
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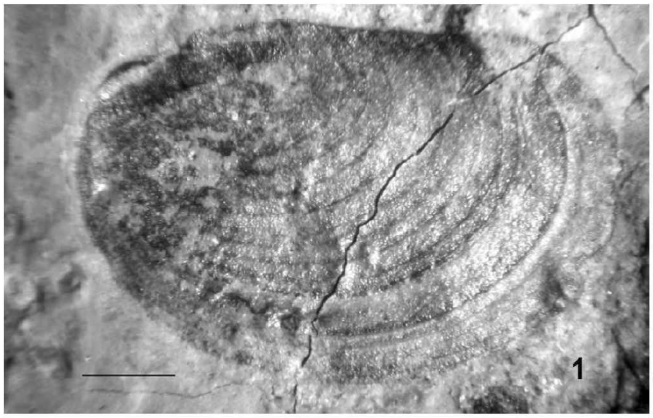
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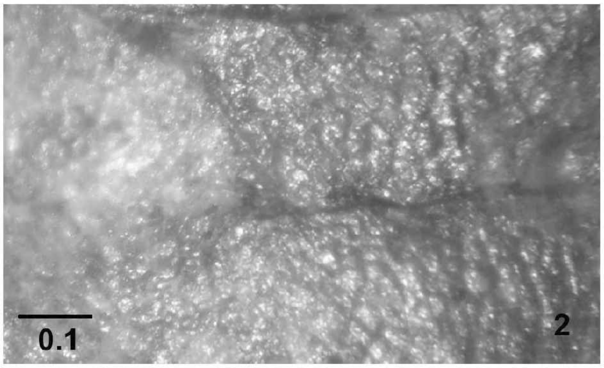

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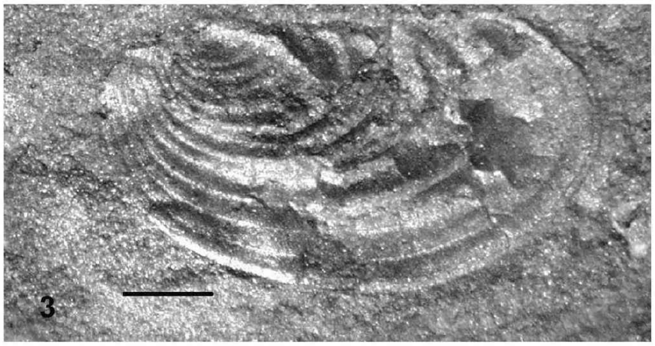
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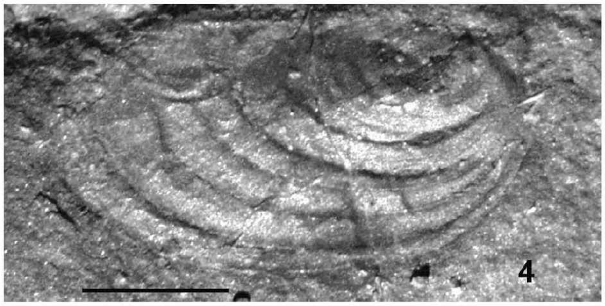
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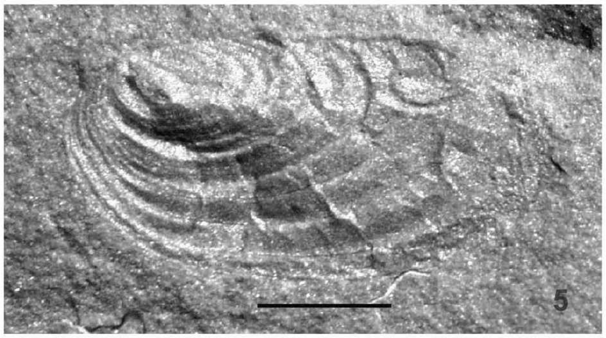
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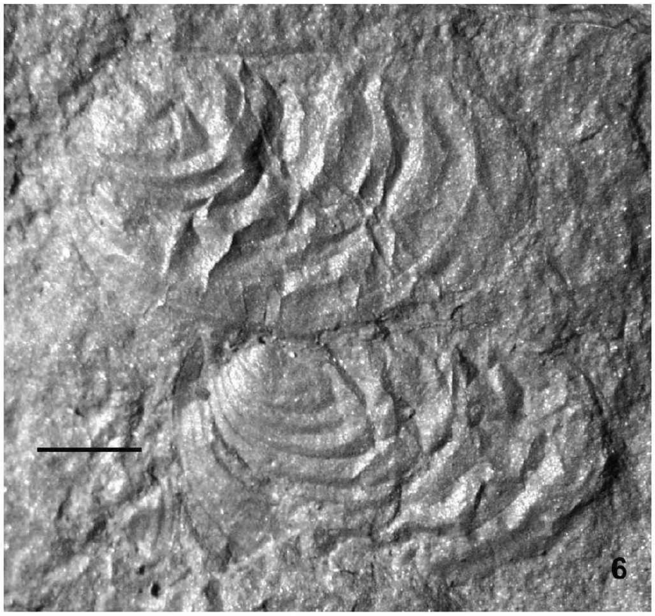
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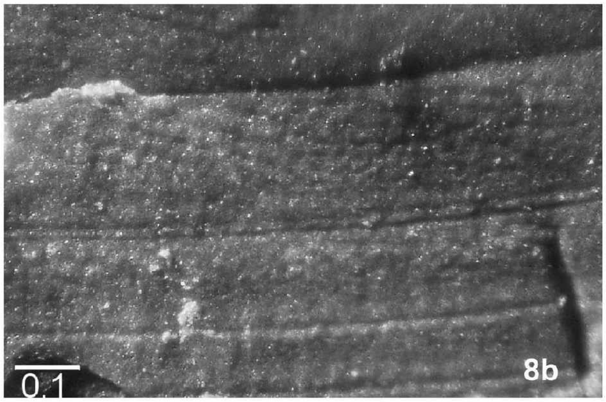

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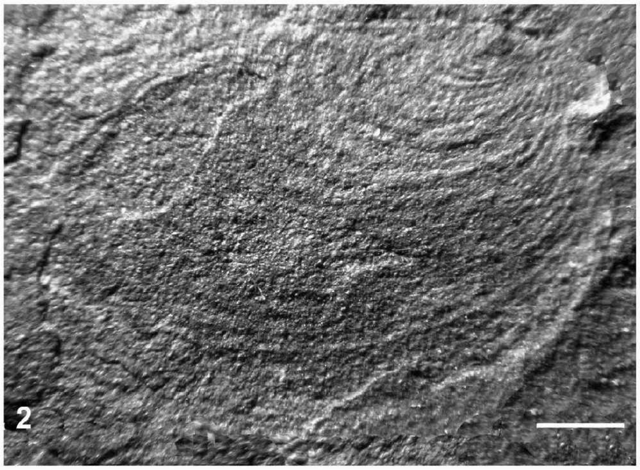

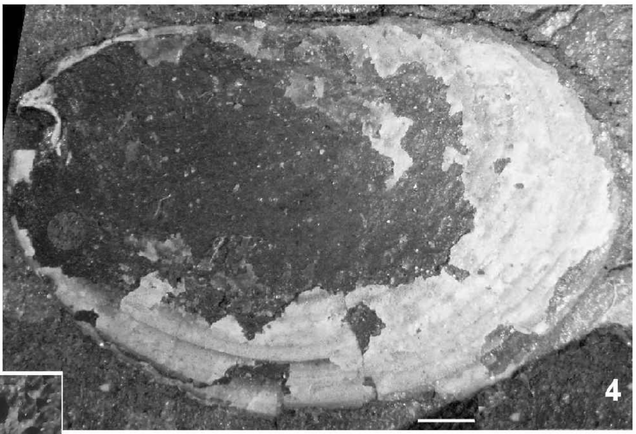

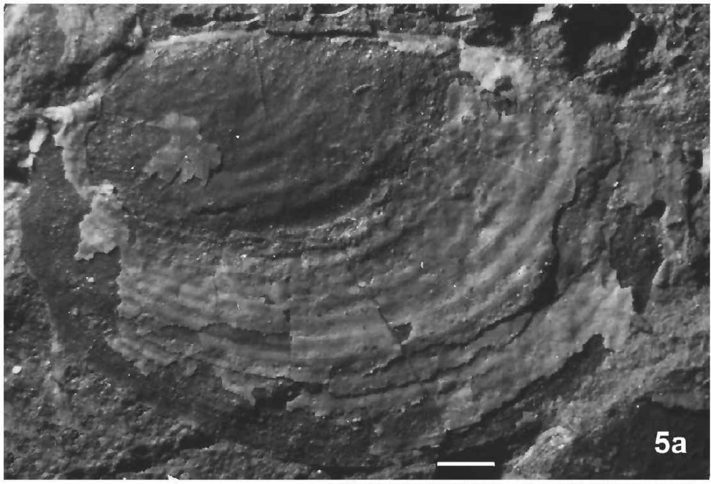

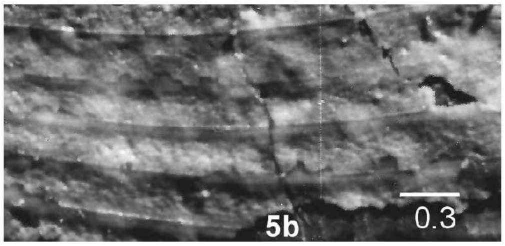

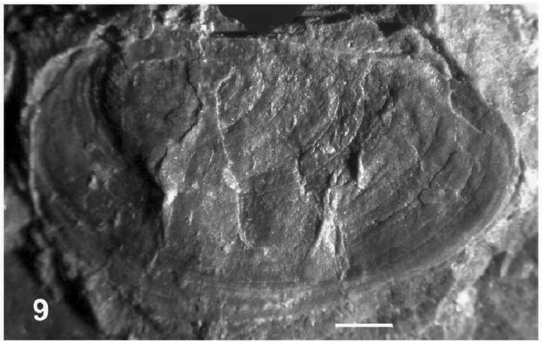

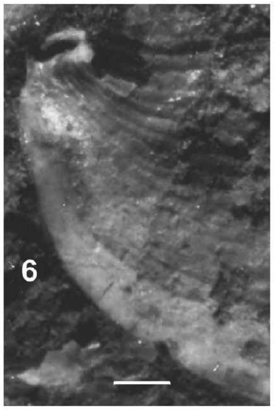

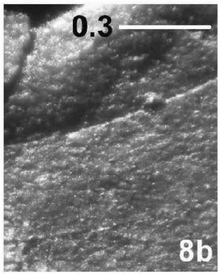

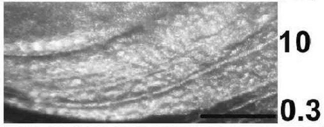

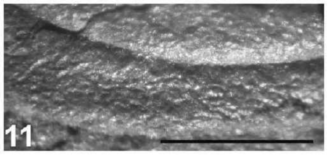

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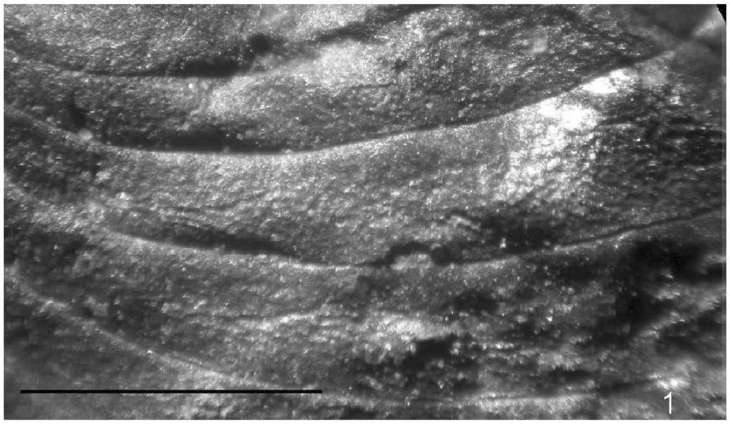
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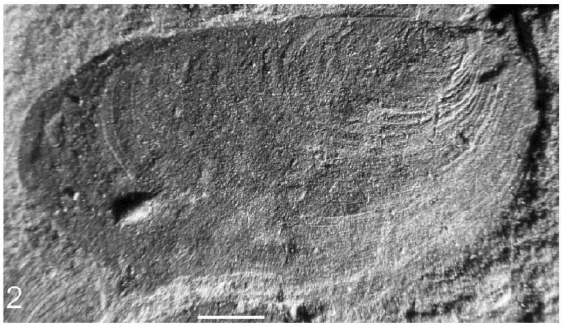
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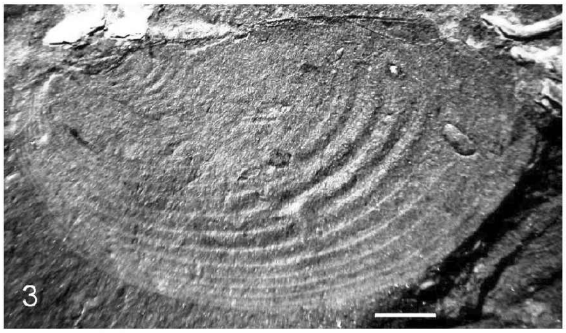
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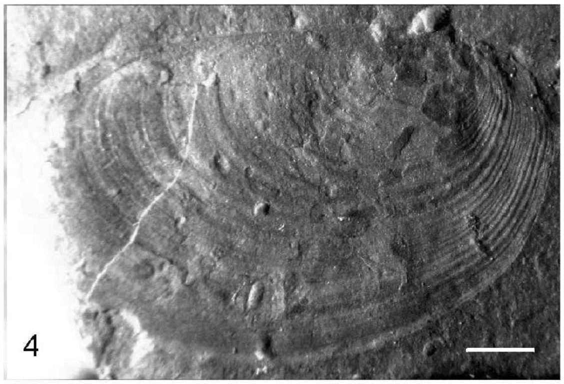
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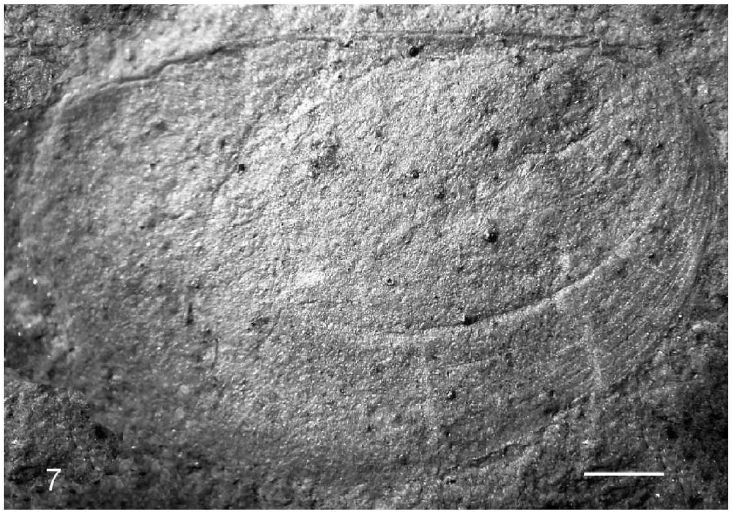
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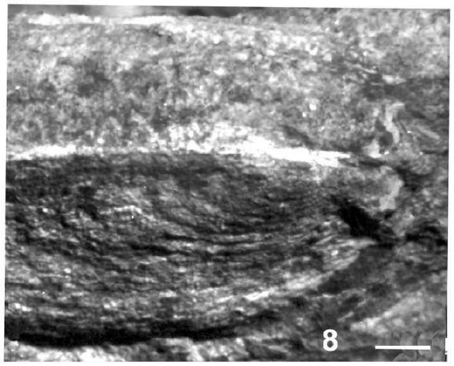
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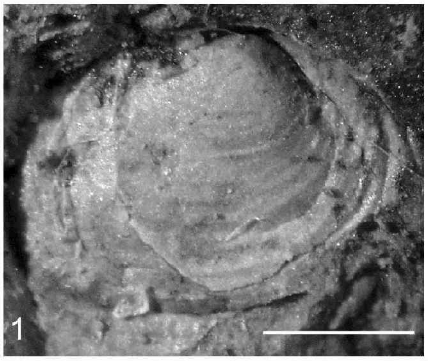

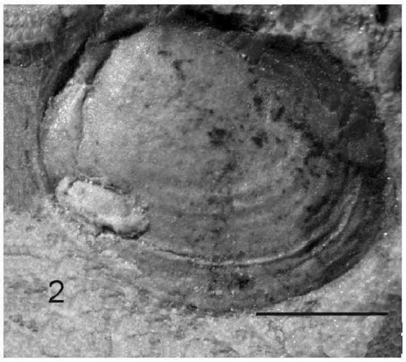

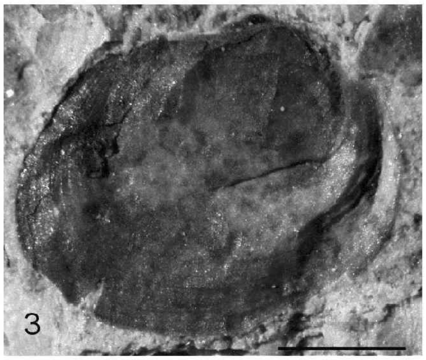

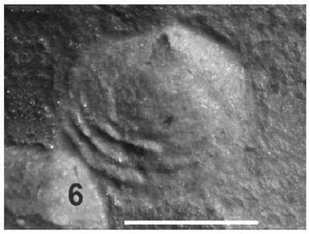

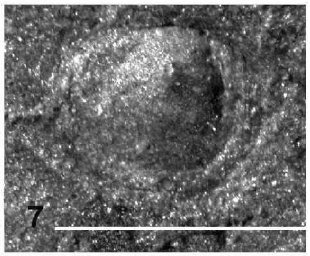

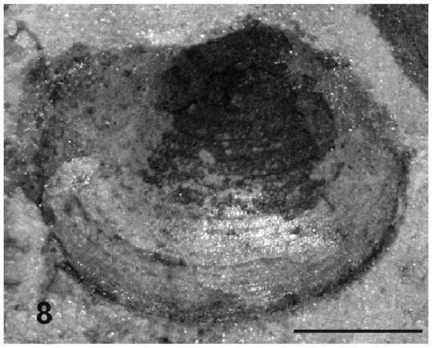

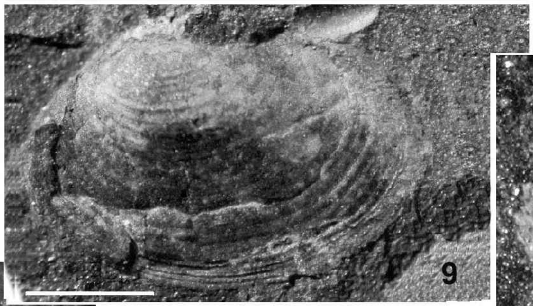

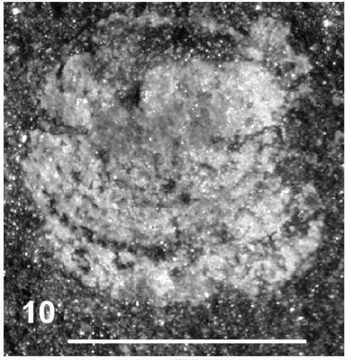

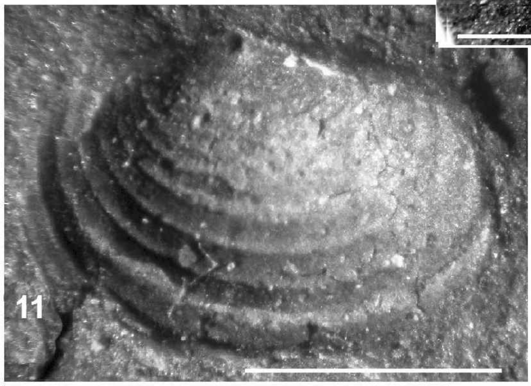

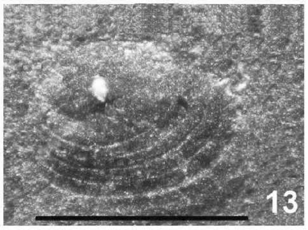

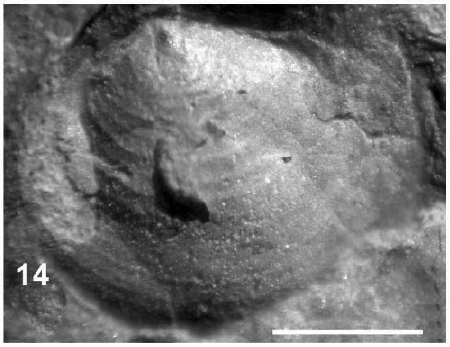

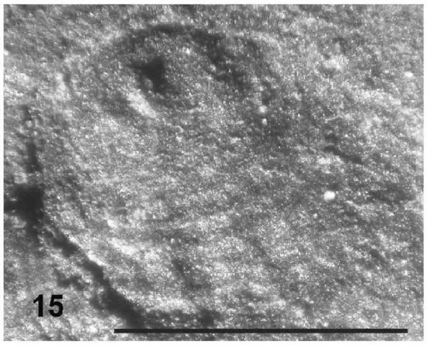

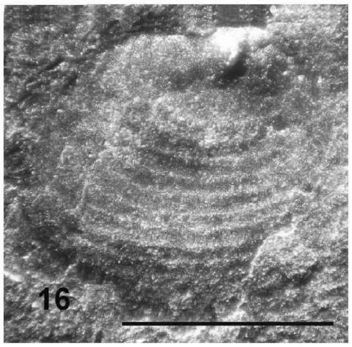

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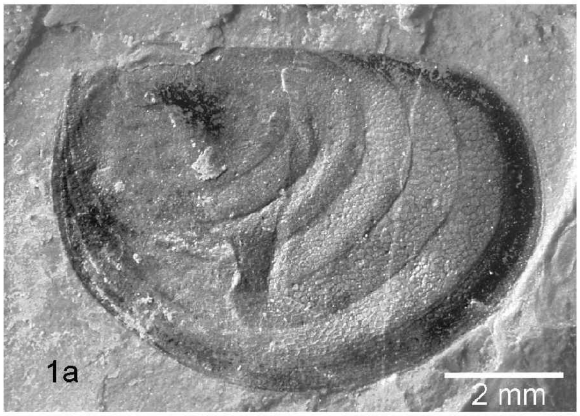

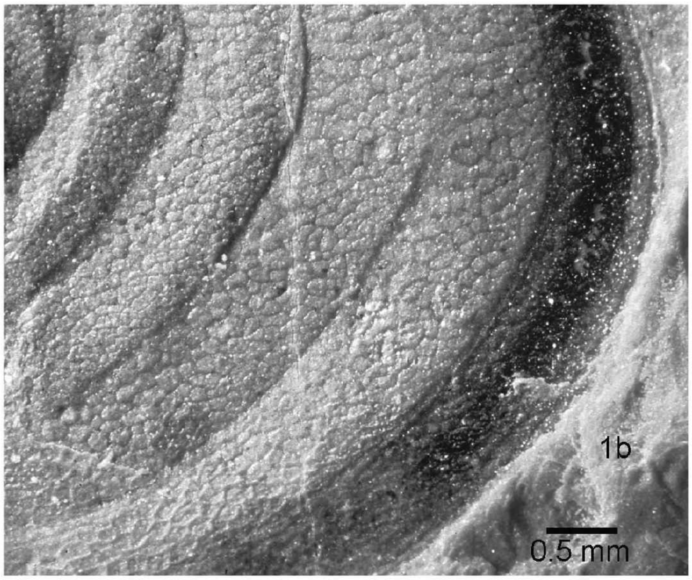

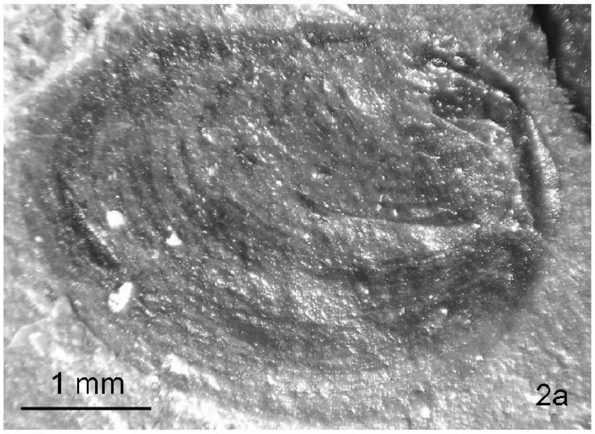

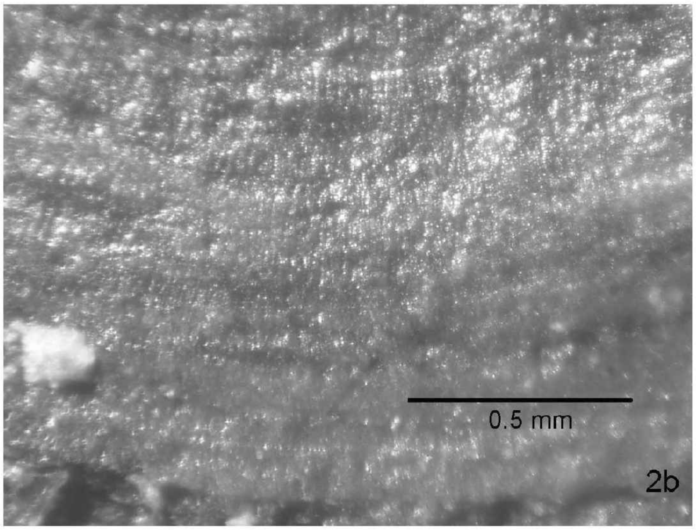

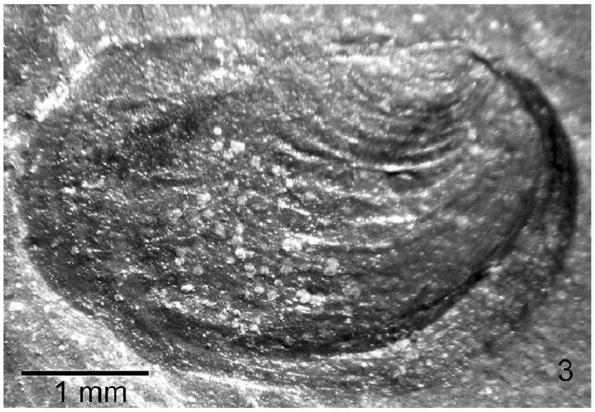

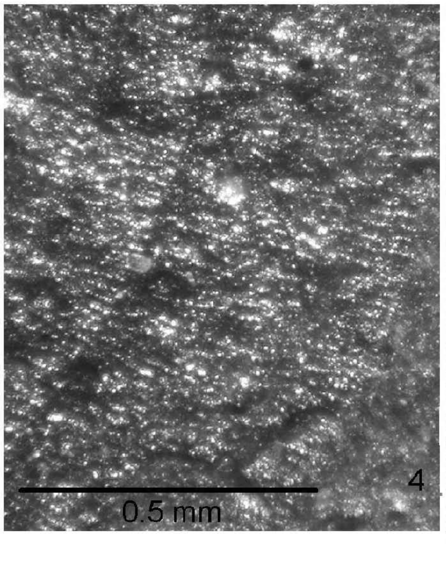

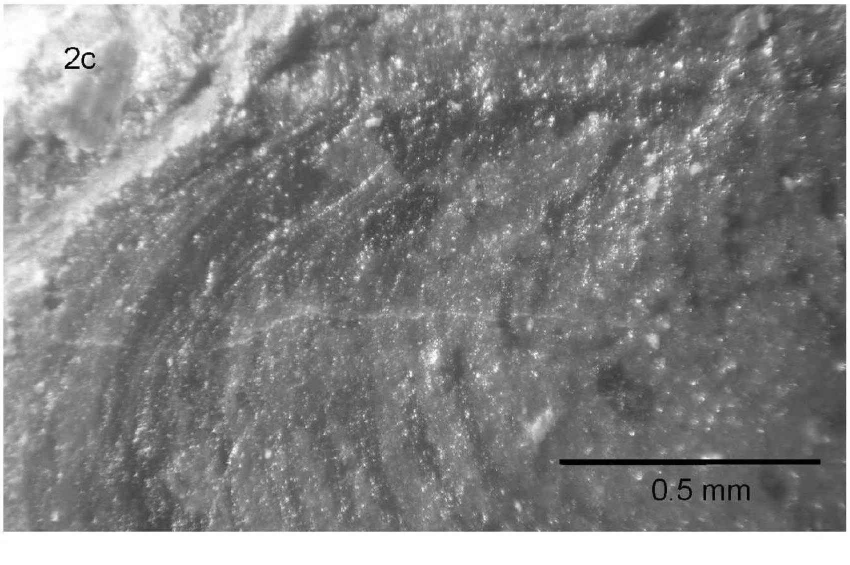

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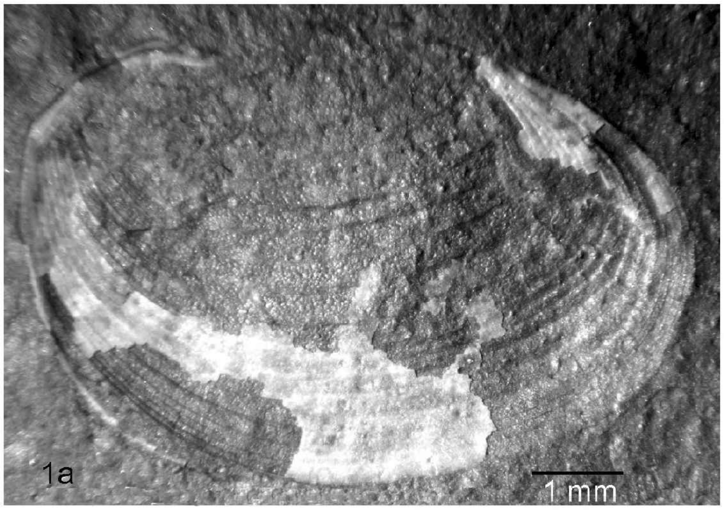

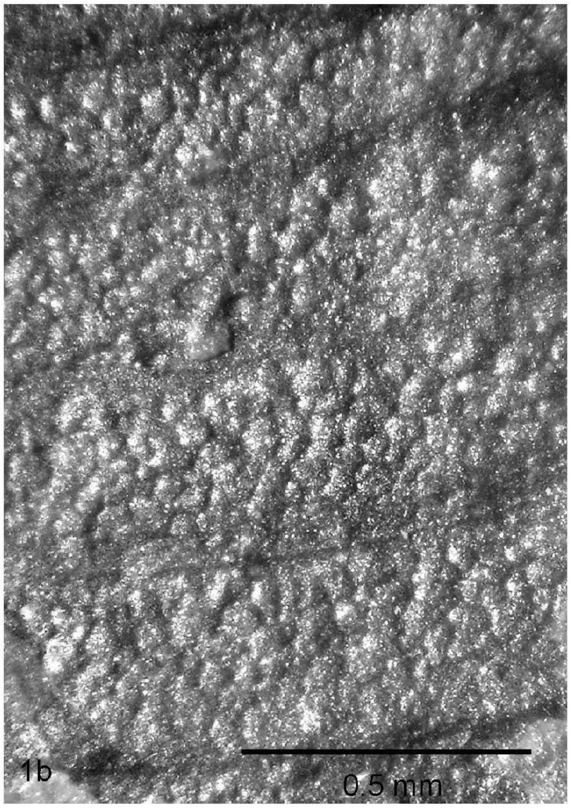

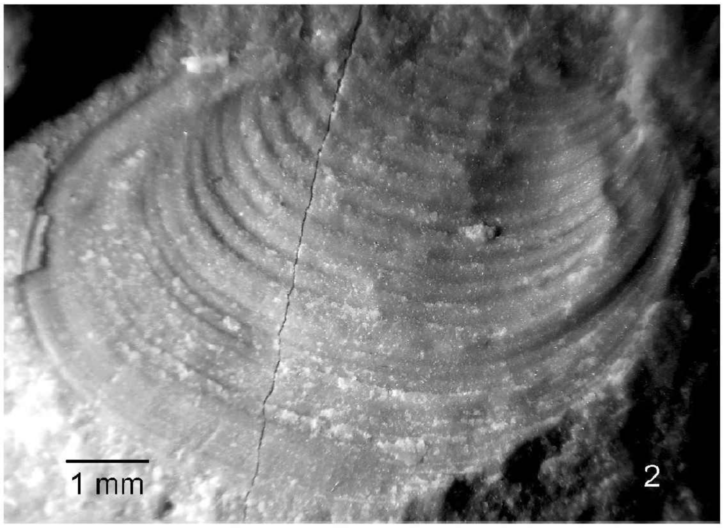

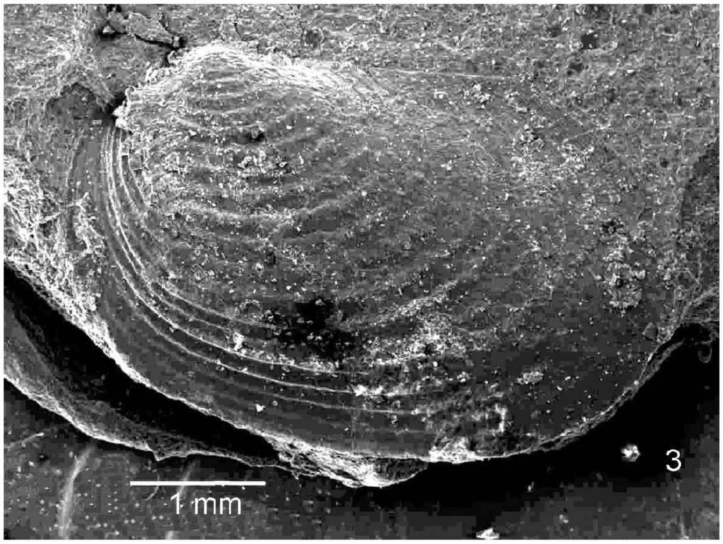

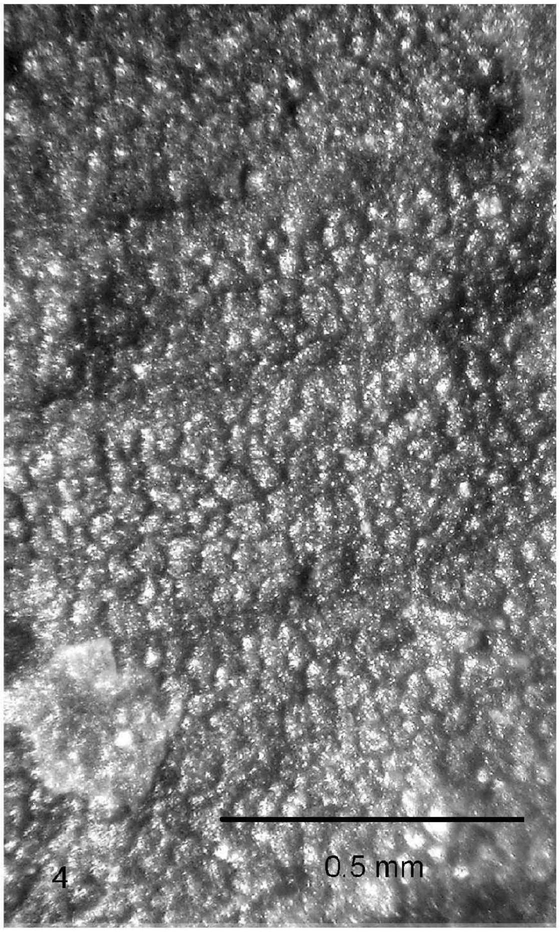

Lucas, S.G. and Spielmann, J.A., eds., 2007, The Global Triassic. New Mexico Museum of Natural History and Science Bulletin 41.

PROPOSAL FOR A CANDIDATE GSSP FOR THE BASE OF THE RHAETIAN STAGE

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Abstract—The Steinbergkogel section near Hallstatt, Salzkammergut, Austria is proposed as candidadate GSSP for the Norian-Rhaetian boundary (NRB). Following a recommendation of the Subcommission on Triassic Stratigraphy the boundary is defined by conodonts, with two alternative positions located closely upon each other. The lower event (option 1) corresponds to the FA of *Misikella hernsteini* 1.80 m above section base, it is followed by the FAD of *Misikella posthernsteini* 40 cm higher up (option 2). Accompanying biostratigraphic boundary markers for option 1 are the FA of the ammonoids *Paracochloceras suessi* coeval to the FAD of *M. posthernsteini* and of *Sagenites* s.str. at about the same level. Option 1 is marked by the LA of *Metasibirites*, a widespread late Norian ammonoid genus, just below the FA of *M. hernsteini*. Another proxy for option 1 is the worldwide disappearance of *Monotis* (*M. salinaria*/*subcircularis* in low palaelatitudes and *M. ochotica* group in the Boreal) closely below the FA of *M. hernsteini*. Half way above the 40 cm thick boundary interval lies a prominent magnetic polarity change from a long Normal to a distinct Reversal which can be recognized in other Tethyan magnetostratigraphies and, by a comparable polarity signature is identified in the lacustrine Newark magnetochronology too. The $\delta^{13}C_{carb}$ record is well preserved but unfortunately no significant variations occur around the two boundary options.

The Steinbergkogel exposes a pelagic basin facies of red and gray Middle Norian to Lower Rhaetian Hallstatt Limestone with a rich ammonoid and conodont fauna that allows a cross-correlation of the respective zonal schemes around the NRB. A lithologically uniform boundary interval, good exposure conditions in an old abondoned quarry and location on public land in a mountainous forested area assure long-time preservation and accessibility.

INTRODUCTION

The Austrian Salzkammergut region fullfills essential requirements for a Rhaetian GSSP: i) it is well known for diverse Norian-Rhaetian low palaeolatitude invertebrate faunas (cephalopods, bivalves, gastropods, brachiopods, reefal organisms) found in different bathymetric and facial environments; ii) knowledge of their temporal and spatial distribution is now well advanced and a high-resolution correlation framework of the relevant pelagic biomarkers (ammonoids, conodonts) linked to abiotic stratigraphic tools such as stable isotopes and magnetostratigraphy has been achieved; iii) adequate lithologies permit the integration of marine and continental palynological events with the new time frame and by this a most widely applicable recognition of the boundary from deeper off-shore settings to marginal marine and terrestrial environments. Especially the latter are fairly common in late Upper Triassic time and cover large areas in the Arctic, in Europe and in south(east)ern Gondwana; iv) the multistratigraphical approach may allow a correlation with the astrochronologically tuned time scale of the Newark basin and thereby a chronological dating of the NRB.

When Guembel (1859) introduced the Rhaetian he possibly could have defined it more carefully knowing the succeeding and nearly 150 years long controversy over scope, content, acceptation or refusal of his stage. His imprecise geographical delineation of the type region allowed a wide range of interpretations (from the Rätikon to R(h)ätische Alpen or the Roman province Rhaetium) and no identification of a type locality. This and a lithostratigraphic unit ("Schichten der *Rhaetavicula contorta*") without age-diagnostic, purely facies dependent shallow-water fossils at the base and no fossils below (Hauptdolomite Formation) were the classical ingredients for the succeeding unstable and confusing stratigraphic nomenclature - for the need of the golden spike concept an absolutely ideal example. When the Upper Triassic stages (and substages) were defined on the basis of ammonoid zones or faunas the Rhaetian still maintained its original status as "Zone der *Avicula contorta*" (Mojsisovics et al., 1895). Later it was substituted by a single ammonoid zone (of *Choristoceras marshi*) before Kozur (1973) concluded that a partial time-overlap must exist between the top-Norian Hallstatt ammonoid fauna and the lower Koessen beds. At the beginning of the eighties of the last century the Rhaetian was already abandoned (Tozer, 1979) and removed from the North American Time Scale. Only ten years later the Subcommission on Triassic Stratigraphy reinstalled the Rhaetian as the top-Triassic stage (Visscher, 1992), again without a proper definition. Ironically, the vivid revival of the Rhaetian was invented in North America when Carter (1993) described a strong radiolarian faunal change that occurred in close temporary proximity to the disappearance of *Monotis,* the appearance of the conodont *Misikella* and of the ammonoid *Paracochloceras*. This boundary has later been adopted by the STS (Orchard, 2003) and forms also the basis for the here proposed boundary options.

GEOGRAPHIC AND GEOLOGICAL LOCATION OF THE PROPOSED CANDIDATE

The Steinbergkogel is a small und unnamed summit (1245 m above sea level) situated in the south-western corner of sheet 96 (Bad Ischl), official topographical map of Austria 1:50,000. It is located just south of the westerly most salt mine gallery symbol (crossed hammers), 250 m to the southwest of the "S" in "Salzberg" (see Fig. 1), corresponding to the entrance of the Ferdinandstollen (Stollen = gallery in English) at an altitude of 1140 m. Access to Steinbergkogel is possible by a forest road that starts in the Echerntal (Tal = valley) and reaches after 7 km the Salzberg and the Ferdinandstollen from where the candidate section can be seen at a distance of 25 m when looking to the south. Alternatively one can reach the Steinbergkogel directly from Hallstatt by taking the cable car to Rudolfsturm (855 m) and following then a marked footpath along the prehistoric burial ground of the Hallstatt (Celtic) period and some Salt mine buildings in a north-westerly direction towards the Plassen peak to arrive at Ferdinandstollen within a one hour walk.

The proposed candidate (coordinates 47°33'50"N, 13°37'34"E) is exposed in a long abandoned quarry where blocks have been extracted to dismantle the galleries of the salt mine. Most of the classical Steinbergkogel ammonoid fauna (Mojsisovics, 1873-1902) may have

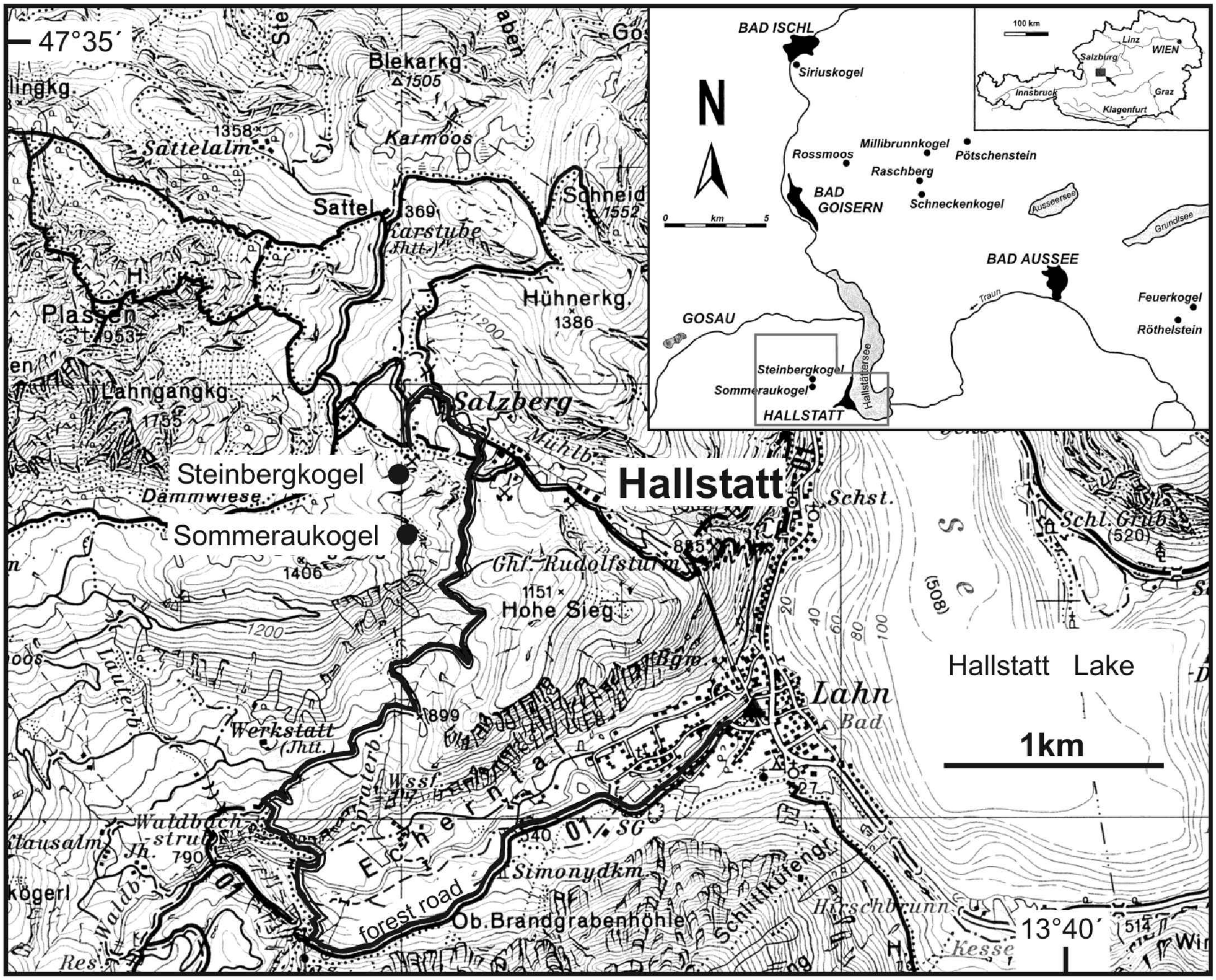

FIGURE 1. Topographic map of Hallstatt with location of the Steinbergkogel.

been collected by miners from that place, but Diener (1926) mentions another fossil locality about 100 m on strike to the west (called ST 2). As the latter is of slightly younger age than the quarry rocks, the old faunal record may be of mixed origin and thus of diachronous age.

The Steinbergkogel is composed of a uniformly (70°N) dipping sequence of different Hallstatt-type limestones (Krystyn et al., 1971) starting with a thick whitish, massive and unfossiliferous Lower Norian variety (Massiger Hellkalk Member) overlain by about 30-40 meters of bedded predominantly red (Hangendrotkalk Member) and in the top gray, fine-grained pelagic limestones (bioclastic wackestones) of Middle Norian to lowermost Rhaetian age (in new sense); the upper half of the gray limestone (Hangendgraukalk Member) develops thin clay interbeds that have eased the quarrying of stones and indicate a gradual transition to gray marls of the Zlambach Formation. The boundary interval corresponds to the basal part of the Hangendgraukalk and is well exposed along strike for 200-300 m along the northern footwall of the Steinbergkogel close to and within a small ravine that follows the lithological boundary from the resistant limestones to the softer transition beds.

Stratigraphically below the quarry section are more than 20 m of red Upper Norian limestones currently under study for bio- and magnetostratigraphy. They contain several layers with *Monotis salinaria, Heterastridium* and ammonoid cross-sections. The quarry consists of 4 meters of medium to thin bedded micritic limestones with the proposed candidate section located at the eastern end (Fig. 2). About 20 beds have been studied in detail, numbered from bottom to top as 103 to 122. Of boundary relevance has been identified bed 108 to bed 112A representing one meter of thickness and differing from over- and underlying rocks by a high bioclastic fossil content made of ammonoids and subordinate echinoderms. Above bed 113 the microfacies changes to a shelly-poor, mud-dominated facies type. Rock colors change around bed 107 from red to gray and return locally to gray-reddish mixed above bed 115. A low CAI of 1 excludes any thermal overprint and favors the preservation of the original paleomagnetic signal and of a primary δ^{13}C-record.

The Steinbergkogel bears beside the candidate section three other ammonoid localities of stratigraphic importance: 1) 30 m west of the GSSP candidate exposes a corresponding sequence at the western quarry end (STK 1 B-C) a promising but still not exploited fossil bed in the basal *Paracochloceras* interval; 2) in the ravine 100 m to the northwest of the quarry lies locality ST 2 with a fossil-rich bed that corresponds to conodont zone 1 (*bidentata-hernsteini* I. Z.); it has delivered *Dionites caesar* and a large *Sagenites reticulatus* and may be the original site of some of the *Sagenites* species described in Mojsisovics (1893) and 3) on top of the Steinbergkogel but without any stratigraphic connection to the GSSP candidate is a local neptunian dike (ST 1) named by Mojsisovics (1893) as "Weisser Crinoidenkalk" with a unique ammonoid assocation containing *Vandaites* (formerly *Choristoceras*) *saximontanum* and *Cycloceltites arduini*. This is now known as the youngest fossil horizon of the Hallstatt Limestone equalling the very top of the *Paracochloceras suessi* or more probably the basal *Vandaites stuerzenbaumi* Zone. The fossils occur in a vertical, up to 50 cm wide, irregular fissure that cuts the whole Hangendgraukalk Member down to a level at least 15 m below the transition from the Hallstatt to the Zlambach Formation (Krystyn, 1991). The fissure is easily distinguished from the surrounding red and micritic host rock by its light gray or whitish color due to the matrix-poor grain-supported, shell- and crinoid-dominated fabric.

FOSSIL RECORD

There is a wealth of literature referring to invertebrate faunas from the Steinbergkogel. Ammonoids have been described by Mojsisovics (1873-1902), pelagic bivalves by Kittl (1912), gastropods by Koken (1897), brachiopods by Bittner (1890) and conodonts by Mosher (1968). A comprehensive faunal list is found in Spengler (1919) with reference to the different locations.

Conodonts

To achieve stratigraphically reliable conodont ranges at least 10 kg of limestone have been dissolved from each bed between 108 and 112. This intense search has led to p-element recoveries of 50-100 specimens per sample, with *Epigondolella bidentata* dominating up to bed 110 and replaced by a *Misikella* dominance above. *Norigondolella steinbergensis*, usually the most frequent faunal element in this time interval is fortunately rare as well as ramiform elements. Taxonomic terminology for conodonts adopted in this paper is for species of the genus *Misikella* from Kozur and Mock (1991) and for *Epigondolella* (including *Mockina*) *bidentata* according to Orchard (1991). Increasing platform and size reduction in the latter species during its phylogenetic end phase (*Cochloceras* interval) leads to a predominance of small platform-less parvigondolellid forms in *Epigondolella* unfavorable environments. Those forms have been named *Parvigondolella andrusovi* Kozur & Mock or *Parvigondolella lata* Kozur & Mock and are described as diagnostic for a time interval younger than that of *E. bidentata*. In *Epigondolella* favorable facies "parvigondolellids" are, however, either fully (*P. andrusovi*) or for a major part (*P. lata*) time equivalent to *E. bidentata* and therefore considered here as morphological variants or ecostratigraphic morphotypes of the latter species.

A first conodont event is seen in bed 109 where *Oncodella paucidentata* and *Misikella hernsteini* appear – without known forerunners named only as FO dates. *Misikella hernsteini* is rare in bed 109 and 110 (5-10 specimens) but gets frequent from 111A onwards (Table 1). Bed 111A marks the FAD of *M. posthernsteini*, as phylogenetic successor of the fore-mentioned species, responsible for the most diagnostic conodont datum in the section and probably the worldwide best-documented FAD of *M. posthernsteini* in co-occurrence with *Paracochloceras*. With just two specimens in 111A and four in 111B *M. posthernsteini* is, however, very rare at the beginning but becomes frequent 30 cm above in bed 112 to get rare again higher up. The initial infrequence highlights the problem of how to recognize the FAD of *M. posthernsteini* in biofacially less favorable environments and use of this event without additional control may cause uncertainties in regional or intercontinental correlations.

Two conodont zones can be distinguished in the NRB interval of the proposed candidate section (Fig. 3) based on the successive appearances of species of the genus *Misikella*:

Zone 1: *Epigondolella bidentata – Misikella hernsteini* Interval Zone

This very short zone (Fig. 4) is characterized by co-occurrence of common *E. bidentata* and rare *M. hernsteini* in beds 109 and 110. The

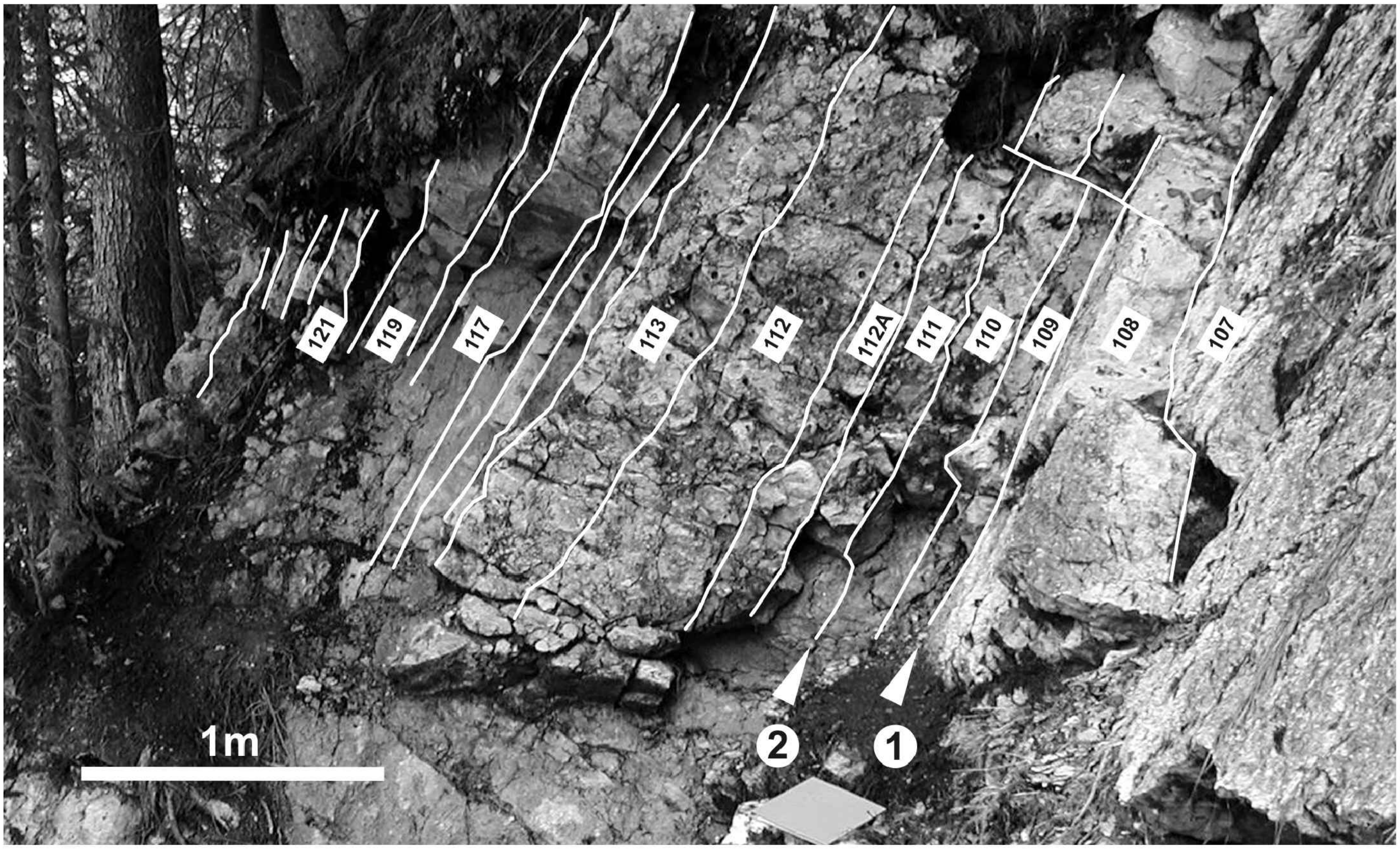

FIGURE 2. Photo of the candidate section showing bed sequence from 107 to 121.

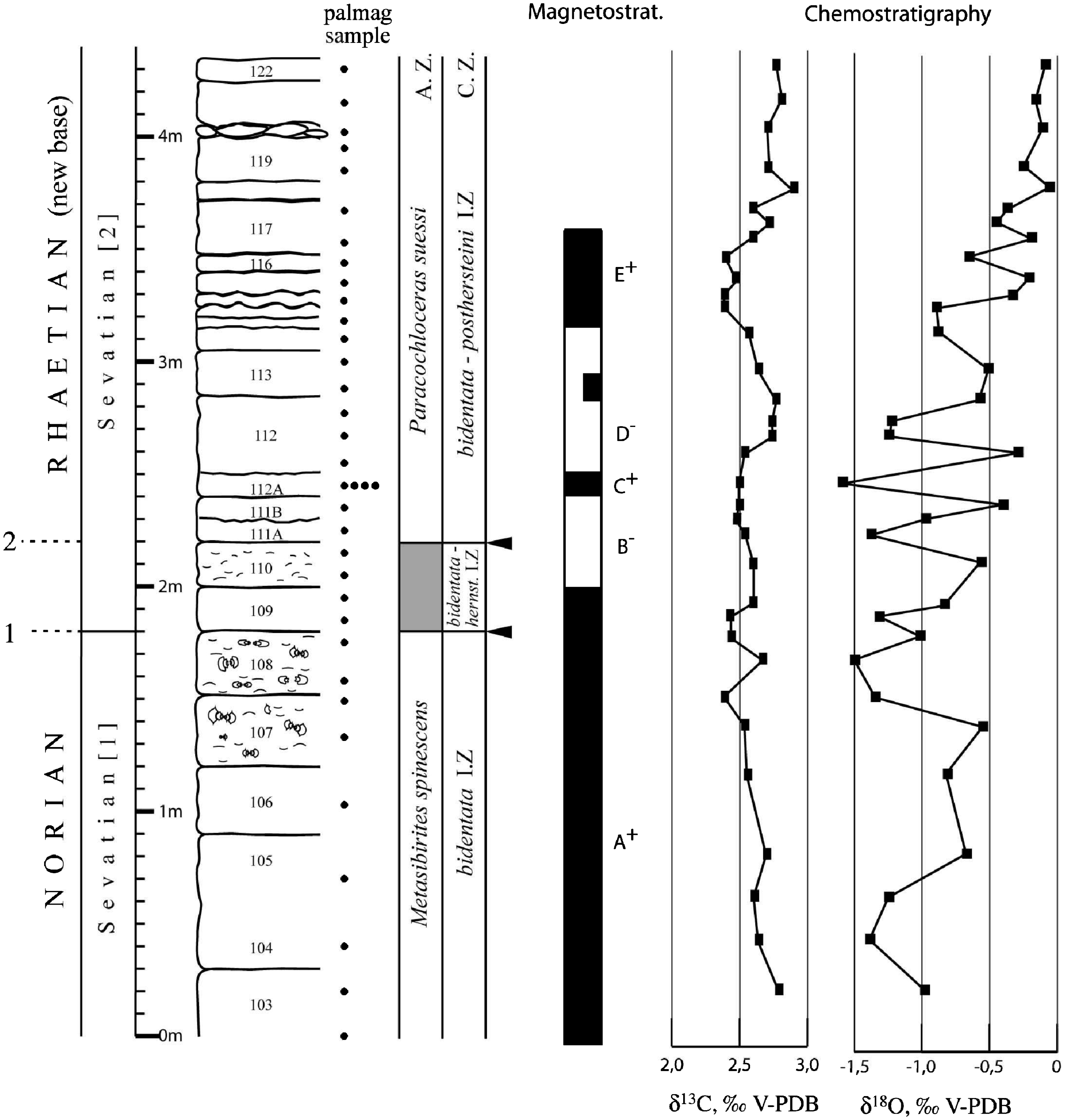

FIGURE 3. Integrated bio-, magneto- and chemostratigraphy of the candidate section. Note boundary options 1 and 2.

zone is most probably the type level of *E. bidentata* (sample Sb-F1of Mosher, 1968, p. 945).

Zone 2: *Epigondolella bidentata – Misikella posthernsteini* Interval Zone

Beds from 111A onwards contain *M. posthernsteini* in low quantities compared to the very frequent *M. hernsteini*. Bearing in mind the large sample size (more than 5 kg) it may be difficult to detect the base of zone 2 with "on average" sampling. Normal sized *Epigondolella bidentata* becomes rare in Zone 2 and is replaced by juveniles resembling the genus *Parvigondolella*.

Considerable provincialism in top-Triassic conodonts limits the above-adopted zonation to the Tethyan realm where it has successfully been applied to sections in Austria (McRoberts et al., in press), Turkey (Gallet et al., 2007), Oman and Timor (Krystyn, unpublished data).

AMMONOIDS

Vertical ranges of newly collected time-diagnostic ammonoids are shown in Figure 3. *Metasibirites spinescens* is very common in beds 107 and 108, *Paracochloceras* starts in bed 111 and is frequently found up to bed 113 with rare occurrences till the top (bed 122). Other trachyostracean

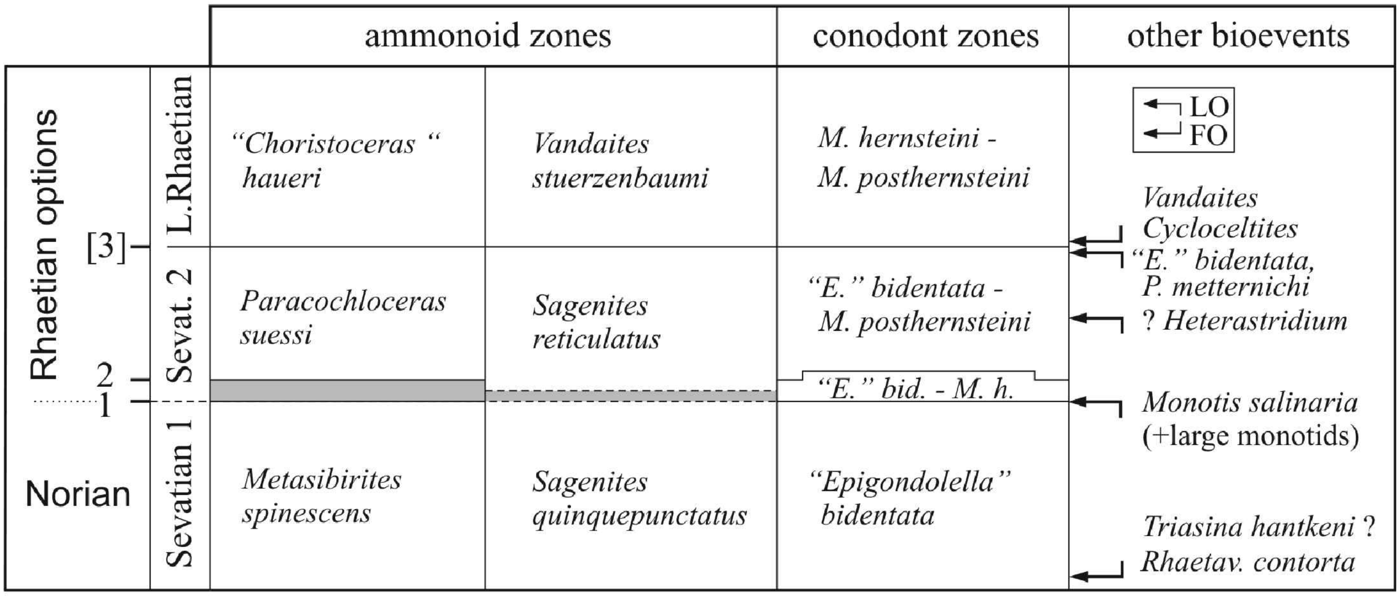

FIGURE 4. Correlation of ammonoid and conodont zones based on Steinberkogel data with integration of additional bioevents.

ammonoids are currently missing except for *Dionites* (beds 109 and 110) and a tiny specimen of *Gabboceras* from bed STK 1B-10 corresponding to bed 109. *Gabboceras* has recently been described by Taylor andGuex (2002) from the basal Gabbs Formation of New York Canyon (Nevada) in a position that may closely match the NRB interval in Steinbergkogel. The genus *Dionites* may have a range across the Norian-Rhaetian boundary and as such may not be boundary-diagnostic. More important is a conodont-dated correlative of bed 110 in ST 2 that contains *Sagenites reticulatus* and *Dionites caesar*.

Combining all above cited faunal records permits the discrimination of two ammonoid zones (Fig. 4), a lower with *Metasibirites* (bed 107 to 108) and an upper with *Paracochloceras* (from bed 111A upwards). An alternative and closely matching zonal scheme with *Sagenites quinquepunctatus* below and *Sagenites reticulatus* above also seems justified under the assumption that the nodose "*Sagenites princeps*" of Mojsisovics (1893, plate 148, fig. 1) has come from bed ST 1B-10 as is suggested from its preservation. Stratigraphically indifferent taxa including *Rhabdoceras suessi, Pinacoceras metternichi, Placites, Arcestes, Cladiscites, Paracladiscites, Rhacophyllites* and *Megaphyllites* are common in all beds. Kozur favours as Lower Rhaetian guide the genus *Cochloceras*, which has led to certain misunderstanding because *Cochloceras suessi* is already a *Paracochloceras* (see Mojsisovics, 1893, p. 581). *Cochloceras* s.str. is nearly monospecific, comparably rare and therefore not useful as a zonal index.

Pelagic Bivalves

Monotids of the *Monotis salinaria* group are common in Steinbergkogel (Kittl, 1912; Spengler, 1919, p. 359) and almost restricted to the Hangendrotkalk Member where they appear in several layers within an interval of 10-15 m. Of special interest is a single unhorizoned large specimen of *M. salinaria* from the Steinberkogel preserved as grey micritic limestone and housed in the collections of the Center of Earth Sciences (of Vienna University). According to the known lithologies the piece must have been derived from the short interval corresponding to beds 108 and 109. This supposed position is in agreement with *Monotis* age data from Hernstein, Lower Austria (McRoberts et al., in press) and would confirm the late Sevatian top-range of *Monotis salinaria* in the Hallstatt Limestone.

Brachiopods and Gastropods

Several species including *Oxycolpella oxycolpos* and the "Norian" *Halorella pedata* have been described by Bittner (1890). Gastropods are represented by 12 genera (Koken, 1897) of more paleoecological and perhaps bathymetrical value.

TOWARDS PALYNOLOGICAL CHRACTERIZATION OF THE BASE OF THE RHAETIAN

Samples from the marly interlayers of the transition zone to the Zlambach Formation in the ravine north of the quarry have turned out to be barren. This is compared to the rather rich palynological content of other Zlambach sections (Krystyn and Kuerschner, 2005), an unexpected and unfortunate result. Several previous palynological studies of Rhaetian reference sections in the Alpine realm, such as Kendelbach, and Weissloferbach (e.g., Morbey, 1975; Morbey and Neves, 1944; Schuurman, 1979) have suggested that the presence of *Rhaetipollis germanicus* may be a valuable biostratigraphic marker to characterize the Rhaetian. However, the entry level of *Rhaetipollis germanicus* is yet unknown because of the carbonaceous nature (facies) of the deposits (e.g. Plattenkalk, Fig. 7) underlying the Rhaetian deposits (Koessen or Zlambach beds). Among dinoflagelate cysts, *Rhaetogonyaulax rhaetica* have been found to be useful, but again, the exact lowest occurrence datum is yet unknown. Our preliminary data from Turkey (Kasimlar Formation, Taurus Mountains) suggest that *R. wiggensii*, associated with *Heibergella* occurs in sediments of Sevatian 1 age (dated by *Monotis salinaria*) while *R. rhaetica* is still absent. Alternatively, succeeding palynological events higher up in the Koessen and Zlambach beds could be useful to characterize the base of the Rhaetian. Current research in the Kleiner Zlambach section revealed the top occurrences of several sporomorphs such as *Enzonalasporites vigens*, *Vallasporites ignacii*, *Patinasporites toralis, Ellipsovelatisporites rugosus, Partitisporites* spp., *Triadispora* spp., while higher up in the section new elements, such as *Chasmatosporites* sp., *Quadraeculina anaeliformis, Limbosporites lundbladii*, enter the record (Fig. 5). These sporomorph assemblages correlate with the transition between the TL and LR concurrent-range zones distinguished by Morbey and Neves (1974) within the Karparthian facies of the Koessen beds in the Kendelbach section. Intriguingly, the marine organic-walled phytoplankton record shows an acme of dinoflagel-

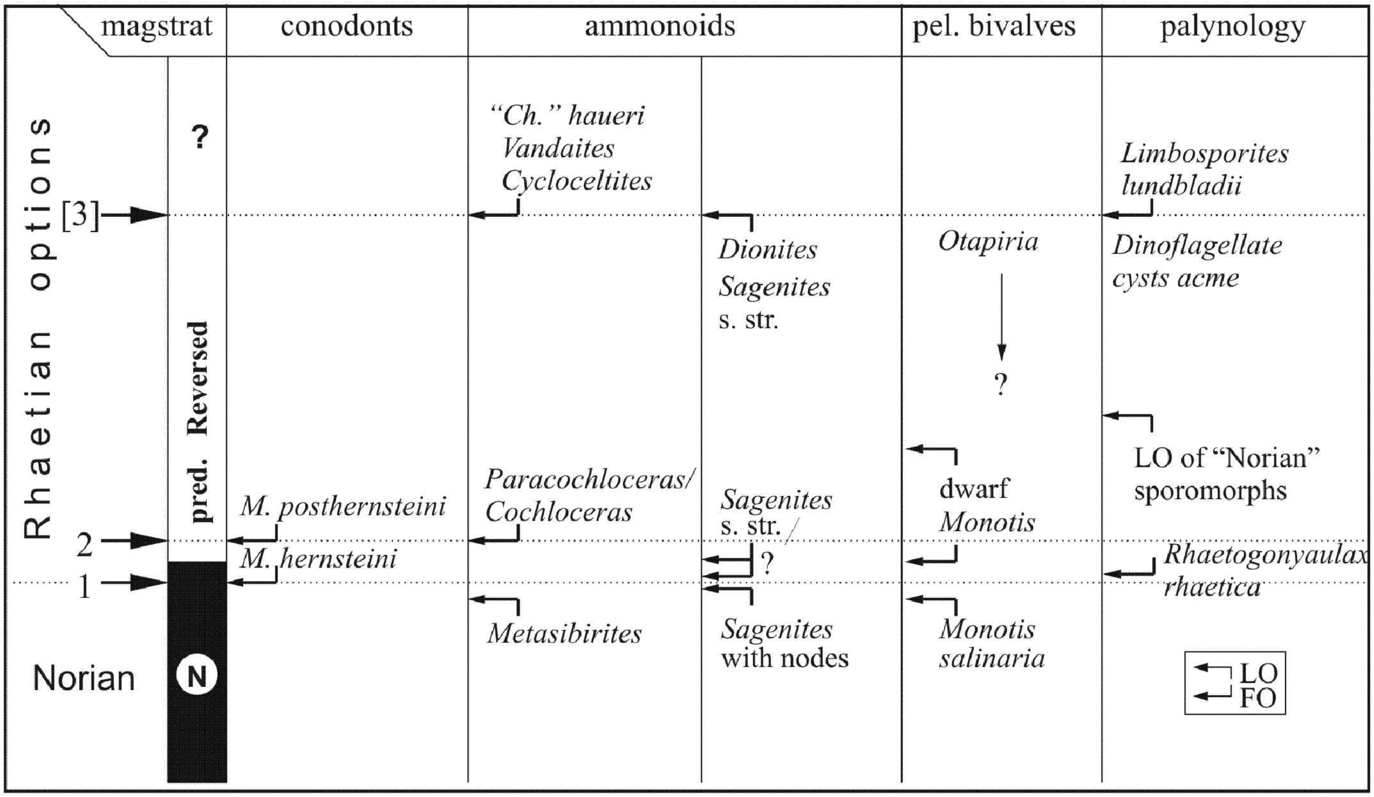

FIGURE 5. First and last appearances/occurrences of biomarkers with respect to Norian-Rhaetian boundary options.

late cysts (*Rhaetogonyaulax, Noricysta, Heibergella*) and coincides approximately with the *Cycloceltites – Vandaites* event in the ammonoid record mentioned above (Fig. 5).

PRELIMINARY NORIAN-RHAETIAN MAGNETOSTRATIGRAPHIC RESULTS

Paleomagnetic analyses have been performed using a three-axis 2G cryogenic magnetometer in the m-metal/steel magnetically shielded laboratory at the Institut de Physique du Globe de Paris. Thermal demagnetization of samples collected through the part of the Steinberkogel section that contains the Norian-Rhaetian boundary reveals a rather complex paleomagnetic behavior characterized by three successive magnetization components. A low unblocking temperature magnetic component is first isolated up to 150°C with a direction close to that of the present day field at the site. A second component is next isolated in the intermediate to high temperature range. Its unblocking spectrum is strongly overlapped by those of the two other components, which prevents the determination of a reliable paleomagnetic direction for this intermediate component. However the latter was clearly acquired while the field experienced a reversed polarity state. Finally a high temperature magnetization component showing dual polarities is obtained below 600°C. Again, because of overlapping unblocking spectra, the directions isolated for this component are often biased, but magnetic polarities could be confidently determined in approximately 2/3 of the sample collection. Figure 6 shows the magnetic zonation hence obtained from the Steinberkogel section and its comparison with previous results from the Scheiblkogel (Austria) and Oyuklu (Turkey) sections (Gallet et al., 1996, 2007). At this step of our study, at least five magnetic polarity intervals are clearly identified in Steinbergkogel, each from several samples; one additional normal polarity zone may also exist within reversed interval D- (half bar in Fig. 1) but it remains poorly defined by only one sample with a biased direction. Nevertheless the magnetic zonation obtained in Steinberkogel agrees quite well with the previous magnetostratigraphic results. The Norian/Rhaetian boundary interval appears to occur very close to a magnetic polarity reversal (magnetic intervals A+/B- in Steinberkogel; Fig. 6), which is also distinctly identified both in the Scheiblkogel and Oyuklu sections and allows an independent proof of the high-resolution correlation of the two Norian-Rhaetian boundary options with the closely successive *Misikella* dates (Fig. 6). These preliminary data therefore encourage further work on the Steinberkogel section.

ISOTOPE CHEMOSTRATIGRAPHY

Samples for carbon isotopes were measured from bed 103 to 122 (Fig. 3) on micro-drilled micrite and analyzed following the method reviewed by Spötl and Vennemann (2003) and described in detail in Richoz et al. (2007). $\delta^{18}O$ values do not co-vary with $\delta^{13}C$ (Fig. 3). The section has not experienced a thermal overprint (CAI 1) and the amount of organic matter, whose diagenesis might impart on the isotopic composition of carbonates, is very low (<1%) with limestones mostly pale gray or red. Moreover, the carbon isotopic curve is well correlatable with two other coeval quarry sections (1B and 1C) within variations as low as 0.2‰ (Richoz, unpublished data). All these observations are seen as conclusive to regard the carbon isotope data as reflecting the initial isotopic composition of seawater with no diagenetic alteration.

The values remain more or less constant all along the measured interval, varying between 2.4‰ to 2.9‰. Changes are thus very low but as certain peaks recur in the two other quarry sections, they are believed to represent primary variations of the seawater isotopic composition. A slow and of small amplitude decrease is observed until the middle of bed 112 followed by a short-term increase of 0.2‰ in top of bed 112. Isotopic values then decrease to reach +2.4‰ between beds 114B and 116, followed by a 0.5‰ increase in the topmost beds of the section. In conclusion, there are no significant carbon isotope variations around the two boundary options and the observed fluctuations are of too small amplitude for long-distance correlation except for the uppermost increase, which is probably a trend correlatable at least Tethys-wide.

The oxygen isotope values show high variability but a general trend can be read. Values stay around a mean value of -1‰ until beds

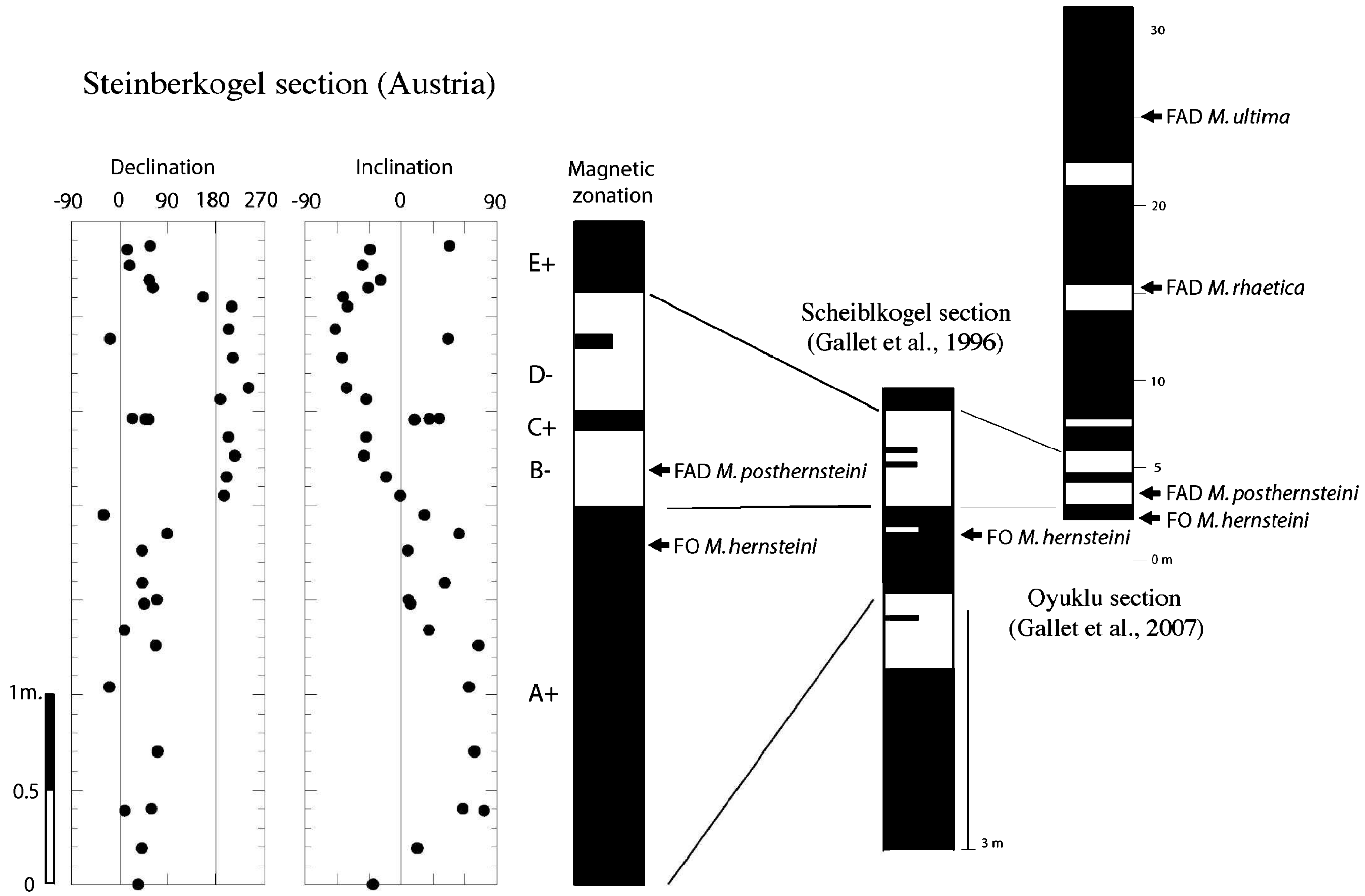

FIGURE 6. Norian-Rhaetian magnetostratigraphic results from the candidate section. These data are compared with the magnetic polarity sequences previously determined from the Austrian Scheiblkogel and Turkish Oyuklu sections (Gallet et al., 1996, 2007). The stratigraphic positions of key conodont events are indicated to the right of the three reported magnetic polarity sequences.

112/114 before increasing to values close to 0‰ in the last beds of the section.

COMPARISON WITH OTHER SECTIONS

From the western Tethyan realm, Muttoni et al. (2004) published a $\delta^{13}C_{carb}$ curve from Pizzo Mondello (Sicily) with constant carbon isotope values around 1.5‰ at the Norian-Rhaetian boundary (relocated at around 400m, Krystyn, oral comm.). Preliminary results from Turkey, Oman and Hernstein (Austria) confirm constant carbon isotope values through the boundary interval with a small increase higher-up in the bidentata-posthernsteini I.Z. (Richoz, unpublished data).

For the Panthalassan realm, Ward et al. (2004) published another $\delta^{13}C_{carb}$ curve from Queen Charlotte Islands (Kennecott Point, British Columbia), but suspect a diagenetically alterted signal. Nevertheless, the $\delta^{13}C_{carb}$ curve is also stable through the Norian-Rhaetian boundary.

Two sections in British Columbia provide $\delta^{13}C$ curves on organic matter material: Kennecott Point, Queen Charlotte Island (Ward et al., 2001 and 2004; Williford et al. 2006) and Black Bear Ridge at Williston Lake (Sephton et al., 2002). First studies at the Kennecott Point section (Ward et al., 2001, 2004) claimed to observe a positive excursion of around 1.5‰ at the extinction level of the bivalve *Monotis* (which is supposed to correspond with the NRB). However, in a new study with higher resolution (Williford et al., 2006, fig. 1), this peak seems to have been incorporated in the variability of $\delta^{13}C_{org}$ measurements and is no more distinguished. At Williston Lake, a peak of 1.5‰ clearly exists despite a low resolution (Sephton et al. 2002). The last occurrence of *Monotis* corresponds to the middle of the positive $\delta^{13}C_{org}$ excursion, which is culminating 2-3m above the boundary. In their reply to a comment from Hall and Pitaru (2003), Wignall et al. (2003) argued that "recent field investigation indicates that the top *Monotis* surface at Black Bear Ridge records an interval of early Rhaetian condensation". Thus, the peak could be in reality higher up in the Rhaetian and not at the boundary.

NORIAN-RHAETIAN BOUNDARY OPTIONS

Following the recommendations of the Subcommission on Triassic Stratigraphy a future Norian-Rhaetian boundary may be defined on the appearance of the conodonts *Misikella hernsteini* or *Misikella posthernsteini*. These two options have been found in the proposed candidate GSSP in a distance of 40 cm above each other and are cross-correlated with ammonoids, magneto- and chemostratigraphy. The events correspond to the base of bed 109 and 111, respectively, and are marked in Figures 3-5 by arrows or numbers. Event 3 in Figures 4 and 5 is considerably younger, well established in the ammonoid fauna (Fig. 4) and palynoflora (Fig. 5) but not recorded in the conodonts (Fig. 5); it is therefore no longer considered and also not represented in the exposed section in Steinbergkogel. No significant C- and O- isotopic variations occur around the two boundary options.

Option 1 (FO of *Misikella hernsteini*)

This lower event corresponds to the FO of *Misikella hernsteini* 1.80 m above section base. It is closely accompanied by the disappearance (LO) of the ammonoid genera *Metasibirites* and *Sagenites* s.l. (with lateral nodes). Another proxy for option 1 is the worldwide disappearance of large *Monotis* (*M. salinaria*/*subcircularis* in low and *M. ochotica* group in high paleolatitudes). A paleomagnetic reversal closely follows boundary option 1 (Fig. 5).

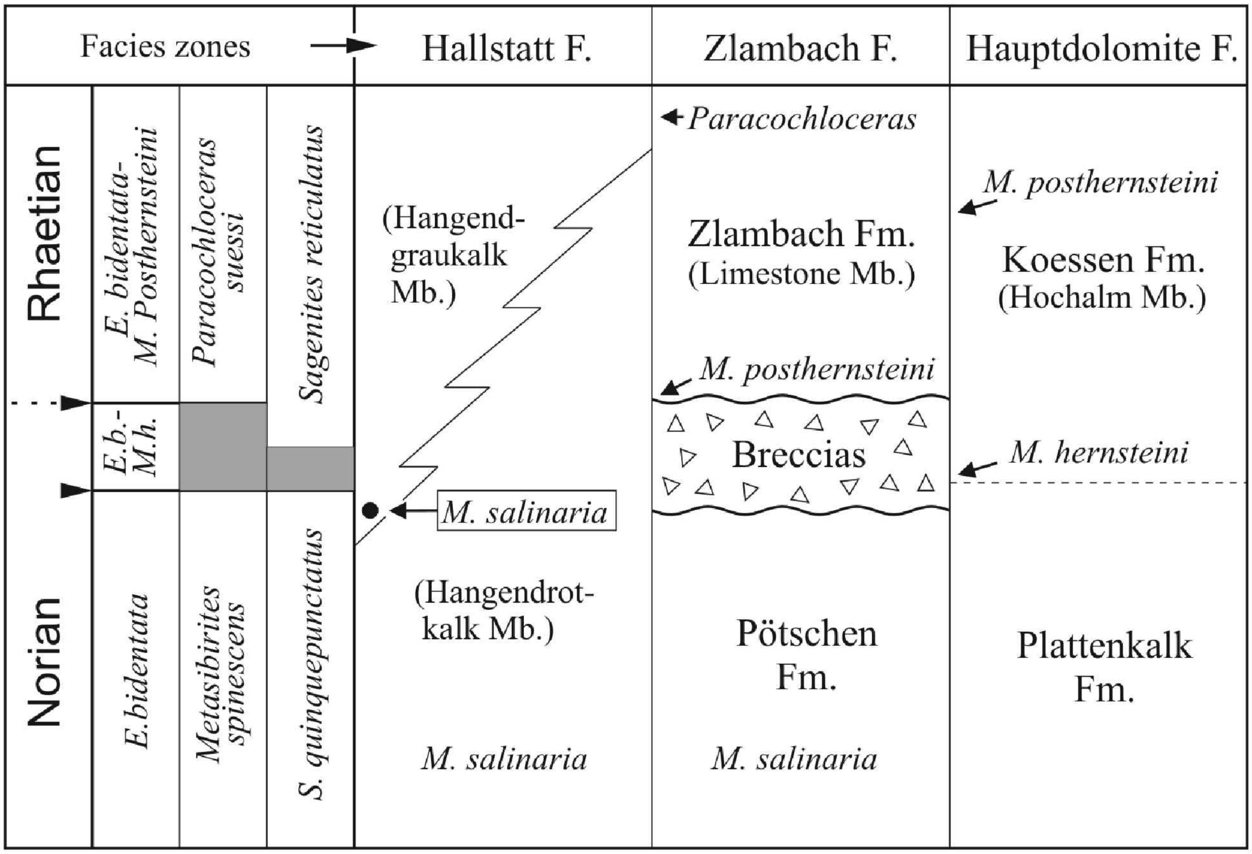

FIGURE 7. Regional correlation of Norian-Rhaetian boundary options within the Northern Calcareous Alps.

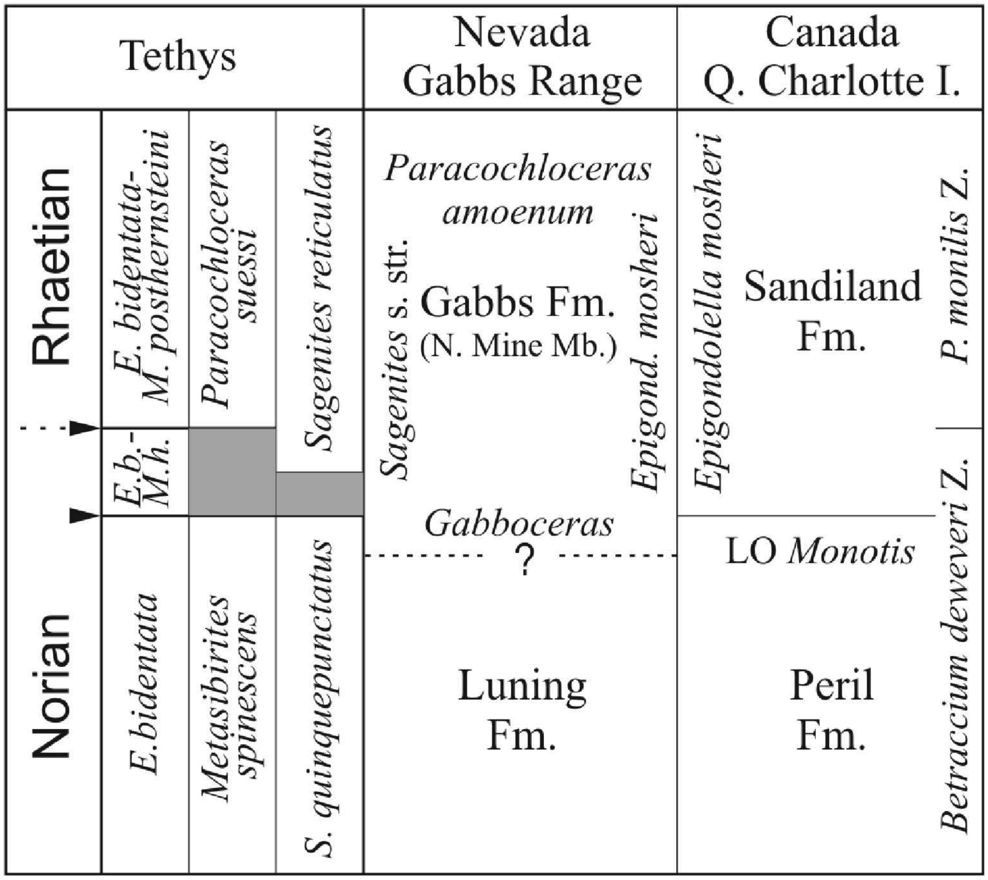

FIGURE 8. Tethys–Panthalassa correlation of the Norian-Rhaetian boundary options.

Option 2 (FAD of *Misikella posthernsteini*)

The FAD of *Misikella posthernsteini* is located 2.20 m above section base and correlates to the FO of *Paracochloceras suessi*. Other proxies are the presence of *Sagenites* s.str. and a position close to the base of a reversal (Fig. 5).

REGIONAL CORRELATIONS

The Zlambach and Koessen formations are two main top-Triassic lithofacies developments in the Northern Calcareous Alps with some importance for the Norian-Rhaetian boundary. New conodont data and geological observations demonstrate contemporaneity of the lower Zlambach Formation (Limestone Member) with the *bidentata-posthernsteini* Zone and a discontinuity towards the underlying Poetschen Formation where the *bidentata-hernsteini* Zone is missing or replaced by breccias (Fig. 7). The Limestone Member is extraordinary in containing radiolarians of the *Precitriduma monilis* Zone (under study by H. Mostler) and a rich marine and terrestrial palynoflora (Krystyn and Kuerschner, 2005). A rare and not much cited conodont record from the basal Hochalm Member of the Koessen Formation (Golebiowski, 1990) has produced *M. hernsteini* far below *M. posthernsteini*, suggesting an age of the base of the Koessen beds close to the *hernsteini* date and close to option 1 (Fig. 7).

INTERCONTINENTAL CORRELATIONS

A global correlation of the two *Misikella* dates seems very difficult because of the high conodont provincialism between the Tethys and the (eastern) Panthalassa realm where *Misikella* appears distinctly later and is extremely rare. *Epigondolella mosheri*, seen as coeval representative of the basal Rhaetian in North America (Orchard and Tozer, 1997), is missing in the Tethys and useless for a high-resolution boundary comparison. The latest data from the Gabbs Formation (Nun Mine Member) indicate a gross age analogy between the two *Sagenites* subzones in New York Canyon (Taylor and Guex, 2002) with the *S. reticulatus* Zone in Steinbergkogel (Fig. 8). *Gabboceras delicatum* may additionally indicate for the lower Nun Mine Member a timely correspondence with the *bidentata-hernsteini* Zone (Fig. 8).

Special attention has been focused on the deepwater succession in Queen Charlotte Islands where the base of the "radiolarian-Rhaetian" is defined and drawn 10 m above the LO of *Monotis* and the FAD of *Epigondolella mosheri*. A comparison with Steinbergkogel implies that the FAD of *E. mosheri* may be taken as a proxy of option 1 and the base of the *P. monilis* Zone as a proxy of option 2 in agreement with Orchard et al. (2007).

ACKNOWLEDGMENTS

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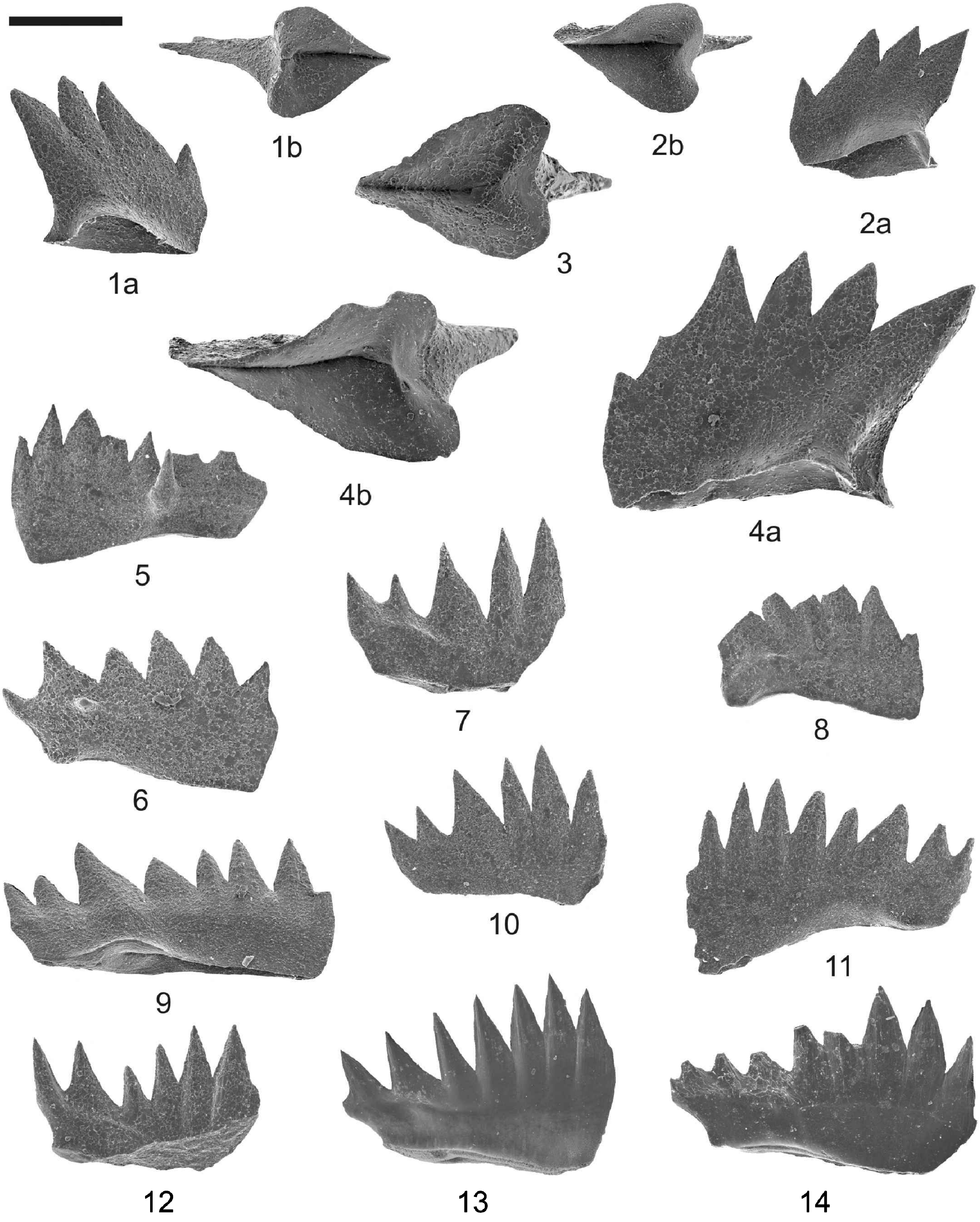
PLATE CAPTION

PLATE 1. Conodonts from the candidate section (Figs. 1-11) and the lower Sevatian *Monotis* bed 15 m below (Figs. 12-14). Scale bar = 180 microns. **Figs. 1-4:** *Misikella posthernsteini* Kozur & Mock; **1-2**: bed 111A (base of 111), **3-4**: bed 112. **Figs. 5-8**: *Epigondolella bidentata* Mosher; **5-6**: bed 113, 7: bed 110, **8**: bed 117. **Figs. 9-11:** *Epigondolella bidentata* Mosher, "*Parvigondolella stage*"; bed 110. **Figs. 12-14:** *Epigondolella bidentata* Mosher, large early growth stage; *Monotis* bed.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Lucas, S.G. and Spielmann, J.A., eds., 2007, The Global Triassic. New Mexico Museum of Natural History and Science Bulletin 41.

LATE TRIASSIC PALYNOSTRATIGRAPHY: THE EARLY RHAETIAN IN THE NORTHERN CALCAREOUS ALPS (AUSTRIA)

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New data from an integrated palynological (pollen/spores, dinoflagellate cysts, acritarchs), (micro)paleontological (ammonoids, bivalves, conodonts, radiolarians) and magnetostratigraphic study of a 50 m thick Sevatian-Rhaetian transition in the Zlambach Formation (Kleiner Zlambachgraben section near Hallstatt, Austria) are presented. This well exposed Western Tethys key section of alternating deeper water limestones and marls shows successive FO and LO events in the marine faunal and phytoplankton record, as well as in the coeval terrestrial pollen/spore record.

Pollen/spore assemblages are dominated by the Classopollis group. However, two distinct palynological zones can be recognized: early Rhaetian assemblages still include a variety of typical Late Triassic elements (*Enzonalasporites*, *Vallasporites*, *Patinasporites, Ellipsovelatisporites*, *Partitisporites, Triadispora*), whereas middle Rhaetian assemblages show the presence of new elements, such as *Chasmatosporites, Quadraeculina, Limbosporites*. Dinoflagellate cysts (*Rhaetogonyaulax*, *Suessia*, *Dapcodinium*), are abundant in the higher part of the studied section. Intriguingly, the transition between the two zones is characterized by an acme of dinoflagellate cysts (*Rhaetogonyaulax, Noricysta, Heibergella*). These events in the palynological record coincide approximately with the FO of characteristic Late Triassic ammonoids (*Choristoceras, Cochloceras*).

The regional and global significance of the nature and magnitude of this event is discussed.

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THE CONTINENTAL TETRAPOD-BEARING TRIASSIC OF SOUTH BRAZIL

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Abstract—The Rosário do Sul Group is one of the better-known tetrapod-bearing continental deposits of Triassic age. It crops out in central Rio Grande do Sul, south Brazil, and has yielded a fauna of more than 40 valid species, including temnospondyl, procolophonoideans, dicynodonts, cynodonts, sphenodontian, rhynchosaurs, and archosaurs. Its fossil record is herein briefly assessed, along with the stratigraphy of its bearing sequences. This includes the Early (perhaps earliest) Triassic Sanga do Cabral Formation, which correlates to the *Lystrosaurus*/ "Impoverished" zones of the Karoo Basin, and a second major stratigraphic sequence of Mid-Late Triassic age that broadly corresponds to the Santa Maria and Caturrita formations. The lower, cynodont-dicynodont dominated fauna of that sequence is partially Chañarian (Ladinian) in age, and encompasses the *Dinodontosaurus* Assemblage-Zone. The Late Triassic fauna includes the *Hyperodapedon* and Ictidosaur assemblage-zones. The former, dominated by rhynchosaurs, includes some of the oldest known dinosaurs, and can be given an Ischigualastian (Carnian) age. The younger fauna contains advanced cynodonts and procolophonids, as well sphenodontians, most probably corresponding to the latest Triassic.

INTRODUCTION

The Rosário do Sul Group, and especially the Santa Maria Formation within it, are well known for their tetrapod record. These Triassic deposits crop out along a 500 km belt in the south-central portion of Rio Grande do Sul, south Brazil (Fig. 1). Fossil tetrapods are, however, not restricted to the Santa Maria Formation, but also abound in the Sanga do Cabral and Caturrita formations, which respectively lay below and above that stratigraphic unit (Andreis et al., 1980). Ages attributed to the Rosário do Sul Group are mainly based on biostratigraphic studies of its tetrapod assemblages, and extend for most of the Triassic, with evidence of Induan-Olenekian (Cisneros and Schultz, 2002), Anisian (Abdala and Sá-Teixeira, 2004), Ladinian (Abdala et al., 2001), Carnian (Langer, 2005a) and Norian (Rubert and Schultz, 2004) faunas.

This contribution includes a review of the fossil tetrapod record of the Rosário do Sul Group. Firstly, this is assessed according to the phylogenetic affinities of the valid taxa (Tables 1, 2), which are discussed based on most recent revisions of their taxonomic status. Thereafter, a second approach is taken, and current knowledge on the depositional sequences of the Rosário do Sul Group is used to order the fossil record of different sites in a stratigraphic framework. Finally, data on sequence stratigraphy of fossil-bearing deposits and phylogeny of fossil taxa are assembled to produce an as comprehensive as possible view of the faunal evolution of the South Brazilian Triassic.

Institutional abbreviations: MCN, Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul; UFRGS, Instituto de Geociências, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brasil. These are indicated only if there is no bibliographic reference to the specimen/taxon in question.

FOSSIL RECORD

The fossil biota of the Rosário do Sul Group includes a minimum of 45 formally proposed, and valid tetrapod species: one temnospondyl, four procolophonoideans, three dicynodonts, 15 cynodonts, one sphenodontian, five rhynchosaurs, and 16 archosaurs. The picture is, however, rather different in terms of abundance. Azevedo et al. (1990) quantified the fossil record of the Santa Maria Formation, where dicynodonts represent about 60% of the specimens collected in most Middle Triassic assemblages, while rhynchosaurs account for about 90% in those of Carnian age. Other faunas are, conversely, dominated by cynodonts (Abdala et al., 2001).

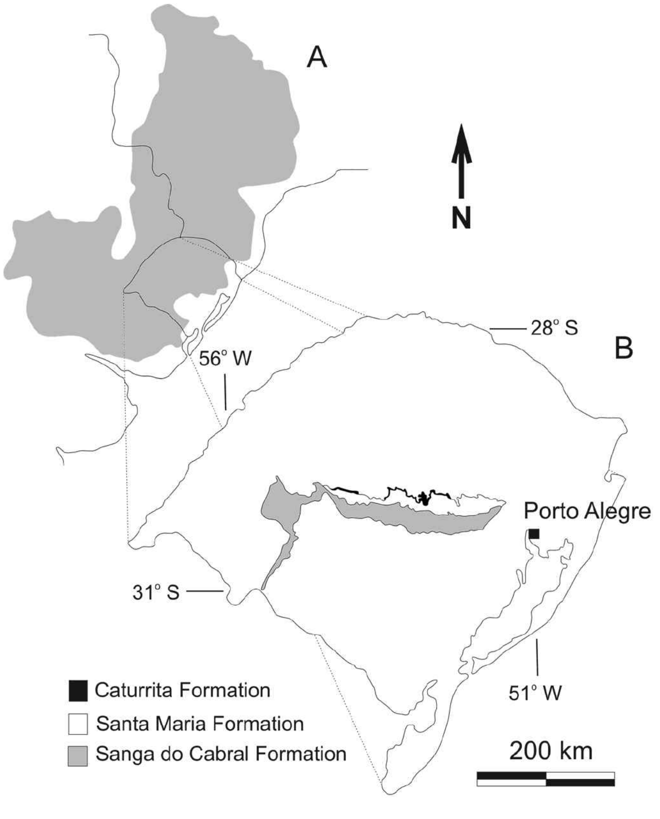


FIGURE 1. A, Map of the Paraná Basin (gray) in east-central South America, showing the location of Rio Grande do Sul, in south Brazil. B, Map of Rio Grande do Sul depicting the outcrop belt of the Rosario do Sul Group (based on DaRosa, 2005; DaRosa and Faccini, 2005).

Temnospondyli

Lavina and Barberena (1985) assigned fragmentary temnospondyl remains from the Sanga do Cabral Formation to the Lydekkerinidae and Rhytidosteidae, but these have been recently reviewed by Dias-da-Silva et al. (2005, see also Dias-da-Silva, 2003), and referred to either Rhytidosteidae or Temnospondyli *incertae sedis*. More complete mate-

TABLE 1. Fossil record presented by monophyletic hierarchy of Temnospondyli, Procolophonoidea, and Therapsida in the Rosário do Sul Group, Triassic of Rio Grande do Sul, Brazil.

Monophyletic hierarchy	Chronological/Stratigraphical range outside Brazil
Rhytidosteidae (Marsicano and Warren, 1998)	Late Permian-Olenekian (Marsicano and Warren, 1998; Warren et al. 2000)
Sangaia lavinai (Dias-da-Silva and Marsicano, 2006)	————
Owenetidae (Cisneros et al., 2004)	Late Permian -Induan (Modesto et al., 2003)
Candelaria barbouri (Cisneros et al., 2004)	————
Procolophonidae (Laurin and Reisz, 1995)	Late Permian -Rhaetian (Sues et al., 2000, Modesto et al., 2001)
Procolophoninae (DeBraga, 2003)	Induan-Olenekian (DeBraga, 2003; Spencer and Benton, 2004)
Procolophon (de Braga, 2003; Cisneros and Schultz, 2002; Dias da Silva et al., 2006)	*Lystrosaurus* Assemblage Zone and “Impoverished zone” (Neveling et al., 1999) and Fremouw Formation (Colbert and Kitching, 1975), Induan-Olenekian, Karoo Basin and Antarctica (Damiani et al., 2000)
P. pricei (Cisneros and Schultz, 2002)	Undefined stratum of the Karoo Basin (Cisneros and Schultz, 2002)
P. brasiliensis (Cisneros and Schultz, 2002)	————
Leptopleurinae (DeBraga, 2003)	Olenekian-Rhaetian (Sues et al., 2000, DeBraga, 2003)
Soturnia caliodon (Cisneros and Schultz, 2003)	————
Kannemeyeriiformes (Maish, 2001)	Olenekian-Norian (Lucas, 1998; but see Thulborn and Turner, 2002)
Dinodontosaurus pedroanum (Lucas and Harris, 1996)	Chañares Formation, Ladinian, Argentina (Cox, 1965)
Stahleckeriidae (Vega-Dias et al., 2004)	Anisian-Norian (Lucas, 1998)
Stahleckeria potens (Vega-Dias et al., 2005)	————
Ischigualastia sp. (Peruzzo and Araújo Barberena, 1995)	Ischigualasto Formation, Carnian, Argentina (Rogers et al., 1993)
Jachaleria (Vega-Dias and Shultz, 2004)	Los Colorados Formation, Carnian/Norian, Argentina (Bonaparte, 1982; Abdala et al., 2001)
J. candelariensis (Vega-Dias and Schultz, 2004)	————
Cynodontia (Hopson & Kitching, 2001)	Late Permian-Recent
Protheriodon estudianti (Bonaparte et al. 2006a)	————
Traversosontidae (Abdala et al., 2006)	Olenekian-Norian (Abdala et al., 2006)
Luangwa (Abdala and Sá-Teixeira, 2004)	Ntawere Formation, Anisian, Zambia (Abdala and Sá-Teixeira, 2004)
L. sudamericana (Abdala and Sá-Teixeira, 2004)	————
Traversodon stahleckeri (Barberena, 1981a)	————
Santacruzodon hopsoni (Abdala and Ribeiro, 2003)	————
Massetognathus (Abdala and Giannini, 2000)	Chañares Formation, Ladinian, Argentina (Abdala and Giannini, 2000)
M. ochagaviae (Barberena, 1981b)	————
Gomphodontosuchus brasiliensis (Hopson, 1985)	————
Exaeretodon (Abdala et al., 2002a)	Ischigualasto Formation, Carnian, Argentina (Bonaparte, 1982)
E. major (Abdala et al., 2002a)	————
E. riograndensis (Abdala et al., 2002a)	————
Chiniquodontidae (Abdala and Giannini, 2002)	Ladinian-Carnian (Abdala and Giannini, 2002)
Chiniquodon (Abdala and Giannini, 2002)	Chañares and Ischigualasto formations, Ladinian-Carnian, Argentina (Abdala and Giannini, 2002)
C. teotonicus (Abdala and Giannini, 2002)	Chañares Formation, Ladinian, Argentina (Abdala and Giannini, 2002)
Clade 8 (Bonaparte et al., 2005)	Norian-Recent (Lucas and Hunt, 1994)
Therioherpeton cargnini (Bonaparte and Barberena, 2001)	————
Charuodon tetracuspidatus (Abdala and Ribeiro, 2000)	————
Prozostrodon brasiliensis (Bonaparte and Barberena, 2001)	————
Tritheledontidae (Sidor and Hancox, 2006)	Norian- Early Jurassic (Lucas and Hunt, 1994; Sidor and Hancox, 2006)
Riograndia guaibensis (Bonaparte et al., 1999)	————
Irajatherium hernandezi (Martinelli et al., 2005)	————
Brasilodontidae (Bonaparte et al., 2005)	————
Brasilodon quadrangularis (Bonaparte et al., 2005)	————
Brasilitherium riograndensis (Bonaparte et al., 2005)	————

rial includes a partial mandible (Dias-da-Silva, 1998) and skull. The latter was described by Dias-da-Silva et al. (2006a) as a new rhytidosteid, *Sangaia lavinai* (Dias-da-Silva and Marsicano, 2006). According to those authors, *Sangaia* is most closely related to the Indian form *Indobatrachops panchetensis*, from the Panchet Formation, Induan of the Damodar Valley (Chatterjee and Roy-Chowdhury, 1974; Lucas, 1998). In addition to these records from the Sanga do Cabral Formation, fragmentary temnospondyl remains were also reported from the Santa Maria Formation (Richter, 2001).

Parareptilia

In the Rosário do Sul Group, parareptiles are known based only on procolophonoideans (*sensu* Lee, 1995), whereas the possible occurrence of a pareiasaur (Schultz and Dias-da-Silva, 1999; Lucas, 2002) was dismissed by Cisneros et al. (2005). Four taxa were described: *Candelaria barbouri* Price, 1947 (see also DaRosa et al., 2004a); *Procolophon pricei* Lavina, 1983; *Procolophon brasiliensis* Cisneros and Schultz, 2002; and *Soturnia caliodon* Cisneros and Schultz, 2003. A further partial skull was

TABLE 2. Fossil record presented by monophyletic hierarchy of Sphenodontia, Rhynchosauria, Prolacertiformes, and Archosauria in the Rosário do Sul Group, Triassic of Rio Grande do Sul, Brazil.

Monophyletic hierarchy	Chronological/Stratigraphical range outside Brazil
Clevosauridae (Bonaparte and Sues, 2006)	Carnian-Early Jurassic (Fraser and Benton, 1989; Sues and Reisz, 1995)
Clevosaurus (Bonaparte and Sues, 2006)	Norian-Early Jurassic (Fraser, 1994; Sues and Reisz, 1995)
C. riograndensis (Bonaparte and Sues, 2006)	————
Rhynchosauridae (Dilkes, 1998)	Anisian-Carnian (Langer and Schultz, 2000a)
"Mariante rhynchosaur" (Schultz and Azevedo, 1990)	————
Hyperodapedontinae (Langer and Schultz, 2000b)	Ladinian?-Carnian (Flynn et al., 1999, Langer et al., 2000)
N. gen. *sulcognathus* (Langer and Schultz, 2000b)	————
Hyperodapedon (Langer et al., 2000)	Ladinian?-Carnian (Flynn et al., 1999, Langer et al., 2000)
H. huenei (Langer and Schultz, 2000b)	————
H. mariensis (Langer et al., 2000)	Ischigualasto Formation, Carnian, Argentina (Langer et al., 2000)
H. sanjuanensis (Langer et al., 2000)	Ischigualasto Formation, Carnian, Argentina (Langer et al., 2000)
Prolacertiformes (Benton and Allen, 1997)	Late Permian-Noriano (Dilkes, 1998)
Archosauria (Gower and Sennikov, 2000)	Late Permian-Recent (Gower and Sennikov, 2000; Benton, 2004)
Spondylosoma absconditum (Galton, 2000, Langer, 2004)	————
Hoplitosuchus raui (Kischlat, 2000)	————
"Prestosuchus" loricatus (Kischlat, 2000)	————
cf. *Tarjardia* (Kischlat, 2000)	Chañares Formation, Ladinian, Argentina (Arcucci and Marsicano, 1998)
Proterochampsia (Kischlat, 2000)	Ladinian-Carnian (Hsiou et al., 2002)
Cerritosausus binsfeldi (Price, 1946)	————
Proterochampsa (Barberena, 1982)	Ischigualasto Formation, Carnian, Argentina (Bonaparte, 1982)
P. nodosa (Barberena, 1982)	————
Rhadinosuchus gracilis (Kischlat, 2000)	————
Chanaresuchus (Hsiou et al., 2002)	Chañares and Ischigualasto formations, Ladinian-Carnian, Argentina (Hsiou et al., 2002)
C. bonapartei (Hsiou et al., 2002)	Chañares Formation, Ladinian, Argentina (Bonaparte, 1982)
Phytosauria (Doyle and Sues, 1995)	Carnian-Rhaetian (Doyle and Sues, 1995; Lucas, 1998)
Aetosauria (Heckert and Lucas, 2000)	Carnian-Rhaetian (Heckert and Lucas, 2000)
Aetosauroides (Desojo and Kischlat, 2005)	Ischigualasto Formation, Carnian, Argentina (Bonaparte, 1982)
Aetosauroides sp. (Desojo and Kischlat, 2005)	————
Rauisuchia (Gower, 2000)	Olenekian-Norian (Gower, 2000)
Barberenasuchus brasiliensis (Kischlat, 2000)	————
Prestosuchidae (Parrish, 1993)	Anisian-Carnian (Gower, 2000)
Prestosuchus chiniquensis (Kischlat, 2000)	————
Procerosuchus celer (Kischlat, 2000)	————
"*Karamuru vorax*" (Kischlat, 2000)	————
Rauisuchidae (Parrish, 1993)	Ladinian-Norian (Gower, 2000)
Rauisuchus tiradentes (Kischlat, 2000)	————
Dinosauriformes (Sereno and Arcucci, 2004)	Ladinian-Recent (Benton, 2004)
Sacisaurus agudoensis (Ferigolo and Langer, 2006)	————
Dinosauria (Padian and May, 1993)	Carnian-Recent (Benton, 2004)
Teyuwasu barberenai (Kischlat, 1999)	————
Saurischia (Langer, 2004)	Carnian-Recent (Langer, 2004)
Saturnalia tupiniquim (Langer, 2003)	————
Guaibasaurus candelariensis (Bonaparte et al., 2006b)	————
Herrerasauria (Langer, 2004)	Carnian-Norian (Langer, 2004)
Staurikosaurus pricei (Novas, 1993)	————
Sauropodomorpha (Langer, 2003)	Carnian/Norian-Late Cretaceous (Gauffre, 1993; Benton et al., 2000; Lucas and Hancox, 2001; Upchurch *et al*., 2004)
Plateosauridae (Yates, 2006)	Norian (Yates, 2003)
Unaysaurus tolentinoi (Leal et al., 2003)	————

also referred to the genus *Procolophon* (Langer and Lavina, 2000, Dias-da-Silva et al., 2006b), but without further detail. According to Cisneros et al. (2004), *Candelaria barbouri* belongs to Owenettidae, and is the sister taxon of "*Owenetta*" *kitchingorum*, from the *Lystrosaurus* Assemblage Zone, Induan of the Karoo Basin, South Africa (Reisz and Scott, 2002), whereas the other three taxa belong to the Procolophonidae (Cisneros, 2006): *Procolophon* species (Cisneros and Schultz, 2002; Dias-da-Silva et al., 2006b) within Procolophoninae and *S. caliodon* within Leptopleurinae (Cisneros, 2006). In addition, *S. caliodon* has been regarded by Cisneros (2006) as the sister taxon of *Hypsognathus fenneri*, from the Newark Supergroup, Norian-Rhaetian of the North American Atlantic Coast (Sues et al., 2000).

Dicynodontia

Dicynodonts have long been recognized in the Triassic of Rio Grande do Sul (Tupí-Caldas, 1936; Huene, 1942; Romer, 1943; Romer and Price, 1944), and considered an important component of its biota (Barberena, 1977; Bonaparte, 1982). Despite this, current knowledge seems to indicate the presence of only three taxa: *Stahleckeria potens* Huene, 1938; *Dinodontosaurus pedroanum* (Tupí-Caldas, 1933; gen. Romer, 1943), and *Jachaleria candelariensis* (Araújo and Gonzaga, 1980; gen. Bonaparte, 1970). The genus *Chanaria* was also reported in south Brazil (Araújo, 1981), but it seems to represent a subjective synonym of *Dinodontosaurus* (King, 1988). In addition, Peruzzo and Araújo-Barberena (1995) assigned a partial skull to *Ischigualastia* sp., a genus otherwise known only in the Ischigualasto Formation, Carnian of Argentina (Cox, 1965; Rogers *et al*., 1993). This material has been referred to *Stahleckeria potens* by Lucas (2001), but for Vega-Dias (pers. com., January 2007) its current status is ambiguous (see also Vega-Dias and Schwanke, 2004a). Even so, Lucas (2001; Lucas and Heckert, 2002) proposed the occurrence of the genus *Ischigualastia* in Rio Grande do Sul, based on the material originally referred to *Jachaleria candelariensis*. Yet, a reassessment of the specimens by Vega-Dias and Schultz (2004; see also Vega-Dias and Schwanke, 2004b) found no evidence for such a taxonomic assignment. Lucas (2002) also proposed the occurrence of a second species of *Stahleckeria*, *S. impotens*, but this was also rejected by Vega-Dias et al. (2005). Beforehand, Lucas (1993a) had considered *Barysoma lenzii* (Romer and Price, 1944; gen. Cox, 1965) a junior synonym of *Stahleckeria potens*, an assignment never contested. Apart from these records (all belonging to the Santa Maria and Caturrita formations), the only other dicynodont reported for South Brazil are isolated stapes from the Sanga do Cabral Formation, one of which was tentatively assigned to *Lystrosaurus* (Schwanke and Kellner, 1999; Langer and Lavina, 2000).

Regarding nomenclatural aspects, following an application by Lucas (1992), the generic name *Diodontosaurus* Tupí-Caldas, 1936, was suppressed (ICZN 1995) in favor of *Dinodontosaurus* Romer, 1943. At the time (Lucas, 1992), *D. turpior* Huene, 1938, was considered the type species of *Dinodontosaurus*. Afterwards, however, Lucas and Harris (1996) regarded both, that species and *D. tener* Huene, 1938, as *nomina dubia*, with type material not even referable to *Dinodontosaurus* at the generic level. These two species were originally described by Huene (1938, 1942) as members of the genus *Dicynodon*, but transferred to *Dinodontosaurus* by Cox (1965). Yet, *contra* Lucas and Harris (1996) the decision of the ICZN (1995) did not suppress the species name *D. pedroanum* Tupí-Caldas, 1936. Therefore, as acknowledged by Lucas and Harris (1996), the first species name proposed in the literature, based on type material attributable to *Dinodontosaurus*, is *D. pedroanum* Tupí-Caldas, 1936, which is here used, following the synonymisation of *D. brevirostris* Cox, 1968, from the Chañares Formation, by Lucas and Harris (1996), as the only valid species of the genus.

Maisch (2001) and Vega-Dias et al. (2004) performed phylogenetic analyses of Triassic dicynodonts, including the three Brazilian genera. The first author placed *Dinodontosaurus* as the basal most Dinodontosauridae, sister taxon of a clade composed of Chinese, Indian, African, Russian, and possibly Argentinean, Early-Mid Triassic forms (Sun, 1963; King, 1988; Cox, 1991; DeFauw, 1993, Battail and Surkov, 2000). In contrast, Vega-Dias et al. (2004) found that genus to represent the sister taxon to the Stahlekeriidae (sensu Maisch, 2001). This is composed of two clades, one composed of *Jachaleria* and *Ischigualastia*, and the other of *Stahleckeria* as the sister taxon to *Angonisaurus*, from the main strata of the Manda Formation (Abdala et al., 2005; "lower Manda" of Lucas, 1998), Anisian of Tanzania.

Cynodontia

Along with archosaurs, cynodonts represent the most diverse tetrapod clade in the Rosário do Sul Group. These include 15 formally proposed taxa, and three forms awaiting formal descriptions: a new chiniquodontid (UFRGS PV0146T; Oliveira, 2006), a basal traversodontid (Reichel, 2006; Reichel et al., 2007), and a probainognathian (UFRGS PV1051T; Oliveira et al., 2007) closely related to *Ecteninion* (Martinez et al., 1996), from the Ischigualasto Formation, Argentina. The described taxa include six traversodontids, eight probainognathians, and a cynodont of ambiguous affinities, *Protheriodon estudianti* (Bonaparte et al. 2006a). All these forms were recorded in the Santa Maria and Caturrita formations, whereas only fragmentary postcranial remains of non-mammalian cynodonts have been collected in the Sanga do Cabral Formation (Abdala et al., 2002a).

The formally described traversodontids include: *Gomphodontosuchus brasiliensis* Huene, 1928 (see Hopson, 1985); *Traversodon stahleckeri* Huene, 1938 (see Barberena, 1981a); *Massetognathus ochagaviae* Barberena, 1981b; *Exaeretodon riograndensis* Abdala, Barberena and Dornelles, 2002; *Santacruzodon hopsoni* Abdala and Ribeiro, 2003; and *Luangwa sudamericana* Abdala and Sá-Teixeira, 2004. Additional records include the poorly known *Exaeretodon major* (Huene, 1938), originally described as a member of the genus *Traversodon* (see Huene, 1942; Barberena, 1974; Abdala *et al*., 2002b), and three unnamed forms described by Abdala et al. (2001) and Abdala and Ribeiro (2002). The genus *Megagomphodon* was also reported in south Brazil (Teixeira, 1995), but it was proposed to represent a subjective synonym of *Massetognathus* (Abdala and Giannini, 2000).

Recent hypotheses dealing with traversodontid phylogeny (Flynn et al., 2000; Hopson and Kitching, 2001; Abdala and Ribeiro, 2003; Abdala et al., 2006) place *Luangwa* as the basal most Brazilian member of the group, whereas *Traversodon* and *Santacruzodon* represent successively more derived forms. Abdala and Ribeiro (2003, but see Abdala et al., 2006) also proposed sister group relationships between *Luangwa* and "*Scalenodon*" *hirschsoni*, from possibly younger parts of the Manda Formation, Tanzania (Abdala and Ribeiro, 2003), and between *Santacruzodon* and *Dadadon isaloi*, from the Isalo Beds, Ladinian-Carnian of Madagascar (Flynn et al., 2000). *Massetognathus* is more derived than these (Godefroit and Battail, 1997; Flynn et al., 2000; Abdala and Ribeiro, 2003; Abdala et al., 2006), and sister taxon of a clade including *Gomphodontosuchus*, at the base, and a group composed of *Menadon besairiei*, from the Isalo Beds, Ladinian-Carnian of Madagascar (Flynn et al., 2000), *Scalenodontoides macrodontes*, from the Lower Elliot Formation, Carnian-Norian of South Africa (Anderson et al., 1998; Lucas and Hancox, 2001) and *Exaeretodon*. Regarding the three unnamed forms described by Abdala et al. (2001) and Abdala and Ribeiro (2002)—traversodontid type I belongs in the *Exaeretodon-Menadon-Scalenodontoides* clade, sharing more similarities with the former two taxa (Abdala and Ribeiro, 2002); type III of Abdala and Ribeiro (2002) shares features with *Boreogomphodon jeffersoni* Sues and Olsen, 1990, from the Turkey Branch Formation, Carnian of the Richmond Basin, Virginia (Sues and Olsen, 1990; Huber et al., 1993); while type III of Abdala et al. (2001) shares plesiomorphies with *Massetognathus*-grade traversondontids (Abdala and Ribeiro, 2002).

On the probainognathian (*sensu* Hopson and Kitching, 2001) part of the cynodont phylogenetic tree, a single formally proposed, and valid chiniquodontid is known for the Rosário do Sul Group (Abdala and Giannini, 2002): *Chiniquodon theotonicus* Huene, 1938, including forms previously assigned to *Belesodon magnificus* Huene, 1938, and *Probelesodon kitchingi* Teixeira, 1982. Further, various more "mammal-like" forms have recently been described or reviewed. These include the Tritheledontidae *Riograndia guaibensis* Bonaparte, Ferigolo and Ribeiro, 2001, and *Irajatherium hernandezi* Martinelli, Bonaparte, Schultz and Rubert, 2005, which respectively represent (Martinelli et al., 2005) the basal most member of the group and a more derived sister taxon of the clade containing *Pachygenelus* and *Diarthrognathus*, from the Lower Jurassic of South Africa and Nova Scotia (Shubin *et al*., 1991; Lucas and Hunt, 1994; Lucas and Hancox, 2001). Two other taxa, *Therioherpeton cargnini* Bonaparte and Barberena, 1975, and *Prozostrodon brasiliensis* (Barberena et al., 1987; gen. Bonaparte and Barberena, 2001), also seem to belong into the tritheledontid-mammal lineage, but are placed either basal to that dichotomy or along either branch (Bonaparte et al., 2005; Martinelli et al., 2005; Sidor and Hancox, 2006; Oliveira, 2006), while

Charruodon tetracuspidatus Abdala and Ribeiro, 2000 (see also Oliveira, 2006), appears to be closely related to *Therioherpeton*. Finally, the brasilodontid cynodonts *Brasilodon quadrangularis* Bonaparte, Martinelli, Schultz and Rubert, 2003, and *Brasilitherium riograndensis* Bonaparte, Martinelli, Schultz and Rubert, 2003, belong in the mammalian branch (Bonaparte et al., 2005; but see Abdala, 2006; Oliveira, 2006).

Sphenodontia

Lepidosaurs of the Rosário do Sul Group are represented only by sphenodontians. Ferigolo (2000) described an unnamed form similar to *Clevosaurus*, while Bonaparte and Sues (2006) erected a new species of that genus, *C. riograndensis*, which may represent the same taxonomic entity described by Ferigolo (2000). According to Bonaparte and Sues (2006), *C. riograndensis* belongs to a clade of *Clevosaurus* species that also include *C. mcgilli* from the Lower Lufeng Formation, Lower Jurassic of China (Wu, 1994), *C. bairdi* from the McCoy Brook Formation, Hettangian of Nova Scotia (Sues et al., 1994), and a South African form from the Upper Elliot-Lower Clarens formations, Lower Jurassic of the Karoo Basin (Sues and Reisz, 1995).

Rhynchosauria

Rhynchosaurs are more diverse in the Rosário do Sul Group than in any other sedimentary deposit worldwide. According to recent reviews (Langer et al., 2000; Langer and Schultz, 2000a, b) five taxa are known. The "Mariante rhynchosaur" (Schultz and Azevedo, 1990), which lacks a formal designation, is closer to Middle Triassic rhynchosaurs, particularly *Stenaulorhynchus* from the Manda Formation, Anisian of Tanzania, than to other South American rhynchosaurs (Langer and Schultz, 2000a), all of which belong to the more derived Hyperodapedontinae (Langer and Schultz, 2000b). This "subfamily" most probably encompasses the material described by Huene (1929) as belonging to six different species: *Scaphonyx fischeri* Woodward, 1903, *S. australis* Huene, 1926, *S. eurichorus* Huene, 1926, *Cephalonia lotziana* Huene, 1926, *Cephalastronius augustispinatus* Huene, 1926, *Cephalastron gondwanicum* Huene, 1926, and *C. brasiliense* Huene, 1926, all of which have been dismissed as *nomina dubia* (Huene, 1942; Sill, 1970; Langer, 1998; Langer and Schultz, 2000a, b). Langer et al. (2000) assigned all the more complete specimens previously referred to either *Cephalonia* (Huene, 1942) or *Scaphonyx* (Huene, 1942; Sill, 1970; Azevedo, 1984), along with that described by Tupí-Caldas (1933) as *Macrocephalosaurus mariensis*, into the widespread genus *Hyperodapedon* (Lucas and Heckert, 2002). They were allocated within two species: *H. mariensis* (Tupí-Caldas, 1933) and *H. sanjuanensis* (Sill, 1970), both of which also occur in the Ischigualasto Formation, Carnian of Argentina. In addition, a new species of *Hyperodapedon*, *H. huenei*, was erected by Langer and Schultz (2000b), while the form described as "*Scaphonyx*" *sulcognathus* (Azevedo and Schultz, 1987) was proposed to represent a new genus of Hyperodapedontinae, sister taxon to *Hyperodapedon* (Langer and Schultz, 2000b).

Prolacertiformes

No prolacertiform has been formally described for the Rosário do Sul Group, but Langer and Lavina (2000, see also Dias-da-Silva, 1998) attributed isolated elongated cervical vertebrae from the Sanga do Cabral Supersequence to that reptile group.

Archosauria

The diverse archosaur fauna of the Rosário do Sul Group includes taxa assigned to Phytosauria, Proterochampsia, "Rauisuchia," Aetosauria, and Dinosauria. At least four proterochampsians are known: *Rhadinosuchus gracilis* Huene, 1938; *Cerritosaurus binsfeldi* Price, 1946; *Chanaresuchus bonapartei* Romer, 1971; and *Proterochampsa nodosa* (Barberena, 1982). The latter has been referred to a new genus, *Barberenachampsa* Kischlat, 2000, but that name was not proposed according to the rules of the ICZN (1999; article 16.1) - i.e., explicitly indicated as intentionally new. In addition, Kischlat and Schulz (1999) included *B. nodosa* along with *Proterochampsa barrionuevoi*, from the Ischigualasto Formation, Carnian of Argentina (Sill, 1967), in a clade of two monospecific genera. Accordingly, we prefer to retain the original generic designation of Barberena (1982, see also Arcucci, 1989).

Kischlat and Schulz (1999) considered *Cerritosaurus* the basal most proterochampsian, whereas *Gualosuchus* and *Chanaresuchus* were proposed to form the clade Rhadinosuchidae (Machado and Kischlat, 2003) with *Rhadinosuchus*. This taxon was first classified as a rauisuchian by Huene (1942), but Kischlat (2000) suggested a proterochampsian affinity instead. Further proterochampsian material from Rio Grande do Sul was assigned to *Chanaresuchus* by Dornelles (1995), but the identity of the described specimen as *Chanaresuchus* instead of *Gualosuchus* or *Rhadinosuchus* can not be determined (Kischlat, 2000; Hsiou et al., 2002), as is also the case of a specimen recently studied by Machado and Kischlat (2003). Likewise, material referred to *Gualosuchus* (Barberena et al., 1985a) might represent either that genus or *Rhadinosuchus* (Kischlat, 2000). More recently, however, *Chanaresuchus bonapartei* was positively identified in South Brazil (Hsiou et al., 2002).

Within the crown-Archosauria (sensu Gauthier, 1986), phytosaurs have only been recorded based on a jaw fragment (Kischlat and Lucas, 2003) and possibly isolated teeth (Dornelles, 1990). Among suchians (sensu Parrish, 1993), aetosaurs are known based on material referred to the genus *Aetosauroides* (Zacharias, 1982; Kischlat, 2000; DaRosa and Leal, 2002). Two species names have entered the literature: *A. subsulcatus* (Zacharias, 1982) and *A. inhamandensis* (Barberena et al., 1985a, b), both of which are nomina nuda. Lucas and Heckert (2001) assigned the south Brazilian aetosaur material to *Stagonolepis robertsoni*, known from the Lossiemouth Sandstone Formation, Carnian of Scotland (Benton and Walker, 1995). That assignment was questioned by Desojo and Kischlat (2005), who proposed that the Brazilian specimens represent a new species of *Aetosauroides*. In fact, the whole synonymization of *Aetosauroides* and *Stagonolepis* (Heckert and Lucas, 2002) seems dubious (Desojo and Baez, 2005).

Most pseudosuchians (sensu Parrish, 1997) of the south Brazilian Triassic have been considered "rauisuchians," a non-monophyletic group of ambiguous affinities (Parrish, 1993; Gower, 2000; Gower and Nesbitt, 2005). The Brazilian forms were reviewed by Kischlat (2000), and five species seem valid: *Prestosuchus chiniquensis* Huene, 1938; *Rauisuchus tiradentes* Huene, 1938; *Procerosuchus celer* Huene, 1938; *Barberenasuchus brasiliensis* Mattar, 1987; and "*Karamuru vorax*" Kischlat, 2000. Kischlat (2000) follows Parrish (1993), including *Rauisuchus* within a group of more gracile, possibly more derived "rauisuchians" - i.e., Rauisuchidae - that may also encompass (Parrish, 1993; Sulej, 2005): *Tikisuchus romeri* from the Tiki Formation, Carnian of India (Chatterjee and Majumbar, 1987); *Batrachotomus kupferzellensis* from the Lettenkeuper, Ladinian of Germany (Gower, 1999); *Teratosaurus silesiacus* from the Krasiejów fauna, Carnian of Poland (Sulej, 2005); *Postosuchus kirkpatricki* from various stratigraphic units (Long and Murry, 1995) within the Chinle Group (Lucas, 1993b), Carnian-Norian of southwestern USA (Lucas, 1998; see also Lehman and Chatterjee, 2005). On the contrary, *Prestosuchus chiniquensis*, and possibly *Procerosuchus celer*, seem to belong into a more basal group of robust "rauisuchians" - i.e., Prestosuchidae - that may also include (Parrish, 1993; Kischlat, 2000; Benton, 2004; Sen, 2005) Anisian forms such as *Ticinosuchus ferox* from the Grenzbitumenzone of Monte San Giorgio, Switzerland (Krebs, 1965), *Yarasuchus deccanensis* from the Yerrapalli Formation, India (Sen, 2005), and those from the Manda Formation of Tanzania (Charig, 1957), as well as the Argentinean forms *Luperosuchus fractus* from the Ladinian Chañares Formation (Romer, 1971), and *Saurosuchus galilei* from the Carnian Ischigualasto Formation (Alcober, 2000). In this context, Kischlat (2000) used various specimens previously attributed to *Prestosuchus chiniquensis*, including a nearly complete skull (Barberena, 1978), to establish a new taxon of Prestosuchidae:

"*Karamuru vorax*". This appears to represent a valid taxonomic entity, with a set of proposed diagnostic features. Yet, the nomenclatural problems raised above for *Barberenachampsa* also apply to "*Karamuru vorax*". Kischlat (2000) assigned the name to Kischlat and Barberena, without indication of a publication year, and none of the two publications referred to those authors in the reference list, Kischlat and Barberena (1999a, b), includes a nomenclatural proposition. It is beyond the scope of this paper to challenge the taxonomic status of "*Karamuru vorax*", but the name is better applied with caution until a formal description of the taxon is available. Finally, *Barberenasuchus brasiliensis*, first described as a sphenosuchid (Mattar, 1987; Mattar and Barberena, 1987), was considered by Kischlat et al. (1999; Kischlat, 2000) as a "rauisuchian" of unclear affinities. In addition, new material under study (Ferigolo et al., 2001; Mastrantonio et al., 2006) seems to represent new prestosuchids.

The dinosaur record of the Rosário do Sul Group is relatively rich for a Triassic deposit, with at least four different valid taxa. *Staurikosaurus pricei* Colbert, 1970, is an herrerasaurid (Novas, 1992; Galton, 2000; Langer, 2004), while *Guaibasaurus candelariensis* Bonaparte, Ferigolo and Ribeiro, 1999, represents a saurischian possibly related to theropods (Bonaparte et al., 2006b; Langer, 2004; Langer and Benton, 2006). Two members of the sauropodomorph lineage are also known: *Saturnalia tupiniquim* Langer, Abdala, Richter and Benton, 1999, and *Unaysaurus tolentinoi* Leal, Azevedo, Kellner and Da Rosa, 2003. The former is the basal-most member of that lineage (Langer, 2003, 2004), while the latter is a member of the "prosauropod" clade Plateosauridae (Yates, 2006), which also includes *Plateosaurus*, known primarily from the Norian of Germany (Yates, 2003). Other putative South Brazilian dinosaurs are *Spondylosoma absconditum* Huene, 1926, *Teyuwasu barberenai* Kischlat, 1999, and *Sacisaurus agudoensis* Ferigolo and Langer, 2006. The latter belongs into the Dinosauriformes, and seems closely related to *Silesaurs opolensis* Dzik, 2003, from the Krasiejów Fauna, Carnian of Poland (Dzik, 2001). Yet, its position either basal to Dinosauria or in the ornithischian lineage is debated (Ferigolo and Langer, 2006). *Spondylosoma absconditum* might represent a "rauisuchian" (Galton, 2000, but see Langer, 2004), while *T. barberenai*, based on part of the material originally ascribed to *Hoplitosuchus raui* Huene, 1938, is too fragmentary to have its affinities defined (Langer, 2004, but see Kischlat, 2000). Further material referred to the Dinosauria has been mentioned by Kischlat and Barberena (1999b).

Regarding archosaurs with uncertain affinities, Kischlat (2000) listed specimens originally described by Huene (1942) as "*Prestosuchus*" *loricatus* and *Hoplitosuchus raui* (partim). In addition, material under study has been preliminarily identified as cf. *Tarjardia* (Kischlat, 2000), a basal crurotarsan according to Arcucci and Marsicano (1998).

STRATIGRAPHIC HIERARCHY AND FOSSIL SITES

The bio- and lithostratigraphy of the tetrapod-bearing Triassic beds of the Paraná Basin in south Brazil are relatively well known (Barberena, 1977; Barberena et al., 1985a, b; Schultz et al., 2000; Scherer et al., 2000; Lucas, 2001; Langer, 2005a). More recently, studies based on stratigraphic sequences (Faccini, 1989; Scherer, 1994; Fonseca, 1999; Zerfass et al., 2003; Rubert and Schultz, 2004) recognized two second-order sequences: Sanga do Cabral and Santa Maria Supersequences (*sensu* Zerfass et al., 2003), the latter of which may be further subdivided (Zerfass et al., 2003; Rubert and Schultz, 2004).

Sanga do Cabral Supersequence

The Sanga do Cabral Supersequence represents the lowest depositional sequence within the Rosário do Sul Group. This second-order sequence (Zerfass et al., 2003) corresponds to the Sanga do Cabral Formation of Andreis et al. (1980), which was deposited in a braided river system under an arid to semi-arid climate (Holz and Scherer, 2000). The poorly confined fluvial channels hosted ephemeral flash flood events (Zerfass et al., 2003) that formed the intraformational conglomerates in which most of the fossil material is found (Holz and Souto-Ribeiro, 2000; Dias-da-Silva et al., 2006b). As a whole, the 50-100 m thick Sanga do Cabral Formation occurs in a nearly continuous 500 km long belt (Fig. 1) extending from the townships of Venâncio Aires to Santana do Livramento (Scherer et al., 2000), but fossils are better known from three areas/localities: Catuçaba, Rincão dos Weiss, and Cachoeira do Sul (Fig. 2).

The first and more thoroughly studied Catuçaba area, south of São Pedro do Sul, (Barberena et al., 1981) has yielded indeterminate cynodonts (Abdala et al., 2002a), prolacertiforms (Dias-da-Silva, 1998; Langer and Lavina, 2000), and temnospondyls, including rhytidosteids (Dias-da-Silva, 2003; Dias-da-Silva et al., 2005), as well as the procolophonid *Procolophon pricei* (Lavina, 1983). From Rincão dos Weiss, south of Mata, *Procolophon brasiliensis* (Cisneros and Schultz, 2002) and an indeterminate species of the same genus (Langer and Lavina, 2000; Dias-da-Silva et al., 2006b) were recorded, while the holotype and only known specimen of *Sangaia lavinai* (Dias-da-Silva et al., 2006a) comes from the more eastern site of Cachoeira do Sul.

Santa Maria Supersequence

According to Zerfass et al. (2003), the Santa Maria Supersequence, an up to 200 m thick second-order sequence, might be subdivided into three third-order sequences, Santa Maria sequences 1, 2, and 3. The former two approximately represents Sequence II of Faccini (1989), and is the only one with tetrapod fossils. The latter corresponds to Sequence III of Faccini (1989), also termed "Mata Sandstone," and is better known for its plant remains (Guerra-Sommer et al., 2000). In terms of lithostratigraphy (Andreis et al., 1980), the tetrapod-bearing rocks of these sequences include the Alemoa Member of the Santa Maria Formation and the Caturrita Formation (Fig. 1). The former corresponds to the red mudstones that occur at the lower-mid levels of Sequence II of Faccini (1989), and at Santa Maria Sequence 1 and lower parts of Santa Maria Sequence 2 (Zerfass et al., 2003). Outcrops of the Alemoa Member typically correspond to deep erosive gullies, the so called "sangas", that are relatively common in central Rio Grande do Sul. The sandier Caturrita Formation corresponds to the upper levels of Santa Maria Sequence 2 plus Santa Maria Sequence 3 (Zerfass et al., 2003), and to the upper levels of Sequence II (Rubert, 2003) plus Mata Sandstone in the scheme of Faccini (1989). As a whole, the Santa Maria Supersenquence crops out along a 250 km west-east belt extending from the townships of Mata to Taquari (Fig. 1).

Santa Maria Sequence 1

This 50 m thick third-order sequence includes a coarser lowstand systems tract, deposited by a high energy, low sinuosity river system, developed under a semi-arid climate, and a transgressive systems tract composed of massive or laminated mudstones, where the tetrapod fossil record is concentrated (Holz and Scherer, 2000; Zerfass et al., 2003). These correspond to deposits of either shallow lakes (Zerfass et al., 2003) or floodplains of an anastomosed fluvial system (Scherer et al., 2000).

Fossil tetrapods of the Santa Maria 1 Sequence occur in two main regions, Chiniquá and Pinheiros (Barberena et al., 1985a), as well as in various isolated localities (Fig. 2). The fossil record from the Chiniquá area, west of São Pedro do Sul, mainly reflects the efforts of Friedrich von Huene and his crew during the fieldwork of 1928-29, including: *Traversodon stahleckeri* (Huene, 1942; Barberena, 1981a), *Chiniquodon theotonicus* (Huene, 1942), *Dinodontosaurus pedroanum* (Tupí-Caldas, 1936), "*Karamuru vorax*" (Huene, 1942; Kischlat, 2000), "*Prestosuchus*" *loricatus* (Huene, 1942), and possibly *Spondylosoma absconditum* (Huene, 1942) from Cynodontier-Sanga (Huene, 1942), or Sanga Beles (Beltrão, 1965); *Stahleckeria potens* (Huene, 1942), *Exaeretodon major* (Huene, 1942), and *Spondylosoma absconditum* (Huene, 1942) from

Baum-Sanga; and *Prestosuchus chiniquensis* (Huene, 1942), *Procerosuchus celer* (Huene, 1942), and possibly *Chiniquodon theotonicus* (Huene, 1942), from Weg-Sanga. Additionally, all those localities have yielded the "*Dinodontosaurus*" material of Huene (1942), considered *nomina dubia* by Lucas and Harris (1996).

The Pinheiros region, south of Candelária (Barberena, 1977), was firstly explored during the thirties by a joint North American-Brazilian expedition (Romer, 1943; Romer and Price, 1944; Romer, 1969), and latter by Brazilian paleontologists (Price, 1947; Barberena, 1977; Araújo, 1981; Barberena et al., 1985b). A plethora of taxa was excavated from the "sangas" of two main areas: Bom Retiro, about 15 km southeast of Novo Cabrais, and Pinheiros itself, about 10 km south of the township of Candelária (Barberena, 1977). *Dinodontosaurus pedroanum* (Romer, 1943; Cox, 1965; Machado, 1992), *Chiniquodon theotonicus* (Romer, 1969; Fernando Abdala, pers. com. January, 2007), and *Massetognathus* (Teixeira, 1987, 1995) appear to occur in "sangas" of both areas, while a dubious record of *Stahleckeria potens* (Romer and Price, 1944; Lucas, 1993a) in the region of Candelária seems to come from Bom Retiro. "*Karamuru vorax*" (Barberena, 1978) and cf. *Ischigualastia* (Peruzzo and Araújo-Barberena, 1995) were also recovered in Bom Retiro, along with *Massetognathus ochagaviae* (Teixeira, 1987), from the site known as Sanga Pascual. In the area of Pinheiros, together with *Massetognathus* (Teixeira, 1995) and *D. pedroanum* (Machado, 1992), a rhadinosuchid proterochampsian (Dornelles, 1992; 1995; Kischlat, 2000) was recovered in the eponymous sanga. Besides, the sites referred to as "Sanga do Ribeiro" by Cox (1965) and Barberena (1977) appear to correspond to different places (see Machado, 1992). The latter is in Bom Retiro, whereas the former is located further south, and has yielded *D. pedroanum* (Machado, 1992). This dicynodont was also registered in other sites around Pinheiros, such as Sanga da Divisa and Sanga Hintz (Machado, 1992), while the holotype of *Candelaria barbouri* (Price, 1947) comes from an undetermined site in the region.

The other sites assigned by Barberena et al. (1985a) to the Pinheiros Local Fauna, Vila Melos and Rincão do Pinhal, are not located in that region (Fig. 2). The former is in the municipality of Vale Verde, and yielded *D. pedroanum* (Araújo, 1981; Machado, 1992), *M. ochagaviae* (Barberena, 1981b), and possibly "*K. vorax*" (UFRGS PV0152T). In the locality of Rincão do Pinhal, south of Agudo, was recorded *C. theotonicus* (Teixeira, 1982), *D. pedroanum* (Teixeira, 1979; Machado, 1992), *M. ochagaviae* (Teixeira 1987), and the new basal traversodontid of Reichel et al. (2007). More recently, various isolated sites (Fig. 2) have yielded a fossil fauna likely coeval to those of Pinheiros and Chiniquá. This is the case of the site of Dona Francisca (Ferigolo et al., 2001) where *Protheriodon* (Bonaparte et al., 2006a) and prestosuchid archosaurs (MCN PV 3585, 10004, 10005; UFRGS PV0629T) occur along with *D. pedroanum* (Machado, 1992) and *Massetognathus* (MCN PV 2293). In addition, the site known as Sítio Cortado, west of Novo Cabrais, has yielded *D. pedroanum*, *Candelaria barbouri*, (DaRosa et al., 2004a), the new traversodontid of Reichel et al. (2007), and most probably *Barberenasuchus brasiliensis* (Mattar, 1987). Nearby sites include Linha da Várzea (DaRosa et al., 2005) and Rincão da Porta (Machado, 1992), both of which yielded *D. pedroanum*.

The fossil fauna of other sites (Fig. 2), previously assigned to faunal associations within the Santa Maria 1 Sequence, are not straightforwardly correlated to those of Pinheiros and Chiniquá, and might correspond to older (Schultz, 1995; Abdala and Sá-Teixeira, 2004) or younger (Abdala et al., 2001) assemblages. The former group includes the type-locality of *Luangwa sudamericana*, between Vera Cruz and Candelária, the precise location of which is unknown (Abdala and Sá-Teixeira, 2004), and the site of Porto Mariante, in Bom Retiro do Sul, that yielded the "Mariante rhynchosaur" (Schultz and Azevedo, 1990) and *D. pedroanum* (Machado, 1992). On the contrary, the possibly younger assemblage of the site of Santuário Schoenstatt, in Santa Cruz do Sul (Abdala et al., 2001; Reichel et al., 2005; Bertoni & Holz, 2006), includes a chiniquodontid (Abdala et al., 2001), *Santacruzodon hopsoni* (Abdala and Ribeiro, 2003), traversodontids with affinities to *Exaeretodon-Menadon*, *Massetognathus*, and *Boreogomphodon* (Abdala et al., 2001; Abdala and Ribeiro, 2002), and a rhadinosuchid archosaur (Machado and Kischlat, 2003).

Santa Maria Sequence 2

This up to 130 m thick third-order sequence includes tetrapod-bearing layers deposited in transgressive and highstand system tracts (Zerfass et al., 2003). In the scheme proposed by Zerfass et al. (2003), the former corresponds to the upper levels of the Alemoa Member, Santa Maria Formation, whereas the latter represents the lower-mid portions of the Caturrita Formation of Andreis et al. (1980). In addition, Rubert and Schultz (2004) found sedimentological evidence to further segregate the upper levels of the Sequence II of Faccini (1989) - i.e., middle portion of the Caturrita Formation (Andreis et al., 1980), into strata bearing their "Ictidosaur Assemblage Zone".

The transgressive systems tract of the Santa Maria 2 Sequence is mainly composed of mudstones, the higher concentration of early diagenetic carbonate in which suggests a drier climate in relation to that of the Santa Maria 1 Sequence (Zerfass et al., 2003). These were deposited in either shallow lakes (Zerfass et al., 2003) or in the floodplains of an ephemeral anastomosed river system (Fonseca and Scherer, 1998; Holz and Scherer, 2000). The latter scenario implies a seasonal climate, as also suggested by the color of the sediments (Holz, 1993). These red beds are typical from the outskirts of Santa Maria (Bortoluzzi, 1974), where Barberena et al. (1985a) defined the Alemoa Local Fauna. This includes the fossil record of two main areas explored by Huene (1942) in the late twenties (Beltrão, 1965; Langer, 2005a), São José and Alemoa, other more recently prospected sites around Santa Maria, as well as outcrops from different areas that seem to bear a coeval fauna (Fig. 2).

Fossil taxa from the Alemoa area include *Staurikosaurus pricei* (Colbert, 1970) and *Teyuwasu barberenai* (Kischlat, 2000) from Sanga Grande, *Gomphodontosuchus brasiliensis* (Huene, 1928), *Saturnalia tupiniquim* (Langer, 2005a), and *Hyperodapedon* sp. from the Wald-Sanga, as well as *Hyperodapedon mariensis* (Tupí-Caldas, 1933), *H. sanjuanensis* (Huene, 1929), and *Cerritosausus binsfeldi* (Price, 1946) from unspecified sites of the area. The sites of São José were mainly explored by Huene (1942), including *Rauisuchus tiradentes* and *Rhadinosuchus gracilis* from Zahnsanga, and *H. sanjuanensis* from Sanga Schramm. Among the other localities around Santa Maria (DaRosa, 2004, 2005), that known as Faixa-Nova has yielded *H. mariensis*, *H. sanjuanensis* (Schultz, 1991), and *Aetosauroides* (Desojo and Kischlat, 2005), while *Therioherpeton cargnini* and *Prozostrodon brasiliensis* were collected in another site nearby Faixa-Nova (Bonaparte and Barberena, 1975; Barberena et al., 1987) that also yielded *H. mariensis* (Langer, 1996).

Outside of Santa Maria, *Hyperodapedon mariensis* and *H. sanjuanensis* were recorded in the municipality of Venâncio Aires (Langer, 1996), as well as from the area of Inhamandá, east of São Pedro do Sul. In the latter area, two sites are recognized, Inhamandá 1 has yelded *H. mariensis*, *H. huenei* (Langer and Schultz, 2000b), and *Aetosauroides* (Zacharias, 1982), whereas *H. sanjuanensis* is the only taxon recorded in Inhamandá 2 (Langer, 1996). Rhynchosaurs and aetosaurs also occur in sites around São João do Polesine, *H. mariensis* (MCN PV 1875) from the locality of Predebon (Azevedo et al., 1999; DaRosa 2005) and *Aetosauroides* (MCN PV 2347) along with an indeterminate rhynchosaur (MCN PV 10101) from the site known as Piche (Outcrop 1 of Perez and Malabarba, 2002). The only temnospondyl remains known from the Santa Maria Supersequence (Richter, 2001) also comes from that area (Outcrop 2 of Perez and Malabarba, 2002). Finally, *Hyperodapedon* (UFRGS PV1063T) also occurs in the site of Picada Escura, south of Candelária.

The highstand systems tract of the Santa Maria 2 Sequence represents a coarsening up succession that transitionally replaces the mudstones of the Alemoa Member (Zerfass et al., 2003). This corresponds to the progressive replacement of an ephemeral anastomosed fluvial-lacustrine system by a perennial braided fluvial system, which indicates an increase in the humid condition along that time (Holz and Scherer, 2000). At least one fossil-bearing site (Fig. 2) within the Caturrita Formation (Rubert and Schultz, 2004; DaRosa, 2005) seems to represent the lower levels of that section, beneath the middle portion of that stratigraphic unit, which yielded the "Ictidosaur Cenozone" of Rubert and Schultz (2004). This is located about 9 km west from Candelária (3 km west of Botucaraí Hill) and includes *Proterochampsa nodosa* (Barberena, 1982), *Exaeretodon riograndensis* (Abdala et al., 2002b), a rhynchosaur with affinities to *Hyperodapedon* (MCN PV3598), and perhaps *Charruodon tetracuspidatus* (Abdala and Ribeiro, 2000). In addition, the site of Linha Facão (Fig. 2), 6 km east of Candelária, has been often (Barberena et al. 1985b; Scherer, 1994; Schultz, 1995) correlated to the type-locality of *E. riograndensis*. It yielded the rhynchosaurs N. gen. *sulcognathus* (Azevedo and Schultz, 1987) and *Hyperodapedon sanjuanensis* (Azevedo, 1984), but it is unclear if both come from the same stratigraphic levels. The former taxon also occurs in the upper levels of Faixa Nova and Wald-Sanga localities (Schultz, 1991), above the strata in which *Hyperodapedon* abound.

Exaeretodon has also been registered alongside rhynchosaurs referable to *Hyperodapedon* in other sites of Santa Maria Sequence 2, such as Várzea do Agudo and Cidade dos Meninos, alluding to their possible correlation to the type-locality of *E. riograndensis*. Yet, although these sites correspond to the upper parts of the Alemoa Member, there is no stratigraphic evidence their beds lay above those bearing the "Alemoa Local Fauna" (DaRosa et al., 2004b; DaRosa, 2005). The site of Várzea do Agudo, also known as Janer or Cooperativa Agudo, yielded *Hyperodapedon* (MCN PV 3509), *Exaeretodon* (UFRGS PV0715T; Oliveira, 2006), a cynodont similar to *Ecteninion* (UFRGS PV 1051T), and possible dinosaur remains (Cabreira et al., 2006), whereas rhynchosaurs possibly referable to *Hyperodapedon* (DaRosa, 2004), an aetosaur similar to *Aerosauroides*, and *Exaeretodon* (Weiss et al., 2003; Malabarba et al., 2005) were recorded in Cidade dos Meninos, north of Camobi. The latter taxon was also found in the lower part (MCN PV10001) of the type-locality of *Sacisaurus agudoensis*, in the outskirts of the town of Agudo.

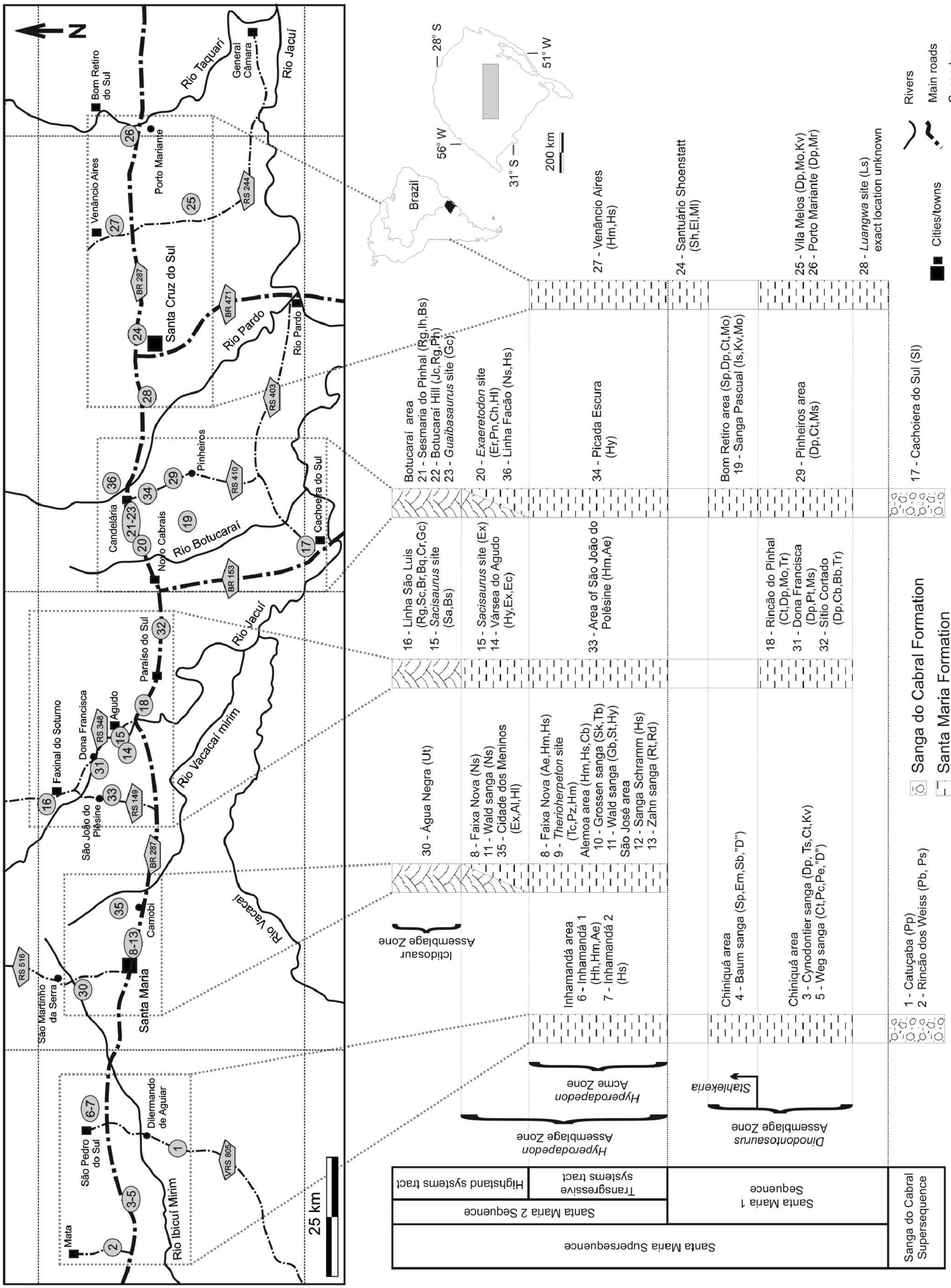
In a detailed stratigraphic revision of the areas of Candelária and Faxinal do Soturno, Rubert and Schultz (2004) defined the sedimentological basis to distinguish the middle part of the Caturrita Formation of Andreis et al. (1980). This represents the full establishment of the braided fluvial system that deposited the coarser sediments of that stratigraphic unit. Tetrapods of this interval come basically from the surroundings of the Botucaraí Hill, west of Candelária, and from the site of Linha São Luiz, about 2 km NW from Faxinal do Soturno (Fig. 2). The latter includes *Clevosaurus riograndensis* (Bonaparte and Sues 206), *Soturnia caliodon* (Cisneros and Schultz, 2003), *Riograndia guaibensis* (Soares, 2004), *Guaibasaurus candelariensis* (Bonaparte et al., 2006b), *Brasilodon quadrangularis* and *Brasilitherium riograndensis* (Bonaparte et al., 2003). Besides, fossils actually collected at Botucaraí Hill, 6 km of Candelária, are solely *Jachaleria candelariensis* (Araújo and Gonzaga, 1980), an indeterminate phytosaur (Kischlat and Lucas, 2003), an isolated tooth of *Riograndia guaibensis* (UFRGS PV1062T), plus fragmentary archosaur remains (Dornelles, 1990; Kischlat & Barberena, 1999b; Kischlat, 2000). Other tetrapods of the area come from the type-locality of *Guaibasaurus candelariensis* (Bonaparte et al., 1999) and from the site of Sesmaria do Pinhal, respectively about 2.0 and 1.2 km west of the hill. The latter has yielded *Riograndia guaibensis* (Bonaparte et al., 2001), *Irajatherium hernandezi* (Martinelli et al., 2005), sphenodontians (MCN PV10104), and brasilodontid cynodonts (MCN PV3001-3002). Isolated teeth (MCN PV10102) of the latter group were also recorded along with *Sacisaurus agudoensis* (Ferigolo and Langer, 2006), while the prosauropod *Unaysaurus tolentinoi* represents a further, but isolated record from the uppermost levels of the Caturrita Formation. According to Leal et al. (2003), it was recovered from a conglomerate in the site of Água Negra, 13 km north of Santa Maria, township of São Martinho da Serra.

FAUNAL TURNOVERS

Early studies of the Sanga do Cabral Biota (Barberena et al., 1981, 1985a; Lavina, 1983; Dias-da-Silva, 1998) suggested its correlation to the *Lystrosaurus* Assemblage-Zone of the Karoo Basin, South Africa (Groenewald and Kitching, 1995). More recently, the general scarcity of that fauna, together with preponderance of the genus *Procolophon*, prompted Cisneros and Schultz (2002; see also Dias-da-Silva et al., 2005) to propose its correlation to the *Procolophon* Zone (= lower part of the so-called "Impoverished zone") of the Karoo Basin, as defined by Neveling et al. (1999). Yet, given that *Procolophon* occurs in both the *Lystrosuarus* Assemblage Zone and *Procolophon* Zone, Dias-da-Silva et al. (2006b) took a more conservative approach (Fig. 3) by correlating the Sanga do Cabral Formation to either of them (i.e., the entire Katberg Formation; see also Langer and Lavina, 2000; Abdala et al., 2002a), as also indicated by its "taphocorrelation" (Souto-Ribeiro and Holz, 1998). Indeed, the prevalence of *Procolophon* in the Brazilian sequence might represent a taphonomic bias (Dias-da-Silva et al., 2006b), and not a strong basis for its correlation to the "Impoverished zone". The correlation with the Karoo Basin only allows the assignment of an undifferentiated Lower Triassic age (Shishkin et al., 1995; Damiani et al., 2000; Hancox and Rubidge, 2001) for the Sanga do Cabral Formation, but the occurrence of a basal rhytidosteid with affinities to *Indobatrachops* (Dias-da-Silva et al., 2006a), from the Panchet Formation (Cosgriff, 1984; Lucas, 1998; Yates and Sengupta, 2002), might prove to represent a complementary basis to define an Induan age for the Brazilian stratigraphic unit.

The fossil record of Santa Maria 1 Sequence (Zerfass et al., 2003) is usually assigned to a single biostratigraphic unit, the Therapsid (Barberena, 1977; Bonaparte, 1982; Schultz et al., 2000) or *Dinodontosaurus* (Barberena et al., 1985b; Lucas, 2001) "zones", correlated to the Argentinean Chañares Formation (Bossi and Stipanicic, 2002). This scheme seems oversimplified, as suggested by the record of putatively older (Abdala and Sá-Teixeira, 2004) and younger (Abdala et al., 2001) fossil assemblages. Barberena et al. (1985a) attempted a geographically based chronologic refinement, proposing the Local Faunas of

FIGURE 2. Index map of part of central Rio Grande do Sul showing the location of main fossil sites, and composite stratigraphic sections of the major fossil-bearing areas. Ae = *Aetosauroides* sp, Al = *Aetosauroides*-like aetosaur, Bb = *Barberenasuchus brasiliensis*, Bq = *Brasilodon quadrangularis*, Br = *Brasilitherium riograndensis*, Bs = brasilodontid, Cb = *Candelaria barbouri*, Cr = *Clevosaurus riograndensis*, Ct = *Chiniquodon teotonicus*, Ch = *Charuodon tetracuspidatus*, "D" = *Dinodontosaurus* of Huene (1935-42), Dp = *Dinodontosaurus pedroanum*, Ec = *Ecteninion*-like cynodont, El = *Exaeretodon*-like traversodontid, Em = *Exaeretodon major*, Er = *Exaeretodon riograndensis*, Ex = *Exaeretodon* sp, Gb = *Gomphodontosuchus brasiliensis*, Gc = *Guaibasaurus candelariensis*, Hh = *Hyperodapedon huenei*, Hl = *Hyperodapedon*-like rhynchosaur, Hm = *Hyperodapedon mariensis*, Hs = *Hyperodapedon sanjuanensis*, Hy = *Hyperodapedon* sp, Ih = *Irajatherium hernandezi*, Is = cf. *Ischigualastia*, Jc = *Jachaleria candelariensis*, Kv = "*Karamuru vorax*", Ls = *Luangwa sudamericana*, Ml = *Massetognathus*-like traversodontid, Mo = *Massetognathus ochagaviae*, Ms = *Massetognathus* sp, Mr = "Mariante rhynchosaur", Ns = N. gen. *sulcognathus*, Pb = *Procolophon brasiliensis*, Pc = *Prestosuchus chiniquensis*, Pe = *Procerosuchus celer*, Ph = indeterminate phytosaur, Pn = *Proterochampsa nodosa*, Pp = *Procolophon pricei*, Ps = *Procolophon* sp, Pt = *Protheriodon estudianti*, Pz = *Prozostrodon brasiliensis*, Rg = *Riograndia guaibensis*, Rd = *Rhadinosuchus gracilis*, Rt = *Rauisuchus tiradentes*, Sb = *Spondylosoma absconditum*, Sc = *Soturnia caliodon*, Sa = *Sacisaurus agudoensis*, Sh = *Santacruzodon hopsoni*, Sk = *Staurikosaurus pricei*, Sl = *Sangaia lavinai*, Sp = *Stahleckeria potens*, St = *Saturnalia tupiniquim*, Tb = *Teyuwasu barberenai*, Tc = *Therioherpeton cargnini*, Tr = traversodontid of Reichel et al. (2007), Ts = *Traversodon stahleckeri*, Ut = *Unaysaurus tolentinoi*.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Santa Maria
Camobi
BR 287
Rio Vacacaí
São João do Polêsine
RS 149
Faxinal do Soturno
Dona Francisca
RS 348
Agudo
Rio Vacacaí mirim
Paraíso do Sul
Rio Jacuí
Novo Cabrais
BR 153
Candelária
Rio Botucaraí
Cachoeira do Sul
Pinheiros
RS 410
RS 403
Rio Pardo
BR 471
Santa Cruz do Sul
Venâncio Aires
RS 244
Porto Mariante
Bom Retiro do Sul
Rio Taquarí
General Câmara
Rio Jacuí
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3-5
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26
Brazil
56° W
51° W
28° S
31° S
200 km
Rivers
Main roads
Secondary roads
RS 244
Route names
Cities/towns
Villages
26
Fossil sites
Sanga do Cabral Formation
Santa Maria Formation
Caturrita Formation
Santa Maria Supersequence
Santa Maria 2 Sequence
Highstand systems tract
Transgressive systems tract
Santa Maria 1 Sequence
Sanga do Cabral Supersequence
Hyperodapedon Assemblage Zone
Hyperodapedon Acme Zone
Ictidosaur Assemblage Zone
Dinodontosaurus Assemblage Zone
Stahleckeria
1 - Catuçaba (Pp)
2 - Rincão dos Weiss (Pb, Ps)
Chiniquá area
3 - Cynodontier sanga (Dp, Ts,Ct,Kv)
5 - Weg sanga (Ct,Pc,Pe,"D")
Chiniquá area
4 - Baum sanga (Sp,Em,Sb,"D")
Inhamandá area
6 - Inhamandá 1 (Hh,Hm,Ae)
7 - Inhamandá 2 (Hs)
30 - Água Negra (Ut)
8 - Faixa Nova (Ns)
11 - Wald sanga (Ns)
35 - Cidade dos Meninos (Ex,Al,Hl)
8 - Faixa Nova (Ae,Hm,Hs)
9 - *Therioherpeton* site (Tc,Pz,Hm)
Alemoa area (Hm,Hs,Cb)
10 - Grossen sanga (Sk,Tb)
11 - Wald sanga (Gb,St,Hy)
São José area
12 - Sanga Schramm (Hs)
13 - Zahn sanga (Rt,Rd)
16 - Linha São Luis (Rg,Sc,Br,Bq,Cr,Gc)
15 - *Sacisaurus* site (Sa,Bs)
15 - *Sacisaurus* site (Ex)
14 - Várzea do Agudo (Hy,Ex,Ec)
33 - Area of São João do Polêsine (Hm,Ae)
18 - Rincão do Pinhal (Ct,Dp,Mo,Tr)
31 - Dona Francisca (Dp,Pt,Ms)
32 - Sítio Cortado (Dp,Cb,Bb,Tr)
Botucaraí area
21 - Sesmaria do Pinhal (Rg,Ih,Bs)
22 - Botucaraí Hill (Jc,Rg,Ph)
23 - *Guaibasaurus* site (Gc)
20 - *Exaeretodon* site (Er,Pn,Ch,Hl)
36 - Linha Facão (Ns,Hs)
34 - Picada Escura (Hy)
Bom Retiro area (Sp,Dp,Ct,Mo)
19 - Sanga Pascual (Is,Kv,Mo)
29 - Pinheiros area (Dp,Ct,Ms)
17 - Cachoeira do Sul (Sl)
27 - Venâncio Aires (Hm,Hs)
24 - Santuário Shoenstatt (Sh,El,Ml)
25 - Vila Melos (Dp,Mo,Kv)
26 - Porto Mariante (Dp,Mr)
28 - *Luangwa* site (Ls) exact location unknown

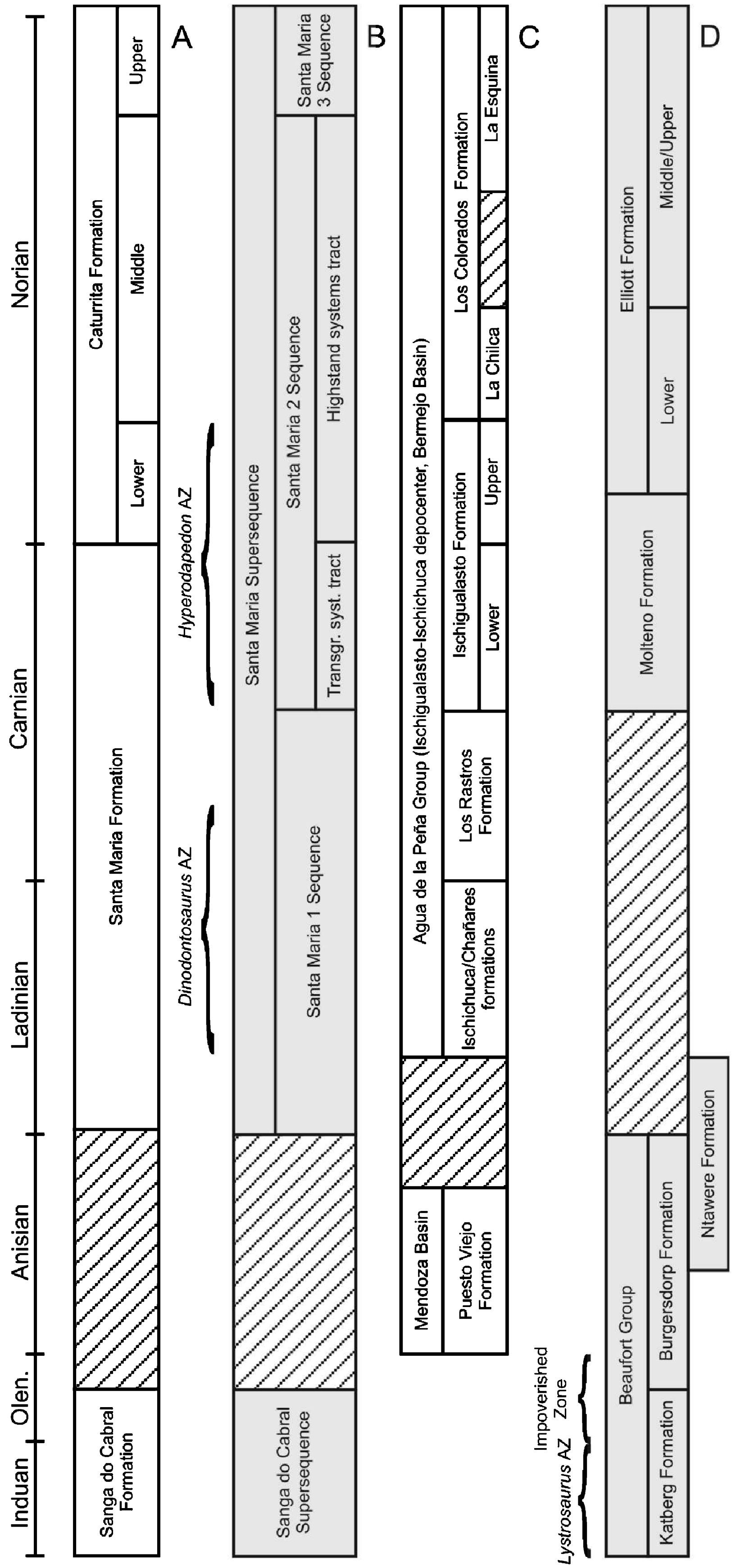

FIGURE 3. Comparison of the lithostratigraphy (**A**) and sequence stratigraphy (**B**) of the Rosário do Sul Group with general stratigraphic charts of the tetrapod-bearing Triassic of Argentina (**C**) and southern Africa (**D**). **A**, based on Andreis et al. (1980). **B**, based on Zerfass et al. (2004). **C**, based on Abdala et al. (2001) and Stipanicic (2002). **D**, based on Neveling et al. (1999), Lucas and Hancox (2001), Abdala and Sá-Teixeira (2004), and Abdala et al. (2005).

Chiniquá and Pinheiros, the latter of which assembles records from different localities from the eastern portion of the outcrop belt of the Alemoa Member, but no further studies followed that path. In the Chiniquá area, the record of *Chiniquodon theotonicus* and *Dinodontosaurus* in the Cynodontier-Sanga allows a rather straightforward correlation to the Chanãres fauna, while more derived forms such as *Stahleckeria potens* and *Exaeretodon major*, from the Baum-Sanga, are suggestive of a younger age (see *Dinodontosaurus* vs. *Stahleckeria* zones of Cooper, 1982), even considering the doubt regarding the latter generic assignment. The situation is similar in the Pinheiros region. Records of *Dinodontosaurus*, *Massetognathus*, and *Chiniquodon theotonicus* support the correlation to that Argentinean stratigraphic unit, while the possible occurrence of *Ischigualastia*/*Stahleckeria* implies a younger faunal stage. The records of *Dinodontosaurus* and *Massetognathus* in Vila Melos, Rincão do Pinhal, and Dona Francisca, and of the former taxon in Sítio Cortado also indicate a correlation to the Chañares fauna, while those of *Luangwa* and perhaps the "Mariante rhynchosaur" suggest an older age for parts of the Santa Maria Formation (Schultz, 1995; Abdala and Sá-Teixeira, 2004). On the contrary, Abdala et al. (2001) proposed a younger age for their "Traversodontid biozone," based on the comparison to a putative Late Ladinian-Early Carnian fauna from Madagascar (Flynn et al., 1999). That biozone includes an assemblage dominated by traversodontids, some of them showing features typical of Ladinian forms and others sharing characters of Carnian forms. This condition, in the absence of dicynodonts, suggests the placement of the Traversodontid Biozone above (Fig. 2) the "typical" faunas of the *Dinodontosaurus* biozone (Abdala et al., 2001; but see Lucas, 2001; Langer, 2005a).

The two antipodal hypotheses that could explain the tetrapod record of the Santa Maria 1 Sequence seem unlikely. It does not appear to correspond to a sole coexisting assemblage, given that the occurrence of *Luangwa* along with *Exaeretodon* or *Ischigualastia*, despite the uncertainty of these latter two records, goes against any current biochronological orthodoxy (Lucas, 1998; Abdala and Sá-Teixeira, 2004; but see Cooper, 1982; Ochev & Shishkin, 1989). It seems equally improbable that faunas of nearby sites, with no apparent stratigraphic separation between them, such as those within the Chiniquá and Pinheiros regions, have radically different ages. Accordingly, the isolated record of *Luangwa* seems to represent the current single evidence of an older, possibly Anisian poorly sampled fauna (Abdala and Sá-Teixeira, 2004, but see Cooper, 1982) within the Santa Maria 1 Sequence. The resemblance of the "Mariante rhynchosaur" to *Stenaulorhynchus* may support an older age also for the Porto Mariante locality. Yet, its poorly constrained phylogentic position precludes more substantiated stratigraphic inferences. Indeed, given the occurrence of *Dinodontosaurus*, that assemblage ("Associação 3" of Schultz, 1995) is better correlated to the bulk of the Santa Maria 1 Sequence, which corresponds to a younger fauna (Fig. 3), the age of which is debatable. It shares index-fossils with the Chañares Formation, implying a Ladinian age (Lucas, 2001), but the record of *Exaeretodon*/*Menadon*–like cynodonts (Barberena, 1974; Abdala et al., 2001) and cf. *Ischigualastia* (Peruzzo and Araújo-Barberena, 1995) provides some evidence of a younger age for certain faunas. If the statuses of these records are confirmed (Abdala et al., 2002b; Lucas, 2001), two alternative scenarios are feasible: the fauna might be intermediate in age between those sampled from the Chañares and Ischigualasto formations of Argentina (see Bonaparte, 1982), but is probably more chronologically extensive (Fig. 3), congregating temporally separate assemblages (Fig. 2). Further taxonomic studies of the above mentioned key-taxa are, however, needed in order to segregate younger faunas from the otherwise typically Chañarian fossil associations.

The fauna of the transgressive systems tract of the Santa Maria 2 Sequence (Fig. 2) belongs entirely in the so-called *Hyperodapedon* Assemblage Zone (Lucas, 2001; Langer, 2005a), first envisaged by Barberena (1977) and assigned different names in the literature (Barberena et al., 1985a, b; Schultz et al., 2000; Abdala et al., 2001). This has been long recognized as partially (Bonaparte, 1982; Barberena et al., 1985a; Langer, 2005a) or totally (Barberena et al., 1985b; Schultz et al., 2000; Abdala et al., 2001; Lucas, 1998, 2002) coeval to the fauna of the Ischigualasto Formation, Argentina (Rogers et al., 1993). Indeed, the record of *Hyperodapedon*, *Aetosauroides*, and herrerasaurid dinosaurs, plainly justifies that hypothesis, whereas the overwhelming dominance of the first genus might allow further scrutinizing. As discussed by Langer (2005a, b), a similar ecological scenario is found in the lower portions of the Ischigualasto Formation, as well as in deposits of other parts of the world, allowing the tentative correlation of a *Hyperodapedon* Acme Zone (Fig. 2) to both the lower portions of that Argentinean stratigraphic unit (Fig. 3) and other parts of Pangea. In chronological terms, a Carnian (= Ischigualastian) age is consensually admitted for that fossil assemblage (Abdala et al., 2001; Lucas, 2001; Schultz et al., 2000; Langer, 2005b; but see Furin et al., 2006).

As stated by Zerfass et al. (2003), the highstand systems tract of the Santa Maria 2 Sequence seems to encompass two distinct "biozones", the lower of which belongs into the *Hyperodapedon* Assemblage Zone. This implies a subdivision of that biostratigraphic unit between transgressive and highstand systems tracts of the Sequence (Fig. 2), as already inferred by Schultz et al. (2000) for their "Rhynchosaur Cenozone". The fauna of the *Hyperodapedon* Assemblage Zone, within the highstand systems tract of Santa Maria 2 Sequence, partly corresponds to "Associação 6" of Schultz (1995), which includes *Exaeretodon*, *Proterochampsa*, and possibly N. gen. *sulcognathus*. The former two taxa are useful for comparison to the Ischigualasto Formation fauna, while the latter allows a correlation (see below) to the lower portions of the highstand systems tract of the Santa Maria 2 Sequence in the area of Santa Maria (Zerfass et al., 2003, fig. 5), which lack records of *Hyperodapedon*. That genus is also missing from the upper part of the Ischigualasto Formation, where the only taxon represented is the abundant *Exaeretodon* (Rogers et al., 1993). This suggests the correlation (Fig. 3) of the upper Ischigualasto fauna to the south Brazilian *Exaeretodon*-bearing deposits (Langer, 2005a) from the type-locality of *E. riograndensis* and the sites of Várzea do Agudo and Cidade dos Meninos. This assumption is, however, jeopardized by both the new records of *Hyperodapedon*-like rhynchosaurs in these sites, and the putative stratigraphic correspondence of the latter two to those yielding the *Hyperodapedon* Acme Zone in the outskirts of Santa Maria (DaRosa 2005). On the contrary, *Exaeretodon* was still not recovered from typical *Hyperodapedon* Acme Zone faunas (Fig. 2). Therefore, although *Exaeretodon*-like forms occur in older assemblages within the Santa Maria Supersequence (Barberena, 1974; Abdala et al. 2001), it is possible to envisage a twofold subdivision (Fig. 4) for the *Hyperodapedon* Assemblage Zone. This includes an older *Hyperodapedon* Acme Zone, encompassing an *Exaeretodon* ghost-lineage, and a younger assemblage where that rhynchosaur is less abundant, occurring along with *Exaeretodon* (Fig. 4; note that these are not segregated in Figure 2).

In the Santa Maria 2 sequence, the record of N. gen. *sulcognathus* roughly matches that of *Exaeretodon*, providing further evidence of the above ordination. It may occur together with *Hyperodapedon* in Linha Facão, a site often correlated to the type-locality of *E. riograndensis*, but also characterizes strata lying above those where *Hyperodapedon* abound in the area of Santa Maria. It is, however, important to stress the conjectural nature of these correlations (Fig. 4). In fact, more collecting effort is needed in order to determine (1) if *Exaeretodon* is really missing from the sites where *Hyperodapedon* abounds, (2) if the latter is really less abundant, or even absent, in sites where *Exaeretodon* occurs, and (3) if *Hyperodapedon* occurs, or not, along with N. gen. *sulcognathus* in some sites. Before that, the task or ordinating these strata may prove unfeasible. In any case, even if slightly younger than the transgressive systems tract of the Santa Maria 2 Sequence (Langer, 2005a, b), there is no reason to assign the *Exaeretodon*-bearing faunas of its highstand systems tract an age other than Ischigualastian (Fig. 3; see also Lucas, 2001).

The upper "biozone" of the highstand systems tract of the Santa Maria 2 Sequence (Zerfass et al., 2003) was fully characterized by Rubert

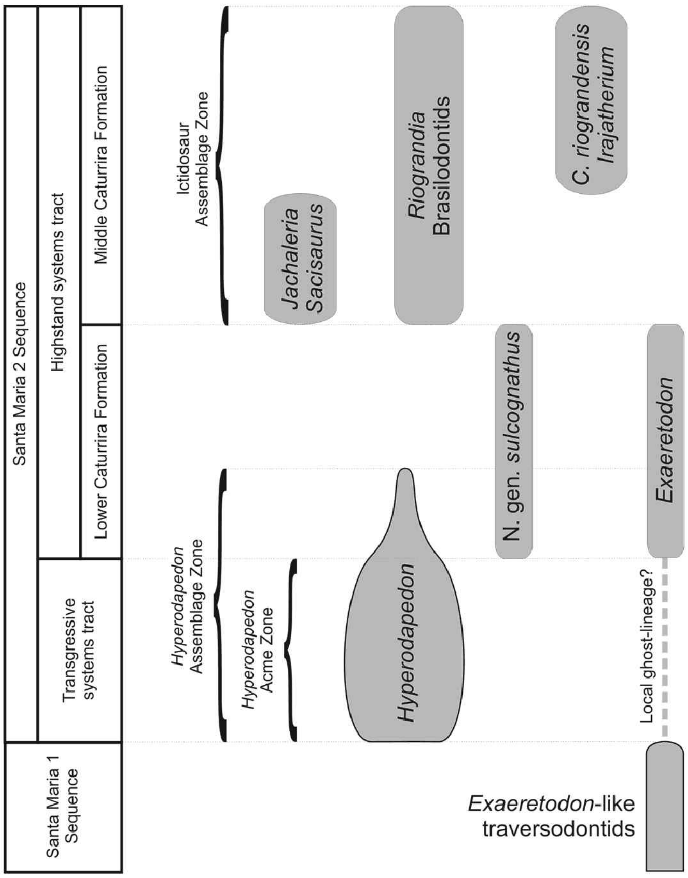

FIGURE 4. Stratigraphic distribution of certain tetrapod taxa in the Santa Maria 2 Sequence, based on the tentative ordination of their fossil assemblages.

and Schultz (2004) as to encompass the *Jachaleria*-level (Scherer et al., 1995; Schultz et al., 2000) and more recently discovered fossil assemblages into the "Ictidosaur Assemblage Zone". This "biozone" is clearly post-Ischigualastian (Langer, 2005a, *contra* Lucas, 2001), and the record of *Jachaleria* allows a direct correlation to the La Chilca fauna of the Los Colorados Formation (Fig. 3). This has been considered of Late Carnian age (Abdala et al., 2001; see also Rogers et al., 1993), but new radiometric data (Furin et al., 2006), supports its placement within the Norian. Although more indicative of the latter (Cisneros and Schultz, 2003), the record of most small tetrapods (e.g., *Riograndia guaibensis*, *Brasilodon quadrangularis*, and *Brasilitherium riograndensis*) does not contradict either age assignment (Langer, 2005a). On the contrary, the sister group relationship between the procolophonids *Soturnia* and *Hypsognathus* (Cisneros, 2006), and those of the cynodont *Irajatherium* (Martinelli et al., 2005) and the sphenodontian *Clevosaurus riograndensis* (Bonaparte and Sues, 2006) to Jurassic forms suggest younger ages. Regarding taxa of other possibly coeval sites, the sister group relation between *Unaysaurus* and *Plateosaurus* (Yates, 2006) suggests a Norian age, while that between *Sacisaurus* and *Silesaurus* (Ferigolo and Langer, 2004) indicates a Carnian age.

The above-mentioned set of ambiguous data prevents an accurate age assignment, and possible ordination of faunas within the "Ictidosaur Assemblage Zone" might help to explain this puzzle. Yet, contrary to the claims of Cisneros and Schulz (2003), there is no lithostratigraphic basis to ordinate any of the fossil bearing strata within that Assemblage Zone (Scherer, 1994; Rubert and Schultz, 2004). Indeed, it seems unlikely that faunas of nearby sites, with no apparent stratigraphic separation between them, such as those of Botucaraí Hill and Sesmaria do Pinhal, have radically different ages. In this case, the whole fauna might be intermediate between those sampled at the localities of La Chilca and La Esquina, both from Los Colorados Formation (Bonaparte, 1982; Abdala et al., 2001), including the earliest records of certain clevosaurid, tritheledontian, and leptopleurine clades. Alternatively, it might congregate temporally separate assemblages. Given their separate occurrences and based on their phylogenetic affinities *Jachaleria candelariensis* and *Sacisaurus agudoensis* would be assigned to an older fauna, while *Irajatherium hernandezi* and *Clevosaurus riograndensis* would characterize a younger one (Fig. 4). In this case, forms that occur together with most of those taxa, such as *Riograndia* and brasilodontid cynodonts would have longer temporal ranger, occurring along that entire time interval (Fig. 4).

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ANOTHER DICYNODONT FROM THE TRIASSIC MUSCHELKALK OF GERMANY AND ITS BIOCHRONOLOGICAL SIGNIFICANCE

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Abstract—An isolated limb bone from the upper Anisian interval of the Muschelkalk in Bavaria, Germany is the radius of a *Dinodontosaurus*-grade dicynodont. This is the third dicynodont bone documented from the German Muschelkalk, and it may indicate that *Dinodontosaurus* records are not strictly Ladinian in age, but could also be late Anisian.

INTRODUCTION

Dicynodonts were a Pangea-wide group of terrestrial tetrapods of the Permian and Triassic that provide important biostratigraphic data for tetrapod biochronology (e.g., King, 1988; Lucas, 1995, 1998, 2006; Lucas and Wild, 1995). Their fossils are particularly abundant in Lower-Middle Triassic strata in Gondwana. In contrast, very few dicynodont fossils have been recovered from the Lower-Middle Triassic of Europe. Here, I add to this meager European record of Triassic dicynodonts a radius from the Anisian interval of the Muschelkalk in southern Germany and discuss its biochronological significance. In this paper, SMNS refers to the Staatliches Museum für Naturkunde, Stuttgart, Germany.

PROVENANCE

The dicynodont fossil described here was collected on 20 July 1974 by M. Wild at Hegenbrunn bei Kulmach in Bavaria, Germany. The fossil came from strata of the upper Muschelkalk that are in the spinosus zone of the standard ceratite zonation of the Muschelkalk. This means that the dicynodont radius is of late Anisian age (e.g., Hagdorn et al., 1998).

DESCRIPTION

SMNS 83875 (Fig. 1) is described here as the nearly complete left radius of a dicynodont. The proximal end has a nearly oval cross section and is broader than the shaft but lacks the epiphyseal cap and/or is eroded proximally. However, it appears that the proximal end of the radius was nearly flat or shallowly concave. There is a sharp radial crest on the antero-medial edge near the proximal end of the bone. The shaft has a trihedral cross section, and the entire bone is slightly bowed (arched), with the most concave side of the arch facing posteriorly. The distal end is much wider than the shaft and wider than the proximal end. It projects antero-medially and has a smooth, saddle-like articular surface, but is crushed in the medio-lateral plane. Maximum length = 109 mm, maximum proximal width = 39 mm and maximum distal width = 52 mm.

IDENTIFICATION

Many tetrapod fossils have been collected from the Muschelkalk, mostly of marine reptiles—nothosaurs, placodonts, pachypleurosaurs, protorosaurs, thalattosaurs and ichthyosaurs (e.g., Lucas, 1997; Hagdorn and Rieppel, 1999). However, some specimens (usually isolated bones) of freshwater or terrestrial tetrapods are also found in the Muschelkalk and include mastodontosaurids, plagiosaurids, tanystropheids and two previously published isolated bones of dicynodonts (Broili, 1921; Lucas and Wild, 1995; Lucas, 1999). Comparison of SMNS 83875 by myself and by O. Rieppel to marine reptile taxa known from the Muschelkalk indicate that it does not belong to any of these groups.

Instead, it appears to be an isolated bone of a terrestrial tetrapod, and it very closely resembles the left radius of a dicynodont, as first suggested to me by R. Wild (cf. Camp and Welles, 1956, fig. 26; Cox, 1965, fig. 17; King, 1981, fig. 26, 1988, fig. 39C-D; Lucas and Harris, 1996, figs. 8.7-8.8; Ray and Chinsamy, 2003, pl. 1, fig. 5, text-fig. 5A; Ray, 2006, pl. 1, fig. 7, text-fig. 1E-F). Indeed, size and shape of the bone are very similar to the radii of *Dinodontosaurus* illustrated by Huene (1935), Beltrão (1965) and Lucas and Harris (1996). Differences, though, between the Muschelkalk bone and the radius of *Dinodontosaurus* include the relative expansions of the ends of the bone and its bowed (curved) shaft. Some or all of these features may, however, be due to distortion (plastic deformation) of the bone. Certainly, an isolated radius cannot be assigned to a dicynodont genus with certainty, so I only identify SMNS 83875 as aff. *Dinodontosaurus* sp., for the same reasons that Lucas and Wild (1995) so identified an isolated dicynodont humerus from the early Ladinian interval of the Muschelkalk near Crailsheim, Germany.

BIOCHRONOLOGICAL SIGNIFICANCE

The specimen described here adds to a sparse Muschelkalk record of isolated dicynodont bones that defy precise identification because of their incompleteness. Two of these records are assigned to aff. *Dinodontosaurus* and are of late Anisian and early Ladinian age. This provides prima facie evidence of *Dinodontosaurus*-grade dicynodonts in marine late Anisian-early Ladinian strata.

Dinodontosaurus is a South American dicynodont known from the Santa Maria Formation in southern Brazil and the Ischichuca (formerly Chañares) Formation of Argentina (Cox, 1965, 1968). These records are in tetrapod assemblages of the Berdyankian land-vertebrate faunachron (lvf) of Lucas (1998) and are generally considered to be of Ladinian age (e.g., Bonaparte, 1982; Lucas, 1998, 1999, 2002), though there is little basis for correlation to the marine timescale. The record of a *Dinodontosaurus*-like dicynodont in late Anisian marine strata of the Muschelkalk opens up the possibility of a late Anisian age for the South American records of *Dinodontosaurus* and the Berdyankian lvf. Thus, at present it may be most defensible to say that the records of *Dinodontosaurus*, and the Berdyankian lvf, likely correlate to late Anisian as well as Ladinian time.

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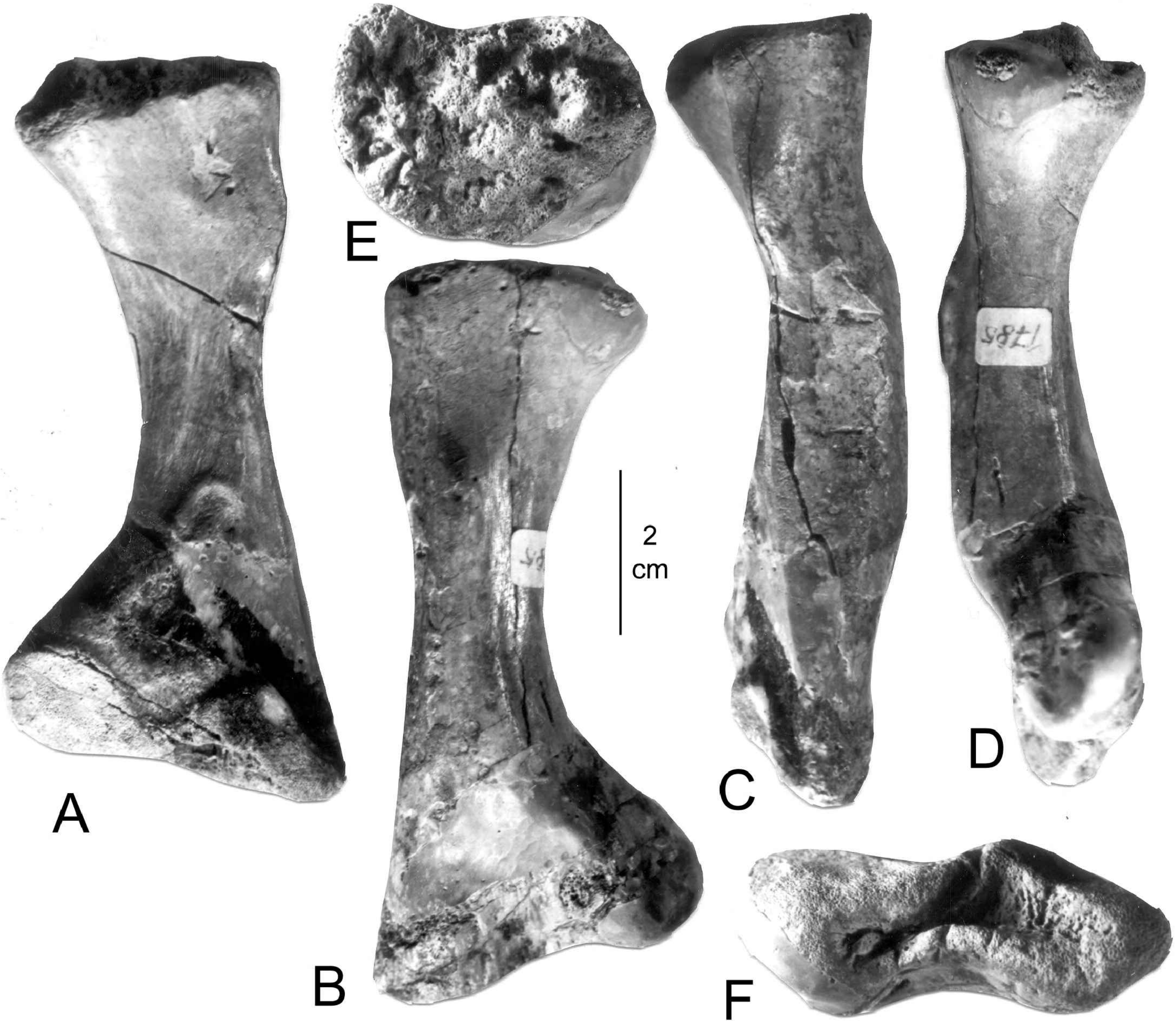

FIGURE 1. SMNS 83875, left radius of a dicynodont (aff. *Dinodontosaurus* sp.) from the upper Muschelkalk at Hegenbrunn bei Kulmach in Bavaria, Germany, in **A**, medial, **B**, lateral, **C**, anterior, **D**, posterior, **E**, proximal and **F**, distal views.

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A GIANT SKULL, ONTOGENETIC VARIATION AND TAXONOMIC VALIDITY OF THE LATE TRIASSIC PHYTOSAUR *PARASUCHUS*

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Abstract—*Parasuchus* (= *Paleorhinus*) is the most primitive known phytosaur, and its fossils define a Carnian biochron recognizable across much of Pangea. The largest known specimen of this primitive taxon, an incomplete skull from the Popo Agie Formation in northwestern Wyoming, demonstrates that the nares remain anterior to the antorbital fenestra throughout the ontogeny of *Parasuchus*, an observation confirmed by an analysis of a broad database. The fact that this character is not variable through the ontogeny of this phytosaur genus, as some previous authors have speculated, helps to cement the taxonomic validity of *Parasuchus*. For the past century, systematists have attempted to establish a classification of organisms rooted in some form of a biological species concept. Cladotaxonomy, on the other hand, is the recognition of cladotaxa, which are low-level taxa (genera and species) that correspond to clades in a cladistic analysis. Cladotaxonomic relegation of all primitive phytosaurs to a metataxon is based on a posteriori evaluation of character polarity that fails to acknowledge the existence of a biotaxon regardless of how a cladist evaluates character polarities millions of years later. We reject assignment of primitive phytosaurs to a metataxon as uninformative, and recognize *Parasuchus* as a diagnosable phytosaur genus.

INTRODUCTION

Phytosaurs are an extinct group of primitive archosaurs whose body fossils are known from Upper Triassic strata in North and South America, Europe, Africa, Madagascar, India, and Thailand (e.g., Hunt, 1994; Hungerbühler, 1998, 2002, and references cited therein). The most primitive known phytosaur is *Parasuchus* (= *Paleorhinus*), which has an essentially Pangean distribution, including an occurrence in marine strata in Austria that reliably calibrates occurrences of *Parasuchus* as Carnian in age (Hunt and Lucas, 1991; Lucas, 1998; Lucas and Heckert, 2000). Indeed, *Parasuchus* is the primary index taxon of the Otischalkian land-vertebrate faunachron (lvf) (Lucas and Hunt, 1993; Lucas, 1998). Because of its widespread distribution and relative abundance, including articulated skeletons from India (Chatterjee, 1978), *Parasuchus* is one of the best-known phytosaurs. In this paper, we describe a specimen collected nearly 50 years ago that is the largest known skull of *Parasuchus*. This specimen is important because it provides insight into the growth of the skull of *Parasuchus*, which we analyze metrically with a preliminary data set. This analysis and the desirability of informative taxonomy lead us to reject cladotaxonomic relegation of all primitive phytosaurs to a metataxon.

In this paper we consider *Parasuchus* to be a subjective senior synonym of *Paleorhinus*, even though *Paleorhinus* was the widely used name by the 1990s. This is because a little advertised application by Chatterjee (2001) to the International Commission on Zoological Nomenclature (only one comment was published on this application: Hungerbühler, 2001a) requested a neotype designation for *Parasuchus hislopi*, the oldest name for a primitive phytosaur genus and a *nomen dubium* based on an undiagnostic holotype (Hunt and Lucas, 1991). The Commission (Opinion 2045) ruled in favor of the application, so *Parasuchus* is a diagnosable taxon that we consider a senior synonym of *Paleorhinus* (and the other synonyms of *Paleorhinus* listed by Hunt and Lucas, 1991, p. 488).

PROVENANCE

The specimen described here, FMNH (Field Museum of Natural History, Chicago) PR 130 (field number PA-75-48) (Fig. 1), was collected in Wyoming by a FMNH party led by G. Snyder in 1948, apparently as an incidental part of an expedition to collect younger fossils. The locality is recorded as the south banks of the river by "Ochre Hill," approximately 1 mile southeast of Dubois in Fremont County, Wyoming. Presumably "the river" refers to the Wind River. The specimen's matrix is a brownish red mudstone containing abundant flecks of whitish analcime, a typical lithology of the Popo Agie Formation in Wyoming (Lucas, 1993).

The Popo Agie Formation in Wyoming yields a relatively sparse, but important, tetrapod assemblage of Otischalkian age. That assemblage includes the metoposaurid temnospondyl *Buettneria*, the dicynodont *Placerias*, the rhynchosaur *Hyperodapedon*, the phytosaurs *Parasuchus* and *Angistorhinus*, the rauisuchian *Heptasuchus*, and the poposaurid *Poposaurus* as well as probable (but fragmentary) dinosaurs and other tetrapods (Williston, 1904; Mehl, 1913, 1915a,b, 1928; Branson and Mehl, 1928, 1929; Branson, 1948; Dawley et al., 1979; Lucas, 1994, 1998; Lucas and Heckert, 2002; Lucas et al., 2002).

DESCRIPTION

FMNH PR 130 is a very large, incomplete phytosaur skull exposed in dorsal view (Fig. 1). Preserved, identifiable portions of the skull include the bones immediately surrounding the external nares, remnants of the septomaxillae, the medial and posterior margins of the antorbital fenestrae, all of the bones surrounding the orbits, and the left lateral temporal fenestra, postfrontals, parietals, and right squamosal. It appears that the entire block broke into at least three pieces and was rather poorly (hastily?) repaired with plaster. Another block with the same catalog number is even more poorly preserved, with a few plates of bone visible on the surface. This block was also "restored" (repaired?) with plaster. No identifiable elements are visible on the second block, although some vertebrae or part of the snout may be present.

The skull has been only partially prepared. As preserved, it measures 590 mm long from immediately anterior to the nares posteriorly to the squamosals. Thus, the skull length of 590 mm includes little of the snout, which usually comprises much of the length of a phytosaur skull (Gregory, 1962; Chatterjee, 1978). At its widest, FMNH PR 130 is approximately 415 mm wide in the vicinity of the quadratojugals, although the lateral margins of the skull are generally missing, poorly preserved if present, and the whole skull appears to have been dorsoventrally crushed. Using the allometric regression for skull width, A-P orbital diameter and postorbital length versus length that we develop

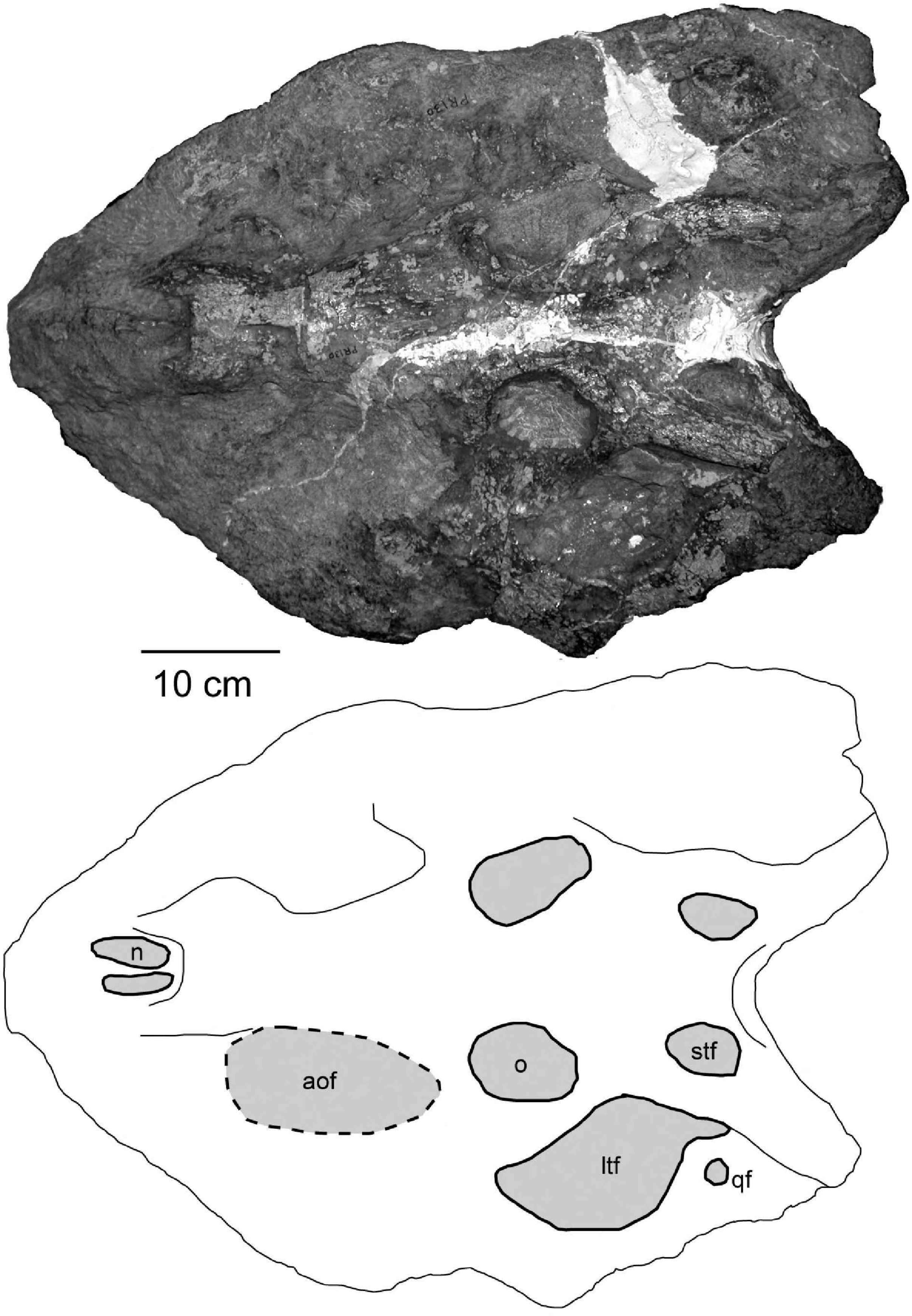

FIGURE 1. Photograph and line drawing of dorsal view of FMNH PR 130, skull of *Parasuchus* sp. from the Popo Agie Formation of Wyoming. Abbreviations are: aof = antorbital fenestra, ltf = lateral temporal fenestra; o = orbit; qf = quadratic foramen; stf = supratemporal fenestra.

later, we calculate that this skull would have been slightly over 1.5 m in length. This is, by far, the largest known skull of *Parasuchus*.

The nares are little, if at all, elevated above the skull roof and their dorsal margins are inclined anteriorly. There is very little bone preserved anterior to the nares, but the 6-7 cm of matrix block preserves no indication of a narial crest. The nares are located almost entirely anterior to the antorbital fenestrae, the primitive condition for archosaurs and one of the diagnostic traits of *Parasuchus* (Hunt and Lucas, 1991; Hunt, 1994; Long and Murry, 1995). In addition, the dorsal margin of the external nares is inclined anteriorly, the orbits are dorsally oriented and a large quadratic foramen is present, all characteristic features of *Parasuchus* (Hunt and Lucas, 1991).

The left orbit is the better-preserved and is ~65 mm long and ~58 mm across. The antorbital fenestrae are poorly preserved, but the left is ~ 120-140 mm long. The right is 100 mm long (minimum) and more likely 140 mm long. The left lateral temporal fenestra is a rhombus with the following dimensions: base ~75 mm, top ~65 mm, anterior margin ~100 mm, posterior margin ~110-130 mm (across curve), with diagonals of 140 and 90 mm. The supratemporal fenestrae are well-preserved, filled with matrix, and essentially at the level of the skull roof and fully exposed as two ovals in dorsal view. The left is ovoid and approximately 35 mm wide by 50 mm long. The right appears to be 30 mm wide by 55 mm long. The right squamosal is thin and rod-like, approximately 30 mm wide and 140 mm long and almost entirely at the level of the skull roof. There is very little, if any, descending process. A quadratic foramen appears to be present on the left side of the skull at the quadrate-quadratojugal juncture.

ONTOGENY AND SIZE OF *PARASUCHUS*

Relatively little is known about the ontogeny of phytosaurs, and this has allowed some speculation about ontogenetic changes in key diagnostic features of the phytosaur skull. With regard to *Parasuchus*, this speculation began with comments by Padian (1994) on an incomplete rostrum (with external nares anterior to the antorbital fenestrae) from the Adamanian *Placerias* quarry of Arizona that Ballew (1989), Hunt and Lucas (1991), Long and Murry (1995) and Lucas et al. (1997) identified as *Paleorhinus*. Padian (1994, p. 405) suggested that this might be a fragment of a juvenile skull based on its small size and the possibility that juvenile phytosaurs may have retained the "plesiomorphic condition" of external nares that are anterior to the antorbital fenestrae with the former "migrating posteriorly and dorsally (through ontogeny) as they do in fact phylogenetically." Nevertheless, as Lucas et al. (1997) noted, no data support this inference of ontogeny recapitulating phylogeny.

Subsequently, Fara and Hungerbühler (2000) correctly recognized that the holotype skull of *Paleorhinus magnoculus*, from the Upper Triassic of Morocco, is that of a juvenile (Fig. 2). Dutuit (1977) originally described this skull as a distinct species of *Paleorhinus*, and Long and Murry (1995) made it the type of a new genus, *Arganarhinus*. However, Fara and Hungerbühler (2000) argued that the relatively large orbits, relatively short snout and overall small size of the holotype of *P. magnoculus* indicate that it is a juvenile specimen, and we concur. Fara and Hungerbühler (2000, p. 836) went on to conclude that "no other characteristics than those deemed here ontogenetically variable have been presented to substantiate the assignment [of the holotype skull of *P. magnoculus*] to *Paleorhinus*," even though they did not in any way demonstrate ontogenetic variation in the diagnostic characters of *Paleorhinus* (such as the nares located anterior to the antorbital fenestrae) that are evident in the holotype skull of *P. magnoculus*.

We have assembled a preliminary metric database from our own data and published information (Appendix) with which to evaluate relative growth of some aspects of the skull of *Parasuchus* across the various species. In an allometry plot (Huxley, 1932) we fit linear equations (slope-intercept form) to the $\log_{10}$-transformed data (Fig. 3). In such a plot, the relative growth of a sector or feature is indicated by the slope of the curve fit line, which is the allometric growth constant, k. If k = 1, isometric growth is indicated, whereas positive and negative allometry are indicated by k > 1 and k < 1, respectively (Gould, 1966).

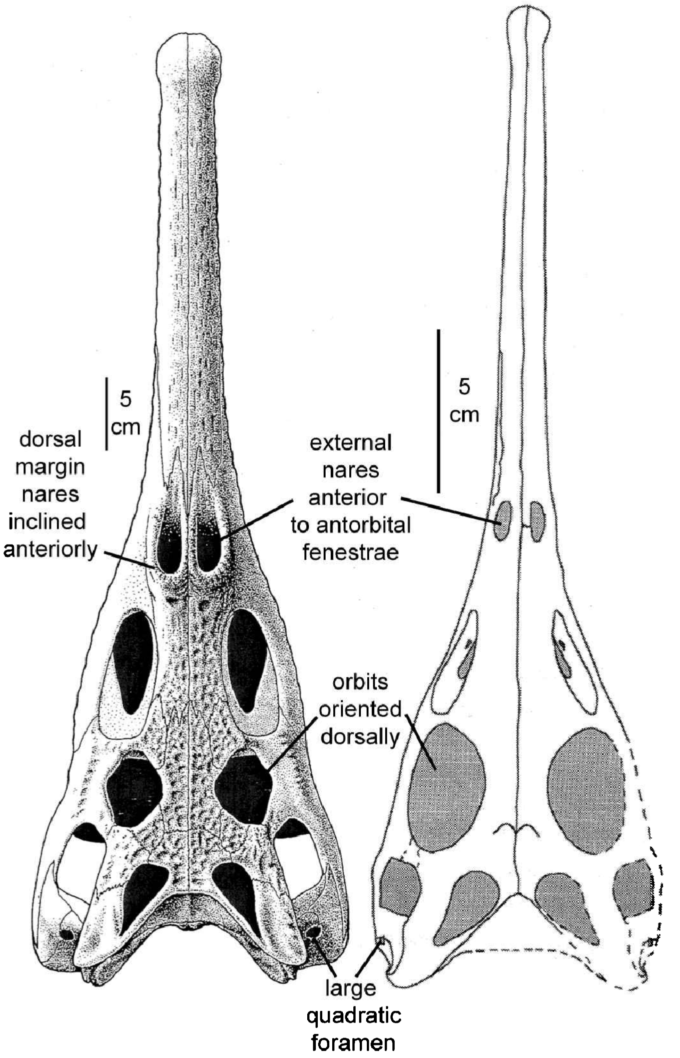

FIGURE 2. Diagnostic features of the skull of *Parasuchus*; adult skull from Poland (after Dzik, 2001) and the holotype juvenile skull of *P. magnoculus* (after Fara and Hungerbühler, 2000).

These data (Fig. 3) show that as the skull length of *Parasuchus* increased, the orbits grew relatively little (strong negative allometry, k = 0.4), whereas prenarial length grew relatively more than skull length (weak positive allometry, k = 1.14). Both preorbital and postorbital lengths increased in very slight positive allometry (k = 1.06 and k = 1.07, respectively). Given the small sample size, it is possible that isometric growth is present in these sectors. Skull width grew relatively less than length (negative allometry, k = 0.83).

Most significantly, there was essentially no growth (extreme negative allometry, k ~ 0.06) in the part of the rostrum between the antorbital fenestrae and external nares (postnaris-aof in the plot). In other words, the absolute distance between the external nares and the antorbital fenestrae remains approximately constant throughout ontogeny in *Parasuchus*. These data show very wide scatter, and the correlation coefficient, R^2, is extremely low (0.001). The data points, however, definitely form a prolate grouping whose poles are essentially horizontal (zero growth). Additionally, the preantorbital fenestra length (pre aof L) shows slight negative allometry (k = 0.95) in spite of the fact that most of its length is made up of the prenarial length, which shows positive allometry. The allometric difference between the prenarial length and preantorbital length

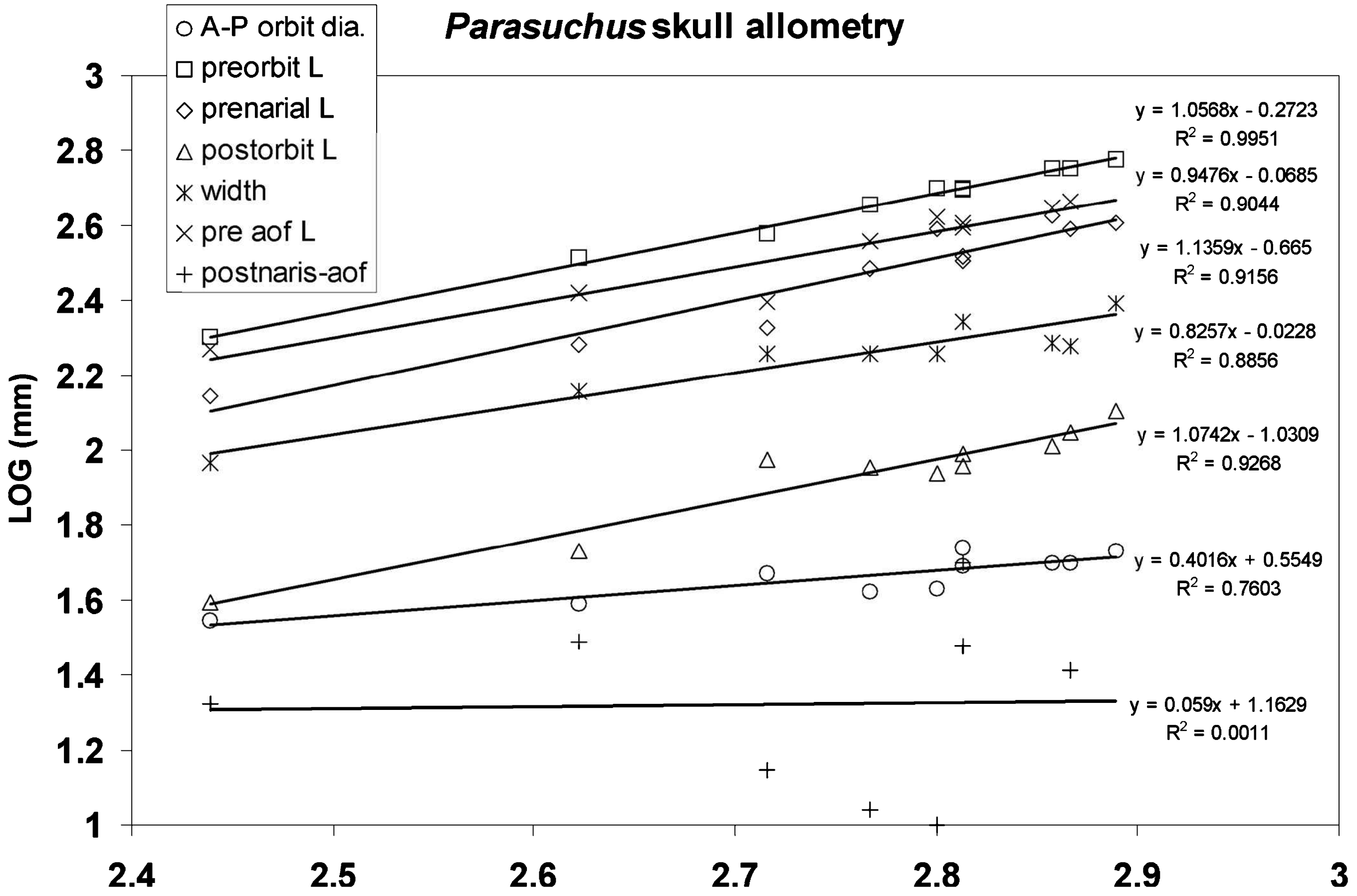

FIGURE 3. Cranial allometry of *Parasuchus* based on metric data listed in the Appendix.

definitely reinforces the idea that the sector between the nares and antorbital fenestra is one of extreme negative allometry. Obviously, at some point very early in ontogeny there must be some growth in this region, but over the span of skull lengths in our database (275 mm to 775 mm) there is practically none. The fact that the area between the nares and antorbital fenestra shows essentially no growth refutes previous suggestions that this key diagnostic character of *Parasuchus* is ontogenetically variable.

Therefore, the skull we document here, while nearly twice the length of any previously described specimen of *Parasuchus,* is certainly congeneric with other published specimens. Importantly, all of the characteristics used by Hunt and Lucas (1991) to diagnose *Parasuchus* (=*Paleorhinus*) are present on this specimen.

The estimated skull length of this specimen places it among the largest known phytosaur skulls. Some of the largest phytosaur skulls documented to date include:

1. The holotype of *Machaeroprosopus gregorii* Camp, 1930, (=*Rutiodon gregorii* of our usage).
2. The holotype of *Brachysuchus megalodon* Case, 1929 (=*Angistorhinus megalodon* of our usage).
3. A large *Rutiodon* (=*Machaeroprosopus*) skull described by Colbert (1947).
4. A large skull of *Redondasaurus* skull described by Heckert et al. (2001).

The first three of these comprise the longest specimens documented by Colbert (1947, table 3) or Gregory (1962, fig. 4) in their analyses of phytosaurs and are based on relatively complete skulls. The fourth specimen was very conservatively estimated to be ~1.17 m long by Heckert et al. (2001) and is based on a skull lacking the snout, as is the specimen here. All of these specimens are robust, as well. If our analyses are correct, the skull we describe here, if it were complete, would probably be the longest known phytosaur skull, as only the gigantic skull described by Colbert (1947) exceeds 1.4 m in length.

CLADOTAXONOMY OF PRIMITIVE PHYTOSAURS

Lucas and Kondrashov (2004) coined the term cladotaxonomy, and defined a cladotaxon as a low-level taxon (genus or species) that corresponds to a clade in a cladistic analysis. We generally reject a cladotaxonomic approach (also see Lucas, 2005) to the alpha taxonomy of fossil vertebrates for four reasons:

1. No attempt at gauging the amount of, and the significance of, variation is incorporated into the cladistic analysis. Instead, the variation, such as it is determined, is assumed to be of phylogenetic significance only. Thus, the possibility of populational variation in characters deemed to be of phylogenetic significance is not addressed. This is of particular concern in phytosaurs, as some characters used in previous cladistic analyses, such as the presence of a rostral crest, are now known to be sexually dimorphic in at least some taxa (Zeigler et al., 2002, 2003).

2. The cladotaxonomy names nearly every branch, stem, and node on the cladogram, and thus results in taxonomic hypersplitting. Because the cladogram artificially imposes a cladogenetic pattern on this splitting, any genus currently considered speciose will be split into multiple genera by the cladotaxonomic approach, and anagenetic evolution within

a lineage cannot be recognized.

3. Cladotaxa only convey the topology of a cladogram and thus are taxa devoid of other biological significance. The cladogram is based on a character atomization that takes discrete characteristics of biological import and divides them into many smaller characters, all deemed to be of equal phylogenetic significance. Thus, any biological significance of the characters is removed from the analysis at the outset.

4. Finally, there is the "cladogram du jour factor." Cladistic analysis has proven highly useful in constructing phylogenetic hypotheses that can be subjected to rigorous evaluation. But, when such hypotheses are instantly turned into new taxonomic names, the taxonomic nomenclature becomes burdened with numerous names based on little-tested hypotheses. In effect, the cladogram of the moment, even if it is the only published cladogram (the "cladogram du jour"), becomes the basis for new taxonomy. New alpha taxonomy based on such a cladogram is premature.

Another aspect of cladotaxonomy that has not been discussed can be called the metataxon problem. To many cladists, a taxon recognized as primitive in a cladistic analysis, and that lacks any supposed autapomorphies, cannot be identified as a taxon, and instead becomes a metataxon. Such metataxa are typically seen as taxonomic garbage cans ("grades") that encompass specimens that defy precise identification. However, in reality, such metataxa are simply an artifact of an a posteriori reasoning process—all cladistic hypotheses must have a symplesiomorphic sister taxon, and if that taxon lacks autapomorphies according to the analysis, it is deemed a metatxon. In reality, the taxon as a biological entity existed, regardless of how a cladist judges character polarities.

Parasuchus provides a good example. Cladistic a posteriori reasoning terms it a metataxon because it is the most primitive phytosaur and lacks autapomorphies in the analysis (e.g., Hungerbühler, 2001b, 2002). However, primitive phytosaurs lived during the Late Triassic and were unaware of subsequent a posteriori cladistic reasoning more than 200 million years later. Those primitive phytosaurs constituted a biological entity that merits a Linnaean name, as do all other diagnosable biotaxa, and that name is *Parasuchus*.

Indeed, *Parasuchus* (=*Paleorhinus*) is one of the best known and longest-recognized phytosaurs (e.g., Williston, 1904; Lees, 1907; Ballew, 1986, 1989; Hunt, 1989; Hunt and Lucas, 1991, Long and Murry, 1995). Furthermore, prior to cladistic a posteriori reasoning and Chatterjee's (2001) unadvertised petition to the ICZN, the name *Paleorhinus* had one of the most stable taxonomic histories of phytosaurs (compare genus-level synonymies in Hunt [1994] and Long and Murry [1995]). Hunt and Lucas (1991) identified four diagnostic characters of *Parasuchus* that distinguish it (and its obvious synonyms: see Hunt and Lucas, 1991, p. 488) from all other phytosaurs: external nares anterior to antorbital fenestrae, dorsal margin of external nares inclined anteriorly, dorsally-oriented orbits and large quadratic foramina (Fig. 2). Referring to this genus as "*Parasuchus*-grade" phytosaurs (phytosaurs with nares clearly anterior to the antorbital fenestra, the primitive archosaurian condition) or "non-phytosaurid phytosaurs" (e.g., Fara and Hungerbühler, 2000; Hungerbühler, 2001b, 2002) simply ignores useful morphological information and thus produces an uninformative taxonomy. We prefer a taxonomy with maximum information that recognizes discrete morphological clusters as taxa, and continue to apply the generic name *Parasuchus* to the most primitive phytosaurs.

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APPENDIX

Parasuchus **skull metrics; various species from various sources.**

										LOG10 transforms							
Taxon	**Reference**	**skull L**	**A-P orbit dia**	**preorbit L**	**prenarial L**	**postorbit L**	**width**	**pre aof L**	**postnaris-aof**	**skull L**	**A-P orbit dia**	**preorbit L**	**prenarial L**	**postorbit L**	**width**	**pre aof L**	**postnaris-aof**
Paleorhinus magnoculus	Fara & Hungerbuhler, 2000	275	35.1	200.4	140	39.5	92.4	186	21	2.4393327	1.54530712	2.301898	2.146128	1.596597	1.965672	2.269513	1.32221929
Promystriosuchus ehlersi *	Case, 1922	720	50	567	426	103	193	444	-15	2.8573325	1.69897	2.753583	2.62941	2.012837	2.285557	2.647383	
Paleorhinus bransoni	Fara & Hungerbuhler, 2000	775	54	599	404	127.5	248			2.8893017	1.73239376	2.777427	2.606381	2.10551	2.394452		
Paleorhinus sp.	Dzik, 2001	650	55	495	330	98	220	405	50	2.8129134	1.74036269	2.694605	2.518514	1.991226	2.342423	2.607455	1.69897
Francosuchus broilii *	Kuhn, 1932	520	47	378	212	95	181	250	14	2.7160033	1.67209786	2.577492	2.326336	1.977724	2.257679	2.39794	1.14612804
Parasuchus hislopi *	Chatterjee, 1978	585	42	453	305	90	182	362	11	2.7671559	1.62324929	2.656098	2.4843	1.954243	2.260071	2.558709	1.04139269
Ebrachosuchus neukami *	Kuhn, 1936	631	43	501	389	87	182	420	10	2.8000294	1.63346846	2.699838	2.58995	1.939519	2.260071	2.623249	1
Paleorhinus bransoni	Williston, 1904	735	50	565	390	112	190	461	26	2.8662873	1.69897	2.752048	2.591065	2.049218	2.278754	2.663701	1.41497335
Paleorhinus AbIII/112	SGL	419	39	326	192	54	144	264	31	2.622214	1.59106461	2.513218	2.283301	1.732394	2.158362	2.421604	1.49136169
Paleorhinus AbbIII/200	SGL	650	49.1	502	322	91.5	221	393	30	2.8129134	1.69108149	2.700704	2.507856	1.961421	2.344392	2.594393	1.47712125

*Synonymized with *Paleorhinus* (Hunt, 1991)

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GLOBAL TRIASSIC TETRAPOD BIOSTRATIGRAPHY AND BIOCHRONOLOGY: 2007 STATUS

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Abstract—The global Triassic timescale based on tetrapod biochronology remains a robust tool for both global and regional age assignment and correlation. The Lootsbergian and Nonesian land-vertebrate faunachrons (LVFs) are of Early Triassic age; cross correlation of part of the Lootsbergian to the Olenekian and all or part of the Nonesian to the Anisian lacks support. In the South African Karoo basin, both the Lootsbergian and the Nonesian can and should be subdivided into sub-LVFs. The upper part of the South African *Cynognathus* zone, previously considered Nonesian in age, is younger, of Perovkan age. We redefine the beginning of the Perovkan as the first appearance datum of the temnospondyl *Eocyclotosaurus*, which resolves uncertainties in the correlation of *Eocyclotosaurus* assemblages and shansiodont assemblages. The Berdyankian LVF equates to parts of Ladinian and Carnian time. Rejection of recent cladotaxonomy of phytosaurs and an incorrect claim of a Revueltian record of the temnospondyl *Metoposaurus*, as well as newly established stratigraphic ranges and new taxonomy of aetosaurs, have improved correlation and temporal resolution within the interval Otischalkian-Apachean. This further supports separation of the Otischalkian and Adamanian and runs contrary to suggestions to merge the two LVFs as a single Ischigualastian LVF. Though readily recognized and correlated in western North America, the Apachean LVF remains the most problematic LVF for global correlation. A recent purported test of the Triassic LVFS based on GIS is rejected as invalid because it is replete with internal inconsistencies, factual errors and questionable interpretations. Continued careful biostratigraphy in the field and improved alpha taxonomies that are not cladotaxonomies will further develop, elaborate and test the Triassic timescale based on tetrapod evolution.

INTRODUCTION

Although the use of tetrapod fossils for biostratigraphy had a long tradition, Lucas (1990) first discussed the possibility and desirability of developing a global Triassic timescale based on tetrapod evolutionary events. Lucas and Hunt (1993) subsequently proposed a series of four land-vertebrate faunachrons (LVFs) for most of Late Triassic time based on a succession of four tetrapod fossil assemblages ("faunas") in the Chinle Group of the western United States. Huber et al. (1993) also proposed a set of LVFs for the Upper Triassic tetrapod assemblages of the Newark Supergroup in eastern North America. Lucas (1993) proposed four LVFs for the Early-Middle Triassic tetrapod assemblages of northern China. Lucas et al. (1997a) presented revised definitions of some of the Late Triassic LVFs.

Lucas (1998) consolidated these earlier works and presented a comprehensive global Triassic tetrapod biochronology (Fig. 1). This scheme, which divides Triassic time based on tetrapod evolution, has now been tested and refined over nearly a decade. Here, we discuss the current status of the Triassic tetrapod-based timescale, reviewing new data and analyses and addressing some of the comments and critiques of some other workers.

In this paper: FAD = first appearance datum; HO = highest occurrence; LO = lowest occurrence; LVF = land-vertebrate faunachron; and SGCS = standard global chronostratigraphic scale (the "marine" timescale).

THE LAND VERTEBRATE FAUNACHRONS

Lootsbergian

Lucas (1998) defined the Lootsbergian LVF as the time between the FADs of the dicynodont *Lystrosaurus* and the cynodont *Cynognathus* (Fig. 1). In essence, it is the time equivalent to the "*Lystrosaurus* zone" of longstanding usage. Based on its principal index fossil *Lystrosaurus*, Lootsbergian-age tetrapod assemblages have long been identified in South Africa, Russia, India, China and Antarctica (see references in Lucas, 1998). Recognition of and correlation within the Lootsbergian appears to be one of the most biostratigraphically stable parts of the Triassic tetrapod timescale.

Nevertheless, three issues merit consideration based on recent work: (1) what is the relationship of the beginning of the Lootsbergian to the Permo-Triassic boundary (PTB)?; (2) what is the precise correlation of the Lootsbergian to the standard global chronostratigraphic scale (SGCS)?; and (3) can the Lootsbergian LVF be subdivided?

Unlike almost all of the Triassic marine stage boundaries, the base of the Triassic (= base of Induan Stage) has been formally defined by the FAD of the conodont *Hindeodus parvus* at a global stratotype section and point (GSSP) located at Meishan in southern China (Yin et al., 2001). This means it is possible to attempt to correlate a potential Triassic base in the nonmarine section to a fixed, agreed-upon point in the marine timescale. Nevertheless, at present there is no precise basis for correlating the beginning of the Lootsbergian (the FAD of *Lystrosaurus*, long considered a nonmarine proxy for the beginning of the Triassic) to the FAD of *H. parvus*.

Magnetostratigraphic data indicate that the PTB is in a normal polarity chron in marine sections, and a normal polarity chron also encompasses the LO of *Lystrosaurus* in the Karoo basin of South Africa and the Junggur basin of northwestern China (Ogg, 2004; Steiner, 2006). However, this only suggests contemporaneity within the duration of the normal chron (assuming, of course, that it is, in fact, the same normal chron), not synchrony.

Most who equate the *Lystrosaurus* FAD to the Permo-Triassic boundary do so by assuming a single mass extinction in the nonmarine and marine realms is the Permo-Triassic boundary (e.g., Retallack et al., 2003). Similar circular reasoning has been used to identify the Triassic-Jurassic boundary in nonmarine strata (see critique of Lucas and Tanner, 2006). Such circular reasoning overlooks two facts: (1) the largest marine extinction at Meishan actually is below the LO of *Hindeodus parvus*; and (2) it is not at all clear that the LO of *Lystrosaurus* is coincident with a terrestrial mass extinction. Thus, the stratigraphic overlap of *Dicynodon*, the classic youngest Permian dicynodont, and *Lystrosaurus* is well (and repeatedly) documented in South Africa and northwestern China. Plant-based criteria used to identify the Permo-Triassic boundary do not coin-

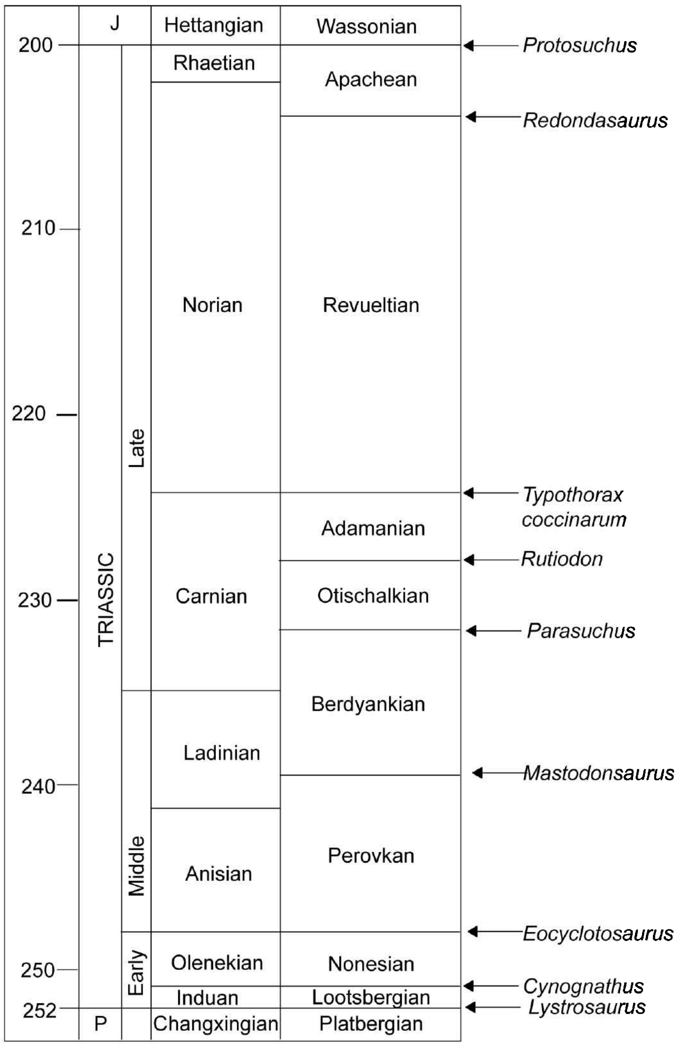

FIGURE 1. The Triassic timescale based on tetrapod evolution showing taxa that define the beginning of each LVF on the right, and correlation of the LVFs to the SGCS.

cide with the LO of *Lystrosaurus* (Hancox et al., 2002). Most of the tetrapod extinctions that occur close to the LO of *Lystrosaurus* are, in fact, stratigraphically below it, and are lesser in number than some of the tetrapod turnovers lower and higher in the section (e.g., King, 1990, 1991; Lucas, 1994). At present, we continue to believe that the beginning of the Lootsbergian is close to the Permo-Triassic boundary, but current data do not demonstrate a precise equivalence.

Correlation of the Lootsbergian to at least part of the marine Induan Stage is clear (Lucas, 1998). However, whether the Lootsbergian equates to part, all or more than Induan time is not possible to determine with the available data. The Wordy Creek Formation in eastern Greenland has a record of Lootsbergian amphibians interbedded with marine late Griesbachian-early Dienerian (middle Induan) age strata (Lucas, 1998). Shishkin (2000, p. 65) asserted that the Lootsbergian includes assemblages younger than Induan, but no credible data support his claim. For example, he stated (p. 65) that "the Hesshanggou assemblage of China [which Lucas, 1998 assigned a Lootsbergian age]…is actually latest Spathian or Spathian-Anisian in age." This undocumented statement is also remarkable considering that there is no direct way to correlate Hesshanggou Formation red beds in Shanxi (long correlated by Chinese workers to the "*Procolophon*" zone of the Karoo: Cheng, 1981) to the SGCS (Lucas, 1993a, 1998, 2001). In another example, Damiani et al. (2000) reported a generically-indeterminate trematosaurid jaw from the South African Lootsbergian strata and claimed it extends Lootsbergian time up to the late Olenekian, largely because of its resemblance to Olenekian *Trematosaurus*. The more likely possibility that Damiani et al. (2000) simply extended the range of that trematosaurid back into the Induan was not considered by them.

Lootsbergian time encompasses both the "*Lystrosaurus* zone" and "*Procolophon* zone" of classic usage (e.g., Broom, 1906). Thus, there may be two or three distinct tetrapod assemblages (at least in the Karoo basin) within the Lootsbergian (the stratigraphic distribution of the cynodont *Thrinaxodon* may be useful here: Groenewald and Kitching, 1995), and this should provide a basis for subdivision of the LVF.

Nonesian

Lucas (1998) defined the Nonesian as the time between the FAD of the cynodont *Cynognathus* and the FAD of the dicynodont *Shansiodon*. In essence, it was intended to be the time equivalent to the South African "*Cynognathus* zone" of classic usage. Cross correlation of the Nonesian to at least part of the Olenekian is clear because of the occurrence of the Nonesian index temnospondyl *Parotosuchus* in marine Spathian strata in the Mangyshlak Peninsula of western Kazakstan (e.g., Lozovsky and Shishkin, 1974).

During the 1990s, careful biostratigraphy in the Karoo basin by John Hancox and collaborators demonstrated that the classic "*Cynognathus* zone" consists of three stratigraphically discrete assemblages (e.g., Hancox et al., 1995, 2000; Hancox, 2000). These assemblages have been called subzones A, B and C by Hancox et al. (1995), and the upper is clearly Perovkan in age (Hancox, 2000). This means the South African Nonesian (which encompasses subzones A and B) is divisible into two biochronological units (Hancox, 2000). However, correlation of these subzones to the Olenekian-Anisian remains somewhat problematic, and the alternatives are well discussed by Hancox (2000). We regard subzones A and B as Early Triassic and C as Anisian, but the jury is still out on whether B could be, at least in part, early Anisian. The important point is that recognizing subzone C as Perovkan does not affect the definition of the Nonesian, it only means that considering all of the "*Cynognathus* zone" to be Nonesian (Lucas, 1998) was incorrect.

Perovkan

Lucas (1998) defined the Perovkan LVF as the time between the FAD of the dicynodont *Shansiodon* and the FAD of the temnospondyl *Mastodonsaurus*. Its characteristic assemblage is the tetrapod fauna from the Russian Donguz Formation, so the land-vertebrate biochronology shifts here from superposed South African assemblages (the characteristic assemblages of the Lootsbergian and Nonesian LVFs) to superposed Russian assemblages (the characteristic assemblages of the Perovkan and Berdyankian LVFs). This geographic shift poses problems for the biochronology, particularly in demonstrating the temporal succession (not overlap) of Nonesian and Perovkan-age assemblages. Indeed, the reassignment of the upper "*Cynognathus* zone" to the Perovkan LVF just discussed well reflects such problems.

Shishkin (2000) argued (on weak evidence) that the Donguz Formation tetrapod assemblage is actually late Anisian, so it is younger than the *Eocyclotosaurus* assemblage that well represents the Perovkan in western Europe and North America and is of unambiguous early Anisian age (Lucas and Schoch, 2002). A more circumspect reading of the data (e.g., Ivakhenko et al., 1997) simply regards the Donguz assemblage as Anisian, with no more precise age correlation.

Lucas (1993b) argued that the LO of the dicynodont *Shansiodon* is Anisian, and this is why Lucas (1998) used it to define the beginning of the Perovkan. If the LO of *Shansiodon* is actually younger than the LO of *Eocyclotosaurus*, then *Eocyclotosaurus* is of Nonesian age. This is not easily resolved, but we do note that the LO of *Kannemeyeria* in China predates the LO of *Shansiodon*, as it does in South Africa, and there is no evidence that the youngest Nonesian assemblage in South Africa (subzone B of Hancox et al., 1995) is equivalent to the *Eocyclotosaurus* zone. It is also important to realize that Shishkin's (2000) arguments are based on his own ideas of temnospondyl evolutionary trajectories (not shared, for example, by Schoch and Milner, 2000) and his willingness to readily correlate nonmarine strata to the SGCS based on conchostracans, nonmarine ostracods and other data that we consider of low biostratigraphic reliability.

Nevertheless, we do recognize problems in establishing the temporal succession of Perovkan assemblages, but believe all are broadly Anisian, and some (part of American Moenkopi Group, German Röt Formation) are clearly early Anisian. The easiest way to reduce ambiguity here is to redefine the beginning of the Perovkan as the FAD of *Eocyclotosaurus*, and we do so (Fig. 1). Nesbitt (2003) has demonstrated that the rauisuchian *Arizonasuarus* is widely distributed and relatively easily recognized, so it can be added to the list of Perovkan index taxa.

Berdyankian

Lucas (1998) defined the Berdyankian LVF as the interval between the FAD of the temnospondyl *Mastodonsaurus* and the FAD of the phytosaur *Paleorhinus* (now correctly called *Parasuchus*). As Lucas (1998) noted, global correlations within the Berdyankian interval are confounded by the near endemism of South American tetrapod assemblages that are apparently of this age (the *Dinodontosaurus* faunas of Argentina and Brazil, classically assigned to the Chanarian land-vertebrate "age" of Bonaparte, 1966, 1967). Recognition of Berdyankian-age assemblages in Russian and Germany is rendered easy by the presence of the key index taxon *Mastodonsaurus* (Lucas, 1999)

The Brazilian and Argentinian *Dinodontosaurus* assemblages are unambiguously correlated to each other, and have generally been considered Ladinian based on flimsy palynostratigraphic evidence (see reviews by Lucas and Harris, 1996 and Lucas, 2002). Tetrapod evidence to correlate the *Dinodontosaurus* assemblages to the European Berdyankian is also not robust; it consists of fragmentary remains of *Dinodontosaurus*-grade and *Stahleckeria*-grade dicynodonts from the German Muschelkalk and Russian Bukobay Formation, respectively, not on shared alpha taxa (Lucas and Wild, 1995; Lucas, 1998). At present, this South American-European correlation remains weakly supported and merits further study. This may be one area where magnetostratigraphy (in South America) is needed.

A much better knowledge of Berdyankian assemblages now can be had from German sections where *Mastodonsaurus* extends through the Lettenkeuper (Schoch, 1999; Lucas, 1999). This firmly establishes the Berdyankian as representing a portion of Ladinian time. Particularly significant are newly collected bone beds in the Lettenkeuper, which have yielded a diverse assemblage of tetrapods, including *Plagiosuchus*, *Gerrothorax*, *Mastodonsaurus*, *Kupferzellia*, trematosaurids, almasaurids, *Batrachotomus*, various archosaurs and a cynodont (e.g., Schoch, 2002).

Otischalkian

The Otischalkian LVF was defined as the time between the FADs of the phytosaurs *Parasuchus* (=*Paleorhinus*) and *Rutiodon* (Lucas and Hunt,1993; Lucas et al., 1997a; Lucas, 1998). It is important to note that a little advertised petition to the International Commission on Zoological Nomenclature by Chatterjee (2001) resulted in establishing a diagnostic lectotype for *Parasuchus* (long a *nomen dubium*: Hunt and Lucas, 1991a), so that this name should be regarded as the senior synonym of *Paleorhinus* (see Lucas et al., 2007a). Furthermore, even though Hunt and Lucas (1991a) provided a careful taxonomic revision of *Parasuchus*, and provided a clear diagnosis of the genus that has never been contested, some cladotaxonomists have relegated all primitive phytosaurs to a metataxon (grade) and then claimed these phytosaurs (long and widely known as *Paleorhinus*/*Parasuchus*) are of no value to biostratigraphy (Rayfield et al., 2005). We reject such a cladotaxonomic approach to primitive phytosaur taxonomy and recognize *Parasuchus* as a diagnosable genus widespread in Otischalkian strata (Lucas et al., 2007a). However, there is one record of *Paleorhinus* in what we have regarded as oldest Adamanian strata, at the *Placerias*/Downs quarries in the Bluewater Creek Formation of the Chinle Group in Arizona (Lucas et al., 1997a). Also, note that the aetosaur *Stagonolepis* is now known to have Otischalkian records in Poland (Dzik, 2001) and in Germany (Heckert and Lucas, 2000), so it is no longer an index fossil of the Adamanian LVF (see below).

The Otischalkian index taxa *Longosuchus* (= *Lucasuchus*) and *Doswellia* still stand. *Metoposaurus* also has only Otischalkian records, though Milner and Schoch (2004) recently claimed its presence in the Revueltian Stubensandstein of Germany. They based this claim on a skull acquired by the British Museum in 1862, listed in the museum records as coming from "the Middle Keuper near Stuttgart, Württemburg." Fraas (1889, p. 137) stated the skull came from "Feuerbacher Heide bei Stuttgart" and provided a brief description of the skull, which had never been illustrated. Despite this description, Milner and Schoch (2004, p. 244) stated that "it is questionable if Fraas ever saw the specimen." Feuerbacher Heide was a small community that is now part of greater Stuttgart, where stone quarries in the Schilfsandstein yielded many tetrapod specimens including *Metoposaurus*, the phytosaur *Zanclodon arenaceus* and the sphenosuchian *Dyoplax* (e.g., Hunt, 1993; Lucas et al., 1998a; Hungerbühler, 2001b). Thus, it makes eminent sense for the British Museum metoposaur skull to have come from a stone quarry at Feuerbacher Heide, as stated by Fraas, who had a detailed firsthand knowledge of the Feuerbacher localities and fossils.

Nevertheless, Milner and Schoch (2004) claimed that the BMNH skull came from the Middle Stubensandstein at Aixheim. They based this conclusion on the preservation of the specimen, stating that the "three dimensional creamy-white bone" and "green coarse sandstone" of the BMNH specimen excludes its provenance as Schilfsandstein. However, not all specimens from the Schilfsandstein are black, crushed bone as Milner and Schoch (2004) claim (see for example, the type of *Zanclodon arenaceus*: Hungerbühler, 2001b, figs. 1-2), and "green coarse sandstone" does not exclude the Schilfsandstein lithologically.

Indeed, the original locality data with the British Museum skull preclude its provenance as middle Stubensandstein at Aixheim. Thus, Aixheim is not near Stuttgart, it is ~90 km to the SSW (Hungerbühler, 1998, fig. 1). In 1862, Aixheim would have been at least a two-day journey by horse from Stuttgart, and thus would not have been described as "near Stuttgart." Furthermore, the original attribution to the "Middle Keuper" excludes the Stubensandstein, as the Schilfsandstein was traditionally considered Middle Keuper in Baden-Württemberg (Geyer and Gwinner, 1991). Finally, no well provenanced German metoposaur has ever been found in the Stubensandstein; all are from the Schilfsandstein-Lehrberg Schichten interval (Lucas, 1999). Thus, we conclude that Milner and Schoch's (2004) claim that the British Museum skull is from the Stubensandstein, and thus Revueltian in age, is based on specious reasoning and reject it.

The last Otischalkian index fossil listed by Lucas (1998) is the phytosaur *Angistorhinus*. Its records are Otischalkian (Long and Murry, 1995) except one, near Lamy, New Mexico, where it co-occurs with *Rutiodon* in the earliest Adamanian (Hunt et al., 1993). This overlap of Otischalkian and Adamanian index fossils (as at the *Placerias* quarry in Arizona) is what may be expected in as good a fossil record as the Chinle Group.

The occurrence of a specimen of *Parasuchus* in marine Upper Carnian (Tuvalian) strata in Austria cross-correlates the Otischalkian, in part, to the late Carnian (Hunt and Lucas, 1991a). However, some Otischalkian tetrapods (e.g., those from the Schilfsandstein) are as old as early Carnian (late Julian), so a cross correlation of the Otischalkian to part of the early and part of the late Carnian is best supported by the data (Fig. 1).

We see the Otischalkian as one of the best supported and most globally correlatable of the LVFs; it represents a slice of Carnian time readily recognized in North America, Europe, North Africa and India. Indeed, Heckert and Lucas (2006) demonstrated that, although some vertebrate taxa do co-occur in strata of both Otischalkian and Adamanian age, there are many microvertebrate taxa that are known only from strata of Adamanian age (see below). Rayfield et al. (2005, p. 347), however, claimed that the Otischalkian "cannot act a global biochronological unit" principally based on their endorsement of the cladotaxonomy of *Parasuchus*/*Paleorhinus* and their acceptance of Milner and Schoch's (2004) incorrect report of *Metoposaurus* in the Revueltian Stubensandstein.

Adamanian

Lucas (1998) defined the Adamanian LVF as the time between the FADs of the phytosaurs *Rutiodon* and *Pseudopalatus*. He listed as index fossils the rhynchosaur *Scaphonyx*, the aetosaur *Stagonolepis* and *Rutiodon*-grade phytosaurs (including *Leptosuchus* and *Smilosuchus*). The dicynodont *Ischigualastia* (= *Jachaleria*) was also considered an Adamanian index taxon. Taxonomic revisions and range extensions have necessitated an update of these index taxa.

Stagonolepis now has well-documented records in the Otischalkian assemblage at Krasiejów in southern Poland (Dzik, 1991; Lucas et al., 2007b). This lends support to Heckert and Lucas' (2000) conclusion that *Ebrachosaurus singularis* Kuhn, 1936, from the Otischalkian German Blasensandstein (type destroyed in World War II) was based on specimens of *Stagonolepis*. These European Otischalkian records of *Stagonolepis* thus raise the possibility that its stratigraphically lowest records in North America, such as at the *Placerias*/Downs quarries in Arizona, may also be Otischalkian (and thus the record of *Paleorhinus* there would also be Otischalkian).

Extensive revisions of rhynchosaurs (Langer and Schultz, 2000; Langer et al., 2000a, b) indicate that specimens previously assigned to *Scaphonyx* are dominantly *Hyperodapedon*. Lucas et al. (2002a) reviewed these records in detail and demonstrated that a *Hyperodapedon* biochron is of Otischalkian and Adamanian age. Thus, at the generic level, rhynchosaurs can no longer be used to discriminate the Otischalkian and Adamanian.

Largely based on this, Langer (2005a, b; also see Schultz, 2005) claimed that the Otischalkian and Adamanian cannot be distinguished and they should be abandoned and replaced by a single LVF, the Ischigualastian. To do so, Langer (2005b) dismissed phytosaur-based distinctions of the Otischalkian and Adamanian, basing his rejection largely on the cladotaxonomy of primitive phytosaurs "documented" in published abstracts by Hungerbühler (2001a; Hungerbühler and Chatterjee, 2002). Langer (2005b) also rejected aetosaur-based correlations based on the taxonomy of South American aetosaurs published by Lucas and Heckert (2001) and Heckert and Lucas (2002). This is particularly significant, as Langer (2005b, p. 228) repudiates the work by claiming, without any documentation, that "*Stagonolepis wellesi* lacks a unique ornamentation pattern of its dorsal paramedian osteoderms," contrary to the published work of Lucas and Heckert, as well as those of Long and Ballew (1989), Parrish (1994), Long and Murry (1995) and Parker (2007), among others. Unlike Langer, we prefer to base our taxonomic conclusions on well justified and documented, published work based on the study of fossils, especially where there is a consensus among all experts, not on single sentence opinions that lack supporting data.

Langer (2005b) also used the conclusions of Sulej (2002) regarding the taxonomy of *Metoposaurus* and *Buettneria* to question using amphibians to distinguish the Otischalkian and Adamanian. However, a review of the metoposaur specimens described by Sulej (2002) does not support some of his basic anatomical observations or his taxonomy (Lucas et al., 2007b). Rayfield et al. (2005) also argued for amalgamation of the Otischalkian and Adamanian based largely on the same arguments as Langer (2005a, b).

What these workers also fail to recognize is that: (1) Otischalkian and Adamanian tetrapod assemblages are stratigraphically superposed and readily distinguished in the Chinle Group of the American Southwest; (2) there is no evidence that the "Ischigualastian" of South America is Otischalkian and much more evidence that it is Adamanian, so Ischigualastian should not be redefined to encompass Otischalkian and Adamanian time; and (3) identification of distinct Otischalkian and/or Adamanian assemblages has been achieved in North America, South America, Europe, India and North Africa. The fact that Langer (2005b) and Rayfield et al. (2005) cannot accept a well-documented alpha taxonomy of Otischalkian and Adamanian index fossils (which they have not studied) is not a valid reason to amalgamate the Otischalkian and Adamanian LVFs.

Recent work in the Chinle Group of the western USA has refined the stratigraphic ranges of known tetrapod taxa and has recognized new records in strata of Adamanian age. These new data are principally from the Petrified Forest National Park in Arizona (Heckert and Lucas, 2002; Hunt et al., 2002; Woody, 2003; Heckert, 2004; Woody and Parker, 2004; Heckert et al., 2005) and the extensive exposures of the Chinle Group in east-central New Mexico (Hunt and Lucas, 1995; Lucas et al., 2002b), with other records from the Tecovas and Trujillo formations in Texas (Heckert, 2004; Heckert et al., 2006; Martz and Small, 2006). Clearly, there is a "transitional" fauna between the Adamanian and Revueltian lvfs (Woody and Parker, 2004), and this prompted Hunt et al. (2005) to subdivide the Adamanian into two sub-faunachrons, St. Johnsian (older) and Lamyan (younger), of regional biochronological significance.

Heckert and Lucas (2006) built upon the microvertebrate collections documented by Heckert (2001, 2004) and demonstrated that there are multiple microvertebrate index taxa of Adamanian (St. Johnsian) time, including the xenacanth "*Xenacanthus*" *moorei*, the enigmatic vertebrate *Colognathus obscurus* and the archosaurs (possibly ornithischian dinosaurs) *Tecovasaurus murryi*, *Crosbysaurus harrisae*, and *Krzyzanowskisaurus hunti*.

Revueltian

Lucas (1998) defined the Revueltian as the time interval between the FADs of the phytosaurs *Pseudopalatus* and *Redondasaurus*. However, Hunt et al. (2005) redefined the beginning of the Revueltian as the FAD of the aetosaur *Typothorax coccinarum*, and we endorse this decision (Fig. 1).

Some of the discussion of the Revueltian has focused on whether or not it is readily distinguished from the younger Apachean LVF (Long and Murry, 1995; Rayfield et al., 2005). These arguments again are rooted in taxonomic disagreements (discussed below), as the type assemblages of the Revueltian and Apachean are stratigraphically superposed in east-central New Mexico and thus are obviously time successive.

Typothorax, *Aetosaurus* and *Pseudopalatus*-grade phytosaurs were listed as Revueltian index fossils (Lucas, 1998). However, recognition of an older, Adamanian species of *Typothorax*, *T. antiquum*, by Lucas et al. (2002b) has modified this; it is the species *T. coccinarum* that is a Revueltian index fossil, and this is part of what prompted Hunt et al. (2005) to redefine the beginning of the Revueltian as the FAD of *T. coccinarum*. Parker (2007) has stated without explanation that *T. antiquum* cannot be distinguished from *T. coccinarum* but we dismiss his undocumented claim and refer to the diagnosis provided by Lucas et al. (2002b).

Rayfield et al. (2005, table 1, p. 340) claim that there is a single osteoderm of *T. coccinarum* from the Tres Lagunas Member of the Santa Rosa Formation of New Mexico, citing both Long and Murry (1995) and Lucas et al. (2002b) as the sources of this record. However, a careful reading of Lucas et al. (2002b) reveals there are no *T. coccinarum* fossils known from the Tres Lagunas Member; indeed, the record claimed by Long and Murry (1995, p. 234) is of a specimen of *T. antiquum* from the younger (but still Adamanian) Garita Creek Formation. *T. coccinarum* thus stands as a robust index fossil of the Revueltian across the Chinle Group. Indeed, its likely descent from *T. antiquum* as part of an anagenetic evolutionary lineage (Lucas et al., 2002b) creates the first place in the Triassic tetrapod biochronology that the beginning of a LVF can be defined by a true species-level evolutionary event, not the appearance of a genus-level taxon. This was another impetus to redefine the beginning of the Revueltian as the FAD of *T. coccinarum*.

Aetosaurus is one of the most robust tetrapod index fossils of the Triassic. Lucas et al. (1998b) presented a detailed taxonomic revision based on study of all North American and European specimens. *Aetosaurus* has a marine record in the middle Norian of northern Italy (Wild, 1989), and all of its nonmarine records are Revueltian. Criticism of the use of *Aetosaurus*, well reflected by Rayfield et al. (2005), claims that because *Aetosaurus* has been portrayed as the plesiomorphic sister taxon of other aetosaurs in cladistic analyses (e.g., Heckert and Lucas, 2000) it "must" have a long ghost lineage that therefore renders it useless in biostratigraphy. This is clearly specious cladotaxonomic reasoning (Lucas et al., 1999). Thus, the position of a taxon on a cladogram has nothing to do with its biostratigraphic utility unless all the assumptions of the cladogram—and the existence of a ghost lineage is nothing more than an assumption—are brought into the biostratigraphic analysis. Indeed, any alternative cladogram of aetosaurs, for example, one that views *Aetosaurus* as a highly derived, dwarfed and simplified form, would produce a very different "ghost lineage."

Rayfield et al. (2005, p. 339) further claim "there is some disagreement over the status of supposed '*Aetosaurus*' remains" but provide no explanation, citation, or justification of this remark. We know of no such disagreement in the primary literature on *Aetosaurus* (e.g., O. Fraas, 1877; Huene, 1921; Walker, 1961; Wild, 1989; Heckert and Lucas, 1998; Small, 1998; Lucas et al., 1998b, 1999) or on aetosaurs in general (Walker, 1961; Parrish, 1994; Heckert et al., 1996; Heckert and Lucas, 2000; Parker, 2007). We conclude that there is no valid reason to question the use of *Aetosaurus* as a Revueltian index taxon.

Pseudopalatus-grade phytosaurs include *Pseudopalatus*, *Nicrosaurus* and *Mystriosuchus*, all taxa restricted to Revueltian time. Like the use of *Rutiodon*-grade phytosaurs to identify the Adamanian, this is a convenient and concise way to refer to a group of broadly contemporaneous phytosaur taxa whose stratigraphic ranges are well established, but whose genus- and species-level nomenclature remain in flux (compare Ballew, 1989; Long and Murry, 1995; and Hungerbühler, 2002).

Heckert and Lucas (1996) first suggested that *Revueltosaurus* might serve as an index taxon of Revueltian time. At that time they (and all other published literature) considered *Revueltosaurus*, which was known solely from teeth, to be an ornithischian dinosaur. Parker et al. (2005) documented associated skulls and postcrania of *Revueltosaurus callenderi,* demonstrating that that taxon is actually a crurotarsan archosaur. However, they noted that, following Hunt (1989), Padian (1990) and others, the teeth are indeed diagnostic, and the taxon is valid. Heckert and Lucas (2006) then showed that *R. callenderi* is restricted to strata of Revueltian (Barrancan) age, and is therefore an index taxon of the Revueltian.

The preceding example is important not so much because it reaffirms the validity of the Revueltian, but because it demonstrates the relative unimportance of phylogeny in biostratigraphy. Indeed, just as the vast majority of the geologic time scale (with all periods save the Ordovician named prior to Darwin's publication of the *Origin of Species*) was constructed with no knowledge of evolution *per se*, the changing phylogenetic position of *Revueltosaurus* alters neither its biostratigraphic significance nor its biochronological utility. Biostratigraphically, what is important about *Revueltosaurus* is that it is distinctive (easily identified), relatively common and/or widespread, and known from a relatively restricted stratigraphic interval. Whether it is an ornithischian (as previously supposed) or a crurotarsan (the current hypothesis) is irrelevant to its biostratigraphic potential, regardless of how interesting the evolutionary questions related to its phylogenetic position may be.

Hunt (1994, 2001) divided the Revueltian into three sub-LVFs of regional utility. Two of these, the Barrancan (early Revueltian) and Lucianoan (later Revueltian) are readily correlated in the western USA using various index fossils (e. g., Heckert and Lucas, 2006).

Apachean

The Apachean LVF was defined as the time between the FADs of the phytosaur *Redondasaurus* and the crocodylomorph *Protosuchus*. As Lucas (1998) noted, the Apachean is very difficult to correlate outside of North America because of latest Triassic endemism, and Rayfield et al. (2005, p. 348) correctly described the Apachean as "useful as a regional, but not global, biochronological unit."

Lucas (1998) listed three Apachean index fossils: the aetosaur *Redondasuchus*, the phytosaur *Redondasaurus* and the dinosaur *Riojasaurus*. Restricted to Argentina, *Riojasaurus* is not a robust index fossil of the Apachean, but the Apachean is readily distinguished in North America by its primary index fossils, *Redondasaurus* and *Redondasuchus*. However, some workers (Long and Murry, 1995; Martz, 2002) have questioned the validity of *Redondasaurus* and *Redondasuchus*, proclaiming the former a synonym of *Pseudopalatus* and the latter a synonym of *Typothorax*, although Martz (2002) did recognize *Redondasuchus* as a distinct species of *Typothorax*, *T. reseri*.

Long and Murry (1995) did not consider the supratemporal fenestra being visible in dorsal view a taxonomically useful character, which could be used to distinguish *Redondasaurus* from *Pseudopalatus* (=*Arribasuchus*). Spielmann et al. (2006a) demonstrated that in the various photographic plates used to illustrate the skulls of *Pseudopalatus*, the supratemporal fenestra can always be seen in dorsal view, usually as slits medial to the squamosals (Long and Murry, 1995, fig. 40A-C). Thus, they considered "supratemporal fenestrae that are essentially concealed in dorsal view" is a character that distinguishes *Redondasaurus* as a genus separate from *Pseudopalatus* (= *Arribasuchus*). This interpretation of *Redondasaurus* as distinct from *Pseudopalatus* was also advocated by the taxonomic analysis of Hungerbühler (2002).

Redondasuchus reseri (Hunt and Lucas, 1991b; Heckert et al., 1996) was identified as a juvenile *Typothorax coccinarum* by Long and Murry (1995) and Martz (2002). They suggested that the paramedian osteoderms illustrated by Hunt and Lucas (1991b) were osteoderms of the cervical or caudal region of the carapace. They also attributed the extreme flexure of the paramedian osteoderms of *R. reseri* to postmortem distortion. Spielmann et al. (2006b) reaffirmed the validity of *Redondasuchus* and noted that many paramedian osteoderms of *Redondasuchus* are not crushed or deformed and still exhibit their characteristic flexure.

Lehman and Chatterjee (2005; also see Lehman, 1994) reported a revised Upper Triassic tetrapod biostratigraphy in West Texas using an interpretation of lithostratigraphy that is unique to them (contrary to all previous published stratigraphy and geologic mapping) and was previously refuted by Lucas et al. (1994). Thus, in reading Lehman and Chatterjee (2005) it is necessary to realize that the lithostratigraphy has been retrofitted to an undocumented model of Chinle Group sedimentation in West Texas, one in which relatively fine-grained strata to the west and north (distal or basinal deposits) are assumed to correlate to relatively coarse-grained strata to the east and south (proximal or basin edge deposits). This assumption allows the type Otischalkian tetrapod assemblage near Big Spring to be correlated to the Revueltian assemblages near Post. Previous work on Chinle lithostratigraphy in West Texas, including our own, arrived at different correlations than do Lehman and Chatterjee (2005). Indeed, pioneering work by Drake (1892) produced more credible lithostratigraphic correlations of the West Texas Upper Triassic strata than do Lehman and Chatterjee (2005).

Relatively recent recognition that Apachean-age strata extend above the Chinle Group into part of the Moenave-Wingate (lower Glen Canyon Group) lithosome has been based, in part, on the occurrence of a *Redondasaurus* skull in the lower part of the Wingate Sandstone in southeastern Utah (Lucas et al., 1997b; Lucas and Tanner, 2007). Improved magnetostratigraphy and recognition of *Aetosaurus* in lower Rock Point Formation strata in Colorado (Small, 1998) and New Mexico (unpublished data) also lead us to suggest that Apachean time may not simply equate to the Rhaetian, but may also include late Norian strata. However, as we have long stressed (e.g., Lucas and Hunt, 1993; Lucas, 1998; Lucas and Tanner, 2007), cross-correlation of the Apachean age rocks in the America Southwest to the SGCS is particularly difficult.

DISCUSSION

The global Triassic timescale based on tetrapod evolution developed in the 1990s has been critiqued because of: (1) perceived problems with the alpha taxonomy of some of its index fossils; (2) possible temporal overlap of the Nonesian and Perovkan LVFs; (3) changes and additions to the stratigraphic ranges of some index taxa; and (4) perceived problems of correlation to the SGCS. Taxonomic disagreements lie at the heart of many arguments over biostratigraphy, and we believe the extensive taxonomies we and others developed for many of the Triassic index taxa, especially metoposaurs, phytosaurs and aetosaurs, provide a sound basis for their use in biostratigraphy. Much of the criticism of these taxonomies comes from cladotaxonomists who are developing a typological, oversplit and biologically uninformative alpha taxonomy of many Triassic tetrapods.

Here, we resolve the problems of potential overlap or gaps around the Nonesian-Perovkan boundary by redefining the beginning of the Perovkan to obviate such problems. Stratigraphic range extensions and changes are the regular outgrowth of collecting and careful biostratigraphic study in the field. They always force adjustments to any biochronological scheme rooted in sound biostratigraphy. Problems with correlation of the Triassic LVFs to the SGCS remain largely because in much of the nonmarine Triassic section few data can be relied on for cross correlation to the marine timescale.

Clearly, we need a nonmarine Triassic tetrapod biochronology with which to sequence the history of tetrapod evolution on land. Advances in the scheme proposed in the 1990s have come from new fossil discoveries, more detailed biostratigraphy and additional alpha taxonomic studies based on sound evolutionary taxonomic principles. Most of the criticisms of the scheme have come from cladotaxonomists who believe that imaginary “ghost lineages” somehow constrain biostratigraphic correlation or from those incapable of undertaking accurate lithostratigraphic and biostratigraphic correlations. Rayfield et al. (2005) represents a flawed synopsis of these criticisms, and further couched their review as a “GIS test” of the Triassic tetrapod biochronology (but see the Appendix). This literature review-based test, however, is replete with errors of commission and omission that undermine its use as an evaluation of Triassic tetrapod biochronology, As the work reviewed here demonstrates, that biochronology will continue to be elaborated, refined and evaluated by careful work in the field and museum.

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APPENDIX

Rayfield et al. (2005) presented a putative "GIS study/test" of the Triassic tetrapod biostratigraphy and biochronology we developed in the 1990s (see text). Here, we review this article in detail to demonstrate that it is replete with factual errors, selective use of the literature, misrepresentations and misinterpretations. Page numbers used as headings here and figure and table callouts refer to Rayfield et al. (2005). "The text" refers to the preceding body of our article.

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1. The "massive and abrupt extinction of marine animals" at the Triassic-Jurassic boundary (TJB) has been called into question by Hallam (2002), Tanner et al. (2004) and Lucas and Tanner (2004), literature not cited by Rayfield et al.

2. Lucas (1994) did not argue for "a gradual, possibly competitive replacement" of tetrapods across the TJB.

3. "The standard stage-level division of the Triassic is based upon the stratigraphical distribution of ammonites in the European Alps" is erroneous. The current SGCS recognizes several stages defined on non-Alpine stratotypes, such as Induan and Olenekian. One of the two agreed-on GSSP's for the Triassic stages (base Induan) is defined by conodont biostratigraphy in China, and conodont biostratigraphy will define others.

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4. "Eight 'Land Vertebrate Faunachrons' ('LVFS') were identified, each comprising successive assemblage zones of Triassic tetrapod fossils" is misleading. The LVFs are time intervals between the FADs of key taxa. They have a characteristic tetrapod assemblage, but they are not temporally coextensive with assemblage zones of tetrapod fossils.

5. The "aim to test the LVF concept for the first time, using a Geographical Information Systems (GIS-based) approach" misleads on two accounts. First, there have already been many published tests of the LVF concept prior to Rayfield et al. (see the text), and, second, GIS is not able to test biochronology (see below).

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6. Figure 2 fails to account for Lucas et al.'s (2002a) reappraisal of the distribution of *Hyperodapedon*, although this is later referred to in the text.

7. The reference to Barnosky and Carrasco (2000) implies that somehow their GIS database (MIOMAP) has some relevance to biochronology, but it is not being used to evaluate biochronology simply because GIS cannot make such evaluations.

PAGES 330-333 (TABLE 1)

Many of the age assignments of the index taxa to the SGCS are identical to ours. However, the table contains numerous errors:

8. There is no verified record of *Mastodonsaurus* in the Bromsgrove Sandstone Formation.
9. Similarly, *Mastodonsaurus* is not known from the Schilfsandstein.
10. *Paleorhinus* (=*Parasuchus*) has no record in the middle Pekin Formation.
11. *Paleorhinus* (=*Parasuchus*) has no record in the Tecovas Formation.
12. *Metoposaurus* has no verifiable record in the Baldy Hill Formation.
13. *Metoposaurus* has no record in the Middle Stubensandstein (see the text).
14. *Rutiodon* does not occur in the lower Bull Canyon Formation.
15. *Rutiodon* has no record in the Owl Rock Formation.
16. *Rutiodon* has no record in the Grès à Avicula Contorta.
17. *Typothorax coccinarum* has no record in the Tres Lagunas Member of the Santa Rosa Formation (see the text).
18. There are no records of *Typothorax coccinarum* in the Trujillo Formation.
19. *Typothorax coccinarum* is not known from the Redonda Formation.
20. *Typothorax coccinarum* (indeed, no aetosaur) has ever been documented from the Sloan Canyon Formation.
21. There is no evidence that the aetosaur record in "Lithofaces Association II" of the Deep River Basin, North Carolina is late Carnian. The cited correlation is based on fishes and "magnetostratigraphy in prep.," neither of which reliably indicate a late Carnian age.

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22. It is interesting that "Early Triassic LVFs are not considered herein…because most of their known assemblages occur outside of the western Northern Hemisphere" even though the same could certainly be said of the Berdyankian LVF.

23. The analysis is so frought with basic errors (see comments on Table 1 above) that the claim that "our chosen area and timeframe offer enough information to provide a thorough test of the validity of Middle and Late Triassic LVFs" is questionable.

24. Supposedly "care was taken to ensure that taxon and formation ages were estimated using tetrapod and megafloral-biochronology-independent means (e.g., magnetostratigraphy, radiometric dating, palynology) in order to avoid circularity and non-independence of data (Tables 1, 2)." But, not enough care was taken to produces tables free of numerous errors (see comments on Table 1, above and Table 2, below). Furthermore, are palynological ages really independent of megafloral ages? And, how do you assign a late Norian-Rhaetain age to the Sloan Canyon Formation based on "tetrapod trackways" only (as is done in Table 1), and then claim this "correlation" is independent of vertebrate biostratigraphy?

25. The claim is made that through a "GIS database analysis" the "distribution of type LVF assemblage taxa and key index taxa…through space and time using attribute selection… " is being evaluated. In reality, once a time ordering of tetrapod assemblages is achieved, the distribution of taxa can be determined without GIS. So, to claim that GIS is somehow being used to evaluate the biochronology is to claim for GIS something it cannot do and is not needed to do.

26. How megafloral data can be used "in testing LVF stability" is impossible to understand. Does conodont biostratigraphy test the stability of ammonite biostratigraphy?

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27. Some of the errors in Table 1 are incorporated into the temporal ranges in Figure 3. However, the figure actually indicates very robust index fossils for the Otischalkian, for example, so it does not support (contradicts) the later claim that the Otischalkian is not a useful biochronologic unit.

28. We agree that grade-level correlations are less desirable than shared alpha taxa, but to state that "ghost lineages between sister-taxa may persist for millions of years, such that taxa related at the familial level need not exist in the same temporal range" is to present an assumed and undocumented hypothetical with regard to erythrosuchid-based Middle Triassic correlations.

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29. Were the Moenkopi erythrosuchid identified as *Shanisuchus*, it would support a China-western North America correlation, which is a global terrestrial correlation across Middle Triassic Pangea. Contrary to what is said by Rayfield et al., this would make *Shanisuchus* a quite useful Perovkan index taxon.

30. We do not consider "regional" to equate to "western Northern Hemisphere" (=North America and Europe). This strikes us as a geographical area larger than a "region."

31. "None of the five index taxa [of the Beryankian LVF] are present in North America" is true but misleading, simply because no Berdyankian-age tetrapod assemblage has ever been found in North America.

32. The Berdyankian is Ladinian-Carnian in age, so the statement that the Berdyankian index taxon *Exaeretodon* "ranges from Ladinian- to Carnian-aged strata in South America" is irrelevant to its utility as an index taxon.

33. As above, there are no documented records of *Mastondonsaurus* in the Bromsgrove Sandstone Formation or in the Schilfsandstein. Therefore, the statement that "*Mastondonsaurus* appears not to be a temporally restricted index taxon" is false.

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34. The temporal ranges claimed for *Macronemus* and *Ticinosuchus* (also see Fig. 3) are much longer than their actual ranges.

35. The cladotaxonomic conclusions of Fara and Hungerbühler (2000) and Hungerbühler (2001b) used by Rayfield et al. to undermine the taxonomy of *Paleorhinus* (=*Parasuchus*) have been refuted by Lucas et al. (2007a).

36. The statement that "*Paleorhinus* has not been diagnosed in terms of derived character states; its diagnostic feature, the position of the external naris relative to the antorbital fenestra, is plesiomorphic" is not followed up, but presumably represents the cladotaxonomic reasoning discussed above in the text and rejected by us.

37. In Table 1 *Paleorhinus* is listed as having a marine Carnian record in the Austrian Opponitzer Schichten, and here it is claimed the specimen

"may represent an indeterminate small basal phytosaur." Which is it?

38. The Bluewater Creek record of *Paleorhinus* (=*Parasuchus*) may be Otischalkian, as discussed in the text.

39. Milner and Schoch's (2004) claim of a *Metoposaurus* record in the Stubensandstein, quoted here, is discussed at length in the text and rejected.

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40. "The taxonomic instability of both taxa [*Paleorhinus* and *Metoposaurus*] renders them problematic global biochronological markers," yet the "taxonomic instability" of *Metoposaurus* is in no way discussed.

41. Again, "the taxonomic status of both genera [*Metoposaurus* and *Paleorhinus*] needs further attention before they can be used confidently for global biochronology," yet not even a cladotaxonomic comment is presented by Rayfield et al. regarding the taxonomy of *Metoposaurus*.

42. As documented by Lucas et al. (2007b), *Stagonolepis* now has a known temporal range of Otischalkian-Adamanian, obviating much of the text on page 338.

43. Martz et al. (2003) are cited as indicating that there are "problems in identifying aetosaurs from isolated and incomplete scutes" (but see Heckert et al., 2007), and then it is claimed this is a factor that "hinder[s] the potential of *Stagonolepis* as a useful global Adamanian index fossil." Yet, no published identifications of *Stagonolepis* are actually questioned by Rayfield et al.

44. *Paleorhinus* and *Rutiodon* do not co-occur in the Tecovas Formation in West Texas; they are stratigraphically separate in West Texas (Hunt and Lucas, 1991).

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45. There are no records of *Paleorhinus* in the middle Pekin Formation of the Newark Supergroup (also see Table 1).

46. There are no records of *Rutiodon* in the Owl Rock Formation in Arizona. The reference cited for this record (Kirby, 1989) makes no definite assignment of an Owl Rock phytosaur to *Rutiodon*. In fact, all subsequent workers have assigned the Owl Rock phytosaurs to *Pseudopalatus* (Kirby, 1991, 1993; Spielmann et al., 2007).

47. Interestingly, *Rutiodon*? is listed from the Grès à Avicula Contorta in France, but here it is acknowledged that this record – based on isolated teeth and a premaxilla – has been dismissed as an unjustified identification (Lucas and Huber, 2003), yet at the same time it is presented as a possible Norian record of *Rutiodon* (also see Fig. 7). Which is it?

48. The conclusion that "there is, therefore, a strong argument for amalgamating the Northern Hemisphere Otischalkian-Adamanian biochrons into a coarser late Carnian unit" does not follow from preceding text. Indeed, once the obvious errors are removed from Table 1 and Figure 3, Rayfield et al.'s (2005) own analysis does not support their conclusion.

49. The statement "there is some disagreement over the status of supposed '*Aetosaurus*' remains" finds no support in the work of those who have actually studied aetosaurs (see the text).

50. The unfounded claim that *Aetosaurus* has a long "ghost lineage" and "therefore, one should expect to find *Aetosaurus* in pre-Norian strata" is made here and addressed above in the text.

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51. Had Rayfield et al. carefully read Lucas et al. (2002b), they would not repeat the error (also see Table 1) of claiming that *Typothorax coccinarum* has a "late Carnian" record in New Mexico.

52. The errors (Table 1) regarding Apachean records of *Typothorax* (especially in the Sloan Canyon Formation of New Mexico, where no aetosaur fossil has ever been found) are repeated here.

53. On the one hand, an abstract by Hungerbühler et al. (2003) is cited as authority that *Redondasaurus* is a synonym of *Pseudopalatus*, yet a published article by Hungerbühler (2002) upholding the distinctiveness of *Redondasaurus* is ignored, clearly demonstrating a selective citing of the relevant scientific literature.

54. The megafloral analysis begun here is heavily rooted in circular correlation built into Table 2 – such as using the plant megafossils to determine the ages of the plant megafossils (example: *Eoginkoites* from the Popo Agie Formation in Table 2). This directly contradicts the statement in point 24 above.

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55. The ranges claimed and depicted in Figure 4 and Table 2 should be compared to the Chinle Group megafloral ranges depicted by Lucas (1997, fig. 23.8). Lucas compiled the actual lithostratigraphic ordering of the megafossil plant genera in the Chinle Group and provide better temporal resolution of the megaflora than Table 2 of Rayfield et al.

56. Rayfield et al. evaluate an out-of-date plant biostratigraphy based on Ash (1980), overlooking Ash (1987), who subdivided his *Dinophyton* floral zone into lower (*Dinophyton*) and upper (*Sanmiguelia*) floral zones. This is part of the reason why some of the "*Dinophyton* floral zone" records listed in Table 2 are erroneously recorded as Norian.

57. The statement that "megafloral records do not allow recognition of distinct Carnian-aged Otischalkian and Adamanian biochrons" is misleading, as Otischalkian and Adamanian are based on vertebrate evolution, not plant evolution. Furthermore, Lucas' (1997) analysis of Chinle plant distribution suggests that there are distinct megafloras in Otischalkian and Adamanian strata.

58. Again, the succeeding statement that "megafloral records neither support nor contradict the LVF biochron divisions proposed for these intervals [Anisian-Ladinian, Norian-Rhaetian]" is irrelevant to tetrapod biostratigraphy.

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59. Some of the problems/errors in Table 2 have already been discussed above. Claims of Norian records of *Pagiophyllum* and *Dinophyton* are erroneous (Ash, 1980; Lucas, 1997).

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60. The claim that "the distribution of the Otischalkian index taxa *Metoposaurus* and *Angistorhinus* appears to be influenced by depositional environment" is based on a very imprecise and error-laden assessment, and readily rejected (see below).

61. "*Metoposaurus* is found in various high-energy environments." But, on the one hand, Rayfield et al. claim that *Metoposaurus* records in the western USA, Nova Scotia and western Europe are "generally found in conglomeratic or channel sandstone deposits" or in "braided river channels." On the other hand they cite Milner and Schoch (2004) as authority that "German *Metoposaurus* remains were more abundant in the playa lake environments [low energy] of the Lehrbergschichten… " Which is it?

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62. The statement that "*Angistorhinus* tends to be deposited [sic, how is a fossil taxon deposited?] in low-energy settings such as the floodplain or low-energy stream deposits" is largely a taphonomic artifact, as a complete enough skull of a phytosaur to be identified as *Angistorhinus* is unlikely to be preserved in a high energy deposit.

63. Figure 5, a supposed "GIS-derived correlation of *Metoposaurus* to high-energy environments and *Angistorhinus* to low-energy environments" is replete with errors. Thus, *Metoposaurus* records in the "playa lake environments" of the German Lehrbergschichten and the marine "Raibl beds Dolomia di Forni" are "high-energy environments" equated by the figure to the fluvial environments of the Blasensandstein, Kieselsandstein and Schilfsandstein. The unverified record of *Metoposaurus* in the Baldy Hill Formation of Oklahoma (see above) is incorporated into the figure. In the map of part of the western USA, the geographic region from Santa Rosa, New Mexico through northeastern Arizona/southeastern Utah is shown on the map (Fig. 5a) as "perceived ocean," even though the Chinle deposits within the "ocean" are also labeled as "conglomeratic or channel sandstone depositional environments." (It has long been known that the Late Triassic shoreline of western Pangea is much farther west than shown in Figure 5a). Clearly, the figure is full of errors that undermine its value as a "GIS derived correlation."

64. "Analysis of Otischalkian taxa reveals that the aetosaur *Longosuchus* is only found in association with coals." Yet, there are no coals in the Upper Triassic of West Texas, where most *Longosuchus* records occur, or associated with its Moroccan record as well. Only in North Carolina are there coal beds in the same depositional basin as *Longosuchus* fossils, though there is no clear association of the tetrapod with a coal bed (which could lead to the kind of paleoclimatic influences that Rayfield et al. hope to make).

65. The follow-up statement that "*Longosuchus* has the potential to act a regional index taxon for North American Otischalkian time if further occurrences appear outside of humid, coal-containing environments" can be dimissed.

66. Figure 6 also embodies many errors, such as omitting the record of *Redondasaurus* in the Wingate Sandstone of southeastern Utah (Lucas et al., 1997b). Note that the western North American seaway shown in Figure 5a is absent in Figure 6a (and Figures 7a and 8a), though all are supposedly derived from the same paleogeographic base map.

67. The statement that "Otischalkian *Paleorhinus* and Adamanian *Rutiodon* only co-occur in warm temperate or tropical environments" misleads, as the taxa have only one co-occurrence in the Chinle Group of Arizona (see text).

68. The statement "*Paleorhinus* is found without *Rutiodon* in the Popo Agie Formation of the western USA" is supposed to convey climate information, but *Rutiodon* does not occur in the Popo Agie Formation because it is Otischalkian, and thus, by definition, pre-dates *Rutiodon* records (also see Table 1).

69. The succeeding statements that "in warmer, wetter climes, an increase in resource availability enabled both taxa [*Paleorhinus* and *Rutiodon*] to co-exist" and "resource depletion in arid conditions may have resulted in *Paleorhinus* succeeding in the western USA, whereas *Rutiodon* succeeded in the east" are unsupportable, given the near total temporal separation of the two genera.

70. Given that there are no Upper Triassic coal deposits in the American Southwest, the statement that "both *Rutiodon* and *Stagonolepis* are found in association with coal deposits across southern North America" is incorrect. The continuation, that they are found "in arid European deposits" is incorrect for several reasons, including there are no European *Rutiodon* records, and *Stagonolepis* records in Europe are in the lower part of the Middle Keuper, a wet interval of sedimentation. Finally, the claim that *Rutiodon* and *Stagonolepis* are found in association with "calcretes and evaporates in the northern basins of the Newark Supergroup" also lacks a factual basis, especially because *Stagonolepis* is not known from any of the Newark basins.

71. The statement that *Aetosaurus* "tends to prefer arid environments" lacks supporting data and is false based on our own documentation of its distribution (e.g., Lucas et al., 1998b).

72. Given the erroneous base maps, incorrect correlations, inconsistencies and imprecise level of discrimination of depositional environments and climatic indicators, it is not surprising that "identifying climatic biases that might have acted on megafloral distribution is also problematic." The entire analysis is problematic because its database is inadequate.

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73. Errors in Figures 7 and 8 have been discussed above; their largest error is that both figures do not accurately depict the distributions of the taxa whose distribution is being analyzed.

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74. The discussion of megafloral restrictions to depositional environments and climate is meaningless, as no information on the taphonomic biases (taphofacies) of the megaplant records are considered.

75. The text repeats reference to the erroneous Revueltian records of *Dinophyton* and *Pagiophyllum* listed in Table 2.

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76. The conclusions reiterate many of the mistakes, misrepresentations and misinterpretations of the previous text. Given the sheer quantity of errors in the text of Rayfield et al. (see above), almost all of the conclusions of the article can be rejected.

Lucas, S.G. and Spielmann, J.A., eds., 2007, The Global Triassic. New Mexico Museum of Natural History and Science Bulletin 41.

TOPOTYPES OF *TYPOTHORAX COCCINARUM*, A LATE TRIASSIC AETOSAUR FROM THE AMERICAN SOUTHWEST

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Abstract—The syntype specimens of the aetosaur *Episcoposaurus horridus* Cope, 1887, are from the type locality of *Typothorax coccinarum* Cope, 1875, in the Painted Desert Member of the Petrified Forest Formation, Chinle Group at Cerro Blanco, Rio Arriba County, New Mexico. The syntypes of *E. horridus* are topotypes of *T. coccinarum,* and some probably represent the same individual as the lectotype of *T. coccinarum*. *E. horridus* is a junior subjective synonym of *T. coccinarum,* and we restrict the lectotype of *E. horridus* to a single caudal dorsal paramedian osteoderm. The topotypes of *T. coccinarum* provide a more complete picture of the anatomy of the species and further confirm its distinctiveness from *T. antiquum*.

INTRODUCTION

Aetosaurs are heavily armored archosaurs known from Upper Triassic strata in North and South America, Greenland, Europe, India, North Africa and Madagascar (Heckert and Lucas, 2000). The first aetosaur named from the American Southwest was *Typothorax coccinarum* Cope, 1875, based on specimens Cope collected in 1874 near Gallina in Rio Arriba County, New Mexico (Fig. 1). In 1881, Cope's hired fossil collector, David Baldwin, collected additional aetosaur specimens from the same locality near Gallina, and they became the type material of *Episcoposaurus horridus* Cope, 1887, long regarded as a synonym of *T. coccinarum*. This material thus is topotypic of *Typothorax coccinarum* and further establishes the distinctive morphology of this biostratigraphically significant species.

Institutional abbreviations: AMNH = American Museum of Natural History, New York; NMMNH = New Mexico Museum of Natural History, Albuquerque.

HISTORY

Camp (1930) and Lucas and Hunt (1992) relocated the type locality of *Typothorax coccinarum*, which is just north of Cerro Blanco near Gallina, New Mexico in the Painted Desert Member of the Petrified Forest Formation (also see Lucas et al., 2005a, b). In 1881, Cope's hired collector David Baldwin collected from the same locality additional aetosaur (and phytosaur) fossils that became the type material (syntypes) of *Episcoposaurus horridus* Cope, 1887. Baldwin's packing label (also see Heckert and Lucas, 2002, p. 203) with the type material reads:

> Sack 3, Box 2.
> 1881 Prof. E.D. Cope,
> 2100 Pine St. Philadelphia.
>
> Contains: Part of fossils— bones dug out Gallina Pan on April 12th to May 1 Triassic or Jurassic 200 ft below Gypsum, 150 ft above Gray sand stone – No head-no foot 3 teeth(?) only.
>
> D. Baldwin
>
> Lower jaw! [note added later, connected to "no head"— this lower jaw is probably the phytosaurian jaw Cope (1887) excluded from the type material (Gregory, 1953, p. 3)]

It is reasonable to infer that Baldwin was collecting at the *Typothorax coccinarum* locality discovered by Cope in 1874. Indeed, Cope (1887, p. 213) stated that "this species [*Episcoposaurus horridus*] is indicated by a number of bones which were excavated at the same place [as the type material of *T. coccinarum*]." Furthermore, Huene (1915, p. 492) noted that "in the Triassic Cope collection many bones and fragments are marked with the same number (2307) as the type specimens; that means they come from the same place." This even raises the possibility that at least some of the type material of *T. coccinarum* and *E. horridus* represents a single individual (see below). Note also that the AMNH online catalog erroneously lists the locality of the type material of *E. horridus* as "Arroyo Seco?," which is many km from Cerro Blanco (Fig. 1).

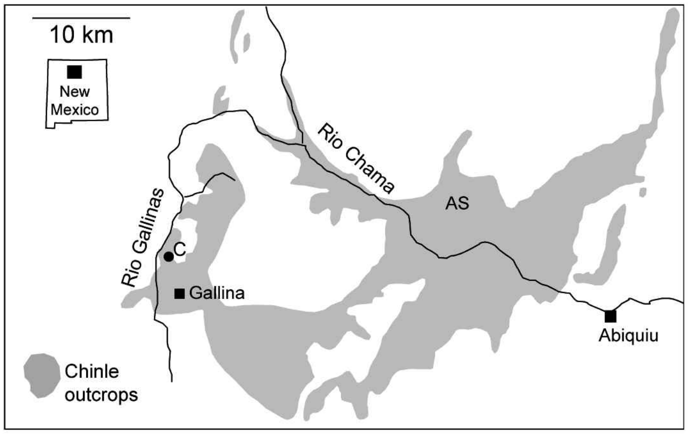

FIGURE 1. Distribution of Chinle Group outcrops in the Chama basin of northern New Mexico showing location of type locality of *Typothorax coccinarum* and *Epsicoposaurus horridus* at Cerro Blanco near Gallina (C) and the location of the Arroyo Seco (AS) area to the east.

In naming *Episcoposaurus horridus*, Cope (1887, p. 213) listed the type material as "two caudal vertebrae, a proximal and a distal; a humerus; two ulnae; a femur lacking the condyles; a proximal part of a fibula; a calcaneum; and a number of dermal bones. The only part of the skull possibly belonging to this animal is a splenial bone." Cope (1887) provided no illustrations of these specimens, but Huene (1915, figs. 12-15, 18-27) did. Huene (1915, p. 492-499) also redescribed the type material of *E. horridus* and (p. 493) excluded the humerus, radius and ulna from it because they "are so very much smaller than those of the hind leg that…it seems impossible that the animal could have been so disproportionate." He thus restricted the type to "the bones of the hind leg as the real type of this species, appending also the splenials, the two caudals and possibly some of the scutes" (Huene, 1915, p. 493).

Gregory (1953a, p. 1-2) noted that "Cope's original type of *Episcoposaurus horridus* is hopelessly mixed with bones of other individuals, some of which were referred by him, and later by von Huene

(1915A), to *Typothorax*, and which include characteristic dorsal armor of that genus." Gregory (1953) went on to conclude that *E. horridus* is a synonym of *T. coccinarum*. He reviewed the history of *E. horridus*, noting that its type material came from the same locality as the type material of *T. coccinarum* and stated that:

> ... the probable association of *Episcoposaurus* femur (lectotype of *E. horridus*) with unmistakable armor of *Typothorax*, and the further likelihood that the supposed distinctive armor of *Episcoposaurus* is merely that of the tail rather than thorax or abdomen, and finally the intimate association of the type specimen of *Episcoposaurus horridus* with bones referred by Cope as well as subsequent students to *Typothorax coccinarum*, all suggest that only one species is present. If this be so (it is probably incapable of absolute proof), *Episcoposaurus* is a synonym of *Typothorax* having been established upon remains of the same species (Gregory, 1953, p. 6).

Gregory (1953a, p. 10) went on to list the type of *Episcoposaurus* as:

> Type of *Episcoposaurus horridus*: A.M.N.H., no 2713 (formerly 2307). Two caudal vertebrae (proximal and distal); humerus; two ulnae; femur lacking condyles; proximal part of tibia; distal part of fibula; calcaneum; a number of dermal bones. Splenial possibly associated. Von Huene (1915, p. 492-493) designated bones of hind leg as lectotype. From same locality as type of *Typothorax coccinarum*. Collected by David Baldwin, April 12, 1881.

Long and Ballew (1985, p. 61-62) supported Gregory's conclusion that the osteoderms that are part of the syntypes of *E. horridus* belong to *T. coccinarum*. Long and Murry (1995, p. 101) thus listed *Episcoposaurus horridus* as a junior subjective synonym of *Typothorax coccinarum* Cope, 1875. They also listed AMNH 2713 as coming from the same locality (Cerro Blanco) as the holotype of *T. coccinarum*. AMNH 2712, a calcaneum, is also from this site, as is AMNH 2710. The splenial included with the type material of *E. horridus* (Huene, 1915, fig. 20) is that of a phytosaur.

Heckert and Lucas (2000) followed previous workers and considered *Episcoposaurus horridus* a junior subjective synonym of *Typothorax coccinarum* in their review of the Stagonolepididae. Heckert and Lucas (2002) also noted that, in spite of the extensive work by Huene (1915), Gregory (1953a, b), Long and Ballew (1985) and Long and Murry (1995), no one had ever designated a lectotype for *Episcoposaurus haplocerus*, widely regarded as the type of *Desmatosuchus haplocerus*. Consequently, they (Heckert and Lucas, 2002, p. 194) designated an osteoderm from the type locality of *Episcoposaurus haplocerus*, in the Tecovas Formation of West Texas as the lectotype. They also described and illustrated (Heckert and Lucas, 2002, figs. 4-5) topotypic material from the type locality of *Typothorax coccinarum*.

LECTOTYPE AND SYNTYPES OF *EPISCOPOSAURUS HORRIDUS*

The aetosaur specimens that are included in the type material of *Episcoposaurus horridus* listed by Cope (1887), Huene (1915) and Gregory (1953a) comprise an assemblage of bones that represent more than a single individual (see below). We therefore regard these listings as designations of syntypes. We advocate restricting the type of *E. horridus* to a single lectotype bone. In this case, we designate the complete left dorsal caudal paramedian osteoderm of AMNH 2713 (Fig. 3A; Gregory, 1953a, fig. 17) the lectotype. This eliminates the confusion over association of the syntypes well discussed by Huene (1915) and Gregory (1953a).

The lectotype corresponds well anatomically to dorsal caudal paramedian osteoderms of *Typothorax coccinarum* (Hunt et al., 1993). As noted above, *Episcoposaurus horridus* has long been considered a junior subjective synonym of *Typothorax coccinarum* (Gregory, 1953; Long and Ballew, 1985; Long and Murry, 1995), and restriction of the lectotype to a single osteoderm does not change, but does formalize, this synonymy.

The various other syntypes of *Episcoposaurus horridus* consist of a caudal centrum (Fig. 2A-C), two left? dorsal paramedian osteoderms (Fig. 2D-G), one right? paramedian osteoderm (Fig. 2H), one left lateral osteoderm (Fig. 2I), two right? lateral osteoderms (Figs. 2J, 3C-D), three left caudal paramedian osteoderms (Fig. 3B, E-G), one right caudal paramedian osteoderm (Fig. 3H), a complete right humerus (Fig. 4A-B), a complete left ulna (Fig. 4C), a proximal right ulna (Fig. 4D-E), a proximal left? radius (Fig. 4F-G), a complete right femur (Fig. 5A), a left proximal tibia (Fig. 5B), two right? proximal tibiae (Fig. 5F-J), a distal tibia (Fig. 5C-E) and a left calcaneum (Fig. K-M).

The dorsal paramedian osteoderms clearly demonstrate the characteristic ornamentation of *Typothorax coccinarum*: random pitting, prominent anterior bar, lack of ornamentation and a ventral keel (compare Figs. 2D-H, 3 to Long and Ballew, 1985, figs. 8-11, pls. 2-3 and Long and Murry, 1995, fig. 100). Likewise, the lateral osteoderms (Figs. 2I-J, 3C-D) show the characteristic dorsoventral compression and laterally-directed sharp edge for which this taxon is known. The caudal paramedian osteoderms (Fig. 3B, E-G) possess an anterior bar and ornamentation identical to the same elements in NMMNH P-12964, a nearly complete articulated specimen of *T. coccinarum* (Hunt et al., 1993). The right humerus (Fig. 4A) has expanded proximal and distal ends, with the distal end having prominent condyles; morphologically this specimen appears identical to a *T. coccinarum* humerus illustrated by Long and Murry (1995, fig. 105). The ulnae (Fig. 4C-E) are anteroposteriorly compressed and lack a prominent olecranon process while the proximal left? radius is elliptical in proximal view; these elements are identical to the ulnae and radii of NMMNH P-12964. The femur (Fig. 5A) bears a small fourth trochanter and prominent distal condyles and appears identical to *T. coccinarum* femora illustrated by Long and Murry (1995, fig. 110). The proximal tibia fragments (Fig. 5B, F-J) are elliptical in proximal view with prominent proximal articulation and a more slender shaft. The distal tibia fragment (Fig. 5C-E) has offset facets on its distal articulation and is kidney-shaped in distal view. The left calcaneum (Fig. 5K-M) is complete with a prominent dorsal process, and a ridge on the ventrolateral margin of the calcaneal shaft. This specimen was previously described and illustrated as *T. coccinarum* by Long and Murry (1995, fig. 112A-D).

DISCUSSION

Because of their anatomical similarity to and co-occurrence with the holotype of *Typothorax coccinarum*, we consider the aetosaur specimens in the AMNH collection from Cerro Blanco (AMNH 2709-2713) to constitute topotypical specimens of *T. coccinarum* (Figs. 2-5). Comparison of these specimens to an essentially complete skeleton of *T. coccinarum* from east-central New Mexico (NMMNH P-12694) documents that they reflect well the diagnostic characteristics of *T. coccinarum*.

Typothorax long served as a wastebasket taxon to which much of the aetosaur material from the Chinle Group was referred. Thus, the aetosaur now recognized as *Longosuchus* was originally a species of *Typothorax* (Sawin, 1947), and specimens of *Paratypothorax* and *Redondasuchus* also have been assigned to the genus (e.g., Long and Murry, 1995; Martz, 2002).

There are two valid species of *Typothorax*: *T. coccinarum* and *T. antiquum* (Lucas et al., 2002). Parker (2007, p. 161) stated that "the holotype specimen of *Typothorax antiquum* Lucas et al. 2002 cannot be differentiated from material of *T. coccinarum*" but provided no justification for this claim. However, a substantial number of differences in the armor distinguish the two species, which are likely temporally successive representatives of an anagenetic evolutionary lineage (Lucas et al., 2002).

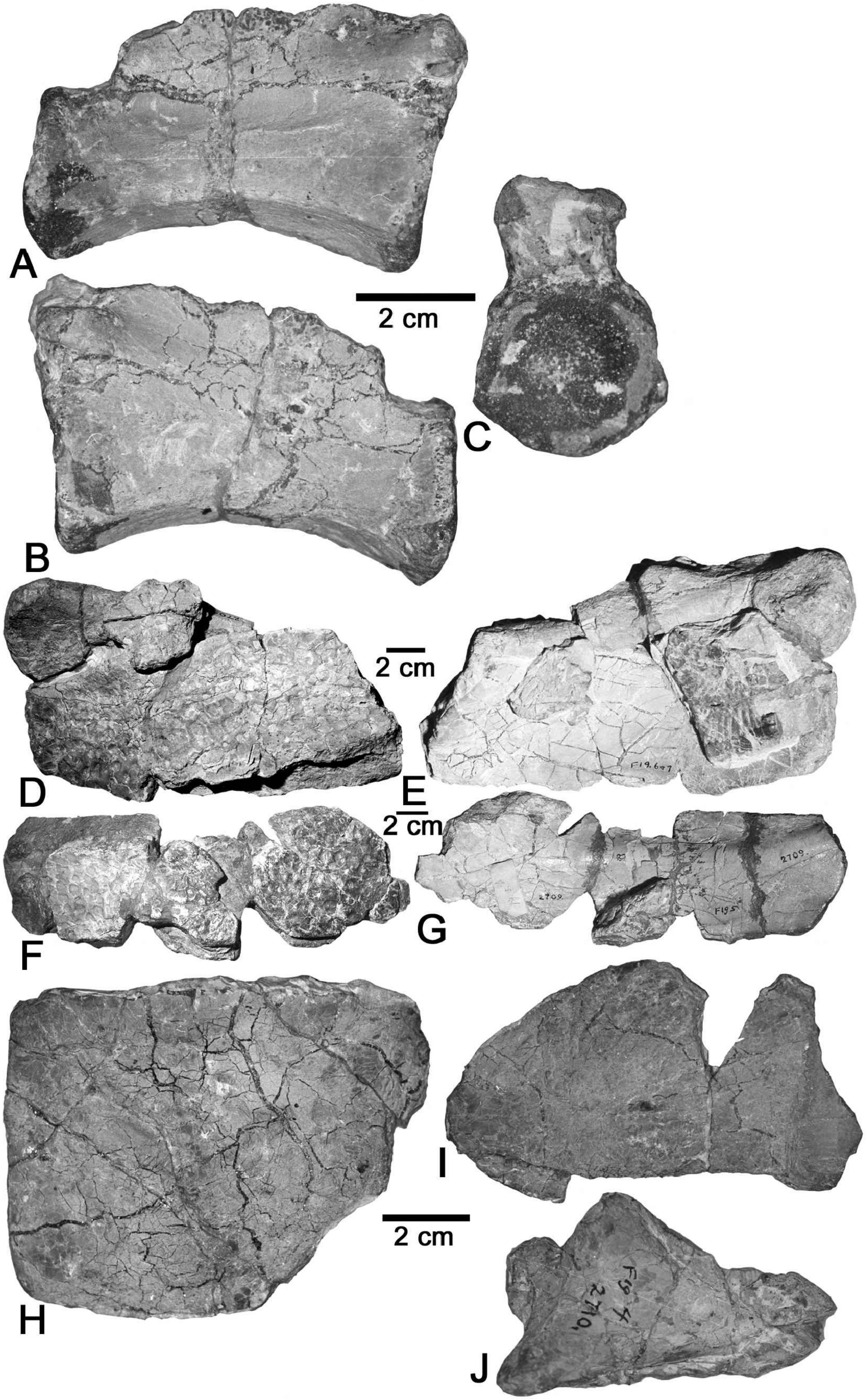

FIGURE 2. Topotypes of *Typothorax coccinarum*. **A**-**C**, **H**-**I**, AMNH 2713. **D**-**G**, AMNH 2709. **J**, AMNH 2710. **A**-**C**, complete caudal? centrum in **A**, right lateral, **B**, left lateral and **C**, anterior views. **D**-**E**, partial left? dorsal paramedian osteoderm in **D**, dorsal and **E**, ventral views. **F**-**G**, incomplete left? dorsal paramedian osteoderm in **F**, dorsal and **G**, ventral views. **H**, partial right? paramedian osteoderm in dorsal view. **I**, left lateral osteoderm in dorsal view. **J**, right? lateral osteoderm in posterior view.

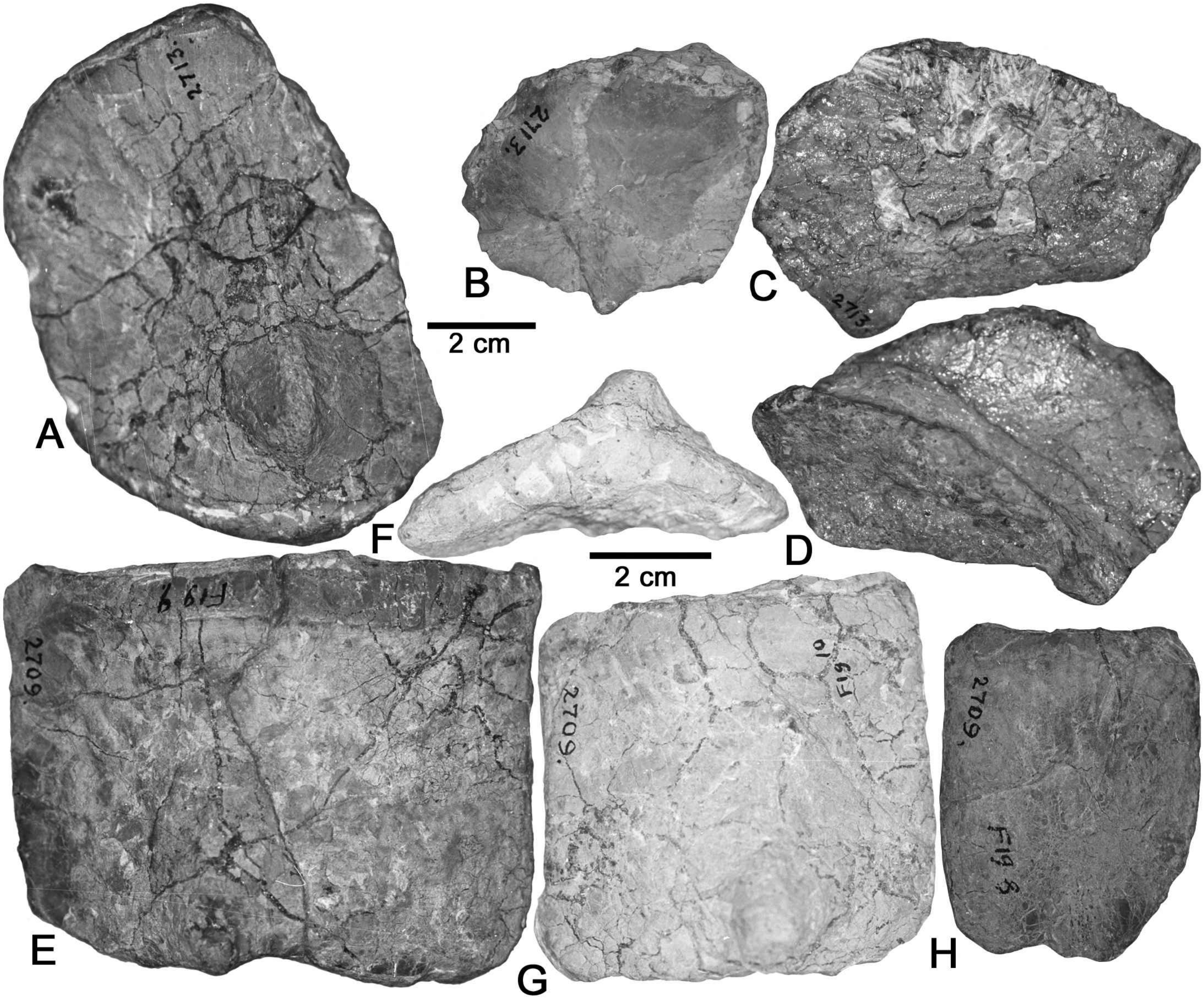

FIGURE 3. Topotypes of *Typothorax coccinarum*. **A**-**D**, AMNH 2713. **E**-**H**, AMNH 2709. **A**, complete left dorsal caudal paramedian osteoderm in dorsal view (lectotype of *Episcoposaurus horridus*). **B**, partial left dorsal caudal paramedian in dorsal view. **C**-**D**, incomplete right ?lateral osteoderm in **C**, dorsal and **D**, ventral views. **E**, partial left dorsal caudal paramedian osteoderm in dorsal view. **F**-**G**, complete left dorsal caudal paramedian osteoderm in **F**, posterior and **G**, dorsal views. **H**, partial ?right dorsal caudal paramedian osteoderm in dorsal view.

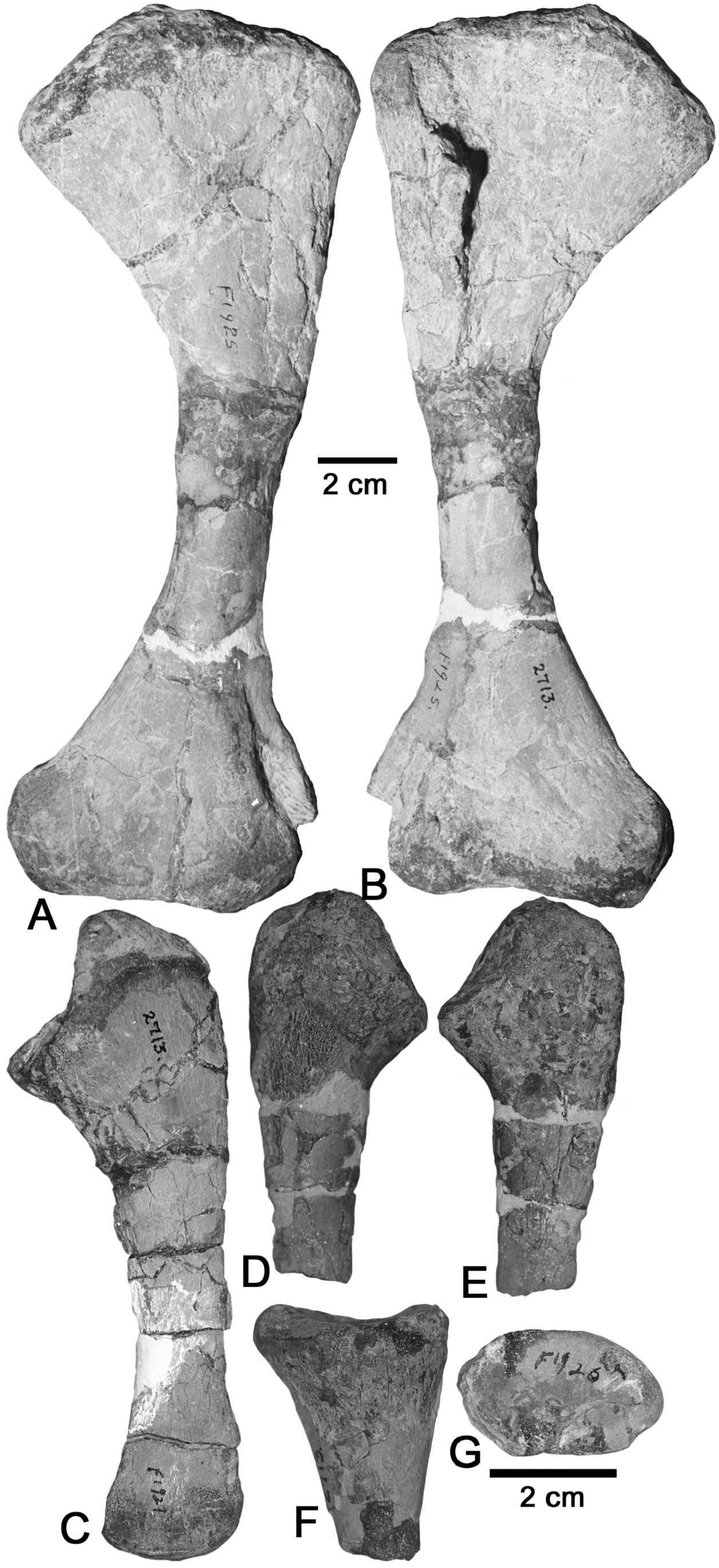

FIGURE 4. Topotypes of *Typothorax coccinarum*. **A-C**, **F-G**, AMNH 2713. **D-E**, AMNH 2711. **A-B**, right humerus in **A**, anterior and **B**, posterior views. **C**, left ulna in lateral view. **D-E**, proximal right ulna in **D**, lateral and **E**, medial views. **F-G**, proximal left? radius in **F**, lateral and **G**, proximal views.

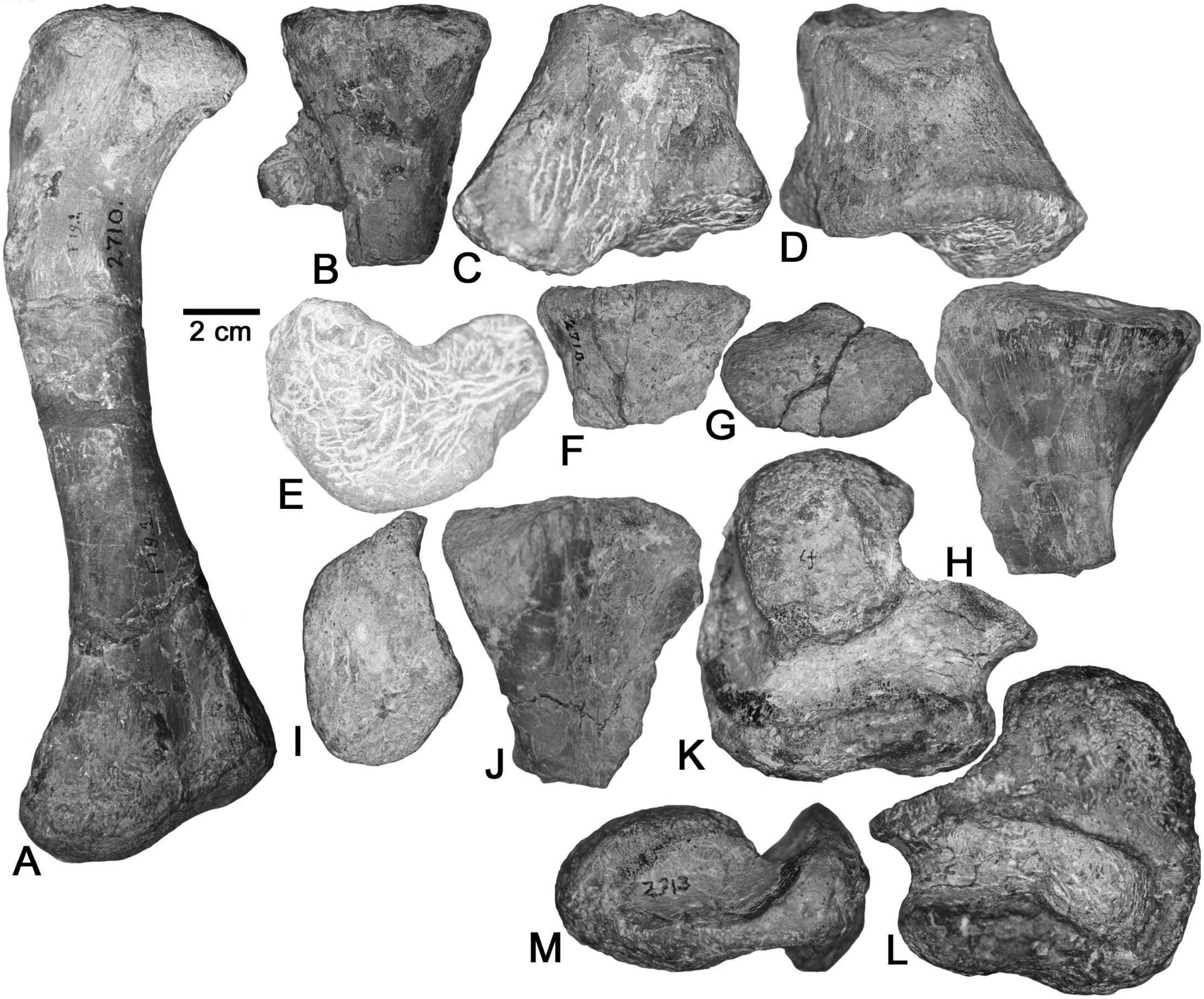

FIGURE 5. Topotypes of *Typothorax coccinarum*. **A-B**, AMNH 2710. **C-G**, **K-M**, AMNH 2713. **H-J**, AMNH 2711. **A**, right femur in posterior view. **B**, left? proximal tibia in ?lateral view. **C-E**, distal tibia in **C**, ?medial, **D**, ?lateral and **E**, distal views. **F-G**, right? proximal tibia in **F**, medial and **G**, proximal views. **H-J**, right? proximal tibia in **H**, medial, **I**, lateral and **J**, proximal views. **K-M**, left calcaneum in **K**, proximal, **L**, distal and **M**, dorsal views.

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BIOCHRONOLOGICAL SIGNIFICANCE OF LATE TRIASSIC TETRAPODS FROM KRASIEJÓW, POLAND

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Abstract—The Krasiejów locality in the Upper Triassic of southern Poland yields the tetrapod taxa *Cyclotosaurus robustus* (= *C. intermedius*), *Metoposaurus diagnosticus* (we reject proposed subspecies of this species), *Stagonolepis robertsoni*, *Teratosaurus suevicus* (= *T. silesiacus*), *Parasuchus bransoni* and *Silesaurus opolensis*. The occurrences of *Parasuchus* and *Metoposaurus* indicate the Krasiejów assemblage is of Otischalkian age, and the presence of *Stagonolepis* at Krasiejów expands its temporal range to Otischalkian-Adamanian. Previous non-vertebrate biostratigraphic correlation of the Krasiejów locality to the German Lehrberg Schichten is confirmed by vertebrate biostratigraphy and provides a good example of how a newly discovered tetrapod assemblage (at Krasiejów) demonstrates the utility of the global Triassic tetrapod biochronology.

INTRODUCTION

One test of a biostratigraphic (biochronologic) framework is how well it accounts for new discoveries. The discovery of an Upper Triassic tetrapod locality at Krasiejów in southern Poland (Fig. 1) provides just such a test of the Late Triassic tetrapod biochronology proposed by Lucas and collaborators (Lucas and Hunt, 1993; Lucas et al., 1997; Lucas, 1998, 1999). The Polish Triassic tetrapod assemblage contains Otischalkian index taxa and comes from a part of the Keuper section that is this age based on other data. Here, we review the Krasiejów tetrapod assemblage and its biochronological significance. In this paper, PAN refers to specimens in the collection of the Paleontological Institute, Polish Academy of Sciences, Warsaw.

PREVIOUS STUDIES

Dzik et al. (2000) provided initial information on what they referred to as "a new *Paleorhinus* fauna" from Krasiejów. They listed the tetrapod assemblage as consisting of a capitosaur, *Metoposaurus diagnosticus*, *Paleorhinus* sp., an aetosaur and a dinosaur. Subsequently, the capitosaur (Sulej and Majer, 2005), metoposaur (Sulej, 2002) and phytosaur (Dzik, 2001) were documented, as was a rauisuchian (Sulej, 2005) and a dinosauromorph (= the "dinosaur" of Dzik et al., 2000: Dzik, 2003). Dzik (2001) illustrated a jaw fragment and tooth of an aetosaur, stating that it is very similar to *Stagonolepis*. Zatón et al. (2005) documented charophytes from the Krasiejów locality, and provided a description of the geological context of the site.

GEOLOGICAL CONTEXT

At Krasiejów (Fig. 1), Triassic tetrapod bones are present in a mudstone-dominated section in a cement plant clay pit. Two beds produce bone, but their close stratigraphic proximity (~7 m) and shared taxa indicate they represent a single biostratigraphic assemblage. The bone-bearing strata have been correlated to the subsurface Drawno Beds, and are estimated to be ~80 m above the top of the Reed Sandstone, the local equivalent of the German Schilfsandstein (Dzik, 2001, 2003; Sulej, 2002; Zatón et al., 2005). The Polish workers thus consider the Drawno Beds correlative to the German Lehrberg Schichten, and conchostracan-based correlations support this conclusion (H. Kozur, written commun., 2007).

TETRAPOD ASSEMBLAGE

Amphibians

Cyclotosaurus

Sulej and Majer (2005) named a new species, *Cyclotosaurus intermedius,* for cranial and postcranial material from both bonebeds at Krasiejów. This material includes a complete skull with associated mandible (the holotype), two incomplete mandibular rami, various disarticulated skull bones, a humerus, a scapulocoracoid, a nearly complete clavicle, a cleithrum and two interclavicles.

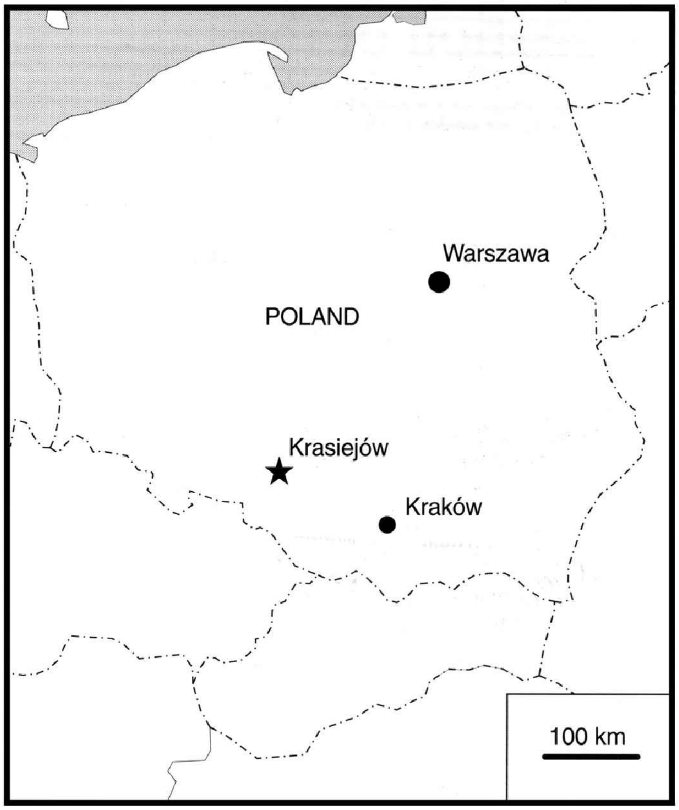

FIGURE 1. Location map of the Krasiejów tetrapod locality in southern Poland (after Sulej, 2002).

C. intermedius is remarkably similar to *C. robustus* from the German Schilfsandstein (Fraas, 1889, 1913; Schoch and Milner, 2000), so we consider *C. intermedius* synonymous with *C. robustus*. Sulej and Majer (2005) listed the following putative differences between the two species: (1) orbits more laterally positioned in *C. intermedius*; (2) interchoanal tooth row gently curved posteriorly (not straight) in *C. intermedius*; (3) para- and interchoanal teeth broadly separated (not a single arcade) in *C. intermedius*; (4) shagreen of denticles on palate in *C. intermedius*; (5) quadrate projects behind margin of skull roof in *C. intermedius*; and (6) *C. robustus* has a wider skull with a more concave posterior border. However, differences (1) and (6) are not metrically significant (see Sulej and Majer, 2005, table 1), and difference (5) is arguably the result of diagenetic distortion (a feature present in some material from the quarry, such as an aetosaur sacral vertebra; see below). Difference (2) can be rejected because Fraas (1889, pl. 10) illustrates a skull of *C. robustus* in which the interchoanal tooth row is curved posteriorly, as in *C. intermedius*. Differences (3) and (4) are apparently real, but we hesitate to make them a basis for species-level distinction because variation in the interchoanal and palatal teeth is common among stereospondyl taxa (e.g., Hunt, 1993).

Metoposaurus

Metoposaurid skulls (Fig. 2) and postcrania are common at the Krasiejów locality, and Sulej (2002) listed the following metoposaurid material: eight complete skulls, four nearly complete skulls, one skull preserving the postorbital region, two skulls preserving portions of the preorbital region, one complete and five incomplete interclavicles and three incomplete and two nearly complete clavicles. Sulej (2002) described the specimens and used them to subdivide *Metoposaurus diagnosticus* into two subspecies – *M. d. diagnosticus* and *M. d. krasiejowensis* – based on a supposed shorter prepineal portion of the parietal in the latter and putative differences in parietal shape between the two nominal subspecies.

However, we find subspecies attributions particularly inappropriate for the *Metoposaurus* sample analyzed by Sulej (2002) because it is a small sample of fewer than 20 individuals, not large enough to gauge variation within one or between multiple populations, let alone within a species. Furthermore, it is clear that Sulej's subspecies are actually "little species," an inappropriate use of subspecies (e.g., Simpson, 1961). Instead, subspecies should be used to subdivide a range of variation within a species (cline) so that "at least a minimum proportion, now usually set at 75 per cent, of individuals of adjacent subspecies will be unequivocally determinable" (Simpson, 1961, p. 173, 175; also see Amadon, 1949).

The differences in the length of the parietal anterior to the pineal foramen used by Sulej (2002) to distinguish the "subspecies" of *M. diagnosticus* are clearly size related: there is a strong correlation between skull size and the length of the parietal anterior to the pineal foramen evident in Sulej's (2002, fig.10B) data. The differences in the parietal angle used by Sulej to distinguish the subspecies of *M. diagnosticus* are also size related and do not convincingly separate the sample into two discrete morphotypes (Sulej, 2002, fig. 10A). Therefore, we do not recognize the subspecies of *M. diagnosticus* proposed by Sulej (2002) and simply refer the Krasiejów metoposaurs to *Metoposaurus diagnosticus*.

Another important point to address is Sulej's (2002) claim that the lacrimal enters the orbit in the Krasiejów metoposaur skulls (contrary to the normal condition in *Metoposaurus*: Hunt, 1993). Indeed, he illustrates the holotype of *Metoposaurus diagnosticus krasiejowensis* (PAN ZPAL AbIII 358) with the lacrimal entering the orbit (Sulej, 2002, fig. 4). However, our close examination of this skull (Fig. 2A) and other metoposaur skulls from Krasiejów does not confirm his claim. Either preservation is too poor to discern the lacrimal in its entirety or it is clear (as is the case in PAN ZPAL AbIII 11) that the lacrimal does not enter the orbit (Fig. 2B-C).

Reptiles

Stagonolepis

The aetosaur *Stagonolepis* is a common constituent of the Krasiejów bonebeds, and previous publications have stated that the

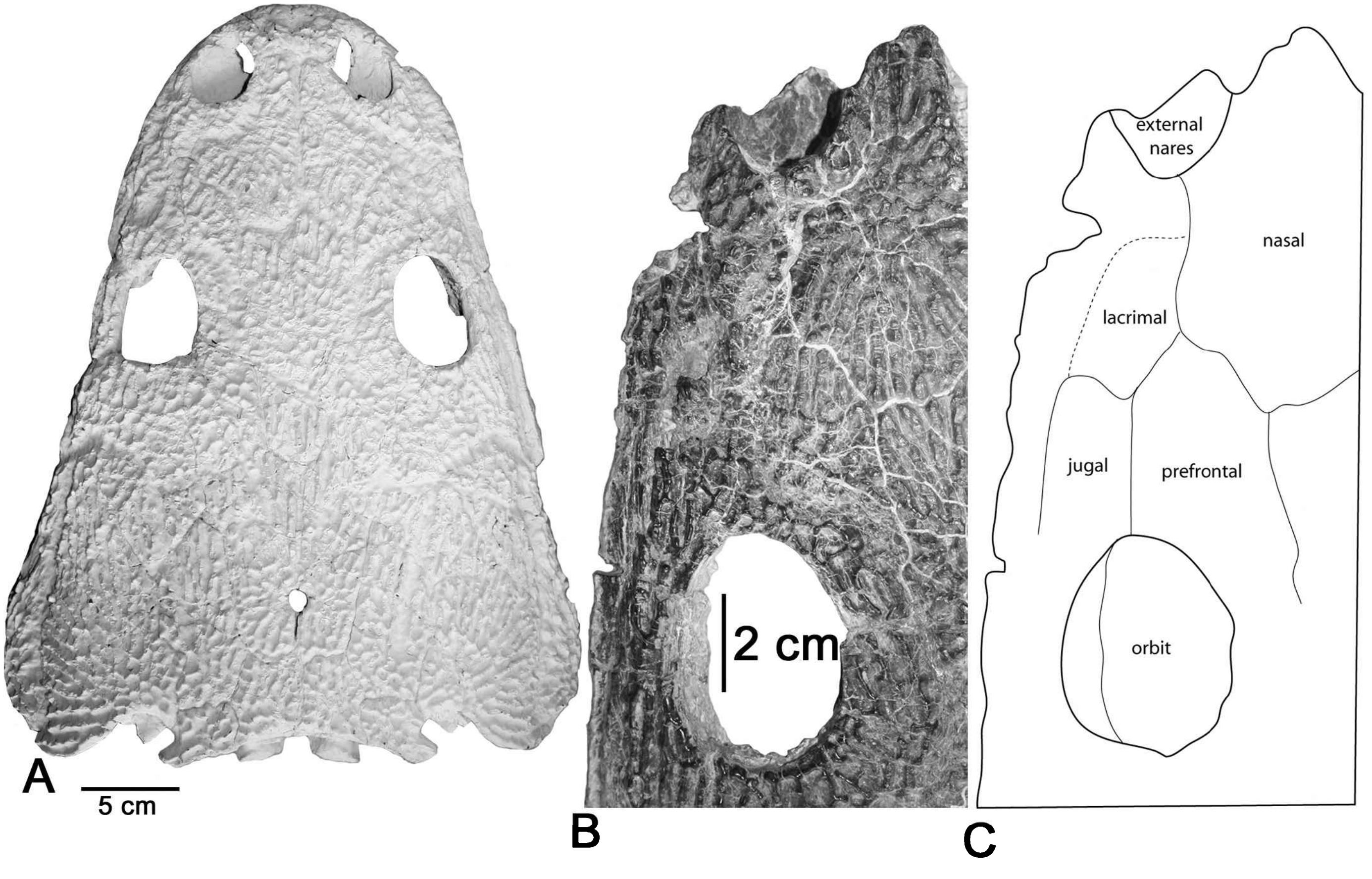

FIGURE 2. **A**, *Metoposaurus diagnosticus*, PAN ZPAL AbIII 358, complete skull in **A**, dorsal view (holotype of *M. diagnosticus krasiejowensis*). **B**-**C**, PAN ZPAL Ab III 11, dorsal view close-up of the preorbital region of an incomplete skull showing exclusion of the lacrimal from the orbit margin.

Polish specimens represent a new species. However, material of *Stagonolepis* we were able to examine in the Warsaw collection cannot be distinguished from *S. robertsoni* (sensu Heckert and Lucas, 2000). The aetosaur material from the Krasiejów bonebeds we examined consists of an isolated dorsal vertebra (Fig. 3A-B), a sacral vertebra (Fig. 3E-H), a rib (Fig. 3C-D), a cervical or caudal paramedian osteoderm (Fig. 4D-F), a dorsal paramedian osteoderm (Fig. 4A-C), an incomplete left scapulocoracoid (Fig. 5A-D), a left humerus (Fig. 5E-J), a left ulna (Fig. 6A-D), a metapodial (Fig. 6E-H), an incomplete left femur (Fig. 7A-D) and a left tibia (Fig. 7E-J).

The single dorsal vertebra (PAN AbIII 502/67) is complete (Fig. 3A-B). The centrum has nearly circular anterior and posterior articular surfaces. The neural canal is elliptical, with the long axis oriented dorsoventrally. The transverse processes are bifurcate with the rectangular dorsal bifurcation projecting farther laterally than the columnar ventral half. The width of each transverse processe is approximately two and one half times the length of the centrum. Heckert and Lucas (2000, 2002) diagnosed *Stagonolepis robertsoni* as having transverse processes that exceed twice the centrum length; thus, the ratio of transverse process width to centrum length supports assignment of the Krasiejów material to *S. robertsoni*. The neural spine is mediolaterally compressed, triangular in cross section and terminates dorsally with a triangular expansion of bone, a typical feature of aetosaur dorsal vertebrae. The tall height of the neural spine compares closely with *S. robertsoni*.

The sacral vertebra is complete, with some slight distortion of the anterior articular surface of the centrum (Fig. 3E-H). The ventral margin of the anterior articular surface appears compressed dorsally, resulting in a kidney-shape in anterior view; this contrasts with the undistorted posterior articular surface, which is elliptical. The neural canal is elliptical and proportionally quite small when compared to that of the dorsal vertebra. The prezygapophyses are triangular in lateral view, project anterodorsally and extend beyond the anterior margin of the centrum. The transverse processes are extensive; the width of each equals the width of the centrum. The processes are triangular in anteroposterior view and angle posteriorly ~45°. The posterior margins of the transverse processes extend beyond the posterior margin of the centrum. The postzygapophyses are triangular, project posteriorly and are approximately half the size of the prezygapophyses. The neural spine is proportionately shorter than in the dorsal vertebrae, considerably thicker, and terminates in a large, circular knob of bone.

The single rib is complete (Fig. 3C-D) and has extensive buttressing, both anteriorly and posteriorly, near its proximal end. The anterior buttress is confluent with the capitulum. The capitulum is displaced laterally from the tuberculum.

Both the left dorsal paramedian osteoderm (Fig. 4A-C) and the left cervical or caudal paramedian osteoderm (Fig. 4D-F) are complete. The dorsal paramedian osteoderm is rectangular, whereas the cervical or caudal paramedian osteoderm is nearly square. Both possess prominent anterior bars, anteroposteriorly-directed keels on the dorsal surfaces of the osteoderm that contact their respective posterior margins, and a radiating pattern of pits and grooves that extend from the dorsal keels. These features readily identify this material as *Stagonolepis robertsoni* (Heckert and Lucas, 2000, 2002).

The scapulocoracoid is nearly complete, missing the ventral margin of the coracoid (Fig. 5A-D). The scapular blade is rectangular along its height but expands both anteriorly and posteriorly at its distal end. This expansion is more pronounced posteriorly, but both expansions are triangular. The glenoid is subcircular and angled posterolaterally. The entire scapulocoracoid is angled; in anteroposterior view, a point of flexure is apparent just dorsal to the glenoid.

The left humerus is complete (Fig. 5E-J), with an expanded proximal end, a shaft that is elliptical in cross-section, and two prominent condyles distally. The shaft is asymmetrically oriented anteriorly; all these are features typical of aetosaur humeri (Long and Murry, 1995; Lucas et al., 2002).

The left ulna is complete (Fig. 6A-D) and lacks a prominent olecranon process. The proximal articulation is subelliptical in proximal view. The shaft thins distally and is anteroposteriorly compressed.

The isolated metapodial is complete (Fig. 6E-H). The proximal articular surface is a flattened ellipse, while the distal articular surface is rectangular. This distal surface also has collateral ligament pits on both side of its distal articulation for the attachment of the extensor muscles of the digits.

The right femur is missing its head, but everything distal to its position is preserved (Fig. 7A-D). The femoral shaft is fairly massive with a rounded, pyramidal fourth trochanter and very large distal condyles. This specimen is identical to a femur Long and Murry (1995, fig. 81) assigned to *Stagonolepis*.

Like the femur, the left tibia is identical to material assigned to and illustrated as *Stagonolepis* by Long and Murry (1995, fig. 84). The tibia is mediolaterally compressed and expanded proximally (Fig. 7E-J). Additionally, a slight crest wraps around the anterior edge of the tibial shaft at its midpoint. Both the Polish specimen and the specimen illustrated by Long and Murry (1995) have elliptical distal ends and shallow sulci on their lateral edges.

Teratosaurus

Sulej (2005) erected the new species *Teratosaurus silesiacus* for disarticulated cranial and mostly disarticulated postcranial material from both bone beds at Krasiejów. He distinguished *T. silesiacus* from the type, and the only other named, species of *Teratosaurus*, *T. suevicus*, by features of the maxilla, the only bone in common between specimens of either species (Fig. 8). According to Sulej (2005), unlike *T. suevicus*, *T. silesiacus* has the medial anterior foramen on the maxilla located on its medial surface, a more strongly oblique dorsal process of the maxilla, and foramina for replacement teeth set in a straight line and not connected by a dental groove.

However, a close comparison of the maxilla of *Teratosaurus silesiacus* (Fig. 8) and that of *T. suevicus* (Galton, 1985, pl. 1) calls into question the distinctiveness of *T. silesiacus*. No obvious difference exists in the obliquity of the maxilla dorsal processes, and the alignment of the foramina for replacement teeth in *T.* "*silesiacus*" is not straighter than that in *T. suevicus*. There is a distinct dental groove connecting these foramina in *T. suevicus* that is present, but not as distinct, in *T. silesiacus*. The medial anterior foramen on the maxilla opens anteriorly on *T. suevicus* and more ventrally on *T. silesiacus*. This relatively minor difference, however, could be due to preservation quality and distortion. We also reject Sulej's (2005) argument that "the great distance in time of about 4 million years between these animals [*T. suevicus* and *T. silesiacus*] suggest that they probably belong to different species." Therefore, we consider *T. silesiacus* to be a junior synonym of *T. suevicus*.

Parasuchus

Dzik (2001) described a skull he identified as *Paleorhinus* sp. from Krasiejów that we assign to *Parasuchus bransoni* (cf. Hunt and Lucas, 1991). Note that creation of a diagnostic neotype for *Parasuchus hislopi* by the International Commission on Zoological Nomenclature in 2003 (opinion 2045, case 3165) renders *Paleorhinus* a junior subjective synonym of *Parasuchus*.

The *Parasuchus* material present from the Krasiejów locality includes two nearly complete skulls and an incomplete, associated torso in a matrix block. One skull (Fig. 9A-D) is nearly complete, missing only part of its left squamosal, and its snout exhibits separation along the midline. The other skull (Fig. 9F-G) is nearly complete, missing a portion of its snout and having its postorbital region partially disarticulated. This skull preserves its lower jaws in articulation with the rest of the skull and has a large percentage (>80%) of its maxillary dentition intact (Fig. 9F). Both skulls have narial openings anterior to their antorbital fenestrae, dorsally directed orbits, dorsal margins of the nares that are

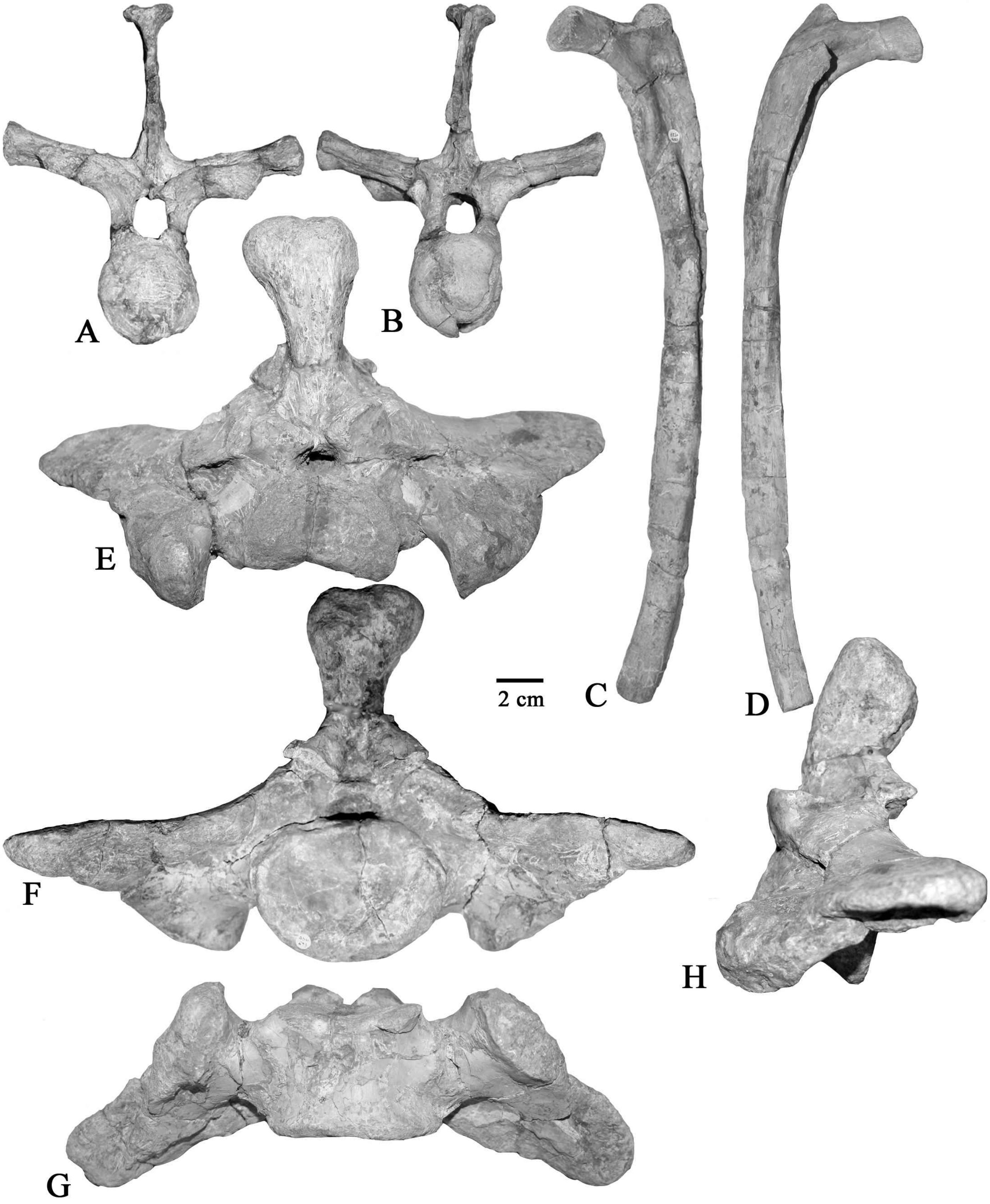

FIGURE 3. **A**-**B**, *Stagonolepis robertsoni*, PAN ZPAL AbIII 502/67, mid-dorsal vertebra in **A**, anterior and **B**, posterior views. **C**-**D**, *Stagonolepis robertsoni*, PAN ZPAL AbIII 1527, complete right? rib in **C**, anterior, and **D**, posterior views. **E**-**H**, *Stagonolepis robertsoni*, PAN ZPAL AbIII 1693, incomplete sacral vertebra in **E**, anterior, **F**, posterior, **G**, ventral, and **H**, left lateral views.

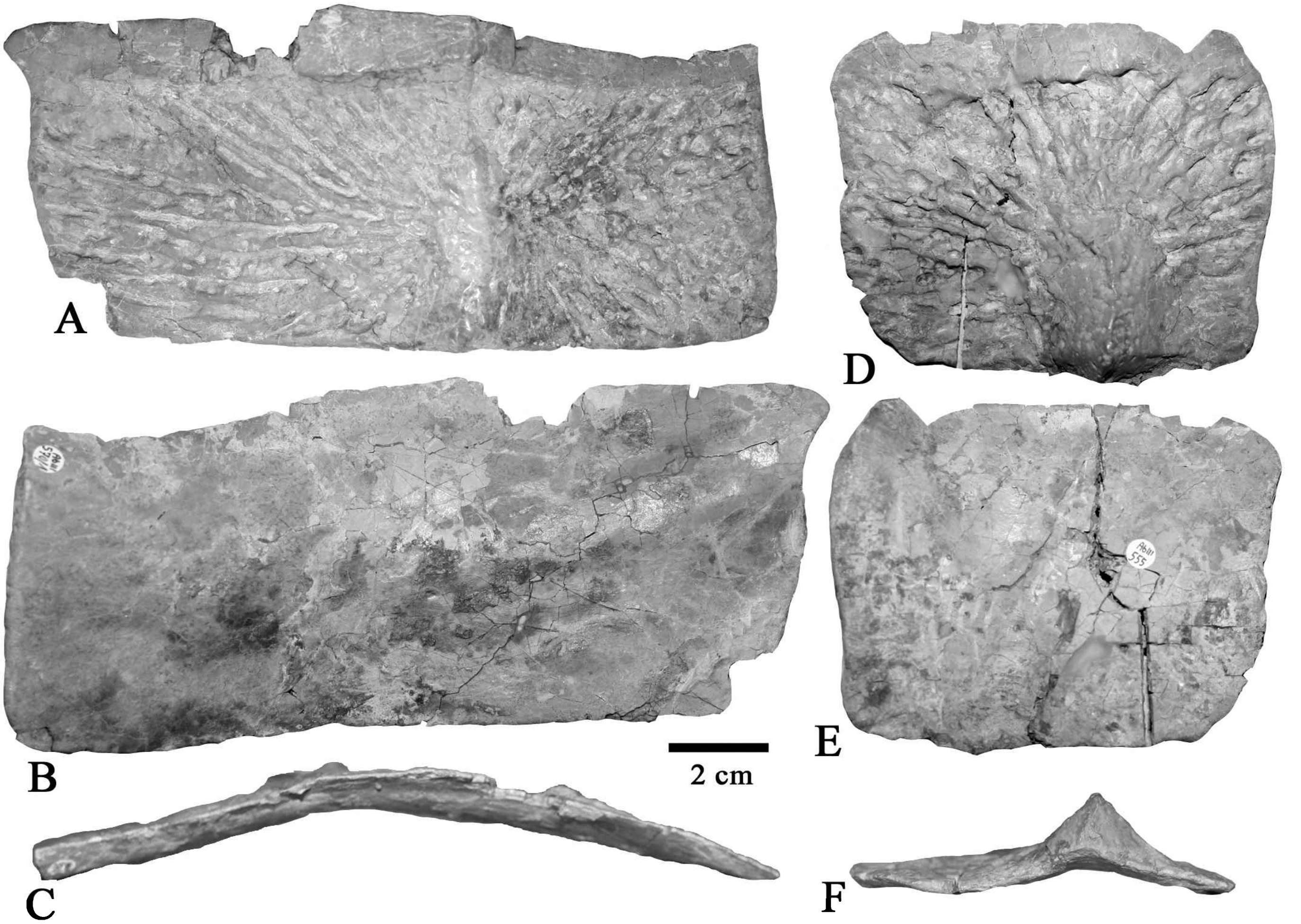

FIGURE 4. **A**-**C**, *Stagonolepis robertsoni*, PAN ZPAL AbIII 57011, left paramedian osteoderm in **A**, dorsal, **B**, ventral, and **C**, posterior views. **D**-**F**, *Stagonolepis robertsoni*, PAN ZPAL AbIII 535, left lateral osteoderm in **D**, dorsal, **E**, ventral, and **F**, posterior views.

inclined anteriorly, and large quadratic foramina, diagnostic features of *Parasuchus* (Hunt and Lucas, 1991) The associated torso is partially disarticulated but consists of numerous dorsal osteoderms, proximal rib fragments and the left scapular blade in a matrix block (Fig. 9E). The two skulls from Krasiejów show a significant range in size (total lengths are ~400 and ~610 mm) and confirm that position of the external nares relative to the antorbital fenestra (a feature diagnostic of *Parasuchus*) does not change ontogenetically.

Silesaurus

Dzik (2003) named the dinosauriform *Silesaurus opolensis* based on cranial and postcranial material from Krasiejów. This taxon is unique to the locality, and thus of little value to biochronological correlation. Indeed, *Silesaurus* is one of the youngest known non-dinosaurian dinosauriforms.

DISCUSSION

Taxonomic descriptions of much of the Krasiejów tetrapod assemblage provide a classic example of what Cooper (1982) termed "provincial taxonomy": virtually all of the taxa described from Krasiejów were assigned to new species, not based on robust morphological differences, but mostly on their location at a new site. However, a careful review of the Krasiejów tetrapod taxa indicates that it contains only one new (and thus far endemic) taxon, the dinosauriform *Silesaurus opolensis*. *Metoposaurus* and *Parasuchus* from Krasiejów are indicators of an Otischalkian age (Lucas, 1998, 1999). The occurrence of *Stagonolepis* is particularly important because it documents an Otischalkian record of this taxon, which can no longer be considered an index taxon of the Adamanian.

Lithostratigraphic and microfossil correlations indicate that the Krasiejów locality is equivalent to the Lerhberg Schichten of the German Keuper. Tetrapod biostratigraphy indicates the Lehrberg Schichten are of Otischalkian age (Lucas, 1999). Therefore, tetrapod biostratigraphy confirms previous correlations based on other data. The Krasiejów tetrapod assemblage thus further demonstrates the value of Triassic tetrapods in biostratigraphic correlation, based on the global Triassic tetrapod biochronology developed in the 1990s.

ACKNOWLEDGMENTS

Lucas thanks M. Borsuk-Bialynicka, J. Dzik and T. Sulej for access to the Krasiejów fossils in Warsaw. Jerry Harris and Larry Rinehart provided helpful reviews of the manuscript.

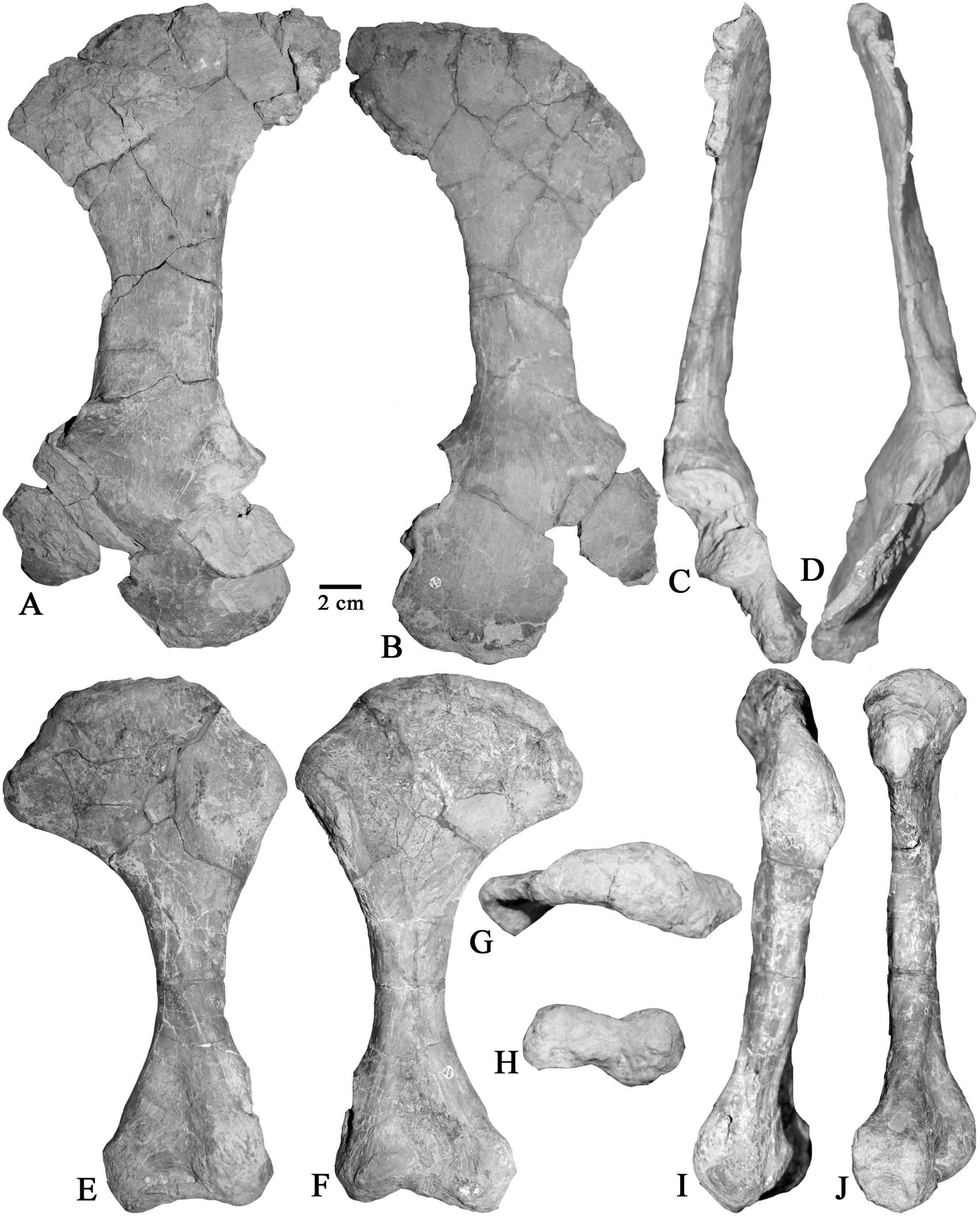

FIGURE 5. **A**-**D**, *Stagonlepis robertsoni*, PAN ZPAL AbIII 694, incomplete left scapulocoracoid in **A**, lateral, **B**, medial, **C**, posterior, and **D**, anterior views. **E**-**J**, *Stagonolepis robertsoni*, PAN ZPAL AbIII 1175, left humerus in **E**, anterior, **F**, posterior, **G**, proximal, **H**, distal, **I**, medial and **J**, lateral views.

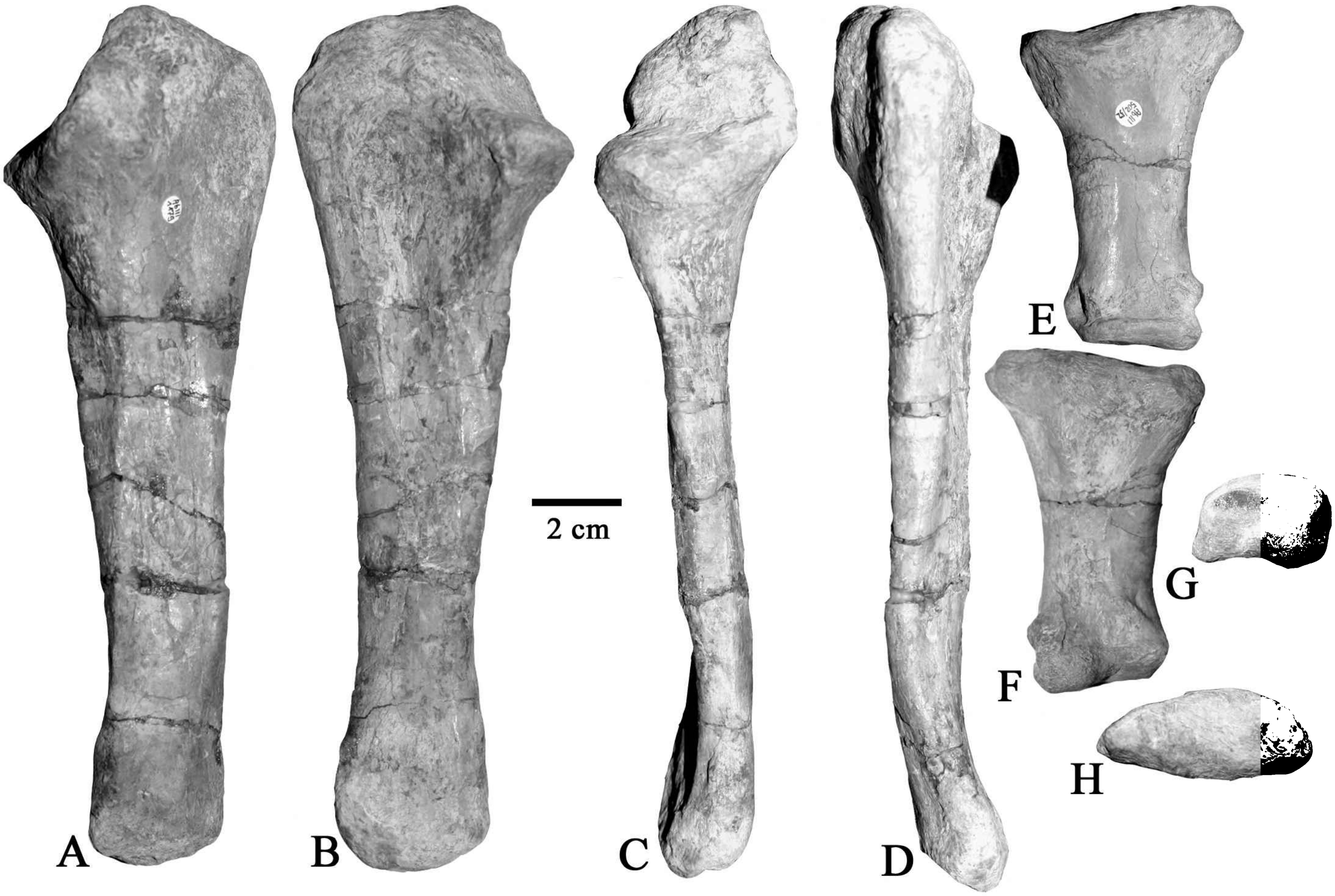

FIGURE 6. **A**-**D**, *Stagonolepis robertsoni*, PAN ZPAL AbIII 1179, left ulna in **A**, anterior, **B**, posterior, **C**, medial, and **D**, lateral views. **E**-**H**, *Stagonolepis robertsoni*, PAN ZPAL AbIII 502/52, right? metapodial in **E**, dorsal, **F**, ventral, **G**, distal, and **H**, proximal views.

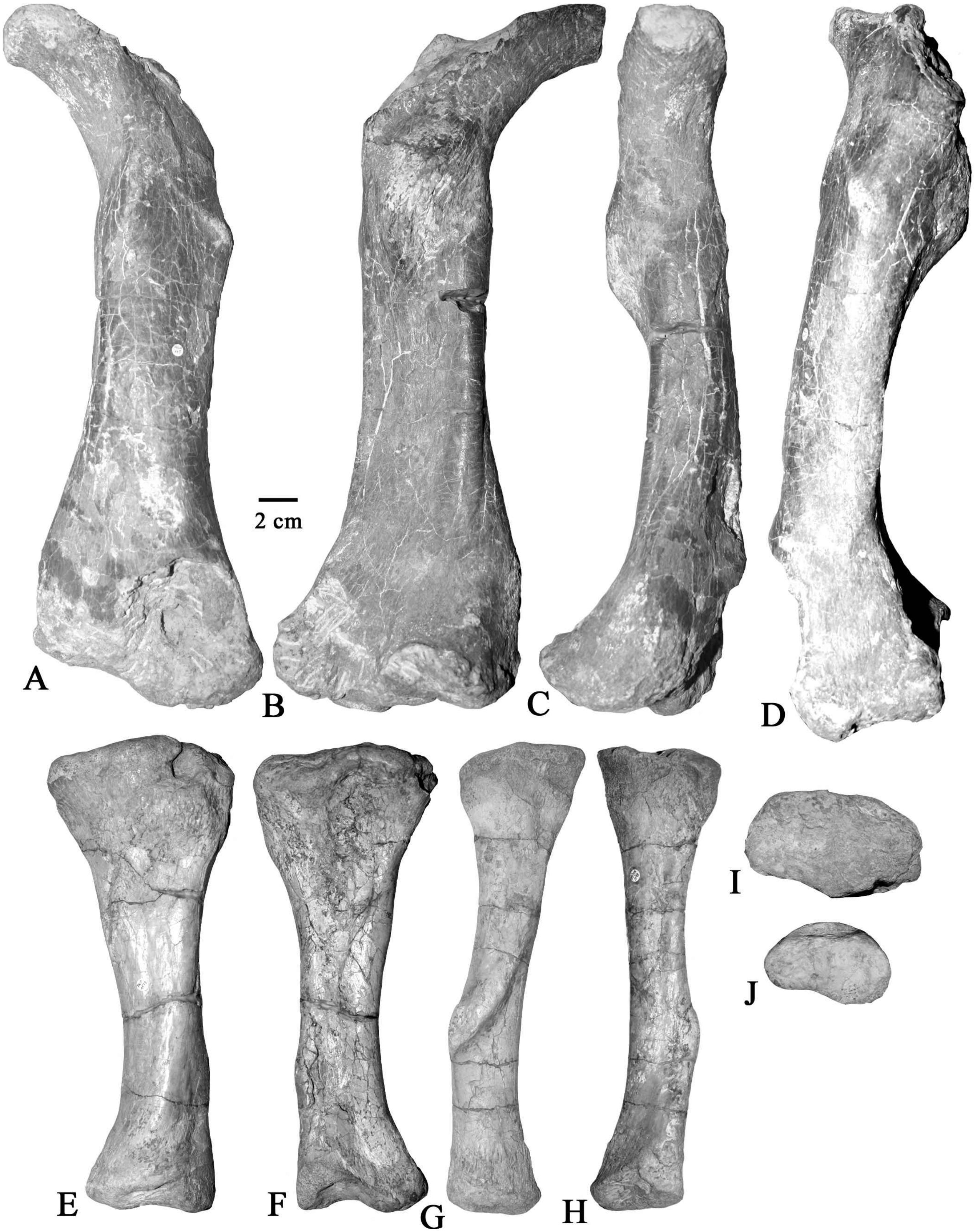

FIGURE 7. **A-D**, *Stagonolepis robertsoni*, PAN ZPAL AbIII 115, incomplete left femur in **A**, anterior view; **B**, posterior view; **C**, medial view; and **D**, lateral view. **E-J**, *Stagonolepis robertsoni*, PAN ZPAL AbIII 1178, left tibia in **E**, medial view; **F**, lateral view; **G**, anterior view; **H**, posterior view; **I**, proximal view; and **J**, distal view.

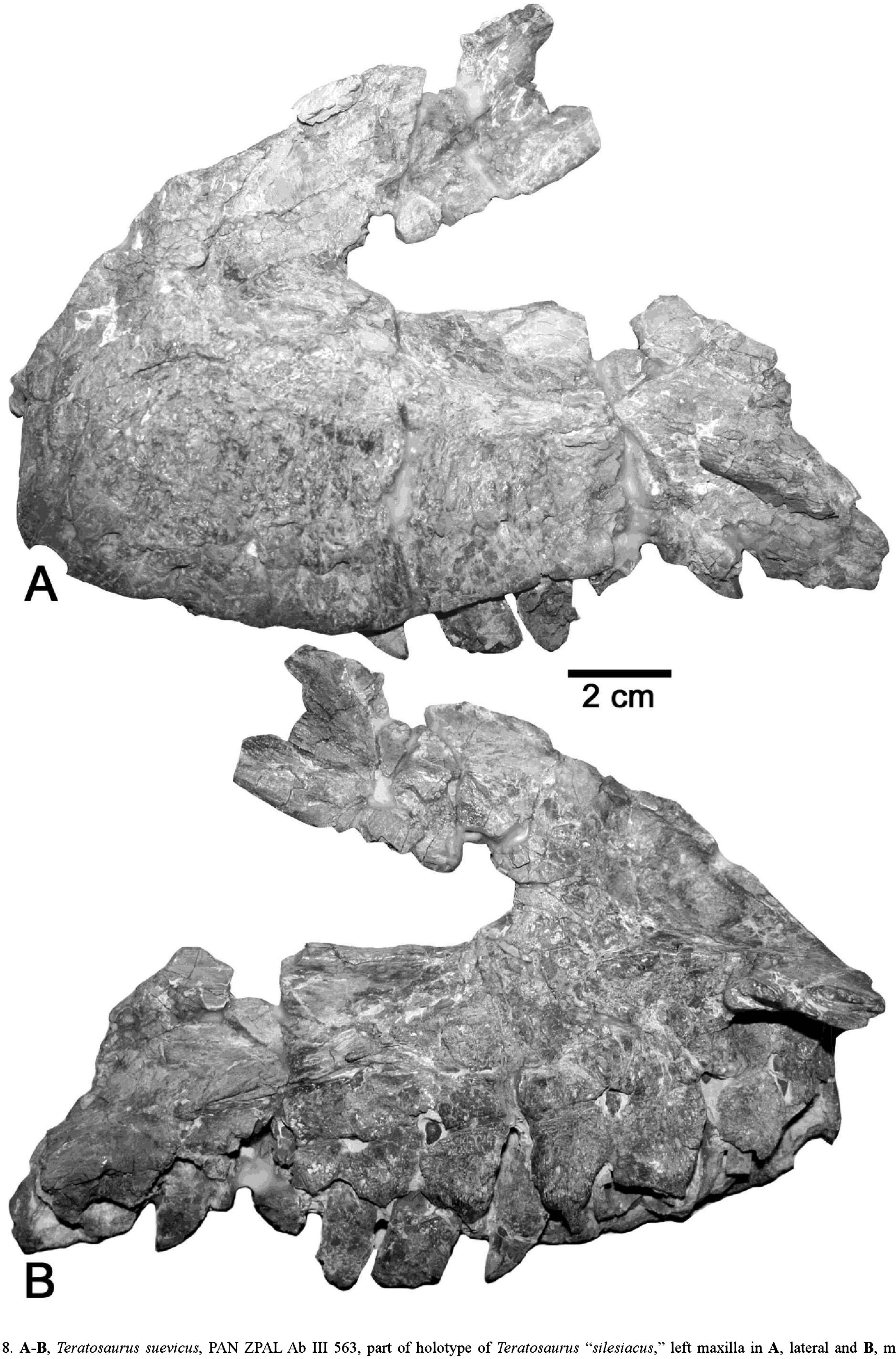

FIGURE 8. **A**-**B**, *Teratosaurus suevicus*, PAN ZPAL Ab III 563, part of holotype of *Teratosaurus* "*silesiacus*," left maxilla in **A**, lateral and **B**, medial views.

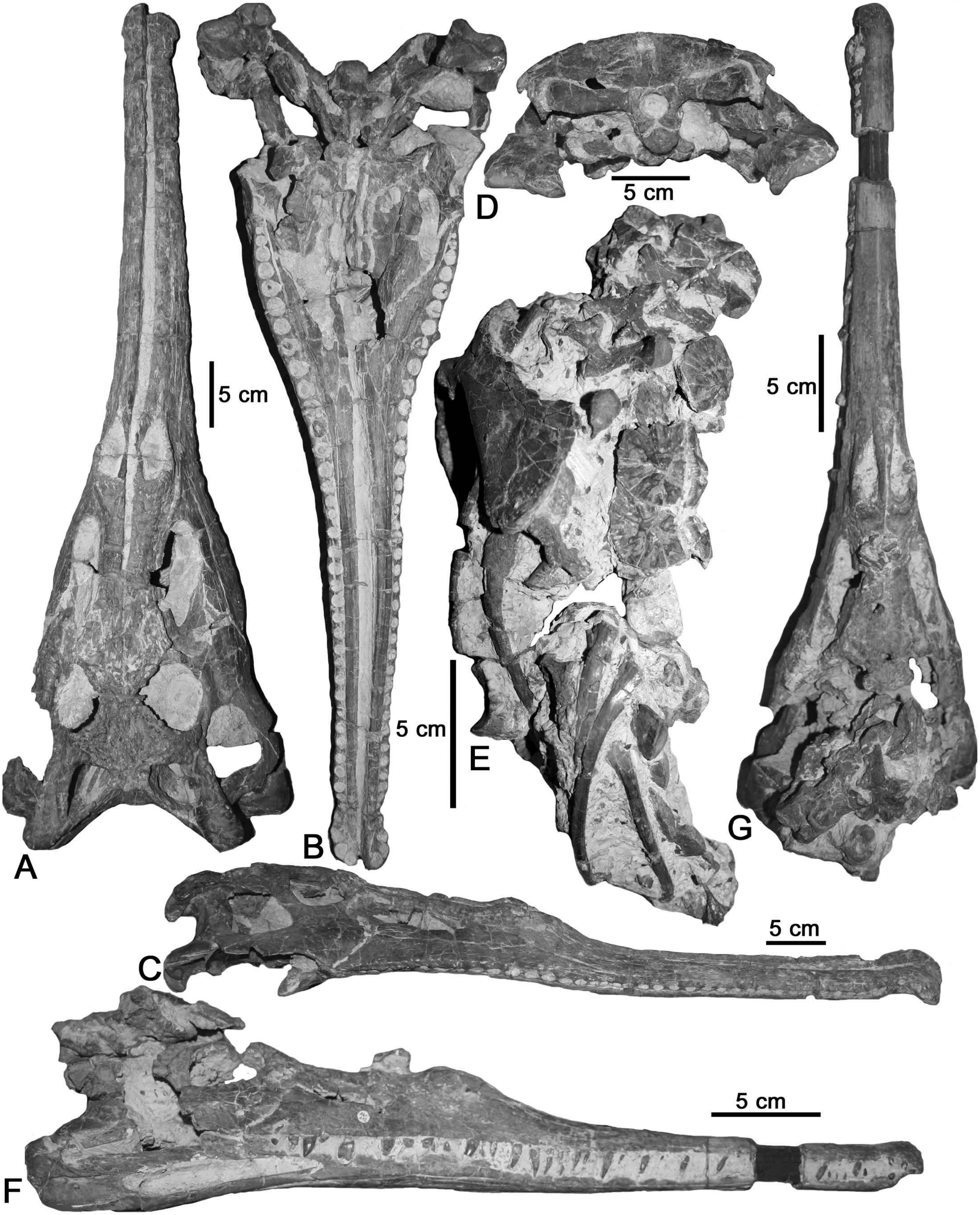

FIGURE 9. **A**-**D**, *Parasuchus bransoni*, PAN ZPAL Ab III 200, nearly complete skull in **A**, dorsal, **B**, ventral, **C**, right lateral and **D**, occipital views. **E**-**G**, *Parasuchus* sp., PAN ZPAL Ab III 112, nearly complete skull in **F**, right lateral and **G**, dorsal views. **E**, incomplete, associated torso of ZPAL Ab III 112, consisting of dorsal osteoderms and ribs, in matrix block.

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TAXONOMY OF *SHUVOSAURUS*, A LATE TRIASSIC ARCHOSAUR FROM THE CHINLE GROUP, AMERICAN SOUTHWEST

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Abstract—The distinctive, edentulous archosaur *Shuvosaurus inexpectatus* Chatterjee, 1993, was named based on a skull, whereas the postcrania of the same taxon were named *Chatterjeea elegans* Long and Murry, 1995. *Effigia okeeffeae* Nesbitt and Norell, 2006, is the name for the associated skull and postcranium of *Shuvosaurus* and *Chatterjeea*. Therefore, only one generic name, *Shuvosaurus* (= *Chatterjeea*, = *Effigia*), is valid, and the supposed diagnostic features of *Effigia* indicate that, at most, its type material represents a species of *Shuvosaurus* (*S. okeeffeae*) distinct from the type species of *Shuvosaurus* (*S. inexpectatus*). *S. inexpectatus* has a well documented, early Revueltian distribution in Texas-New Mexico, whereas *S. okeeffeae* is well documented from only one Apachean locality in New Mexico.

INTRODUCTION

One of the most unusual tetrapods recovered from the Upper Triassic Chinle Group of the American Southwest is *Shuvosaurus* from the Bull Canyon Formation in West Texas. Originally described as an ornithomimosaurian dinosaur by Chatterjee (1993), *Shuvosaurus* has an edentulous beak, enormous orbits and other features that are, indeed, reminiscent of an ostrich dinosaur. Recently, Nesbitt and Norell (2006) and Nesbitt (2007) described a remarkably similar taxon, *Effigia*, from the Rock Point Formation of the Chinle Group in New Mexico. Here, we argue that *Effigia* is a junior subjective synonym of *Shuvosaurus*.

Institutional abbreviations: AMNH = American Museum of Natural History, New York; TTUP = Texas Tech University Museum, Lubbock.

PREVIOUS STUDIES

Chatterjee (1993) named *Shuvosaurus inexpectatus* for TTUP 9280, a nearly complete skull, left lower jaw and a dorsal vertebra (holotype) and additional, less complete cranial material, part of an atlas and a right scapula (referred specimens) from the Post quarry in the Revueltian Bull Canyon Formation in West Texas. Chatterjee (1993) regarded *Shuvosaurus* as a coelurosaurian theropod dinosaur close to ornithomimosaurs based on a cladistic analysis.

Long and Murry (1995) named *Chatterjeea elegans* for relatively small postcranial material (most notably the holotype, TTUP 9001, a nearly complete postcranial skeleton) of an archosaur from the Post quarry. Chatterjee (1985) had earlier considered these specimens to be juvenile postcrania of *Postosuchus*. Puzzled by the relative abundance of *Chatterjeea* postcrania in the Post quarry, and apparent absence of cranial material of this taxon, Long and Murry (1995, p. 162) suggested that the cranial material named *Shuvosaurus* might belong with the postcranium named *Chatterjeea*. As Long and Murry (1995) acknowledged, this would make *Shuvosaurus* the senior synonym of *Chatterjeea*.

Rauhut (1997) briefly redescribed the skull of *Shuvosaurus* and reaffirmed Chatterjee's conclusion that it is a theropod dinosaur. However, Hunt et al. (1998) argued against the dinosaurian affinities of *Shuvosaurus* and tentatively supported the argument of Long and Murry (1995) that *Shuvosaurus* and *Chatterjeea* are one taxon. Heckert and Lucas (2000) considered *Shuvosaurus* to be a non-dinosaur, as did Mackovicky et al. (2004).

Rauhut (2003) continued to regard *Shuvosaurus* as a bizarre theropod. He also suggested that *Gojirasaurus* from the Revueltian Bull Canyon Formation of east-central New Mexico (Carpenter, 1997) is based on postcrania of *Shuvosaurus*. The type material of *Gojirasaurus* consists of partial postcrania of a large (>5 m total length) theropod dinosaur, and cranial material of *Shuvosaurus* was found at the type locality of *Gojirasaurus* (Carpenter, 1997; Hunt, 2001). This association, and Rauhut's conclusion that the type skull of *Shuvosaurus* is that of a juvenile (hence its adult postcrania would be as large as those of *Gojirasaurus*), were the basis for Rauhut's suggestion.

Lehane (2005) provided a very detailed description of the cranial anatomy of *Shuvosaurus*. He also assigned it to the Theropoda.

Nesbitt and Norell (2006) and Nesbitt (2007) recently erected *Effigia okeeffeae* for associated cranial and postcranial specimens from the Whitaker quarry at Ghost Ranch, New Mexico, in the Apachean Rock Point Formation of the Chinle Group. *Effigia* has a skull nearly indistinguishable from that of *Shuvosaurus*, and a postcranium remarkably similar to that of *Chatterjeea*, so we argue here that the two taxa are synonymous. The association of a *Shuvosaurus* skull and *Chatterjeea* postcranium in *Effigia* confirms previous suggestions that *Shuvosaurus* and *Chatterjeea* represent one taxon.

SHUVOSAURUS AND *CHATTERJEEA*

The associated postcrania and skull of *Effigia* demonstrate that the *Shuvosaurus* skull belongs with a *Chatterjeea* postcranium as was postulated previously (Long and Murry, 1995; Hunt et al., 1998; Nesbitt and Norell, 2006; Nesbitt, 2007). Thus, *Chatterjeea elegans* Long and Murry, 1995 is a junior subjective synonym of *Shuvosaurus inexpectatus* Chatterjee, 1993. Furthermore, the associated postcrania demonstrate that *Shuvosaurus* is a suchian archosaur, not a theropod dinosaur (Nesbitt and Norell, 2006; Nesbitt, 2007). The postcrania of *Gojirasaurus* are those of a dinosaur, so despite a taphonomic association, *Gojirasaurus* and *Shuvosaurus* do not represent the same taxon.

TAXONOMIC STATUS OF *EFFIGIA*

Effigia is very similar to *Shuvosaurus* in many anatomical features that distinguish both from other suchians, especially the edentulous premaxilla, maxilla and dentary and the long dorsal process of the premaxilla (Fig. 1). Nesbitt and Norell (2006, p. 1045) and Nesbitt (2007, p. 6) listed six characteristics that supposedly distinguish *Effigia* from *Shuvosaurus*. Here, we evaluate these characteristics:

1. "Presence of both a dorsal and posterior process of the maxilla": In *Shuvosaurus*, the skull has a relatively small maxilla that sutures to the nasal dorsally, and thus is excluded from contacting the lacrimal. In other words, the maxilla does not form much of the dorsal margin of the antorbital fenestra. In contrast, *Effigia* has been reconstructed to have a dorsal process of the maxilla that forms much of the dorsal border of the antorbital fenestra and meets the lacrimal. This difference appears to us to be genuine, despite damage to and distortion of the holotype skulls of both *Shuvosaurus* and *Effigia*.

2. "Small posterior process of the premaxilla": Both *Shuvosaurus*

and *Effigia* have a long posterior process of the premaxilla that contacts and separates the nasals dorsal to the external nares. There is no difference between the taxa in the shape of this process, or its relative length. Nesbitt (2007) correctly abandoned this putative diagnostic feature listed by Nesbitt and Norell (2006).

3. "Relatively shorter dentary": The lower jaw of the holotype of *Shuvosaurus* is not complete, and most of it between the symphyseal region and the mandibular fenestra has been reconstructed (Chatterjee, 1993, fig. 5A; Rauhut, 1997, fig. 1; Lehane, 2005, fig. 5) (Fig. 1C). Existing bone maps of the lower jaw of *Shuvosaurus* do not distinguish dentary-surangular or dentary-angular sutures, which should be anterior to the posterior end of the reconstructed missing portion of the lower jaw. Nesbitt (2007, p. 32) states that "the dentary of *Shuvosaurus* (TTUP 9280) is slightly longer than that of *Effigia*" but no quantification or documentation of this statement is provided, and given the reconstruction in the former, would be difficult to assess at best. Based on available data, we conclude that relative lengths of the dentaries of *Shuvosaurus* and *Effigia* are not demonstrably different.

4. "Presence of a large pit on the posterior side of the lacrimal:" Nesbitt (2007, p. 15) clarifies this by stating that "even though preservation of the lacrimal of *Shuvosaurus* is poor, the element lacks the posterior fossa and is much more mediolaterally compressed than that of *Effigia*." The bone is mediolaterally compressed and damaged in the *Shuvosaurus* skull (TTUP 9280) so whether or not it has a small fossa, as in the *Effigia* skull, might be problematic. Nevertheless, this may be a genuine difference between *Shuvosaurus* and *Effigia,* although the biological significance of the "large pit" is undetermined.

5. "Absence of posterior process of squamosal": Nesbitt (2007) describes a supposed difference in shape between the squamosals of *Shuvosaurus* and *Effigia*. The *Shuvosaurus* squamosal is tetraradiate with a prominent posterior process. That of *Effigia* is supposedly triradiate, with a posterior convexity, but lacks a distinct posterior process (Nesbitt, 2007, fig. 14). However, Nesbitt's (2007, fig. 4) illustration of the holotype of *Effigia okeeffeae*, AMNH FR 30587, shows a tetraradiate squamosal with a distinct posterior process (Fig. 1A), as does the reconstruction of the skull of *Effigia* by Nesbitt and Norell (2006, fig. 1) (Fig. 1B). However, Nesbitt's (2007, fig. 14) illustration shows a somewhat different squamosal outline for *Effigia*.

According to Nesbitt (2007), the quadratojugals are unknown in *Effigia*, so the long, trapezoidal quadratojugals shown in the reconstruction of Nesbitt and Norell (2006, fig. 1) are hypothetical. One possibility, suggested by Nesbitt's (2007, fig. 14A) close-up photograph of the left squamosal of AMNH FR 30587, is that part of the quadratojugal is present as part of the ventral end of what he identifies as the squamosal. Given the great similarity of the skulls of *Effigia* and *Shuvosaurus*, a small and triangular quadratojugal in *Effigia* seems more likely than the long, trapezoidal element hypothesized by Nesbitt and Norell (2006).

6. "Small fossa on posterolateral side of squamosal": Nesbitt (2007, p. 18) clarifies this feature, stating that "a small, well-defined depression is located on the posterior portion of the [squamosal] body. This depression opens ventrally and is surrounded by a small rim of bone." *Shuvosaurus* apparently lacks this depression (Nesbitt, 2007), and like the pit on the lacrimal the biological significance of this fossa is unknown.

DISCUSSION

Of the six putative diagnostic differences between *Effigia* and *Shuvosaurus*, the shape of the maxilla, a pit of unknown significance in the lacrimal and some differences in squamosal shape appear to be unambiguous differences. The other supposed differences are not replicable (premaxilla, dentary). The difference in the maxilla (longer dorsal process in *Effigia*) is a difference in the degree of development of a feature, which can vary ontogenetically, dimorphically, or simply with individual variation, not in strict presence/absence. The biological significance of the distinctive features of the lacrimal and squamosal are unknown, so there is no way to evaluate the significance of variation in these features with the small sample at hand. Indeed, so little is known of cranial variation in *Shuvosaurus*/*Effigia* that the taxonomic significance of the differences is open to question.

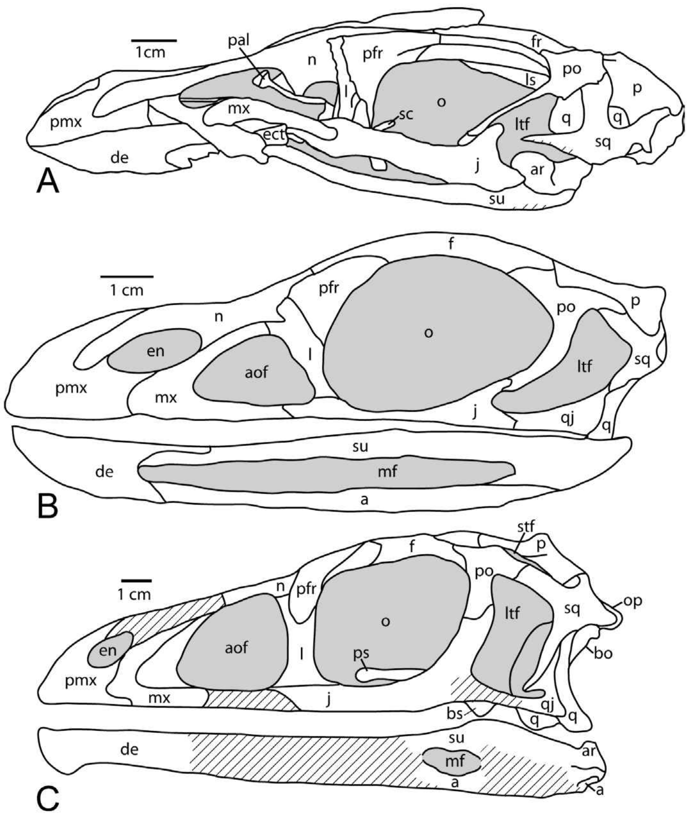

FIGURE 1. Comparison of the skulls of *Effigia* and *Shuvosaurus*. **A**, Drawing of left side of holotype skull of *Effigia okeeffeae*, AMNH FR 30587, as preserved (after Nesbitt, 2007, fig. 4). **B**, Reconstruction of skull of *Effigia okeefeae* in left lateral view (after Nesbitt and Norell, 2006, fig. 1). **C**, Reconstruction of skull of *Shuvosaurus inexpectatus* in left lateral view (after Lehane, 2005, fig. 5). Diagonal lines represent reconstructed portions. Abbreviations are: a = angular, aof = antorbital fenestra, ar = articular, bo = basioccipital, bs = basisphenoid, de = dentary, en = external nares, f = frontal, j = jugal, l = lacrimal, ltf = lateral temporal fenestra, mf = mandibular fenestra, mx = maxilla, n = nasal, o =orbit, op = opisthotic, p = parietal, pfr = prefrontal, pmx = premaxilla, po = postorbital, ps = parasphenoid, q = quadrate, qj = quadratojugal, sq = squamosal, stf = supratemporal fenestra, su = surangular.

We conclude that the anatomically minor difference(s) used to diagnose *Effigia* from *Shuvosaurus* do not merit generic separation. We note that in Nesbitt's (2007) detailed description of *Effigia*, he mentions some other anatomical differences between it and *Shuvosaurus* that are not part of the diagnosis of *Effigia*. However, these differences, and those that were used to diagnose *Effigia* from *Shuvosaurus* strike us as minor anatomical differences, almost all of which are of unknown biological significance, that could easily represent variation within a taxon. Indeed, in the cladistic analysis of *Effigia* among basal archosaurs published by Nesbitt (2007, fig. 54), *Effigia* and *Shuvosaurus* are scored identically (for known characters) for the 83 characters analyzed (Nesbitt, 2007, appendix 5). This means that there are no phylogenetically informative differences between *Effigia* and *Shuvosaurus* by Nesbitt's (2007) analysis, so they are not even distinct cladotaxa.

Many of the differences in the drawings of the reconstructed skulls of *Effigia* and *Shuvosaurus* (Fig. 1) reflect artistic license in the reconstruction of damaged, distorted and incomplete fossils. Thus, for example, if the posterior portion of the skull of the *Effigia* skull were raised dorsally so that the long axis of the lateral temporal fenestra were vertical (and there is no reason not to do this since the distortion there is clearly diagenetic and artificial), the two reconstructions would be much more similar.

We thus consider *Effigia* Nesbitt and Norell, 2006 to be a junior subjective synonym of *Shuvosaurus* Chatterjee, 1993. Pending further information on cranial variation in *Shuvosaurus*, we very tentatively regard the Ghost Ranch material as a distinct species, *S. okeeffeae*, distinguished from *S. inexpectatus* by the difference in the maxilla originally used to differentially diagnose *Effigia* from *Shuvosaurus*. *S. inexpectatus* has a well documented early Revueltian distribution in Texas-New Mexico (Hunt, 1991), whereas *S. okeeffeae* is well documented only from one Apachean locality in New Mexico.

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CONODONTS VIEWED AS EVOLVING HEAVY-MINERAL GRAINS

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Abstract—Conodonts are common in lag deposits near unconformities. Within these lag deposits, conodonts behave as heavy-mineral grains and represent the ages of the units underlying the unconformity rather than the age of the overlying rock unit. More importantly, the biology of conodonts is unknown, as are the ranges and phylogenies of many species. The burden of proof that any conodont has not been reworked rests with those conodont investigators who have, thus far, generally failed to demonstrate this fact conclusively. Furthermore, we believe that the "Standard Zonation" and environmental interpretations based on conodont biofacies is open to question. Much more attention should be given to "the stratigraphic evidence of a well-marked unconformity" than to these "other classificatory or correlative criterion."

INTRODUCTION

Are conodonts a panacea of stratigraphic and sedimentologic information or are they biologically derived heavy minerals? Conodonts are microscopic (generally 0.1 to 1 mm maximum dimension) hard parts of an unknown group of organisms and are composed of apatite (approximating the mineral fancolite; Epstein et al., 1977). Conodonts are never preserved as whole organisms (except for a very few questionable soft-body traces, Benton, 1987) and their biology is unknown. They have been considered as either internal supports for soft tissues (Hass, 1941) or as teeth of everything from worms to vertebrates (Benton, 1987). Contenders for the conodont-bearing animal extend back to Silurian time, although conodonts occur as early as the Cambrian (Epstein et al., 1977; Mikulic et al., 1985). We have examined the literature to assess some of the applications of conodont studies to geologic problems. This examination brings to mind myriad questions about the validity of these applications, and we conclude that particular care must be taken in the interpretation of this organic silt.

Conodont biostratigraphy accounts for much of the present interpretation of the Paleozoic record. In fact, many of the geologic models presently in use, especially in the Midwest and in the eastern Great Basin, are conodont-driven paleogeographic reconstructions (see, for example Sandberg and Poole, 1977; Metzger, 1989).

Conodont biostratigraphy has been offered as an error-free means of dating strata and as the key to detailed biofacies interpretations used for paleogeographic reconstructions (see, for example Sandberg et al., 1982, and references cited therein). Conodonts, it is claimed, provide "the most refined time-measuring tool for the Late Devonian" (Ziegler and Sandberg, 1990, foreword), and Upper Devonian conodont zones are thought to represent times spans as short as 0.3 Ma (Sandberg et al., 1983, Ziegler and Sandberg, 1982). Conodonts are the basis of a "Standard Zonation" to act "as a standard [sic] against which all other biozonal schemes can be measured" (Ziegler and Sandberg, 1990, p. 14). Conodonts have been used to date tectonic activity with amazing precision, even when most workers cannot agree on anything else about the event (see, for example, Sandberg in Nelsen and Stewart, 1980; Sandberg, 1981). Conodonts have also been used as golden spikes to tag three of the most elusive boundaries in the geological column—the Devonian-Mississippian, the Mississippian-Pennsylvanian, and the Permian-Triassic (Sandberg in Streel, 1972; Sweet, 1988; Brown et al., 1990). Conodonts have also been used by the petroleum industry as an inexpensive tool to measure thermal maturation (the conodont alteration index or CAI; Epstein et al., 1977)

Proponents of conodont biofacies models differentiate many sedimentary environments in minute detail based solely on the conodont fauna. Conodonts have been interpreted as key indicators of eustatic sea-level fall (Sandberg and Ziegler, 1984), bolide impacts (Sandberg et al., 1988; Wang et al., 1991), and many other facets of geology, only a few of which we can enumerate here. If the predictions and interpretations based on this phosphatic Rosetta stone are valid, conodont studies should revolutionize the way geology is done. Before field geologists retire their rock picks, however, an examination of the literature is in order. Because conodonts are so similar to heavy mineral grains, the positions of faunal collections in relationship to "well-marked" unconformities are especially important.

Most of our examples are from the Devonian and Mississippian. Thus reference to Gunter Bischoff, E.B. and E.R. Branson, Charles Collinson, W.M. Furnish, Gilbert Klapper, M.G. Mehl, C.B. Rexroad, C.A. Sandberg, A.J. Scott, and Willi Ziegler seem conspicuous only because these workers have been among the most prolific conodont specialists working on this geologic time period.

CONODONT OCCURRENCES AND EXPLANATIONS

When, as commonly happens, conodont studies contradict macrofaunal and sedimentologic interpretations, conodont specialists offer a host of ad hoc explanations (compare, for example, Williams, 1943 and Scott and Collinson, 1961, and see Alberti et al., 1974). Most of these fall into one or a combination of seven categories: reworking, stratigraphic leakage, homeomorphy, polyphylogeny, multiple morphotypes, ontologenetic development, and subspeciation. Our examination of the literature suggests that reworking of conodonts near unconformities explains many of these contradictions and casts doubt on many of the claims for the utility of conodonts.

Reworking and Stratigraphic Leakage of Conodonts

Conodont abundances, measured as specimens per kilogram of sample, are extremely variable. Most marine sedimentary rocks sampled for conodonts, it appears, do not contain them (see, for example, Uyeno et al., 1982; Sando and Sandberg, 1987). Limestones commonly contain on the order of one to ten specimens per kg (see, for example, Scott and Collinson, 1961), although Uyeno et al. (1982) report recovering only four conodonts from a 263 kg limestone sample. Conodonts, however, are often extremely abundant, especially near the bases of marine sedimentary rock units. These conodont-rich horizons have been the target of extensive study (see, for example, Branson and Mehl, 1934b; Sandberg and Klapper, 1967).

Conodonts are so common at some horizons that they can be expressed as percent phosphate. Sandberg and Klapper (1967) report phosphate content, primarily as conodonts, of 4-15 percent P_2O_5 from the Cottonwood Canyon Member at the base of the Mississippian Madison Limestone in Montana. These horizons would be targets for mining, except they are generally only a few inches thick. These horizons are invariably near unconformities where the conodonts have been hydraulically concentrated (see, for example, Ellison, 1987). Although conodonts are remnants of the material removed by erosion, they have been used frequently to date overlying units (see, for example, Sandberg and Klapper, 1967).

Conodont specialists recognize that many horizons contain reworked conodonts and weed out the older forms to compile "representative" faunal lists (see, for example Sandberg and Klapper, 1967, p. B48). A common assumption used to recognize reworked conodonts is that water-transported conodonts show signs of "marked wear" (Branson and Mehl, 1934b, p. 267). Broadhead and Driese (1991) demonstrated, however, that conodonts, like other heavy mineral grains, may not be abraded during subaqueous sedimentary transport. In order to identify indigenous conodonts, therefore, specialists must depend on the a priori knowledge of the age of the host formation and of the ranges and habitats of the conodonts (see, for example, Ziegler and Sandberg, 1990, foreword) rather than on physical evidence.

Examples of conodonts collected from lag deposits overlying unconformities are quite common in the literature, although they are not always cited as such. These lag deposits include, for example, the basal Chattanooga and New Albany Shale of Tennessee and adjacent areas (Devonian: Ulrich and Bassler, 1926; Bassler, 1932; Hass, 1956); the Mississippian Bushberg Sandstone of Missouri (Branson and Mehl, 1934b); the clastic unit at the base of the Madison Limestone in South Dakota, Wyoming, and Montana (Klapper and Furnish, 1963; Sandberg and Klapper, 1967); the Mississippian fish "tooth" beds of Iowa (Straka, 1968); and the uppermost part of the Jacobs Chapel bed at the top of the New Albany in southern Indiana (considered Mississippian in age by Rexroad, 1969, and others).

Horizons containing less than thousands or tens of thousands of conodonts per kilogram of sample also can contain reworked conodonts, and reworking is not confined to beds immediately overlying unconformities. Examples of such include the lower Hannibal Formation (Mississippian) at Monroe City, Missouri (Branson, 1934), the "Devonian clays" of Iowa (Stauffer, 1940), and the lower Milligen Formation (Devonian (?) and Mississippian) of Idaho (Sandberg et al., 1975). Although reworked conodonts commonly occur with detrital clastics, there are many examples of reworked conodonts in limestone. The Middle Devonian Lingle Formation of southern Illinois (Orr, 1964) and the Cedar Valley Limestone in Iowa (Stauffer, 1940) include reworked specimens, as does the lower Chappel Limestone of Texas (Mississippian: Hass, 1959; Ellison, 1987), and the Louisiana Limestone of Illinois and Missouri (considered Devonian in age by Scott and Collinson, 1961). Examples of faunal mixing are especially common near the Devonian-Mississippian boundary.

In the Mississippi Valley, several workers have reported conodonts from the Devonian Grassy Creek Formation reworked into the Mississippian Bushberg Sandstone and the equivalent Hannibal Formation in some areas but not in others (Branson, 1934; Branson and Mehl, 1934b; Ziegler et al., 1974; Chuauff and Bombrowsik, 1977). The New Albany Shale in southern Indiana and the Chattanooga Shale in Alabama and correlative formations in neighboring areas (Ulrich and Bassler, 1926; Holmes, 1928; Huddle, 1934; Hass, 1956), including the Grassy Creek in Missouri (Branson and Mehl, 1934a), contain conodonts that commonly are reworked into younger strata (see, for example *Polygnathus rhomboidea* in Collinson et al., 1962).

So many species of conodonts are considered as reworked within their ranges that reports of their indigenous occurrences are open to question. The Sheffield (Devonian), Maple Mill (Devonian or Mississippian), and Prospect Hill (Mississippian) Formations of Iowa contain specimens of *Polygnathus semicostata* that "appear to be reworked" because "some specimens are abraded" as well as specimens of *Polygnathus perplexus* and *Polygnathus praehassi* that Metzger (1989, p. 521) considered reworked in the Prospect Hill but indigenous to the Sheffield and Maple Mill. Conodonts that Ellison (1987) considered to be reworked in the Canutillo Formation (Mississippian) of Texas (see, for example, *Polygnathus nodocostatus*) have been reported as indigenous in many other formations of Upper Devonian and Lower Mississippian age including the Grassy Creek Formation (Branson, 1944) and the Louisiana Limestone of the Mississippi Valley, the New Albany and Chattanooga Shales (Campbell, 1946; Hass, 1956), the Sheffield Formation (Anderson, 1966), the Sappington Member of the Three Forks Formation and the Leatham and Pinyon Peak formations of Wyoming, Montana and adjacent areas (considered Devonian in age by Sandberg, 1976), as well as the Upper Devonian Wabamun Formation of southern Alberta (Mound, 1968).

In Europe, a Lower Carboniferous conglomerate of the western Harzgeröder Zone (Südharz) graphically illustrates the problems of reworked conodonts. Only about half the samples from the conglomerate include Lower Carboniferous conodonts. All samples show stratigraphic admixture of conodonts, mostly of Late Devonian age, but Early Devonian conodonts and rare Middle Devonian forms are also present (Buchholz and Luppold, 1990). Understandably, a Carboniferous conglomerate containing clasts of Early, Middle, and Late Devonian age should contain older conodonts, but what happens to the conodonts basinward of the conglomeratic facies?

The Frasnian and Famennian type sections in Europe appear to be no more reliable a guide to conodont distributions than are many of the American sections. The basal Frasnian zone "was originally defined in extremely condensed sequences in the Rhenish Slate Mountains, West Germany" (Klapper, 1989, p. 449), and the Frasnian-Famennian boundary in Belgium is largely a section of mixed detrital clastics and carbonates (Bouckaert et al., 1972). The type section of the Famennian Stage (Upper Devonian) in Belgium is largely detrital clastic material (see, for example, Bouckaert and Ziegler, 1965).

Conodonts that are considered younger than the age assigned to the host formation can present an awkward problem, but they are dismissed by a second working hypothesis—stratigraphic leakage (see, for example, Branson and Mehl, 1934b). Sandberg and Klapper (1967) report that Mississippian age "conodonts have infiltrated downward through cracks" into the top 2.5 cm of the Sappington Sandstone (p. B11) at one locality and have leaked downward 2 m through "hairline fractures" in a regolith at another (p. B13).

Homeomorphy and Polyphylogeny

Not all the difficulties that have arisen in application of the standard conodont sequence have been attributed to faunal mixing. "Past inconsistency in the taxonomic concepts" also "precludes direct application of the . . . standard zones" in many instances (Klapper and Lane, 1989, p. 469).

Two related "taxonomic concepts" commonly invoked by conodont specialists are homeomorphy and polyphylogeny—recurring leitmotifs in the conodont literature. Look-alike species and look-alike genera, generally referred to as homeomorphs, appear throughout the geologic column. Specialists supply these look-alikes with distinct ancestry, although some are explicitly described as morphologically indistinguishable. Homeomorphy implies that evolution has repeated itself. Polyphylogeny, on the other hand, implies that multiple ancestors (as many as three) converged to form a single species (see, for example, *Palmatolepis marginifera duplicata, P. marginifera*, and *P. quadrantinodosa quadrantinodosa* in Sandberg and Ziegler, 1973; *Bispahtodus costatus* in Ziegler et al., 1974; *Scaphignathus ziegleri* in Sandberg and Ziegler, 1979; and *Palmatolepis praetriangularis* in Ziegler and Sandberg, 1990). The similarity of conodont species is frequently tucked away in formal synonymies and cloaked in erudite terms that thwart the uninitiated.

Homeomorphy of species may be valid in instances involving multielement taxonomy. The multielement genus *Kladognathus* Rexroad has been described as an example of related species that differ only in one or two elements used to give the assemblage its specific epithet (Rexroad, 1981). In another case of multielement taxonomy, the genus *Cavusgnathus* Harris and Hollingsworth, several of the elements appear to be shared among closely related species (Brown et al., 1990). In single-element taxonomy, however, the claims of homeomorphic development are more tenuous and generally include unwarranted assumptions about intraspecific variability.

The genus *Gnathodus* Pander offers an entertaining story of homeomorphy and polyphylogeny (for a discussion of the phylogeny of the genus *Gnathodus*, see Rhodes et al., 1969). *Gnathodus commutatus* is reported in the Lower Carboniferous in Germany (Bischoff, 1957), Spain (Thompson, 1972), and Great Britain (Reynolds, 1970), and the Late Meramecian through middle Chesterian in North America (Upper Mississippian, Thompson, 1972). Branson and Mehl (1941, p. 98) noted that "this species [*G. commutatus*] is of special interest because of its similarity to the simpler gnathodids . . . It is likely that a comparable species of an earlier time gave rise to [the genus] *Gnathodus.*" *G. commutatus*, under its various generic and specific aliases, or one of its look-alikes, has also been reported from the Devonian Gassaway Member at the base of the Chattanooga Shale (Hass, 1956), and from supposedly Upper Devonian units, including the Saverton and Louisiana in Illinois and Missouri (Scott and Collinson, 1961), and the Sappington, Leatham, Pinyon Peak, and related units in Utah, Wyoming, and Montana (Sandberg, 1976).

To avoid the problem of a Mississippian genus occurring in the Devonian, Ziegler (1969) defined a new genus, *Protognathodus*. In the definition, he explains that "Die neue Gattung [*Protognathodus*] ist eine homeomorphe Vorläufer-Form der Gattung *Gnathodus*, mit ihr aber phylogenetisch nicht direkt verbunden." Ziegler therefore claims that the genus *Protognathodus* is homeomorphic with, but unrelated to, the genus *Gnathodus*. Numerous species and subspecies of the genus *Protognathodus* have been defined, redefined, combined, and otherwise offered up for examination by conodont specialists. *Gnathodus*, *Protognathodus*, and "broadly homeomorphic" Silurian forms (Rhodes and Austin, 1971, p. 342) are apparently only distinguishable by their ages although conodonts specialists have given them distinct phylogenies. Because all of these genera have been reported from numerous horizons known to contain reworked conodonts, their continued use in chronostratigraphy seems to be an act of faith.

Alberti et al. (1974) reviewed the conodont and macrofauna, information bearing on the age of the "*Protognathodus* fauna" of Ziegler (1969) and concluded that the fauna was unsatisfactory for defining the Devonian-Carboniferous boundary. Nonetheless, despite the problems of homeomorphy and polyphylogeny, the genus *Protognathodus* has been used to redefine the ranges of ammonites (the ammonite genus *Imitoceras* in the Stockum Limestone of Germany: Ziegler, 1969), and the *Protognathodus* fauna is considered an important key to the Devonian-Mississippian boundary by many specialists.

Other examples of alleged homeomorphically and polyplylogenetically derived genera abound. For example, Chauff and Klapper (1978, p. 151) consider the Late Devonian genus *Apatella* to be a possible homeomorph of the Osagean (Early Mississippian) genus *Bactrognathus*: "Despite the considerable stratigraphic gap in occurrence (Kinderhookian Series), the possibility that the two genera are of the same phyletic lineage can not be excluded, thus the homeomorphous relationship is suggested with question."

Multiple Morphotypes and Ontogenetic Development

At the opposite end of the spectrum from the problems of homeomorphy is that of intraspecific variability, generally labeled under the headings of multiple morphotypes and subspecies. Most commonly, multiple morphotypes are delineated and justified because all the morphotypes are within a single sample, whether or not the sample is known to contain reworked conodonts. Examples of both multiple morphotypes and polyphylogenitic lineages seem to be especially common from stratigraphically mixed assemblages. Many subspecies and morphotypes are named and abandoned, depending on who is doing the taxonomy.

Polygnathus inornata Branson and Mehl and *P. communis* Branson and Mehl are two examples of species containing multiple morphotypes (Scott and Collinson, 1961; Straka, 1968). *P. communis* has been described as "a characteristic Lower Mississippian fossil" (Hass, 1959, p. 390), although it has been reported from the lower Upper Devonian in Europe (Delfour and Gigot, 1985). *P. inornata* and *P. communis* have been reported from many horizons containing reworked conodonts.

Icriodus latericrescens robustus Orr, originally described from the Middle Devonian Dundee Formation of Ontario, is an example of a subspecies having three morphotypes that show "no apparent stratigraphic restrictions" (Uyeno et al., 1982, p. 32). The Dundee shows signs of subaerial exposure and reworking, and, not surprisingly, "yielded the most diverse conodont fauna of any unit in the Devonian of southwestern Ontario" (Uyeno et al., 1982, p. 17).

Siphonodella sulcata and *Siphonodella praesulcata* present an even more disturbing problem, primarily because the change from *S. praesulcata* to *S. sulcata* is the golden spike for the Devonian-Mississippian boundary (Sandberg et al., 1972, 1978), a convention followed by most conodont specialists. In their definition of *Siphonodella praesulcata*, Sandberg et al. (1972, p. 19) state: "The great differences in shape, length, and ornamentation of the platform of *Siphonodella praesulcata* n. sp. appear to be intraspecific, because they occur within single collections, no two individuals of which bear entirely the same characteristic. . . . *Siphonodella praesulcata* n. sp. closely resembles *S. sulcata*, and transitional forms, which are difficult to assign, have been observed."

All the units from North America from which Sandberg, Streel, and Scott's collections were derived have been discussed earlier, including the Sappington, the Cottonwood Canyon, the Leatham, the "Glen Park" (and a "pre-'Glen Park' regolith"), the basal Hannibal, and the New Albany. We have already alluded to problems with the upper Famennian. *S. sulcata* is also reported from the Hangenberg Limestone in Germany (Klapper's 1963 resampling of Voges' (1959) localities, cited in Sandberg and Klapper, 1967; also Ziegler, 1969, who cites Sandberg and Klapper, 1967), which is a mixed limestone and detrital clastic section (Voges, 1959). The problems of multiple morphotypes of *S. sulcata* is compounded by Sandberg et al.'s (1972) identification of a specimen called *S. sulcata* by Canis (1968) as a gerontic form.

Pseudopaleontologic Dating: The Myth of the Golden Spike

Siphonodella is considered to be a "characteristic Mississippian genus" (Hass, 1947, p. 137) that "has not been noted in strata older or younger than the Kinderhook" (Branson and Mehl, 1934b, p. 295) and is "perhaps the most distinctive 'Early' Carboniferous genus in North America, Germany, and elsewhere" (Rhodes and Austin, 1971, p. 330). *Polygnathus plana*, described by Huddle (1934) from the New Albany Shale in southern Indiana and reported from the base of the Upper Devonian in Germany by Bischoff and Ziegler (1956), however, has been synonomized by Rexroad (1969) with *S. duplicata*, the type species of the genus.

Siphonodella sulcata, the golden spike for the Devonian-Mississippian boundary, is not without problems. It occurs rarely and generally with reworked conodonts. Huddle (1934) reported a single broken specimen of *S. sulcata* (*Polygnathus sulcata*) from the upper part of the New Albany at Rockford, Indiana. Hass (1959) reported one broken specimen from the Chappel Limestone of Texas (reported as *Siphonodella duplicata* according to Canis, 1968). Boogaert (1967) reported a single broken specimen of *S. sulcata* from the Devonian and Lower Carboniferous of the Cantabrian Mountains, Spain, and two specimens of *Siphonodella*? n. sp. a, which were from a sample containing reworked fauna. Boogaert (1967, p. 186) suggested "it is very probable that *S.*? n.

sp. a . . . is also reworked." One of the highest concentrations of *S. sulcata* (23 specimens) reported is from a lag deposit in the Cottonwood Canyon (Sandberg and Klapper, 1967, p. B51). The lag deposits of the Cottonwood Canyon "are characterized by abundant conodonts; fish plates, teeth, bones, and scales; glauconite grains; phosphatic coprolites, nodules, and pellets; large quartz sand grains and granules; and granules, pebbles, and cobbles derived from the underlying rocks" (p. B29).

Paproth and Streel (1984, p. 256), discussing the absence of specimens transitional between *S. praesulcata* and *S. sulcata* at the type boundary locality, quote Sandberg and Ziegler (1984): "'a brief eustatic fall in sea level' occurred just before the first entry of *S. sulcata* and that the 'short stratigraphic interval wherein the pelagic siphonodella biofacies is interrupted' might be recognized by a shallower protognathodid biofacies, characterized by *Pr. kockeli* (the lower *Protognathodus* Fauna)."

DISCUSSION

All the tales of homeomorphs, heterochronic homeomorphy, polyphylogeny, stratigraphic leakage, subspeciation, ontogeny, and intraspecific variability provide colorful reading. More than that, however, they provide a clue to the truth. All these tales point toward a single cause: reworking of conodonts.

Many species, especially the platform elements, have been reported somewhere in the geologic literature as having been reworked or as occurring with reworked forms. The common occurrence of reworked specimens near the Devonian-Carboniferous boundary is relatively simple to explain. The Late Devonian and Early Mississippian was generally a time of orogenesis along all of the North American margins and in northern Europe. Orogenesis was accompanied by erosion and sedimentation.

Furthermore, conodonts are frequently sampled from units in which they have been hydraulically concentrated for obvious reasons: limestones may require tens of kilograms of sample to produce a reasonable number of conodonts. Naturally occurring concentrates, on the other hand, can provide hundreds or thousands of individuals from a small sample (see, for example Sandberg and Klapper, 1967; Sandberg and Ziegler, 1973). Multielement taxonomic analysis of conodonts suggest that conodont assemblages contain four to eight bars and blades and only one or two platform elements. Conodont suites that deviate from the ratio of elements established using recurring natural assemblages undoubtedly represent a hydraulically sorted population. One rule of thumb for recognizing reworked conodont suites has been proposed: a suite that contains 60-80 percent platform elements probably represent a hydraulically concentrated sample (Ellison, 1987). Even this estimate is probably too high.

Information Loss

When a mixed population from a lag concentrate is treated as a representative time slice, a great deal of evolutionary development is packed into a single species under the label of intraspecific variability. Intraspecific variability is commonly assumed simply because all specimens were derived from a single sample. Incorrect interpretation of intraspecific variability can mask evolutionary development and results in a loss of stratigraphic information.

Further loss of information also occurs when reworking of specimens during erosional intervals is incorrectly interpreted. Reworking of conodonts at higher levels in the geologic column can lead to extension of species ranges and, at least in some instances, to apparent repetition of evolution cloaked in the guise of homeomorphy. The potential of conodonts for the study of erosional history is unique in the sedimentary record. Just as a zircon or another radiometrically datable heavy mineral grain can provide useful information about sources of clastic material and timing of tectonic events, so too, could conodonts provide information on source areas and uplifts. Much of the previous application of conodonts, however, has precluded this potentially important avenue of investigation.

Information Gain

From a geologic perspective, as important as the loss of information caused by the study of mixed faunal populations is the gain of meaningless information, which comes in many forms. One is a misconception of the amount of geologic time represented by the rock record. Conodont assemblages embodied in the "Standard Zonation" may be recognized within lag deposits, which produces phantom zones that expand the apparent time represented by a rock interval and represent clastic provenance and hydraulic sorting rather than time. Workers commonly cannot agree on the number of zones in a section. One such example is the upper *Bispathodus costatus* through *Siphonodella sandbergi* Zones in the Pinyon Peak Limestone and the Fitchville Formation, Late Devonian-Early Mississippian in Utah, zones that may or may not be present (compare Gosney, 1982, with Sandberg and Poole, 1977).

Phantom zones have greatly influenced the geologic interpretation of Paleozoic rocks throughout North America. Examples include the Deseret basin in the eastern Great Basin and the Borden basin in the Illinois basin. Nichols and Silberling (1990) demonstrated that the relative numbers of different kinds of conodonts used to calibrate the conodont deep-basin biofacies in the eastern Great Basin are a function of dissolution of limestones and consequent concentration of insoluble elements, including conodonts. Macke (1991) questioned the conodont-based interpretation of rapid subsidence in the Illinois basin postulated by earlier workers. These postulated starved basins and events of rapid crustal subsidence necessary to form them have been based largely on conodont biostratigraphy applied to rocks containing reworked assemblages. As such, and lacking any other reasonable corroborative evidence, we conclude that these deep basins are part of the myth that surrounds conodont biostratigraphy and are unreasonable in light of more substantiative geologic evidence.

Mixed conodont assemblages can also produce phantom thermal maturities. Because conodonts in mixed assemblages represent the thermal maturity of the source rocks rather than of the host sediments, a variation in CAI should be one of the hallmarks of stratigraphic admixtures. Interpretation of the thermal maturity, therefore, depends on the conodonts having been thermally altered within the host sediments and not within older formations from which they were derived.

Many geologists feel a certain uneasiness when faced with a list of italicized Latin names, especially for fossils that cannot be readily studied, even with a hand lens, and that are present only as fragments in the rocks. This uneasiness has frequently given way to blind faith in the conodont specialists. Reviewing the literature on conodonts suggests that the uneasiness is justified. Many conodont studies seem unconstrained by the geology of the host formations and buck the common sense we acquired in our biology and paleontology classes. Conodonts must be viewed primarily as heavy mineral grains and secondarily as fossils. Conodont studies graphically illustrate the assertion of Keyes (1912, p. 156) that "In the delimitation of geologic formations" too much weight has been placed on "the occurrences of a fauna" and not enough weight has been placed "on the stratigraphic evidence of a well-marked unconformity."

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PALEOECOLOGY OF THE LATE TRIASSIC EXTINCTION EVENT IN SOUTHWEST BRITAIN

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A high-resolution paleoecological study of the shelly invertebrate macrofauna across two marine Triassic/Jurassic boundary sections in the United Kingdom (St Audrie's Bay, southwest England; Lavernock Point, south Wales) is presented, utilizing a sampling and study regime designed to control for lithofacies and paleoenvironmental biases. Analyses fail to reveal convincing evidence of a catastrophic marine extinction event. Instead, the Late Triassic crisis in southwest Britain appears to be expressed in outcrop as a small-scale turnover event. There is, however, good evidence for significant paleoecological change in the marine ecosystem at this time. The immediate post-event recovery interval is characterized by assemblages of low abundance, low diversity, high dominance and low evenness that persisted for approximately one ammonite subzone, and animals of small body size for approximately one ammonite zone. Benthic paleoecological recovery was disrupted by an episode of anoxia. The pattern of body-size changes recorded in the shelly macrofauna closely matches that of the trace fossil record. Trends in shell thickness do not support the presence of a biocalcification crisis during the Late Triassic biotic turnover.

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TRIASSIC PALEOGEOGRAPHIC AND TECTONIC EVOLUTION OF SOUTHWESTERN LAURENTIA THROUGH JURASSIC TECTONIC OVERPRINT

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The undeformed to broadly folded Triassic and Jurassic stratigraphy of the Great Plains and Laramide broken foreland of the western North American craton belie the increasingly complex task of reassembling the Triassic paleogoeography and tectonic evolution of the Cordilleran margin. Indeed, the location and configuration of the western margin of the Triassic North American craton remain obscure. From the leading eastern edge of the Cretaceous Sevier fold and thrust belt westward, the reassembly of Triassic paleogeography and tectonic evolution becomes increasingly clouded by Cenozoic extension and volcanism, Cretaceous contraction and plutonism, and poorly understood Jurassic contraction, extension, and large-scale translation. Across much of the Basin and Range, outcrops of Triassic and Jurassic rocks decrease in number and become widely separated. The Early Mesozoic Marine Province of west-central Nevada and adjacent parts of California is a collage of structurally bounded stratigraphic assemblages of lower Mesozoic rocks, each displaying different stratigraphic successions and tectonic histories. Spatial relations of these terranes among each other and to the craton prior to arriving in their present configuration, and the timing of their accretion to the North American craton remain controversial. The site of origin, timing and magnitude of displacement, and time of accretion of suspect terranes, which lie within or west of the batholithic belt, become increasingly obscure.

A first approximation of pre-Cretaceous geology is obtained by: 1) removing the relatively small amount of Cenozoic extensional deformation north of the Great Basin and Snake River Plain (western Montana and Idaho) and east of the Idaho Batholith; 2) balancing cross sections to restore the Idaho batholith to its pre-Cretaceous site of origin; and 3) aligning the Sierra Nevada and Coast Range batholiths with the restored site of origin of the Idaho batholith. The pre-Cretaceous distribution of Triassic rocks in the Basin and Range, extending from northern Nevada to Sonora, Mexico, is, in the main, controlled by: 1) the distribution of middle Early Jurassic normal faults; 2) obduction of island arc and cratonal margin rocks onto the craton in the late Early to early Middle Jurassic; and 3) 1,000 to 1,5000 km of left-lateral displacement of North America relative to Triassic rocks of southwestern Laurentia.

Removal of the Jurassic tectonic overprint reveals a Triassic paleogeography with a prominent reentrant centering on western Wyoming and southeastern Idaho. Two nearly right-angle bends turned the margin westward across what is now northern and west-central Nevada and central California. The westward extent of the southwestern margin of Laurentia is unknown. This reentrant in the cratonal margin served as a prominent sediment sink throughout the Middle and Late Triassic. The prominent unconformity separating the Permian and Triassic systems does not appear to be related to a tectonic event but resulted from the latest Permian to Permo-Triassic drawdown in global sea level. The tectonic framework in which the Triassic System of the Cordillera was deposited was established with the Mid-Permian depositional overlap of the Early Permian Sonoman orogeny. Within this framework, the Triassic System of southwestern North American is divisible into five tectonosequences, the Lower Triassic Moenkopi; lower Middle Triassic Holbrook; the upper Middle to lower Upper Triassic Panther Canyon; the Upper Triassic Chinle; and the Upper Triassic to Lower Jurassic Dinosaur Canyon. These tectonosequences provide a high resolution record of five paleogeographic time slices, which document Triassic tectonic evolution of southwestern Laurentia.

1.) Lowest Moenkopi tectonosequence deposition was restricted to the extensional reentrant in the Triassic Cordilleran cratonal margin. The reconstructed Moenkopi tectonosequence displays a passive-margin-like stratigraphic architecture, which overlaps extensional structures. Recovery from Panthalassan anoxia is recorded within the Moenkopi tectonosequence.

2.) The Holbrook tectonosequence records a dramatic change in paleoslope from east to west in the Moenkopi tectonosequence to south to northwest in the Holbrook tectonosequence. The change in plaeoslope evidences creation of a cryptic active margin across southern Laurentia.

3.) Within the collage of terranes in the Early Mesozoic Marine Province, the Panther Canyon tectonosequence or younger rocks rest on thick successions of upper Paleozoic and lower Mesozoic rocks dominated by thick accumulations of volcanic rocks and boulder conglomerates, with lesser thicknesses of sedimentary rocks that contrast markedly with overlying unconformity-bounded sequences of marine-shelf facies correlative and lithofacies having affinities with the Panther Canyon, Chinle, Dinosaur Canyon, and Jurassic Glen Canyon tectonosequences. These relationships document Ladinian south to southeastward accretion to the craton and depositional overlap of the allochthonous terranes during deposition of the Panther Canyon tectonosequence. The pre-accretion location of allochthonous terrains is unknown.

East and southeast of the Early Mesozoic Marine Province, pre-Chinle tectonosequence erosion removed all but the lowest part of the Middle Triassic Series – lower Holbrook tectonosequence - from the western craton.

4.) The voluminous volcanogenic sediment in the Chinle tectonosequence was transported northwestward and northward from a volcanic source, which exposed crystalline basement. The volcanic source extended from at least eastern Chihuahua, Mexico to the present Gulf of California. Absence of evidence of a western source of volcanic rocks precludes the Upper Triassic volcanic Koip Group from having occupied a location along the present Sierra Nevada crest during the Late Triassic. Rather, the Koip arc appears to have been accreted to the craton during late Early to early Middle Jurassic obduction.

The active-margin source of sediment which lay along the southern boundary of Laurentia from initiation of the Holbrook tectonosequence to the close of the Chinle tectonosequence has not been identified. It appears to have been rifted from the southern margin of Laurentia at the close of the Triassic.

5.) The Dinosaur Canyon tectonosequence, which contains the Triassic–Jurassic boundary, was deposited during a magmatic null marking the major plate rearrangement from the configuration that dominated Middle and Late Triassic time to the continental-margin-arc configuration that has persisted from the Early Jurassic to the present.

The preceding overview begs the following speculations on the site of origin, timing of translation, and final accretion of Wrangellia and related terranes. The interpreted paleolatitude and collective Triassic stratigraphy of these terranes is compatible with the stratigraphy envisioned for the missing Middle to Late Triassic source terranes of the Holbrook and Chinle tectonosequences along the cryptic active margin of south westerern Laurentia. Pre-Jurassic rifting of these terranes from the Laurentian craton during Dinosaur Canyon plate rearrangement preserves the Triassic stratigraphy intact. Unfortunately, the paleobio-geography implies one or more pre-rifting, trans-Pangean Tethyan connections. Limited paleobiogeographic and paleomagnetic evidence suggest displacement during the large-scale, middle Early Jurassic right-lateral translation and contemporaneous transtensional(?) normal faults. Accretion coincided with the postulated late Early to early Middle Jurassic obduction event prior to large-scale, left-lateral translation.

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THE SEQUENCE-STRATIGRAPHIC SETTING OF THE TRIASSIC-JURASSIC BOUNDARY, NEW YORK CANYON, GABBS VALLEY RANGE, WESTERN NEVADA

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The Triassic–Jurassic boundary in the stratigraphic section at New York Canyon resides within a single tectonosequence generated by a short-lived tectonic disturbance, a major plate rearrangement involving the southern and western margins of Laurentia. The lower sequence boundary is overlain by the Gabbs Formation, whose base is early Rhaetian (*Amoenum* zone). The location of the upper sequence boundary at New York Canyon is ambiguous. Two surfaces in the overlying Ferguson Hill Member of the Sunrise Formation potentially may be the upper boundary; one lies near the base, and the other in the middle, of the Ferguson Hill Member. However, the same tectonosequence is observed at El Antimonio, Sonora, Mexico. The biostratigraphic age control on the upper surface of the tectonosequence at El Antimonio implies that the upper sequence boundary is late Hettangian (*Sunrisense* zone), therefore the upper surface at New York Canyon is the surface near the base of the Ferguson Hill Member. The stacking pattern of lower shoreface to intertidal facies associations within the sequence in New York Canyon are interpreted to indicate that the Triassic – Jurassic boundary lies within the highstand systems tract. The Triassic – Jurassic boundary tectonosequence of marine strata at New York Canyon is also manifest in non-marine strata of the Dinosaur Canyon and Whitmore Point members of the Moenave Formation on the Colorado Plateau in southern Utah where this sequence has been defined as the Dinosaur Canyon tectonosequence. The sequence boundaries of the Dinosaur Canyon tectonosequence are synonymous with the boundaries of the Apachaen land vertebrate faunachron. Pollen from the upper part of the Dinosaur Canyon tectonosequence indicates an early to late Hettangian age. Magnetostratigraphy throughout strata included within the tectonosequence indicates normal polarity of the geomagnetic field. These observations indicate the Triassic–Jurassic boundary is located within the Dinosaur Canyon tectonosequence. Therefore, the stratigraphic section at New York Canyon can be correlated with sections containing the magnetostratigraphic, palynological, and vertebrate records of this time.

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DIVERSITY DYNAMICS AND EVOLUTIONARY ECOLOGY OF MIDDLE AND LATE TRIASSIC HALOBIID AND MONOTID BIVALVES

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Middle and Late Triassic halobiid and monotid bivalves represent an ecologically similar group belonging to two separate clades: the Halobiidae (Order Pterioida) and the Monotidae (Order Pectinoida). A significant attribute shared between these groups is their persistent occurrence in monospecific or paucispecific shell accumulations that are frequently found in deep-water, and in many cases oxygen deficient, marine settings. Approximate age durations of species are comparable to typical ammonoids and/or conodont zones during the Triassic and in some instances have temporal resolutions demonstrably shorter, making them among the best macroinvertebrate biochronologic indexes of the Middle and Upper Triassic.

Diversity metrics including species richness, raw and per-taxon rates of origination and extinction and taxic turnover and volatility were determined for *Daonella s.l.*, *Halobia s.l.*, *Monotis s.l.* for the Middle and Late Triassic. Approximately 45 species of *Daonella* are known and have temporal durations typically confined to one or two ammonoid zones and the per-genus volatility rate is high (v = 0.32). *Daonella* species richness is bimodal with a strongest peak (14 species) in the upper Anisian and the second and lesser peak during the middle part of the upper Ladinian (Gredleri zone). The lower Ladinian has the fewest species, when high extinction and origination result in essentially complete turnover at the Anisian/Ladinian boundary and again in the early part of the upper Ladinian. *Halobia* is species rich (slightly more than 60 valid species are known) and is less volatile (v = 0.17) than *Daonella* and monotids. *Halobia* diversity remains relatively low during the lower Carnian (< 10 species) rising to just under 15 species by the end of the stage (Macrolobatus zone). *Halobia* diversity peaks in the lower Norian (about 17 species) and remains relatively high until the middle Norian (Columbianus I zone) with a few species co-occurring with *Eomonotis* in the upper middle Norian (Columbianus II zone). *Monotis s.l.* is highly volatile (v = 0.25), including approximately 30 well-established species of which 12 *Eomonotis* are known from the middle Norian. A nearly complete turnover occurs between middle and upper Norian. *Monotis s.s.* achieves a diversity peak of approximately 16 species in the uppermost Norian (Cordilleranus zone) and is followed by near complete extinction at the Norian/Rhaetian boundary. At least two dwarfed *Monotis* species are known to occur in the Rhaetian (Misikella posthernsteini zone).

Halobiid and monotid species richness, extinction and origination, turnover may be related to short-term changes in the physical marine setting and in turn were driven by high within-species genetic diversity, Sea-level changes are not correlated with origination or extinction patterns, and, except for the Norian/Rhaetian boundary where high extinction rates coincide with a positive $\delta^{13}C$ excursion, turnover peaks are not correlated with known fluctuations in the global carbon cycle. Instead, their high turnover and occurrence in dense shell beds is best explained by population instability along oxygen deficient gradients. A model involving initial colonization and substrate dominance and subsequent local disappearance. Metapopulations of sister and sibling species are replaced without competition in subsequent threshold conditions. It is hypothesized that halobiid and monotid bivalve metapopulations were controlled by rapid fluctuations in environmental conditions that would tend to favor eurytopic species with high genetic diversity and exhibit higher evolutionary turnover rates.

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CALIBRATION OF EARLY AND MIDDLE TRIASSIC TIME SCALES USING ORBITAL-CLIMATE CYCLES

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During the last decades, the time-relationship between the Early, Middle and Late Triassic epochs changed dramatically. Starting with an assumed relationship of 10:10:12.5 my (Harland et al., 1964), recently the well based relationship is about 5:10: 35 my. Duration of stages within the Early and Middle Triassic has varied significantly in publications of 1987 through 2007: Induan (Indusian) 1–6 my, Olenekian 3.1–5 my, Anisian 1.6–8 my, and Ladinian 3–9 my. The stabilization of stage definitions by GSSPs, attainment of higher analytical precision on radio-isotopic age determinations on tuffs, recognition of climatic cycles recorded in the sedimentary record that are induced by periodic orbital changes (Milankovitch cycles), and the integration of these elements using biostratigraphic and magnetostratigraphic correlations leads to a more precise numerical time scale. There is a systematic offset of ~ 1.5 my between single and multigrain U-Pb ages from the Late Permian to the Middle Triassic (Menning et al., in prep.), therefore our calibrations for all stage boundaries rely on single-grain results.

We focus on cycles as time indicators from the Germanic Triassic, particularly from the Buntsandstein (s) and Muschelkalk (m), which are completely developed in the migrating center of the Central European Basin. Extending the cycle-stratigraphy into the Late Triassic is uncertain, because recent estimates of a ~ 35-my duration for that epoch imply that the lithostratigraphic units of Central Europe are probably punctuated with gaps of uncertain duration.

The base of the Triassic at the GSSP in Meishan, South China is synchronous with the First Occurrence Datum (FOD) of the conodont *Hindeodus parvus* (Yin et al., 2001). Single-grain ID-TIMS ages for beds 25 and 28 constrain the Permian-Triassic boundary (PTB, Bed 27c) as ~ 252.5 Ma (Mundil et al., 2001, 2004; Menning et al., 2005). Following Kozur (1999), the PTB in Central Europe is within the small-scale cycle s1.2, which allocates an age of ~ 252.6 Ma to the Zechstein-Buntsandstein boundary. This anchor point has been used to age-calibrate the Regional Stratigraphic Scale (RSS) of Central Europe to durations derived from orbital-climatically induced cycles (Menning et al., 2005).

The Buntsandstein contains ~ 60 small-scale cycles obtained by Szurlies, who applied magnetostratigraphy to prepare a regional framework (Szurlies et al., 2003; Szurlies, in Menning et al., 2005). These cycles appear to be associated with climatic changes induced by the 100 ky eccentricity cycle acting on precession. Therefore, the Buntsandstein has a duration of ~ 6 my (Szurlies, in Menning et al., 2005) and spans ~ 252.6 Ma to 246.6 Ma. These Buntsandstein cycles are grouped into 7 Folgen, which are bounded by quasi-isochronous boundary planes: Calvörde-Folge (s1: s1.1–s1.10, ~ 1 my), Bernburg-Folge (s2: s2.1–s2.10, ~ 1 my), Volpriehausen-Folge (s3: s3.1–s3.12, ~ 1.2 my), Detfurth-Folge (s4: s4.1–s4.4, ~ 0.4 my), Hardegsen-Folge (s5: s5.1–s5.12, ~ 1.2 my), Solling-Folge (s6: s6.1–s6.4, ~ 0.4 my), and Röt-Folge (s7: s7.1–s7.8, ~ 0.8 my).

The Early Muschelkalk contains ~ 20 small-scale cycles (m1: m1.1–m1.9, m2: m2.1–m2.5, m3: m3.1–m3.6), the Middle Muschelkalk contains ~ 12 (m4: m4.1–m4.2, m5: m5.1–m5.8, m6: m6.1–m6.2) and the Late Muschelkalk has ~ 34 (m7: m7.1–m7.14, m8: m8.1–m8.8, m9: m9.1–m9.12) (Hagdorn et al., in Menning et al., 2005). These imply a total Muschelkalk duration of ~ 6.4 my, and a span from ~ 246.6 to 240.2 Ma.

According to magnetostratigraphic and biostratigraphic evidence, the base of the Olenekian (FOD of *Neospathodus waageni*) is at about the boundary of cycles s2.6-s2.7, the base of the Anisian (*Chiosella timorensis*) is at about the boundary of Folgen s6-s7, and the base of the Ladinian (*Eoprotrachyceras curionii*) is in the early Folge m9. Applying this cycle stratigraphy projects the durations of these Early and Middle Triassic stages as: Induan (Indusian) ~ 1.5 my, Olenekian ~ 3.6 my, Anisian ~ 6.4 my, and Ladinian ~ 4 my (Menning et al., 2005). More radio-isotopic age determinations, including using the methods Rb-Sr on clays and Re-Os on black shales, are necessary to check and confirm these estimations.

The durations of ~ 6.0 my for the Buntsandstein and ~ 6.4 my for the Muschelkalk are shorter than in previous publications. However, they are consistent with: a) radio-isotopic ages within the Changhsingian, Induan (Indusian), Olenekian, Anisian and Ladinian stages in China, Alps and Hungary (Menning et al. in prep.), b) the duration of magnetic zones (Szurlies et al., 2003; Szurlies, 2004; Menning et al., 2005), which corresponds to that of the Late Cenozoic, c) a very long Late Triassic Epoch deduced from Milankovich-cycles from the Newark Basin (Olsen & Kent, 1999), and d) radio-isotopic ages for the Triassic-Jurassic boundary of ~ 202–200 Ma (Dunning & Hodych, 1990; Pálfy et al., 2000).

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NEW CONSTRAINTS FOR THE LADINIAN-CARNIAN BOUNDARY IN THE SOUTHERN ALPS: SUGGESTIONS FOR GLOBAL CORRELATIONS

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INTRODUCTION

The Ladinian-Carnian boundary interval is represented in many localities of the Southern Alps (Northern Italy) by continuous and expanded basinal successions. The boundary interval is best exposed in Badia and Cordevole valleys (Dolomites); there, the Stuores Wiesen section has been indicated as a possible GSSP site for the Carnian stage (Broglio Loriga et al., 1999). The purpose of this study is to critically review the potential of Stuores Wiesen as a GSSP candidate, in the light of new data and interpretations that have arisen in the last eight years (e.g., Manco et al., 2004; Mietto et al., 2004).

GEOLOGICAL AND STRATIGRAPHIC SETTING

The Late Ladinian-Early Carnian sedimentation of the Dolomites is characterized by the growth and progradation of carbonate platforms on small, connected and articulated basins several hundred meters deep (Bosellini et al., 2003). The dismantling of volcanic edifices in the Dolomites (e.g., Predazzo) or in adjacent regions provided an abundant and continuous supply of volcanic arenites and clays. Active growth of platforms shed abundant carbonates into the basins during the Early Carnian.

This continuous supply of carbonate and terrigenous materials led to constantly high sedimentation rates, and guaranteed the expansion and continuity of stratigraphic series. The Ladinian-Carnian boundary interval in the Badia Valley is represented, in the basinal series, by the Wengen/La Valle and San Cassiano formations.

The Wengen/La Valle Formation is a flysch-like succession of turbiditic arenites, siltites and shales, organized in a long-term fining upward trend. A conglomeratic unit (Conglomerato della Marmolada) is present at its base. Calciturbidites or carbonate olistoliths and/or olistostromes are also present, and are thought to derive from the erosion of a subaerially exposed Ladinian carbonate platform or from local fringing reefs.

Above the Wengen/La Valle Formation lies the San Cassiano Formation, constituted by shales, marls, micritic limestones and fine to coarse calciturbidites, including oolites. The carbonate content of the San Cassiano Formation derives from the active growth of mostly prograding carbonate platforms (Cassian platforms 1 and 2).

STUDIED STRATIGRAPHIC SECTIONS

Being the most complete and thoroughly studied section of the Badia and Cordevole valleys area (Fig. 1), the Stuores Wiesen section is the natural choice as candidate for the GSSP of the Carnian stage (Fig. 2). The section is located at Pralongià, a few km south of the village of San Cassiano, in the high Cordevole Valley, and is accessible from the village of Corvara by chair-lift and an easy walk in less than one hour. It consists of a ca. 220-m-long composite succession encompassing the La Valle and San Cassiano formations (Fig. 3).

Other sections have been selected in the type area to better illustrate the faunal changes in the boundary interval. The Antersass section is located on the northern flank of Gardenaccia, south of the village of Longiarù in the middle Badia Valley. This section is totally within the San Cassiano Fm. and is noticeable for the abundance of fairly well preserved ammonoids. It contains the best record of the boundary between the *canadensis* and the *aon* subzones (Fig. 4).

The Bec de Roces section is located on the eastern flank of the Sella massif, near Passo Campolongo at the head of Cordevole Valley. It is a short section within the lower San Cassiano Fm. that best illustrates the ammonoid associations typical of the *canadensis* Subzone (Fig. 5).

Other stratigraphic sections of the Badia Valley or surroundings (Col da Oi, Passo Gardena, Passo Sella) have also been studied in the past years. Descriptions of these localities may be found in the literature (Mietto and Manfrin, 1995a, b).

MAGNETO-, CHEMO-, AND SEQUENCE STRATIGRAPHY

The magnetostratigraphic setting has not been modified after Broglio Loriga et al. (1999). The correlation with the coeval Mayerling section (Gallet et al., 1998, fig. 10) by comparison of magnetostratigraphic data and the vertical distribution of conodont taxa proposed at that time has been further confirmed by the new find of the conodont *Paragondolella polygnathiformis noah* (Hayashi) 70 cm above the first occurrence of *Daxatina canadensis* (Whiteaves). Stable C and O isotope investigations are still in process at the University of Innsbruck and will be reported soon.

The sequence stratigraphic framework is the same presented in Broglio Loriga et al. (1999) across the proposed boundary as well as its global correlation. The boundary is placed at the beginning of the regressive trend just after the Car 1 maximum flooding surface (sensu Gianolla et al., 1998) in a section presenting very high sedimentation rates (Gianolla, 1995). The mfs is one of the best traceable surfaces for basin-wide correlation. Thus the potential for correlation of the proposed boundary is enhanced by sequence stratigraphic interpretation, especially with sections characterized by lower sedimentation rates.

BIOSTRATIGRAPHY

Ammonoids

The taxonomic revision of the ammonoids from the Stuores Wiesen section and the joint studies of a rich fauna recovered at the Antersass and Bec de Roces sections and surroundings allow us to delineate better the faunal association of the *canadensis* Subzone from the Southern Alps, and to recognize those taxa which are useful to correlate different paleobiogeographic domains.

With reference to previous data (Mietto and Manfrin, 1995a, b; Broglio Loriga et al., 1999), the most important observations, chiefly new, regard the following taxa:

a) genus *Daxatina*: the comparison of Southern Alps specimens belonging to genus *Daxatina* with type materials from Canada (courtesy of M. Balini), demonstrates that *Daxatina canadensis* (Witheaves) occurs, indeed, in the Southern Alps. Thus, the previous *Daxatina* cf. *canadensis* Subzone should now be considered as *canadensis* Subzone, whose base coincides with the FAD of the index species. Among the material from the Stuores Wiesen section, another *Daxatina* species is present. Moreover, from the debris of the Antersass section, a specimen comparable with the Canadian species *Daxatina laubei* Tozer has been collected.

b) genus *Frankites*: a further paleontological study of the species

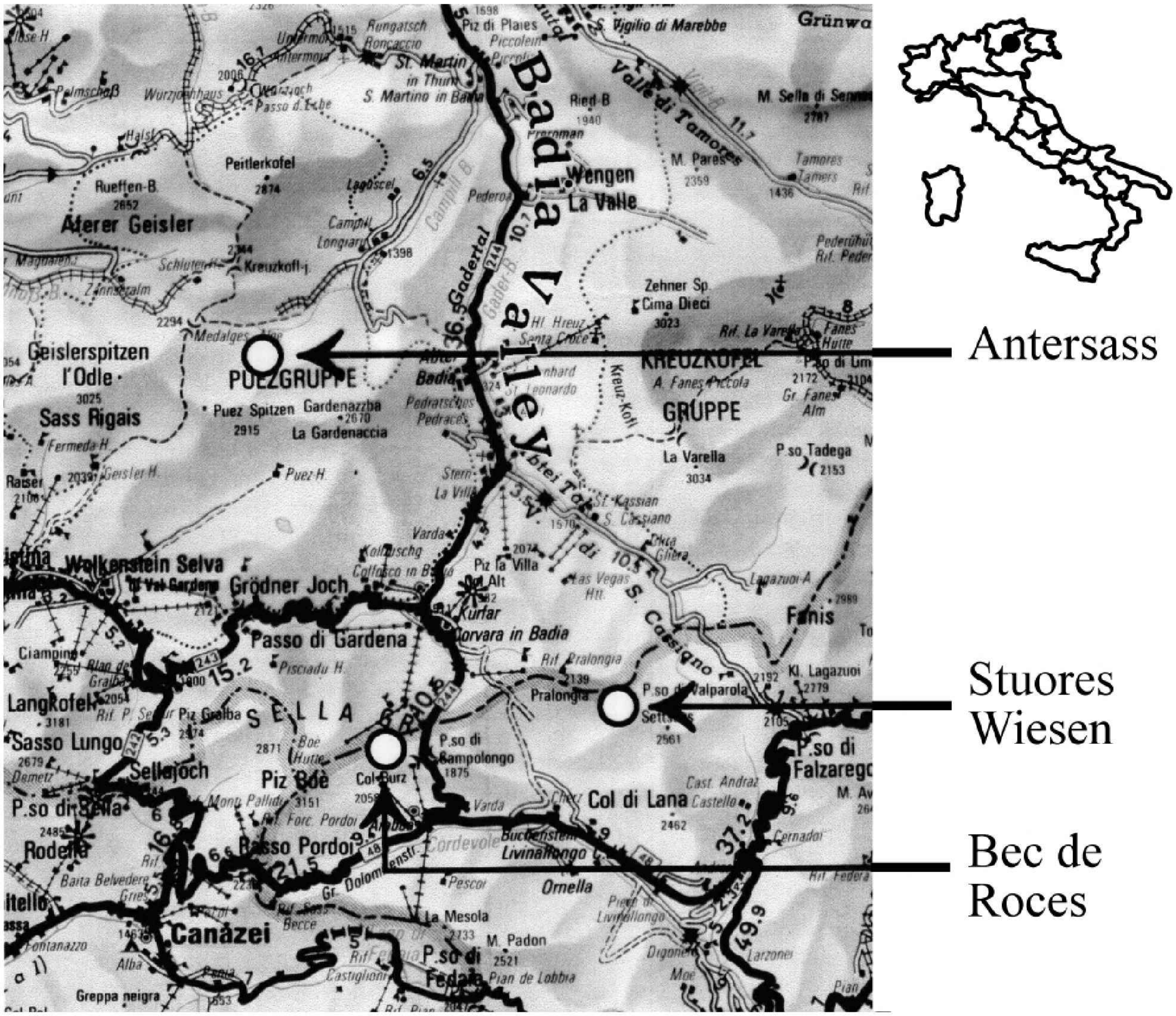

FIGURE 1. Sketch map of the studied area.

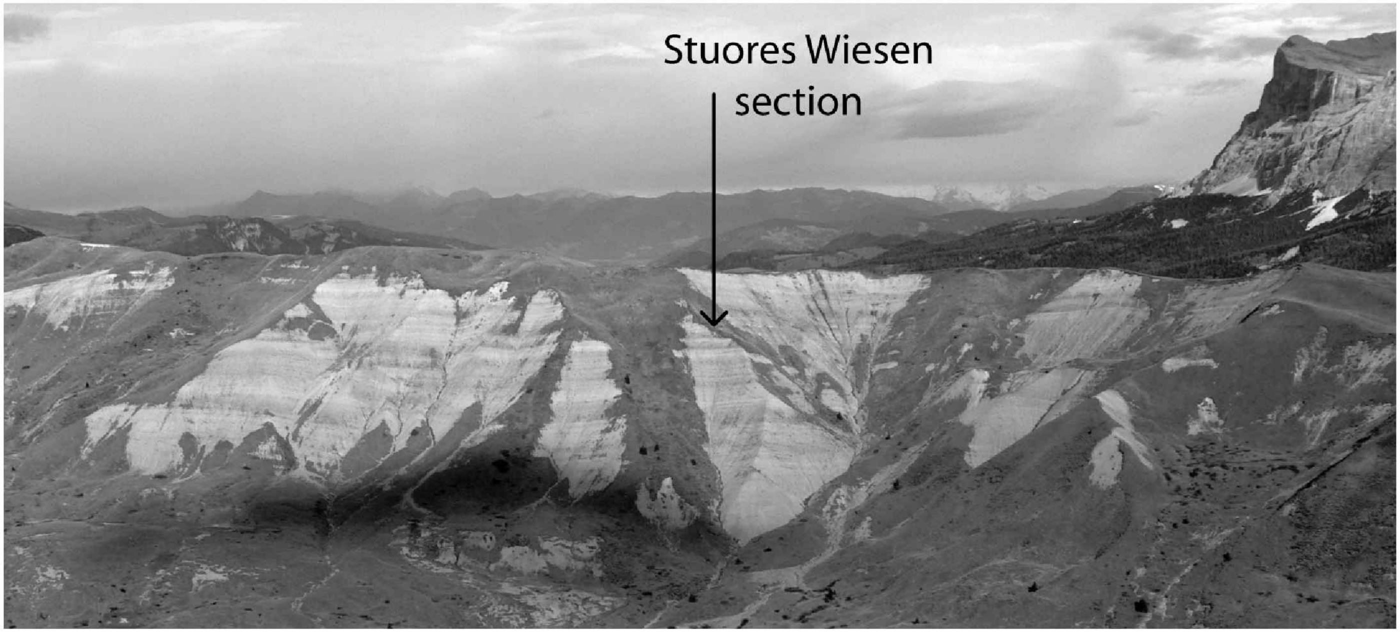

FIGURE 2. Panoramic view of the Stuores Wiesen section.

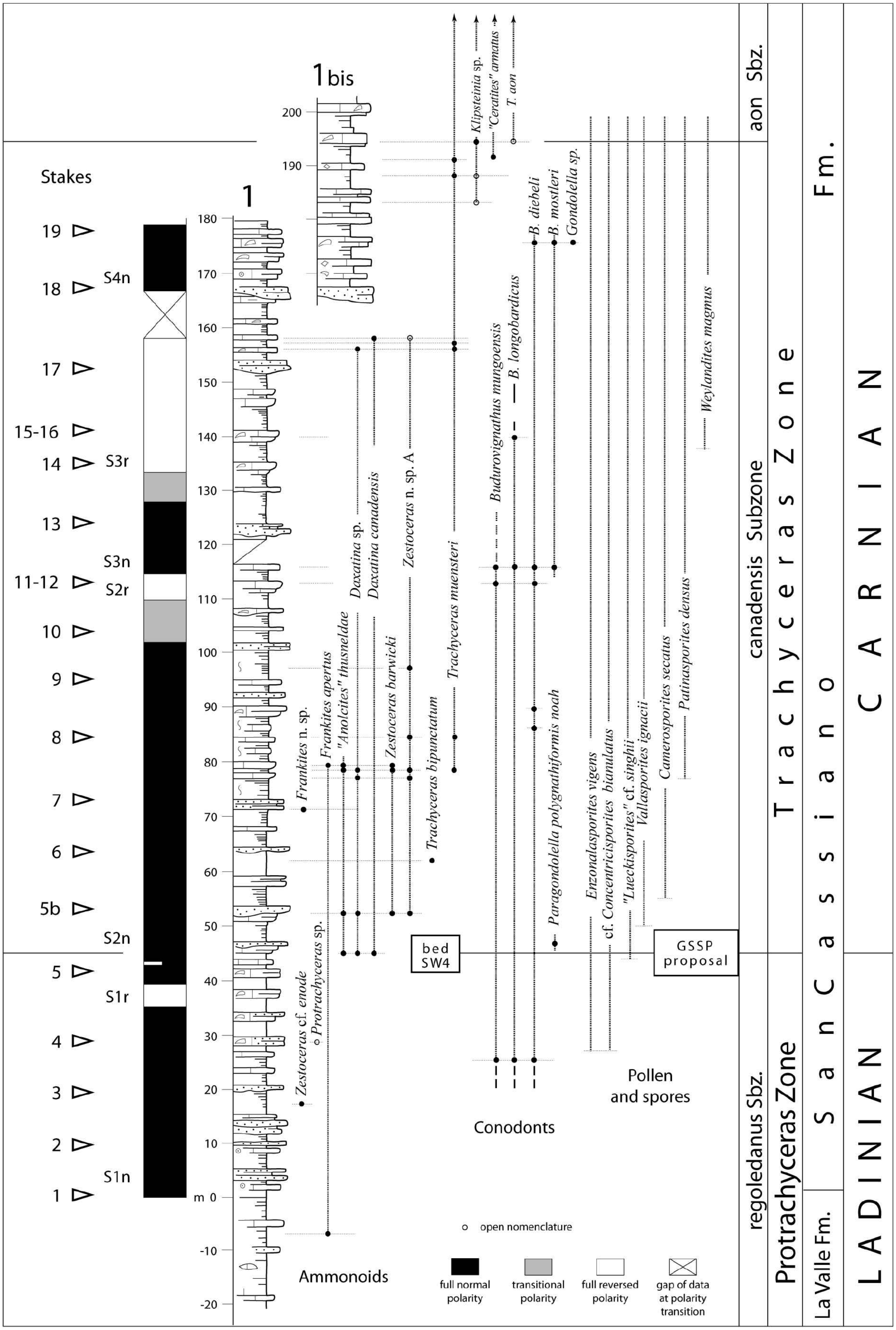

FIGURE 3. Stuores Wiesen section.

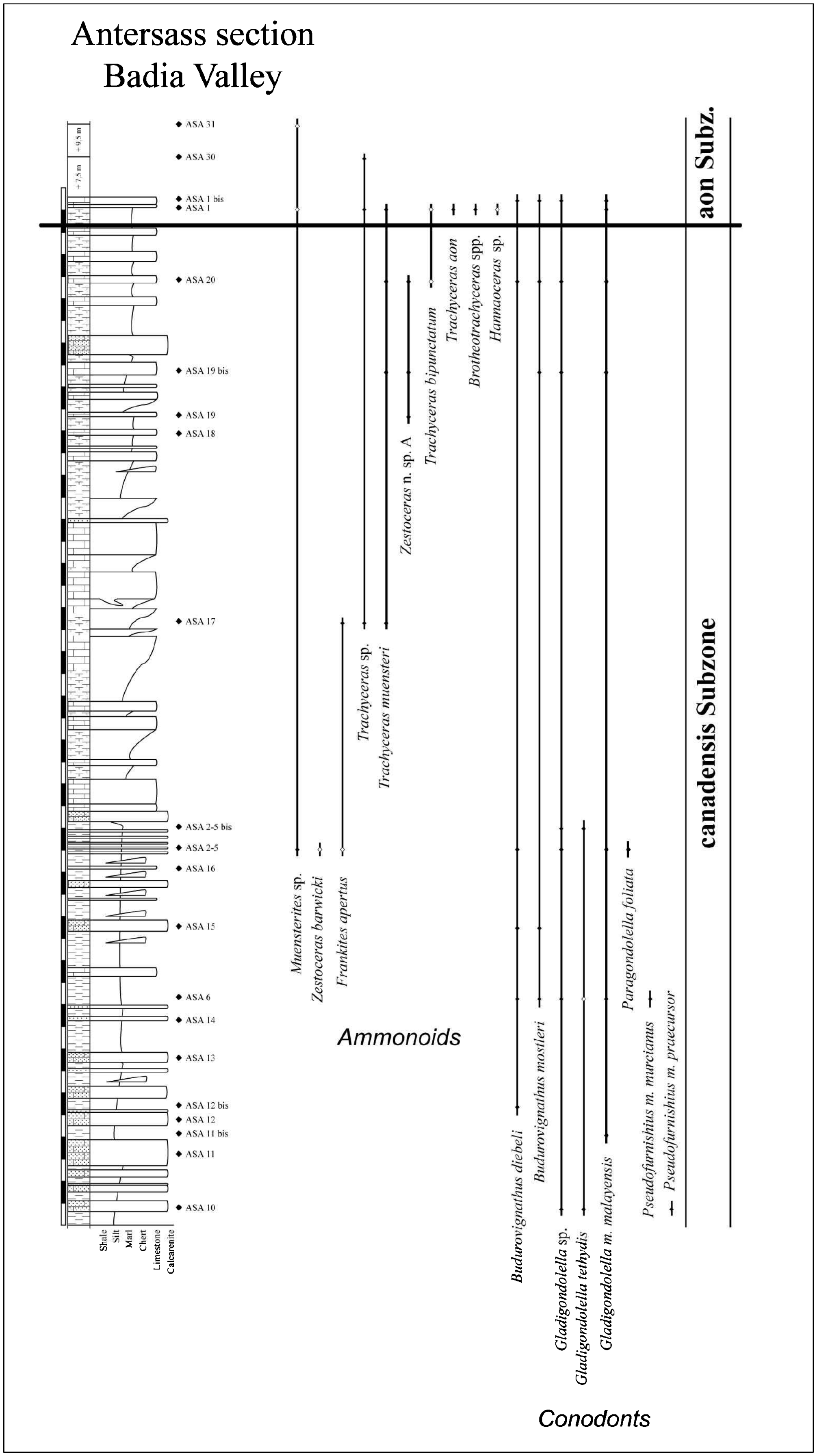

FIGURE 4. Antersass section.

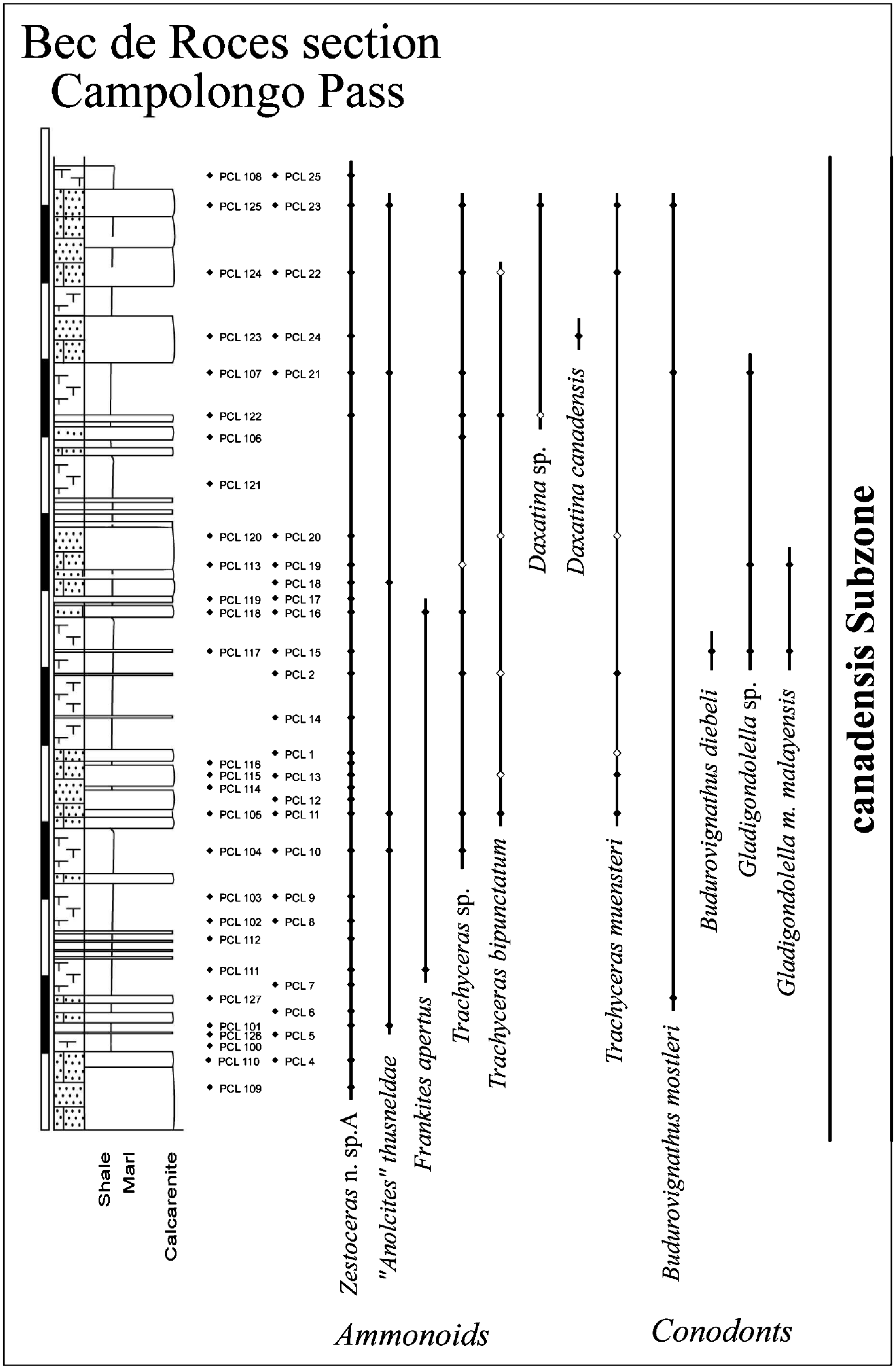

FIGURE 5. Bec de Roces section.

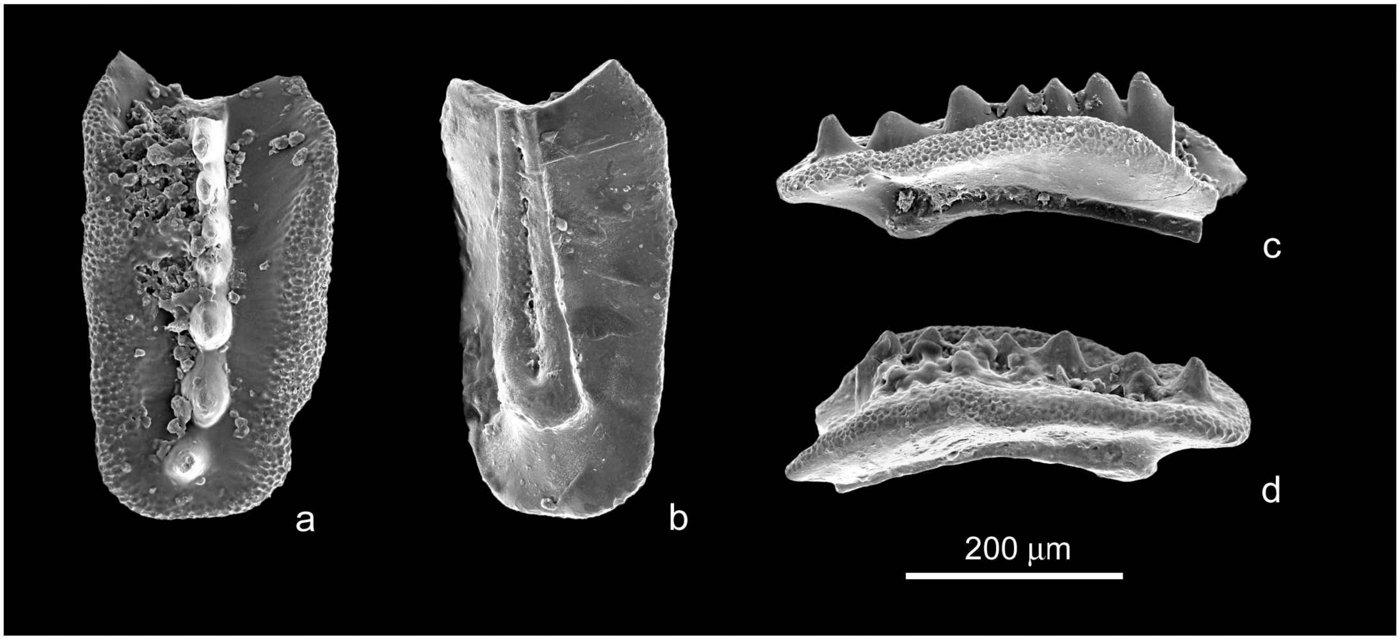

FIGURE 6. SEM Photomicrographs. *Paragondolella polygnathiformis noah* (Hayashi). Stuores Wiesen section, SW 4c; **a**, upper view, **b**, lower view, **c**-**d**, lateral view.

Frankites apertus (Mojsisovics) showed it is distinguished from *Frankites regoledanus* (Mojsisovics), but coincides with the North American species *Frankites sutherlandi* (McLearn). Another *Frankites* species has been recovered in the *regoledanus-canadensis* subzones. This species, indicated as *Frankites* n.sp. in Figure 3, is characterized by a rather low number of ribs per whorl compared to the other species of the genus;

c) genus *Trachyceras*: at least two different species belonging to the genus *Trachyceras* have been documented within the biostratigraphic studied interval: *Trachyceras bipunctatum* (Münster) and *T. muensteri* (Wissmann). An exemplar of the latter species exhibits a subammonitic suture line typical of the genus *Trachyceras*, which is quite different from that of the genus *Daxatina*. Furthermore, in some species, the shape and dimensions of the nodes in ventral position seem to be useful to distinguish the two genera even if the suture line cannot be checked. In the Antersass section, the joint occurrence of *Trachyceras aon* (Münster) and *Brotheotrachyceras* spp. marks the base of the *aon* Subzone. This subzone boundary is not so well documented in the Stuores Wiesen section.

d) genus *Zestoceras*: the Canadian species *Zestoceras enode* (Tozer) prudentially identified here with open nomenclature, is documented in the *regoledanus* Subzone. In the *canadensis* Subzone, *Zestoceras* n. sp. A is instead common. This species is also recognizable in the ammonoid succession from the *sutherlandi* Subzone 2 of British Columbia (see Tozer, 1994. pl. 82, fig. 5, identified as *Zestoceras enode*). Specimens of Stuores Wiesen section previously referred to *Clionitites* sp. are now identified as *Zestoceras barwicki* (Johnston), a species known from the New Pass Range (Nevada, USA). As suggested by Johnston (1941), we consider *Zestoceras barwicki* (Johnston) exactly like the exemplar from Pozoritta (now Pojorita) in Bukowina (Rumania), labelled as *Trachyceras armatum* (Münster) by Mojsisovics (1882, pl. 34, fig. 2). More recently Tozer (1994) noticed the resemblance of the previous exemplar with the Canadian species *Zestoceras cerastes* Tozer, from the *sutherlandi* Subzone 2 of Tozer (1994). Since we consider those specimens as belonging to the same taxon, they should be identified as *Zestoceras barwicki* (Johnston) by priority.

e) Specimens previously determined as *"Anolcites"* ex gr. *laricus* (Mojsisovics) are now assigned to *"Anolcites" thusneldae* Mojsisovics. This species firstly occurs together with *Daxatina canadensis* (Witheaves) in bed SW 4 at Stuores Wiesen.

f) *"Ceratites"* sp., recovered in the upper part of the Stuores Wiesen section just below the *canadensis/aon* subzones boundary (Broglio Loriga et al., 1999), is now identified as *"Ceratites" armatus* (Münster), a taxon also documented in the *aon* Subzone. In the same part of the section *Badiotites eryx* (Münster) occurs.

The *canadensis* Subzone is chiefly characterized by the species *Daxatina canadensis*, *Trachyceras muensteri* , *T. bipunctatum*, *Frankites apertus*, *Zestoceras* n. sp. A, *Z. barwicki* and *"Anolcites" thusneldae*. *Daxatina canadensis* is documented in the Himalayas (Balini et al., 2001; Krystyn et al., 2004), in Alaska (Martin, 1926), in Canada (Tozer, 1994) and in the Svalbard Islands (Böhm, 1903, 1904; Mørk et al., 1992).

The ammonoid assemblage of the *canadensis* Subzone of the Southern Alps best resembles that of the *sutherlandi* Subzone 2 of North America. Because of the wide distribution of this species, *D. canadensis* is an excellent candidate as the primary marker for the base of the Carnian stage. The latter was historically marked by the occurrence of *Trachyceras aon*, which was considered the first *Trachyceras*. In the *canadensis* Subzone, two *Trachyceras* species different from *T. aon* predate the first appearance of the quoted genus. Hence, the assignment of a Carnian age to the *canadensis* Subzone perfectly fits also with an historical point of view.

The choice of *Daxatina canadensis* (Witheaves), a fairly cosmopolitan species, as biomarker for the base of the Carnian stage, and consequently the proposal of the Stuores Wiesen section as GSS and the bed SW4, in which *D. canadensis* appears, as Point for the base of the Carnian guarantees a global correlation among several domains. This correlation potential is also confirmed by other taxonomic groups as well as by physical signals.

Conodonts

Although the Prati di Stuores/Stuores Wiesen section has been investigated several times for conodont biostratigraphy, a poor fauna has been recorded. This fauna is composed of *Budurovignathus mungoensis* (Diebel), *Budurovignathus mostleri* (Kozur), *Budurovignathus diebeli* (Kozur & Mostler), *Budurovignathus longobardicus* (Kovàcs) and by the long-ranged species *Gladigondolella malayensis malayensis* Nogami and *Gladigondolella tethydis* (Huckriede) (Broglio Loriga et al., 1999). All these species range at least from the upper part of the Longobardian (upper Ladinian) to the lower part of the Julian (lower Carnian).

Recently, *Paragondolella polygnathiformis noah* (Hayashi) has been recovered in the Prati di Stuores/Stuores Wiesen section (Fig. 6). This species is from sample SW 4c, 70 cm above the first occurrence of *Daxatina canadensis* (Whiteaves) (bed SW 4). The first occurrence of *Paragondolella polygnathiformis noah* (Hayashi) seems to be the most useful conodont biomarker to recognize the base of the Carnian stage.

Palynomorphs

Palynological assemblages from the Stuores Wiesen section are characterized by a well-diversified microflora, mainly including spores, pollen grains and subordinately organic-walled marine elements (acritarchs, foraminiferal linings and tasmanitids). The microflora of the *regoledanus* Subzone primarily includes sporomorphs ranging in age from the Ladinian to the Carnian. Successive steps of significant diversity increase are well recognizable throughout this subzone: the upper part is characterized by the first occurrence of *Enzonalasporites vigens* and *Concentricisporites* cf. *Concentricisporites bianulatus*, and the uppermost part by the first occurrence of "*Lueckisporites*" cf. *singhii*. The association correlates with the uppermost part of *secatus*-*vigens* phase of Van der Eem (1983). A more gradual microflora diversification is registered at the *regoledanus*/*canadensis* subzones boundary as in the entire *canadensis* Subzone. The first occurrence of *Daxatina canadensis* at Stuores Wiesen is very close to a significant compositional change, mainly consisting in the replacement of Upper Ladinian-Carnian sporomorphs by typical Carnian taxa. The first occurrence in the section, from 3.2 to 48.1 m above the bed SW4 (see Fig. 3), of the Carnian species *Vallasporites ignacii*, *Patinasporites densus* and *Aulisporites* cf. *A. astigmosus,* in association with *Enzonalasporites vigens*, allows us to refer the palynological associations from the lower part of the *canadensis* Subzone to the *vigens-densus* phase of Van der Eem (1983) as previously proposed by Broglio Loriga et al. (1999).

Other Groups

No new data on other fossil groups (e.g., foraminifers, microcrinoids, holothurian sclerites, molluscs and brachiopods and bivalves) have been reported since Broglio Loriga et al. (1999). The presence of "praehalobid" bivalves has been confirmed within the *canadensis* Subzone also in the Bec de Roces section (R. Posenato, pers. comm.).

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NEW PALEONTOLOGICAL, BIOSTRATIGRAPHIC AND PALEOGEOGRAPHIC RESULTS FROM THE TRIASSIC OF THE MERSIN MÉLANGE, SE TURKEY

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Abstract—The Mersin Mélange consists of remnants of three major Tethyan oceans, the Palaeotethys, the Pindos-Huğlu Ocean and the Neotethys. The geological setting of the Mersin Mélange is briefly discussed. Exact biostratigraphic investigations are the basis for paleogeographic reconstructions. In the present paper, four new conodont species are described. Biostratigraphically important is above all the Alaunian *Epigondolella praeslovakensis* Kozur, Masset and Moix n. sp., so far erroneously assigned to "*E.*" *slovakensis*. *E. praeslovakensis* and *Metapolygnathus mersinensis* Kozur and Moix are important paleobiogeographic markers for a Neotethyan origin. Important Upper Triassic conodont species, such as *Epigondolella abneptis*, the type species of *Epigondolella*, have been revised, and *Carnepigondolella nodosa,* the genus *Mockina*, *Mockina bidentata,* and *Parvigondolella rhaetica* (=*Misikella rhaetica* Mostler) are discussed. The Sevatian age of true *M. slovakensis* and of *Parvigondolella vrielyncki* has been confirmed.

One new radiolarian family, one new genus, seven new species and two new subspecies are described. The new radiolarian species *Spongotortilispinus moixi* Kozur and Mostler n. sp. defines the lower Tuvalian *S. moixi* radiolarian zone, which is also characterized by a rapid radiation of the Xiphothecidae, numerous new species of genera which originated in Julian or older radiolarian faunas, the beginning of new radiolarian genera, such as *Protunuma*, which are especially characteristic for parts of the Jurassic, and the absence of *Capnodoce*, which appears in younger Tuvalian time.

INTRODUCTION

The Permian and Triassic rocks of the Mersin mélange are not yet well studied. Many sections and units were for the first time accurately dated by Masset and Moix (2004) by using mainly conodonts and radiolarians. Deciphering the complicated stratigraphy allows us to establish a possible origin and transport direction for the clasts and the blocks. For this aim, a systematic sampling was undertaken, and the description of the newly found faunas will be made in several papers beginning with the present paper, in which we will describe some new conodont species that are partly important for solving longstanding biostratigraphic problems. Moreover, several new radiolarian species are described that define a newly established lower Tuvalian radiolarian zone. Many Pennsylvanian, Permian and triassic conodont, ostracod and radiolarian species will be described in several forthcoming papers. They will improve the Late Pennsylvanian, permian and Triassic Tethyan conodont and radiolarian biostratigraphy and paleobiogeography.

The material of the Mersin mélange is derived from three different major Tethyan oceans. These are, from north to south: (1) the Palaeotethys (very common remnants, proven mainly by pelagic deep water Pennsylvanian and Lower Permian conodont and radiolarian faunas), (2) the Pindos-Huğlu Ocean (very common remnants, proven mainly by Upper Triassic and Jurassic facies and magmatic succession, partly by Upper Triassic faunas), and (3) the Neotethys *sensu* Stampfli (1978), Kozur (1999, 2000) and Stampfli and Kozur (2006) with a few remnants assumed to be of Neotethyan origin by an uppermost Carnian fauna with *Metapolygnathus mersinensis* Kozur and Moix and by a peculiar middle Norian conodont fauna with *Epigondolella praeslovakensis* Kozur, Masset and Moix, n. sp. Depending on palaeogeography, the faunistic content of the different Tethyan oceans is varying in space and time. In the present paper, we discuss in the palaeogeographic chapter only possible faunistic differences between the very similar middle Carnian to Rhaetian faunal succession of the Pindos Huğlu Ocean and the Neotethys s.s.

GEOLOGICAL SETTING (MOIX, KOZUR AND STAMPFLI)

The Mersin Ophiolitic Complex (MOC) belongs to the South-Taurides ophiolitic belt and crops out on the southern flank of the Bolkardağ, northwestward of the coastal cities of Mersin and Erdemli (Fig. 1). It is bounded by the sinistral Ecemis Fault to the east and is thrust over the para-autochthonous series of the Bolkardağ to the north. The Bolkardağ is mainly made of platform-type limestones ranging from Permian to Upper Cretaceous. The Upper Cretaceous is known as the Cehennemdere Formation (Demirtaşlı et al., 1984; Özer et al., 2004) and consists of shallow water limestone with some brecciated episodes showing the first instabilities of the platform, indicating the arrival of the southwards progressing nappes. The uppermost Cretaceous represents the flysch-like sedimentation and is known as the Yavca Formation and is made of sandstones, conglomerates and debris-flows. It directly overlies the Scaglia-type facies of the Upper Campanian-lowermost Maastrichtian, showing the flexure of the Anatolian-Tauric composite plate and shortly preceding the obduction of the Phrygian Ocean (see Moix et al., in press, for discussion). The Bolkardağ was formerly considered as a tectonic window of the Afro-Arabian platform by Ricou et al. (1975) and was defined as the "Calcareous Axis". The MOC consists of three distinct structural elements represented by numerous tectonic slices: an ophiolitic mélange, a sub-ophiolitic metamorphic sole and an oceanic ophiolitic series (Fig. 1). The sedimentary sequences of the MOC represent in fact a typical "colored mélange" composed of blocks of massive limestones, radiolarites, pillow-lavas and sandstones (Juteau, 1980; Parlak, 1996).

The Mersin Ophiolite (Parlak, 1996) is a junior synonym of the Çamlı Ophiolite (Pampal, 1987) and generally crops out in the valleys under the tabular Miocene rocks of the Silifke-Karaman Formation that cap the entire region. According to Parlak and Delaloye (1996, 1999), the Mersin Ophiolite formed in a supra-subduction zone (SSZ) tectonic setting during the Late Cretaceous. The trace elements geochemistry of the cumulative rocks also indicates that the ophiolite developed in an arc

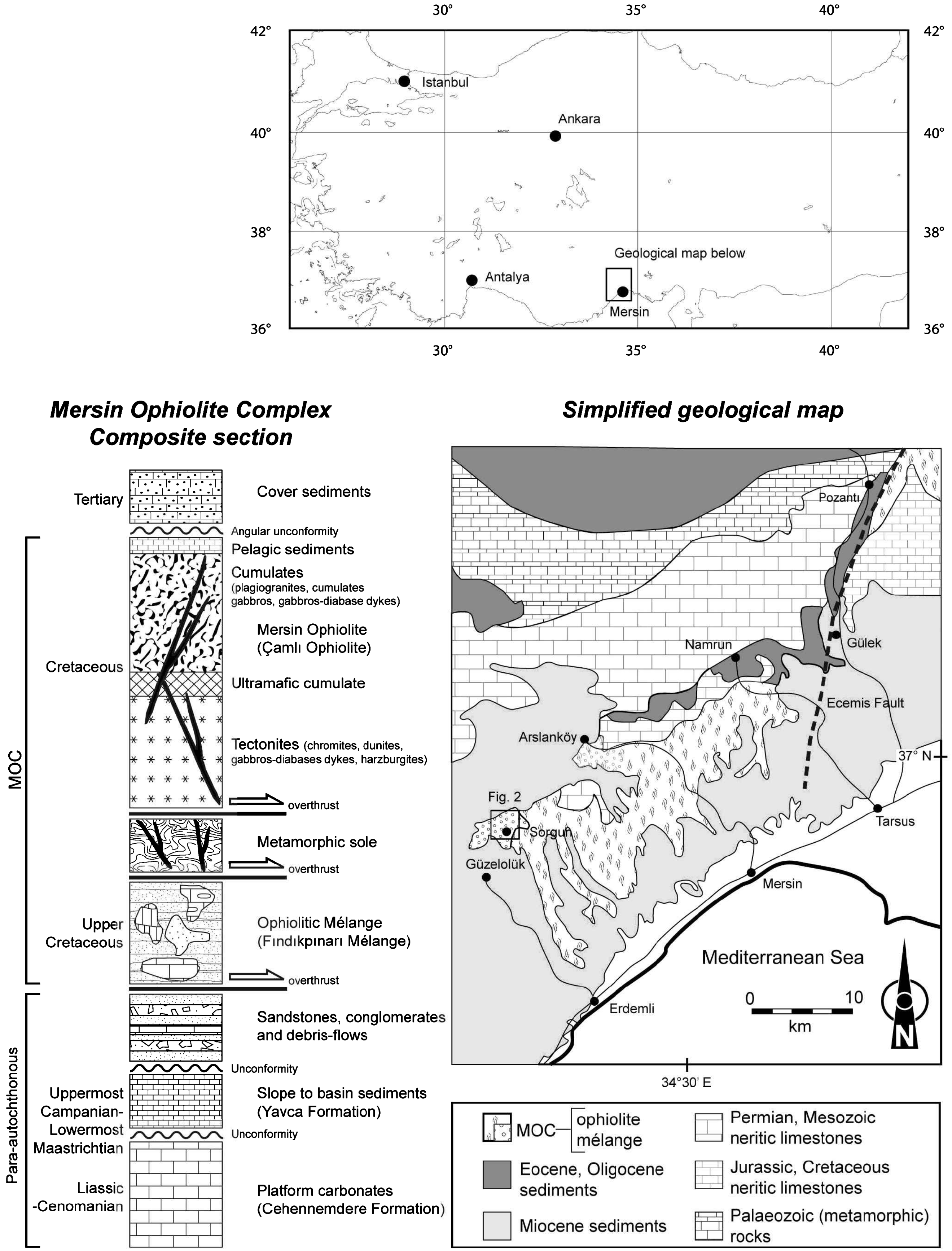


FIGURE 1. General map, composite section and simplified geological map of the Mersin Ophiolitic Complex (MOC). Compiled from Parlak (1996) and Özer et al. (2004).

environment. The oceanic crustal section is about 6 km thick and comprises the following sequence: mantle tectonites, ultramafic/mafic cumulates, and basaltic pillow-lavas associated with deep-marine sediments (Fig. 1).

In the Mersin area, only a few outcrops exhibit pieces of the metamorphic sole. Tholeiitic, microgabbroic-diabasic dykes intruded the metamorphic rocks. From a geochemical point of view and based on the REE and trace elements patterns, these dykes show a MORB and/or VAB signature, suggesting also a supra-subduction zone setting (Parlak et al., 1995; Parlak, 1996; Parlak et al., 1996; Parlak and Robertson, 2004). The various dykes intruding these metamorphites should represent the initial detachment of the oceanic lithosphere and the beginning of the compressional regime during the closure of the supra-subduction ocean (Phrygian Ocean) related to slab roll-back of the older Huğlu-Pindos Ocean. ^{40}Ar/^{39}Ar radiometric dates of the sole indicate ages ranging from 101 ± 4 Ma to 91.0 ± 0.8 Ma, with an average between 92.6 ± 0.2 Ma and 93.4 ± 2 Ma (Parlak, 1996; Parlak and Delaloye, 1999; Dilek et al., 1999; Thuizat et al., 1981; Parlak et al., 1995). In addition, diabase seams cutting the metamorphic sole, and thus posterior to its formation, gave a medium age ranging from 91.0 ± 0.6 Ma to 63.8 ± 0.9 Ma (Parlak and Delaloye, 1996; Parlak, 1996; Dilek et al., 1999).

From a general point of view, the Mersin mélange was thrust onto the Tauric platform and is tectonically overlain by the sub-ophiolitic metamorphic rocks and the ophiolitic suite. The mélange appears directly above the Scaglia-type limestones of Upper Campanian/lowermost Maastrichtian age of the Bolkar Dağ. In the Güzeloluk-Sorgun area, the Mersin mélange is sealed by Burdigalian limestones (Pampal, 1987). The Mersin mélange consists of a chaotic accumulation of blocks and rocks in a tectonic and sedimentary mixture (olistostrome) of ophiolitic material, and oceanic and exotic blocks of various ages. Blocks in the mélange typically range in size from meters to several hundreds of meters. Locally, broken formations are represented by elongated bodies ranging in size from hundreds of meters to kilometers. Large-scale sampling and systematic dating allow constraint of = the timing, setting and origin of the Mersin mélange. According to these data and based on thorough field observations and many fossil determinations, the so-called Mersin mélange was separated into two different new units (Masset and Moix, 2004): the first unit is the Upper Cretaceous Sorgun Ophiolitic mélange (SOM) situated in the north and the second is the Anisian-Ladinian Hacialanı mélange (HM) situated in the south. The distinction of these two mélanges was based on the following criteria: (1) the presence or absence of ophiolitic material; (2) the age of the components and the type of lithologies; (3) the age of the matrix; (4) the Color Alteration Index of the conodonts (CAI) and (5) the Thermal Alteration Index (TAI) of the palynomorphs.

The northerly SOM was investigated in detail, and some of the newly described sections are of high interest to explain the derivation of a part of the Mersin mélange. Seemingly, the SOM could correspond to the Fındıkpınarı Formation of Özer et al. (2004), and to the mélange described also eastwards in the Arslanköy area by Demirtaşlı et al., (1984). The matrix of the SOM may partly correspond to the Başpınar Formation of Pampal (1987), which contains deep sea radiolarites, pelagic limestone and ophiolitic-derived rocks such as volcanites and serpentinites (see below). Biochronological data (foraminifers) from the limestone provide a Cenomanian to Santonian–Campanian age (Pampal, 1987). Many blocks with kilometric lateral extent mapped as coherent bodies have been identified within the SOM, and are regarded as broken formations (or nappes).

In addition to these kilometric blocks, there are a multitude of smaller blocks represented by the following lithologies: meters to several hundreds of meters blocks of carbonates ranging from Lower Carboniferous to Late Triassic. These limestones are not discriminating in terms of palaeogeography, as shallow water sedimentation of that age is well developed both in the Anatolian and Taurus terranes; meters to tens of meters blocks of radiolarite ranging from Anisian for the oldest to Turonian-Coniacian for the youngest, suggesting that a deep open basin remained open until the Coniacian stage; rare, tens of meters blocks of amphibolite; blocks of partially serpentinous peridotite; tens of meters blocks of gabbros and pillow-lavas; blocks of debris-flows (ophiolitic debris); blocks of sandstones.

The southerly HM (outside the area shown on Fig. 2) lies tectonically below the Çamlı Ophiolite, and is separated from the SOM by a tectonic contact. Tertiary sediments, especially visible north of Gâvuruçtuğu and near Hacialanı, cover the ophiolite, the SOM and the HM. The matrix of the HM could partly correspond to the Sorgun Formation of Pampal (1987) and is made of argillite and silts. The sporomorph association is mainly composed of land plant-derived bisaccates, giving an upper Anisian to middle Carnian age with some reworked Lower Triassic sporomorphs. Thus, at least a part of the HM is a Middle to Late Triassic olistostrome/accretionary complex that contains all of the pelagic Pennsylvanian (calcarenites) and Lower Permian (radiolarites and calciturbidites) blocks recognized in the Mersin mélange. So far, the minimum ages of the HM are coming from two radiolarite samples (Bajocian and Valanginian) and from a block of micro-breccia that contains both fusulinids and rudists fragments. These younger blocks were obviously admixed during the final emplacement and juxtaposition of both mélanges, but they could also represent the younger sequence above the Triassic olistostrome.

The HM is a Palaeotethyan-derived unit, a Middle Triassic to Upper Triassic Palaeotethyan flysch to molasse with olistostromes of that age, probably deposited on the lower plate. This flysch to molasse has passed over the lower Tauric plate and was finally deposited in the Neotethys south of it, where no platform deposits were deposited after that, and where it was admixed with the Cretaceous mélanges when this went over it. Only so can it be explained that no post-Triassic carbonate platform was on this flysch, which had to be involved in the HM when it was deposited on then Tauric lower plate. Very similar olistostromes are present in Sicily (Catalano et al., 1991, Carcione et al., 2004; Stampfli et al., 2001). Pennsylvanian to Permian pelagic rocks would have been reworked during the Eocimmerian orogenic event. The components of the HM are genetically different from the ones of the SOM. The HM is mainly composed of radiolarites, sandstones, conglomerates and pillow-lavas. These lithologies, i.e., the sandstones with plants and the micro-conglomerates rich in quartz, lydites and rhyolite pebbles, represent the Cimmerian flysch to molasse due to the closure of the Palaeotethys and the soft collision between the Tauric and Anatolian terranes.

LOCATION AND PREVIOUS WORK (MOIX)

The Mersin mélange, poorly studied until now, represents a key area for any palaeogeographic/tectonic reconstructions in southern Turkey. The investigated area in the mélange is situated north of Erdemli (Mersin, southern Turkey) and is framed by the villages of Gâvuruçtuğu to the north and Sorgun to the south (Fig. 2). Historically, a 1:25,000 scale geological map of the Mersin Ophiolite and associated units was drawn in the Güzelolük–Sorgun region by Pampal (1987). The latter defined the Çamlı Ophiolite (synonym of Mersin Ophiolite) consisting of a nearly complete ophiolitic series. He defined also the Başpınar Formation of Cenomanian-Campanian age characterized by deep sea radiolarites, pelagic limestones and ophiolitic rocks. According to Pampal (1987), this formation was emplaced on the Tauric margin during the Late Cretaceous-Early Tertiary interval. Pampal (1987) defined also the Göktepe limestones and mapped this formation as a thrust sheet overriding the Mersin mélange. The Göktepe limestones have an age ranging from Carboniferous to Early Cretaceous, and are overlain by medium-bedded limestones and gray massive limestone, defined as the Kevençukuru limestones of Berriasian age. The Göktepe limestones may be correlated either to the Cehennemdere Formation of Özer et al. (2004) and Demirtaşlı et al. (1984), whose ages range from Jurassic to Cenomanian in the Arslanköy area, or to the Çağıloluktepe limestones of Pampal (1984), described in the Arslanköy–Tepeköy area, whose ages range from Jurassic to Late Cretaceous.

Finally, the Göktepe limestones, the Cehennemdere Formation and the Çağıloluktepe limestones are similar, and most probably belong to the para-autochtonous sequences of the Bolkardağ, defined as a part of the "Calcareous Axis" of Ricou et al., (1975). Between Gâvuruçtuğu and Sorgun in the SOM (see Fig. 2 for location), Parlak and Robertson (2004) reconstructed intact Upper Permian to Lower Cretaceous shallow-water carbonate sequences similar to those of the Bolkardağ (para-autochthonous or Tauric Carbonate Platform). According to these authors, the platform units in the Mersin mélanges are considered as thrust sheets of the para-autochthonous platform carbonate sequences incorporated into or covering the ophiolitic mélange. Finally, Pampal (1987) defined the Maastrichtian-Lower Palaeocene Sorgun Formation made of turbiditic material incorporating Permian, Upper Triassic, Jurassic and Lower Cretaceous limestone and Cenomanian-Campanian radiolarite olistoliths.

Then, Parlak (1996) worked mainly on the ophiolitic suite and defined the Mersin mélange where he identified different rock assemblages comprising continental margin units, rift series, platform fragments, slabs of metamorphic rocks and fragments of oceanic lithosphere. Later, four distinctive associations have been identified by Parlak and Robertson (2004). They are: (1) a shallow-water carbonate association; (2) a volcanogenic-terrigenous-pelagic association; (3) a basalt-radiolarite-pelagic limestone association; and (4) an ophiolite-derived association. Nevertheless, the main problem was the lack of palaeontological constraints in the previous studies. Consequently, the scarcity of age data made it impossible to extend local observations to the regional scale, and to correlate in a proper way local stratigraphic sequences laterally throughout Turkey and adjacent areas.

Parlak and Robertson (2004) recognized that some lithostratigraphic units could be well compared with other units in the Beyşehir-Hoyran Nappes, i.e., the Huğlu Unit and the Boyalı Tepe Unit (Monod, 1977), using facies similarities but without clear paleontological evidence. Nevertheless, as no biostratigraphic investigations were made in detail, many sections were misinterpreted and, therefore, wrongly assigned. For example, Parlak and Robertson (2004) compared the Carnian Ammonitico Rosso (considered as Lower Jurassic) of Tavusçayırı Tepe (Fig. 3) to the Liassic Boyalı Tepe Unit near Beyþehir. They also compared the Boyunyurt Tepe section (Masset and Moix, 2004) *pro parte* to the Boyalı Tepe Unit using Upper Oxfordian-Lower Kimmeridgian radiolarites (considered as Upper Jurassic-Lower Cretaceous) and did not realize that the uppermost Jurassic and Lower Cretaceous is represented by pelagic limestones (Majolica) preceding a second radiolaritic episode of Barremian to Cenomanian age. Recently, detailed field work was carried out by Masset and Moix (2004) with a special focus on the ophiolitic mélange where important components were dated for the first time. Several sections and single samples have been investigated and yielded shallow water and pelagic rocks developing from the Lower Carboniferous up to the Upper Cretaceous. Finally, Moix et al. (in press) developed a new terrane subdivision of Turkey and proposed a new interpretation for the Mersin ophiolitic complex in the Tethyan realm.

Investigated Sections

The three broken formations and the smaller block presented in this paper belong exclusively to the SOM (see Fig. 2 for location and Figs. 3 and 4 for the logs). The broken formations are the Tavusçayırı, Gâvuruçtuğu and Kocatabur blocks. The small-scale Fırıntaş Block probably belongs to the Kangal Formation defined by Masset and Moix (2004). The latter is made of gray to red pelagic limestones in Hallstatt facies. The Kangal Formation is often represented by small-scale blocks of identical lithologies throughout the mélange, but never showing exactly the same lithological succession nor presenting exactly the same range of ages. The following facial development and ages can be found in the investigated blocks:

(i) The Fırıntaş Block (Fig. 3) ranges from the upper part of middle Norian to the lowermost Rhaetian. It is mainly made of medium-bedded pink limestones in Hallstatt facies at the base passing upwards to thin-bedded red limestones at the top. This block shows similarities with the Kangal Block and the Gerdemelipınarı Block. It is thus supposed that these blocks should have a common origin. The base of the sequence shows thicker beds with ammonoids of probable Norian age. Interesting is the occurrence of *Epigondolella abneptis* (Huckriede) s.s. in the basal part of the sequence (sample I 5). The accompanying conodonts, *Mockina postera* (Kozur and Mostler), *M. zapfei* Kozur and *Norigondolella steinbergensis* (Mosher), indicate a late Alaunian age, important for the dating of *E. abneptis* s. s. The next younger but considerably higher sample I 4 has a Sevatian conodont fauna with *Mockina bidentata* (Mosher) and *Parvigondolella vrielyncki* Kozur, confirming the assignment of *P. vrielyncki* Kozur and Mock to the lower Sevatian, which changes the late Alaunian age assignment of palaeomagnetic successions in the Antalya nappes by the *P. vrielyncki* fauna (= "*Epigondolella*" n. sp. E fauna) in Gallet et al. (1992, 1993, 1996, 2000). Sample I 3 has an unspecific, but rather lower Sevatian conodont fauna with *Norigondolella kozuri* (Gedik). Sample I 2 cannot be dated by conodonts, whereas sample I 1 with *Misikella posthernsteini* Kozur and Mock, *M. hernsteini* (Mostler), advanced forms with 2-3 denticles, *Oncodella paucidentata* (Mostler) and *Zieglericonus rhaeticus* Kozur and Mock is a typical lower Rhaetian conodont fauna.

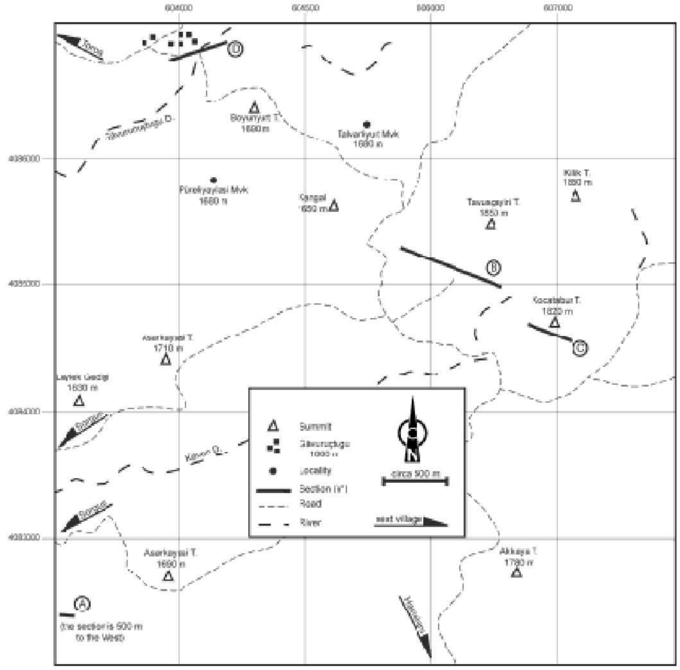


FIGURE 2. Locality chart for the Fırıntaş Block (A), Tavusçayırı Block (B), Kocatabur Block (C) and Gâvuruçtuğu Block (D). Location is on Figure 1.

(ii) The Tavusçayırı Block (Fig. 3) *sensu* Masset and Moix (2004) will be described in detail in another paper and differs considerably from the dating of the Tavusçayırı section by Parlak and Robertson (2004). The sequence starts with brecciated beds followed by polygenic conglomerates, which rest with erosive contact over the breccia. It is followed by black calciturbidites passing upwards to a thin platform development of early Carnian age. The top of the platform represents a paleorelief that is filled by red pelagic limestones rich in ammonoids of middle Carnian age. This is in turn overlain by a volcanic (tuffitic) interval where pelagic and redeposited limestones are interstratified. It passes then to a thick sequence made of pelagic limestones where several debris-flows and calciturbidites are intercalated. This sequence ends normally with a large breccia, at places overlain by a well-developed ammonitico rosso of Lower Jurassic age. The uppermost part of the section is made of a

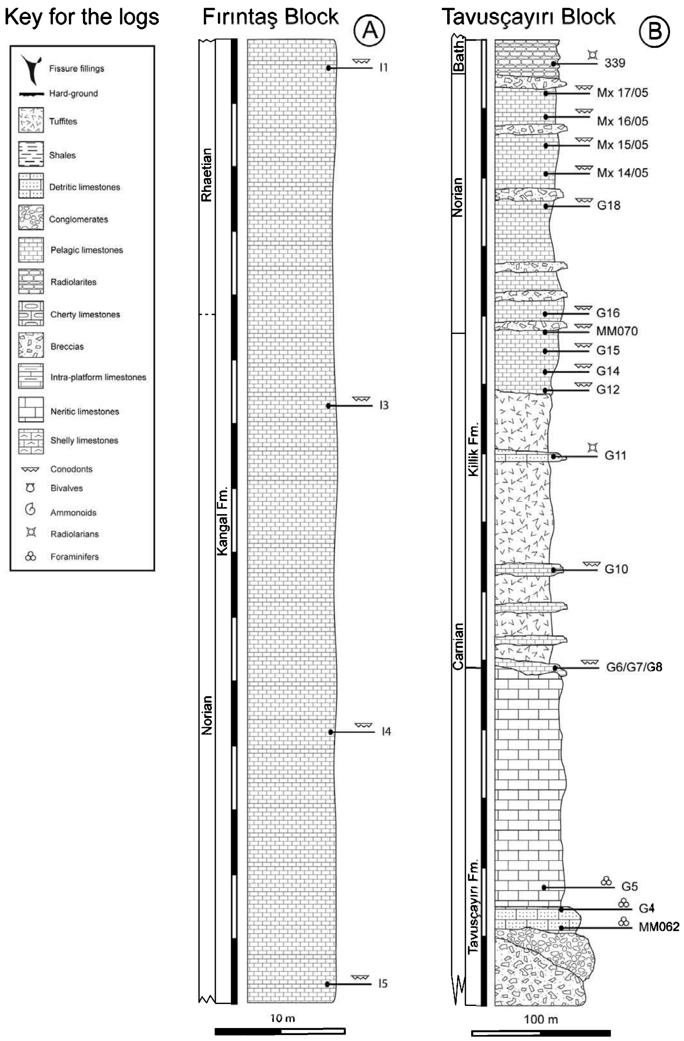


FIGURE 3. Synthetic lithostratigraphic sections of the Fırıntaş Block (A) and Tavusçayırı Block (B). Location is on Figure 2.

breccia followed by Dogger radiolarites. This succession corresponds to the Huðlu-type development farther to the west, first described by Monod (1977) in the Beyşehir-Hoyran Nappes or in the Bozkır Units by Özgül (1976) and stratigraphically revised by Kozur (1997).

Eight conodont samples (G 6, G 7, G 7A-E, G 8) were taken from the ammonitico rosso (Hallstatt Limestone facies) at the beginning of the pelagic part of the sequence. Most of them had a poor conodont fauna, and only sample G 7 had a rich fauna. The conodont association with *Carnepigondolella nodosa* (Hayashi, 1968) s. s. (=*Epigondolella carnica* Krystyn, 1975), *Gladigondolella tethydis* (Huckriede) and *Paragondolella noah* (Hayashi) indicates a correlation with the *Austrotrachyceras austriacum* ammonoid Zone, the same age that was obtained by ammonoids (det. Krystyn). The next younger sample G 10 yielded a fauna consisting mainly of siliceous sponge spicules, a few radiolarians and very few conodonts, among them *Gladigondolella* sp., indicating that this level belongs still to the Julian. Sample G 11 has a very rich and well preserved radiolarian fauna that will be described in a monographic paper (see section below on systematics). It belongs to *Spongotortilispinus moixi* Zone of the basal Tuvalian. This age is indicated by the rather poor conodont fauna, consisting exclusively of *Paragondolella noah* (Hayashi) and the absence of *Gladigondolella*. Siliceous sponges are also very common and well preserved. Ostracods are moderately common and well preserved. They indicate a water depth of about 150-200 m.

From samples G 12 to G 15, upper Tuvalian conodont faunas representing the *Carnpoigondolella pseudodiebeli-M. communisiti* Zone and the *Epigondolella orchardi* Zone are present, whereas *E. quadrata* Orchard indicates the base of the Norian in sample MM070. Sample G 16 belongs to the *E. triangularis* Zone. Sample G 18 with the co-occurrence of *Mockina bidentata* (Mosher) and *M. postera* (Kozur and Mostler) belongs to the lower Sevatian. Samples Mx 14/05 and Mx 15/05 with numerous *Misikella hernsteini* (Mostler) and *Oncodella paucidentata* (Mostler), but without *E. bidentata* (Mosher), belong to the lower part of the upper Sevatian *M. hernsteini* Zone. It is very interesting that already at this stratigraphic level the first *Misikella koessenensis* (Mostler) was found (see also section below on biostratigraphic evaluation). There is surely not contamination because no samples with *M. koessenensis* were dissolved, when sample Mx 15/05 was dissolved.

As we have observed in several other Tethyan sections, after the disappearance of *E. bidentata* and replacement by the *M. hernsteini-P. andrusovi* fauna or the *M. hernsteini* fauna without *Parvigondolella*, in sample Mx 16/05 *M. bidentata* comes back, but with distinctly different forms (two morphotypes, one of them comprises the holotype morphotype). Especially interesting are forms with a rather long posterior carina with up to 5 denticles, *Mockina* cf. *bidentata* (Mosher) (Pl. 2. Fig. 2). They are similar to but not identical with *Orchardella mosheri* (Kozur and Mostler). For sample Mx 17/05 an early Rhaetian age cannot be excluded. From *Misikella* only *M. hernsteini* was found , but only with few specimens and, therefore, it cannot be excluded that *M. posthernsteini* is already present in this level with a poor conodont fauna.

(iii) The Gavuruçtuğu Block (Fig. 4) ranges from middle Norian to probably Rhaetian. The stratigraphic sequence begins with medium-bedded gray to brownish fetid micritic limestones. rich in organic matter and framboidal pyrite, a common diagenetic phase in many types of shales, especially abundant in strata formed under oxygen-poor depositional conditions (Wignall et al., 2005; Wilkin and Barnes, 1997) and characteristic of a (restricted) basinal/ramp environment. The sequence passes upwards to an alternation of thin- to medium-bedded black to gray micritic argillaceous limestone and marls. The sequence ends with highly recrystallized massive gray limestone with replacement cherts. The neritic limestone sequence continues upwards and is of unknown thickness.

The conodonts assemblage of the Gavuruçtuğu Block yielded from sample D 4 to E 5 a typical monospecific conodont fauna characteristic of intraplatform basins. It consists exclusively of *Epigondolella praeslovakensis* Kozur, Masset and Moix n. sp. Above this level open sea deposits occur (samples MM031 to P 4, see Fig. 4), in which *E. praeslovakensis* occurs together with *M. medionorica* Kozur and *M. zapfei* Kozur. This is the same conodont association as from the ammonoid-dated late Alaunian from Timor (see chapter biostratigraphic evaluation). By this the upper range of *M. praeslovakensis* can be well dated as late Alaunian. These pelagic limestones are overlain by shallow water carbonates without conodonts, but with foraminifers. Only long-ranging species were found which indicate Norian to Rhaetian ages.

(iv) The sequence of the Kocatabur Block (Fig. 4) begins with thin-bedded gray to pink micritic and nodular limestones of uppermost Carnian age and passes upwards to highly recrystallized massive neritic limestones. The presence of fissure fillings in the upper part of the section indicates the fracturing of the platform during the Late Triassic. Fissure fillings are mainly composed of red pelagic micrites and one of them gave an uppermost Rhaetian age.

The oldest conodont assemblage of the Kocatabur Block (sample H 1) yielded *Carnepigondolella zoae* (Orchard) and *Metapolygnathus communisti* Hayashi, partly transitional to *Paragondolella noah* (Hayashi). This fauna is interesting as it shows the beginning of *M. communisti* within the *C. zoae* Zone. This clearly Carnian fauna shows that the FAD of *M. communisti* cannot be used to define the Norian base. A similar age can be assumed until sample 396 with *M. communisti* and *P. noah* (Hayashi), partly transitional to *M. communisti*. In samples H 40 and H 60, there occur *M. communisti*, *E. praetriangularis* Kozur and

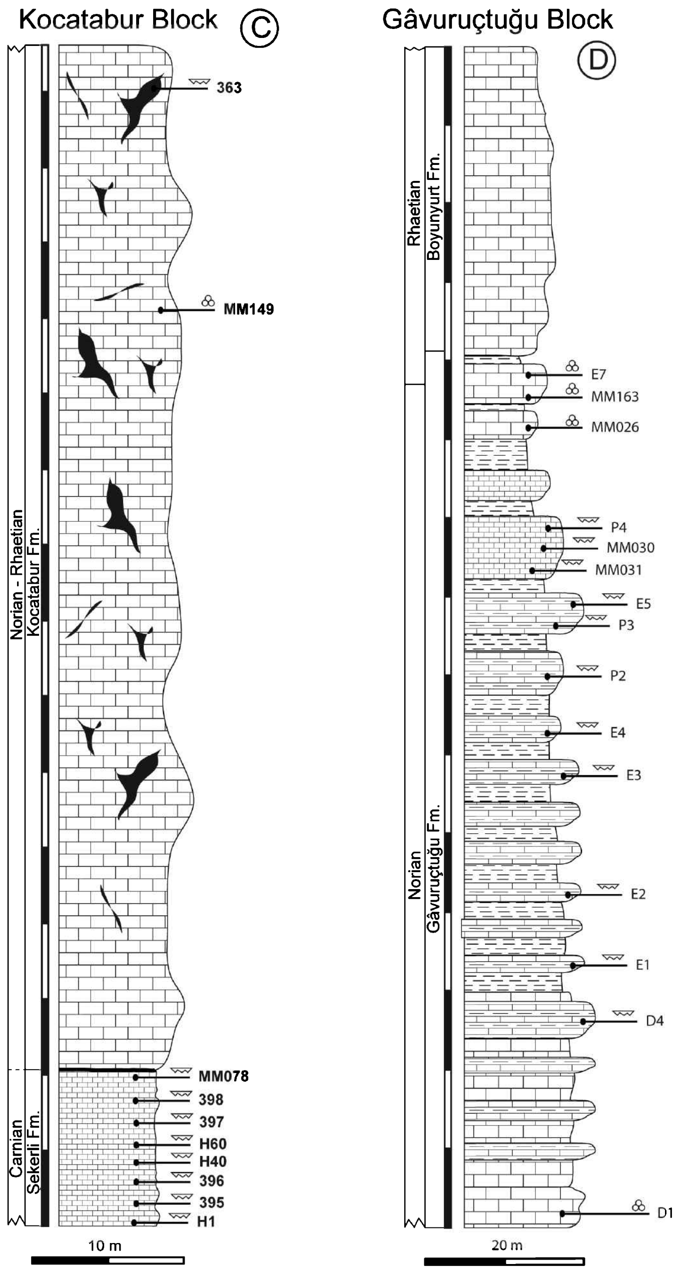


FIGURE 4. Synthetic lithostratigraphic sections of the Kocatabur Block (C) and Gâvuruçtuğu Block (D). Location is on Figure 2. Key is on Figure 3.

Moix n. sp. and transition forms between *M. communisti* and *M. mersinensis* Kozur and Moix n. sp. A similar fauna occurs until sample 398. In sample MM078 *E. orchardi* Kozur and *Metapolygnathus mersinensis* Kozur and Moix n. sp. are present, indicating the *E. orchardi* Zone of the uppermost Carnian and - because of *M. mersinensis* – Neotethyan character. Somewhat deeper a similar fauna was found, where additionally *M. communisti* is present. The overlying shallow water limestones have no conodonts, but in a fissure filling of red pelagic micritic limestones within this shallow water limestones a pelagic upper Rhaetian conodont fauna with *Misikella posthernsteini* Kozur and Mock und *M. ultima* Kozur and Mock is present.

PALEOTECTONIC SETTING
(MOIX, KOZUR AND STAMPFLI)

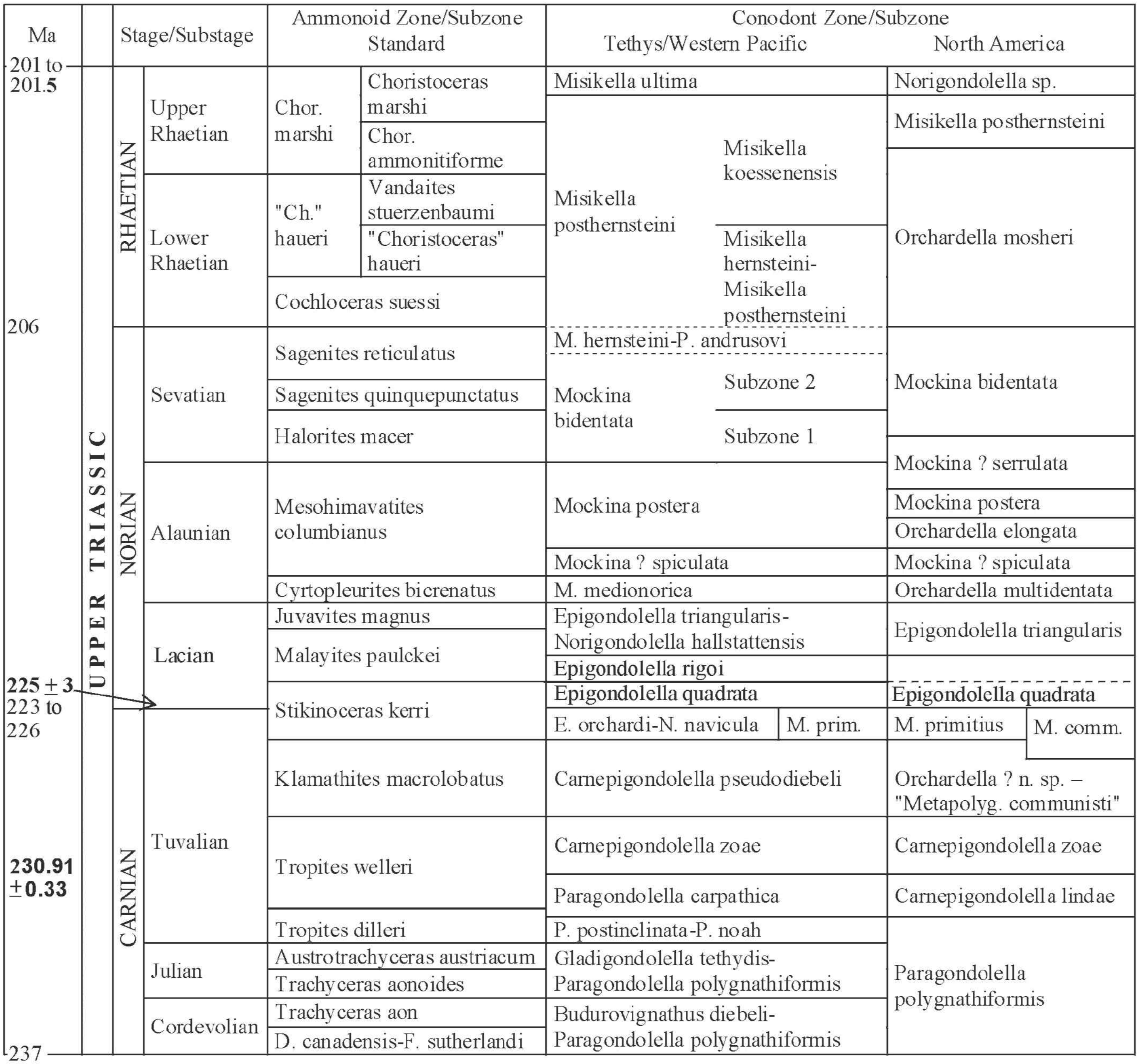
Several terranes of different origin composed the Turkish segment of the Tethysides. These terranes are separated by complex suture zones of different ages representing the remnants of different oceanic domains. A complete description of these terranes/domains/sutures is given in Moix et al. (in press). Since the Carboniferous, the north-verging subduction of Palaeotethys developed a diffuse rifting zone on the southern margin of Eurasia (Stampfli and Kozur, 2006; Ziegler and Stampfli, 2001). First, this phenomenon caused the collapse of the Variscan cordillera and the opening of different back-arc basins such as Küre, Meliata, Maliac and then Pindos. At the same time, the Paleotethyan slab-pull induced the detachment and drifting of the Cimmerian terranes (e.g. Greater Apulia-Beydağları domain, Taurus terrane, Sanandaj-Sirjan, Alborz, Central Afghanistan, Pamir-Tibetan terranes) from the northern border of Gondwana. The direct consequence of it was the opening of the Neotethys/East-Mediterranean domain during the Early Permian (Stampfli et al., 2001, Stampfli and Borel, 2004; Stampfli and Kozur, 2006). Back-arc rifting associated with the Palaeotethys subduction zone caused the Permo-Triassic opening of the Maliac-Meliata-Küre-Svanetia system of marginal basins along the still active Eurasian margin (Fig. 6).

The Küre Ocean

The Küre oceanic unit consists of ophiolites and a main sedimentary unit, the Akgöl Group (Ketin, 1962), in which the dark middle Carnian to Middle Jurassic siliciclastic turbidites and olistostromes represent a wide-spread flysch sequence characteristic of the active southern margin of the Küre Ocean. The middle Carnian to lower Norian part of the matrix can be dated by different *Torlessia* species (Kozur, 1998; Kozur et al., 2000). The olistoliths contain basalts and ultramafic rocks as well as shallow water Scythian and pelagic, slope and shallow water sediments (limestones and radiolarites) of Anisian and Ladinian age. The oldest pelagic rocks contain *Chiosella timorensis*, the conodont guide form of the basal Anisian. In the *Neogondolella regalis* Zone, the second conodont zone of the Anisian, the first palaeopsychrosphaeric deep water ostracods appear, which indicate a broad connection to the world ocean. The opening of the Küre Ocean is placed within the late Olenekian, indicated by the first appearance of similar pelagic sediments in the Kotel Zone and in the Dobrudzha Trough (in western continuation of the Küre Ocean), also accompanied by the emplacement of Scythian E-MORB (Nicolae and Seghedi, 1996; Seghedi, 2001). The presence of siliciclastic flysch in the southern margin, and of a passive margin with Late Triassic Hallstatt Limestone in the north at the same time (Kozur et al. 2000), indicates a southwards-directed subduction as already assumed by Şengör (1984) and Şengör and Yılmaz (1981). The northern slope of the Küre Ocean is represented by the Çalça Unit which is characterised by Pelsonian to uppermost Norian or lowermost Rhaetian Hallstatt Limestones which have the same facies succession as in the Hallstatt type area in Austria (Kozur et al., 2000).

The Meliata-Hallstatt Ocean

The Meliata-Hallstatt Ocean of the Eastern and Western Carpathians and Northern Alps, was located in the western prolongation of the Küre Ocean. Former direct connections are apparently missing due to major lateral displacements around the Moesian promontory. But, a connection to the Küre Ocean through the south Moesian aborted rift (Georgiev et al., 2001) certainly existed. The widespread occurrence of palaeopsychrosphaeric ostracods in the Middle Triassic to Liassic of the Meliata-Hallstatt Ocean and its slope and outer shelves (Kozur, 1991) speaks in favour of a broad enough deep-water connection (below 500 m water depth) with the world oceans. The easternmost remnants of the Meliata-Hallstatt domain occur as exotic blocks in the Transylvanian Nappes. As in the Küre Ocean, the lower Anisian consists of pelagic limestone and pillow-lava, but pelagic upper Olenekian rocks were not yet found. In the typical Meliaticum of the Western Carpathians and Eastern Alps, a rifting phase occurred during the Late Permian. The first pelagic conditions begin in the late Bithynian. Pelagic limestones with



Ma		Stage/Substage		Ammonoid Zone/Subzone Standard		Conodont Zone/Subzone Tethys/Western Pacific		Conodont Zone/Subzone North America
201 to 201.5	UPPER TRIASSIC	RHAETIAN	Upper Rhaetian	Chor. marshi	Choristoceras marshi	Misikella ultima		Norigondolella sp.
						Misikella posthernsteini	Misikella koessenensis	Misikella posthernsteini
					Chor. ammonitiforme			Orchardella mosheri
			Lower Rhaetian	"Ch." haueri	Vandaites stuerzenbaumi			
					"Choristoceras" haueri		Misikella hernsteini-Misikella posthernsteini	
				Cochloceras suessi				
206		NORIAN	Sevatian	Sagenites reticulatus		M. hernsteini-P. andrusovi		Mockina bidentata
				Sagenites quinquepunctatus		Mockina bidentata	Subzone 2	
				Halorites macer			Subzone 1	Mockina ? serrulata
			Alaunian	Mesohimavatites columbianus		Mockina postera		Mockina postera
								Orchardella elongata
						Mockina ? spiculata		Mockina ? spiculata
				Cyrtopleurites bicrenatus		M. medionorica		Orchardella multidentata
			Lacian	Juvavites magnus		Epigondolella triangularis-Norigondolella hallstattensis		Epigondolella triangularis
				Malayites paulckei		Epigondolella rigoi		
225 ± 3 223 to 226				Stikinoceras kerri		Epigondolella quadrata		Epigondolella quadrata
		CARNIAN	Tuvalian			E. orchardi-N. navicula	M. prim.	M. primitius M. comm.
				Klamathites macrolobatus		Carnepigondolella pseudodiebeli		Orchardella ? n. sp. – "Metapolyg. communisti"
230.91 ±0.33				Tropites welleri		Carnepigondolella zoae		Carnepigondolella zoae
						Paragondolella carpathica		Carnepigondolella lindae
				Tropites dilleri		P. postinclinata-P. noah		Paragondolella polygnathiformis
			Julian	Austrotrachyceras austriacum		Gladigondolella tethydis-Paragondolella polygnathiformis		
				Trachyceras aonoides				
			Cordevolian	Trachyceras aon		Budurovignathus diebeli-Paragondolella polygnathiformis		
237				D. canadensis-F. sutherlandi				

FIGURE 5. Upper Triassic stages, substages, ammonoid, Tethyan and North American conodont zones and numeric ages. Modified after Kozur (2003; Bachmann and Kozur, 2004). Changes of numeric ages discussed in Kozur and Weems, this volume.

some mafic volcanics characterising the Pelsonian; sea-floor spreading began in the Illyrian. Upper Illyrian, Ladinian and Cordevolian are characterised by wide-spread pillow-lava and red radiolarites. As in the Küre Ocean, sea-floor spreading suddenly stopped in the middle Carnian. Late Carnian and Norian thermal subsidence caused drowning of outer shelves, characterised by a transition from shallow water limestones to Hallstatt Limestones. The subduction of the Meliata Ocean began during the Jurassic and its closure was within the Oxfordian, as in Küre, where, however, the subduction began earlier.

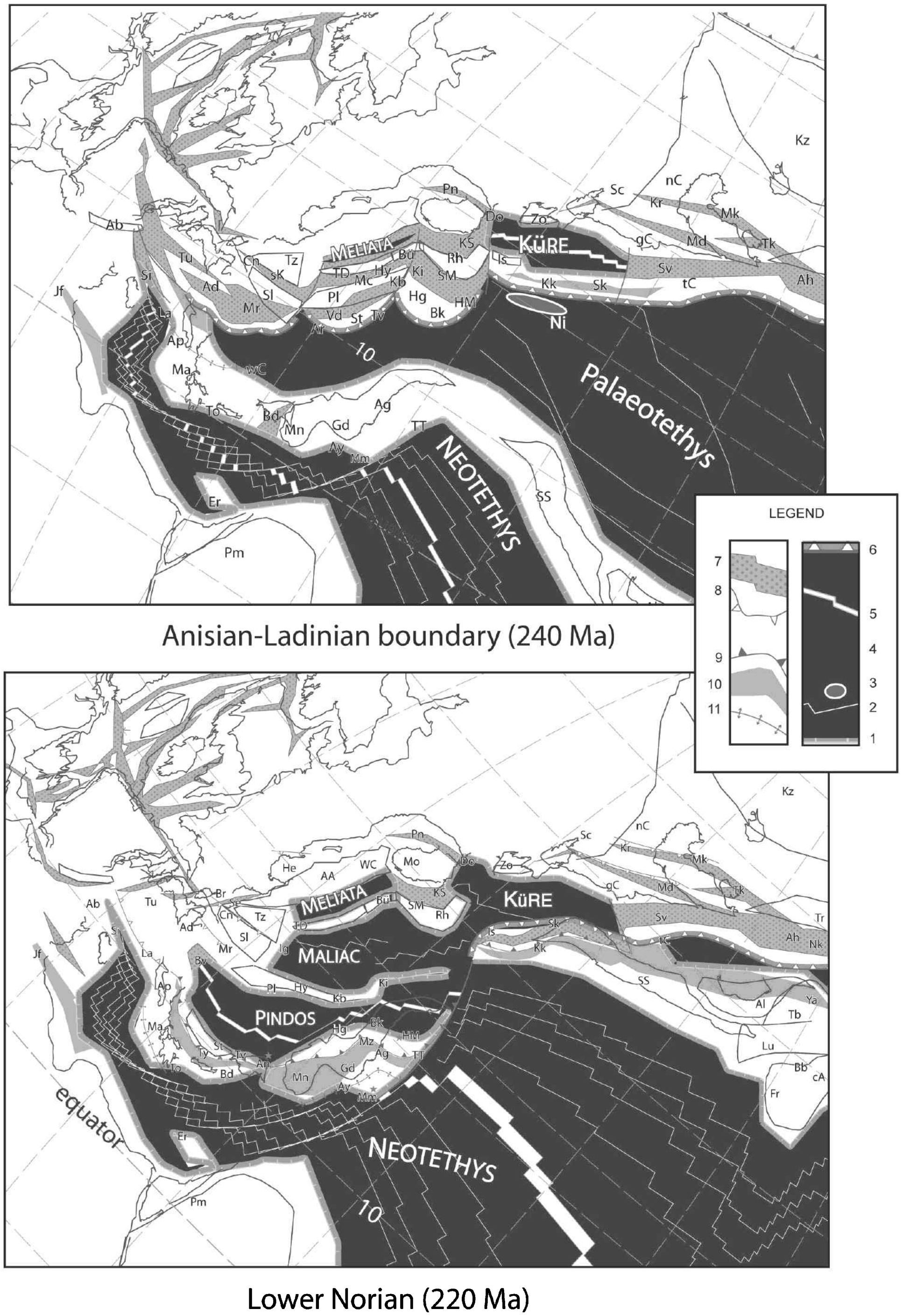
The Maliac Ocean

In the Maliac Ocean, sea-floor spreading started at the beginning of the middle Carnian (Ferrière, 1974; Ferrière, 1976; Ferrière, 1977; De Bono, 1998; De Bono et al., 1999) when it stopped in the Küre and Meliata-Hallstatt oceans (Kozur, 1991). This is locally connected with a pronounced shoulder uplift in the outer shelf of the Maliac domain. Deep water late Olenekian to Cordevolian sediments (pelagic limestones and radiolarites connected with widespread intermediate volcanism) are overlain by middle Carnian shallow water carbonates. This "Maliac signal" is opposite to the "Meliata signal" (thermal subsidence of the slope and outer shelf).

The Maliac Ocean was subducted during the Jurassic, contemporaneous with the Meliata Ocean. The northwestern evidence of Maliac remnants are found in the Mts. Kalnik and Medvednica (northwestern Croatia, Halamiæ and Gorièan, 1995), but the "Maliac signal" can also be observed in the eastern Drauzug. The "Maliac signal" is also well recognisable in the Karaburun peninsula in Turkey (Stampfli et al., 2003), but its eastern continuation was nearly totally subducted in the Izmir-Ankara Belt.

The Pindos Ocean

The Pindos domain was a deep-water basin since the Late Trias-



Anisian-Ladinian boundary (240 Ma)

Lower Norian (220 Ma)

FIGURE 6. Anisian-Ladinian boundary (240 Ma) and lower Norian (220 Ma) palaeotectonic reconstructions of the Mediterranean domain. **Key for the figures: AA**, Austro-Alpine; **Ab**, Alboran; **Ad**, Adria *sensu stricto*; **Ag**, Aladağ-Bolkardağ; **Ah**, Agh-Darband; **Al**, Alborz; **An**, Antalya, Alakir Cay; **Ap**, Apulia *sensu stricto*; **Ar**, Arna accretionary complex; **Ay**, Antalya; **Bb**, Band e Bayan; **Bd**, Beydağları; **Bk**, Bozdağ-Konya fore-arc; **Br**, Briançonnais; **Bü**, Bükk; **Bv**, Budva; **cA**, central Afghanistan, Hazarajat**; Cn**, Carnic ; **Do**, Dobrogea; **Er**, Eratosthen; **Fr**, Farah basin; **gC**, great Caucasus; **Gd**, Geyikdağ-Anamas-Akseki; **He**, Helvetic rim basin; **Hg**, Huğlu-Boyalı Tepe; **HM**, Huğlu-Mersin; **Hy**, Hydra; **Ig**, Igal trough; **Is**, Istanbul; **Jf**, Jeffara rift; **Kb**, Karaburun; **Ki**, Kirşehir; **Kk**, Karakaya fore-arc; **Kr**, Kermanshah Ophiolite; **KS**, Kotel-Strandja rift; **Kz**, Kazakhstan; **La**, Lagonegro; **Lu**, Lut; **Ma**, Mani; **Mc**, Maliac rift/ocean; **Md**, Mozdak; **Mk**, Mangyshlak rift; **Mm**, Mamonia accretionary complex; **Mn**, Menderes; **Mo**, Moesia; **Mr**, Mrzlevodice fore-arc; **Mz**, Munzur dağ-Keban; **NC**, North Caspian; **Ni**, Nilüfer seamount; **Nk**, Nakhlak fore arc; **Pl**, Pelagonian; **Pm**, Palmyra rift; **Pn**, Pienniny rift; **Rh**, Rhodope; **SC**, South Caspian; **Se**, Sesia (western Austroalpine); **Si**, Sicanian; **Sl**, Slavonian; **sK**, south-Karawanken fore arc; **Sk**, Sakarya; **SM**, Serbo-Macedonian; **SS**, Sanandaj-Sirjan; **St**, Sitia E-Crete; **Sv**, Svanetia rift; **Tb**, Tabas; **tC**, trans-Caucasus; **TD**, Transdanubian; **Tk**, Tuarkyr; **To**, Talea Ori; **Tr**, Turan; **TT**, Toros transform margin; **Tu**, Tuscan; **Tv**, Tavas Nappe; **Ty**, Tyros fore-arc; **Tz**, Tizia; **Vd**, Vardousia; **wC**, western-Crete (Phyl-Qrtz) accretionary Complex; **WC**, West Carpathian; **Ya**, Yazd; **Zo**, Zonguldak. **Key for the legend: 1-** passive margin; **2-** magnetic anomalies or synthetic anomalies; **3-** seamount; **4-** oceanic crust; **5-** spreading ridges; **6-**subduction zone; **7-** rifts; **8-** sutures; **9-** active thrusts; **10-** foreland basins; **11-**flexural bulge.

sic, located between the Gavrovo-Tripolitza (Greater Apulia) and the Pelagonian units. The Pindos-Olonos zone comprises a well-known sedimentary continuous sequence of pelagic facies from Late Triassic to Palaeocene followed by a Palaeocene-Oligocene flysch (De Wever and Cordey, 1986; De Wever and Origlia-Devos, 1982; Fleury, 1980; Richter and Müller, 1993a; Richter and Müller, 1993b; Richter et al., 1993). The basal part of the Pindos stratigraphic column, as shown by Aubouin et al. (1970) and Fleury (1980) is characterised by a formation, mainly of Carnian age, called "Détritique triasique". Degnan and Robertson (1998) proposed the name Priolithos Formation for this formation, and have shown the orogenic origin of the re-sedimented clasts. We attribute the main source of detritus to the uplifted continental basement located to the southwest (Sitia micro-continent and Tyros fore-arc, future Tripolitza), corresponding to the most external detached piece of the former Variscan cordillera. The middle to late Carnian age of this flyschoid formation, points to a possible mixed origin, either syn-rift of the Pindos back-arc opening and/or tectonic inversion related to the Eocimmerian event.

Our own investigations (Bellini, 2002; Payer, 2001; Stampfli et al., 2003) have shown the presence of early to middle Carnian basaltic lava flows and tuffites in the Pindos basal sequence (Priolithos Formation) in eastern Crete (Kalos Potamos) (also present in the Pindos Mountains, Kozur and Mock unpublished data). REE distribution and other discriminative diagrams show a dominant volcanic arc affinity with minor E-MORB signature, confirming a Carnian back-arc position for the Pindos Ocean. No proof of spreading younger than Carnian has been found so far.

A part of the Triassic arc was abandoned in the northern margin of the Pindos, in the Vardoussia region, characterised by sub-alkaline to calc-alkaline and shoshonitic (Mt. Ghiona) lavas with subduction-related geochemical signatures (Lefèvre et al., 1993; Pe-Piper, 1998; Pe-Piper and Mavronichi, 1990). Recent investigations in the Chamezi area of eastern Crete (Champod and Colliard 2003), have shown the presence of Early to Middle Triassic rift related series, potentially belonging to the southern margin of the Pindos domain. They can be correlated with the "Tyros"-type Middle Triassic fore-arc sequences of Vai through a common Late Permian pelagic substratum and to the Pindos remnants of Kalos Potamos through a similar pelagic Late Triassic. The Chamezi-Pindos rift opened within an Early to Middle Triassic arc and was separated from the Vai fore-arc basin by a ridge made of the Variscan basement units of the Sitia micro-continent.

Eastwards, the Pindos sequences can be extended to the Antalya domain, as proposed by Brunn et al. (1976). The Lower and Median Antalya Nappes (e.g. Alakır Çay Nappe) are characterised by Carnian and Norian deep-water facies rich in detritism and locally in volcanics (Carnian pillow lavas, Marcoux, 1970), similar to the lower Pindos sequences (Dumont et al., 1972; Gutnic et al., 1979; Marcoux, 1987). One characteristic of these sequences is the presence of Late Triassic clastic material (locally reworking rhyolitic pebble) marking the Eocimmerian event.

We also assign to an eastern continuation of the Pindos-Antalya domain (southern slope and shelf) the Huğlu and Boyalı Tepe units of the Central Taurus (Gutnic et al., 1979), from the Beyþehir-Hoyran Nappes (Andrew and Robertson, 2002), assigned to the so-called "Neotethys northern branch" remnants by the latter authors. In the Huğlu Unit, thick middle Carnian and lower Tuvalian tuffs and basalts with a few intercalations of cherty limestones are present, overlain by Late Triassic cherty limestones and cherts with Jurassic radiolarians (Kozur, 1997; Tekin, 1999). The Gülbahar Nappe of the Lycian domain with lower to middle Norian cherty limestones, cherts and tuffs may also be derived from the southern margin of the Pindos Ocean, but exposed Carnian rocks are not known from there.

The western continuation of the Pindos is represented by the Budva domain of the external Dinarides (Gorièan, 1994). Upper Triassic rocks (pelagic *Halobia* limestones) are underlain by sandstones, marls, shales, limestones, cherts, tuffs, basalts and intermediate volcanics, for which a Middle Triassic age is indicated, but without good faunal evidences. This lower sequence may correspond to the Palaeotethyan accretionary/fore-arc complex. This westernmost part of the Pindos basin could have been located on a major transcurrent fault, and locally inverted in Late Triassic times during the Eocimmerian phase and later on during lateral displacement between Africa and Eurasia.

Tectonic Evolution

The Palaeotethys closed definitely during the Carnian-early Norian times between the Eurasia-derived terranes (Anatolian terrane) and the Gondwana-derived terranes (Cimmerian terranes). This event provoked the development of flysch-like deposits followed by molassic developments, both usually sealed by Lower Jurassic carbonate platforms. This is for example the Shemshak Formation in Iran or the Çayır Formation in the Beyşehir-Hoyran Nappes in Turkey. The unified Cimmerian and Anatolian terranes formed a new micro-continent that was progressively covered by large carbonate platforms, extending from Apulia to Eastern Turkey, forming the northern passive margin of the East-Mediterranean Neotethys Ocean. Eastward, the same collision induced subduction reversal, and instead of the northward subduction of the Paleotethys, the Küre basin started to subduct southwards, leading to the opening of the Vardar and Izmir-Ankara oceans in the Jurassic. The latter became a back-arc ocean of the Neotethys Ocean, whereas the Vardar followed the west directed roll-back of the Maliac Ocean. The closure of the Küre, Maliac and Meliata oceans took place in the Late Jurassic, whereas the Pindos Ocean was not affected by these late Cimmerian events, and started to close only in the Late Cretaceous (first Pindos flysch). It finally was totally closed only in the Oligocene. On the contrary, its eastern Huğlu branch was affected by major ophiolite obduction in the Late Cretaceous and disappeared at that time.

This complicated scenario, although quite well constrained, explains the difficulties encountered so far in the understanding of the evolution of these different marginal oceans. Most of them are only known through exotic blocks found along their disappeared margins, and usually associated to younger ophiolites (Jurassic ones for Maliac, and Cretaceous ones for Huğlu), then most of these areas were involved in the Alpine shortening and collisional events. The other important point is the lateral (E-W) displacement of major blocks in regard of each other. This can be measured using Figure 6, where the southern part of Turkey is located south of Austria and the external Hellenides south of France. It is was through the opening of the Atlantic that these blocks were transferred eastwards, and through the Alpine shortening transferred northwards to their present location.

SYSTEMATICS

Conodonts

Only some Upper Triassic conodonts will be discussed. Pelagic Carboniferous, Permian and Lower Triassic conodonts and further Upper Triassic conodonts will be described and discussed in forthcoming papers. The material is housed in the Institut de Géologie et de Paléontologie, Université de Lausanne.

Genus *Carnepigondolella* Kozur, 2003

Type species: *Metapolygnathus zoae* Orchard, 1991.

Carnepigondolella nodosa (Hayashi, 1968)
(Plate 2, Figures 4-8)

Remarks: *C. nodosa* is one of the most problematical Upper Triassic conodont species. It was described from cherts which were originally assigned by Hayashi (1968) into the Permian, but the figured and described conodonts, among them several new species and the new genus *Metapolygnathus* Hayashi, indicate that conodonts from the late

Ladinian to the early Norian were present in this material. Unfortunately, Hayashi (1968) did not mention which species occur together. Thus, the age of the holotypes cannot be concluded from faunas but only from the species themselves. If no specific age can be assigned to a species, its age can be only determined as late Ladinian to early Norian. Normally the age assignment of the new species established by Hayashi (1968) does not generate too much problems, because several guide forms from the late Ladinian to Early Norian interval were described, which have a short range. However, *C. nodosa* is problematic regarding its age and, therefore, the age of the holotype can be only determined as late Ladinian to early Norian and under consideration, where such types do not occur as Julian to late Tuvalian. This species was for many years regarded as a middle Tuvalian guide form and even a middle Tuvalian *nodosa* Zone was used both in Tethys and in North America despite the fact that most of the Tuvalian forms are rather different from the holotype.

Krystyn (*in* Kristan-Tollmann and Krystyn, 1975) described an "*Epigondolella*" *carnica* Krystyn which is a stratigraphic species, mainly discriminated because it occurs in the upper Julian. However, as the holotype may be from the Julian or from the Tuvalian (see above), age differences cannot be used to confirm a separation of *carnica* from *nodosa*. The morphologic differences which Krystyn (in Kristan-Tollmnn and Krystyn, 1975) mentioned cannot be used to separate the upper Julian from the middle Tuvalian forms because the characters for the Julian forms are all also present in the Tuvalian forms and partly rather ontogenetic than taxonomic differences.

Kozur (2003) discussed the differences between both forms and concluded that the upper Julian forms correspond to the holotype which he had re-studied. Therefore, "*E.*" *carnica* Krystyn, 1975 is junior synonym of *C. nodosa* (Hayashi, 1968) s. s. He pointed out that in the upper Julian most forms have the largest platform width in the anterior third of the platform, whereas the middle Tuvalian forms are mainly widest close to the posterior end. However, superadult upper Julian forms are also widest close to the posterior end. The upper Julian forms have strongly upturned, narrow platform margins. The middle Tuvalian forms have only slightly upturned broad lateral platform margins with broad nodes. Taking these differences Kozur proposed to name the upper Julian forms as *C. nodosa* s. s and to use for the middle Tuvalian forms the names given by Orchard (1991). But he also mentioned that there is a certain overlap in the features between the upper Julian and the middle Tuvalian forms.

Further careful studies of the *C. nodosa* group from the upper Julian and middle Tuvalian have shown that the differences in Julian and Tuvalian *C. nodosa* may be ecologically controlled. Thus, even the *baloghi* morphotype of *C. carnica* can be found in the higher Tuvalian of the Northern Calcareous Alps and Western Carpathians. Especially interesting in this connection is the paper of Martini et al. (1991) from the Tuvalian part of the Mufara Formation in Sicily. The Mufara Formation comprises predominantly siliciclastic sediments related to the Reingraben Event. From the accompanying conodonts and sporomorphs, an Early Tuvalian age can be concluded. Thus, the Tuvalian types of the *C. nodosa* group should be expected. However, exclusively the late Julian morphotypes of typical *C. nodosa* are present with narrow, strongly upturned lateral platform margins, and the platform is widest in the anterior third. If these forms would occur in an upper Julian conodont fauna with *Gladigondolella tethydis* (Huckriede), it surely would be assigned to *C. carnica*. One illustrated more subtriangular form, widest at the posterior end (assigned by Martini et al. (1991) to *Paragondolella carpathica* Mock) has narrow lateral platform margins and such forms occur also in the late Julian type material. Thus, seemingly in the time of the Reingraben Event with predominantly siliciclastic sedimentation always the *carnica* morphotype (*C. nodosa* s.s.) is present, equal whether these sediments belong to the late Julian or early Tuvalian. However, also in cherty limestones of Sicily the upper Julian morphotype is present beside typical Tuvalian *C. zoae* (Orchard), as recognizable from the illustrations in Cafiero and De Capoa Bonardi (1982). The general absence of *C. nodosa* in earliest Tuvalian beds is not unusual for the distribution of Triassic conodonts. Thus, *Grodella delicatula* (Mosher) is common in the Early Anisian, Pelsonian, Cordevolian, late Norian and Early Rhaetian, but absent in most of the late Anisian–Ladinian, Julian and Tuvalian. As the example from the Mufara Formation shows, *C. nodosa* s.s. seemingly occurs not only in the late Julian but also in the Tuvalian. If the above mentioned features, which characterizes also the holotype, are present (platform widest in the anterior part, lateral platform margins strongly upturned and narrow), the forms should be assigned to *C. nodosa*, independent from a late Julian or a Tuvalian age. It seems that *C. nodosa* (including "*E.*" *carnica* Krystyn) represents a long –ranging form (upper Julian-upper Tuvalian), whereas forms with the character of Tuvalian forms (Kozur, 2003) are restricted to the middle and lower pat of upper Tuvalian (e.g. *C. zoae*).

Genus *Epigondolella* Mosher, 1968

Type species: *Polygnathus abneptis* Huckriede, 1958.

Epigondolella abneptis (Huckriede, 1958)
(Plate 1, figures 1, 2)

1958 *Polygnathus abneptis* n. sp. – Huckriede, p. 156-157, Pl. 14, only Figs. 12, 13, 16, 17, non ! Pl. 11, Fig. 33; Pl. 12, Figs. 30-36; Pl. 14, Figs. 1-3, 5, 14, ?18, 26, 27, 32, 47-58

Occurrence: So far only known from the Alaunian (type material and our material from the Fırıntaş Block (section A on Fig. 2) and Gâvuruçtuğu Block (section D on Fig. 2).

Remarks: *Epigondolella abneptis* (Huckriede) is one of the most used species names among the Norian conodonts, but nearly all forms assigned to this species, do not belong to it. In recent years, mostly lower Norian forms were assigned to *E. abneptis*, mainly *E. quadrata* Orchard (1991), but the holotype of *E. abneptis* is from the Alaunian of Sommeraukogel, and is distinctly different from all lower Norian *Epigondolella*. The unclear systematic position of *E. abneptis* is especially problematic because Mosher (1968) has chosen this species as the type species of *Epigondolella* Mosher. Originally, "*Polygnathus*" *abneptis* Huckriede included several species of different genera from the upper Anisian up the upper Norian. The upper Anisian form is a nodose gondolellid, which occur rarely in this level. The Carnian forms belong to different species of *Carnepigondolella* Kozur, 2003, the Norian forms belong partly to *Epigondolella*, e.g. *E. abneptis* (Huckriede) s.s., *E. quadrata* Orchard, *E. triangularis* (Budurov), partly to *Mockina*, e.g. *M. postera* (Kozur and Mostler), *M. bidentata* (Mosher).

Mosher (1968) left nearly all species, illustrated by Huckriede (1958), in *Epigondolella abneptis* (Huckriede), except one *Mockina bidentata*. Therefore, the original definition of *Epigondolella* based on its type species *E. abneptis*, is inaccurate. Likewise inaccurate was the *E. abneptis* Zone which has to be abandoned.

Kozur (2003) pointed out that the Alaunian holotype of *E. abneptis* is characterized by a low number of large denticles on the short free blade. Such forms from the upper Alaunian are illustrated in the present paper (Pl. 1, Figs.1, 2). *E. abneptis* should be restricted to such forms which correspond to the holotype and are derived from the same stratigraphic level as the holotype. In the other features (platform outline, denticulation of the anterior platform margin, undenticulated posterior platform, position of the pit), this *E. abneptis* s. s. is similar to *E. quadrata* Orchard. The closest relations exist to *E. praeslovakensis* n. sp. which has also a short free blade, but its posterior end descends quite abruptly, wall-like, as in *Mockina slovakensis* (Kozur).

Epigondolella praeslovakensis Kozur, Masset and Moix n. sp.
(Plate 1, Figs. 4-8)

Derivatio nominis: Forerunner of *Mockina slovakensis* (Kozur).

Holotype: The specimen on Pl. 1, Fig. 6.

Locus typicus: Mersin Mélange, section D, Gâvuruçtuğu Block (Figs. 2, 4).

Stratum typicum: Pelagic upper Alaunian limestone, sample MM030 (Fig. 4).

Material: More than 100 specimens.

Diagnosis: Platform slender to wide, outline variable, subrectangular to subtriangular. Platform margin with 2-3 large denticles in the anterior 2/3. Posterior third of the platform without denticles or with a denticle in each corner of the posterior margin. Additionally often a denticle on the posterior margin in continuation of the carina is present. Rarely an additional small denticle may be present on the posterior platform margin. The posterior platform margin is broadly rounded, often blunt, in the middle part often pointed by the denticle in continuation of the carina. The platform margins are only slightly elevated. The anterior carina with a short free blade is high, short, with a mostly short anterior denticle and 4-7 long, slender, highly fused denticles which are straight or slightly reclined. The posterior end of the anterior carina is abrupt, very high, wall like, only rarely a denticle is present which has the half length of the other denticles (except the first one) of the free blade. These forms (Pl. 1, Fig. 5) show transitional character to the anterior carina of *E. abneptis.* The posterior carina has conical small to moderately long denticles which are closely spaced in the anterior part and widely separated in the posterior part.

The lower side of the conodont has a wide to very wide, flat keel (attachment surface), in adults with a blunt, distinctly bifurcated posterior end. The bifurcation is symmetrical or slightly to moderately asymmetrical. The basal cavity lies below the middle of the platform. It has two indistinct oval pits at the anterior and posterior end of the basal cavity, which are only slightly widened compared with the broad basal furrow.

Occurrence: So far only known from the Neotethys or from areas with Neotethyan faunas and the Gâvuruçtuğu Block of the Mersin Mélange. Very common in the Gâvuruçtuğu Block. In limestones from intra-platform basins, it is the only present species. In pelagic limestones, it occurs together with *Epigondolella abneptis* s.s. (only in sample P 4, Fig. 4), *Mockina medionorica* Kozur and *M. zapfei* (Kozur), which allows an assignment to the upper Alaunian. Rare in the upper Alaunian of Sicily. Obviously Alaunian of Timor (in Martini et al., 2000 assigned to "*Epigondolella*" *slovakensis*). Alaunian of the middle part of the lower Member of the Dolomia di Forni Formation, Carnia, NE Italy.

Remarks: So far, *Epigondolella praeslovakensis* Kozur, Masset and Moix was assigned by Krystyn, for the last time in Martini et al. (2000) and Kovács (in Budai and Kovács, 1986, Kovács and Nagy) to "*Epigondolella*" *slovakensis* (Kozur). This misidentification lead to serious stratigraphic mistakes especially in determination of the age of monospecific *Mockina slovakensis* faunas from shallow intra-platform basins (e. g., Donofrio et al., 2003, Budai and Kovács, 1986, Kovács and Nagy, 1989), but perhaps also in some dating of *M. slovakensis*-bearing beds for palaeomagnetic studies (Gallet et al., 1992, 1993, 1996, 2000), see chapter biostratigraphic evaluation.

The main reason for the misindentification of *Epigondolella praeslovakensis* as "*Epigondolella*" *slovakensis* is the insufficient consideration of the development of the lower side. As we know from the well studied Palaeozoic conodonts, the development of the lower side, especially of' the position of the pit is decisive important for separation of genera and partly also species. Except some Triassic conodont workers, e.g. Budurov, Kozur, Metcalfe, Nicoll, and Wang Cheng-yuan, all with experience in Palaeozoic conodonts too, the majority of the Triassic conodont workers do not sufficiently regard the importance of the development of the lower side for separation of genera and species. Thus, for example, *Paragondolella polygnathiformis* (Budurov and Stefanov) and *P. noah* (Hayashi) are assigned to the *Metapolygnathus* Hayashi, despite the fact that the adults have a terminal to subterminal pit, whereas the adults of type *Metapolygnathus* have a pit in front of, rarely in the middle of the platform; in juvenile forms the pit is even located at the anterior end of the platform.

In *Epigondolella praeslovakensis,* the adults have a typical lower side of *Epigondolella* with broad, blunt posterior end of the keel (attachment surface) which is always distinctly bifurctated. The pit lies in or somewhat behind the middle of the platform. In adults of *Mockina slovakensis* (Kozur), the posterior end of the keel is mostly pointed or narrowly rounded with a pit in front of the middle of the platform as typical for *Mockina*. Only very rarely and mainly in the lower range of *M. slovakensis*, the posterior end of the keel is blunt, but even in these forms the pit lies in front of the middle of the platform. In several of the 1,000 investigated specimens, no *M. slovakensis* has a distinctly bifurcated posterior end of the keel as it is present in all adults of *E. praeslovakensis*. The posterior platform end of *M. slovakensis* is mostly pointed or narrowly rounded, but some specimens have a broad, blunt posterior platform end. The carina is identical in both species. Especially the abrupt, high, wall-like posterior end, which is not present in any other Triassic platform conodont, is present in both species and this feature together with the insufficient regarding of the development of the lower side, is obviously the reason for the misidentification by Krystyn and Kovács.

E. praeslovakensis has probably evolved from *E. abneptis* s. s. (see under this species) by development of the last denticle of the anterior carina to a very large denticle causing the abrupt, wall-like posterior end of the anterior carina.

E. postera (Kozur and Mostler) has also a rather abrupt posterior end of the anterior carina, but in general the last denticle of the anterior carina is distinctly smaller than the preceding one. By this and by the small size of adult *M. postera* the wall-like posterior end of the anterior carina is not so prominent. Moreover, adults of *M. postera* are much smaller than adult *E. praeslovakensis*. As within the *praeslovakensis-slovakensis* lineage the size becomes smaller, it is to expect that the forerunner of *E. praeslovakensis* was either as big as or bigger than *E. praeslovakensis*. The main argument against the derivation of *E. praeslovakensis* from *M. postera* is that *M. postera* has the typical Mockina lower side with a pointed posterior end of the keel in adults forms, whereas *E. praeslovakensis* has a terminally distinctly bifurcated typical *Epigondolella* keel. As the forerunner charácter of *E. praeslovakensis* to *M. slovakensis* is obvious (transitional forms in the Dolomia di Forni), the development of *E. praeslovakensis* and *M. slovakensis* from *M. postera* can be excluded.

Epigondolella praetriangularis Kozur and Moix n. sp.
(Plate 1, Figures 9, 10)

Derivatio nominis: Forerunner of *E. triangularis* (Budurov, 1972).

Holotypus: The specimen on Pl. 1, Figs. 9a,b.

Locus typicus: Mersin Mélange, Kocatabur Block (section C in Figs. 2, 4).

Stratum typicum: GRAY to pink micritic pelagic limestone, uppermost Carnian *E. orchardi* Zone, sample MM078 (Fig. 4).

Material: More than 50 specimens from the Mersin Mélange and Silická Brezová (Slovakia).

Diagnosis: Platform moderately large, subtriangular to triangular, broadest at the blunt posterior margin. Platform margins only slightly elevated, with short denticles. The lateral margins have 2-4 denticles which are concentrated to the anterior half of the platform. On the posterior platform only one denticle is developed, which may be also absent on one side. The posterior margin has 2-4 small denticles. The anterior carina with a long free blade is long, high, in the height regularly curved. The 9-11 denticles are highly fused, but their uppermost part is free. The last denticle is the small cusp which is only insignificantly larger then the forgoing denticle. After the cusp is mostly a gap, followed by a relatively large denticle considerably before the platform end. The keel on the lower platform side is wide with strongly bifurcated broad posterior end. The basal cavity lies about under the middle of the platform. The distinct basal furrow ranges into the basal cavity and is at its end and at the beginning of the basal cavity slightly widened.

Occurrence: The species occur from the Meliata-Hallstatt and Küre Oceans in the North to the Neotethys in the South, but it is never common. It can be found in the *E. orchardi* Zone and in the *E. quadrata* Zone, where it get more and more similar to *E. triangularis* (Budurov).

Remarks: *Epigondolella praetriangularis* is a transition form from *Carnepigondolella pseudodiebeli* (Kozur) to *Epigondolella triangularis* (Budurov). *C. pseudodiebeli* has in adults broad nodes on the lateral platform margins, whereas the posterior platform margin is smooth or has a node on each corner of the posterior margin. The basal cavity lies behind the middle of the platform. The transition between both species is in the *E. orchardi* Zone. *E. triangularis* has the same position of the basal cavity and the same platform outline, especially in *E. triangularis uniformis* Orchard. However, the denticulation of the platform margin is stronger and the platform denticles are longer. The transition between both species is in the lower *E. quadrata* Zone.

Epigondolella rigoi Kozur n. sp.
(Plate 2, Figure 1)

Derivatio nominis: In honour of Dr. Manuel Rigo, Padova, for his outstanding work on the conodont fauna of the Lagonegro Basin.

Holotypus: The specimen of "*Metapolygnathus abneptis spatulatus* (Hayashi)" illustrated by Noyan and Vrielynck (2000, Fig. 8-4), re-figured as *Epigondolella rigoi* in Noyan and Kozur, in press.

Locus typicus: Stefanion section (Argolis, Peloponnes, Greece)

Stratum typicum: Cherty limestone, sample L 157, *E. rigoi* Zone (middle Lacian).

Material: Several hundreds of specimens.

Diaguosis: Platform relatively short, its posterior part is strongly widened sometimes on one side but usually on both sides; platform outline subtriangular. In some forms there is only a slight widening in the posterior platform (mainly in late juvenile or subadult specimens), but even so these forms still have a relatively short platform. The posterior platform is flat, without marginal platform denticulation, but sometimes its posterior margin is wavy. When, in some specimens, an oblique or bifurcated ridge-like prolongation of the carina reaches to the posterior margin, a short denticle may be present as in several other *Epigondolella* species. In the anterior part of the platform, 2-4 denticles are present on each side. The carina is high in the anterior part (with a rather long free blade) and becomes steadily lower towards its posterior end which is located distinctly anterior to the platform end. The cusp is the last or penultimate denticle of the carina. Sometimes the carina may be bifurcated behind the cusp and both branches may bear 2 small denticles. Usually only one branch is distinct and the other one is indistinct or missing.

The keel is strongly bifurcated in its posterior part, the pit lying more or less beneath the middle of the platform. The distinct basal furrow runs from the pit to the anterior end of the keel.

Occurrence: *E. rigoi* Zone (lower Norian between the *E. quadrata* Zone and the *N. hallstattensis-E. triangularis* Zone) to Alaunian throughout the entire Tethys.

Remarks: *E. rigoi* Kozur n. sp. will be described *in* Noyan and Kozur (in press). As we have used in Fig. 5 the *E. rigoi* Zone and it is not clear, whether the Noyan and Kozur paper or the present paper will appear earlier, *E. rigoi* is described here to avoid the use of a nomen nudum. The former assignment of *E. rigoi* and the relations to other species is discussed *in* Noyan and Kozur (in press). Additionally a good example for assignment of *E. rigoi* to *E. triangularis* is Martini et al. (2000, Pl. 5, Figs. 3, 4).

Genus *Metapolygnathus* Hayashi, 1968

Type species: *Metapolygnathus communisti* Hayashi, 1968.

Metapolygnathus mersinensis Kozur and Moix n. sp
(Plate 1, Figures 14, 15)

Derivatio nominis: According to the occurrence in the Mersin Mélange.

Holotypus: The specimen on Pl. 1, Fig. 14.

Locus typicus: Kocatabur Block of the Mersin Mélange, section C (Fig. 2, 4).

Stratum typicum: Gray to pink micritic pelagic limestone of the *Epigondolella orchardi* Zone, uppermost Carnian. Sample MM078 (see Fig. 4).

Material: More than 100 specimens.

Diagnosis: Platform slender, subrectangular, with blunt, often slightly oblique posterior margin, mostly laterally slightly curved by one convex side and a concave to straight other side. The platform margins are moderately, in the posterior third only slightly upturned. In the anterior part of the platform there are on each side 2-3, rarely on one side 4 short denticles or long nodes. The anterior carina is high, with a long free blade. The denticles are there high and highly fused. Their length increases from the anterior margin gradually and then decreases gradually from the level, where the platform begins. The last denticle of the anterior carina is the cusp. It is small, not large, but mostly a little broader than the preceding denticle and not separated by a gap. After the cusp is a gap and then two relatively large, especially broad, widely separated denticles follow. The carina ends distinctly before the platform end, but sometime it continues in a low, undenticulated ridge which ranges until one posterolateral corner of the platform. The keel is rather broad and has a bifurcate broad posterior end. The basal cavity lies below the middle of the platform. Two indistinct pits indicated by a slight widening of the basal furrow are present at the anterior and posterior end of the basal cavity. The distinct and rather broad basal furrow reaches from the basal cavity until the anterior end of the conodont.

Occurrence: Common in the Neotethys of western Sicily and Oman. Common in the Neotethyan Kocatabur Block, very rare in the Kangal Block (the studies of this block are not yet finished). Not present in any northern Tethyan ocean and probably not present or very rare in the Pindos-Huğlu Ocean. *M. mersinensis* begins in the upper part of the C. *pseudodiebeli-M. communisti* Zone and is most common in the *E. orchardi* Zone of uppermost Carnian.

Remarks: Most similar is *Metapolygnathus primitius* (Mosher) to which this species was assigned until now. Platform outline, denticulation and lower side are identical or very similar (often *M. primitius* has a somewhat longer platform). The posterior carina is, however, distinctly different. In *M. primitius* the small cusp is followed after a gap by 3 densely spaced small denticles which are followed, after a gap by a further very small to rather large denticle. In more than 100 investigated adults of *M. mersinensis* after the cusp two, widely separated, relatively large denticles are present, very rarely a third denticle was observed which is also widely separated from the second one.

Genus *Misikella* Kozur and Mock, 1974

Type species: *Misikella longidentata* Kozur and Mock, 1974.

Misikella koessenensis Mostler, 1978/
"*Misikella*" *rhaetica* Mostler, 1978
(Plate 2, Figure 1)

Remarks: Kozur and Mock (1991) have shown that *Misikella ultima* Kozur and Mock evolved from *M. posthernsteini* Kozur and Mock by development of a secondary posterior blade with 1-3 denticles behind the primary blade of *M. posthernsteini*. The same development can be observed from *Misikella hernsteini* (Mostler) to *M. koessenensis*

Mostler, but the latter species develops mostly only one denticle behind the primary blade of *M. hernsteini*. Rarely, however, also a second small denticle is developed (Kozur and Mock, 1991, Pl. 7, Fig. 1). Mostler (in Mostler et al., 1978) described also a second species, “*Misikella*” *rhaetica* Mostler which has typically a posterior blade with 2-3 denticles, in so-called transition forms also one denticle. However, he figured only forms with 2 and 3 denticles on the posterior blade which he regarded correctly as the typical “*Misikella*” *rhaetica*. Forms with only one rather large and broad denticle have been separated by Kozur and Mock (1991) from “*M.*” *rhaetica* as *Parvigondolella rhaetica* Kozur and Mock. In contrast to all other *Misikella* species, in “*M.*” *rhaetica* then basal cavity is not present under the entire lower part of the blade, but only under the posterior half to 2/3 of the blade. In lateral view, the lower margin abruptly changes to a somewhat higher level as well shown by Mostler et al. (1978, Pl. 2, Fig. 4). Both these features (basal cavity only present in the posterior half to 2/3 of the conodont and characteristic abrupt change of the lower margin line in lateral view with the beginning of the basal cavity) are characteristic for *Parvigondolella* and never appear in *Misikella*. Therefore, we assign “*M*”. *rhaetica* Mostler, 1978 to *Parvigondolella*. By this, *Parvigogondolella rhaetica* Kozur and Mock, 1991 becomes a secondary homonym of *Parvigondolella rhaetica* (Mostler, 1978). We replace therefore the name *Parvigondolella rhaetica* Kozurand Mock, 1991 by *Parvigondolella prorhaetica* Kozur and Mock n. sp. Type locality, type stratum, holotype and description as for *Parvigondolella rhaetica* Kozur and Mock, 1991, p. 276.

For discussion of the stratigraphical importance of *Parvigondolella rhaetica* (Mostler), see chapter biostratigraphic evaluation.

Genus *Mockina* Kozur, 1990

Type species: *Tardogondolella abneptis postera* Kozur and Mostler, 1971.

Remarks: Orchard (2005) used the same scope of *Mockina* as Kozur (1990), but he regarded in the multilement taxanomy *Mockina* as a junior synonym of *Cypridodella* Mosher, 1968 because the holotype of the type species *Cypridodella conflexa* Mosher has been derived from beds with *Mockina bidentata* (Huckriede). How dangerous is this kind of apparatus reconstructions the *Cornudina apparatus* of Orchard (2005) shows. *Cornudina* was established in the Germanic Basin and it occurs there in large parts of the Germanic Basin in monospecific faunas which contain only the apparatus with *Cornudina* (Pa element). In the reconstruction by Orchard only the Pa and Pb element belong to the *Cornudina* apparatus. All other elements are part of a gondollelloid apparatus, whereas *Cornudina* belongs even to another superfamily then these elements. In the true *Cornudina* apparatus from monospecific faunas in the Germanic Basin *Chirodella* (M element), *Diplododella meissneri* (Tatge) (Sa element) and different *Neohindeodella* species (Sb and Sc elements) are present. Sa, Sb, Sc and M elements have an inverted lower side without basal cavity and basal furrow, but the ramiform element which Orchard (2005) assigned to *Cornudina* have all a well developed basal cavity and basal furrow and none of them is even a little similar to the true apparatus of *Cornudina*. Thus, apparatuses should be only constructed in monospecific faunas which have only one type of Pa element. In the sample with *Cypridodella conflexa*, not only *Mockina bidentata*, but also *Misikella hernsteini* (Mostler) with a very similar apparatus, *Norigonolella steinbergensis* (Mosher), all with Gondolellacea apparatuses, are present. But this is not the main problem. In the Paleozoic was a long discussion, whether the *Ozarkodina* apparatus should be named after the Pa element (*Ozarkodina*) or after the Sc element (*Hindeodella*), which has in the form taxonomy the priority. Finally, it was decided to use the name of the Pa element because it is specific for the genus, whereas the *Hindeodella* Sc element occurs in different species. According to Mosher (1968), *Cypridodella conflexa* occurs from the Lower Triassic up to the Norian from North America and Europe. *Mockina*, however, occurs only in the middle and upper Norian. Thus, these elements, like with the Paleozoic *Hindeodella*, occur in different multielement genera. Even if we use a more restricted scope of *Cypridodella conflexa*, this form species occurs from the Middle Triassic to the Rhaetian, clearly indicating that it belongs to different multielement genera. For this reason, a M element of gondolellid conodonts (*Cypridodella*) should never be used for the name of a multielement genus because it occurs in different multielement genera. What has be proven after many years of discussion to be correct in the Palaeozoic should be also applied in the Triassic. The names of multielement genera must be derived from specific elements which occur only in one multielement genus, the Pa elements. Kozur (2003) separated the North American stock of the former *Mockina* s.l. as *Orchardella* (*Orchardella multidentata* stock). This stock does not occur outside of the shelf of continental North America, but also this stock was assigned by Orchard (2005) into *Cypridodella* despite the fact that the type species of *Cypridodella* was established in the European Tethys (slope of the Meliata-Hallstat Ocean), where the *Orchardella* stock is not present.

Mockina bidentata (Mosher 1968)
(Plate 2, Figures 2, 3)

Remarks: Gallet et al. (2007) regarded *Parvigondolella andrusovi* and *P. lata* as morphological variants or ecostratigraphic morphotyps of “*Epigondolella*” *bidentata*. They pointed out that these forms replace “*E.*” *bidentata* in *Epigondolella* unfavourable environments. This is surely not the case. The replacement of *Mockina bidentata* by *Parvigondolella* occurs in quite different facies, red and gray Hallstatt Limestones, dark pelagic limestones, radiolarites. And it never occurs in the lower Sevatian (where only juvenile *M. bidentata* are similar to *Parvigondolella*, as all *Mockina* and even *Epigondolella* species have an earliest ontogenetic *Parvigondolella* stage followed by a *M. bidentata* stage, see Kozur, 1972), even if the facies is not favourable for *Mockina*, then often a *Norigondolella*-dominated fauna replaces *M. bidentata*. Moreover, *Mockina slovakensis* (Kozur) is very common in faunas dominated by *Parvigondolella andrusovi* Kozur and Mock and *P. lata* Kozur and Mock, as in the Neotethys of western Sicily. In several Tethyan sections, and so also in Tavusçayırı Block a very interesting development can be observed without facial changes. In the lower and middle Sevatian, the size of *M. bidentata* is reduced and the small forms below the *Misikella hernsteini-Parvigondolella andrusovi* Zone have in general only 1-3 denticles behind the cusp. They finally loose the lateral denticles and changed into *Parvigondolella*, which may be partly as large as or even larger than small *M. bidentata*. Then a fauna follows which is dominated by *M. hernsteini* and *Parvigondolella andrusovi* and *P. lata*. After this fauna, still within the *M. hernsteini-P. andrusovi* Zone, *M . bidentata* re-appears, but with distinctly different morphotypes than below the *M. hernsteini-P. andrusovi* Zone. The holotype of *M. bidentata* comes from this high level of *M. bidentata* which ranges up to the lower Rhaetian. Two morphotypes occur in this level with the type *M. bidentata*. One morphotype has a long anterior blade with numerous slender, highly fused denticles and a rather long posterior carina with 3-5 denticles. Such forms do not occur below the M. *hernsteini-P. andrusovi* Zone. The holotype belongs to this morphotype, but forms with 5 denticles on the posterior carina get close to *Orchardella mosheri*, but are not identical with it. They are here named as *M.* cf. *bidentata* (Pl. 2, Fig. 2). The second morphotype, which is somewhat smaller, is probably related to the *M. bidentata* below the *M*: *hernsteini-P. andrusovi* Zone. These forms have a short anterior carina with few, but big, especially broad denticles which are not so highly fused as in the other morphotype. These forms (Pl. 2, Fig. 3) look rather different from the first morphotype including the holotype and may represent a new species. But the development of the *M. bidentata* group must be studied in detail in several densely sampled sections before the subdivision of the *M. bidentata* group can be finished. Especially must be studied, what are the relations of *M. bidentata* below the *M. hernsteini-P. andrusovi* Zone to the two morphotypes in the younger *M. bidentata* fauna.

Radiolarians

Masset and Moix started to investigate the Mersin Mélange in 2002. The latter found new sections presenting very interesting Upper Triassic development of the Huðlu-type sequence. upper Carnian radiolarians were discovered already in 2002, and this was confirmed by detailed field studies in 2003. In 2003, several new species from the lower Tuvalian were also found. These results were briefly presented in Masset and Moix (2004) where it is written (p. 63) "il s'agit d'un calcaire micritique à radiolaires qui livre une faune impressionnante dont beaucoup de nouvelles espèces", proving this discovery before 2004. Since 2003, we are working on a monographic paper about the lower Tuvalian radiolarians of the Mersin Mélange which are rather characteristic for the Huğlu Unit of the Pindos-Huğlu Ocean and can be found also in other occurrences of the Huğlu Unit. As there are more than 300 species, more than 200 of which are new, this monographic investigation, in which also Dr. Péter Ozsvárt, Budapest, is involved, will take several years. Therefore, some of the new taxa, e.g. the index species of the lower Tuvalian radiolarian zone will be described in this and forthcoming short papers. In the monographic paper, the inner structure of the species will be documented in detail. To avoid parallel studies, some colleagues working in the same units or in the same age were informed about our monographic work on this radiolarian fauna after the discovery of this unique radiolarian fauna (see Kozur and Mostler, 2006) as Kozur and Mostler did since they started a monographic work on the Longobardian radiolarian fauna of Bosnia.

Family Gomberellidae Kozur and Mostler, 1981

Genus *Karnospongella* Kozur and Mostler, 1981

Type species: *Karnospongella bispinosa* Kozur and Mostler, 1981.

Karnospongella multispinosa Kozur, Moix and Mostler n. sp.

(Plate 2, Figure 11; Plate 4, Figure 1)

Derivatio nominis: After the distal spines on the two main spines.

Holotype: The specimen on Pl. 2, Fig. 11.

Locus typicus: Tavusçayırı Block (section B on Fig. 3).

Stratum typicum: Limestone intercalation in tuffs, sample G 11 (see Fig. 3), lowermost Tuvalian, *P. postinclinata-P. noah* conodont zone, *S. moixi* radiolarian zone.

Material: More than 100 specimens.

Diaguosis: Shell bottle-like, spongy. The two apical main spines include an angle of about 90 degrees. They are thick, moderately long, have narrow and very high ridges which are separated by deep and broad furrows. The ridges are strongly twisted (3-4 turns). At the terminal end of the main spines 4-5 short to moderately long, needle-like denticles branch off from the distal part of the ridges. These spines run in different directions. In the distal half of the shell 2 or 3 long, needle-like denticles are present, which are obliquely downward directed.

Occurrence: Lower Tuvalian of Sicily, Lagonegro Basin, Huğlu Unit of the type area and the Mersin Mélange.

Remarks: *Karnospongella bispinosa* Kozur and Mostler from the Julian of the Alps, Sicily, Lagonegro Basin and Huğlu Unit has two main spines with a pointed terminal end, in which the terminal part of the strongly twisted ridges do not bear spines.

Family Spongotortilispinidae Kozur and Mostler n. fam.

Diaguosis: Shell sphaerical, rarely discoidal, spongy. It consists of numerous (7-9) concentric layers (very densely spaced, somewhat irregular shells around a microsphaere which are connected by numerous bars. Two polar spines or 3 main spines in triangular arrangement are present. The ridges of the main spines are strongly twisted. Often also a secondary spiral torsion of the spines with the twisted ridge is present.

Assigned genera: *Spongotortilispinus* Kozur and Mostler n. gen., *Vinassaspongus* Kozur and Mostler, 1979

Occurrence: Upper Ladinian to Lower Norian.

Remarks: *Spongotortilispinus* was assigned to the recent genus *Spongostylus* Haeckel, 1882 by Kozur and Mostler (1979, 1981) and subsequent authors (e.g. Lahm, 1984, Tekin, 1999). This genus was assigned to the Stylosphaeridae Haeckel, 1882. However, the Stylosphaeridae with Spongostylinae Haeckel, 1882 have a different inner structure. The Spongostylinae either consist only of one spongy cortical shell or the include a latticed medullary shell (*Spongostylus*).

The Oertlispongidae Kozur and Mostler (*in* Dumitricã et al., 1980) which have a similar inner structure (but with more regular shells) are distinctly heteropolar with one strongly modified polar spine whereas the other polar spine is round and unmodified, and sometimes replaced by several needle like spines. The modification of the main polar spine is quite different from the Spongotortilispinidae. The round main polar spine is mainly curved or bifurcated and modifies into a blade-like, often spiny main pine.

The Zhamojdasphaeridae Kozur and Mostler, 2006, have, like the Oertlispongidae, numerous more clearly separated shells. The 3 main spines modify similar as the main polar spine at the Oertlispongidae to form twisted blades. In the Oertlispongidae and Spongotortilispongidae those parts of the main spines are unmodified, which are situated within the shell. In the Zhamojdasphaeridae the main spines are also modified to blades inside the shell (Pl. 4, Fig. 6).

Genus *Spongotortilispinus* Kozur and Mostler n. gen.

Type species: *Spongotortilispinus moixi* Kozur and Mostler n. sp.

Derivatio nominis: After the spongy shell and the strongly twisted spines.

Diagnosis: Shell sphaerical, spongy, consisting of numerous (7.-9) concentric layers which built somewhat irregular, very densely spaced shells around a microsphaere. The shells are connected by numerous short beams. The two polar spines show a strong torsion of the three ridges. Additionally, often also the spines are curved or show a distinct spiral torsion independent from the torsion of the ridges.

Assigued species: *Spongotortilispinus moixi* Kozur and Mostler n. gen. n.sp. *Spongostylus carncius* Kozur and Mostler, 1979; *Spongostylus tortilis* Kozur and Mostler, 1979; *Spongostylus aequicurvistylus* Lahm, 1984; *Spongotortilispinus inaequispinosus* Kozur, Moix and Mostler n. sp.; *Spongotortilispinus ozvarti* Kozur, Moix and Mostler n. sp.; *Spongotortilispinus turkensis* Kozur, Moix and Mostler n. sp.; *Spongotortilispinus tuvalicus* Kozur, Moix and Mostler n. sp.

Occurrence: Uppermost Ladinian to lower Norian of the Tethys.

Remarks: *Spongotortilispinus* Kozur and Mostler n. gen. was since Kozur and Mostler (1979) assigned to the recent genus *Spongostylus* Haeckel, which has a spongy cortical shell and only one medullary shell. Therefore the inner structure of this genus is quite different.

Vinassaspongus Kozur and Mostler, 1979 has three strongly twisted spines in triangular arrangement.

Spongotortilispinus moixi Kozur and Mostler n. gen. n. sp.

(Plate 2, Figure 9, 10; Pl. 3, Figs. 1-3)

Derivatio nominis: In honour of PhD Patrice Moix, Lausanne, for his outstanding work on the Mersin Mélange and the discovery of the well preserved rich radiolarian fauna.

Holotype: The specimen on Pl. 2, Fig. 10.

Locus typicus: Tavusçayırı Block (section B on Fig. 3).

Stratum typicum: Limestone intercalation in tuffs, sample G 11 (see Fig. 3), lowermost Tuvalian, *P. postinclinata-P. noah* conodont zone, *S. moixi* radiolarian zone.

Material: More than 50 specimens.

Diaguosis: With the character of the genus. The polar spines have 3 narrow high ridges separated by deep furrows. Proximal they are straight or only a little twisted. In a short middle part the ridges are twisted with only 2-3 turns. In the long distal part they are straight or only a little twisted and toward the distal end the ridges become lower and the separating furrows shallower and finally both disappear and the distal part of the polar spines becomes roundish without ridges. Independent from the torsion of the ridges, there is a distinct spiral torsion of one polar spine with maximally one turn. The other polar spine is strongly curved, but only a little twisted.

Occurrence: Lowermost Tuvalian of the Huğlu Unit in the type area and in the Mersin Mélange. Lower Tuvalian of the Lagonegro Basin and western Sicily.

Remarks: Kozur and Mostler wanted describe this species from the lower Tuvalian of western Sicily and the Lagonegro, before they had seen the very rich and well preserved material from sample 11. Later P. Moix allowed them to take the holotype from the better preserved material in sample 11, it was named as *Spongotortilispinus moixi*. As this species was chosen as type species for the lowermost Tuvalian, it is described in the present paper under Kozur and Mostler together with the new genus and the new family. The other new *Spongotortilispinus* species are described by Kozur, Moix and Mostler.

In most *Spongotortilispinus* species only the ridges are strongly twisted, whereas the polar spines are straight or curved, but not twisted. Only in *S. turkensis* Kozur, Moix and Mostler n. sp. also the spines are twisted. This species has, however, much stronger twisted ridges (7-9 turns against 2-3 in *S. moixi*).

Spongotortilispinus aequicurvistylus (Lahm, 1984)
(Plate 3, Fig. 8)

1984 *Spongostylus aequicurvistylus* n. sp. – Lahm, p. 69, 70, Pl. 12, Fig. 5

Occurrence: Upper Julian and lower Tuvalian of the Alps, Hungary, Lagonegro Basin, Sicily, Huğlu Unit of the type area and of the Mersin Mélange.

Spongotortilispinus inaequispinosus
Kozur, Moix and Mostler n. sp.
(Plate 3, Figure 5)

Derivatio nominis: According to the strongly different polar spines.

Holotype: The specimen on Pl. 3, Fig. 5).

Locus typicus: Tavusçayırı Block (section B on Fig. 3).

Stratum typicum: Limestone intercalation in tuffs, sample G 11 (see Fig. 3), lowermost Tuvalian, *P. postinclinata-P. noah* conodont zone, *S. moixi* radiolarian zone.

Material: 18 specimens.

Diagnosis: With the character of the genus. The polar spines have high narrow ridges separated by deep furrows. Straight proximal part of the polar spines rather long. In one polar spine follow a long middle part with strongly twisted ridges with 9-10 turns. It has a short straight proximal portion and a long oblique distal portion. The distal part of this polar spine consists of a long, needle-like distal spine. The distal part of the shorter second polar spine is also oblique, but in the opposite direction to the first one. The oblique part is shorter than or as long as the short straight part with twisted ridges. Because the oblique part of the second polar spine is much shorter than then in the first one, there are only 4-5 turns in the twisted part.

Occurrence: Huğlu Unit in the Mersin Mélange.

Remarks: There are three species, in which the distal part of the polar spines are curved in opposite directions. In *Spongotortilispinus carnicus* (Kozru and Mostler, 1979) both spines have a short oblique part and the larger part of the twisted portion in both polar spines is straight. In the lower Tuvalian *Spongotortilispinus ozsvarti* both polar spines have a long oblique part. The part with the strongly twisted ridges (on both polar spines with 8-9 turns) begins a little above the surface of the shell, and therefore the proximal part of the polar spines with straight ridges is very short.

Spongotortilispinus ozsvarti Kozur, Moix and Mostler n. sp.
(Plate 3, Figure 4)

Derivatio nominis: In honour of Dr. Péter Ozsvárt, Budapest, for his important Triassic and Jurassic radiolarian studies in Hungary.

Holotype: The specimen on Pl. 3, Fig. 4.

Locus typicus: Tavusçayırı Block (section B on Fig. 3).

Stratum typicum: Limestone intercalation in tuffs, sample G 11 (see Fig. 3), lowermost Tuvalian, *P. postinclinata-P. noah* conodont zone, *S. moixi* radiolarian zone.

Material: 7 specimens.

Diagnosis: With the character of the genus. The two polar spines are similar, but distally curved into opposite direction. The 3 ridges are very narrow, the furrows between them deep and broad. The proximal part with straight ridges is very short, the following part with strongly twisted ridges (8-9 turns on both polar spines) is long. The needle-like distal spine is also very long in both polar spines.

Occurrence: Only known from the type locality.

Remarks: See also under *Spongotortilispinus inaequispinosus* Kozur, Moix and Mostler n. sp. In *S. carnica* (Kozur and Mostler, 1979) also both polar spines are similar are curved in opposite direction. However, the oblique distal part is much shorter and only 4-6 turns can be observed in the part with twisted ridges.

Spongotortilispinus turkensis Kozur, Moix and Mostler n. sp.
(Plate 3, Figures 6, 7)

Derivatio nominis: After the occurrence in Turkey.

Holotype: The specimen on Pl. 3, Fig. 7.

Locus typicus: Tavusçayırı Block (section B on Fig. 3).

Stratum typicum: Limestone intercalation in tuffs, sample G 11 (see Fig. 3), lowermost Tuvalian, *P. postinclinata-P. noah* conodont zone, *S. moixi* radiolarian zone.

Material: 12 specimens.

Diagnosis: With the character of the genus. Both polar spines have 3 narrow, high ridges, separated by deep and broad furrows. The proximal part of the polar spines with straight or very slightly twisted ridges is relatively long. The following part has strongly twisted ridges with 7-9 turns. The distal spine is needle-like, on one polar spine very long, on the other polar spine moderately long. On polar spine is slightly spiral twisted (half to one turn). The other polar spine is curved in the same direction but not or only slightly twisted.

Occurrence: Lower Tuvalian of the type locality.

Remark: In *Spongotortilispinus moixi* Kozur and Mostler n. sp. the ridges on the polar spine are much fewer twisted (only 2-3 turns).

Spongotortilispinus tuvalicus Moix and Mostler n. sp.
(Plate 3, Figure 9)

Derivatio nominis: After the occurrence in the Tuvalian.

Holotype: The specimen on Pl. 3, Fig. 9.

Locus typicus: Tavusçayırı Block (section B on Fig. 3).

Stratum typicum: Limestone intercalation in tuffs, sample G 11 (see Fig. 3), lowermost Tuvalian, *P. postinclinata-P. noah* conodont zone, *S. moixi* radiolarian zone.

Material: 21 specimens.

Diagnosis: With the character of the genus. The 3 ridges on the polar spines are very high, narrow. The furrows between the ridges are very deep, broad. The proximal part with straight to very slightly twisted ridges is moderately long. The part with strongly twisted ridges is in one polar spine strongly curved perpendicularly to the axis. In the other polar spine this part is only slightly to moderately curved and often slightly twisted. A long, needle-like distal spine is present.

Occurrence: Lower Tuvalian of the type locality and of the type Huğlu Unit.

Remarks: Most similar is *Spongotortilispinus aequicurvistylus* (Lahm, 1984), in which, however, both polar spines are curved in the same manner.

Family Zhamojdasphaeridae Kozur and Mostler, 2006

Genus *Zhamojdasphaera* Kozur and Mostler, 1979

Type species: *Zamojdasphaera latispinosa* Kozur and Mostler, 1979.

Zhamojdasphaera latispinosa mersinensis Kozur, Moix and Mostler

(Plate 4, Figure 3)

Derivatio nominis: After the occurrence in the Mersin Mélange.

Holotypus: The specimen on Pl. 4, Fig. 3.

Locus typicus: Tavusçayırı Block (section B on Fig. 3).

Stratum typicum: Limestone intercalation in tuffs, sample G 11 (see Fig. 3), lowermost Tuvalian, *P. postinclinata-P. noah* conodont zone, *S. moixi* radiolarian zone.

Material: 9 specimens.

Diaguosis: Shell in upper view subsphaerical to subtriangular. The shell is spongy and consists of 6-7 very densely spaced shells around a microsphaere which are connected by numerous short bars. The 3 main spines in triangular arrangement are blade-like, very broad, twisted in propeller-like manner, so that their total widths is recognizable in the distal part before they become narrower, as typical for Upper Triassic *Zhamojdasphaera*. Distally the spines are gradually pointed and on the distal end a very long, needle-like distal spine is present.

Occurrence: Lower Tuvalian of the Huğlu Unit in Turkey and of the Lagonegro Basin.

Remarks: *Zhamojdasphaera latispinosa latispinosa* Kozur and Mostler, 1979 from the Julian of the Alps and Sicily has also blade-like, twisted, distally pointed main spines, but if a needle-like distal spine is present, it is very short.

Zhamojdasphaera rigoi Kozur, Moix and Mostler n. sp.

(Plate 4, Figures 2, 4-6)

Derivatio nominis: In honour of Dr. Manuel Rigo, Padova, for his help for our paper.

Holotype: The specimen on Pl. 4, Fig. 2.

Locus typicus: Tavusçayırı Block (section B on Fig. 3).

Stratum typicum: Limestone intercalation in tuffs, sample G 11 (see Fig. 3), lowermost Tuvalian, *P. postinclinata-P. noah* conodont zone, *S. moixi* radiolarian zone.

Material: More than 100 specimens.

Diaguosis: Shell in upper view subtriangular, spongy, consisting of 6-7 very densely spaced shells which are connected with each other by numerous short beams; the inner continuation of the 3 very broad, blade-like main spines is also blade-like within the shell (Pl. 4, Figs. 6a,b). The 3 main spines are in triangular arrangement, in their proximal part not or only a little twisted, in the distal part strongly twisted in propeller-like manner. The distal part of the main spines is broadly rounded, partly blunt, with a short, needle-like to narrow triangular distal spine or with a long, needle-like distal spine.

Occurrence: Lower Tuvalian of Sicily, Lagonegro Basin and Mersin Mélange.

Remarks: In *Zhamojdasphaera latispinosa* Kozur and Mostler, 1979 the distal end of the broad, blade-like main spines is gradually pointed with short or long spine at the tip. Two subspecies can be distinguished according to the length of the distal spine.

Zhamojdasphaera rigoi rigoi Kozur, Moix and Mostler n. sp.

(Plate 4, Figs. 2, 6)

Holotype, locus typicus and stratum typicum: As for the species.

Material: 43 specimens.

Diagnosis: With the species character. Distal spine very long, needle-like.

Occurrence: In the lower Tuvalian of the Lagonegro Basin and the Mersin Mélange.

Remarks: *Zhamojdasphaera rigoi brevispinosa* Kozur, Moix and Mostler n. subsp. has short need-like, rarely narrow triangular distal spines.

Zhamojdasphaera rigoi brevispinosa

Kozur, Moix and Mostler n. sp.

(Plate 4, Figures. 4, 5)

Derivatio nominis: After the short dirsal spines.

Holotype: The specimen on Pl. 4, Fig. 5

Locus typicus: Tavusçayırı Block (section B on Fig. 3).

Stratum typicum: Limestone intercalation in tuffs, sample G 11 (see Fig. 3), lowermost Tuvalian, *P. postinclinata-P. noah* conodont zone, *S. moixi* radiolarian zone.

Material: More than 100 specimens.

Diagnosis: Material: 81 specimens.

Diagnosis: With the species character. Distal spine short, needle like, rarely narrow triangular.

Occurrence: Lower Tuvalian of Sicily, Lagonegro Basin and Mersin Mélange.

Remarks: *Zhamojdasphaera rigoi rigoi* Kozur, Moix and Mostler n. subsp. has very long, needle like distal spines.

BIOSTRATIGRAPHIC EVALUATION

Conodonts

The conodonts belong to the stratigraphically most important fossils in the Triassic. However, there are still some problems which lead to serious miscorrelations. Two of these problems will be discussed in the following chapter.

The age of *Mockina slovakensis* and *Parvigondolella vrielyncki*

Kozur (1972) established *Mockina slovakensis* from beds immediately above the uppermost Norian *Misikella hernsteini* Zone and below the Rhaetian *M. posthernsteini* Zone. In the type stratum among the conodonts also after re-sampling only some specimens of *M . slovakensis* and no other conodonts (except few ramiform elements of the *M. slovakensis* apparatus) occur, the original sampling yielded only one specimen. Kozur (1972) assigned these beds to the uppermost Sevatian, but an earliest Rhaetian age cannot be excluded. uppermost Norian age was confirmed by Gullo (1993, 1996) who found *M. slovakensis* throughout the entire Sevatian, especially common in open sea pelagic limestones of the *M. hernsteini-P. andrusovi* Zone, but no more in the Rhaetian. Kozur has seen this material and could confirm all determinations by Gullo. In the open sea shelves and slopes of the Meliata-Hallstatt and Küre oceans, *M. slovakensis* is present throughout the Sevatian, but not in the Rhaetian. Its uppermost occurrence is in the uppermost Norian beds. However, as shown by the detailed conodont studies of Channell et al. (2003) in the Silická Brezová section (Slovakia), this species is always very rare in open sea environments around these oceans. In the contrast, it is very common, and occurs there in monospecific associations in Norian intraplatform basins, especially within the Hauptdolomit, which can be only dated by *M. slovakensis*. More than 20 years ago, Krystyn found well dated middle Norian "*E. slovakensis*" in Timor, which he never published or illustrated. He has shown this material to Kovács, who was so convinced from the middle Norian age of

M. slovakensis that he pointed out that the type material comes from an allodapical limestone with reworked conodonts according to his opinion supported by later stratigraphic data (the middle Norian *M. slovakensis* of Timor found by Krystyn). However, the type stratum is not an allodapical limestone but a strongly marly dark gray micritic limestone to hard calcareous marl without any sign of reworking at the conodonts and foraminifers as already mentioned by Kozur (1972) in the original description. Later stratigraphic data especially from Gullo (1993, 1996) have not confirmed that *M. slovakensis* is reworked from older beds but it is most common in the uppermost Norian immediately below the Rhaetian (Gullo, 1993, 1996 and own material). Kovács and Nagy (1989), found *M. slovakensis* in the level of *Rhabdoceras suessi*. Mainly on the base of *M. slovakensis* with its assumed middle Norian age the Seefeld Formation of the Alps was assigned to the middle Norian (Donofrio et al., 2003) using the unpublished data of Krystyn and the published data of Budai and Kovács (1986) and Kovács and Nagy (1989) which have used the unpublished middle Norian *M. slovakensis* of Timor.

In Martini et al. (2000) Krystyn finally illustrated his "*Epigondolella slovakensis*" from Timor. In the explanation of the plates, the were assigned to the Lower Norian, but this is surely a printing mistake because in the text the occurrence of *E. slovakensis* was used to confirm the middle Norian age of the beds. Thus, still in 2000 Krystyn was convinced that *M. slovakensis* is a middle Norian guide form! The three specimens illustrated in Martini et al. (2000) are really typical middle Norian (partly latest middle Norian) guide forms, but they do not belong to *M. slovakensis*. The specimen in Martini et al., 2000, pl. 5, figs. 21-22 belongs to *Epigondolella praeslovakensis* Kozur, Masset and Moix n. sp. No lower side was figured which is very important for distinction between *E. praeslovakensis* and *M. slovakensis*. However, in the upper view is clearly to seen that the end of the carina is bifurcated into two smooth ridges which run into the posterolateral corners. This feature indicates that the end of the keel is bifurcated as in *E. praeslovakensis*. Moreover, slender forms with blunt posterior end as the figured specimen are common in *E. praeslovakensis* but absent in *M. slovakensis*. The rare forms of *M. slovakensis* with blunt posterior end of the platform have all a very broad short platform.

The other two specimens illustrated under *E. slovakensis* do even not belong to the *M. slovaken*sis group, because they have a gradual descending of the posterior end of the carina. The specimen in Martini et al. (2000), pl. V, figs. 13-14 is *Mockina zapfei* (Kozur), a guide form for the uppermost Alaunian and lower Sevatian. The specimen on pl. V, figs. 7-18 is *Mockina* ? *medionorica* Kozur a guide form of the middle Norian in the entire Tethys. These illustrations clearly indicate that *M. slovakensis* reported by Krystyn and co-authors from the middle Norian of Timor are really middle Norian, but at least to the largest part not *M. slovakensis*. Thus, the papers where the middle Norian age of he upper Norian *M. slovakensis* were used, has to be revised. Most important is the age of the Seefeld Formation of the Alps. Beside *M. slovakensis* the dating as middle Norian is based on two further species, "*Epigondolella*" *carinata* Orchard and "*Epigondolella*" *postera* (Kozur and Mostler). Denticulation of the posterior platform occur in some *M. slovakensis* and also in *E. praeslovakensis*. The two illustrated specimens determined by Donofrio et al. (2003) as "*E.*" *carinata* have a wall like posterior end of the anterior carina. They belong to *M. slovakensis*. In *M. carinata* the posterior end of the anterior carina is rapidly, but gradually descending. *M. postera* is smaller, but similar to those specimens of *M. slovakensis* which have on one side of the lateral platform margin one denticle on the other side two denticles. This is especially the case in those forms of *M. slovakensis* in which the last denticle of the anterior carina has about half the length of the preceding denticle. This feature can be also observed in some *E. praeslovakensis* (Pl. 1, Fig. 5). In *M. slovakensis* this feature can be occasionally observed until the *M. hernsteini*-*P. andrusovi* Zone. Such forms belong in a population to *M. slovakensis* and not to *M. postera*, which is never present in the *M. hernsteini*-*P. andrusovi* Zone. The dominating typical *M. slovakensis* in the Seefeld Formation and the total absence of *E. praeslovakensis* indicate a Sevatian age of the Seefeld Formation. The Rezi Dolomite below the Rhaetian Kössen Beds in the Keszthelyi Mts. (Hungary) also contains typical *M. slovakensis* correctly determined by Budai and Kovács (1986). The conodonts occur there between the underlying Hauptdolomit and the overlying Rhaetian Koessen Beds in the upper part of the Rezi Dolomit Formation, closer to the Koessen Beds than to the Haudolomit. Already from the stratigraphic position in the sequence a late Sevatian age is probable, and this is also indicated by the rather advanced *M. slovakensis*. Budai and Kovács (1986) assigned these beds into the upper part of Alaunian regarding that age for "*E. slovakensis*" from Timor, but they did not exclude early Sevatian age because in that time Kovács and Nagy had already known the occurrence of *M. slovakensis* together with *Rhabdoceras suessi* in the Pilis Mts., later published in Kovács and Nagy (1989) A late Alaunian to early Sevatian age was also assigned to the Avicula Limestone of the Pilis Mts., where, however, *M. slovakensis* occurs together with the Sevatian to Rhaetian *Rhabdoceras suessi*. For the Alaunian age they again referred to Krystyn's unpublished material from Timor which is, as pointed out above, not *M. slovakensis*. The determinations of *M. slovakensis* by Kovács and Nagy (1989) were correct. Morphotypes which Donofrio et al. (2003) assigned to *Epigondolella carinata*, they correctly assigned to *M. slovakensis*, and also morphotypes with the *M. postera* denticulation they assigned to *M. slovakensis* as we do.

The Dolomia di Forni (Carnia area, NE Italy) was also assigned to the Alaunian on the base of the Alaunian age of "*E. slovakensis*" from Timor. The material is well documented by Roghi et al. (1995). On their pl. I, figs. 1-4 they illustrated typical *M. slovakensis*, including that morphotype, which Donofrio et al. (2003) erroneously put into *M. carinata* (Orchard). These specimens are correctly determined as "*E.*" *slovakensis* and they are derived from the uppermost part of the lower member of the Dolomia di Forni, which can be assigned according to these typical *M. slovakensis* to the Sevatian. From the middle part of the lower member of the Dolomia di Forni Roghi et al. (1995) illustrated one lower side of a form which can be regarded as a very advanced *E. praeslovakensis*, transitional to *M. slovakensis*. It has a slightly bifurcated posterior end of the keel. Thus, this level is probably latest Alaunian. *E. praeslovakensis* is surely present in the deeper part of the Dolomia di Forni Formation, because Roghi et al. (1995) reported also forms with bifurcated posterior end of the keel. From the lower part of the lower member of the Dolomia di Forni Formation a very short and broad, arrow-like form is illustrated in which the two posterior denticles of the anterior carina are broken in their fused part. Thus, an exact determination is difficult. This form is very small, but nevertheless an adult form, as also pointed out by Roghi et al. (1995). It is much too small for an adult *M. slovakensis*, but also too small for an adult *E. praeslovakensis*. It could be a *M. postera*. In any case, such small *Mockina* of the *M. postera* group are known from the upper Alaunian. Thus the Alaunian-Sevatian boundary lies obviously within the higher part of the lower Dolomia di Forni Formation of Carnia (NE Italy).

Further published occurrences of true *M. slovakensis* are all from the Sevatian (e.g., Amodeo et al., 1993 in the Lagonegro Basin), including the upper Sevatian *M. hernsteini* Zone (e.g., Meço, 1999). In evaluation of all our material from *M. slovakensis* and *E. praeslovakensis* we can conclude that monospecific faunas which consist only of true *M. slovakensis* belong to the Sevatian up to the top of the *M. hernsteini* Zone. The FAD of *M. slovakensis*, as already assumed by Channell et al. (2003), is in the latest Alaunian, where it occurs together with advanced *E. praeslovakensis*. Monospecific faunas which consist exclusively of *E. praeslovakensis* belong to the middle to late, but not latest Alaunian.

The illustrations of middle Norian "*E. slovakensis*" from Timor in Martini et al. (2000) also are very important for the evaluation of the ages of faunas with "*Epigondolella* n. sp. D" which was used by Gallet et al. (1992, 1993, 1996, 2000) as a guide form for the upper Alaunian for dating palaeomagnetic samples in the Antalya nappes. In Gallet et al.

(2000) it was stated that this form is very similar to "*E.*" *slovakensis*. As I was not illustrated, there were several possibilities of interpretation. (1) *M. slovakensis* could be a long-ranging middle-upper Norian form, but then I would not be clear, why this species is neither in Sicily nor in Slovakia found in the middle Norian, except primitive forms in the latest Alaunian in Sicily (and in the Dolomia di Forni Formation). (2) The upper Alaunian in Gallet et al. (1992, 1993, 1996, 2000) could be lower Sevatian, but the palaeomagnetic correlations rather indicate that the middle Norian with "*Epigondolella* n. sp. D" is really middle Norian and only the *Parvigondolella vrielyncki* fauna (= "*Epigondolella* n. sp. E" fauna) is Sevatian and not Alaunian as corrected by Channell et al. (2003). The early Sevatian age of the *P. vrielyncki* fauna and by this the correction by Channell et al. (2003) of the dating of the magnetozones in Gallet et al.(1992, 1993, 1996, 2000) was confirmed in the Fırıntaş Block, where sample I 5 has a late Alaunian fauna, the next younger sample I 4 with *Parvigondolella vrielyncki* Kozur and Mock and *M. bidentata* (Mosher) a lower Sevatian fauna (see Fig. 3 and chapter investigated sections). (3) "*E. slovakensis*" sensu Krystyn from the Antalya nappes is *E. praeslovakensis* but this would be the only rich occurrence of *E. praeslovakensis* outside the Neotethys. (4) A middle Norian *Epigondolella* or *Mockina* not belonging to the *M. slovakensis* group was erroneously determined as "*E.*" *slovakensis,* but this was difficult to imagine because the *M. slovakensis* group is clearly distinguished by the very high, wall like end of the anterior carina. As in Martini et al. under "*E.*" *slovakensis*" three different Alaunian or upper Alaunian species were illustrated, none of which belong to *M. slovakensis* and only one is *E. praeslovakensis*, this problem is solved, the upper Alaunian dating for the "*Epigondolella* n. sp. D Zone" can be confirmed and this must not be based on *E. praeslovakensis* which would bring problems with the palaeobiogeographic conodont distribution. The "*Epigondolella* n. sp. E Zone" (*Parvigondolella vrielyncki* fauna), however, is not late Alaunian, but Sevatian.

Parvigondolella rhaetica Zone versus *Misikella koessenensis* subzone

In our conodont zonation we use for the lower part of upper Rhaetian (middle Rhaetian) the *Misikella koessenensis* Subzone of the *M. posthernsteini* Zone. Krystyn in Gallet et al. (2007) and former papers uses for the same interval the "*Misikella*" *rhaetica* Zone. As shown in the systematic part true "*Misikella*" *rhaetica* is a *Parvigondolella*, in which the basal cavity does not reach the anterior end of the conodont (correctly stated in the diagnosis by Mostler (in Mostler et al., 1978) as in all *Misikella* species. The use of *Parvigondolella rhaetica* (Mostler) as zonal index species is very problematical because this species is the most rare Triassic conodont species. We have made many conodont studies in this interval in the European Tethys and have investigated more than 300 *Misikella* specimens from this interval. *M. koessensis* is also a rare form, but we have more than 30 specimens form this species. From *Parvigondolella rhaetica* (Mostler) we have only 3 specimens and also Mostler (in Mostler et al., 1978) had not much more specimens. Moreover, this species was revised by Kozur and Mock (1991) which have restricted the species to typical forms (according to Mostler, 1978) with 2-3 denticles on the posterior blade. Gallet et al. (2007) regarded *Oncodella paucidentata* (Mostler) as so rare that in cannot be used as an index species. However, it is much more frequent than *P. rhaetica*. Taking this into consideration it was rather clear, that "*Misikella*" *rhaetica* sensu Krystyn cannot be "*M.*" *rhaetica* sensu Mostler. However, before Gallet et al. (2007) this form was never illustrated by Krystyn. Mostler (in Mostler et al., 1978) regarded the short basal cavity in "*M.* " *rhaetica* as decisive feature. This basal cavity is only present under the posterior half to 2/3 of the conodont, unknown from any *Misikella* species (see chapter systematics). As to expect, none of the forms illustrated in Gallet et al. (2007) as "*Misikella" rhaetica* belongs to this species; figs. 3-7, 3-9 and 3-10 are typical *Misikella* with a basal cavity under the entire lower side, as diagnostic for the genus *Misikella*. By this can be clearly excluded that these forms belong to *Parvigondolella rhaetica* (Mostler). They have one denticle behind the anterior blade and correspond to *Misikella koessenensis*, which has mostly one denticle behind the anterior blade which can be very small, slender or rather large and broader. All transitions between the forms with different size of the posterior denticle are present throughout the entire range of this species. The taxonomic position of the specimen on figs. 3-8 is not quite clear, but surely also this form is not a *Parvigondolella rhaetica* because it has only one very broad denticle behind the anterior blade, whereas typical *P. rhaetica* have 2-3 slender denticles. The anterior part of the specimen was slightly downward tilted during taking the picture, and therefore it is unclear whether the basal cavity reaches until the anterior end (in is case it would be *Misikella* cf. *koessenensis*) or (more probably) the basal cavity covers only the posterior half of the lower side and in this case it would be *Parvigondolella prorhaetica* Kozur and Mock (new name for *Parvigondolella rhaetica* Kozur and Mock, 1991 because of secondary homonymy with *Parvigondolella rhaetica* (Mostler, 1978, see chapter systematics). Thus, obviously, true *Parvigondolella rhaetica* (Mostler) is also in Krystyn`s material as rare as in our material and he was not able to figure a single specimen of this species. As obviously most of his "*Misikella*" *rhaetica* are in reality *Misikella koessenensis* and he wrote that his "*M.*" *rhaetica* Zone is defined by the co-occurrence of "*M.*" *rhaetica* with *M. koessenensis* and *M. psosthersteini*, also the fauna of Krystyn`s "*M.*" *rhaetica* Zone is not characteriszed by *M. rhaetica* but by *M. koessenensis.* Thus, the name of the zone/subzone should be in all cases *M. koessensis* Zone/Subzone. We prefer the name *M. koessenensis* Subzone of the *M. posthernsteini* Zone because *M. koessenensis* is much less frequent than *M. posthernsteini* (ratio *koessenensis*:*posthernsteini* generally below 1: 10). The second reason is that *M. koessenensis* begins much earlier, already in the lower part of the *M. hernsteini* Zone. There it is very rare (ratio *koessenensis* : *hernsteini* below 1:100), but nevertheless, in such case it is better to use only a *koessenensis* Subzone for the level, where *M. koessenensis* is no longer extremely rare. A *M. koessensis* from the lower *M. hernsteini* Zone is illustrated on Pl. 2, Fig. 1.

Gallet et al. (2000) pointed out that in the Oyuklu section (Turkey) in contrast to the Csõvár section, there is no space for a post-*ultima* conodont interval because the conodont record ends with *M. ultima* just below the boundary clay. This situation is identical with Csövár. Also there the *M. ultima* Zone reaches immediately below a clayey-silty horizon which may be named as Gallet et al. (2007) did, as a boundary clay. This boundary clay is situated below the first Liassic radiolarians and ammonoids and belong to the Rhaetian. Very rarely, *N. detrei* is present in these beds and it becomes then more common in beds with Liassic radiolarians before the conodonts finally disappear. In Figure 5 the *detrei* Zone is not shown, because it straddles the Rhaetian-Hettangian boundary and has so far no ammonoid correlation. Thus, our Figure 5 ends with the top of the *Choristoceras marshi* Zone and the top of the *M. ultima* Zone.

Radiolarians

The Middle and Upper Triassic radiolarians belong to the most important biostratigraphic groups. Their resolution potential is from the Illyrian to Rhaetian higher than that of the conodonts and as high as or higher than that of the ammonoids. The problem is that most of the Triassic species are not yet described and for original description very well preserved faunas are necessary, in which also the inner structure can be observed. One such fauna we have found in the lowermost Tuvalian which we study since 2003. More than 2000 SEM pictures have been taken. We have found so far more than 300 species, most of them are new. This fauna is very interesting because it has lived close to the end of the Reingraben Event. The likewise very rich and well preserved radiolarian fauna from the Julian of Austria described by Kozur and Mostler (1972, 1978, 1979, 1981, 1982, 1983, 1994) and Lahm (1984) has been collected from beds immediately below the Reingraben Event (0.5 – 5 m below the middle Carnian shales). Thus, after finishing our monographic work, we can evaluate the importance of the ecological changes connected with the Reingraben Event for radiolarian faunas. Until now can be recognised that the majority of the genera straddles the Reingraben Event, but most of the lower Tuvalian species are different from the upper Julian species of the same genera. Moreover, a clear diversification can be observed in some families, e.g. within the Xiphothecidae, and some forms appear for the first time which are common only in the Jurassic, e.g. *Protunuma*. A new radiolarian zone, the *Spongotortilispinus moixi* Zone is established for the lower Tuvalian.

Spongotortilispinus moixi Zone

Definition: Range Zone of *Spongotortilispinus moixi* Kozur, Moix and Mostler n. gen. n. sp., together with numerous Xiphothecidae, Spongotortilispinidae, *Protunuma* spp., *Karnospongella multispinosa* Kozur, Moix and Mostler n. sp., *Zhamojdasphaera rigoi* Kozur, Moix and Mostler n. sp.

Lower boundary: FAD of *Spongotortilispinus moixi* Kozur, Moix and Mostler n. gen. n. sp., *Karnospongella multispinosa* Kozur, Moix and Mostler n. sp., *Zhamojdasphaera rigoi* Kozur, Moix and Mostler n. sp., first *Protunuma* and many highly specialized Xiphothecidae.

Upper boundary: FAD of first *Capnodoce*, LAD of *Spongotortilispinus moixi* Kozur, Moix and Mostler n. gen. n. sp., *Karnospongella multispinosa* Kozur, Moix and Mostler n. sp.

Remarks: As Kozur an Mostler (1994) established the upper Julian *Tetraporobrachia haeckeli* Zone , they could not exactly define the upper boundary of this zone because from the lower Tuvalian only badly preserved or not well dated radiolarian faunas were present. With the establishment of the well dated *S. moixi* Zone, the upper boundary of the *Tetraporobrachia haeckeli* Zone can be well defined. Most genera of the *T. haeckeli* Zone can be also found in the *S. moixi* Zone, but mostly with other species than in the *T. haeckli* Zone. Especially important is the FAD of the new *Spongotortilispinus* species, which have been described in the present paper and which are not yet present in the *T. haeckeli* Zone as well as the FAD of *Karnospongella multispinosa* Kozur, Moix and Mostler n. sp. and *Zhamojdasphaera rigoi* Kozur, Moix and Mostler n. sp., which are also not yet present in the rich *Karnospongella* and *Zhamojdasphaera* faunas of the *T. haeckeli* Zone. Very important is also rapid radiation of the Xiphothecidae, with highly specialized forms which are not yet present in the *T. haeckeli* Zone, and the FAD of *Protunuma*. Most important for the definition of the upper boundary is the FAD of *Capnodoce* because the immediate forerunner of *Capnodoce* is already present in the *S. moixi* Zone.

Palaeo(bio)geographic Evaluation

Depending on the paleogeographic constellation, the faunistic connections and differences between the Tethyan oceans changed in different times. In the Lower and Middle Permian, the conodont and radiolarian fauna is rather uniform in the Tethys. Only in the eastern Neotethys and its Perigondwana margin, a Gondwanide cool-water conodont fauna is present. In the Upper Permian the western Neotethys and Palaeotethys have totally different radiolarian faunas. In the Neotethys, the *Ishigaconus* fauna is present, which can be traced until New Zealand, and in the Palaeotethys, the *Neoalbaillella-Imotoella* fauna is present. The Upper Permian *Ishigaconus* and *Neoalbaillella-Imotoella* faunas are also separated in different terranes in Japan, but there not so strictly different as in the western Tethyan realm. Lower Triassic faunas are uniform in the Tethys. During the Middle Triassic to Cordevolian (lower Carnian) an increasing separation of the Neotethyan fauna from the Palaeotethyan fauna can be observed which has its maximum in the Cordevolian. During the Longobardian and Cordevolian the conodont, ostracod, holothurian sclerite and even sponge spicule faunas of the Neotethys and its shelves are quite different from the faunas north of the Apulian-Tauride High and its eastern continuation into the eastern Tethys. To the latter palaeobiogeographic realm belong shelves, rift basins, and oceanic basins in the Pindos-Huğlu Paleogeographic Realm, in which during the Julian (middle Carnian) the Pindos-Huğlu Ocean opened, the remnant Paleotethys and its back-arc basins (Maliac Ocean, Karakaya Basin, Meliata-Hallstatt Ocean, Küre Ocean).

A total change in the boundaries of the palaeobiogeographic realms occurred with the Reingraben Event (Schlager and Schöllnberger, 1974), which is in the Tethys more than only the Middle Carnian Pluvial Event (sensu Simms and Ruffell, 1989) of the continental Basins, like the Germanic Basin and in the Newark Supergroup of the eastern North American Upper Triassic-Liassic rift basins (see Kozur and Weems, this volume). In the Tethys, tectonic movements play also an important role which is related to the closure of the Paleotethys and opening of the Pindos-Huğlu Ocean. By these palaeogeographic changes the Apulian-Tauride High was broken in the middle Carnian in two places (Kozur, 2000, Stampfli and Kozur, 2006). By this, warm water currents from the equatorial Neotethys could penetrate the vast area of the western Tethys north of the Apulian-Tauride High. This may have caused a drastic temperature rise in this vast area and by this a mega-monsoon system was established which caused the Middle Carnian Pluvial Event in the continental areas north and northwest of the Tethys (Germanic Basin, rift basins in eastern North America. This event, in interaction with the tectonic movements caused an enhanced fresh water and siliciclastic input in marginal parts of the Tethys, where it caused a carbonate productivity crisis that included the demise of carbonate platforms and widespread siliciclastic sedimentation (often with land plant remains, as in the Lunz Beds, brackish water ostracods and conchostracans). Thus, the upper Julian ostracod guide form *Simeonella brotzenorum* Bunza and Kozur is an euryhaline brackish water ostracod, which is common in the Lunz and Raibl beds of the Alps and facially equivalent beds in Hungary.

By the connection with the Neotethys, the Pindos-Huğlu Ocean has got since the Reingraben Event (middle Carnian) a very similar Upper Triassic fauna as that of the Neotethys. There are still some distinct differences in parts of the Upper Triassic between the Neotethys and the northernmost Tethyan oceans (Meliata-Hallstatt Oceans and Küre Ocean). Unfortunately, the oceanic basins between these two oceanic are not yet well enough studied to figure out exactly the middle Carnian to Rhaetian faunistic similarities and differences to the southernmost oceanic realm (Neotethys and its shelves) and the northernmost oceanic realm (Meliata-Hallstatt and Küre Oceans and their shelves). Especially it cannot be in all cases decided whether the conodont faunas of the Pindos-Huğlu Ocean and the Neotethys are in the entire post-Cordevolian-Upper Triassic time identical or faunistic differences between both oceans existed in certain intervals of the post Cordevolian-Upper Triassic interval. Our studies have shown that there are some differences between both oceanic realms in certain time itnervals, but further studies in both areas are necessary to show that the differences are generally present and are not caused or strengthened by local factors.

In the upper Julian *Carnepigondolella nodosa* (Hayashi), junior synonym *Epigondolella carnica* Krystyn *in* Kristan-Tollmann and Krystyn, 1975 (see systematic part), is wide-spread in the Pindos-Huğlu Ocean and Maliac Ocean. The holotype of "*Epigondolella*" *carnica* was described by Krystyn from Hallstatt Limestones of the Antalya Nappes. Krystyn (1983) and Vrielynck (1987) described the upper Julian *Carnepigondolella nodosa* from Hallstatt Limestones of the inner Maliac Epidauros section in Greece. In more than 100 big samples from the upper Julian Hallstatt Limestones in Slovakia, Hungary, the Alps and from the Küre Ocean in northern Turkey, no single specimen of *C. nodosa* s.s. has been found. If they would be present, they can be only extremely rare. Also in the Neotethys of Sicily, we did not find this species in the upper Julian. Dr. Manuel Rigo (Padova) found one specimen in the Neotethyan sequence of the Lagonegro Basin. Thus, it seems that the upper Julian *C. nodosa* s.s. is common in Hallstatt Limestones only in the Pindos-Huğlu Ocean and Maliac Ocean, whereas in the

Neotethys and in the Meliata-Hallstatt and Küre Oceans it is either missing or extremely rare in this facies. We have found this species in upper Julian ammonitico rosso (Hallstatt Limestone facies) of section G in the Tavusçayırı Block (see above for description). This section is in the Triassic facies and facies succession identical with the Huğlu Unit of the Bozkýr area, Central Taurus in the revised stratigraphic dating by Kozur (1997). In one sample (G7), it was very common, in the other samples of these limestones conodonts are very rare, but the upper Julian *C. nodosa* s.s. was found, but as rare as the other conodonts. Thus, the correlation with the Huğlu Unit by facies succession and magmatism (Masset Moix, 2004, Parlak and Robertson, 2004) can be confirmed by the common occurrence of *C. nodosa* s.s. in the upper Julian ammonitico rosso of Hallstatt Limestone facies.

As mentioned in the systematic part, most of *Metaplygnathus primitius* (Mosher) formerly reported from the Tethys (e.g. Krystyn, 1980; Channell et al., 2003) are not *M. primitius* and even not closely related to this paper. This is definitely the case for all reported occurrences from the Meliata-Hallstatt Ocean, and also for the Küre Ocean (own studies). However, in the Neotethys, there are forms which are very similar to but not identical with *M. primitius* (material from Pizzo Mondello, Muttoni et al., 2004 and SEM pictures for this paper determined and presented to Triassic conodont workers in Vancouver by Prof. Alda Nicora and Prof. Muttoni, Milano; own material from a section close to Pietra di Salomone, western Sicily), which we describe in this paper as *M. mersinensis*.Kozur and Moix n. sp. Krystyn (*in* Gallet et al., 1992) reported *M.* cf. *primitius* from sections of the Antalya Nappes (Pindos-Huğlu Ocean) in Turkey. Unfortunately, Gallet et al. (1992, 1993, 1994, 1996, 2000) did not figure a single conodont and thus, it is not clear, whether they are the forms which Krystyn (and Kozur) had so far assigned to *M. primitius*, but which are unrelated to this species, or *M. mersinensis*. Noyan and Kozur (in press) investigated the upper Carnian and lower Norian beds from the northern shelf of the Pindos Ocean in Greece. They did not find *M. mersinensis*. We have investigated several sections across the Carnian-Norian boundary. When the typical Huğlu-type development is present, *M. mersinensis* was not found. Thus, seemingly, *M. mersinensis* is also absent from the Pindos-Huðlu Ocean, and the forms which Krystyn in Gallet et al. had mentioned but not illustrate, do not belong to *M. mersinensis* but belong to those forms formerly assigned to *M. primitius* which are not related to his species (see above).

However, in the Kocatabur Block, we have found *M. mersinensis* in two samples indicating a latest Carnian age in a fauna which corresponds to the Neotethyan fauna of the same age from western Sicily. We assume that this block has been derived from the Neotethys. However, further studies of the conodonts around the Carnian-Norian boundary in the Pindos-Huğlu Ocean and its shelves are necessary to exclude definitely that *M. mersinensis* is also common in that ocean.

As discussed in the systematic and biostratigraphic chapter, *Epigondolella praeslovakensis* Kozur and Moix has considerable biostratigraphic importance. However, it has also palaeobiogeographic importance. Krystyn had permanently (for the last time in Martini et al., 2000) regarded *Mockina slovakensis* Kozur as a middle Norian guide form based on well dated material from Timor, which was for long time not illustrated or described. Kovács (*in* Budai and Kovács, 1986 and Kovács and Nagy, 1989) who had seen the material of Krystyn followed him, but *in* Kovács and Nagy (1989), he modified the age assignment of Krystyn into middle to late Norian. Kozur had permanently (for the last time in Channell et al., 2003) regarded *M. slovakensis* as a guide form for the Sevatian which is especially common in the late Sevatian. This was confirmed by Gullo (1993, 1996) in the Neotethys of western Sicily and also there this species is especially common in the late Sevatian *Misikella hernsteini-Parvigondolella andrusovi* Zone. Kozur has seen the material of Gullo, her determinations were correct. The view of Krystyn that *M. slovakensis* is a guide form for the middle Norian is difficult to understand because the holotype is from the uppermost Norian just below the Norian-Rhaetian boundary. For this reason, very much material from the uppermost middle Norian of Slovakia was investigated, but *M. slovakensis* could not be found. As in the Meliata-Hallstatt Ocean and its shelves, *M. slovakensis* is very common in intra-platform basins, but rare (however, regularly present) in open sea deposits, the middle Norian of Sicily was also investigated, where *M. slovakensis* is very common in open sea deposits. There, *Epigondolella praeslovakensis* Kozur, Masset and Moix n. sp. was found in the upper Alaunian. It is seemingly present along the entire Neotethys because one of the forms illustrated by Martini et al. (2000) from Timor belongs to this species. No lower side was illustrated, but on the upper side the end of the carina is bifurcated into two low undenticulated ridges. All *E. praeslovakensis* which shows this feature have long bifurcated ends of the keel. In *M. slovakensis* this feature is unknown. By this is proven that the middle Norian forms of Krystyn are not *Mockina slovakensis* but *Epigondolella praeslovakensis*. What is more important for our palaeogeographic reconstructions, it is proven that this species occurs in the entire Neotethys. As we have not found it outside the Neotethys, we use it as an indicator for Neotethys. Interesting is also the occurrence of *E. praeslovakensis* in the Dolomia di Forni in NE Italy (see chapter biostratigraphic evaluation). There, Nicora (1981) found in the Cordevolian *Pseudofurnishius murcianus*, the typical late Longobardian and Cordevolian conodont of the Neotethys and its shelves. The Neotethyan faunistic affinity was now also proven for the middle Norian for the Southern Alps in NE Italy.

The evidence for the wide spread occurrence of Palaeotethyan remnants is not part of the present paper. It is mainly based on pelagic Pennsylvanian to pre-Kungurian limestones with deep water conodonts (mainly gondolellids) and radiolarians, mainly *Albaillellaria*, which are characteristic for water depth below 500 m. Such sediments are unknown from the western Neotethys. Also Kungurian radiolarites indicate a Palaeotethyan origin. Kungurian pelagic limestones are partly known from the Neotethys (Batain in Oman, Kozur, unpublished data) but not radiolarites which are, in turn, common in the Palaeotethys. These Palaeotethyan fauna will be described and discussed in forthcoming papers.

CONCLUSIONS

The Mersin Mélange contains remnants from the Palaeotethys, Pindos-Huğlu Ocean and the Neotethys. Remnants from the first two oceanic areas are common, Neotethyan remnants are rather rare. The recognition of the different oceanic units is partly based on characteristic facies and magmatic successions (Huğlu Unit of the Pindos-Huğlu Ocean) partly on faunistic characters. Especially difficult is the separation of the post-Cordevolian faunas from the Neotethys and the Pindos-Huğlu Ocean because the fauna of the two domains is in post-Cordevolian time very similar, whereas until the Cordevolian both domains have a quite different fauna. So far, we have used the occurrence of the latest Carnian *Metapolygnathus mersinensis* Kozur and Moix n. sp. and of the middle Norian *Epigondolella praeslovakensis* Kozur, Masset and Moix n. sp. as evidence for Neotethyan origin. However, further studies are necessary to exclude that these two species may be also common in the Pindos-Huğlu Ocean. The occurrence of *Carnepigondolella nodosa* s. s. (= "*E.*" *carnica*) in upper Julian Hallstatt Limestones/ammonitico rosso seems to be characteristic for the Pindos-Huğlu Ocean and Maliac Ocean.

Some important taxonomic and biostratigraphic problems among the Upper Triassic conodonts could be solved. We have described 4 new conodont species. Especially important is *Epigondolella praeslovakensis* which was in Timor and partly also in the Dolomia di Forni (NE Italy) assigned to "*E.*" *slovakensis*. By this, an incorrect age assignment for the Sevatian *E. slovakensis* was made and by this several sections and lithostratigraphic units were incorrectly dated. For instance, the *M. slovakensis* fauna of the Seefeld Formation in the Northern Calcareous Alps has not an Alaunian, but a Sevatian age. The same is true for the Rezi Dolomit of the Keszthely Mts. SW of the Lake Balaton, Hungary, and the Avicula Limestone of the Pilis Mts. north of Budapest. The Dolomia die Forni has in its lower part with *E. praeslovakensis* and ?*M. postera* a late Alaunian age, from the upper part of the lower Member it belongs to the Sevatian. Important is also the uppermost Carnian *Metapolygnathus mersinensis,* which can be used as indicator for Neotethyan origin (see above).

Epigondolella abneptis, the type species of *Epigondolella* has been revised and *Carnepigondolella nodosa* has been discussed. Faunas, which consist exclusively of *Mockina slovakensis* have a Sevatian age. Middle Norian occurrences of *M. slovakensis* are either based on other species, such as *Epigondolella praeslovakensis* Kozur, Masset and Moix n. sp., *Mockina medionorica* Kozur and *M. zapfei* (Kozur) or are based on incorrect dating of monospecific *M. slovakensis* faunas on the basis of assumed middle Norian age of this species in Timor, which is based on the above mentioned species, but not on *M. slovakensis*.

The "*Misikella*" *rhaetica* Zone of Gallet et al. (2007) is mainly based on *Misikella koessenensis* which was erroneouly assigned to "*M.*" *rhaetica*. True *Parvigondolella rhaetica* with a posterior blade which bears 2-3 denticles is too rare to be used as zonal index form. None of the 4 specimens of "*M.*" *rhaetica,* illustrated by Gallet et al. (2007) belongs to this species; 3 of them are *M. koessenensis*. Instead of the "*M.*" *rhaetica* Zone the *M. koessenensis* Subzone of *M. posthernsteini* Zone with the same stratigraphic scope is used. It is better to discriminate only a *M. koessenenis* Subzone of the *M. posthernsteini* Zone because *M. koessenensis* is not as extremely rare as *P. rhaetica*, but also clearly subordinate compared with *M. posthernsteini*. Moreover, *M. koessenensis* begins already extremely rarely in the lower *M. hernsteini-P. andrusovi* Zone.

The *Spongotortilispinus moixi* radiolarian zone is established for a very rich lower Tuvalian radiolarian fauna. This zone is also present in the Huğlu Unit, in the Neotethyan Lagonegro Basin and in the Maliac Ocean. Most of the genera of the Julian *Tetraporobrachia haeckeli* Zone are also present in the lower Tuvalian *S. moixi* Zone, but represented by other species. Characteristic for this zone is also the strong radiation of the Xiphothecidae and the beginning of new radiolarian groups, which have their main occurrence in the Jurassic, such as *Protunuma*. Younger Tuvalian faunas are distinguished by the presence of *Capnodoce*. Only the forerunner of *Capnodoce* is present in the *S. moixi* Zone.

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PLATE CAPTIONS

PLATE 1. Scale = 100 µm **Figs. 1, 2**: *Epigondolella abneptis* (Huckriede, 1958) s. s., middle Norian (Alaunian), Fırıntaş Block (section A on Fig. 2), sample I 5; **Fig. 1**: upper view, rep.-no. 8-12-03/III-100; **Fig. 2**: rep.-no. 8-12-03/III-98, a) upper view, b) lateral view. **Fig. 3**: *Mockina postera* (Kozur and Mostler, 1971), upper view, middle Norian (Alaunian), Fırıntaş Block (section A on Fig. 2), sample I 5, rep.-no. 8-12-03/III-102. **Figs. 4-8**: *Epigondolella praeslovakensis* Kozur, Masset and Moix n. sp., upper Alaunian, Gâvuruçtuğu Block (section D on Fig. 2); **Fig. 4**: sample MM 030, rep.-no. 10-9-03/I-23, a) lateral view, b) lower view; **Fig. 5**: some transitional character in the posterior end of the free blade to *E. abneptis,* sample MM 030, rep.-no. 10-9-03/I-23, a) lateral view, b) upper view, c) lower view; **Fig. 6**: holotype, sample MM 030, rep.-no. 10-9-03/I-20, a) lateral view, b) upper view, c) oblique lower-lateral view; **Fig. 7**: sample MM 031, rep.-no. 10-9-03/I-17, a) lateral view, b) upper view, c) lower view; **Fig. 8**: sample MM 030, rep.-no. 10-9-03/I-19, a) lateral view, b) upper view, c) lower view. **Figs. 9, 10**: *Epigondolella praetriangularis* Kozur and Moix n. sp., uppermost Carnian *E. orchardi* Zone. Kocatabur Block (section C on Fig. 4), sample H 60; **Fig. 9**: holotype, rep.-no. 3-07/IV-59, a) lateral view, b) lower view; **Fig. 10**: upper view, rep.-no. 3-07/IV-63. **Figs. 11, 12**: *Metapolygnathus communisti* Hayashi, 1968, uppermost Carnian *E. orchardi* Zone. Kocatabur Block (section C on Fig. 4); **Fig. 11**: exemplar with small nodes at the anterior platform margin, lower view, sample H 60, rep.-no. 3-07/IV-68A; **Fig. 12**: another exemplar, upper view, sample H 40, rep.-no. 3-07/IV-68. **Fig. 13**: *Carnepigondolella pseudodiebeli* (Kozur), upper view, uppermost Carnian *E. orchardi* Zone. Kocatabur Block (section C on Fig. 4), sample MM078, rep.-no. 27-7-03/I-15. **Figs. 14, 15**: *Metapolygnathus mersinensis* Kozur and Moix n. sp., uppermost Carnian *E. orchardi* Zone; **Fig. 14**: holotype, Kocatabur Block (section C on Fig. 4), sample MM078, rep.-no. 10-9-03/I-14, a) lateral view, b) oblique lateral-upper view, c) lower view; **Fig. 15**: Kangal Block (the fauna of this block is not yet finally studied and will be described in a forthcoming paper), sample B 2, rep.-no. 8-12-03/II-85, a) lateral view, b) lower view.

PLATE 2. Scale = 100 µm. **Fig. 1**: *Misikella koessenensis* Mostler, lateral view, upper Sevatian, lower *Misikella hernsteini-Parvigondolella andrusovi* Zone, Tavusçayırı Block (section B on Fig. 3), sample Mx 15/05, rep.no. 3-07-III/49A. **Fig. 2**: *Mockina* cf. *bidentata* (Mosher), lateral view, upper Sevatian, upper *Misikella hernsteini-Parvigondolella andrusovi* Zone, Tavusçayırı Block (section B on Fig. 3), sample Mx 16/05, rep.no. 3-07-IV/22. **Fig. 3**: *Mockina bidentata* (Mosher), morphotype II, lateral view, upper Sevatian, upper *Misikella hernsteini-Parvigondolella andrusovi* Zone, Tavusçayırı Block (section B on Fig. 3), sample Mx 16/05, rep.no. 3-07-IV/24. **Figs. 4-6**: *Carnepigondolella nodosa* (Hayashi), different morphotypes, upper Julian, Tavusçayırı Block (section B on Fig. 3), sample G 7; **Fig. 4**: rare morphotype with partly denticulated posterior margin, widest at the posterior end, rep.-no. 10-9-03/I-31, a) upper view, b) lateral view; **Fig. 5**: juvenile form, upper view, rep.-no. 10-9-03/I-26; **Fig. 6**: widest at the posterior end, otherwise similar to the holotype, upper view, rep. no. 10-9-03/I-28. **Fig. 7**: Ramiform element of *Gladigondolella*, upper Julian, Tavusçayırı Block (section B on Fig. 3), sample G 7, rep.-no.10-9-03/I-35. **Fig. 8**: *Spongotortilispinus* sp., inner structure, innermost part broken out, lowermost Tuvalian, *P. postinclinata-P. noah* conodont zone, *S. moxi* radiolarian zone, Tavusçayırı Block (section B on Fig. 3), sample G 11, re.-no. 23-9-04/II-58. **Figs. 9, 10**: *Spongotortilispinus moixi* n. gen. n. sp., lowermost Tuvalian, *P. postinclinata-P. noah* conodont zone, *S. moixi* radiolarian zone, Tavusçayırı Block (section B on Fig. 3), sample G 11; **Fig. 9**: re.-no. 23-9-04/II-7; **Fig. 10**: holotype, rep.-no. 23-9-04/I-188. **Fig. 11**: *Karnospongella multispininosa* Kozur, Moix and Mostler n. sp., holotype, lowermost Tuvalian, *P. postinclinata-P. noah* conodont zone, *S. moxi* radiolarian zone, Tavusçayırı Block (section B on Fig. 3), sample G 11, re.-no. 23-9-04/VI-33.

PLATE 3. Scale = 100 µm, if not otherwise indicated. **Figs. 1-3**: *Spongotortilispinus moixi* Kozur and Mostler n. gen. n. sp., lowermost Tuvalian, *P. postinclinata-P. noah* conodont zone, *S. moixi* radiolarian zone, Tavusçayırı Block (section B on Fig. 3),sample G 11; **Fig. 1**: rep.-no. 23-9-04/II-7; **Fig. 2**: rep.-no. 8-12-03/I-25H; **Fig. 3**: rep.-

no. 8-12-03/I-59. **Fig. 4**: *Spongotortilispinus ozsvarti* Kozur, Moix and Mostler n. sp., holotype, lowermost Tuvalian, *P. postinclinata-P. noah* conodont zone, *S. moixi* radiolarian zone, Tavusçayırı Block (section B on Fig. 3),sample G 11, rep.-no. 8-12-03/I-13. **Fig. 5**: *Spongotortilispinus inaequispinosa* Kozur, Moix and Mostler n. sp., holotype, lowermost Tuvalian, *P. postinclinata-P. noah* conodont zone, *S. moixi* radiolarian zone, Tavusçayırı Block (section B on Fig. 3), sample G 11,rep.-no. 23-9-04/II-46. Figs. 6, 7: *Spongotortilispinus turkensis* Kozur, Moix and Mostler n. sp., lowermost Tuvalian, *P. postinclinata-P. noah* conodont zone, *S. moixi* radiolarian zone, Tavusçayırı Block (section B on Fig. 3), sample G 11; **Fig. 6**: rep.-no. 23-9-04/II-1; **Fig. 7**: holotype, 27-11-04/II-101. **Fig. 8**: *Spongotortilispinus aequicurvistylus* (Lahm, 1984), lowermost Tuvalian, *P. postinclinata-P. noah* conodont zone, *S. moixi* radiolarian zone, Tavusçayırı Block (section B on Fig. 3), sample G 11, rep.-no. 8-12-03/I-38. **Fig. 9**: *Spongotortilispinus tuvalicus* Kozur, Moix and Mostler n. sp., holotype, lowermost Tuvalian, *P. postinclinata-P. noah* conodont zone, *S. moixi* radiolarian zone, Tavusçayırı Block (section B on Fig. 3), sample G 11, rep.-no. 23-9-04/II-37.

PLATE 4. Fig. 1: *Karnospongella multispininosa* Kozur, Moix and Mostler n. sp., lowermost Tuvalian, *P. postinclinata-P. noah* conodont zone, *S. moxi* radiolarian zone, Tavusçayırı Block (section B on Fig. 3), sample G 11, re.-no. 8-12-03/I-15. **Figs. 2, 6**: *Zhamojdasphaera rigoi rigoi* Kozur, Moix and Mostler n. sp., lowermost Tuvalian, *P. postinclinata-P. noah* conodont zone, *S. moixi* radiolarian zone, Tavusçayırı Block (section B on Fig. 3), sample G 11; **Fig. 2**: holotype, rep.-no. 23-9-04/V-90; **Fig. 6**: lateral (equatorial) view on the open shell and spines, inner structure well visible, rep.-no. 23-9-04/VI-159, a) detail, b) total view.**Fig. 3**: *Zhamojdasphaera latispinosa mersinensis* Kozur, Moix and Mostler n. sp., holotype, lowermost Tuvalian, *P. postinclinata-P. noah* conodont zone, *S. moixi* radiolarian zone, TavusçayırıBlock (section B on Fig. 3), sample G 11, rep.-no.- 23-9-04/IV-30; **Figs. 4, 5**: *Zhamojdasphaera rigoi brevispinosa* Kozur, Moix and Mostler n. sp., lowermost Tuvalian, *P. postinclinata-P. noah* conodont zone, *S. moixi* radiolarian zone, Tavusçayırı Block (section B on Fig. 3), sample G 11; **Fig. 4**: rep.-no. 8-12-03/I-12; **Fig. 5**: holotype, rep.-no. 23-9-04/V-200.

PLATE 1

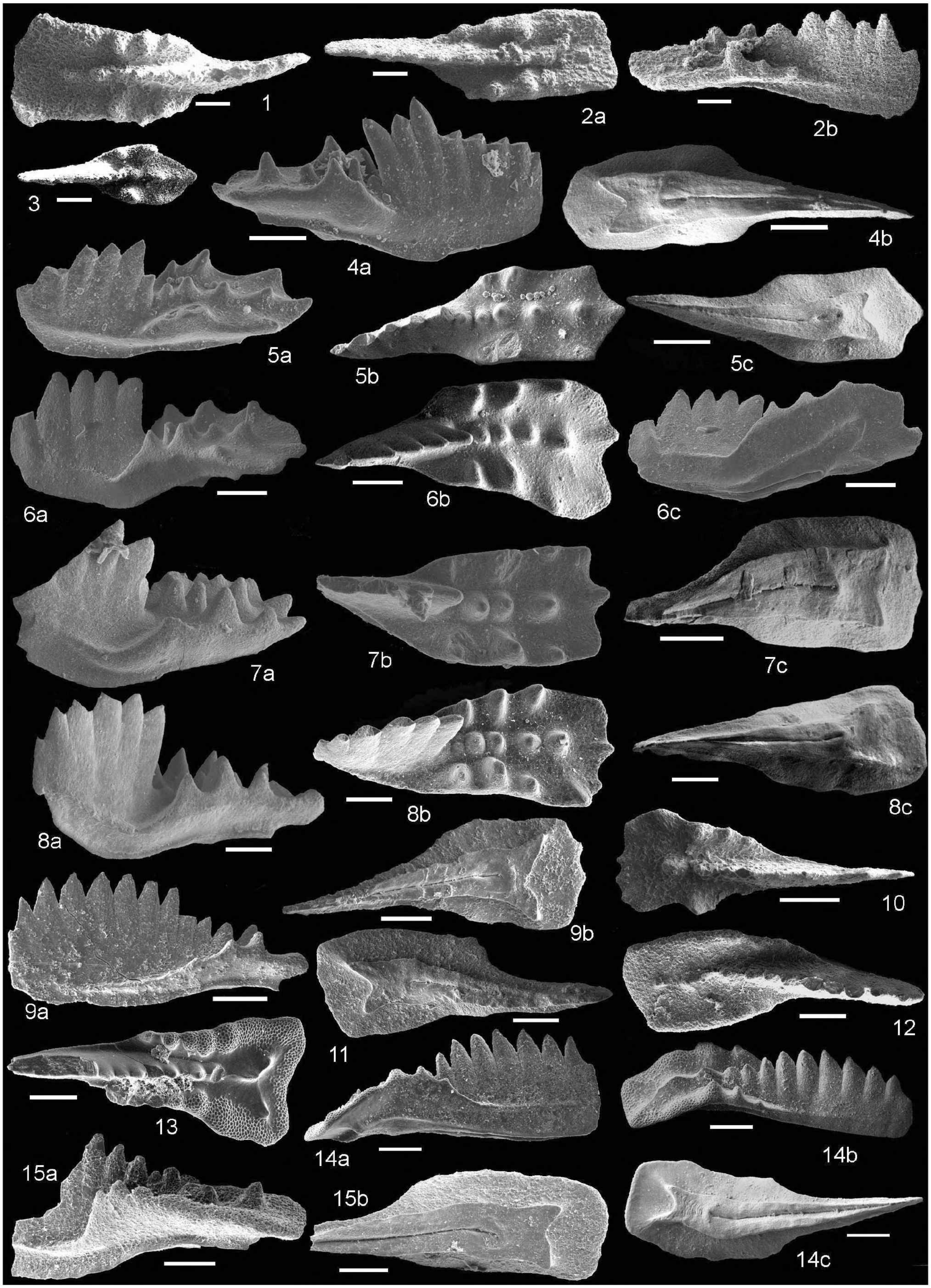
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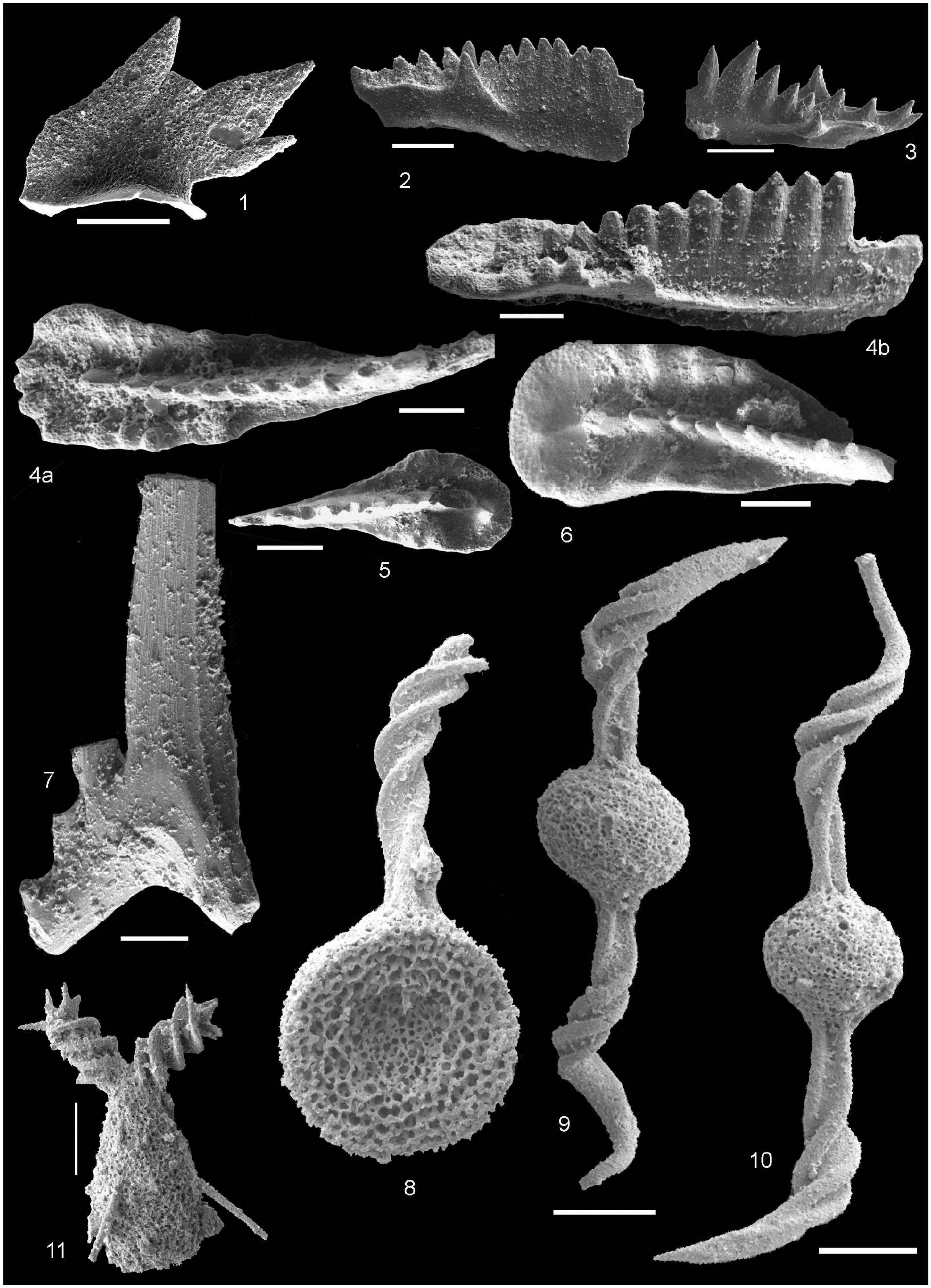
PLATE 2



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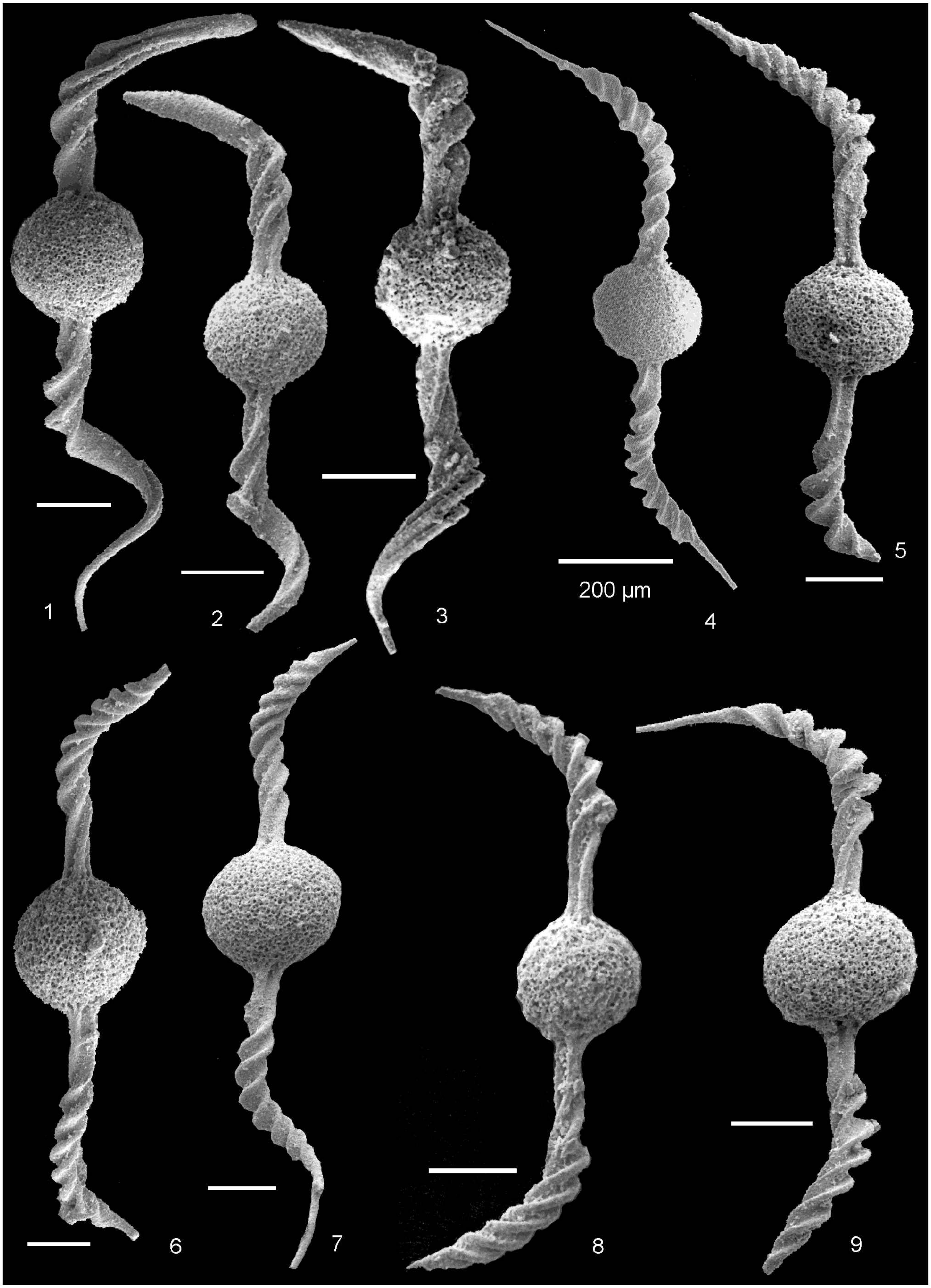

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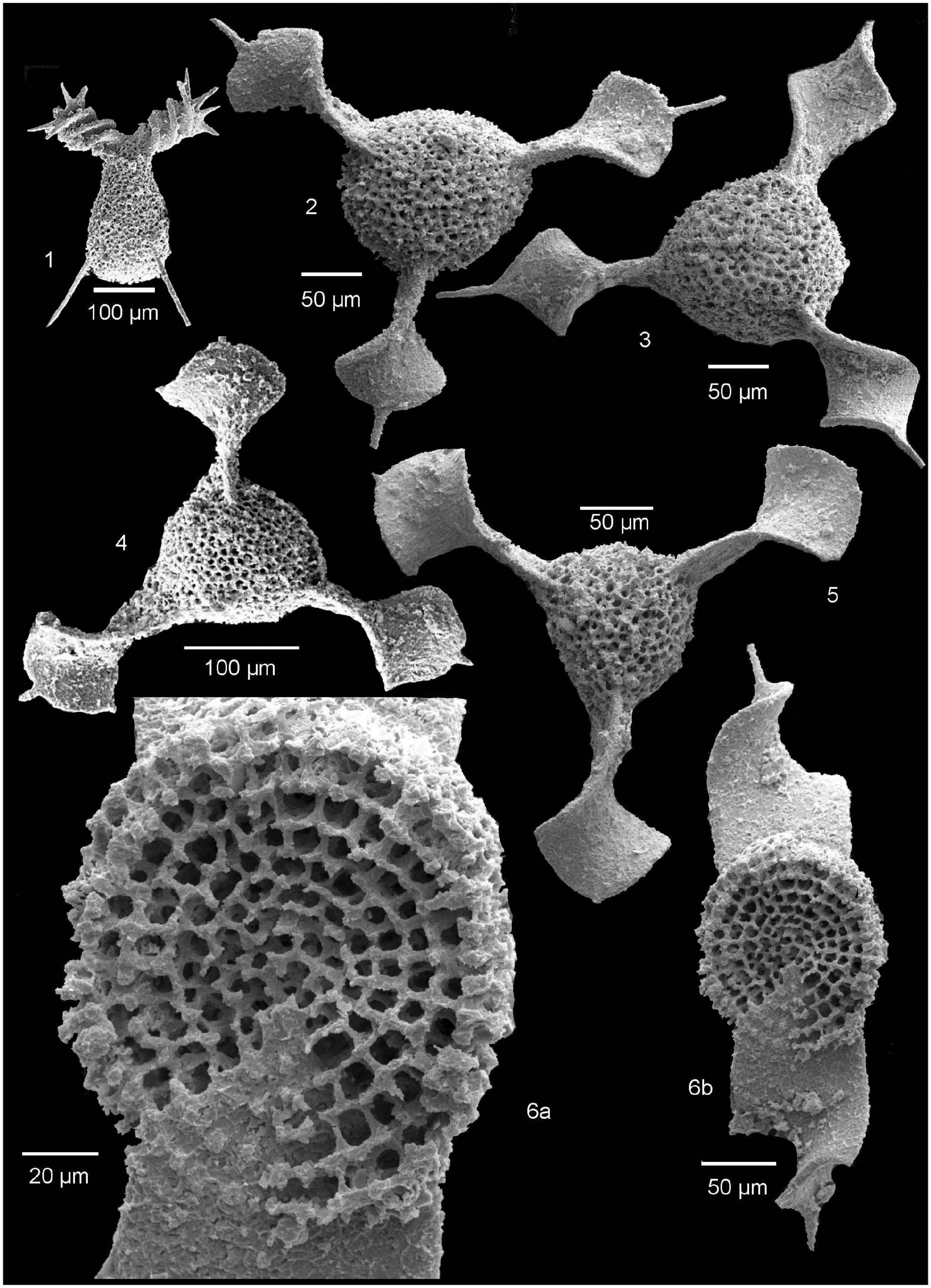

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AMMONITE-BASED CORRELATION OF THE MIDDLE/LATE ANISIAN BOUNDARY (MIDDLE TRIASSIC) BETWEEN NEVADA AND THE SOUTHERN ALPS

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This study presents the preliminary results of ammonite-based correlation of the middle/late Anisian (Pelsonian/Illyrian) boundary (Middle Triassic) between Nevada and the Southern Alps (Fig. 1). On the basis of new collections from a new locality in eastern Lombardy (Monte Guglielmo) and from classical sections in Giudicarie, these ammonoid faunas allow revising the taxonomic interpretation of *Ceratites cimeganus* Mojsisovics, 1882 and of the genus *Paraceratites* Hyatt, 1900. *Ceratites cimeganus* is here assigned to the North American genus *Rieppelites* Monnet and Bucher, 2005.

An improved age calibration of the regional transition from shallow to deep water environments is then obtained through the assessment of these new fossil finds and literature data. In eastern Lombardy-Giudicarie, *R. cimeganus* is diagnostic of a distinct biochronological unit (*cimeganus* Zone) bracketed between the older *Bulogites zoldianus* Zone and the younger *Judicarites euryomphalus-Paraceratites trinodosus* zones.

This refined ammonoid succession is then compared with the recently revised Anisian ammonoid record from Nevada (Monnet and Bucher, 2005, 2006). The recognition of this *cimeganus* Zone significantly improves worldwide correlation since it is recognized in several other Tethyan basins (Dolomites, Northern Calcareous Alps) as well as in North America (Nevada). These new data allow a redefinition of the middle/late Anisian boundary in the western Tethys, which is here drawn between the *zoldianus* and *cimeganus* zones. This limit is marked by a clear ammonoid turnover (e.g., disappearance of *Acrochordiceras* and *Balatonites*, diversification of Paraceratitinae).

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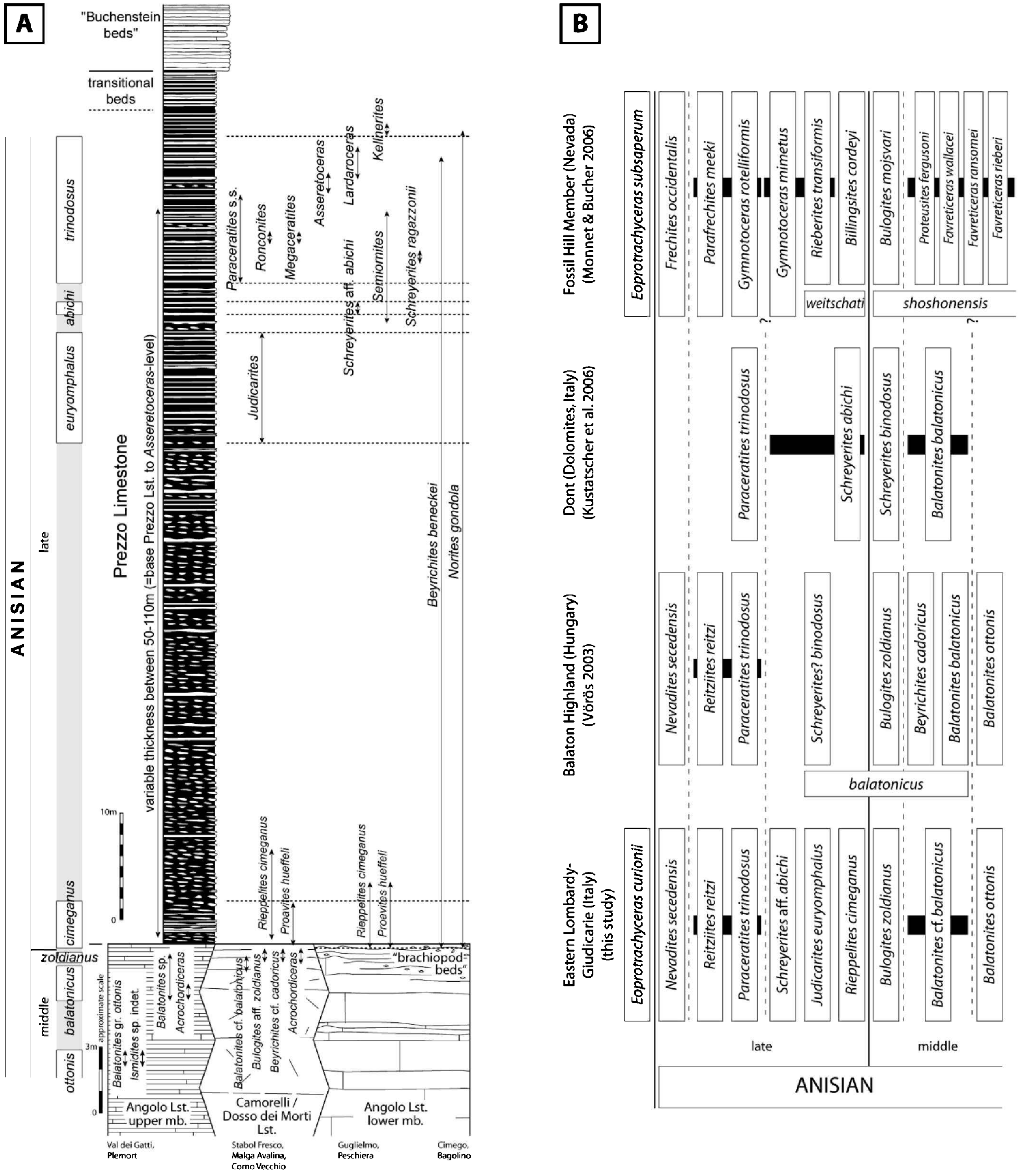

FIGURE 1. **A**, Schematic summary distribution of major ammonoids around the middle/late Anisian boundary in eastern Lombardy-Giudicarie (compiled and modified after Gaetani, 1969, Balini, 1992, Balini et al., 1993, Brack et al., 1999, 2005, and this study). **B**, Correlation of the middle/late Anisian boundary (Pelsonian/Illyrian) between major Tethyan basins and Nevada (vertical black bars indicate amount of uncertain correlation).

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CRITICAL VIEW OF THE CALIBRATION OF THE TRIASSIC TIME SCALE

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The calibration of the geologic time scale by means of radio-isotopic dating techniques is instrumental for an accurate reconstruction of events and processes in Earth's history, including biotic evolution, climate and environmental change, tectonic and magmatic processes, et cetera.

In this contribution, the importance of high-quality radio-isotopic ages will be illustrated using examples of geologic events during Triassic times, for example the observed changes in ocean chemistry (Payne and Kump, 2007; Payne et al., 2004) and the recovery of life after the most severe mass extinction in the Lower Triassic (Ovtcharova et al., 2006), and the events leading to the End Triassic biotic crisis (Mundil et al., 2005; Olsen et al., 2003; Pálfy et al., 2000), including the timing of the Siberian Trap volcanism in latest Permian to earliest Triassic times (Renne and Basu, 1991; Renne et al., 1995) and the CAMP (Central Atlantic Magmatic Province) volcanism in latest Triassic times (Knight et al., 2004; Marzoli et al., 1999). In addition, different hypotheses on the timing and recording of purported climatic signals in Middle Triassic shallow marine carbonates will be discussed with respect to radio-isotopic ages from intercalated volcanic ash falls and resulting implications for the Triassic time scale (Kent et al., 2004; Mundil et al., 1996; Mundil et al., 2003; Preto et al., 2001; Zühlke et al., 2003).

This contribution is aimed at expanding the understanding of users of geologic time scale compilations, most of which are based on an often arbitrary selection of data and sometimes questionable interpretations (the latest for the Triassic being Ogg, 2004). It is to be expected that the quality of data, in this case radio-isotopic ages from different isotopic systems, is subject to change as new analytical techniques are discovered and applied (e.g. Mattinson, 2005), and the knowledge about primary input values such as decay constants is growing. For example, the accuracy of radio-isotopic ages mainly depends on two prerequisites: (1) a closed isotopic system of the analyzed mineral or rock, i.e., no gain or loss of the parent and/or daughter element, and (2) the quality of the calibration of reference materials (natural or artificial standards) and decay constants.

Whereas the former is often not given, resulting in ages which are slightly too young (due to the loss of the radiogenic daughter isotope), it has often either been ignored or was not recognized (see Mundil et al. (2001) for discussion). The latter imposes a problem if ages from different isotopic systems are compared. For example, recent studies show evidence that the decay constant for ^{40}K is substantially miscalibrated by as much as 1%, which vastly exceeds the currently attainable analytical precision of ca. 0.1% (Min et al., 2000; Mundil et al., 2006). In particular, research aimed at studying the synchronicity of events has to take this complication into consideration. A prime example is the age of the Permian-Triassic mass extinction, which is mostly constrained by U-Pb ages, in relation to the age of the Siberian Flood volcanism, which is primarily constrained by ^{40}Ar/^{39}Ar ages (Renne et al., 1995; Bowring et al., 1998; Kamo et al., 2003; Mundil et al., 2004).

Accounting for these complications and taking only radio-isotopic ages into consideration that pass specific criteria (no evidence of redeposition, closed isotopic system, adjustment for systematic biases), the proposed new time scale for the Triassic is significantly different from even the latest published compilation (Brack et al., 2005), which has severe implications for the interpretation of events associated with the Permian-Triassic and Triassic-Jurassic transition (Mundil et al., 2004; Pálfy and Mundil, 2006).

Recent community efforts are aimed at addressing some of these complications by resolving inter-laboratory biases (Condon and Members of the Earthtime U-Pb working group, 2005). In addition, the application of promising new isotopic dating techniques, such as Re-Os dating of black shales (Creaser et al., 2005; Selby and Creaser, 2005) and U-Pb dating of paleosols and carbonates (Rasbury et al., 1998), may provide additional valuable data for time scale calibration where traditional dating techniques fail, for example due to the lack of volcanic products in the Upper Triassic.

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CONODONT BIOSTRATIGRAPHY AND PALEOGEOGRAPHY OF THE TRIASSIC OF THE AUSTRALIAN PLATE AND OF THE ACCRETED TERRANES OF NEW ZEALAND

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After the paucity of Permian conodont faunas recorded in the Australian and New Zealand sectors of Gondwanaland, the Triassic conodont record for insitu Australian marine sediments, and for the accreted terranes of New Zealand is encouraging, both in geographic spread and stratigraphic range. In neither area have conodonts of the early Griesbachian, that is the *Hindeodus parvus* and *Isarcicella* spp. faunas, been recorded, but after that apparent gap scattered (both geographic and stratigraphic), faunas are found from sequences of Dienerian to Rhaetian age.

AUSTRALIA AND THE NORTHERN MARGIN

In the Triassic the northern margin of Gondwanan Pangea opened onto the Meso-Tethys Ocean (Nicoll, 2002). The then continental margin was formed by the Lhasa and West Burma Blocks, parts of the Banda Arc and the New Guinea portion of the Australian Plate. Along what would become the margin of the Australian Plate were a series of cratonic basins, from the Perth Basin in the south, through the Bonaparte Basin to poorly defined Triassic basin structures on islands of the Banda Arc. In terms of the present day Australian Plate, only along the northern margin of present-day New Guinea and some of the islands of the Northern Banda Arc did continental margin shelf areas open directly onto the Meso-Tethys Ocean. Within this setting Triassic sediments were deposited in tectonically controlled basins. Conodonts and other fossils are beginning to allow high resolution correlation of sedimentary sequences and events within and between these basins.

Almost all of the Australian Triassic record is found in sedimentary basin sequences that are now either located offshore or when onshore are buried by younger sediments. For this reason the biostratigraphic record of the Early and Middle Triassic intervals have been only sketchily studied (McTavish, 1973; Nicoll & Foster, 1998). In addition, the sediments of the Middle and Late Triassic in the Perth, Carnarvon and Canning Basins are largely non-marine (Gorter, 1994). In the Perth Basin the Early Triassic is represented by the marine Kockatea Shale. Conodonts from several wells have provided Dienerian to Spathian ages. In the Carnarvon Basin the laterally equivalent Locker Shale ranges in age from Dienerian through Early Anisian, as documented by the presence of *Chiosella timorensis*. The equivalent interval in the Canning Basin in the Early Triassic is represented, in part, by the Blina Shale (onshore) and/or the Locker Shale (offshore). In the Canning Basin these intervals have not been seriously studied for conodonts.

On the outer margins of the Australian Plate, on the Wombat Plateau, Rowley Terrace and Ashmore Platform, only the upper part of the Triassic sequence has been effectively sampled. However, on the Sahul Platform wells have penetrated the interval from Rhaetian to Anisian.

Investigation of the Triassic on the island of Timor has recorded an extensive interval of marine Triassic sedimentation ranging from Dienerian through Rhaetian. The tectonically generated structural complexity of these sediments, related to their early rifting away from the margin of the Australian Plate and their later re-attachment have tended to mask the depositional relationship of the Timor sequences to the equivalent sediments of the Australian margin. Recent sampling of selected intervals is now demonstrating the close faunal similarities of the two areas.

Triassic sediments have yet to be extensively investigated in other islands of the Indonesian Banda Arc and New Guinea (Nicoll, 2002). Thus far only Rhaetian conodont faunas have been identified.

NEW ZEALAND

Unlike the northern margin of the Australian Plate that faced the Tethys Ocean and was subject to progressive rifting of continental blocks, the southeastern margin faced the broad Panthalassa Ocean and was subjected to both inboard small-scale rifting and the accretion of exotic terranes on the outboard margin. All of the known New Zealand Carboniferous, Permian and Triassic conodont faunas are from sequences within these accreted terranes.

The New Zealand Triassic conodont faunas appear to represent three distinctive ages, Early Triassic (Dienerian to Smithian), Middle Triassic (Anisian) and Late Triassic (Carnian to Norian). The ages of the incorporated conodont faunas do not, at least at this stage of investigation, appear to be in any way related to the order of terrane incorporation. The Arrow Rocks locality in the Waipapa Terrane of the North Island contains Induan (Dienerian, *N. dieneri* Zone) and upwards to *N. waageni* Zone (Early Olenekian = Smithian) faunas. The *N. dieneri* Zone (late Induan = Dienerian) fauna includes *Clarkina carinata, Neospathodus cristagalli, N. dieneri*, and *Sweetospathodus kummeli*. The upper fauna of the *N. waageni* Zone (Early Olenekian = Smithian) includes *Neospathodus cristagalli, N. dieneri, N. pakistanensis, N. waageni*, and *Sweetospathodus kummeli*.

The majority of the Triassic conodont faunas known from New Zealand are of Norian Age and have been recovered from various localities within the Torlesse Terrane. The conodonts from the Ruahine Range locality in the Torlesse Terrane Complex of southeastern North Island were all recovered from a single limestone block (Marden et al. 1987). The fauna includes *Paragondolella polygnathiformis* and *Norigondolella navicula*. The age of the Ruahine Range fauna appears to be latest Carnian to earliest Norian.

The conodont faunas of the Torlesse Terrane of the South Island (Jenkins & Jenkins 1971; Silberling et al. 1988) are of Norian age. Jenkins and Jenkins (1971) were the first to report and illustrate the presence of Triassic conodonts from New Zealand. They described two low-diversity faunas, one from the Mount Mason Limestone containing *Norigondolella navicula* (early Norian) and a second from the Okuku Limestone that is of early Late Norian age and contains *Norigondolella steinbergensis*. Silberling et al. (1988) recovered Triassic conodonts from 10 localities. Eight localities, including the Mount Mason and Okuku localities of Jenkins and Jenkins (1971b), were from the Esk Head Subterrane (or Melange) and duplicated the faunas found during the earlier study. Only at one locality, at Studleigh Range, were both *Norigondolella navicula* and *N. steinbergensis* faunas recovered, but from samples (142, 143) at least 10 metres stratigraphically apart.

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^{40}AR-^{39}AR AND U-PB AGE CONSTRAINTS ON THE TRIASSIC-JURASSIC AND NORIAN-RHAETIAN BOUNDARIES, NORTHERN VANCOUVER ISLAND, CANADA

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^{40}Ar-^{39}Ar and U-Pb dating of Late Triassic-Early Jurassic sedimentary and intrusive rocks in the Wrangellia Terrane, northern Vancouver Island, has placed constraints on the absolute age of the Triassic-Jurassic (Tr-J) and Norian-Rhaetian (N-R) boundaries. Classic Wrangellian stratigraphy (Jones et al., 1977) is represented on Vancouver Island by mid- to Late Triassic rocks of the Vancouver Group, comprising Karmutsen flood basalts (Ladinian-Carnian) and platformal Quatsino limestone (Carnian-Early Norian), succeeded by latest Triassic (Carnian-Rhaetian) volcanic-sedimentary sequences of the Parson Bay Formation at the base of the Late Triassic-Middle Jurassic Bonanza Group (Nixon and Orr, 2006). A stratigraphic section (327 m) through strata of the Parson Bay Formation was measured west of Kathleen Lake (92L/6) where the succession is affected by localized, distal skarn alteration associated with nearby intrusions of the Early to Middle Jurassic Island Plutonic Suite (Nixon et al., 2006). Parson Bay strata in the measured section comprise thin to medium bedded, impure limestone, calcareous mudstone, siltstone and minor shale interbedded with hornblende- and augite-bearing feldspathic wacke, crystal-lithic tuff and reworked equivalents, and minor volcaniclastic debris-flow deposits. The top of the section is overlain by a thick sequence (>1 km) of poorly bedded, waterlain volcanic breccias, lithic wackes and subaerial basaltic to andesitic flows; the latter represent the main phase of Bonanza arc volcanism.

Bivalves and conodont faunas collected from Parson Bay sedimentary lithologies indicate an age range of (late) Early Norian to Late Norian-Rhaetian. Hornblende phenocrysts in a porphyritic andesite cobble from a debris-flow deposit located 12m below silty limestone beds containing *Monotis subcircularis* Gabb in the Late Norian part of the section yield a ^{40}Ar-^{39}Ar plateau age of 199.4 ± 3.4 (2σ) Ma (for 50% of the ^{39}Ar released). Limestone beds ~50 m above the *Monotis* locality yield latest Norian-Rhaetian conodont faunas (*Epigondolella* ex. gr. *bidentata* Mosher 1968). Thus, according to the ^{40}Ar-^{39}Ar systematics, the maximum age of the Norian-Rhaetian stage boundary is 202.8 Ma at the 2σ level of confidence, which is slightly younger than the age of 203.6 ± 1.5 Ma given by Gradstein *et al*. (2004).

The composite Merry Widow pluton, which intrudes the Triassic-Jurassic stratigraphy, yields concordant U-Pb zircon ages of 197.1 ± 0.5 (2σ) and 196.7 ± 0.7 (2 σ Ma from gabbro pegmatite and monzonitic phases of the intrusion, respectively. A crystal of metasomatic phlogopite in calc-silicate skarn gives a ^{40}Ar-^{39}Ar plateau age of 197.9 ± 1.3 (2σ) Ma, in good agreement (within error) with the U-Pb dates. The mean U-Pb age of 196.9 Ma for the Merry Widow pluton and the ^{40}Ar-^{39}Ar date from the Late Triassic stratigraphy constrain the absolute age of the Tr-J boundary to approximately 200 ± 3 Ma, consistent with the more precise age of 199.6 ± 0.4 Ma proposed for this boundary by Palfy et al. (2000). Further U-Pb geochronology is presently being conducted on detrital zircons recovered from tuffaceous wackes in the measured section in an attempt to refine the latest Triassic time scale.

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TRIASSIC CHRONOSTRATIGRAPHIC DATABASE AND A DISPLAY INTERFACE

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The numerical ages on the Triassic time scale have undergone a major revision since 2002 and will probably remain in flux for some intervals for the next few years. At the same time, the inter-calibrations and taxonomic nomenclature among and within different faunal groups, magnetic polarity zones, sequences and other stratigraphic scales are constantly being revised. This can create headaches, not only for Triassic specialists, but for other geoscientists working with Triassic strata. Ideally, as new information becomes available and is confirmed, an online public database and visualization system would allow users to access both the current "standard" scales and annotations that explain the inter-calibrations, uncertainties and history of those scales. This ideal system will probably never be practical, but a greatly simplified version is possible.

A project of the International Commission on Stratigraphy (ICS) is to provide detailed global and regional "reference" scales of Earth history. Such scales integrate biostratigraphy (zones, datums for marine and terrestrial realms), sea-level (curves, sequences), geochemistry (trends, events), magnetic polarity chrons and astronomical cycles. These summarize our current consensus on the inter-calibration of events, their relationships to international divisions of geologic time and their estimated numerical ages. The current Phanerozoic database (about 10000 events and zones in April 2007) includes definitions of geologic stages, major zonations and markers of all significant fossil groups, primary and secondary magnetic polarity scales, and other stratigraphic information. Annotations on each entry include source, reliability, selected taxonomic notes, inter-calibrations, and methods of interpolating numerical age. A primary initial source for the Triassic was the extensive "Mesozoic and Cenozoic Sequence Chronostratigraphic Framework of European Basins" chart series of inter-calibrated bio-, magneto-, chemo- and sequence stratigraphy (Hardenbol et al, 1998), which had been calibrated to the geologic time scales of 1995. We recalibrated all these chronostratigraphic and sequence stratigraphy events to Geologic Time Scale 2004 (Ogg, in Gradstein et al., 2004) and included selected post-1995 biostratigraphic schemes, marker events and geochemistry correlated to Tethyan and Boreal ammonite zones.

Within these databases, all inter-calibrations and derived numerical ages are in the form of relational equations. Therefore, when a primary age is adjusted or a calibration is revised, then all other associated ages are also rescaled. These databases need to be enhanced through the efforts of the subcommissions of the ICS and other stratigraphic and regional experts.

However, a database is not nearly as convenient as graphics. Onscreen display and production of user-tailored time-scale charts from the databases is provided by the *Time-Scale Creator*, a JAVA package available from the ICS/CHRONOS websites (*www.stratigraphy.org* or *www.chronos.org*). After specifying the time interval and vertical scale, a user selects a subset of stratigraphic columns and trends (e.g., Gradstein and Ogg, 2006). In addition to screen views and a scalable-vector graphics (SVG) file for importation into popular graphics programs (e.g., Adobe Illustrator), the on-screen display has "hot-curser-points" to open windows providing additional information on events, zones and boundaries or to link to external URLs for in-depth details. Visualization options also include lithologic columns and range charts. The database and visualization package are envisioned as a convenient reference tool, chart-production assistant, and a window into the geologic history of our planet.

This poster is the current Triassic suite within the TimeScale Creator databases, after recalibration to selected radiometric ages, revised Upper Triassic magnetostratigraphic correlations, and Lower Triassic cycle stratigraphy (e.g., Menning et al., this conference). Revisions and contributions are welcome!

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NEW CONODONTS AND ZONATION, LADINIAN-CARNIAN BOUNDARY BEDS, BRITISH COLUMBIA, CANADA

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Abstract—Conodonts from the Ladinian-Carnian boundary interval in British Columbia are described. The study interval embraces the upper Ladinian/lower Carnian Maclearni, Sutherlandi, Desatoyense, Obesum, and Nanseni ammonoid zones. The following new species are described: *Metapolygnathus acuminatus, Metapolygnathus intermedius*, *Metapolygnathus lobatus, Metapolygnathus zonneveldi, Neogondolella liardensis, Paragondolella willistonensis*, and *Paragondolella*? *sulcata*. Based on the distribution of these and other conodont taxa, the following new faunal intervals are defined, from the oldest: *sulcata* Subzone, *acuminatus* Subzone, *intermedius* Zone, and *tadpole* Zone. The *sulcata* Zone is equivalent to the upper Maclearni Zone, and probably part of the lower Sutherlandi Zone wherein the *acuminatus* Zone is defined. The appearance of *Daxatina* within Sutherlandi Zone faunas may be coincident with the base of the *intermedius* Zone. The *tadpole* Zone extends from high in the Sutherlandi Zone through the Obesum and Nanseni zones. The Sutherlandi and Desatoyense zones appear partly equivalent.

INTRODUCTION

Conodont faunas from the Ladinian-Carnian boundary (LCB) interval in British Columbia occur in direct association with ammonoids (Orchard et al., 2002) in several key localities (Fig. 1). A new taxonomy for the conodont collections distinguishes several new taxa that may be of value in deliberations on the placement of the LCB. This contribution introduces these new species and narrows the definition of several other well known species. Through this taxonomy, it is hoped that an improved biochronologic framework may be developed. In North America, ammonoid biochronology about the LCB has been described by Tozer (1967, 1994). This study embraces the upper Ladinian zones of *Maclearnoceras maclearni* and *Frankites sutherlandi*, and the lower Carnian zones of *Trachyceras desatoyense*, *Austrotrachyceras obesum*, and *Sirenites nanseni* (Fig. 2).

Recent discussions about placement of the LCB have considered the distribution of key ammonoid genera *Frankites*, *Daxatina*, and *Trachyceras*. One of these genera, *Daxatina*, has been proposed as an index for the base Carnian (Broglio Loriga et al., 1999). *Daxatina* has been regarded as an element of the North American Sutherlandi Zone, with one species reported from the Desatoyense Zone (Tozer, 1994, p. 35). The Sutherlandi Zone is the terminal ammonoid zone of the Ladinian, although Silberling and Tozer (1968, p. 45) discuss the possibility that it may overlap with the Desatoyense Zone and hence range into the lower Carnian.

In Canada, conodont faunas associated with these key ammonoid genera are species of *Budurovignathus*, *Neogondolella*, *Metapolygnathus*, *Mosherella*, and *Paragondolella*. In this study, the distribution of conodonts associated with each of the ammonoid zones is documented with a view to providing new indices or proxies for correlation of LCB strata. Available data from the Stuores in the Italian Alps (Broglio Loriga et al., 1999) and from important sections in Spiti (Balini et al., 2001; Krystyn et al., 2004) have not previously identified contemporaneous appearances of key conodonts and ammonoids.

BIOSTRATIGRAPHY OF LADINIAN-CARNIAN BOUNDARY LOCATIONS

The following descriptions are based on the available biostratigraphic framework provided by Tozer (1994, appendix) for ammonoid collections representative of his ammonoid zones. These are supplemented by spot sampling of ammonoid-bearing strata by the author and J.P. Zonneveld during regional studies, the details of which are in preparation.

Liard River

This area includes the type localities for each of the upper Ladinian ammonoid zones and for each of the subzones of both the Maclearni and Sutherlandi zones of Tozer (1967, 1994). It is also the type area for *Daxatina canadensis* Whiteaves.

Conodont collections have been recovered from the matrix of five ammonoid faunas. Those from the type stratum of the Maclearni Subzone III (GSC loc. O-68236) in Boiler Canyon were reported as *Metapolygnathus polygnathiformis* by Mosher (1973) but assigned to a new species, *Paragondolella* n. sp. S, by Orchard and Tozer (1997): this is here introduced as *P? sulcata* sp. nov. A second collection (O-68231) from 122 m higher in the section and a third (O-68229), 36 m above that, both contained the ammonoids *Daxatina canadensis* and *Nathorstites macconnelli* and yielded conodont faunas dominated by *Neogondolella liardensis*. Tozer (1994) selected hypotypes of *D. canadensis* from both these faunas. The lower *Daxatina* collection (O-68231), also associated with *Asklepioceras laurenci*, contained also *Metapolygnathus lobatus*, *M. acuminatus*, and *M. intermedius*.

From Middle Canyon, 2.3 km downstream from Boiler Canyon, two further conodont collections from ammonoid matrix are both dominated by *Neogondolella liardensis*. The stratigraphically lower one (O-68266), which contained *Frankites sutherlandi* and *Nathorstites macconnelli*, yielded also a few *Budurovignathus mungoensis*, plus *Paragondolella inclinata* and *Metapolygnathus acuminatus*. About 50 m up-section, a further collection (O-68272) containing *Daxatina canadensis* produced common *Metapolygnathus tadpole* and *Mosherella newpassensis*, plus a few *Metapolygnathus intermedius, M. polygnathiformis*, and *M.* n. sp. H.

Conodonts from the matrix of four ammonoid collections of Sutherlandi Zone age from west of Hells Gate on the Liard River were reported by Mosher (1973). Most of these he referred to *"Neogondolella navicula"* and, although none were figured, they were presumably examples of *Paragondolella inclinata* and/or *Neogondolella liardensis.* The only other significant conodont recorded from these levels was *Budurovignathus mungoensis*. Two other collections reported by Mosher (1973) from elsewhere were essentially the same. In contrast, several Sutherlandi Zone collections recovered by the author from the Fossil Gate locality on Liard River contained *Metapolygnathus acuminatus*, *M. intermedius, M. polygnathiformis*, *Neogondolella liardensis*, *Paragondolella inclinata*, and *P*? *sulcata*, but lacked *Budurovignathus.*

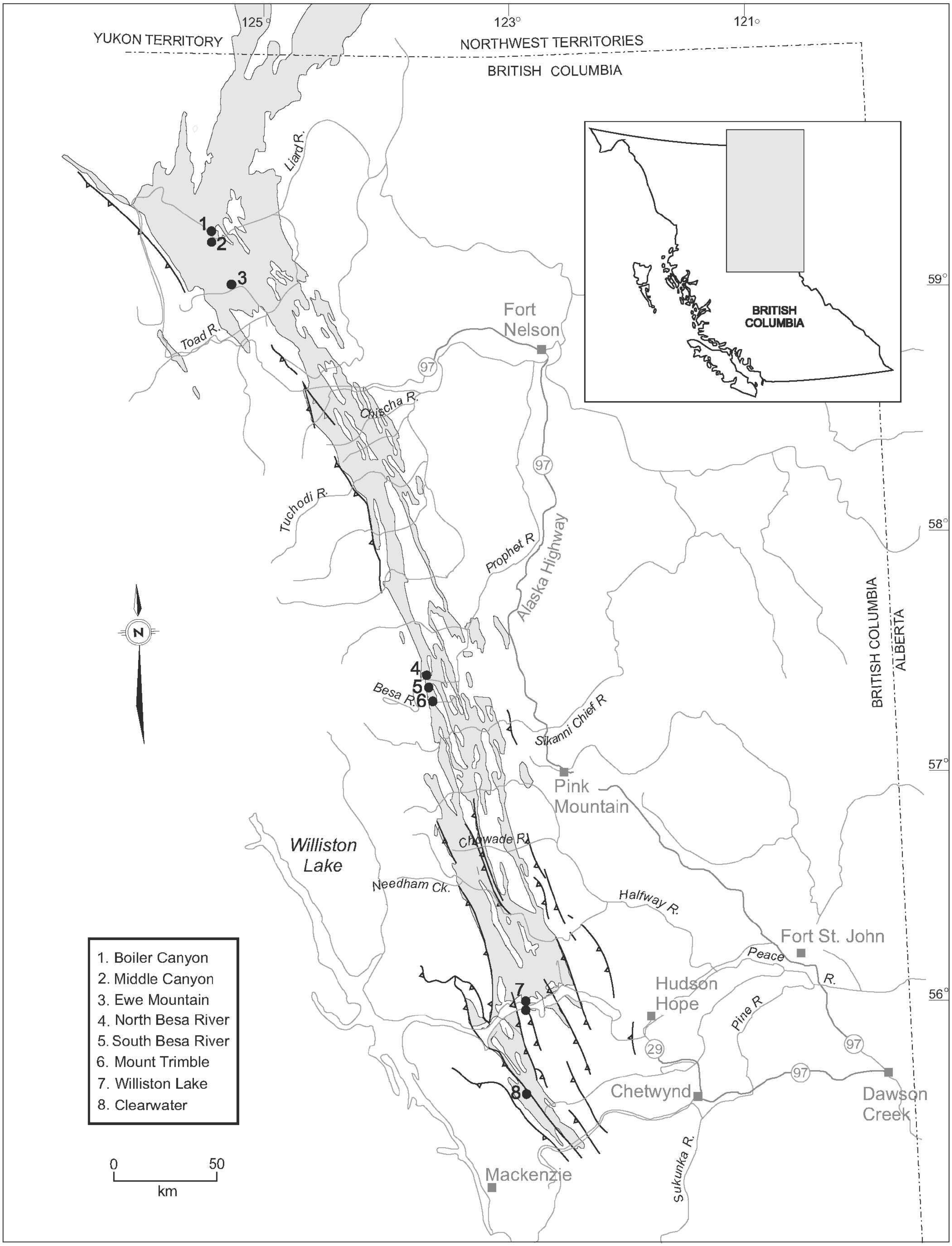


FIGURE 1. Map of northeastern British Columbia showing localities cited in text. Shaded areas are Triassic outcrop. Inset shows coverage within B.C.

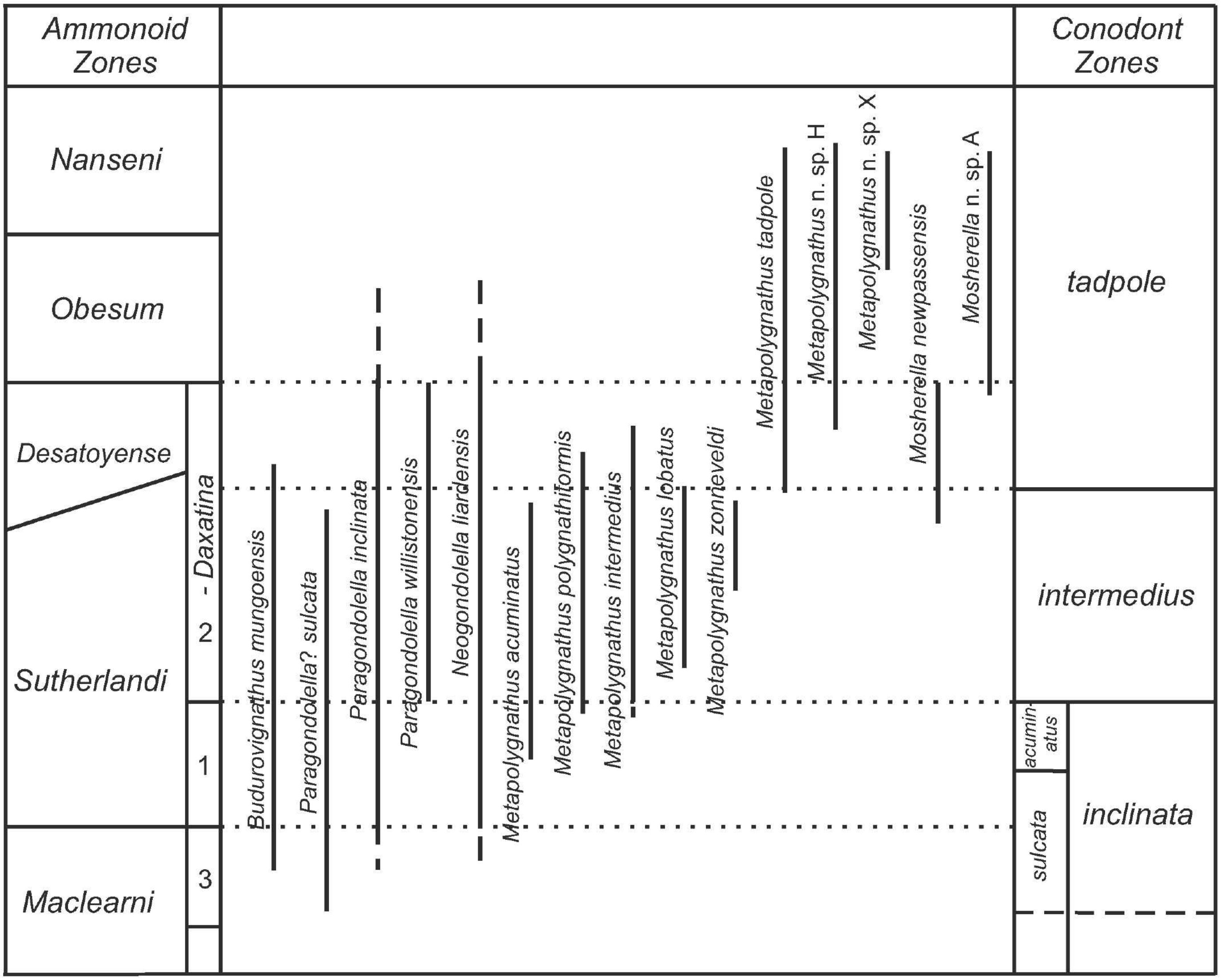


FIGURE 2. Comparative ammonoid and conodont zonations for the Ladinian-Carnian boundary interval, and the range of conodont species in British Columbia. The diagonal line between the Sutherlandi and Desatoyense zones expresses the suggestion that the two zones are in part time-equivalent.

Ewe Mountain

This area is the type area for the lower Carnian *Austrotrachyceras obesum* and *Sirenites nanseni* zones of Tozer (1994). Four conodont collections were recovered by the author, and a further two were reported by Mosher (1973). They span the interval from Subzone II of the Sutherlandi Zone, with *Daxatina canadensis* (including a hypotype of that species), through to the type strata of the lower Carnian zones.

Both the *Daxatina* fauna (O-42316) and the type stratum for the Nanseni Zone (O-42311) contained questionable *Metapolygnathus tadpole*, but that species does occur in both the type stratum of the Obesum Zone (O-42308, 100 m below 42311), and a higher collection (O-42310) with *Sirenites* sp. of probable Nanseni Zone age.

Mosher (1973, pl. pl. 18, fig. 36) reported a single *Neospathodus* sp. E in the type Obesum fauna, a form referred here to *Mosherella* n. sp. A (see section on Clearwater). A collection from the Nanseni Zone (O-42309) was reported as *Metapolygnathus polygnathiformis* (Mosher, 1973) although the new collections from the Nanseni Zone reported here yielded *Metapolygnathus* n. sp. H and *M.* n. sp. X.

North Besa River

Six samples, three with ammonoids, collected by J-P Zonneveld yielded conodonts. A ~150 m thick section contains *Nathorstites* sp. and *Daonella elegans* at 120 m above its base, and *Frankites sutherlandi* and *N. macconnelli* at 147 m. A further spot sample off-section included *Daxatina canadensis* and *Daonella* sp.

The lowest conodont fauna occurs at 37.5 m (C-305047) and is dominated by *Budurovignathus mungoensis* with fewer *Neogondolella liardensis*. At 120 m (C-305048), the *Daonella* level includes the same conodont species in reverse abundance, plus *Paragondolella inclinata*. A smaller collection at 144 m (C-305049) is similar but lacks *Budurovignathus*. The *Frankites* fauna at 147 m (C-305050) is associated with abundant *Neogondolella liardensis*, plus fewer *Mosherella newpassensis* and *Metapolygnathus lobatus*.

The sample with *Daxatina canadensis* (C-305045) produced a conodont collection that lacks *Neogondolella*, but which contains a unique fauna dominated by *Metapolygnathus zonneveldi* and *Paragondolella? sulcata*, with fewer *M. intermedius* and *P. inclinata*.

South Besa River

Samples collected by J-P Zonneveld yielded four conodont faunas from a ~147 m section that includes a record of *Maclearnoceras ensio* at 77.5 m, *Nathorstites* at 129 and at 135 m, and an association of *Daxatina canadensis*, *Frankites sutherlandi,* and *N. macconnelli* at 137 m.

The stratigraphically lowest conodont collection taken between 72-75 m (C-305221) contains only *Budurovignathus mungoensis*, which also occurs in higher samples with *Neogondolella liardensis* at 81 m (C-305222), and at 87 m (C-305223); a single specimen of *Metapolygnathus acuminatus* occurs in the latter collection. The conodonts from the highest bed (C-305224), with *Daxatina* and *Frankites,* contain abundant *Neogondolella liardensis*, *Metapolygnathus intermedius*, and *Mosherella newpassensis*, with fewer *Metapolygnathus lobatus*, *M. zonneveldi*, and *M. polygnathiformis.*

Mount Trimble

Several samples were collected from a short section that included in one bed (C-304828) *Asklepioceras laurenci* and *Nathorstites* sp. Therein, common *Budurovignathus mungoensis* and *Paragondolella inclinata* occur with *Metapolygnathus polygnathiformis*, *M. intermedius*, and rare forms close to *M. tadpole*. Adjacent beds collected over about 6 m contain essentially the same fauna but with variable proportions of *Budurovignathus* compared with other taxa, plus *Metapolygnathus acuminatus*.

Williston Lake

Two localities on opposite sides of the lake reveal similar successions of ammonoid-bearing strata. At West Glacier Spur, four successive ammonoid levels collected over ~8 m contain *Muensterites glaciensis* plus *Nathorstites* sp. at 0 m (C-303346), *Frankites sutherlandi*, *Nathorstites macconnelli*, and *Lobites ellipticus* at 0.4 m (C-304347), all the previous taxa plus *Daxatina canadensis* at 0.6 m (C-304349), and *Lobites ellipticus* alone at 8 m (C-304349).

The conodont faunas are essentially the same but start with a dominance of *Paragondolella inclinata* in the lowest three collections, and end with dominant *Neogondolella liardensis* in the highest sample; *Budurovignathus mungoensis* is common throughout the section. Metapolygnathids are less common, with *M. polygnathiformis* throughout and *M. intermedius* and rare *Paragondolella? sulcata* in the *Daxatina* level.

Brown Hill, on the north side of the lake, has similar ammonoid-conodont beds that have yielded *Paragondolella inclinata* dominated faunas (C-305932) giving way 6 m higher to one (C-305933) in which *Neogondolella liardensis* is dominant. The type species of *Paragondolella willistonensis* also comes from this locality.

Clearwater

Four conodont collections were obtained from macrofossil matrix samples from this area, which is the general location of a fauna (O-83824) that includes *Daxatina limpida* and the type material of *Halobia daonellaformis* (McRoberts, 2000). No conodonts are known from that stratum but a bed about 150 m higher (O-83825) includes mostly *Neogondolella liardensis* plus *Mosherella* n. sp. A and rare *Paragondolella willistonensis*. The new species of *Mosherella* is also known from the Nanseni Zone at Ewe Mountain and in strata above the Desatoyense Zone at South Canyon, New Pass, Nevada (Orchard & Balini, this volume).

A questionable *Daxatina* occurrence (O-83822) includes abundant *Neogondolella liardensis*, and far fewer *Paragondolella inclinata. A* third collection (O-84212) includes *Trachyceras desatoyense* in association with mostly *Metapolygnathus tadpole*, fewer *N. liardensis*, and rare *P. willistonensis*, which is essentially the same as a fourth collection (O-84270) which contains undetermined brachiopods and bivalves.

BIOSTRATIGRAPHIC SUMMARY

The features of the conodont distribution about the LCB in British Columbia can be summarized as follows:

The highest subzone of the Maclearni Zone is dominated by *Paragondolella? sulcata* (Liard River), which ranges up through the Sutherlandi Zone with scattered occurrences in beds that contain both *Frankites* and *Daxatina* (West Glacier Spur, North Besa River).

The conodont *Budurovignathus mungoensis* also appears in the latest Maclearni Zone and ranges up through the Sutherlandi Zone into beds containing both *Frankites* and *Daxatina* (Williston Lake, North Besa River), although most *Daxatina* faunas lack *Budurovignathus mungoensis*.

Ammonoid faunas from the Maclearni and Sutherlandi Zone (without *Daxatina)* are often dominated by *Budurovignathus mungoensis* and *Neogondolella liardensis* (South Besa River), with less common *Paragondolella inclinata* (North Besa River).

Sutherlandi Zone collections with *Daxatina* from Williston Lake and others with *Asklepioceras* from Mount Trimble still contain abundant *Budurovignathus mungoensis* and but also include new paragondolellids, and show diversification of the metapolygnathids: *M. acuminatus, M. intermedius, M. polygnathiformis*, and *P. willistonensis.*

Metapolygnathus acuminatus is the earliest metapolygnathid and occurs first with abundant *Budurovignathus mungoensis* in the Sutherlandi Zone prior to *Daxatina* (Liard River); *M. polygnathiformis* sensu stricto appears about the same time.

Daxatina-bearing faunas assigned to the Sutherlandi Zone may be divided into two based on the successive occurrences of *Metapolygnathus intermedius* and *M. tadpole* (e.g. Liard River). The first appearance of *M. intermedius* may correspond to that of *Daxatina*. Both *Metapolygnathus lobatus* and *Paragondolella willistonensis* also appear at about this time.

Neogondolella liardensis dominates the youngest LCB conodont collections from Williston Lake, and most or all of the collections from Liard River, South Besa River, North Besa River, and the Clearwater area. In contrast, at Mount Trimble there are no *Neogondolella* and the faunas are dominated by *Paragondolella inclinata*, as are the stratigraphically lower beds at the Williston Lake localities. There are no *Paragondolella* species at South Besa River.

The first *Metapolygnathus tadpole* appears within the uppermost range of *Budurovignathus mungoensis* (Mount Trimble), but is more commonly associated with *Mosherella* spp. It ranges from within *Daxatina* beds of the Sutherlandi Zone through the Obesum and Nanseni Zones, first with *Mosherella newpassensis* and later with *M.* n. sp. A.

Budurovignathus mungoensis and *Mosherella newpassensis* have mutually exclusive ranges in the studied samples from British Columbia, where the two species more commonly succeed each other, as in North Besa River. At New Pass, Nevada, the two species do overlap, although *Budurovignathus* is rare (Balini et al., 2007; Orchard & Balini, 2007).

The conodont *Mosherella newpassensis* occurs with *Daxatina* in the some Sutherlandi Zone collections from B.C., and in the Desatoyense Zone at New Pass. These two zones may be, in part, time equivalent (Fig. 2). In South Besa River, *Metapolygnathus zonneveldi* also occurs with *Mosherella*.

Most of the conodont species identified here from the LCB interval occur up to the lowest part of the range of *Metapolygnathus tadpole*, but have not been recovered from higher beds assigned to the Nanseni and Obesum zones.

A CONODONT ZONATION FOR THE LCB INTERVAL

The Ladinian-Carnian boundary interval in British Columbia (B.C.) can be very broadly divided into a lower part characterized by *Budurovignathus mungoensis* and an upper part with *Mosherella newpassensis*. This division is also quite evident at New Pass in Nevada (Orchard & Balini, this volume) although at that locality there is an overlap between the two species that is not observed in B.C., possibly as a result of insufficient sampling of beds between ammonoid horizons. This succession of genera lacks clear speciation events to serve as biochronological markers; however, the development of *Metapolygnathus* from *Paragondolella* and the diversification within the former does provide scope for proposing a biochronology.

It is here proposed that a new conodont zonation based on the successive appearance of *Metapolygnathus acuminatus*, *M. intermedius*, and *M. tadpole* can serve as a temporal framework for our understanding of LCB events. *Paragondolella inclinata* represents the root stock for this evolutionary trend that involved the progressive reduction of the anterior platform. In addition, *Paragondolella*? *sulcata* serves as an index for the Maclearni and Sutherlandi zones prior to the appearance of *Metapolygnathus*. Speciation in *Budurovignathus* is not evident in the B.C. collections although species other than *B. mungoensis* do occur rarely at New Pass (Orchard and Balini, 2007). A zonation based on this genus, as is possible in Europe, is unavailable in North America. However, higher strata do seem amenable to subdivision based on *Mosherella* species.

Two new subzones and two new zones based on evolution within *Paragondolella-Metapolygnathus* lineages are introduced here (Fig. 2). These are calibrated with the ammonoid zones of Tozer (1994) and rest on the same superpositional relationships.

1) *Paragondolella*? *sulcata* Subzone of a broad "*inclinata* Zone." Type locality same as Subzone III of the Maclearni Zone in Boiler Canyon, GSC loc. O-68236, with a diverse ammonoid fauna (see Tozer, 1994, p. 329). This conodont collection contains only the name giver. The base of this subzone is defined by the first appearance of *P*? *sulcata*, and the top by the appearance of *Metapolygnathus acuminatus*.

2) *Metapolygnathus acuminatus* Subzone of a broad "*inclinata* Zone". Type locality is Middle Canyon on Liard River, GSC loc. O-68266, with *Frankites sutherlandi* and *Nathorstites macconnelli*. It contains *Neogondolella liardensis, Budurovignathus mungoensis*, *Paragondolella inclinata*, and *Metapolygnathus acuminatus*. The base of this subzone is defined by the first appearance of the name giver, and the top by the appearance of *Metapolygnathus intermedius*.

3) *Metapolygnathus intermedius* Zone. Type locality is Boiler Canyon on Liard River, GSC loc. O-68231, 122 m above the type *sulcata* Subzone, with *Daxatina canadensis, Asklepioceras laurenci*, and *Nathorstites macconnelli*. It contains a conodont fauna dominated by *Neogondolella liardensis*, plus *Metapolygnathus intermedius, M. acuminatus,* and *M. lobatus.* Also present in this zone are all the species of the previous subzones plus *M. zonneveldi* and the first *Mosherella newpassensis.* The base of this subzone is defined by the first appearance of the name giver, and the top by the appearance of *Metapolygnathus tadpole*.

4) *Metapolygnathus tadpole* Zone. Type locality is Middle Canyon on Liard River, GSC loc. O-68272, containing *Daxatina canadensis*, about 50 m stratigraphically above the type *acuminatus* Zone. It yields abundant *Neogondolella liardensis*, common *Metapolygnathus tadpole* and *Mosherella newpassensis*, plus a few *Metapolygnathus intermedius, M. polygnathiformis*, and *M.* n. sp. H. Also present in this zone is *Paragondolella willistonensis* and the last *Budurovignathus mungoensis*. This zone is currently defined as a range zone.

SYSTEMATIC PALEONTOLOGY

Genus *Metapolygnathus* Hayashi, 1968

Remarks: The genus *Metapolygnathus* embraces mostly Carnian species, in which a reduced anterior platform can be observed in lateral view, upper view, or both. In the oldest representatives, it is generally most obvious in lateral view as the anterior platform 'steps down' on one or both sides. Later, the anterior platform margins 'shrink' both laterally and longitudinally so that the anterior fixed blade is bordered by narrow flanges and ultimately becomes 'free'. *Paragondolella* differs in its more uniform high crested blade-carina and a flatter platform that tapers evenly to the anterior end of the blade without marked deflection in any view.

Kozur (2003, p. 69) adopted a narrower view of *Metapolygnathus*, preferring to restrict the genus to forms, like the type species *Metapolygnathus communisti*, that have a pit located at, or anterior to the middle of the platform, as well as being anteriorly shifted with respect to the end of the keel. The problem with applying these criteria is that most Carnian conodont lineages show progressive anterior pit migration and separation of species on this basis alone is difficult.

Metapolygnathus acuminatus sp. nov.
(Fig. 3. 10-12)

Holotype: GSC 120358, Fig. 3. 10-12.

Etymology: Latin *acumin*, referring to the narrow, relatively pointed posterior platform.

Type stratum: Liard Formation (sample TRIM-2A).

Type locality: GSC loc. C-304781, Mount Trimble, northeast British Columbia.

Diagnosis: In upper view, the P1 element varies from symmetrically to asymmetrically ovoid with its maximum width at midlength. The platform extends to the anterior end of the element. The outer margin is often more convex than the inner margin, which may be straight to concave in its posterior part; the axis may be straight, curved, or inturned at the posterior end. In profile, the element is arched and has one or both lateral margins downturned at a point about one-third from the anterior end of the element: this may appear as a marked change in slope but is typically marked by an irregular 'step'. The nodes of the blade-carina tend to be fused in the central part of the platform where they rise a little above the platform margins; anteriorly, the carina extends as a well differentiated fixed blade that maintains a constant height and therefore projects well above the downturned anterior platform margins. Towards the posterior, the carina terminates in a few larger, partly fused denticles, including the cusp, that are separated from the posterior end of the element by a narrow platform brim. The underside bears a small, posteriorly located pit lying in a narrow loop with raised edges, and a narrower grooved keel extending to the anterior end.

Remarks: Compared with those of *Paragondolella inclinata*, the P1 elements are more pointed and have their maximum width about their midlength rather than posterior of that position; the margins are also commonly more upturned. The species is close to *Metapolygnathus polygnathiformis*, from which it differs principally in platform shape. The latter has a more quadrate posterior platform, a more pronounced, better differentiated cusp, and a broader posterior platform brim. In common with *M. polygnathiformis*, the early reduction of the anterior platform and the differentiation of the anterior and medial blade-carina is seen in lateral view: a geniculation point or step in the lateral platform margin on one or both sides, and a fused medial carina often contrasting with a higher anterior blade. There is no significant platform reduction evident in upper view because the tapering of the platform is generally uniform, as it is in *P. inclinata.*

Canadian occurrences: Liard River, Mt. Trimble, and South Besa River, northeastern British Columbia. Found in Sutherlandi Zone associated with both *Frankites* and *Daxatina*, or with *Daxatina* alone.

Metapolygnathus intermedius sp. nov.
(Fig. 3. 13-15)

2006 *Metapolygnathus* aff. *tadpole* (Hayashi) – Orchard, pl. 6, figs. 13, 14.

Holotype: GSC 120359, Fig. 3. 13-15.

Etymology: The species occupies an intermediate morphology between *M. polygnathiformis* and *M. tadpole*.

Type stratum: Liard Formation (Sample TRIM-2).

Type locality: GSC loc. C-304828, Mount Trimble (NTS 94G/5), northeastern British Columbia.

Diagnosis: Lachrymiform to ovoid, symmetrical to asymmetrical, arched and sometimes curved, often strongly tapered P1 elements with a strongly reduced anterior platform whose margins are moderately to strongly both downturned and inturned at about one-third element length from the anterior end. This is evident in both upper and lateral views. The platform may extend as a very narrow flange to within 1-2 denticles of the anterior end of the blade but commonly the free blade is longer. Platform margins may be subparallel, or commonly biconvex in smaller specimens, and often rather irregular and undulating. In lateral profile, the geniculation of the anterior platform margins often differs on the two sides. The posterior platform is generally narrowly rounded, but may be pointed in smaller specimens in which the terminal cusp projects beyond the platform margin; a very narrow posterior platform brim is present in later growth stages. Some elements have a cusp offset from the longitudinal axis of the carina. The underside bears a small posterior pit lying in a narrow loop with raised edges, and a narrower grooved keel extending to the anterior end.

Remarks: This species was derived from *M. acuminatus* through the further reduction in the anterior platform, which is apparent in lateral and, unlike both the latter species and *M. polygnathiformis*, in upper view. This species shares most of the attributes of *M. acuminatus*, but has a clearly differentiated blade, which may be lower than in older species.

Canadian occurrences: Liard River, Mt. Trimble, South Besa River, North Besa River, and Williston Lake, northeastern British Columbia. Pelly Mountains, Yukon (Orchard, 2006). Found in Sutherlandi Zone associated with both *Frankites* and *Daxatina*, or *Daxatina* alone. The type stratum contains *Asklepioceras laurenci* and *Nathorstites* sp.

Metapolygnathus lobatus sp. nov.
(Fig. 3. 7-9)

Holotype: GSC 120357, Fig. 3. 7-9.

Etymology: Referring to the posterior platform lobe.

Type stratum: Liard Formation, 147 m above base of section (sample NWB-6).

Type locality: GSC loc. C-305048, North Besa River, northeast British Columbia.

Diagnosis: The P1 element is characterized by a medially broad, biconvex platform with margins that taper evenly to the anterior end of the elements and equally strongly towards the posterior end, near which the platform margins are constricted so as to define a lobate posteriormost part of the platform that surrounds the cusp. In lateral view, the anterior lateral margins are turned strongly downward. The anterior platform margins commonly show some subdued nodose ornamentation. The blade-carina is divided into two parts, the posterior one-half elevated to about the height of the platform margins, and the anterior one-half appearing as a higher, mostly fixed blade.

Remarks: This species has a similar platform shape to *Paragondolella willistonensis* but it has a much lower blade-carina. It also resembles some upper Carnian elements that have a similar posterior constriction, but the new species has a relatively well developed platform and lacks a free blade.

Canadian occurrences: Liard River, South Besa River, and North Besa River, northeastern British Columbia. Found in Sutherlandi Zone associated with both *Frankites* and *Daxatina*, together or alone. Occurs with *Frankites sutherlandi* and *Nathorstites macconnelli* in the type collection.

Metapolygnathus polygnathiformis (Budurov & Stefanov, 1965)
(Fig. 3. 22-24)

1965 *Gondolella polygnathiformis* sp. nov. - Budurov and Stefanov, p. 118-19, Pl. 3, fig. 7.
2007 *Metapolygnathus polygnathiformis* (Budurov & Stefanov) – Orchard & Balini, Fig. 6.14-19, 46-51.

Diagnosis: In upper view, the P1 element is typically subquadrate with subparallel margins, especially in later growth stages, with its maximum width near the posterior end. The platform extends to the anterior end of the element. In profile, the element is arched and has one or both lateral margins downturned at a point about one-third from the anterior end of the element; this is typically marked by an irregular 'step'. The nodes of the blade-carina tend to be fused in the central part of the platform, where they rise a little above its margins, and then extend anteriorly as a well differentiated fixed blade that maintains a constant height and therefore stands out well above the downturned anterior platform. The posterior carina terminates in a large, usually well differentiated cusp that lies close to the posterior end of the element but is commonly separated from it by a narrow platform brim. The underside bears a small, posteriorly located pit lying in a narrow loop with raised edges, and a narrower grooved keel extending to the anterior end.

Remarks: See *M. acuminatus* for comparisons, and Orchard & Balini (this volume) for discussion.

Canadian occurrences: Liard River, South Besa River, Mount Trimble, and Williston Lake, northeastern British Columbia. Found in Sutherlandi Zone associated with both *Frankites* and *Daxatina*, or *Daxatina* alone.

Metapolygnathus tadpole (Hayashi, 1968)
(Fig. 3. 19-21)

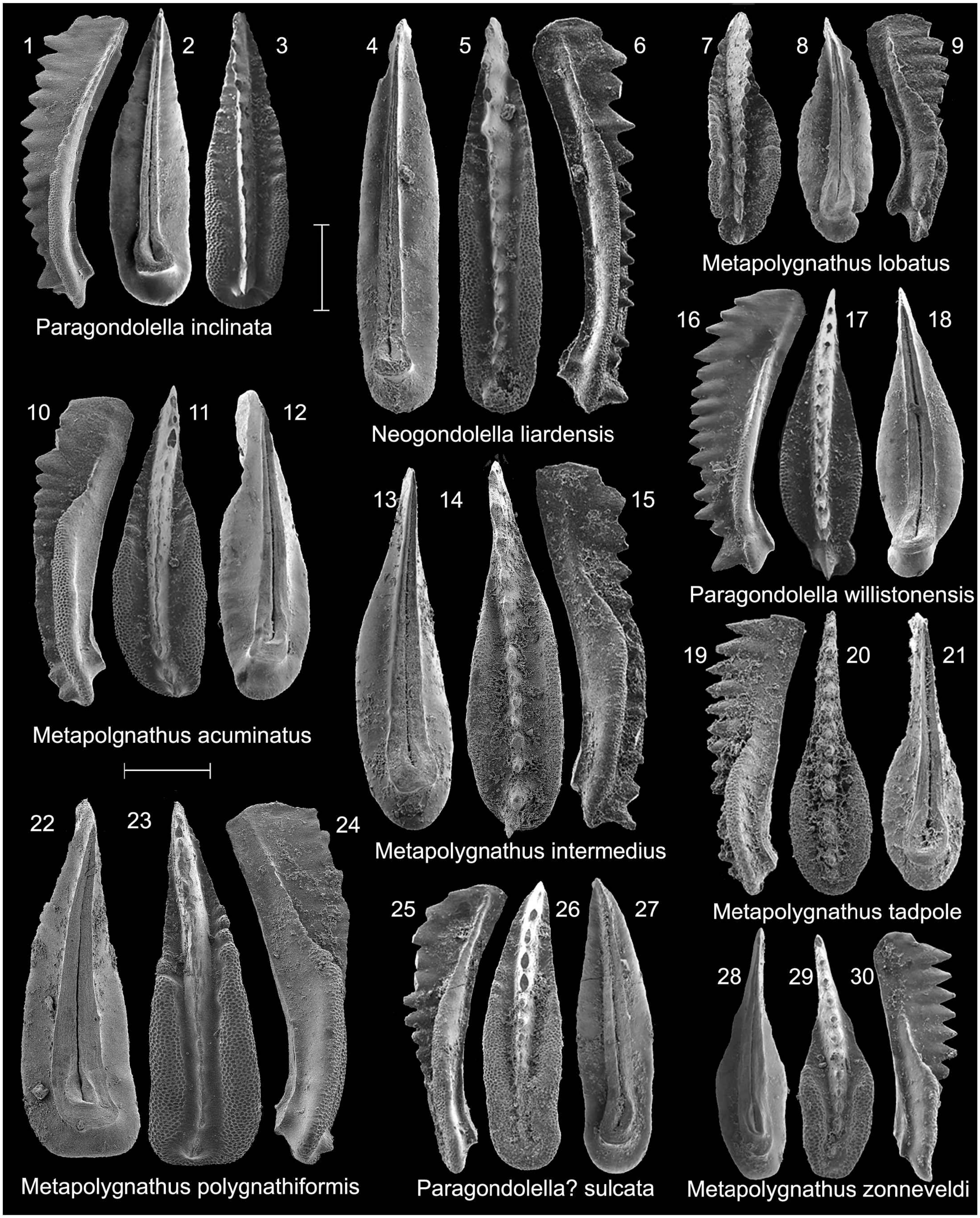
1968 *Gondolella tadpole* sp. nov. - Hayashi, p. 71, pl. 1, Figs. 6a, b.
2006 *Metapolygnathus tadpole* (Hayashi) – Orchard, pl. 4, figs. 1-3; pl. 6, 11, 12, 15, 16.

Diagnosis: P1 elements of this species have a strongly reduced platform that is confined to the posterior one-half of the element, and a free blade that is at least one-half the total element length. The platform is narrow in smallest growth stages and becomes medially broader with growth so that later stages have elliptical platforms; the posterior margin is generally rounded. In lateral view, the anterior platform margins may end abruptly or may downturn in an even curve. The free blade is composed of equal denticles that maintain a uniform height, and pass posteriorly into a carina that projects slightly above the level of the upturned platform margins. The underside bears a small posterior pit that lies in a thick-lipped loop with raised edges that occupies much of the underside of the platform in small specimens, and still appears relatively large in mature elements. A broad grooved keel extends to the anterior end of the blade.

Remarks: This species is an end-member of a series that begins with the reduction of the anterior platform as seen in *M. acuminatus* and *M. polygnathiformis* and which continues with *M. intermedius*. The free blade is distinctly longer than that of the latter. It resembles *M. zonneveldi* in its relative blade:platform ratio, but differs in its well developed carina.

Canadian occurrences: Liard River, Mount Trimble, Ewe Mountain, and Clearwater, northeastern British Columbia. Table Mountain formation, Sylvester Allochthon, and Big Campbell window, Yukon (Orchard, 2006). Found in Sutherlandi Zone associated with *Daxatina*, and

FIGURE 3. Examples (mostly holotypes) of conodont taxa described in text. Scale bars = 200 microns (x80). **1-3,** *Paragondolella inclinata* (Kovacs). GSC 120355 from GSC loc. C-305932 (BHE-1). **4-6,** *Neogondolella liardensis* sp. nov. GSC 120356 from GSC loc. O-86266. **7-9,** *Metapolygnathus lobatus* sp. nov. GSC 120357 from GSC loc. C-305045 (NWB-1). **10-12,** *Metapolygnathus acuminatus* sp. nov. GSC 120358 from GSC loc. C-304781 (TRIM-2A). **13-15,** *Metapolygnathus intermedius* sp. nov. GSC 120359 from GSC loc. C-305045 (NWB-1). **16-18,** *Paragondolella willistonensis* sp. nov. GSC 120360 from GSC loc. C-305932 (BHE-1). **19-21,** *Metapolygnathus tadpole* (Hayashi). GSC 120361 from GSC loc. O-68272. **22-24,** *Metapolygnathus polygnathiformis* (Budurov & Stefanov). GSC 120362 from GSC loc. C-304828 (TRIM-2). **25-27,** *Paragondolella*? *sulcata* sp. nov. GSC 120363 from GSC loc. C-305045 (NWB-1). **28-30,** *Metapolygnathus zonneveldi* sp. nov. GSC 120364 from GSC loc. C-305045 (NWB-1).


1
2
3
Paragondolella inclinata
4
5
6
Neogondolella liardensis
7
8
9
Metapolygnathus lobatus
10
11
12
Metapolgnathus acuminatus
13
14
15
Metapolygnathus intermedius
16
17
18
Paragondolella willistonensis
19
20
21
Metapolygnathus tadpole
22
23
24
Metapolygnathus polygnathiformis
25
26
27
Paragondolella? sulcata
28
29
30
Metapolygnathus zonneveldi

in Nanseni and Obesum zones.

Metapolygnathus zonneveldi sp. nov.

(Fig. 3. 28-30)

Holotype: GSC 120364, Fig. 3. 7-9.

Etymology: Named for J-P, Zonneveld, GSC Calgary.

Type stratum: Liard Formation (spot sample NWB-1).

Type locality: GSC loc. C-305045, North Besa River (NTS 94G/5), northeast British Columbia.

Diagnosis: Short ovoid to quadrate P1 elements with a sunken carina, an inconspicuous cusp, and a substantially shortened platform showing reduction in both upper and lateral views. The unreduced part of the platform is about one-half element length, and the blade is free for part or all of the remainder. The anterior platform may extend as a reduced flange for a variable distance anterior of the strongly stepped down margins. The blade shows a characteristic straight upper and lower profile, at least anterior of the pit, which lies within a narrow loop with raised edges. A narrow grooved keel extends on the underside of the anterior end of the blade.

Remarks: This species differs from *Paragondolella? sulcata* in having a shortened platform and a free blade. Its distinctive carina readily distinguishes it from all other metapolygnathid species. The straight profile is reminiscent of that of *P. foliata*, which differs in having a strong carina and large cusp.

Canadian occurrences: South Besa River and North Besa River, northeastern British Columbia. Found in Sutherlandi Zone associated with both *Frankites* and *Daxatina*, or with *Daxatina* alone.

Neogondolella Bender & Stoppel, 1965

Remarks: The multielement *Neogondolella* apparatus has been reconstructed by Orchard & Rieber (1999), and further examples are given by Orchard (2005). In the latter work, the apparatus described as "*Neogondolella inclinata*" is now referred to *N. liardensis.*

Neogondolella liardensis sp. nov.

(Fig. 3. 4-6)

2005 *Neogondolella inclinata* (Kovacs) - Orchard, p. 85, text-fig. 11.
2006 *Neogondolella inclinata* (Kovacs) – Orchard, pl. 6, figs. 1, 2, 9, 10.

Holotype: GSC 120356, Fig. 3. 4-6.

Etymology: From the type locality on Liard River.

Type stratum: Liard Formation, 74.9 m below contact with uncomformably overlying Cretaceous unit.

Type locality: GSC loc. O-68266, Middle Canyon, Liard River (Tozer, 1994, p. 330), northeast British Columbia.

Diagnosis: Arched P1 elements are relatively narrow and elongate with subparallel margins for most of their length, tapering gradually at both anterior and posterior ends. During growth, the posterior end of the platform varies from pointed to round to subquadrate with rounded corners; a slight constriction may be present. The platform extends to the anterior end of the blade, and posteriorly extends beyond the cusp where it forms a narrow brim. The blade-carina is low throughout, rising slightly to the anterior of the evenly downturned platform margins, more so in large specimens. The cusp is large and prominent, twice the size of the adjacent carinal denticles, and occasionally shows fusion to an adjacent denticle: a small accessory posterior denticle is seen in some juveniles. The carinal nodes, typically 14-15 in number in adults, are low, their pointed apices being visible in profile. The underside bears a small posterior pit lying in a narrow loop with raised edges, and a narrower grooved keel extending to the anterior end.

Remarks: This species has been confused with *Paragondolella inclinata* in the past, partly because large specimens may show some elevation of the anterior blade, whereas larger specimens of the *P. inclinata* may show relative lowering of the posterior carina. However, the platform is generally longer and narrower in the new species, the carina and blade consistently lower, and the cusp much more differentiated. Large populations of this species show variation in carinal development. Some elements have larger and fewer denticles, whereas others have a greater number of small denticles.

Canadian occurrences: Liard River, South Besa River, North Besa River, Clearwater, and Williston Lake, northeastern British Columbia. Found in Sutherlandi Zone associated with both *Frankites* and *Daxatina*, together or alone, and in the Desatoyense Zone.

Paragondolella Mosher, 1968

Remarks: The characteristic morphology of typical Middle Triassic *Paragondolella* species is a posteriorly rounded, relatively flat platform, high blade/carina, and a platform brim posterior of the carina. Orchard (2005) reconstructed a multielement apparatus for *P.* ex gr. *excelsa*, to which the type species belongs. In particular, this multielement species has an S0 element in which the anterior lateral processes diverge far anterior to the cusp. In *Metapolygnathus*, the anterior processes are thought to lie immediately behind the cusp, as in contemporaneous *Neogondolella* species (e.g., *N. liardensis*). However, the multielement apparatuses of younger species, including *P. inclinata*, have yet to be reconstructed.

Paragondolella inclinata (Kovacs, 1983)

(Fig. 3. 1-3)

1983 *Gondolella foliata inclinata* n. subsp. – Kovacs, p. 110-112, pl. 1, figs. 1-4; pl. 3, fig. 2.

Diagnosis: P1 elements of this species are characterized by a high blade-carina that when viewed in profile forms an arcuate crest throughout the length of the element. The blade descends progressively to the posterior where the carinal nodes become progressively submerged with platform growth; the cusp is surrounded by a narrow platform brim. The posterior margin is rounded to subquadrate in outline. Overall platform shapes vary from subparallel to distinctly biconvex, with the broadest point lying a little posterior to platform midlength. The anterior platform margins descend gradually to the anterior end of the element without any pronounced geniculation or inturning. Some specimens have subdued or pronounced nodes on the anterior downturned platform margins. The underside bears a small posterior pit lying in a narrow loop with raised edges, and a narrower grooved keel extending to the anterior end.

Remarks: As discussed under *Neogondolella liardensis*, the P1 element *P. inclinata* has been confused with those of the former species but small specimens in particular can be distinguished by reference to the high blade-carinal denticles, which are also smaller and more numerous in this species. Through increasing differentiation of the blade and medial carina and in the reduction of the anterior platform, *P. inclinata* leads to *Metapolygnathus.*

Canadian occurrences: Liard River, North Besa River, Clearwater, and Williston Lake, northeastern British Columbia. Found in Sutherlandi Zone associated with both *Frankites* and *Daxatina,* together or alone, and in the Desatoyense Zone.

Paragondolella willistonensis sp. nov.

(Fig. 3. 16-18)

Holotype: GSC 120360, Fig. 3 16-18.

Etymology: From the type locality on Williston Lake.

Type stratum: Liard Formation (spot sample BHE-1).

Type locality: GSC loc. C-305932, Brown Hill east, Williston Lake, northeast British Columbia.

Diagnosis: P1 elements of this species have a broad, arched platform divided into two parts: a larger, biconvex anterior part and a narrow, bulbous posterior part. Between them there is a distinct narrowing or constriction in front of the prominent cusp. The blade-carina is high and forms an arcuate crest that descends in both directions from its apex at element midlength. The platform tapers gradually to the anterior without geniculation. The pit lies beneath the cusp and is surrounded by an ovoid loop that occupies most of the constricted portion of the platform, and extends anteriorly as a grooved keel.

Remarks: This species is similar to *Metapolygnathus lobatus* but differs in having a high prominent blade-carina like that of *Paragondolella inclinata*, from which it is readily separated on the basis of its distinctive posterior constriction and more posteriorly centred platform.

Canadian occurrences: Clearwater and Williston Lake, northeastern British Columbia. Found in Sutherlandi Zone associated with both *Frankites* and *Daxatina* together, or with *Daxatina* alone, and in the Desatoyense Zone.

Paragondolella? *sulcata* sp. nov.
(Fig. 3. 25-27)

1997 *Paragondolella* n. sp. S – Orchard & Tozer, p. 683.

Holotype: GSC 120363, Fig. 3. 25-27.

Etymology: Referring to the deep medial trough in which the carina lies.

Type stratum: Liard Formation (spot sample NWB-1).

Type locality: GSC loc. C-305045, North Besa River, northeast British Columbia.

Diagnosis: The arched P1 elements have a distinctive subdued carina that lies in a deep medial trough with well defined adcarinal grooves. The carinal nodes in the posterior one-half of the platform are small, often fused in later growth stages, and terminate in a very small or indistinct cusp that lies well in front of the posterior platform margin that is surrounded by a wide posterior brim. The platform is elongate and has subparallel lateral margins and a rounded to slightly quadrate posterior margin. In lateral view, the posterior carina lies below the platform surface and cannot be seen, whereas the anterior carina rises into a high fixed blade in the anterior one-half to one-third of the element. The platform extends to, or close to the anterior tip of the blade. Downturning of the anterior platform margins is generally gradual in mature specimens but may be more abrupt in smaller specimens. The underside bears a small posterior pit lying in a narrow loop with raised edges, and a narrower grooved keel extending to the anterior end.

Remarks: The sunken carina of this species differentiates it from contemporary elements like those of *Paragondolella inclinata* or *Neogondolella liardensis* that may have a similar platform shape. The derivative *Metapolygnathus zonneveldi* has the same carina but is shorter with a distinctive free blade.

The species is included with question in *Paragondolella* because, like *P. inclinata*, the blade rises to the anterior, although the low posterior carina is quite unlike that of *Paragondolella*. In fact the carinal features are reminiscent of mature specimens of the older species "*P.*" *trammeri*, for which an independent (but preoccupied) genus ("*Trammerella*") was introduced by Orchard (2005). That species differs in having a lower fixed blade and a distinctive, more posteriorly positioned cusp, especially in smaller growth stages.

Canadian occurrences: Liard River, North Besa River, and Williston Lake, northeastern British Columbia. Typical of the Maclearni Zone, and in the Sutherlandi Zone associated with both *Frankites* and *Daxatina* together, or with *Daxatina* alone.

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Lucas, S.G. and Spielmann, J.A., eds., 2007, The Global Triassic. New Mexico Museum of Natural History and Science Bulletin 41.

CONODONT LINEAGES FROM THE CARNIAN-NORIAN BOUNDARY AT BLACK BEAR RIDGE, NORTHEAST BRITISH COLUMBIA

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At Black Bear Ridge on Williston Lake, northeast British Columbia, a continuous outcrop of Ludington and Pardonet formations deposited in a deep marine slope setting on the north-western margin of Pangea has yielded a succession of abundant and diverse late Carnian and early Norian conodonts. These show progressive evolutionary change in platform margin profile and ornament, in relative blade length, in carina height and fusion, and/or in basal pit position. These lineages include that of *Carniepigondolella* spp. (Fig 1.1-3, etc.), and metapolygnathids of the '*polygnathiformis*' – *carpathicus* – *nodosus* lineage (Fig. 1.4-6, etc.); *noah* - n. sp. G – *primitius* lineage (Fig. 1.7-9, etc.); aff. *communisti* – '*parvus*' – *echinatus* lineage; and several others are featuring new taxa. These collectively provide a refined biochronology for the Carnian-Norian boundary interval in which several horizons are identified as suitable datums for correlation and definition.

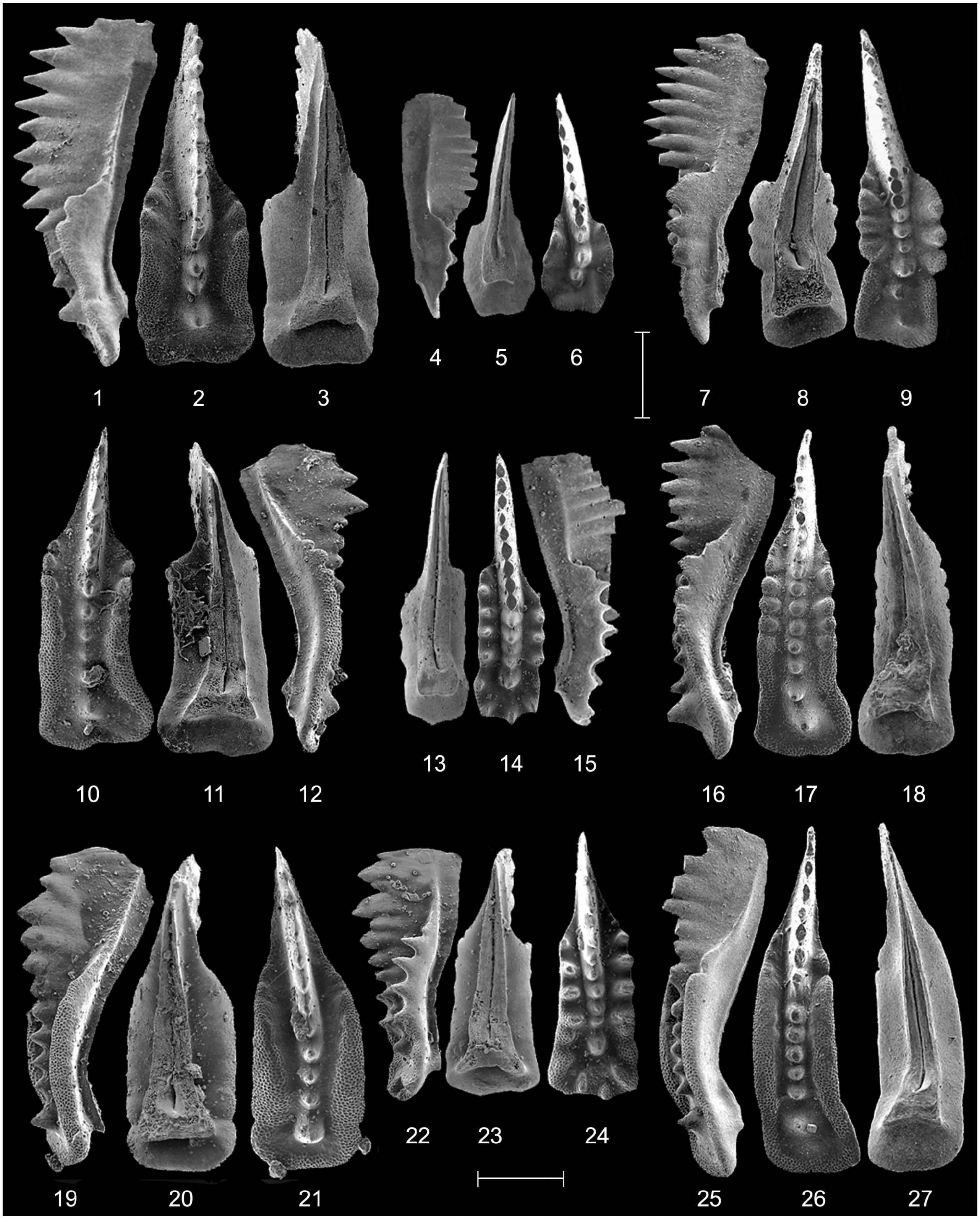

FIGURE 1. Examples of lineages of Carnian-Norian boundary conodonts. Scale bar = 200 microns (x 80). Oldest species are at the bottom and they young upward. **1-3, 10-12, 19-21,** Respectively, *Metapolygnathus nodosus*, *M. carpathicus*, *M. polygnathiformis* s.l. lineage. **4-6, 13-15, 22-24,** Respectively, *Carniepigondolella pseudoechinatus*, *C.* n. sp. N, *C. samueli* lineage. **7-9, 16-18, 25-27,** Respectively, *Metapolygnathus primitius*, *M.* n. sp. G., *M. noah* lineage.

Lucas, S.G. and Spielmann, J.A., eds., 2007, The Global Triassic. New Mexico Museum of Natural History and Science Bulletin 41.

CONODONTS FROM THE LADINIAN-CARNIAN BOUNDARY BEDS OF SOUTH CANYON, NEW PASS RANGE, NEVADA, USA

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Abstract—Conodonts from the Augusta Mountain Formation in the New Pass Range area of Nevada are documented and compared with those recently described from Ladinian-Carnian boundary strata in British Columbia. *Budurovignathus mungoensis* dominated faunas from the Lower Member of the formation correlate with conodont faunas known from the lower Sutherlandi Zone in B.C. Conodont faunas from around the lithological boundary of the Lower and Middle members comprise a diverse association of several new species that are assigned to the new *intermedius* Zone and suggest a position within the higher part of the Sutherlandi Zone at about the appearance of *Daxatina*. Similarly, the appearance of *Metapolygnathus tadpole* with *Mosherella newpassensis* at ~6 m above the base of the Middle Member denotes the base of the *tadpole* Zone, which equates with the highest occurrence of *Frankites* in B.C. The implication is that the Sutherlandi and Desatoyense zones are in part equivalent. The youngest faunas recovered from New Pass yield *Mosherella* n. sp. A and correlate with strata as young as the Nanseni Zone.

INTRODUCTION

This report presents details of the conodont succession at South Canyon in the New Pass Range of central Nevada (Fig. 1). A history of study, details of the succession, and a summary of the biostratigraphy have been given previously in Balini et al. (2007), for which this provides a supplementary record. South Canyon is notable as the type locality for the Lower Carnian Desatoyense Zone, and its superposition above a Sutherlandi Zone ammonoid fauna (Silberling and Tozer, 1968). As such, it is crucial for discussions of the Ladinian-Carnian boundary (Fig. 2).

Mosher (1968) was the first to study conodonts from South Canyon, from both the Favret and Augusta Mountain formations. He found abundant collections of "*Epigondolella*" = *Budurovignathus mungoensis* starting at ~140 m below the Lower-Middle Member contact of the Augusta Mountain Formation, and ranging up to ~1.5 m above that contact. Mosher (1968, p. 911) also recorded "*Neospathodus*" = *Mosherella newpassensis* from ~6.7 m above the base of the Middle Member through ~136 m, and "*Paragondolella*" = *Metapolygnathus polygnathiformis* sensu lato from ~12 m and questionably through ~113 m above the base. Records of "*P. excelsa*" and "*P. navicula*" at the base of the Middle Member are probably assignable to *P. inclinata* and perhaps *N. liardensis* of this report. The occurrence of "*Neospathodus*" *lanceolatus* from near the top of the Middle Member (Mosher, 1968) is now attributed to *Mosherella* n. sp. A (see below). Mosher (1968) also reported many ramiform or "compound" elements from South Canyon, including three new species: *Cypridodella scolosculptura*, *Hindeodella torta,* and *Parachirognathus jungi*. These are now reconstructed as part of the multielement apparatuses of *Budurovignathus* and *Mosherella* (see below).

In 1989, Leopold Krystyn (U. Vienna) collected several conodont samples from South Canyon and shared them with the senior author: these essentially replicated the earlier data of Mosher (1968). A sample from the base of the Middle Member (sample 155) contained abundant *Budurovignathus mungoensis*, and a sample from the Desatoyense Zone (sample 105) yielded abundant *Mosherella newpassensis*, *Paragondolella inclinata,* and *Metapolygnathus polygnathiformis* sensu lato. Several samples from higher in the section yielded *Mosherella* n. sp. A (samples 131, 137). Subsequently, the present authors visited South Canyon in 2002 and made detailed collections through sections A and B. In 2005, these were supplemented by collections from section D (Balini et al., 2007).

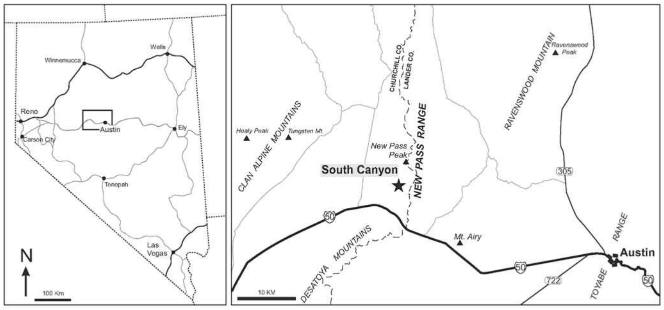

FIGURE 1. Location map of South Canyon.

THE CONODONT SUCCESSION

Conodont samples were taken from four sections reported in Balini et al. (2007): sections D(1), A, B, and D(2). The first of these covered the Lower-Middle Member boundary, the next two an additional 9-18 m of the Middle Member, and section D(2) the interval from about 35-45 m within the Middle Member.

A few meters below the top of the Lower Member, a conodont collection (D31) taken from gray bioclastic packstones with brachiopods yielded the conodonts *Budurovignathus mungoensis*, *Neogondolella liardensis*, and *Paragondolella inclinata.*

In so much as this fauna lacks *Metapolygnathus*, the association is typical of the lower parts of the Sutherlandi Zone in British Columbia. However, within the highest meter of the Lower Member in Sections A and B (Figs. 3-4), they are joined by metapolygnathids that suggest, by comparison with those in B.C., a position within the higher, *Daxatina*-bearing beds of the Sutherlandi Zone.

In general, conodont collections from both sections A and B at South Canyon show a tripartite division spanning the upper Lower and lower Middle members of the Augusta Mountain Formation. Samples from below 1 m from the top of the Lower Member are virtually monospecific *Budurovignathus mungoensis* faunas and, although this species continues into the Middle Member, it becomes subordinate to species of *Metapolygnathus*, *Neogondolella*, and *Paragondolella* (M-N-P) around the lithological boundary. Higher still, from ~6 m above the base of the Middle Member in section A, M-N-P in turn suddenly become subordinate to *Mosherella newpassensis*, which also forms virtually monospe-

		Ammonoid Zone	Type locality
CARNIAN	Upper	*Klamathites macrolobatus*	Shoshone Mts., Nevada
		Tropites welleri	Shasta County, CA
		Tropites dilleri	Shasta County, CA
	Lower	*Sirenites nanseni*	Ewe Mountain, BC
		Austrotrachyceras obesum	Ewe Mountain, BC
		Trachyceras desatoyense	South Canyon, Nevada
LADINIAN	Upper	*Frankites sutherlandi*	Boiler Canyon, BC
		Maclearnoceras maclearni	Fossil Gate, BC
		Meginoceras meginae	Boiler Canyon, BC

FIGURE 2. The North American Upper Ladinian–Carnian ammonoid Standard Scale (Tozer, 1994) showing the position of the *Trachyceras desatoyense* Zone (shaded area). BC=British Columbia; CA=California.

cific faunas in higher beds. The pattern of these dramatic biofacies shifts can be used to correlate between the two sections. Hence, the unexposed base of the Middle Member in Section B is tentatively placed higher than shown in Balini et al. (2007).

Section A (Fig. 3) contains the most complete conodont record for the Ladinian-Carnian boundary (LCB) interval at South Canyon. Above monospecific *B. mungoensis* collections (#SCAN8bis, #B2), the fauna consists of that species plus *Paragondolella inclinata*, *P.*? *sulcata*, *Neogondolella liardensis*, *Metapolygnathus acuminatus*, *M. intermedius*, *M. lobatus*, and *M. polygnathiformis* sensu stricto (#SCAN8 and up). None of these species are common compared with those of *Budurovignathus* and *Mosherella*, but by comparison with conodont faunas from LCB strata in British Columbia (Orchard, this volume), they can be assigned to the *intermedius* Zone, equivalent to the upper Sutherlandi Zone. In section A, many of the species range up through the lower ~5 m of the Middle Member where *Misikella longidentata* also occurs sporadically (#SCAN6 thru #SCAN4). *Budurovignathus mungoensis* is very rare at these levels, too. Faunas above the level of the incoming of *Mosherella newpassensis* (#A19, #B5E) are rather poor in other species and appear less diverse, although *Mosherella* itself is extremely abundant. The taxon overlaps with the range of *Frankites* in B.C., as is the case in section B (#SCAN14, 15).

Higher strata in both sections A and B are dominated by *M. newpassensis* but also contain *Metapolygnathus tadpole* in section A (SCAN3) and in section B (SCAN15): this association is typical of the younger *Daxatina* faunas in British Columbia, which are newly referred to the *tadpole* Zone (sensu Orchard, this volume). Rare *Budurovignathus* sp. A also occurs in these higher strata (SCAN3, B11), above the range of *B. mungoensis*.

Higher parts of the Middle Member exposed in section D(2), yield conodont faunas dominated by *Mosherella newpassensis*. This species forms monospecific faunas in samples D1, D2, and D4, whereas in D9 and D10 it is far more abundant than associated *Paragondolella inclinata*, the only other taxon recovered. In spite of the absence of metapolygnathids, these levels can be correlated with the *tadpole* Zone, known to embrace the Desatoyense Zone in British Columbia. Higher strata of the Augusta Mountain Formation with *Mosherella* n. sp. A can be correlated with the Lower Carnian Nanseni Zone in B.C.

SUMMARY

Many of the conodonts identified in South Canyon (New Pass Range area) have recently been described from LCB strata in British Columbia (Orchard, this volume). This facilitates more refined correlation of the Nevadan successions.

Budurovignathus mungoensis dominated faunas of the Lower Member of the Augusta Mountain Formation correlate with conodont faunas known from the lower Sutherlandi Zone in B.C., broadly equivalent to the *Paragondolella inclinata* Zone differentiated by Orchard (this volume). Those associations known from around the lithological boundary of the Lower and Middle members are assigned to the *intermedius* Zone and suggest, in comparison with B.C., a position within the higher part of the Sutherlandi Zone at about the appearance of *Daxatina*. Similarly, the appearance of *Mosherella newpassensis* and *M. tadpole* at ~6 m above the base of the Middle Member argues for a position, in relation to B.C. faunas, at and above the highest occurrence of *Frankites*, assignable to the *tadpole* Zone of Orchard (this volume). This implies that the Sutherlandi and Desatoyense zones are in part equivalent, as was tentatively suggested by Tozer and Silberling (1968, p. 45). The youngest faunas recovered from South Canyon with *Mosherella* n. sp. A correlate with strata as young as the Nanseni Zone.

TAXONOMIC NOTES

The new taxa reported from South Canyon are described in a companion paper in this volume (Orchard, 2007) and are not discussed further here. Remarks on other elements of the fauna are provided here.

Budurovignathus mungoensis (Diebel)
(Figure 5. 1-10)

1956, *Polygnathus mungoensis* n. sp. – Diebel, p. 431, pl. 1, figs. 1-20; pl. 2, figs. 1-4; pl. 3, fig. 1; pl. 4, fig. 1.
1968, *Epigondolella mungoensis* (Diebel) - Mosher, p. 936-7, pl. 116, figs. 16-19.
1968, *Hindeodella torta* n. sp. – Mosher, p. 929, pl. 114, figs. 11, 12 (= P2 element).

Remarks: This is an extremely abundant species in the Lower Member of the Augusta Mountain Formation. It displays some variation in platform shape, often terminating in a point in small specimens and in many larger 'typical' sinuous representatives. Some other large specimens have broadened posterior platforms resulting from outgrowth of one postero-lateral margin. In those forms, a weak secondary keel may be developed (Fig. 5. 6). These are judged to be intraspecific variants of *B. mungoensis* although similar forms have been assigned to *B. diebeli*, which appears to be a Tethyan endemic.

The paratype of *Hindeodella torta*, the P2 element of the multielement *Budurovignathus* (Orchard, 2005), came from sample NL-1 of Mosher (1968), that is from ~6 m below the Lower-Middle Member boundary, and not from the Middle Member as was stated in the plate description (op. cit., p. 926).

Budurovignathus sp. A
(Figure 5. 15, 16, 25, 26)

Remarks: Two incomplete specimens from the Desatoyense Zone at South Canyon are characterized by rounded anterior nodes, which are only poorly defined in one specimen. The pit is located close to the anterior end of the platform. These specimens are broader than *B. mungoensis* and lack the sharp, well defined platform nodes of that species.

Metapolygnathus polygnathiformis (Budurov and Stefanov)
(Figure 6. 14, 19, 46-51)

1965, *Gondolella polygnathiformis* sp. nov. - Budurov & Stefanov, p.

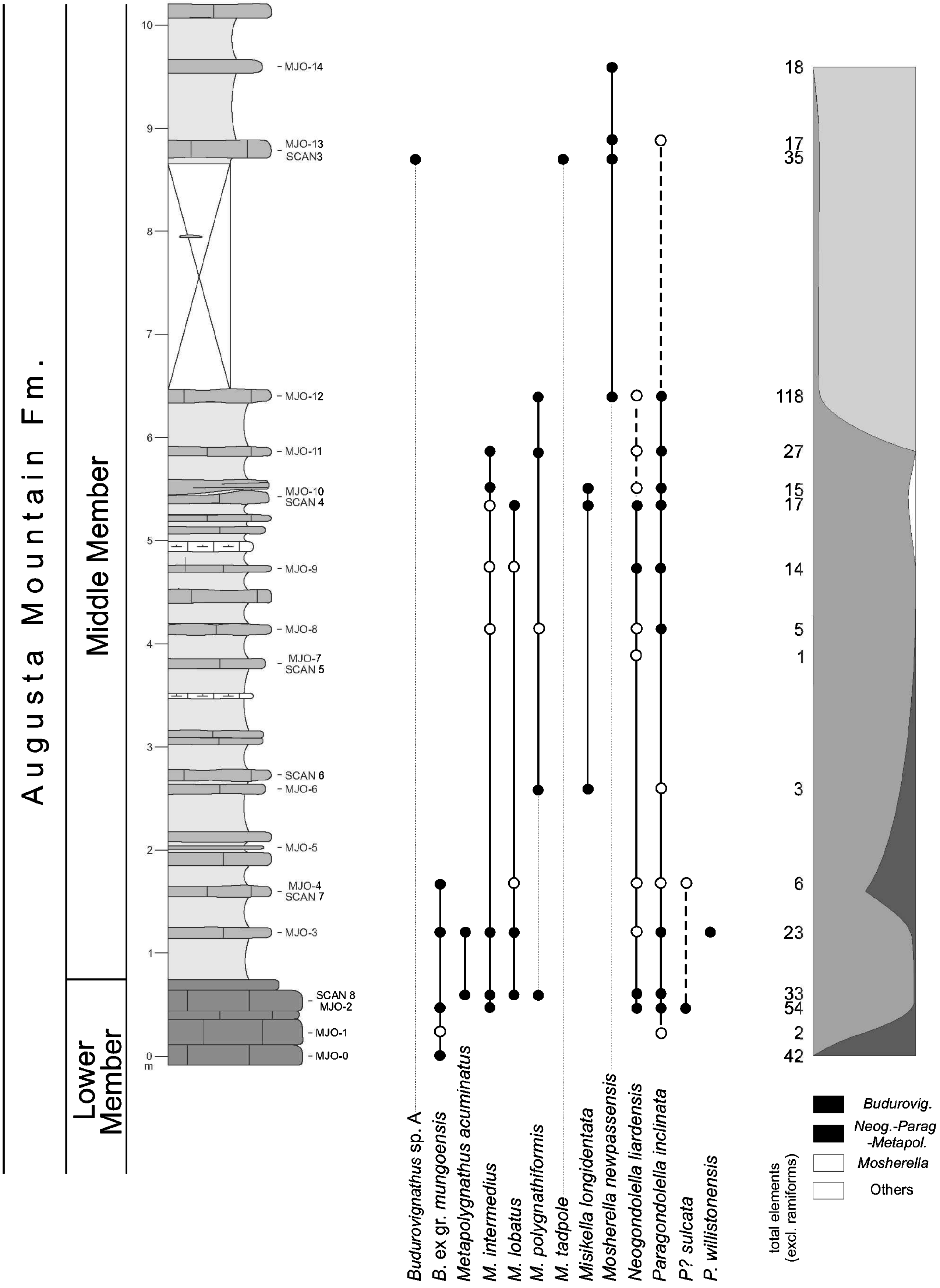

FIGURE 3. Conodont distribution in Section A in South Canyon. Solid circles are occurrences, open circles are questionable. Column on right shows total numbers of elements recovered and variation in the ratio of the principal conodont groups.

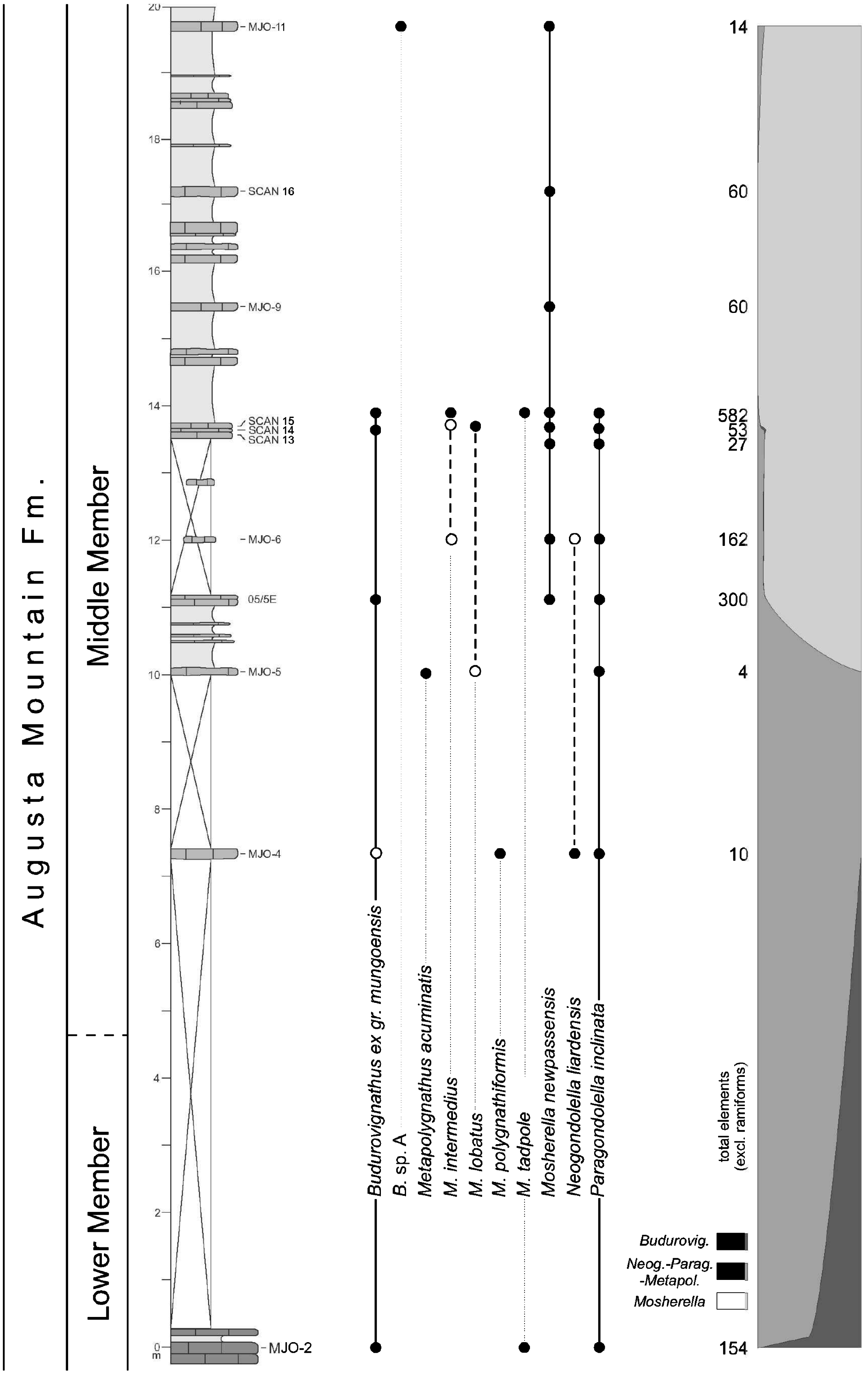

FIGURE 4. Conodont distribution in Section B in South Canyon. Solid circles are occurrences, open circles are questionable. Column on right shows total numbers of elements recovered and variation in the ratio of the principal conodont groups.

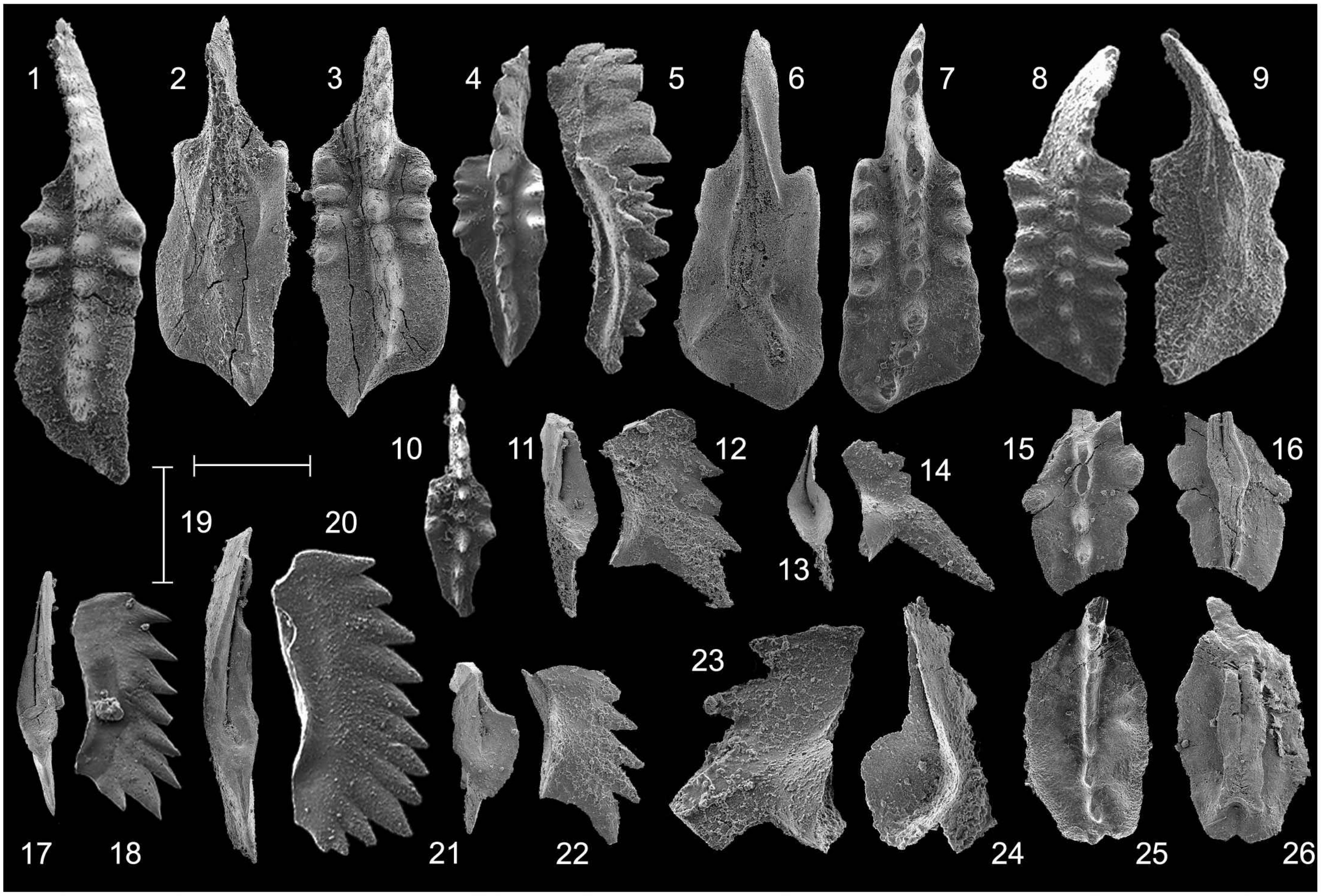

FIGURE 5. Upper, lower, and lateral views of conodonts from South Canyon. Scale bars = 200 microns (x80), except figs. **23**, **24** (x160). **1-10**, *Budurovignathus* ex gr. *mungoensis* (Diebel). **1**, GSC 120393 from SC-B2. **2**, **3**, GSC 120394 from SC-B2. **4**, **5**, GSC 120395 from 155. **6**, **7**, GSC 120396 from SC-A10. **8**, **9**, GSC 120397 from 155. **10**, GSC 120398 from 155. **11**, **12**, **21**, **22**, *Mosherella* n. sp. A. **11**, **12**, GSC 120399 from 131. **21**, **22**, GSC 120400 from 137. **13**, **14**, **23**, **24**, *Misikella longidentata* Kozur & Mostler. **13**, **14**, GSC 120401 from SCAN-4. **23**, **24**, GSC 120402 from 110. **15**, **16**, **25**, **26**, *Budurovignathus* sp. A. **15**, **16**, GSC 101824 from SC-B11. **25**, **26**, GSC 101825 from SCAN-3. **17-20**, *Mosherella newpassensis* (Mosher). **17**, **18**, GSC 101826 from 105. **19**, **20**, GSC 101827 from 105.

118-19, pl. 3, fig. 7.

2004, *Paragondolella polygnathiformis* (Budurov & Stefanov) – Krystyn et al., p. 49, fig. 10, unnumbered illustrations from samples MVc5, MV19.

Remarks: This species was originally described from a collection taken at the south end of the village of Snezha in the Burgas District of Bulgaria, in strata close to the Ladinian-Carnian boundary. According to H. Kozur (pers. comm., 2007), it occurred with abundant specimens of *Paragondolella inclinata* and is probably of "latest Ladinian" age. The original illustration of the holotype is poor and so, too, apparently, is its preservation. However, an essential feature of its morphology is the geniculation of the lateral anterior platform margins and it is this character that has been used as diagnostic in all subsequent reports of the species. As such, the species has been broadly interpreted and used as a guide for both Lower and Upper Carnian strata. Hence, the *polygnathiformis* Assemblage Zone of Mosher (1968, p. 911) and Sweet et al. (1971, p. 458) was based on Upper Carnian *Tropites* beds in Europe and North America with the Hallstatt Limestone at Someraukogel designated as the type locality for zone. The breadth of interpretation subsequently given to *Metapolygnathus polygnathiformis* is demonstrated by the records of Mosher (1973, p. 164), who recorded it from as low as the upper Ladinian Maclearni Zone as well as from the Lower Carnian Nanseni Zone, and Upper Carnian Welleri Zone. In Europe, Krystyn (1980, p. 78) also showed *polygnathiformis* as ranging from near top of late Ladinian Sutherlandi Zone through the Upper Carnian Subbullatus Zone and *Anatropites* Beds; his more restricted *polygnathiformis* Assemblage Zone was largely Tuvalian in age.

Elements from the Upper Carnian show significant differences when compared with specimens from the Ladinian-Carnian boundary interval. In this report, the species *polygnathiformis* is restricted to elements that have the following features:

1) A platform that is posteriorly rounded to more commonly subquadrate in outline.

2) A platform that extends the entire length of the element and, when viewed from above, has gradually tapered anterior margins without inward deflection.

3) When viewed from the side, at least one anterior lateral margin has a geniculation point or anterior 'step'.

4) The carina is moderately high and fused but may be more or less submerged by the upturned platform margins when viewed in profile.

5) The fixed blade is generally well differentiated and partially fused and projects above the down turned platform margins.

6) The cusp is large, prominent, well differentiated from the fused carinal nodes, subterminal in position, and surrounded by a narrow posterior platform brim.

Metapolygnathus polygnathiformis is close to *M. acuminatus* but differs particularly in platform shape. *Metapolygnathus intermedius* is the next evolutionary step within the group, which involves further

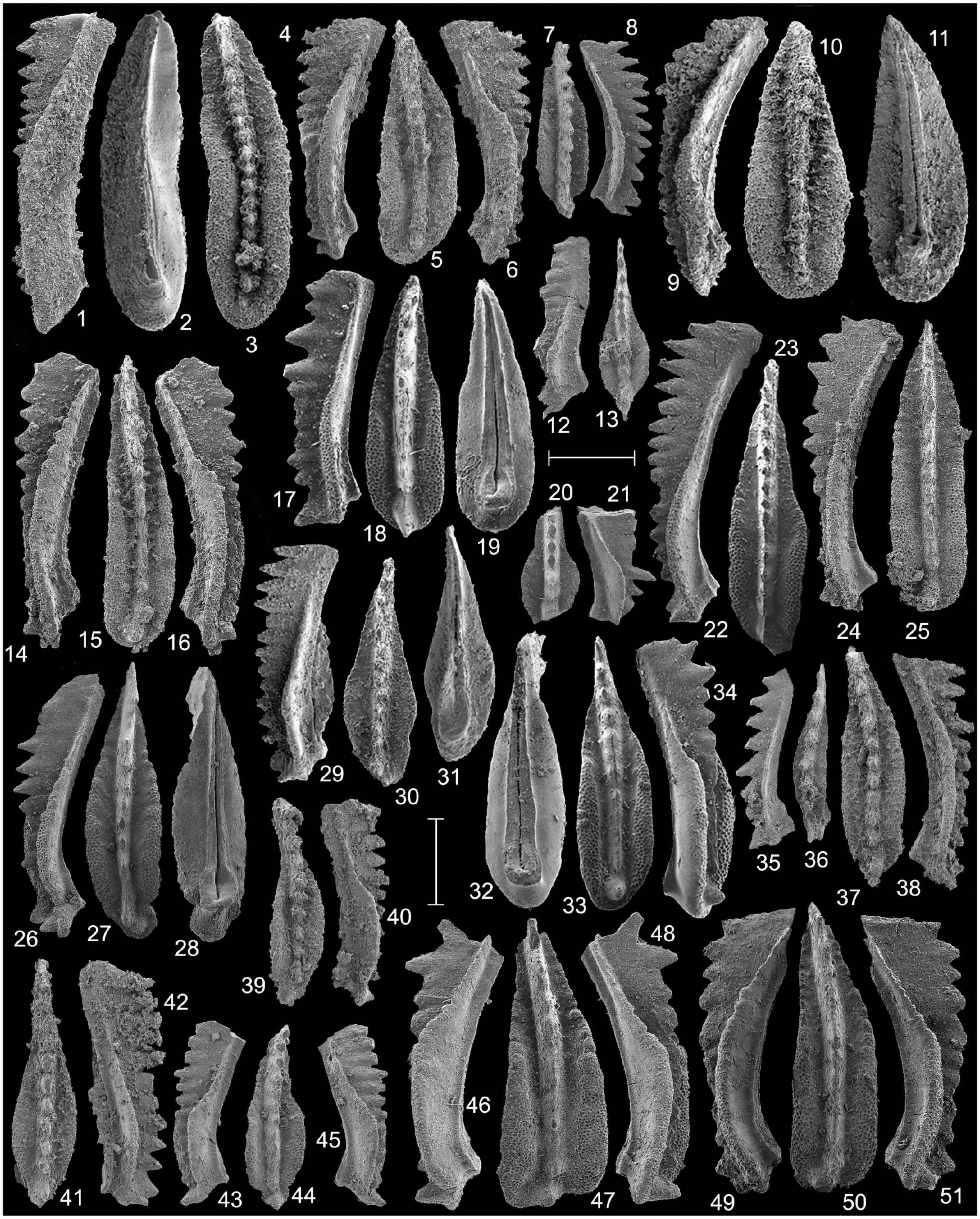

FIGURE 6. Upper, lower, and lateral views of conodonts from South Canyon. Scale bars = 200 microns (x80).**1-3**, *Paragondolella? sulcata* Orchard. GSC 120374 from GSC loc. 306596 (SC-A2). **4-6**, *Metapolygnathus acuminatus* Orchard. GSC 120374 from SC-A3. **7-11**, **24**, **25**, *Paragondolella inclinata* (Kovacs). **7**, **8**, GSC 120375 from SC-A9. **9-11**, GSC 120376 from SC-A2. **24**, **25**, GSC 120377 from SCAN-4. **12**, **13**, **20**, **21**, *Metapolygnathus tadpole* (Hayashi). **12**, **13**, GSC 120378 from SCAN-15. **20-21**, GSC 120379 from SCAN-3. **14-19**, **46-51**, *Metapolygnathus polygnathiformis* (Budurov & Stefanov). **14-16**, GSC 120380 from SC-B4. **17-19**, GSC 120381 from 105. **46-48**, GSC 120382 from SC-A1149-51. GSC 120383 from SC-A12. **22**, **23**, **32-34**, **39-45**, *Metapolygnathus intermedius* Orchard. **22**, **23**, GSC 120384 from 105.39. **40**, GSC 120385 from SCAN-8. **32-34**, GSC 120386 from SC-105. **41**, **42**, GSC 120387 from SCAN-8. **43-45**, GSC 120388 from SCAN-15. **26-28**, *Metapolygnathus lobatus* Orchard. GSC 120389 from SCAN-4. **29-31**, *Paragondolella willistonensis* Orchard. GSC 120390 from SC-A3. **35-38**, *Neogondolella liardensis* Orchard. **35**, **36**, GSC 120391 from SCAN-4. **37**, **38**, GSC 120392 from SC-A9

reduction of the anterior platform, which becomes evident in upper view as well as in lateral view, and which involves the appearance of a 'free blade'. This trend continues to produce *Metapolygnathus tadpole*, in which the free blade is at least half the total element length. Derivatives *of M. polygnathiformis* sensu stricto with a reduced anterior platform have been referred to *Metapolygnathus noah* Hayashi by Kozur (pers. comm., 2007). However, that species has more discrete nodes, a wide brim, and seemingly a more anterior pit than LCB species. *Metapolyganthus noah* corresponds to elements from the Upper Carnian, for which this species name is now restricted.

Misikella longidentata Kozur & Mock
(Figure 5. 13, 14, 23, 24)

1974, *Misikella longidentata* n. sp. – Kozur & Mock, p. 136-37, pl. 1, figs. 4, 5.
1988, *Misikella longidentata* Kozur & Mock – Fahraeus & Ryley, p. 1256, pl. 1, figs. 11, 13.
2003, *Misikella longidentata* Kozur & Mock – Channel, Kozur, Sievers, Mock, Aubrecht, & Sykora, fig. A2 - 4, 5.

Remarks: Four specimens of this species were recovered in Section A and one from sample 110 of Krystyn (collected ~4 m above the base of the Middle Member). They show the characteristic large terminal cusp and few short anterior denticles. Cited records of this species are mostly late Carnian and Norian in age, so these early Carnian occurrences may be the oldest known.

Mosherella newpassensis (Mosher)
(Figure 5. 17-20)

1968, *Neospathodus newpassensis* n. sp. – Mosher, p. 931, pl. 115, figs. 5, 6, 9 (= P1 element).
1968, *Cypridodella scolosculptura* n. sp. – Mosher, p. 921, pl. 113, figs. 13, 22 (=S2 element).
1968, *Parachirognathus jungi* n. sp. – Mosher, p. 933, pl. 115, figs. 18, 19 (= S3/4 element).
2005, *Mosherella newpassensis* (Mosher) – Orchard, p. 92, text-fig. 18H-J.
2006, *Mosherella newpassensis* (Mosher) – Orchard, p. 247, pl. 6, fig. 19.

Remarks: This species is abundant in the Desatoyense Zone at South Canyon, and in B.C. it is also known from *Frankites*-bearing beds in North Besa River, with both *Frankites* and *Daxatina* at South Besa River, and with *Daxatina* alone on Liard River (Orchard, this volume). The species also occurs in the Pelly Mountains, Yukon Territory (Orchard, 2006).

Multielement *Mosherella* was reconstructed by Orchard (2005) based largely on New Pass material. Mosher (1968) formerly described the S2 and S3/4 elements as new species.

Mosherella n. sp. A
(Figure 5. 11, 12, 21, 22)

1968, *Neospathodus lanceolatus* n. sp. – Mosher, p. 930-31, pl. 115, fig. 10 (only).
1973, *Neospathodus* sp. E – Mosher, p. 173, pl. 18, fig. 36.

Remarks: This new species apparently developed from *Mosherella newpassensis* through the loss of denticles posterior of the cusp. This reduction of the posterior process appears to be progressive because in a collection from the Desatoyense Zone in the Clearwater area in British Columbia (GSC loc. 83825), some elements retain a single tiny posterior denticle.

Mosher (1968) referred five specimens from South Canyon (sample NP-116) to a new species for which he selected a holotype from the Upper Norian Hallstatter Kalk at Steinbergkogel, Austria. The holotype is an example of *Misikella* whereas that from South Canyon is not. The South Canyon specimens came from near the top of the Middle Member of the Augusta Mountain formation, and were replicated in several collections made by L. Krystyn. The specimen reported by Mosher (1973) came from a Nanseni Zone collection from the Ludington Formation ("Grey Beds") at Ewe Mountain in B.C. (GSC loc. 42308).

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A SUMMARY OF THE CONODONT SUCCESSION AROUND THE OLENEKIAN-ANISIAN BOUNDARY AT DEŞLI CAIRA, NORTH DOBROGEA, ROMANIA

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Abstract—The occurrence of conodonts in the Olenekian-Anisian boundary (OAB) beds at the Deşli Caira section in Romania is documented. Eight conodont first and last appearances occur at five different horizons spanning 4.25 m of strata. Of these, the fourth is the appearance of *Chiosella timorensis*, which coincides with the ammonoid-defined OAB. The other conodont events help to constrain the boundary.

INTRODUCTION

The Deşli Caira Hill lies in the province of Dobrogea in the south-easternmost part of Romania, between the lower course of the Danube and the Black Sea coast (Fig.1). Having an altitude of 175 m, the hill is located approximately 6 km east of Mihail Kogălniceanu village, and approximately 8 km west of Agighiol village. The coordinates are $28^0$48’ 08”E and $45^0$04’ 27”N. The name Deşli Caira is Turkish in origin, and the feature is actually known in Romanian toponymy under the name of Stânca Mare (Big Stone) or Muchea Ascuţită (Sharp Summit).

The area of the Deşli Caira Hill is included in the Agighiol Zone of the North Dobrogea (Fig.1), which is famous in classic literature for the spectacular development of Triassic ammonoid faunas (Kittl, 1908; Simionescu, 1913). The Agighiol Zone, which has an external position in the framework of the Triassic carbonate platform of the Tulcea Unit (Grădinaru, 2000), is characterized by the development of thick sequences of Hallstatt-type massive limestones interbedded or grading laterally or vertically to Ammonitico Rosso-type nodular siliceous lime-

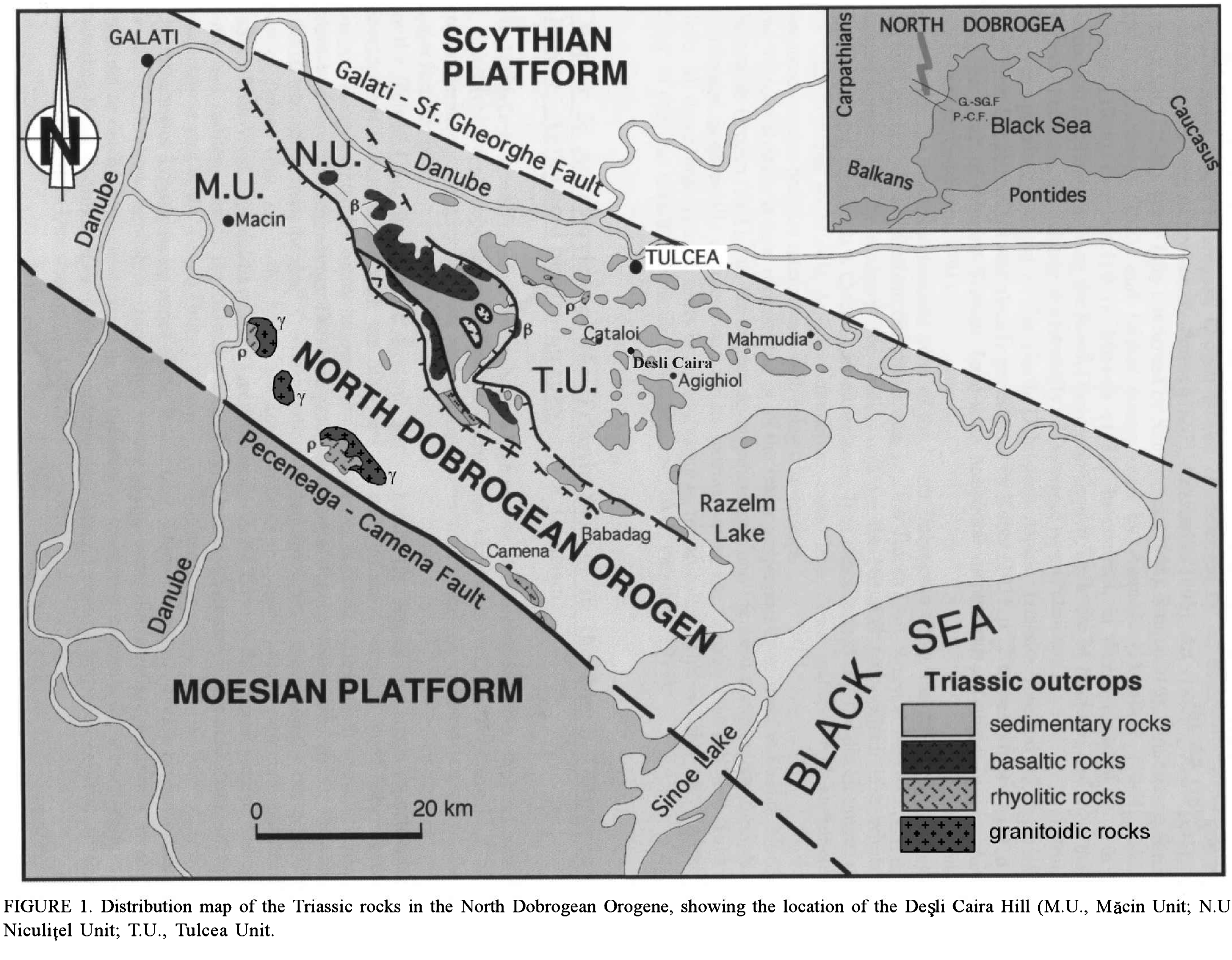


FIGURE 1. Distribution map of the Triassic rocks in the North Dobrogean Orogene, showing the location of the Deşli Caira Hill (M.U., Măcin Unit; N.U., Niculiţel Unit; T.U., Tulcea Unit.

stones. The Tulcea Unit is the lowermost tectonic unit of the Early Alpine North Dobrogea fold and thrust belt (Grădinaru, 2000), which in its turn represents the westernmost prolongation of the Cimmeride Orogenic System. During the Triassic, the North Dobrogea region was situated closer to the main Tethys region but post-Triassic large-scale horizontal movement displaced the North Dobrogea terrane, which is an exotic terrane docked to Eurasia (Grădinaru, 2000).

Deşli Caira Hill is a candidate location for the Olenekian-Anisian boundary (OAB) Global Stratotype Section and Point (GSSP). The present contribution summarizes the conodont succession at the site and thereby contributes to our understanding of the correlation and definition of the OAB.

BIOSTRATIGRAPHY

The Deşli Caira section exposes a sequence of 60+ m thick, Hallstatt-type massive to well-bedded micritic limestones. These limestones are variously colored, mainly reddish, and are interbedded with subordinate "*Posidonia*"-bearing coquinoid limestones of possible tempestite origin, mainly in the lower half of the sequence. The Hallstatt-type limestones are extensively bioturbated at some levels, whereas at other levels they show condensed sedimentation.

The limestone sequence exposed at the Deşli Caira Hill was first studied by Kittl (1908) and Simionescu (1910), who described ammonoid faunas, including new taxa. During the last decades ammonoid faunas have been intensively collected from several stratigraphic levels by the second author (EG). This work has resulted in the recognition of at least eleven levels of distinct, stratigraphically successive ammonoid faunas in the upper half of the Deşli Caira section (Grădinaru, 2000). The late Olenekian is demonstrated by the occurrence of very abundant and diversified ammonoid faunas including species of well-known late Spathian genera such as *Procarnites*, *Albanites*, *Proptychitoides*, *Preflorianitoides*, *Ziyunites*, *Leiophyllites*, etc., and several new ammonoid taxa. Of outstanding value is the occurrence in the latest Spathian of an olenikitid-like ammonoid species group informally assigned to the genus *Deslicairites* by Grădinaru (2003).

The basal Anisian is documented by the *Paracrochordiceras-Japonites* Beds, in which the presence of a *Karangatites*-akin ammonoid and also of "*Romanites*" cf. *simionescui* Welter are recorded. The ammonoid and nautiloid faunas from around the OAB in the Deşli Caira section are of remarkable importance for the correlation of the Triassic in the Tethyan and Boreal realms (Grădinaru & Sobolev, 2006). The next Anisian ammonoid assemblage in the section of the Deşli Caira section is diagnostic for the *Aegeiceras ugra* Beds, which are well known from other classic localities in the Tethyan Realm (Assereto et al., 1980; Gaetani et al., 1992; Balini & Krystyn, 1997; Waterhouse, 1999; Krystyn et al., 2004).

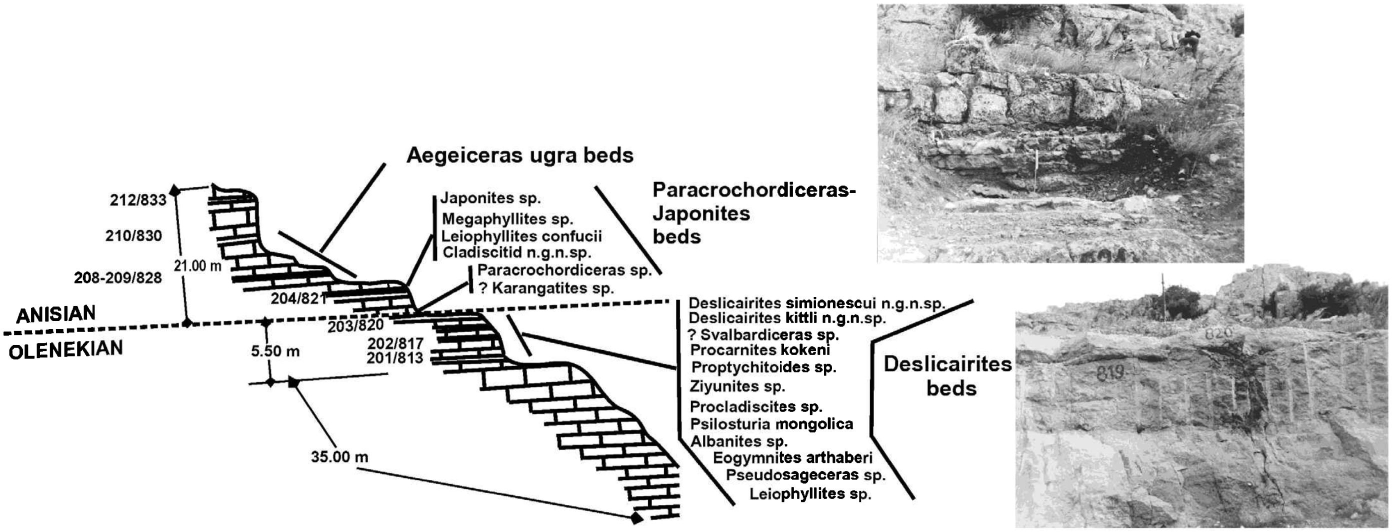
Based on the ammonoid faunal succession, the OAB in the Deşli Caira section can be accurately placed between samples GR6 (=203/4) and GR7 (Figs. 3 and 4). A concurrent bioevent appears to be the first appearance datum (FAD) of *Chiosella timorensis* in a continuum that begins within the *Triassopathodus* ex gr. h*omeri* and passes through the immediate predecessor *Chiosella gondolelloides* (Grădinaru et al., 2002, 2006).

CONODONT SUCCESSION

Conodonts from Deşli Caira were collected over many years and by several workers. Some of these data have been presented in preliminary papers by Mirăuţă (1974, 2000), Grădinaru et al. (2002, 2006).

The present contribution summarizes the conodont succession at Deşli Caira and thereby contributes to our understanding of the correlation and definition of the OAB. Figures 3 and 4 show several generations of sample numbers assigned to conodont collections as well as ammonoid collection levels (prefix GR). During a visit to Bucharest in 2000, two of us (MJO and AN) were shown the conodont collections made by the second author (EG) and these were divided into two subsets for further study in Vancouver and Milan. On the same occasion, the Deşli Caira section was visited and new continuous sampling took place on each side of the OAB defined by ammonoids. Results from this more detailed section spanning the immediate interval of the OAB is shown in Figure 4.

Conodont samples reported here come from about 25 m of section, of which about three-quarters post-date the OAB. Several species present in the samples from the upper Olenekian – *Triassospathodus*, *Cratognathus* spp. (Fig. 5. 11, 12, 18-22), *Spathiscuspus*, *Gladigondoella carinata*, and New genus A (Fig. 5. 10) – probably have a longer history



Remarks:
1 - Lower Anisian has two distinct successive ammonoid assemblages: Paracrochordiceras-Japonites beds and Aegeiceras ugra beds
Occurrence of ? Karangatites sp. in base of Anisian
Karangatites is a zonal marker for the base of the Lower Anisian in Arctic Siberia (Dagys and Sobolev, 2000)
2 - Topmost Olenekian has the outstanding occurrence of the olenikitids in Tethyan province: Deslicairites n.g.n.spp and ? Svalbardiceras sp
3 - The Late Olenekian ammonoid assemblages from Deşli Caira section with Deslicairites n.g.n.spp can be correlated with
Subzone 1a from Qinghai (China) described by He, Wang and Chen (1896)

FIGURE 2. Ammonoid sequence in the Olenekian-Anisian boundary in the Deşli Caira section, North Dobrogea, Romania.

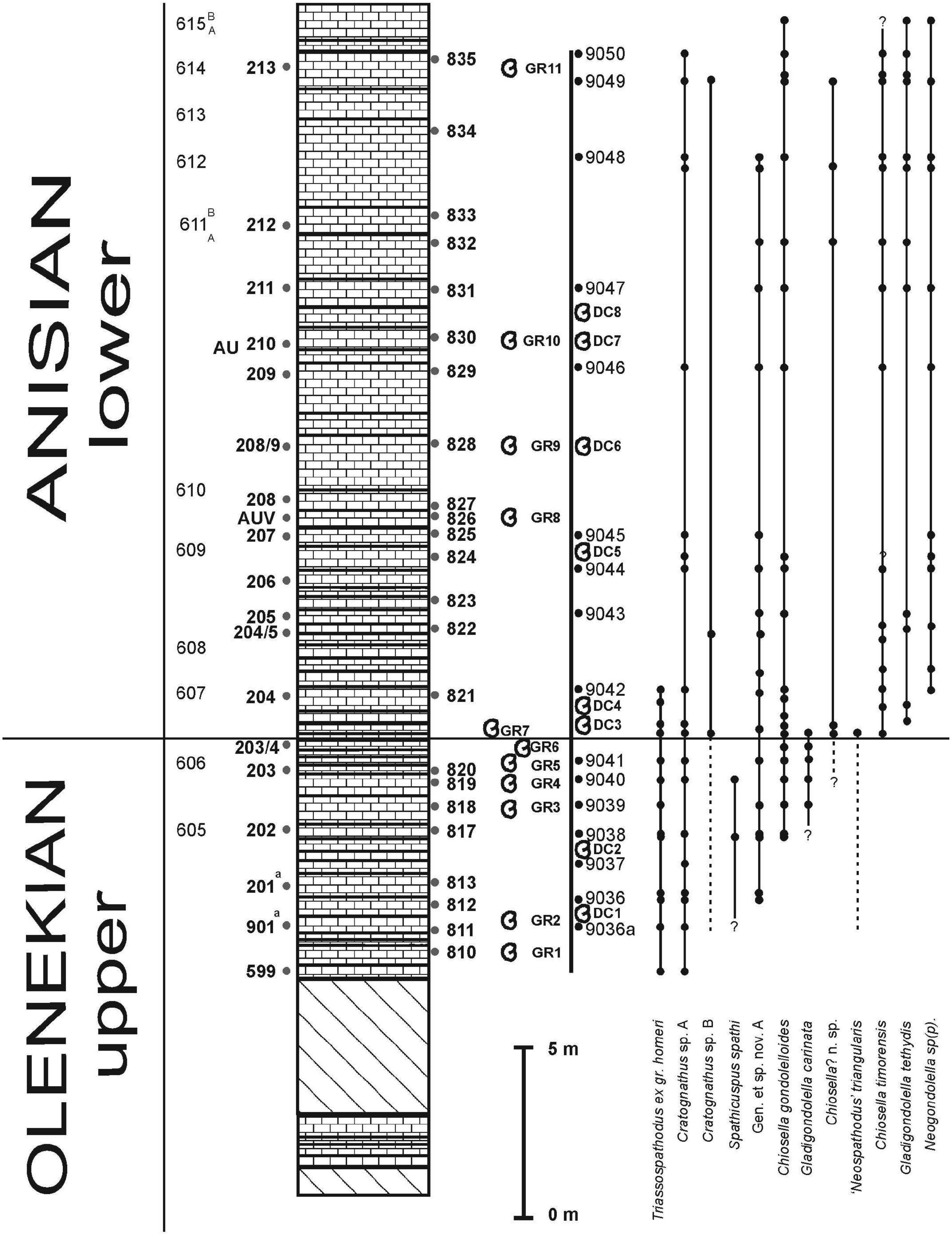


FIGURE 3. Occurrence of conodont taxa from the section at Deşli Caira.

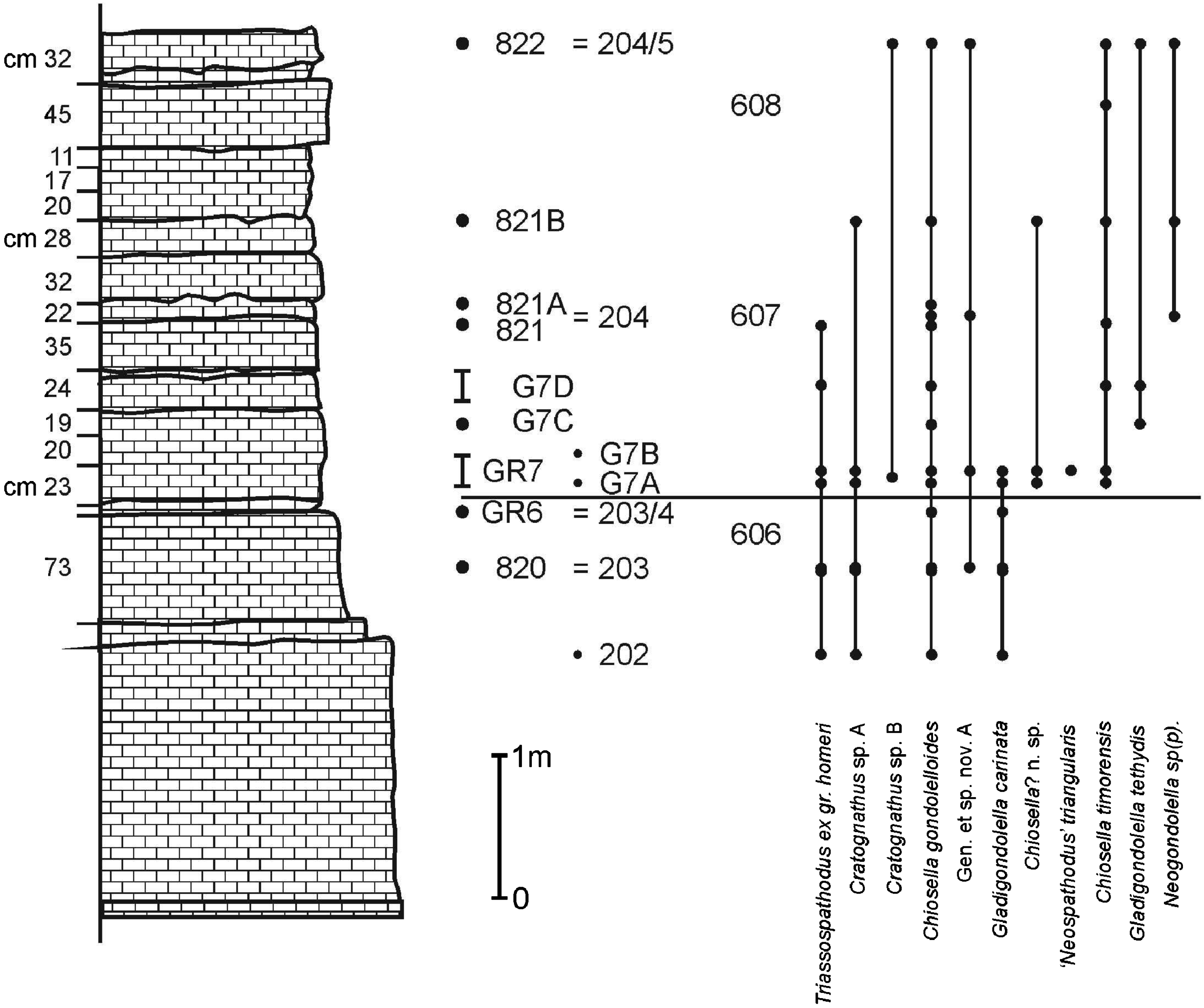


FIGURE 4. Occurrence of conodont taxa from the boundary beds at Desli Caira.

prior to the latest Olenekian (as shown on Figs. 3 and 4), so their apparent FAD in this section is not regarded as significant. In contrast, nine conodont appearances (i.e., FAD) and disappearances (i.e., LAD) are identified as guides to identify the OAB in the Deşli Caira section. Several of these are coincident, and all occur within about 4.25 m of strata. For the remaining 20 m of section, the fauna maintains a relatively constant composition. Each of the OAB conodont taxa have been discussed elsewhere by Orchard et al. (2007). These conodont events are (with positions relative to the OAB):

1 FAD of *Chiosella gondolelloides* (-3 m)
2 LAD of *Spathiscuspus* (-1 m)
3 LAD of *Neospathodus triangularis* (0 m)
4 FAD of *Chiosella timorensis* (0 m)
5 LAD of *Gladigondolella carinata* (0 m)
6 FAD of *Chiosella* n. sp. A (0 m)
7 FAD of *G. tethydis* (+0.5 m)
8 LAD of *Triassospathodus* (+1.25 m)
9 FAD of *Neogondolella* (+1.25 m)

These conodont events are grouped so as to define five datums at Deşli Caira:

FIGURE 5. Illustrations of conodonts from Desli Caira. Scale bars = 200 microns (x80) for all figures except **1, 3** = 100 microns (x160). **1, 2,** *'Neospathodus' triangularis* Bender, GSC 101561, from sample G7. **3, 4,** *Spathicuspus spathi* (Sweet), GSC 101562, from sample 9036A. **5, 6,** *Triassospathodus* ex gr. *homeri* (Bender), GSC 101563, from sample 9036A. **7-9,** *Gladigondolella carinata* Bender. **7, 9,** GSC 101564, from sample G7A, **8,** GSC 101565, from sample G7B. **10,** Genus et sp. nov. A, GSC 101566, from sample 9038. **11, 12, 22,** *Cratognathus* sp. A. **11, 12,** GSC 101567, from sample 9036, **22,** GSC 101568, from sample 9049. **13-15, 23-25,** *Chiosella gondolelloides* (Bender). **13-15,** GSC 101569, from sample 9047, **23-25,** GSC 101570, from sample 9039. **16?, 17?, 31-34,** *Chiosella timorensis* (Nogami). **16, 17,** GSC 101571, from sample 9044; element transitional to *C.* n. sp. A, **31,** GSC 101572, from sample G7D, **32-34,** GSC 101573, from sample 9044. **18-21,** *Cratognathus* sp. B. **18, 19,** GSC 101574, from sample 204/5, **20, 21,** GSC 101575, from sample 9049. **26-28,** *Chiosella* n. sp. A, GSC 101576, from sample 821B. **29, 30,** *Gladigondolella tethydis* (Huckriede), GSC 101577, from sample 9043. **35-37,** *Neogondolella* sp., GSC 101578, from sample 9043.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Datum 1

The first significant datum is the FAD of *Chiosella gondolelloides* (Fig. 5. 13-15, 23-25) at about 3 m below the OAB. The appearance of *C. gondolelloides* is an easily recognized datum since the separation of the species from its apparent forebear and common associate, *Triassospathodus* ex gr. *homeri* (Fig. 5. 5, 6), is straightforward. Less so is the separation of small specimens of the former species from *C. timorensis* (Fig. 5. 31-34), early growth stages of which may be indistinguishable. This poses problems in small, isolated collections of juveniles.

Datum 2

The LAD of *Spathiscuspus spathi* (Fig. 5. 3, 4) at 1 m below the OAB is an earlier LAD than is seen elsewhere (e.g., at Guandao, China), where the species ranges into basal Anisian strata. The species is far less common in the Romanian faunas, and this datum is not a useful one for correlation.

Datum 3

This is the major faunal change of the succession and involves two conodont FADs and two LADs, as well as change in the ammonoid fauna from characteristic Spathian to typical Anisian taxa. These all occur within the lowest part of bed 7 (Fig. 4). Most notable are the FADs of *Chiosella timorensis* and *Chiosella* n. sp. A (Fig. 5. 26-28), the latter being distinguished by its distinctive terminal cusp. This datum also coincides with the LAD of both *Gladigondolella carinata* (Fig. 5. 7-9) and *'Neospathodus' triangularis* (Fig. 5. 1, 2). These four conodont events are not entirely synchronous elsewhere, but they all cluster around the OAB. In Guandao, China, *N. triangularis* disappears earlier, and both the FAD of *C.* n. sp. A and LAD of *G. carinata* are later with respect to the FAD of *C. timorensis*. This may reflect relative condensation in the Deşli Caira succession.

Datum 4

The FAD of *Gladigondolella tethydis* (Fig. 5. 29, 30) occurs 0.5 m above the OAB. This appearance in the early Anisian is consistent with records elsewhere (e.g., Orchard et al., 2007).

Datum 5

At 1.25 m above the OAB, the LAD of *Triassospathodus* ex gr. *homeri* coincides with the FAD of *Neogondolella* sp. (Fig. 5. 35-37). These two taxa are known to overlap elsewhere in Tethys and also in North America. In Tethyan successions, the overlap is within the basal Anisian, as it is in the Deşli Caira, but in North America it occurs first in the late Spathian. Although the overlap of taxa is not a reliable datum worldwide, the LAD of *T.* ex gr. *homeri* is nevertheless a reliable early Anisian event.

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CONODONTS FROM THE OLENEKIAN-ANISIAN BOUNDARY BEDS, GUANDAO, GUIZHOU PROVINCE, CHINA

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Abstract—Two complementary sections in Guandao, Guizhou Province, China yielded abundant conodont faunas that bracket the Olenekian-Anisian boundary (OAB) and provide a high resolution standard succession. The faunal turnover about the OAB is profound, with the complete replacement of *Triassospathodus*-dominated faunas by those in which *Chiosella* is abundant. Including the FAD (first appearance datum) of *Chiosella timorensis* as a proxy for the OAB, there are a total of nine conodont biotic events identified as useful in constraining the boundary. These are, in ascending order: LAD (last appearance datum) of *Neospathodus triangularis*; FAD of *Chiosella gondolelloides*; FAD of *C. timorensis*; LAD of *Gladigondolella carinata*; FAD of *Chiosella* n. sp. A; FAD of *G. tethydis*; LAD of *Spathiscuspus*; LAD of *Triassospathodus*; and FAD of *Neogondolella*. The succession of datums is essentially synchronous in the two sections. All occur prior to the peak of a positive carbon isotope excursion and the shift from dominantly reversed to dominantly normal magnetic polarity. Dated tuffs bracket the OAB as ~247 Ma.

INTRODUCTION

Carbonate platforms and their adjacent deep-marine basin margin facies in the Nanpanjiang basin of south China provide ideal opportunities to study Permian-Triassic stratigraphy. The Nanpanjiang basin forms a deep marine embayment in the southern margin of the South China plate (Fig. 1A, inset), which drifted northward across the eastern Tethys, crossed the equator during the Permian to approximately 12° N latitude by the beginning of the Middle Triassic, and eventually docked with the north China plate during the Late Triassic (Enkin et al., 1992; Van-der-Voo, 1993; Lehrmann et al., 2006). The Nanpanjiang basin is surrounded by the vast Yangtze carbonate platform and contains several isolated carbonate platforms (Enos et al., 2006; Lehrmann et al., 2007). The Great Bank of Guizhou (GBG) is the northernmost of the isolated platforms and occurs in southern Guizhou Province (Fig. 1).

The GBG has proven to be one of the best sites in the basin for study of Permian-Triassic stratigraphy because it contains the longest and most complete Permian-Triassic record among the isolated platforms and exposes a continuous cross-section from shallow-marine platform interior facies to deep-marine basin margin facies (Lehrmann et al., 2007). Guandao section, which occurs on the northern basin margin of the GBG (Fig. 1B), is particularly important for chronostratigraphy around the Olenekian-Anisian boundary (OAB) because: 1) it occurs in deep-marine facies without unconformity, 2) it is physically correlated with an adjacent shallow-marine platform, and 3) it contains abundant conodonts, several dated volcanic ash horizons (Lehrmann et al., 2006), primary magnetic signature, and strata useful for carbon isotope chemostratigraphy (Payne et al., 2004).

Previous studies in the area focused on the depositional environments and evolution of the GBG (e.g. Lehrmann et al., 2007), the record of the end-Permian extinction and biotic recovery (e.g., Payne et al., 2004, 2006a, 2006b), and the geochronology and biostratigraphy of the OAB at Guandao section (Lehrmann et al., 2006). The purpose of this study is to: 1) provide detailed documentation of the conodont succession across the OAB from a new high resolution data set and to 2) integrate the new biostratigraphy with existing geochronological, paleomagnetic, and carbon isotope data.

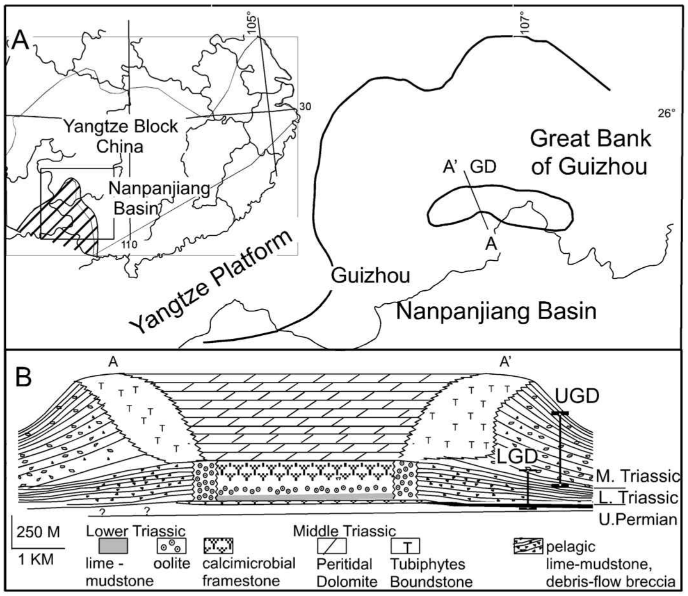


FIGURE 1. A) Early Triassic paleogeographic map of the Nanpanjiang basin. Inset upper left shows position of Nanpanjiang basin in southern margin of south China plate. B) Schematic stratigraphic cross-section of the Lower-Middle Triassic strata of the Great Bank of Guizhou showing location of Lower Guandao section (LGD) and Upper Guandao section (UGD).

STRATIGRAPHY

The GBG evolved from a low-relief bank rimmed with oolite shoals and gentle basin-margin slopes in the Late Permian and Early Triassic to a *Tubiphytes* reef-rimmed platform with steep basin-margin slopes in the Middle Triassic (Fig. 1B). Finally, the GBG developed into a high-relief erosional escarpment before it was drowned and buried with siliciclastic turbidites at the beginning of the Late Triassic (Lehrmann et al., 2007).

Guandao section occurs in two overlapping segments in the basin margin north of the GBG (Fig. 1B). Lower Guandao section spans the Upper Permian through lower Anisian and occurs in the proximal slope adjacent to the platform; whereas the Upper Guandao section spans the upper Olenekian through Carnian and occurs in the distal basin margin (toe of slope) strata farther north of the platform (Fig. 1B). The OAB in Guandao section spans strata regionally mapped as the Lower Triassic Luolou Formation and the Middle Triassic, Anisian Xingyuan Forma-

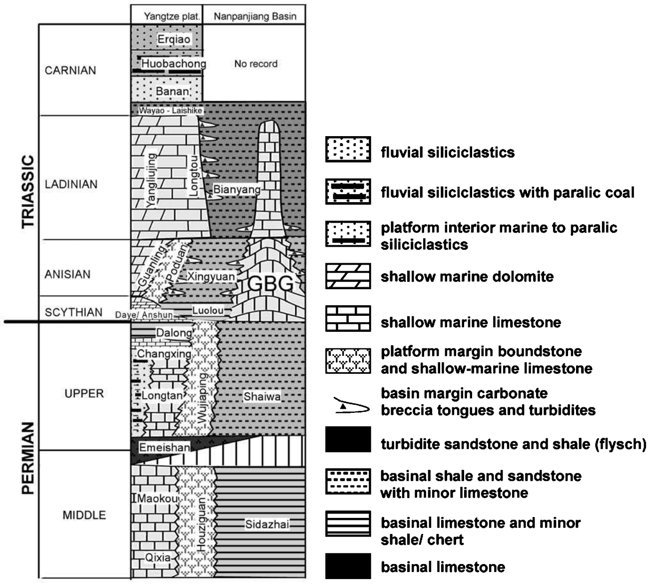


FIGURE 2. Schematic stratigraphic column illustrating regional Permian and Triassic stratigraphy of the Yangtze platform and Great Bank of Guizhou in the Nanpanjiang basin of Guizhou Province (see Enos et al., 2006, Lehrmann et al. 2007; and Guangxi Bureau of Geology, 1987 for more details). Formations represented in Guandao section of this study are the basinal Lower Triassic Luolou Formation and Xingyuan Formation.

tion (Fig. 2). The two formations are bounded by a regionally widespread tuffaceous interval named the "green bean rock" by Chinese geologists (Guizhou Bureau of Geology, 1987).

Facies at Guandao section are primarily thin-bedded pelagic lime mudstone, intraclastic oolitic or skeletal packstone beds that represent carbonate turbidites shed from the adjacent platform and polymict debris flow breccias also shed from the adjacent platform (Fig. 3). Allochthonous shallow-water grains within turbidites in Guandao section reflect evolution of shallow-marine environments in the adjacent GBG. Lower Triassic strata at Guandao section contain abundant ooids whereas Middle Triassic facies contains more diverse skeletal debris such as crinoids, *Tubiphytes* and sphinctozoan sponges (Fig. 3). This change reflects the progressive evolution of the GBG from a low-relief bank containing ooid shoals and low biodiversity in the Early Triassic to a rimmed platform with biologically diverse reef margins in the Middle Triassic (Fig. 3; Payne et al., 2006a). The increase in fossil diversity and fossil abundance across the OAB at Guandao also reflects the pattern of biotic recovery after the end-Permian extinction (Payne et al., 2006b).

Magnetic reversal stratigraphy at Lower Guandao section defines 10 normal and 10 reversed magnetozones from the Lower Triassic and lower Anisian (Lehrmann et al., 2006). Around the OAB in Guandao, normal polarity occurs in the middle Spathian and is followed by a predominantly reversed zone with a few brief normal intervals in the uppermost Spathian and Aegean, and predominantly normal polarity in the Bithynian to lower Pelsonian (Fig. 3). The shift from predominantly reversed in the upper Spathian and Aegean to normal polarity near the beginning of the Bithynian (Fig. 3) should be a useful marker to assist in correlation of the OAB. The Olenekian-Anisian magnetostratigraphy of Guandao section correlates reasonably well with that of the OAB in western Tethys (Muttoni et al., 2000; Nawrocki and Szulc, 2000), as well as the global compilation (Ogg, 2004).

Carbon isotope data contain evidence for several large positive and negative carbon excursions during the Early Triassic followed by stabilization of the carbon curve in the Middle Triassic (Payne et al., 2004). The last positive carbon isotope excursion prior to Middle Triassic stabilization of carbon values occurs in the Aegean substage of the early Anisian (Payne et al., 2004) and thus should also be a useful marker to assist in correlation of the OAB.

The Olenekian-Anisian boundary in the ammonoid-rich Desli Caira section of Dobrogea, Romania is placed between beds with *Deslicairites* below and *Paracrochordiceras-Japonites* above (Gradinaru et al., 2006). A concurrent bioevent is the first appearance datum (FAD) of *Chiosella timorensis* in a continuum that begins with *Triassospathodus* ex gr. *homeri* and passes through the first appearance of *Chiosella gondolelloides* prior to the OAB (Gradinaru et al., 2006). In the following account the *C. timorensis* datum is used as a proxy for the OAB.

THE CONODONT FAUNAS

Several suites of conodont samples were collected from Late Permian to early Carnian strata outcropping in Lower and Upper Guandao sections. Samples prefixed QGC and WG were reconnaissance in nature and were followed by a more comprehensive but relatively widely spaced sampling through the entire succession (prefixes GDL and UGD). For this latest study, the interval identified as likely to contain the OAB boundary was sampled at a scale of every 10-50 cm over 14 m in Lower Guandao (from ~232 m to ~246 m in the cumulative section), and over 7 m in Upper Guandao (from ~9 m to ~16 m in the cumulative section). The entire data set is summarized in Figures 4 and 5, which show both the occurrence of taxa, and the relative ratios of six species or species groups. These figures also show a lithostratigraphic column with paleomagnetic and isotopic data, and the position of ash beds.

Most of the conodont fauna in Lower and Upper Guandao sections are composed of six species or species groups: *Triassospathodus* ex gr. *homeri*, *Spathicuspus spathi*, *Cratognathus* spp., *Gladigondolella tethydis*, *Chiosella* spp., and *Neogondolella* sp(p). Of these, *Triassospathodus* and *Spathicuspus* are dominant in the Olenekian, *Chiosella* and *Neogondolella* are dominant in the Anisian, and conservative *Cratognathus* and different species of *Gladigondolella* range through the entire interval. The nature, range and relative abundance of these groups are discussed below. To arrive at the abundance, the absolute numbers of pectiniform conodont elements (ramiform elements were excluded) in each collection were summed and the percentages of each of these six common taxa groups were calculated. The results are depicted in the right-hand columns of Figures 4 and 5.

Other conodont taxa that occur in the Guandao sections are uncommon but include late Olenekian *Neospathodus triangularis* (Fig. 6. 18), which ranges up to the boundary, and *Cornudina* (Fig. 6. 17) and New Genus A (Fig. 6.16), which occur sporadically both above and below the boundary. The last of these taxa appears to be a useful indicator of the OAB interval, whereas the two others are longer ranging.

Triassospathodus ex gr. *homeri*
(Fig. 6. 10-12)

This group includes the posteriorly asymmetrical *T. homeri*, the posteriorly symmetrical *T. symmetricus*, the posteriorly denticulate *T. brochus*, and *T. sosioensis*. These are all variations on a relatively elongate segminate P1 element with inclined posterior denticles and a distinctive apparatus (Orchard, 2005, text. fig. 19). The appearance and distribution of individual 'morphotypes' is uncertain, but representatives occur first in the middle Spathian (Orchard, 1995) and range upward across the O-A boundary for a short distance.

Representatives of this group are the most common and ubiquitous members of late Spathian conodont faunas in Eurasia and North America, often occurring to the exclusion of other taxa. This is true in Guandao, in Nevada where the *Neopopanoceras haugi* Zone commonly produces such collections, and in British Columbia where the *Keyserlingites subrobustus* Zone contains a very similar fauna. In Lower Guandao, *Triassospathodus* ex gr. *homeri* constitutes at least 70% of Olenekian faunas for 10 m below the boundary, then drops above the boundary to about 50% for 2 m and then declines over 2 m more before disappearing. In Upper Guandao, the lowest 2 m contain predominant

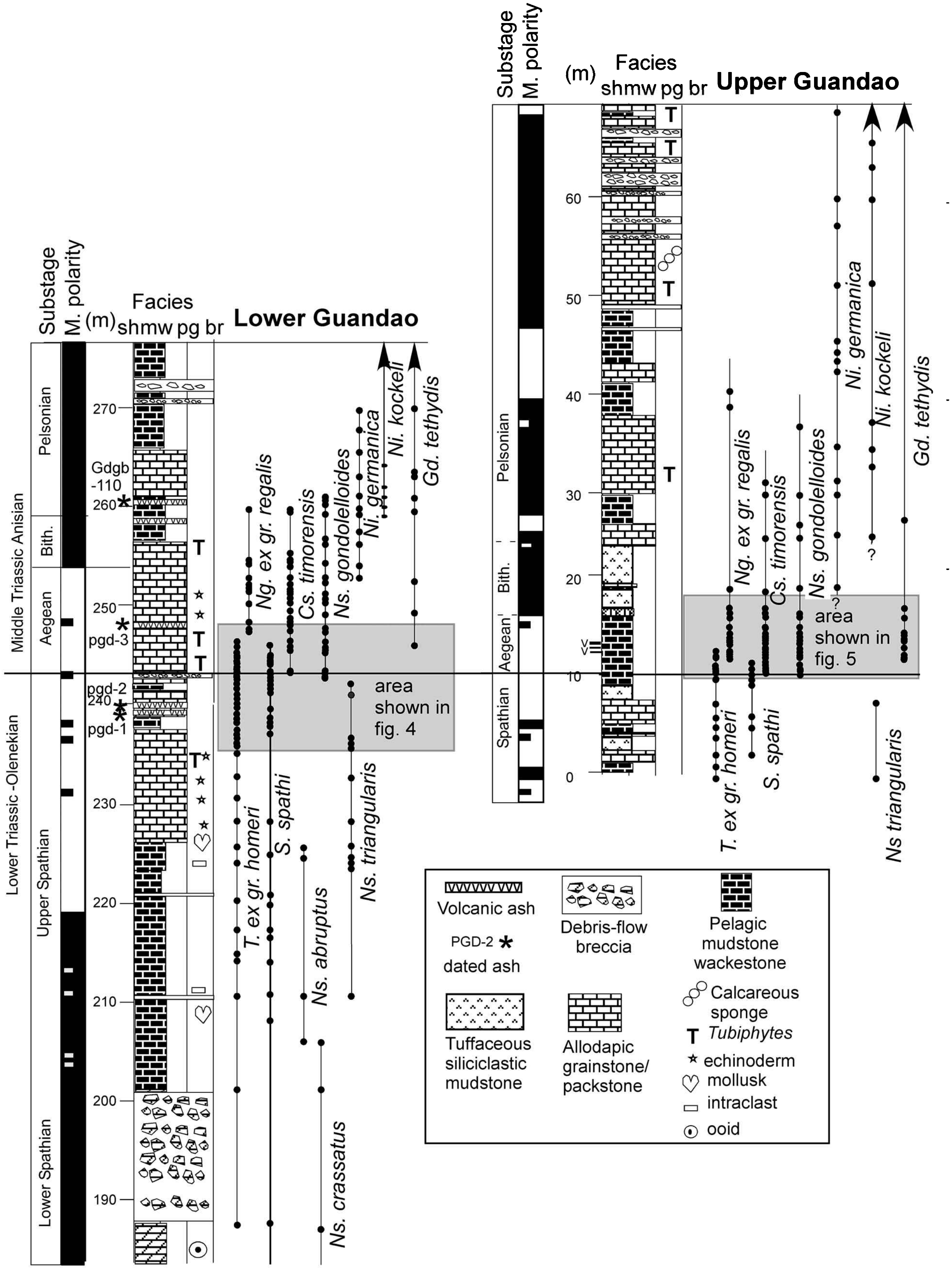


FIGURE 3. Olenekian-Anisian boundary section in basin-margin facies in Lower Guandao and Upper Guandao sections (see Figure 1 for location). Magnetic reversal stratigraphy (black is normal polarity) is shown at left of sections. High-resolution U-Pb ages of volcanic ash units PGD-1, 2, 3 and GDGB-110 were reported in Lehrmann et al. (2006). The Olenekian-Anisian boundary, as delineated by conodont biostratigraphy is bracketed between PGD-2 (247.32 ± 0.08 Ma) and PGD-3 (247.13 ± 0.12 Ma). Gray rectangles show the stratigraphic interval covered by high-resolution conodont data presented in Figures 4 and 5.

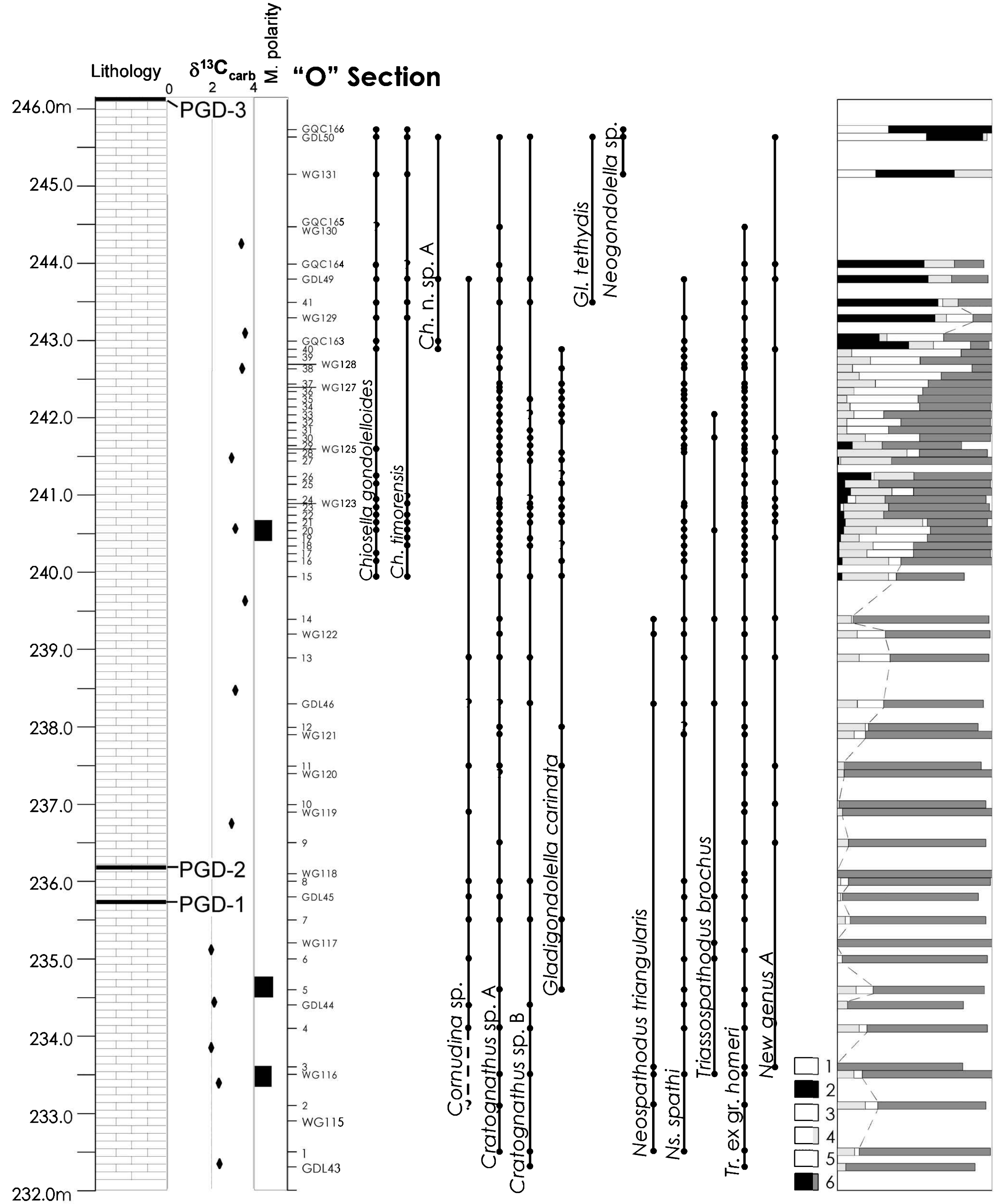


FIGURE 4. High resolution conodont data (bed-by bed; decimeter to sub-decimeter sampling) from pelagic carbonate spanning the Olenekian-Anisian boundary of Lower Guandao section. See Figure 3 for position of stratigraphic interval. Limestone symbol is skeletal packstone with pelagic lime mudstone interbeds; bedding 1-20 cm thick. Black beds (PGD-1,2,3) indicates dated volcanic ash horizons (Lehrmann et al., 2006). Carbon isotope values are from Payne et al. (2004). Note OAB as delineated by conodont biostratigraphy occurs below the peak in the Anisian (Aegean) positive isotope excursion (see Payne et al., 2004). Note stratigraphic elevations differ slightly from those of Lehrmann et al. (2006) because of remeasurement during detailed sampling. Bar graph at right shows relative abundance of conodonts: (1) *Neogondolella*, (2) *Chiosella*, (3) *Gladigondolella tethydis*, (4) *Cratognathus,* (5) *Spathicuspus spathi*, and (6) *Triassospathodus* ex gr. *homeri*.

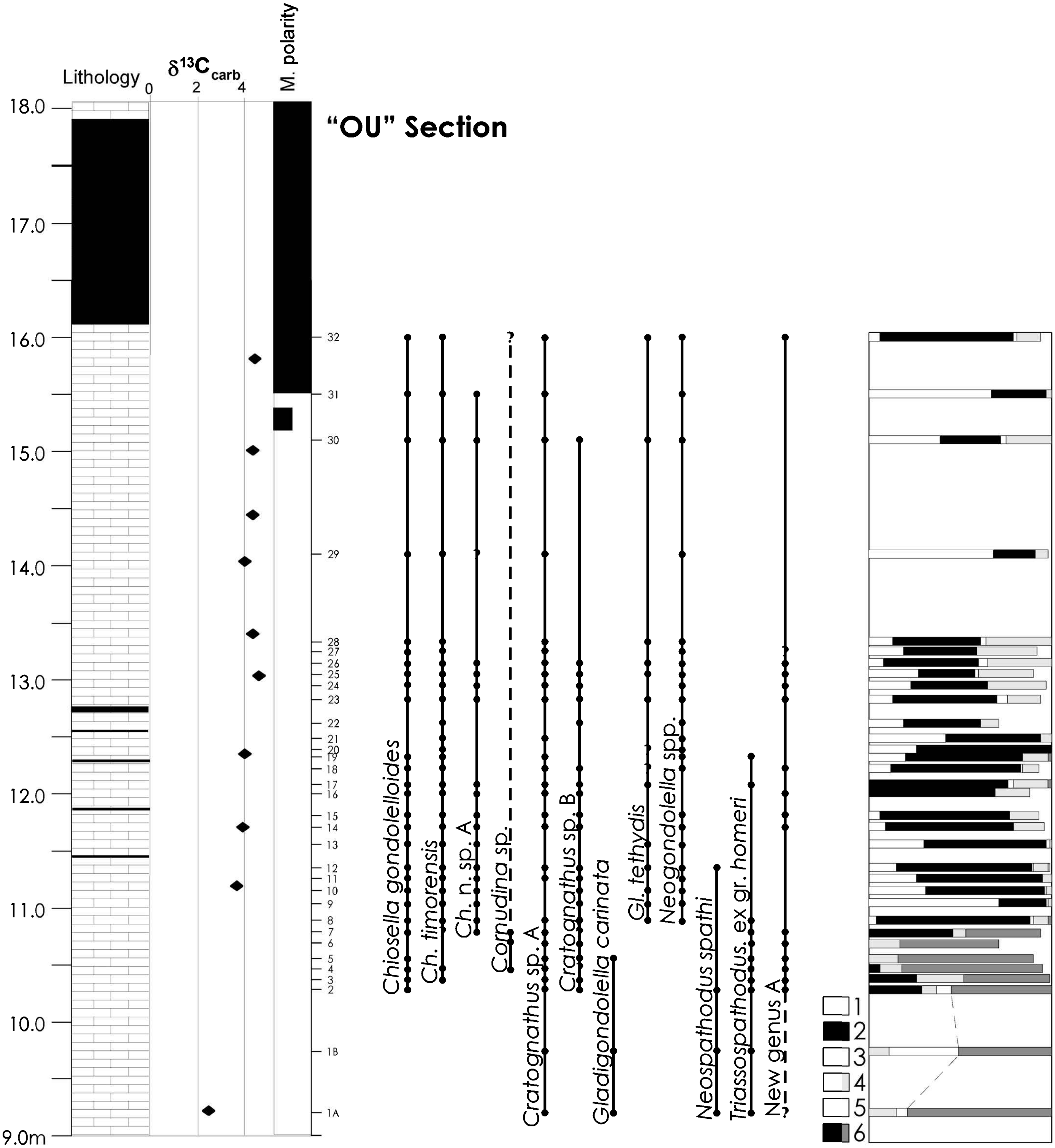


FIGURE 5. High resolution conodont data (bed-by bed; decimeter to sub-decimeter sampling) from pelagic carbonate spanning the Olenekian-Anisian boundary of Upper Guandao section. See Figure 3 for position of stratigraphic interval. Limestone symbol is pelagic lime mudstone with skeletal packstone interbeds; bedding 1-10 cm thick. Black indicates volcanic ash horizons. Carbon isotope values are from Payne et al. (2004). Note OAB as delineated by conodont biostratigraphy occurs below the peak in the Anisian (Aegean) positive isotope excursion (at 13.0 m in this section) (see Payne et al., 2004). Note stratigraphic elevations differ slightly from those of Lehrmann et al. (2006) because of remeasurement during detailed sampling. Bar graph at right shows relative abundance of conodonts: (1) *Neogondolella*, (2) *Chiosella*, (3) *Gladigondolella tethydis*, (4) *Cratognathus*, (5) *Spathicuspus spathi*, and (6) *Triassospathodus* ex gr. *homeri*.

homeri group, but the decline is rapid thereafter with only scattered occurrences for an additional 1 m. This contrast in tempo of the *Triassospathodus* extinction in the two sections may result from differing paleoenvironments in the upper slope (Lower Guandao) and basin (Upper Guandao), with the faunal change more rapid in the latter.

Spathicuspus spathi

(Fig. 6. 1-3)

The P1 element is a small segminate element with a large prominent cusp and a few anterior denticles. Elements of this type first appear in *Columbites* beds in North America. In Lower Guandao, the species is commonly present in small numbers (~10%) throughout the Olenekian part and extends into the basal 1 m of the Anisian. It shows three narrow intervals of relative abundance at 238-239 m, 240-240.5 m, and 241.5-243 m; the magnitude of these 'bulges' also increases from ~20% to ~40% and finally to ~70%. The first of these fluctuations shortly precedes the boundary, the second occurs just above it, and the third is immediately prior to the disappearance of the species at 243.5 m. In deeper water Upper Guandao, only the uppermost 2.5 m of the range of *Spathicuspus* is seen, with a single bulge of about 40% preceding the rapid disappearance.

Cratognathus spp.

(Fig. 6. 13-15)

Two species of *Cratognathus, C.* sp. A (Fig. 6. 13) and the less common *C.* sp. B (Fig. 6. 14, 15), range throughout both sections. They are distinguished by the terminal cusp and more discrete denticles in *C.* sp. B. Also included here for the purposes of the abundance study is the related *Gladigondolella carinata* (Fig. 6. 7-9), only a few of which occur in any single Olenekian fauna. This species disappears at 243 m in Lower Guandao, which is about 3 m above the boundary, and occurs in Upper Guandao in the lowest 1.5 m sampled (up to 10.5 m).

In Lower Guandao, this group generally constitutes less than 20% of the fauna up to 240 m, then increases to 30-50 % through 241.5 m, and then drops back to previous levels through the remainder of the section. In Upper Guandao, a similar 'background' level is seen through the lower 4 m and then the group increases to about 30%.

Gladigondolella tethydis

(Fig. 6. 35)

This species is a very distinctive form that is exclusively Anisian. It appears at 243.5 m in Lower Guandao, some 3.5 m above the boundary. In Upper Guandao it appears at ~11 m, which is in the lowest 2 m sampled, and ranges throughout the OU samples and into higher strata. *Gladigondolella tethydis* occurs in about one-half of the collections and constitutes a few percent of the total fauna.

Chiosella spp.

(Fig. 6. 22-29, 32-34)

Discrimination of two species, *Chiosella gondolelloides* (Fig. 6. 22-29) and *C. timorensis* (Fig. 6. 32-34) has been most recently discussed by Gradinaru et al. (2006) and the criteria presented therein is followed here. As a consequence of the results obtained from the relatively widely spaced sampling done earlier, bed by bed sampling for 3 m below the appearance of *C. timorensis* (at the 243 m level) was undertaken in Lower Guandao section. The results indicate that the genus appears earlier, but in relatively small numbers, 3 m lower in the section (at 240 m). Furthermore, both species of the genus occur first in bed O15. At 239.5 m, O14 contains no *Chiosella*, which is assumed to make its appearance within the intervening 0.5 m interval, which would also be the maximum duration of the *gondolelloides* Zone.

In Lower Guandao, *Chiosella* occurs for about 1.5 m above its FAD and comprises up to 5% of the collections, which are still dominated by *Triassospathodus* ex gr. *homeri.* It then disappears for about 1 and therefore of the OAB, could be up to 3 m below the base of OU samples. However, sedimentation rates were likely higher on the upper slope (Lower Guandao) compared with the basin (Upper Guandao) so the thickness between these various biotic events may be compressed in the latter section, i.e. 2.5 m compared with 5 m in Lower Guandao.

The most significant feature in comparing the two sections is the almost identical relative position of the faunal events. For Lower Guandao, these events are, in ascending order:

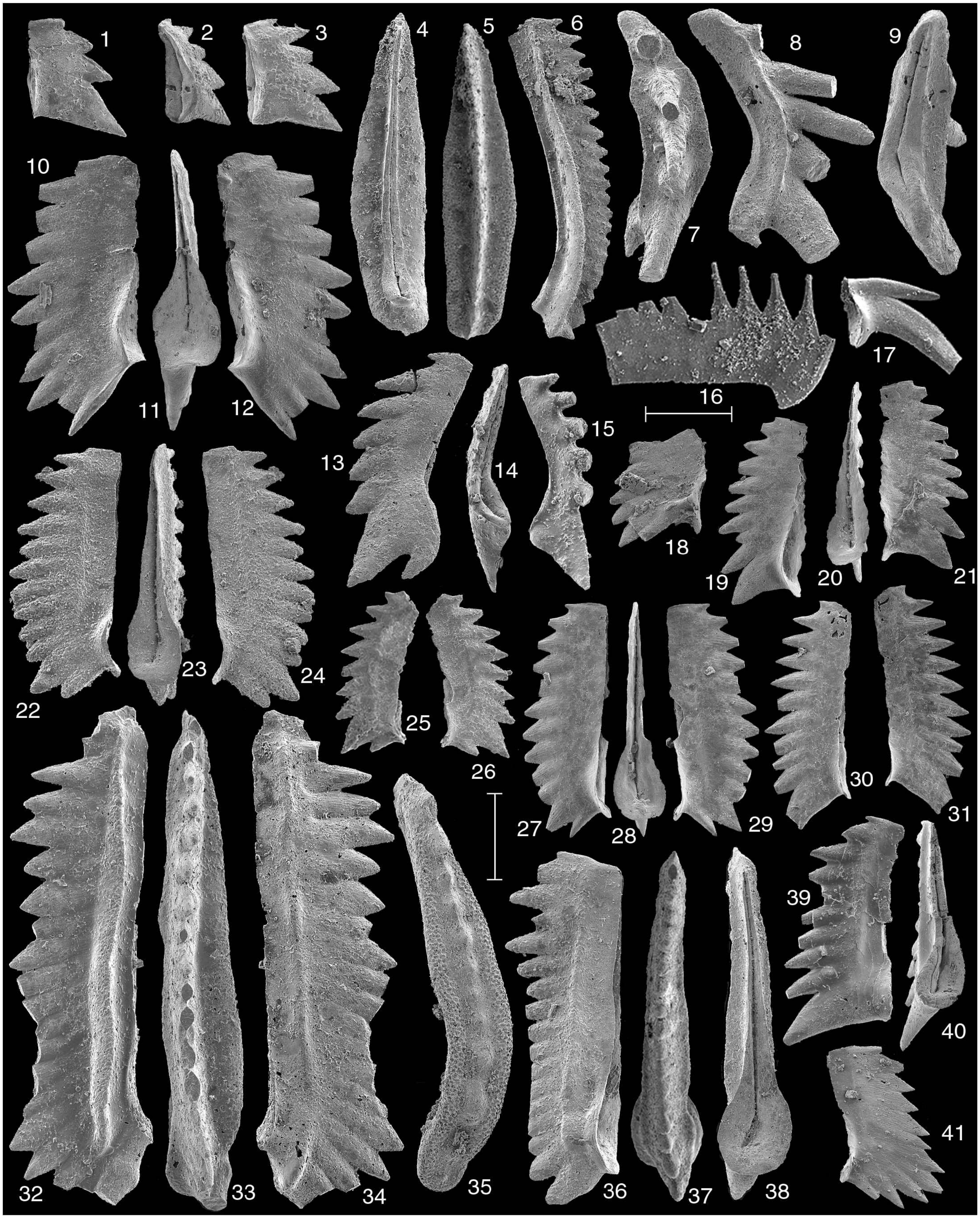
1) LAD of *Neospathodus triangularis* (-0.5 m)
2) FAD of *Chiosella gondolelloides* (<0 m, 0 m) (assumed to be separable from event 3 with additional sampling)
3) FAD of *Chiosella timorensis* (0 m)
4) LAD of *Gladigondolella carinata* (+3 m)
5) FAD of *Chiosella* n. sp. A (+3 m)
6) FAD of *G. tethydis* (+3.5 m)
7) LAD of *Spathiscuspus* (+4 m)
8) LAD of *Triassospathodus* (+4.5 m)
9) FAD of *Neogondolella* (<+5 m) (assumed to be earlier in unsampled interval)

In Upper Guandao, event 1 occurs below the OU sampling; events 2 and 3 occur in adjacent beds; and event 9 occurs concurrently with event 6. In the lower section, events 2 and 9 may be modified through sampling of the gaps immediately beneath both observed events. That being the case, there would be almost perfect synchronicity between the two sections in spite of their differing positions on the slope and in the basin. The stratigraphic thickness over which the entire suite of events takes place is a maximum of about 5 m.

SUMMARY

Two complementary sections in Guandao, Guizhou province, China yield abundant conodont faunas that bracket the Olenekian-Anisian boundary (OAB) and provide a high resolution yardstick against which other boundary sections can be compared. Including the FAD of *Chiosella timorensis* (used as a proxy for the OAB), there are a total of nine conodont biotic events identified as useful in constraining the OAB. In ascending order, the sequence of events are: the LAD of *Neospathodus triangularis*; the FAD of *Chiosella gondolelloides*; the FAD of *C. timorensis*; the LAD of *Gladigondolella carinata*; the FAD of *Chiosella* n. sp. A; the FAD of *G. tethydis*; the LAD of *Spathiscuspus*; the LAD of *Triassospathodus*; and the FAD of *Neogondolella*. All datums occur in both sections, and only the second and last vary between the two; this is thought to be due to collection failure. There is more variation in relative abundance of taxa between the two sections, probably reflecting differing biofacies in slope and basin environments, but overall trends are the same.

FIGURE 6. Illustrations of conodonts from Guandao. Bar scale is 200 microns (x 80). **1-3,** *Spathicuspus spathi* (Sweet). **1,** GSC 101541, from sample O39, **2, 3,** GSC 101542, from sample O35. **4-6,** *Neogondolella* sp., GSC 101543, from sample GDL50. **7-9,** *Gladigondolella carinata* Bender, GSC 101544, from sample O33. **10-12,** *Triassospathodus* ex gr. *homeri* (Bender), GSC 101545, from sample O-33. **13,** *Cratognathus* sp. A, GSC 101546, from sample O20. **14, 15,** *Cratognathus* sp. B, GSC 101547, from sample OU3. **16,** New Genus et sp. A, GSC 101548, from sample UGD-11. **17,** *Cornudina* sp., GSC 101549, from sample UGD-19. **18,** *'Neospathodus' triangularis* Bender, GSC 101550, from sample O3. **19-21,** *Chiosella* n. sp. A, GSC 101551, from sample O40. **30, 31,** *Chiosella* n. sp. A, GSC 101552, from sample O40. **39, 40,** *Chiosella* n. sp. A, GSC 101553, from sample OU7. **22-29,** *Chiosella gondolelloides* (Bender). **22-24,** GSC 101554, from sample OU-2, **25, 26,** GSC 101555, from sample GDL-49, **27-29,** GSC 101556, from sample 0-40. **32-34, 36-38,** *Chiosella timorensis* (Nogami). **32-34,** GSC 101557, from sample OU-3, **36-38,** GSC 101558, from sample GDL-50. **35,** *Gladigondolella tethydis* (Huckreide), GSC 101559, from sample OU-23. **41,** *Nicoraella germanica* (Kozur), GSC 101560, from sample NMC-104.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Both the total composition of the conodont faunas and the eight (or nine) datum events have value in locating the position of the OAB. Non-biotic criteria are provided by the calibrated magneto- and chemostratigraphic profiles, and with dated tuff beds (Lehrmann et al., 2006). These data show that both the peak of a positive carbon isotope excursion and the shift from dominantly reversed to dominantly normal magnetic polarity lies within the early Anisian, several meters above the OAB and all identified faunal datums. The dated tuffs bracket the OAB as ~247 Ma. Hence, Guandao presents an extremely important reference section for the Lower-Middle Triassic boundary.

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LATEST TRIASSIC CONODONTS AND RADIOLARIAN-BEARING SUCCESSIONS IN BAJA CALIFORNIA SUR

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Abstract—Late Triassic (late Norian-Rhaetian) conodonts and radiolarians are reported from three members of the San Hipólito Formation of Baja California Sur, part of the Vizcaíno Sur terrane. The (lower) limestone member is late Norian based on conodonts of the *bidentata* Zone, and sparse radiolarian fauna of the *Betraccium deweveri* Zone. The overlying breccia member includes re-worked upper Norian limestone and questionably includes basal Rhaetian radiolarians. The sandstone (upper) member is Rhaetian in age based on common and variably preserved radiolarians of the *Proparvicinugla moniliformis* Zone (lower to middle Rhaetian), and abundant and well preserved radiolarian faunas assigned to the *Globolaxtorum tozeri* Zone (upper Rhaetian). Conodont faunas from the sandstone member includes Rhaetian *Epigondolella mosheri*, well known in North America, and species of *Misikella*, *Oncodella*, and *Zieglericonus* that are better known from low latitude Eurasian Tethys. The radiolarians from the sandstone member compare closely with the Rhaetian faunas from the Sandilands Formation of Queen Charlotte Islands (QCI), British Columbia but there is minor variation in the range of a few species, and other low latitude, Tethyan taxa occur that are unknown in QCI. The Baja faunas appear to be intermediate in character between those of eastern Panthalasssa and Tethys, which may reflect the relative paleogeographic position of the Vizcaíno Sur terrane. Conodont ranges are calibrated with the Rhaetian radiolarian zonation, and one new conodont, *Bajadontus unicornis* gen. et sp. nov., is described.

INTRODUCTION

The marine sedimentary rocks of the San Hipólito Formation at Punta San Hipólito on the Vizcaíno Peninsula of Baja California Sur (Fig. 1) were formally named by Mina (1957) and described in detail by Finch and Abbott (1977) and Finch et al. (1979), who studied the petrology and sedimentology of the formation. The formation is exposed over a 20 km2 area and is inferred to be in fault contact with the overlying Cretaceous Valle Formation, a unit that covers much of the Vizcaíno Peninsula. The formation is approximately 2400 m thick with good outcrops along the coast and inland; the exact thickness is unknown because the upper part is concealed beneath the sea.

Finch and Abbott (1977) divided the San Hipólito Formation into four informal members (from the base): chert, limestone, breccia, and sandstone (Fig. 2). The oldest member is a radiolarian-bearing chert, which rests on mafic pillow basalts (La Costa Ophiolite of Moore, 1985

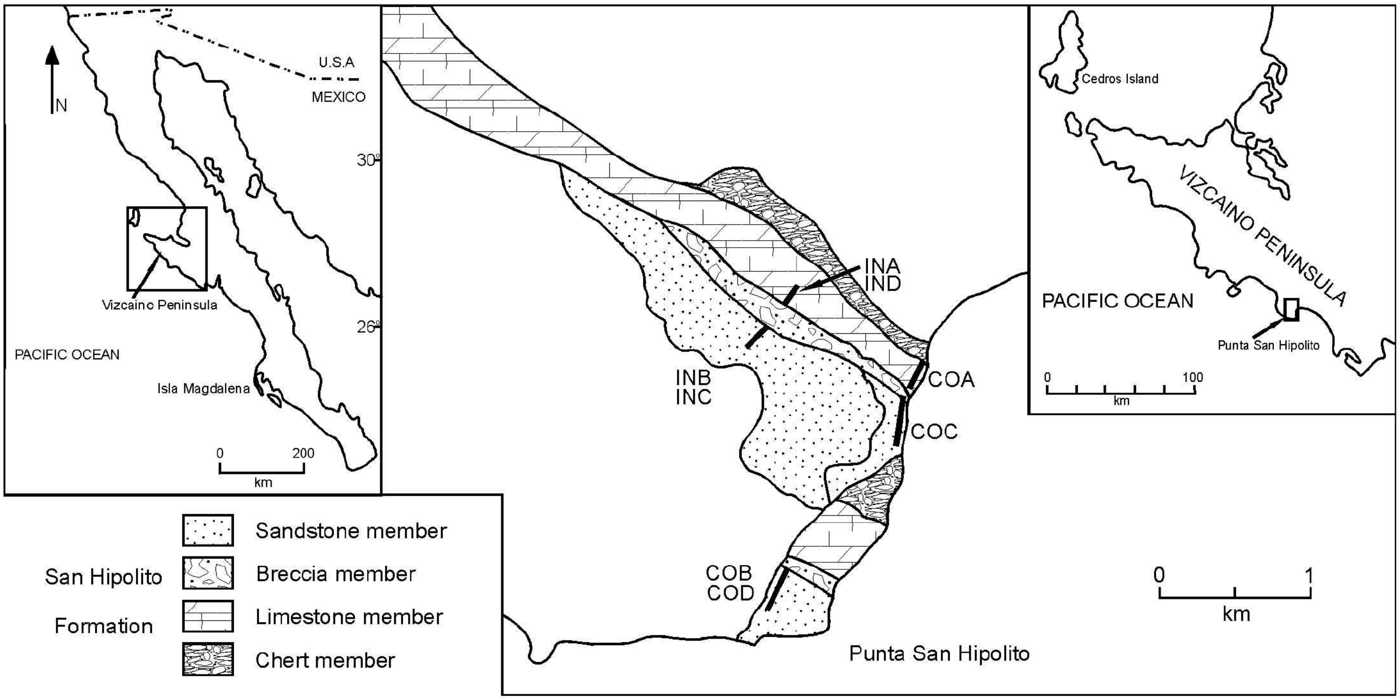


FIGURE 1. Location map of the study area in southwestern North America.

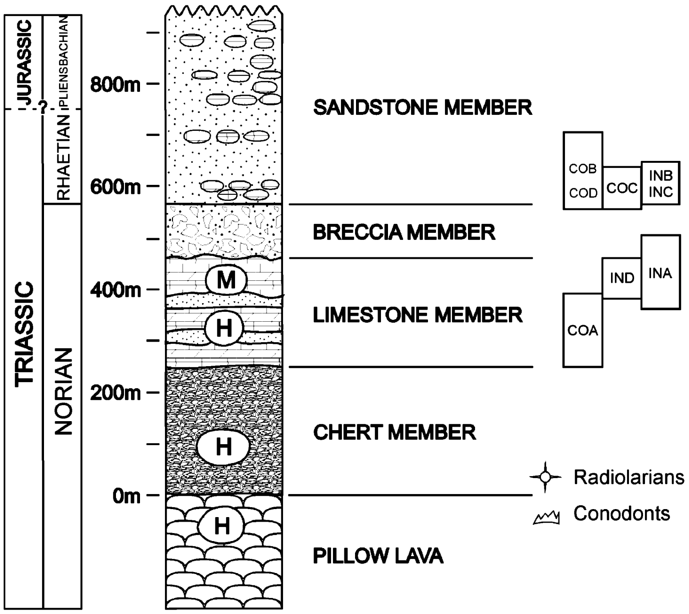


FIGURE 2. Lithostratigraphic column of units in study area, the extent of the six sections described in the Appendix, and symbols for microfossils. In column, H = *Halobia*, M= *Monotis*.

and Vizcaíno Peninsula Ophiolite of Kimbrough and Moore, 2003). *Halobia lineata* (middle Norian) occurs both in the basalt, in interpillow sediments, and in the chert, from which Pessagno et al. (1979) described late Carnian?/ Norian radiolarians.

The limestone member varies in thickness from 95 to 210 m and consists of finely recrystallized limestone with volcaniclastic sandstone. Chaotic folds and autobreccias, locally common, suggest syndepositonal sliding on a depositional slope (Finch and Abbott, 1977). Abundant but poorly preserved calcified radiolaria co-occur with *Halobia*? sp. (Carnian to middle Norian) in the lower part and *Monotis* sp. cf. *M. subcircularis* in the upper part (Finch et al. 1979), implying a middle to late Norian age range for the unit. This constrains the top beds of the limestone member to the upper Norian, equivalent in age to ammonites of the Cordilleranus Zone of Tozer (1979, 1994)

The contact between the limestone and overlying breccia is a submarine erosional surface with considerable relief; the breccia member varies in thickness from 0 m at the coast to 105 m inland. Shallow water reefoid organisms - corals, mollusks, foraminifers and calcareous algae - preserved in limestone clasts and blocks in the breccia member are interpreted as tropical, shallow shelf, and reef accumulations transported into deeper water by submarine slides and deposited in a matrix of volcaniclastic debris (Finch and Abbott, 1977; Finch et al., 1979). Stanley (1979) noted the similarity of the fauna in the limestone blocks to those in allochthonous Upper Triassic reefs of western North America.

The overlying sandstone member, measuring over 1840 m, is the thickest of the formation and consists of poorly sorted volcaniclastic sandstone. Rhaetian radiolarians and conodonts reported here are present in interbedded, thin limestone beds and concretions near the base of the member. Other radiolarian faunas recovered from about 700-900 metres higher in the sandstone member are Lower Jurassic (late Pliensbachian; Whalen and Pessagno, 1984; Whalen and Carter, 2002). Hence, the Triassic-Jurassic boundary may be present in the intervening beds, which appear to be continuous.

The radiolarian data presented here are preliminary (Whalen et al., 1998). They largely utilize the zonation (Fig. 3) developed by Carter (1993) in Queen Charlotte Islands (QCI). The samples were collected during two visits to Baja: P. Whalen and J. Helwig in 1982, accompanied by E.S. Carter in 1996. Conodont samples were processed at GSC Vancouver.

TECTONIC SETTING

Major structural units in the disrupted Mesozoic oceanic rocks in the western part of Baja California are recognized by Sedlock (1993, 2003): an upper plate of amalgamated arc and ophiolitic terranes of Triassic and Jurassic age overlapped by Cretaceous turbidites (Valle Formation) that were most likely deposited in a forearc basin; and a lower plate of blueschist-facies and metasedimentary rocks (the Puerto Nuevo melange). The arc and ophiolitic rocks of the upper plate are recognized in three different terranes in western Baja: Choyal, Vizcaíno Norte, and Vizcaíno Sur (Moore, 1985; Kimbrough, 1985; Kimbrough and Moore, 2003). Sedlock (1993, 2003) considered these three terranes as subterranes of the Cochimí terrane.

The tuffaceous cherts, limestones, and volcaniclastic sandstones of the San Hipólito Formation at Punta San Hipólito, part of the Vizcaíno Sur terrane, overlie the La Costa Ophiolite, the structurally lowest and oldest unit in the terrane. The composition of the volcanic and tuffaceous rocks above the ophiolite (mafic to intermediate, with no continentally derived debris) indicates that both the ophiolite and San Hipólito Formation were deposited adjacent to an active oceanic volcanic arc (Barnes, 1984).

The rock assemblages have been regarded as exotic to North America. Engebretson (1982) and Moore (1985) suggested original deposition several thousand kilometers to the southwest of their present position, with subsequent transportation and accretion to North America due to motion of the Farallon and North American plates. Paleomagnetic studies of the San Hipólito Formation by Hagstrum et al. (1985) inferred 18° ± 11.3°of northward latitudinal displacement since the time of magnetization. Sedlock (1993) concluded that the oceanic rocks on the western edge of Baja California moved northward about 1500 km during the Late Cretaceous and Early Tertiary. Kimbrough and Moore (2003) disagreed and argued that evidence has yet to prove that any of the terranes in the Baja region are far-traveled with respect to one another. The distinct Triassic-Jurassic assemblages are interpreted by these authors to be facies of a single oceanic volcanic arc rather than disjunct terranes; they propose geographic continuity of these terranes in the same paleogeographic setting beginning in Late Triassic time.

CONODONT BIOSTRATIGRAPHY

In this account, conodonts of the San Hipólito Formation are described and their association with radiolarian faunas are noted; the latter are mostly referred to in terms of the numbered assemblages shown in Figure 3. Information on the sampled sections, prefixed IN (inland) and CO (coastal), are given in the Appendix and in Figures 4-6. The conodonts are illustrated in Figures 7 and 8. Authorship of conodont species is given at first mention.

The oldest conodonts recovered from the San Hipólito Formation are from the *Monotis*-bearing limestone member. Those from sections INA, IND, and COA typically comprise *Epigondolella bidentata* Mosher, *E. carinata* Orchard, *Norigondolella steinbergensis* (Mosher) and *Parvigondolella* sp. A. The named species are well known and widespread in *Monotis*-bearing upper Norian strata in British Columbia (Orchard and Tozer, 1997). In one collection from IND, *Bajadontus unicornis* gen et sp. nov., *Norigondolella* sp. A, and *Parvigondolella* sp. B also occur; this fauna is not known elsewhere. In both INA and IND, limestone member strata also contain radiolarians of the *Betraccium deweveri* Zone (Fig. 3).

Conodonts from clasts within the breccia member in both INA and COB are the same as those from the limestone member. This is consistent with a derivation of the clasts, some of which contain *Monotis*, from the underlying limestone member, although a radiolarian collection from the breccia member in INA yielded questionable Rhaetian Assemblage1 radiolarians. The highest occurrences of both *Epigondolella carinata* and *Norigondolella steinbergensis* are from clasts within this unit, whereas both *E. bidentata* and *Parvigondolella* sp. A range higher.

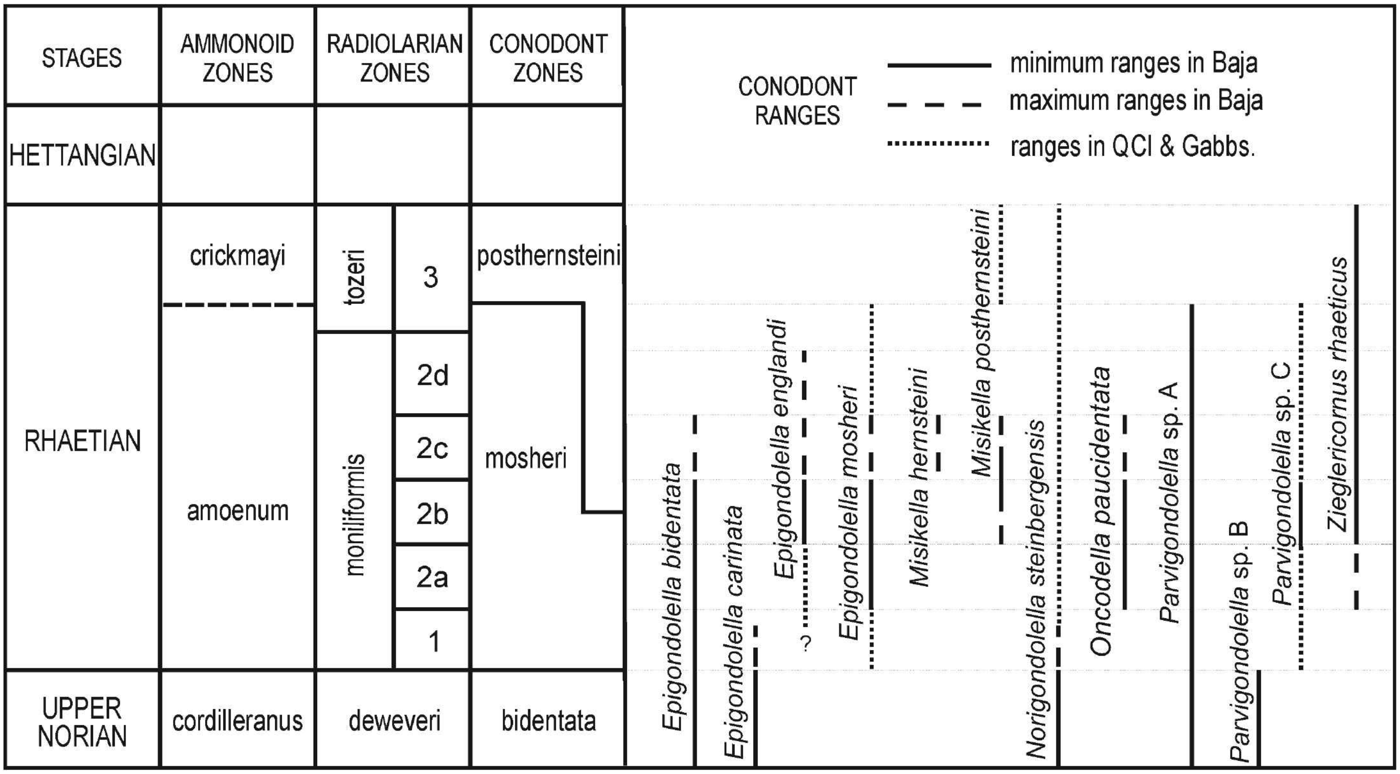


FIGURE 3. Latest Triassic biochronology and the range of conodonts in North America.

In the zonation presented by Kozur and Mock (1991), the disappearance of *Epigondolella bidentata* marks the base of the *Misikella hernsteini – Paragondolella andrusovi* Zone. More recently, Channel et al. (2003, p. 89) revised the definition of the base of that zone to include the predominance of *P. andrusovi* Kozur and Mock over *E. bidentata.* This is confirmed by Krystyn and Kuerschner (2005), who showed *Epigondolella bidentata* extending into the succeeding *M. posthernsteini* Zone at Steinbergkogel, Austria. In collections from British Columbia and Nevada (see below), *Epigondolella bidentata* extends into the Amoenum Zone but is not known to co-occur with *Misikella posthernsteini* Kozur & Mock anywhere in North America. In Baja, *E. bidentata* ranges upwards into the sandstone member of the San Hipólito Formation and is associated with radiolarians of Assemblage 2b in COC, and 2b-c in INC and COB.

Norigondolella steinbergensis is a cosmopolitan, long ranging species that is strongly facies-controlled and prefers fully pelagic conditions. It appears in the middle Norian and is found as high as the late Rhaetian *ultima* Zone at Csõvár, Hungary (Pálfy et al., 2006). In North America, it also has a long range in the Sandilands Formation on QCI, extending to within a few metres of the Triassic-Jurassic boundary, above the only record of *M. posthernsteini* known from the formation (Tipper et al., 1994). *Norigondolella steinbergensis* appears to be absent from the Gabbs Formation in Nevada, as it is from the sandstone member in Baja; these units were evidently not favorable facies for the taxon.

The other element of the upper Norian fauna that ranges from the limestone into the sandstone member is *Parvigondolella* sp. A, which is associated with radiolarians indicative of 2a-b in INB, and of 2b-d and 3 in COC. This taxon bears some resemblance to *P. andrusovi*, the upper range of which is the base of the *posthernsteini* Zone (Kozur and Mock, 1991). Additional uncommon species of *Parvigondolella* have uncertain stratigraphic utility: *P.* sp. B is confined to the limestone member, whereas *P.* sp. C occurs only with radiolarians of 2b in section COC. Both species have comparable occurrences in the Gabbs Formation in Nevada (Orchard et al., 2007).

At the base of the sandstone member in section INB, *Epigondolella mosheri* (Kozur and Mostler) sensu lato appears with *Oncodella paucidentata* (Mostler) and radiolarians of 2a. In higher beds in sections INB/ INC, additional epigondolellids that resemble *E. englandi* Orchard also occur with 2a-b and 2b-c radiolarians. Similar elements occur in section COB/ COD with 2b-2c radiolarians, and in COC with 2b and 3 radiolarians.

Epigondolella mosheri was recognized by Orchard (1991a) as being typical of those from collections from the *Cassianella* beds of Tyaughton Creek in south-central British Columbia (Umhoefer and Tipper, 1998), the type section for the *Cochloceras amoenum* Zone (Tozer, 1994). *Epigondolella mosheri* also occurs above upper Norian *Monotis* beds in both the Pardonet Formation and Bocock Limestone in northeast British Columbia (Orchard, 1991a), and in the Sandilands Formation at both Kennecott Point and Kunga Island on QCI (Orchard, 1991b). *E. mosheri* was originally described from the Nun Mine Member of the Gabbs Formation in Nevada (Mosher, 1968; Kozur and Mostler, 1976; Orchard et al., 2007). The Rhaetian age of *E. mosheri* is thus well established in western North America. The upper limit of *E. mosheri* at both Tyaughton Creek and Kennecott Point is below single occurrences of *Misikella posthernsteini* in the Crickmayi Zone. However, on Kunga Island (QCI), *E. mosheri* occurs with radiolarians of the *Globolaxtorum tozeri* Zone, which is regarded as equivalent to the Crickmayi Zone. This suggests that the latter radiolarian zone ranges below the Crickmayi Zone, or that *E. mosheri* ranges into it (Fig. 3). *Epigondolella englandi*, originally described from Late Triassic strata of the Lewes River Group in Yukon (Orchard, 1991a), also occurs in the Amoenum Zone of Tyaughton Creek, Queen Charlotte Islands, and the Gabbs Valley Range.

Oncodella paucidentata was originally described from Hallstatt Limestone at Hernstein, Austria (Mostler, 1967). Typical of pelagic sequences, the species ranges in Europe through the Rhaetian and up to the upper *posthernsteini* Zone (Kozur and Mock, 1991). In North America the species is known from a single specimen recovered from Kunga Island on QCI (Carter, 1993, fig. 9, section 3, sample 89/13), where it is found in association with radiolarians from 2a. In Baja, *Oncodella paucidentata* occurs with Assemblage 2b radiolarians in section COC,

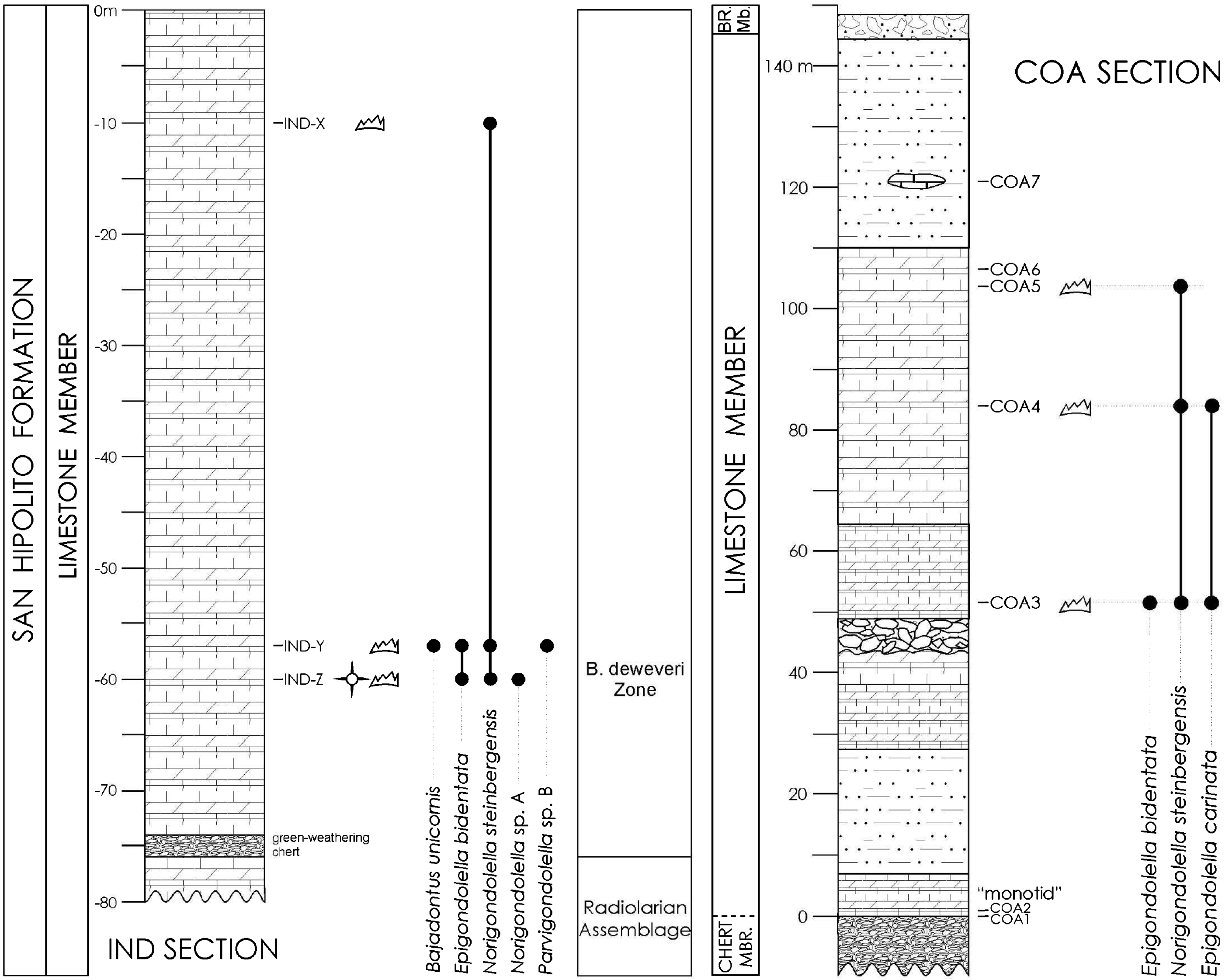


FIGURE 4. Sections IND and COA showing occurrence of conodonts and coeval radiolarian assemblages (see Figure 3).

with those of 2b-c in COB and INC, and with 2a, 2a-b, and 2b-c in INB.

Oncodella paucidentata is accompanied by the first occurrences of both *Misikella hernsteini* and *Zieglericonus rhaeticus* Kozur and Mock at ~10 m above the base of the sandstone member in COB. All these taxa are typical of low latitude "Tethyan" faunas. In common with *Oncodella, Misikella hernsteini* was originally described from the latest Sevatian of Hernstein, Austria (Mostler, 1967). The species apparently ranges into the uppermost part of the *posthernsteini* Zone in Europe, disappearing just before the appearance of *M. ultima* Kozur and Mock at Csõvár, Hungary (Pálfy et al., 2006). In Baja, it occurs with 2b-d radiolarians in COC, and with those of 2b-c in COB and INC.

Zieglericonus rhaeticus was first described from Csõvár, Hungary, where it occurs only in the upper subzone of the *Misikella posthernsteini* Zone, and possibly the terminal Triassic *M. ultima* Zone (Kozur and Mock, 1991). In England, the species also occurs also very high in the Late Triassic in the Langport Member of the Lilstock Formation in the Normanton Hills (Swift, 1995). In North America, *Zieglericonus rhaeticus* has recently been reported, with *M. posthernsteini*, from the upper part of the Mount Hyatt Member of the Gabbs Formation at the proposed GSSP site at Ferguson Hill in the Gabbs Valley Range of Nevada, where it occurs with radiolarians of the *Globolaxtorum tozeri* Zone (Orchard et al., 2007). In Baja, the species occurs with radiolarians of 2a-b in INB, 2b-c in COB, and 2b-d and 3 in COC, which includes a lower range than seen in Hungary. The report of *Zieglericonus* n. sp. in the lowermost Sevatian in Slovakia (Channel et al., 2003, fig. A3. 35) suggests that the genus has a range throughout the Rhaetian.

A single element of *Misikella posthernsteini* was recovered from section INC in association with radiolarians indicative of 2b-c: this is the first record of the species from the *Proparvicingla moniliformis* Zone in North America. In Tethys, *M. posthernsteini* appears concurrently with the ammonoid *Cochloceras* in the Steinbergkogel section in Austria (Krystyn and Kuerschner, 2005); this datum is favored for definition of the Norian-Rhaetian boundary (e.g. Carter, 1993; Kozur, 1999). In North America, the first appearance datum (FAD) of *E. mosheri* seems to represent a proxy for the base Rhaetian in the absence of *Misikella posthernsteini*, which appears later. This is evidently the case both in Nevada (Orchard et al., 2007) and in Baja. In Nevada, as in the two *Misikella posthernsteini* localities in British Columbian allochthonous terranes (QCI and Tyaughton Creek), the species is restricted to the latest Triassic Crickmayi Zone sensu Tozer (1994). In both QCI and Nevada, *M. posthernsteini* occurs with *tozeri* Zone radiolarians. In comparison with known North American occurrences, this suggests that the present Baja collection may be of Crickmayi Zone age. However, in comparison with Tethys, *Misikella posthernsteini* might be expected throughout the entire lower sandstone member and its absence may result from the general sparseness of the Baja faunas. Hence, it is difficult

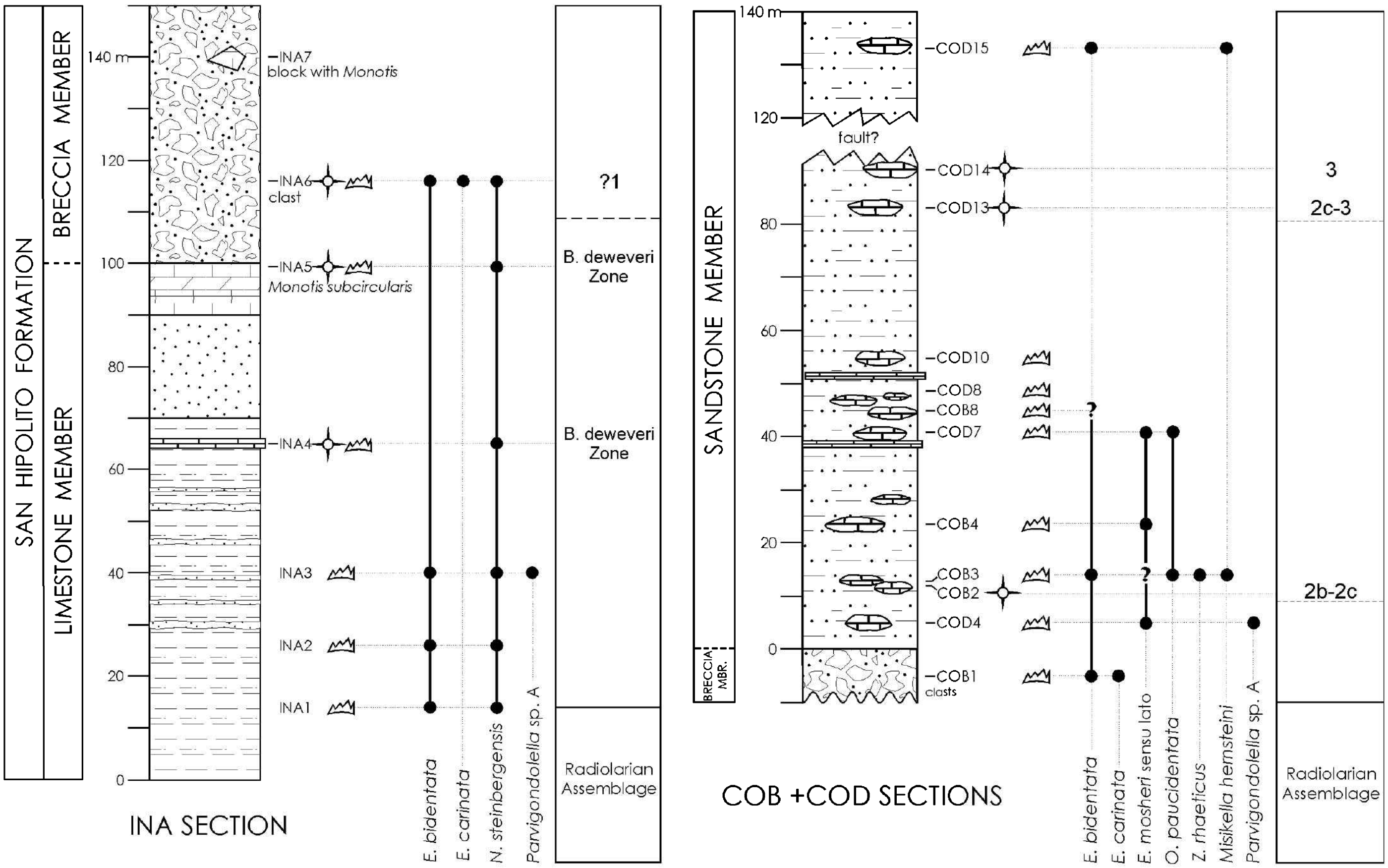


FIGURE 5. Sections INA and COB/D showing occurrence of conodonts and coeval radiolarian assemblages (see Figure 3).

to delineate a *posthernsteini* Zone. The other conodonts from the sandstone member do not resolve this issue because all of them have been shown to range in both the early and late Rhaetian.

RADIOLARIAN BIOSTRATIGRAPHY

The study of Rhaetian radiolarians has developed mainly since the finding of complete faunal successions in the Sandilands Formation of Queen Charlotte Islands (Carter et al., 1989; Carter, 1990). Many new species were described and Unitary Associations (UA) zonation was developed based on independent dating by conodonts and rare ammonoids (Carter, 1993) (Fig. 3). In turn, this detailed zonation now provides a framework for determining conodont ranges in the San Hipólito Formation of Baja California Sur.

The Baja radiolarian fauna is sparse in limestone beds assigned to the *Betraccium deweveri* Zone. However, micrite nodules from the overlying sandstone member have yielded common, variably preserved faunas from the *Proparvicingla moniliformis* Zone (Assemblages 1 + 2a-d), and abundant, well-preserved faunas in higher beds assigned to the *Globolaxtorum tozeri* Zone (Assemblage 3). Some differences have been noted in the range of certain species, e.g. *Nabolella trispinosa* (Carter), which seems to range higher in Baja. These differences plus the rarity of the zonal indicator *Proparvicingula moniloformis* have contributed to a less precise age assignment for assemblages of the *P. moniliformis* Zone. *Globolaxtorum tozeri* faunas are distinctive, however, and compare very closely with those in Queen Charlotte Islands.

The Baja fauna is dominated by species of *Canoptum*, *Citriduma*, *Fontinella*, *Globolaxtorum*, *Haeckelicyrtium*, *Laxtorum*, *Livarella*, *Nabollela* (= *Squinabolella*), *Paronaella*, *Paratriassoastrum*, *Serilla* (= *Risella,* see Carter, in press), and *Tipperella*. Many of these species are cosmopolitan in distribution with occurrence in Oregon (Yeh, 1989), Nevada (Orchard et al., 2007), Philippines (Yeh, 1992; Yeh and Cheng, 1996), Japan (Yao, 1982, Yoshida, 1986; Sugiyama, 1997; Carter and Hori, 2005), China (Yang and Mizutani, 1991; Yeh and Yang, 2007), New Zealand (Spörli and Aita, 1988), Italy (Amodeo, 1999; Reggiani et al., 2005), Austria (Kozur and Mostler, 1981; Kozur, 1984), Turkey (Tekin, 1999, 2002), and Russia (Bragin, 1991).

In comparison with Queen Charlotte Islands, Baja faunas show clear differences in the composition of assemblages. As with *Proparvicingla moniliformis*, the genera *Canutus*?, *Eptingium*, *Ferresium*, and the pantanelliids *Betraccium*, *Cantalum* and *Pantanellium* are also relatively rare in Baja whereas they are abundant in QCI. In contrast, a number of species described from more low latitude localities are common in Baja, but are rare to absent in QCI. These include: *Deflandrecyrtium carterae* and *Haeckelicyrtium takemurai* described from the Philippines (Yeh and Cheng, 1996); *Deflandrecyrtium ithacanthum* and *Haeckelicyrtium breviora* described by Sugiyama (1997) and *Livarella longus* Yoshida from Japan; *Syringcapsa rhaetica* from Austria (Kozur and Mostler, 1981); and *Tricornicyrtium dikmetasensis* and the genus *Parvicrachiale* described from Turkey (Tekin, 1999). The affinity between the Baja faunas and those of more Tethyan regions (particularly Philippines, Japan, and Turkey) implies a more southerly and ?westerly position of the Vizcaíno Sur terrane during the Late Triassic-Early Jurassic.

SUMMARY

Late Triassic faunas found in the San Hipólito Formation demonstrate that the limestone member is late Norian in age based on conodonts of the *bidentata* Zone and on sparse radiolarian fauna of the *Betraccium deweveri* Zone. The breccia member represents re-working of the upper Norian limestone, but radiolarians suggest that the breccia may include basal Rhaetian strata. Hence, the exact position of the Norian –Rhaetian boundary is undetermined. Collections from the sandstone member are Rhaetian in age, but neither the conodonts nor the radiolarians indicate the latest Rhaetian is present in the collections recovered.

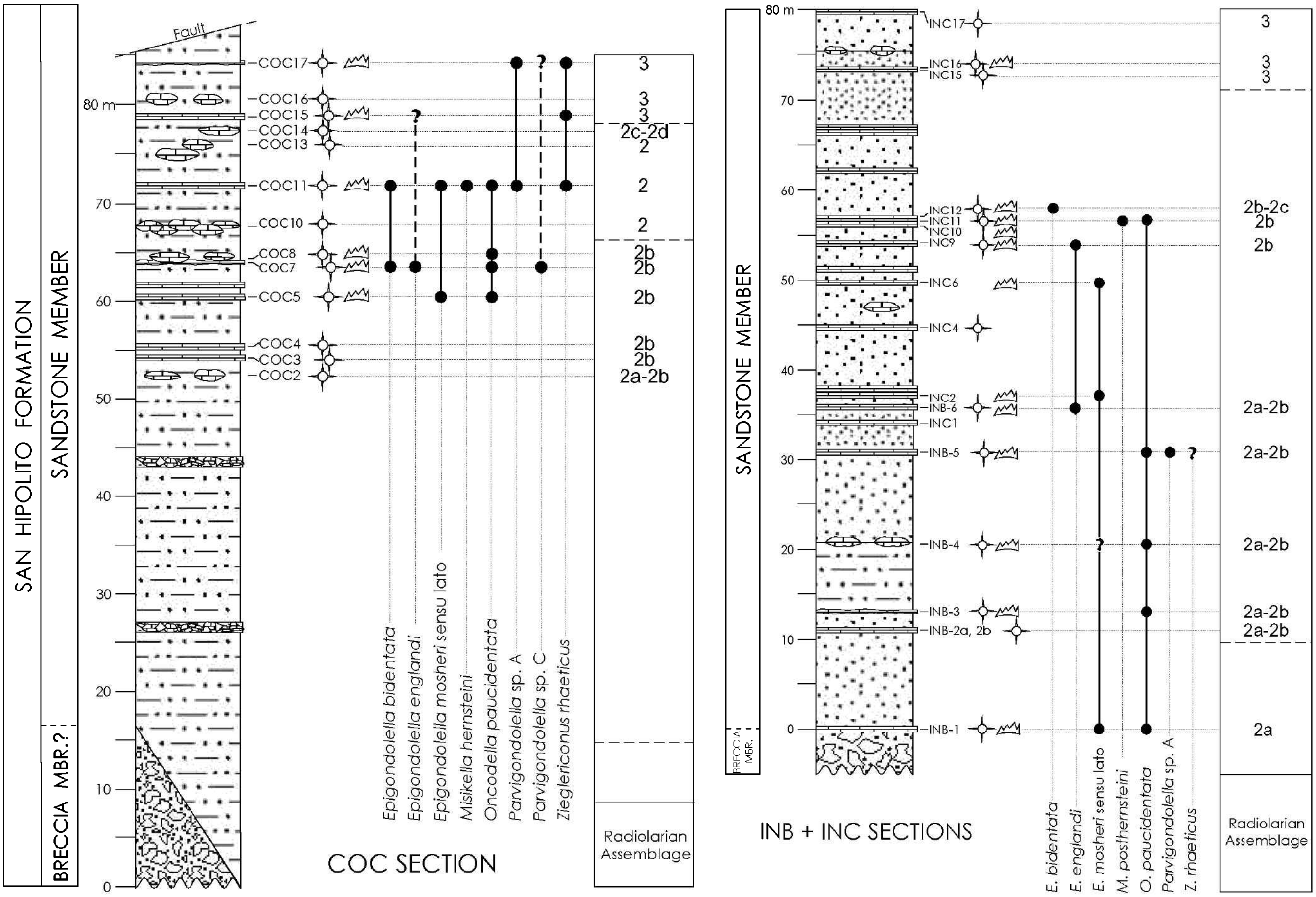


FIGURE 6. Sections COC and INB/C showing occurrence of conodonts and coeval radiolarian assemblages (see Figure 3).

Conodont faunas from the sandstone member include species of *Epigondolella* that are well known in the Rhaetian of North America, accompanied by elements that are not. Rather, the Baja species of *Misikella*, *Oncodella*, and *Zieglericonus* characterize low latitude Eurasian Tethys. Contemporaneous strata in the accreted terranes of British Columbia (Queen Charlotte Islands, Tyaughton Creek) are dominated by *Epigondolella mosheri*, with very rare occurrences of *Oncodella* and *Misikella*. In cratonal North America, *Misikella posthernsteini* and *Zieglericonus rhaeticus* are known only from the latest Rhaetian of Nevada where they occur, as with *M. posthernsteini* in QCI, only above beds with *Epigondolella* and in association with Crickmayi Zone ammonoids. Hence, the Baja conodont faunas appear to be intermediate between those of eastern Panthalasssa and Tethys, which may reflect an intermediate biogeographic provenance.

The radiolarians from the sandstone member compare closely with those from the Rhaetian *Proparvicingula moniliformis* Zone (lower to middle Rhaetian) and *Globolaxtorum tozeri* Zone (upper Rhaetian) in the Sandilands Formation of Queen Charlotte Islands, British Columbia (Carter, 1993), but minor variation is recognized in the range of a few species. Furthermore, the faunas are also accompanied by forms that characterize low latitude regions of Tethys (i.e. Philippines, central Japan, and Turkey) but are unknown in Queen Charlotte Islands.

The recent discovery of both *Misikella* and *Zieglericonus* in New York Canyon, Nevada, and their absence in cratonal successions further north, suggests that these taxa preferred low latitude environments but it does not necessarily imply a distal westerly origin (Orchard et al., 2007). Rather, they appear as late Rhaetian immigrants into an *Epigondolella* dominated biofacies. The Baja faunas are closer to those of Tethys where *Misikella* and its associates became dominant in the early Rhaetian.

TAXONOMIC NOTES

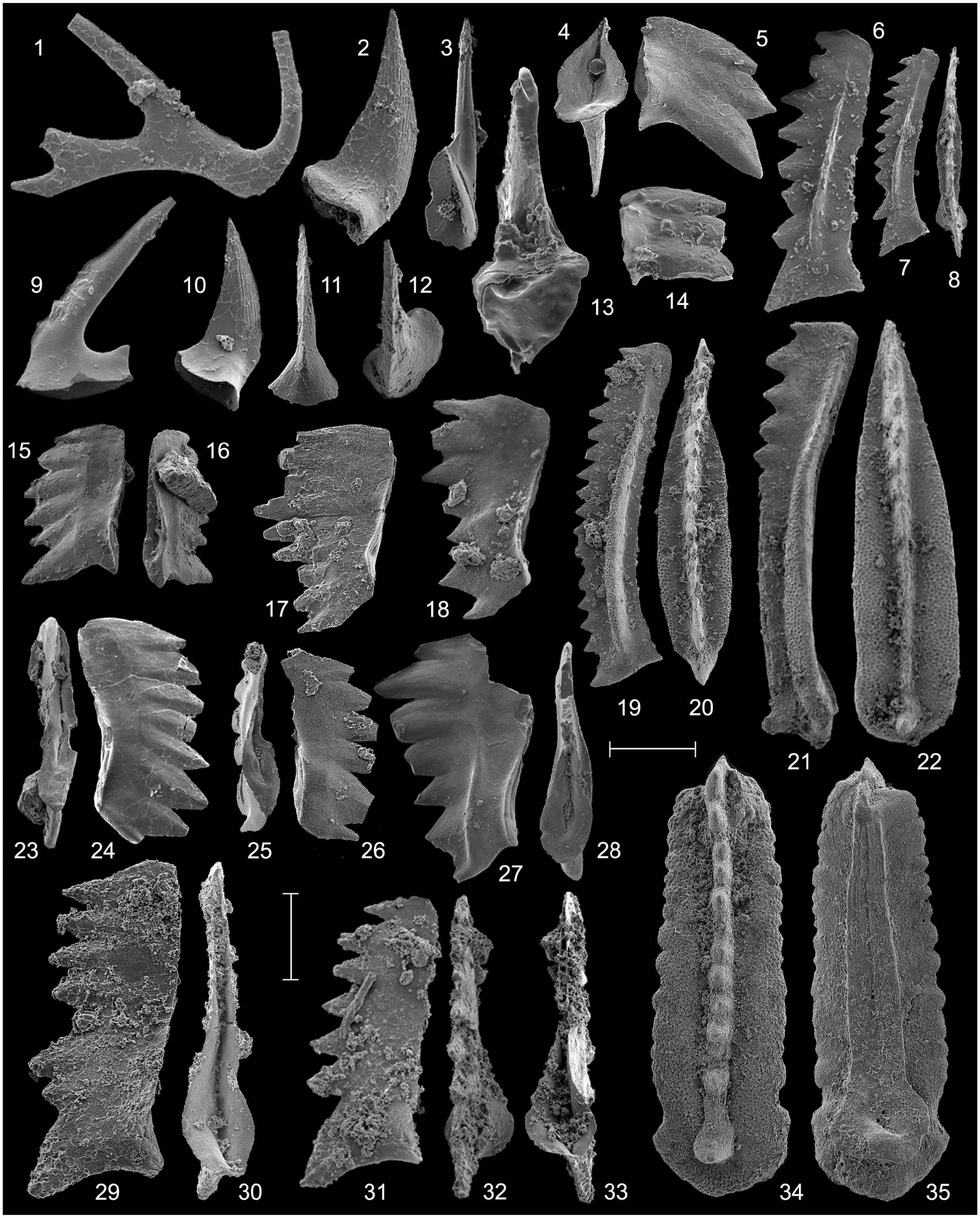
Bajadontus Orchard gen. nov.

Etymology: From a combination of its geographic origin and tooth-like function

Diagnosis: As for the only known species.

Bajadontus unicornis Orchard sp. nov.
(Fig. 7. 29-33)

FIGURE 7. Illustrations of conodonts. Scale bar = 200 microns for numbers **7, 8, 19-22, 34, 35** (x 80), =100 microns for remainder (x 160), =50 microns for number **13** (x 320). **1, 9,** *Oncodella paucidentata* (Mostler). **1,** GSC 101509, and **9,** GSC 101510, both from GSC loc. C-173442 (COC-11). **2, 3, 10-12,** *Zieglericonus rhaeticus* Kozur & Mock. **2, 3,** GSC 101511, and **10-12,** GSC 101512, both from GSC loc. C-173442 (COC-11). **4, 5,** *Misikella hernsteini* (Mostler), GSC 101513, from GSC loc. C-173442 (COC-11). **13, 14,** *Misikella posthernsteini* Kozur & Mock, GSC 101514, from GSC loc. C-177459 (INC-11). **6-8, 19-22,** *Norigondolella steinbergensis* (Mosher). **6,** GSC 101515, and **7, 8,** GSC 1015016, both from GSC loc. C-173414 (IND-X), **19, 20,** GSC 101517, from GSC loc. C-173391 (INA-3), and **21, 22,** GSC 101518, from GSC loc. C-173422 (COA-4). **15, 16, 23-26,** *Parvigondolella* sp. A. **15, 16,** GSC 101519, **23, 24,** GSC 101520, and **25, 26,** GSC 101521, all from GSC loc. C-173442 (COC-11). **17,** *Parvigondolella* sp. B, GSC 101522, from GSC loc. C-173415 (IND-Y). **18,** *Epigondolella bidentata* Mosher, juvenile, GSC 101523, from GSC loc. C-173427 (COB-3). **27, 28,** *Parvigondolella* sp. C, GSC 101524, from GSC loc. C-173438 (COC-7). **29-33,** *Bajadontus unicornis* gen et sp. nov. **29, 30,** Holotype, GSC 101525, and **31-33,** GSC 101526, both from GSC loc. C-173415 (IND-Y). **34, 35,** *Norigondolella* sp. A, GSC 101527, from GSC loc. C-173416 (IND-Z).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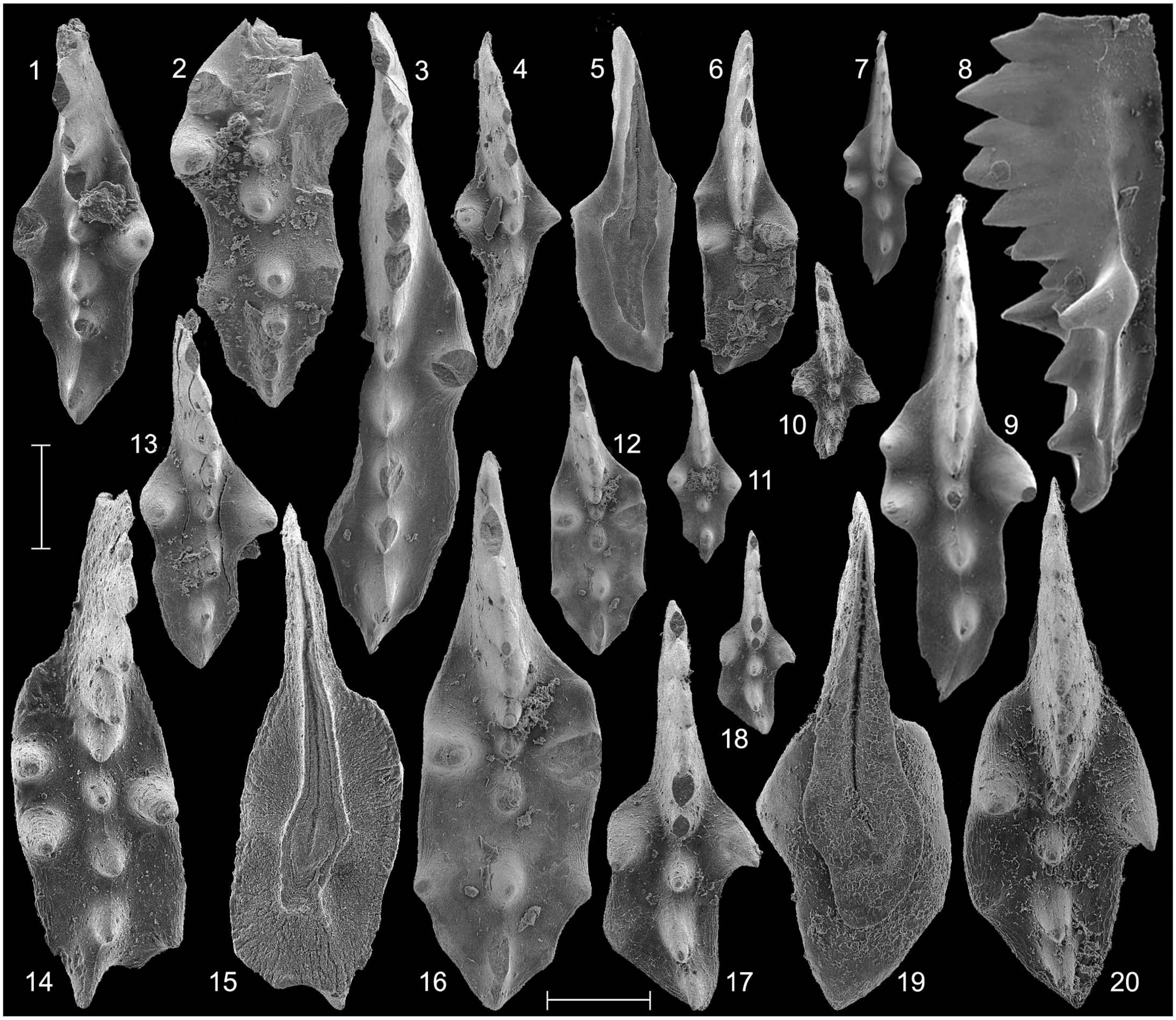

FIGURE 8. Illustrations of conodonts. Scale bar = 200 microns for numbers **5-7, 10-13, 18** (x 80), 100 microns for the remainder (x160). **1-9,** *Epigondolella mosheri* (Kozur & Mostler) *sensu lato.* **1,** GSC 101528, from GSC loc. C-173436 (COC-5), **2,** GSC 101529, from GSC loc. C-177468 (COD-4), **3,** GSC 101530, from GSC loc. C-173436 (COC-5), **4,** GSC 101531, from GSC loc. C-177455 (INC-6), **5, 6,** GSC 101532, from GSC loc. C-177452 (INC-2), and **7-9,** GSC 101533, from GSC loc. C-173445 (COC-15). **10, 11, 13, 17-20,** *Epigondolella bidentata* Mosher. **10,** GSC 101534, from GSC loc. C-173384 (INA-1), **11,** GSC 101535, from GSC loc. C-177460 (INC-12), **13,** GSC 101536, from GSC loc. C-177459 (INC-11), and **17, 18,** GSC 101537, and **19, 20,** GSC 101538, both from GSC loc. C-173425 (COB-1). **12, 16,** *Epigondolella englandi* Orchard, GSC 101539, from GSC loc. C-173399 (INB-6). **14, 15,** *Epigondolella carinata* Orchard, GSC 101540, from GSC loc. C-173393 (INA-6).

Holotype: GSC 120359, Fig. 7. 29, 30.

Etymology: Referring to the large terminal cusp.

Type stratum: Bed IND-Y, ~70 m below the top of the upper Norian limestone member, San Hipolito Formation

Type locality: GSC loc. C-173415. Section IND, Punta San Hipólito on the Vizcaino Peninsula of Baja California Sur.

Material: About 20 specimens.

Diagnosis: The segminate P1 element has a posterior cusp that is about three times as large as the other denticles, of which there are up to 7; these slightly decrease in size and elevation to the anterior. The cusp is posteriorly inclined and has a concave posterior margin. The lower surface is deeply excavated, asymmetrically flared with a slight posterolateral expansion beneath the cusp, and strongly tapered to the anterior. The lateral margins of the element lack any flange development.

Remarks: This new conodont resembles small elements of *Norigondolella steinbergensis* (e.g. Fig. 7. 6), from which it may well have developed, but they differ in lacking a platform and in having a more deeply excavated and flared basal cavity. The latter feature is shared by Rhaetian taxa like *Misikella* and *Zieglericonus*, but any relationship with those hinges on a comparison of the multielement apparatuses of the new taxon, which is unknown.

Epigondolella spp.
(Fig. 8)

Remarks: Several different *Epigondolella* species are thought to occur in the San Hipolito Formation, although none are common. This makes it difficult to assess intraspecific variation, which has not been established for several species of late Norian and Rhaetian age. Broadly contemporaneous or overlapping species include *E. bidentata*, *E. slovackensis* Kozur, and *E. zapfei* Kozur from Europe, and *E. carinata*, *E. englandi*, *E. humboldensis* Meek, and *E. mosheri* (several morphotypes) from North America. There is an urgent need to delineate these taxa taxonomically and thereby demonstrate their stratigraphic utility.

Elements here included in *E. mosheri* sensu lato lack the very long posterior platforms of specimens from the Amoenum Zone of Nevada and Queen Charlotte Islands but they are distinctly longer and narrower than the stratigraphically older specimens of *E. bidentata*. They also commonly have an accessory anterior denticle on one platform margin and thus resemble *E. zapfei* from the *bidentata* Zone in Europe. However, this variation is denticulation is also shown by *E. mosheri* and other populations elsewhere (e.g., Orchard 1983, 1994), so for now they are kept united. Broader, more ornate specimens are referred *to E. carinata* and *E. englandi*.

Norigondolella sp. A
(Fig. 7. 34, 35)

Remarks: The platform of the large P1 specimen has irregular and nodose lateral margins, particularly anteriorly. The large posterior cusp lies within a lobe defined by marginal indentations and is surrounded by a broad platform brim. The single specimen may be a gerontic element of *Norigondolella steinbergensis*.

Parvigondolella sp. A
(Fig. 7. 15, 16, 23-26)

Parvigondolella sp. A – Orchard, Carter, Lucas & Taylor, pl. 1, fig. 20.

Remarks: This species resembles small growth stages of *E.* ex gr. b*identata but* it lacks a platform and lateral nodes. The carinal denticles are of uniform size but decrease in height to the posterior, where the cusp is not well differentiated. The basal edge is straight. This species differs from the holotype of *Paragondolella andrusovi* Kozur and Mock in lacking a large cusp and downturned posterior process, but some elements assigned to the latter species are similar. A similar specimen was previously reported from near the base of the Nun Mine Member of the Gabbs Formation (Orchard et al., 2007).

Parvigondolella sp. B
(Fig. 7. 17)

2007 *Parvigondolella* sp. B – Orchard, Carter, Lucas & Taylor, pl. 1, fig. 21

Remarks: These elements have a well differentiated cusp, and a short downturned posterior process carrying one or two denticles; it lacks both platform and nodes. The basal cavity is elongate and expanded beneath the short posterior process. A specimen was also reported from the lower Nun Mine Member of the Gabbs Formation in Nevada (Orchard et al., 2007). This species resembles the holotype of *Paragondolella andrusovi* with its large cusp and downturned posterior process, but the anterior and posterior parts of the blade are not well differentiated.

Parvigondolella sp. C
(Fig. 7. 27, 28)

2007 *Parvigondolella* sp. C – Orchard, Carter, Lucas & Taylor, pl. 1, figs. 12-15.

Remarks: This element is similar to small growth stages of *E.* ex gr. b*identata* but it lacks lateral denticles. Rather, it has narrow lateral flanges that extend along both sides of the posterior part of the element. Similar but longer elements occur in the uppermost Nun Mine Member of the Gabbs Formation (Orchard et al., 2007), and in the Sandilands Formation of QCI.

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APPENDIX

Information on each of the sampled sections is provided below.

IND (FIG. 4)

This 80 m section is in the limestone member, collected in 1996. Three conodont collections consist largely of *Epigondolella* and *Norigondolella* species, but one the most diverse of those recovered from the unit. *Bajadontus unicornis* gen. et sp. nov. occurs immediately above radiolarians of the *B. deweveri* Zone.

COA (FIG. 4)

This ~140 m section, collected in 1996, begins at the base of the lithogically variable limestone member, which rests on the chert unit and includes monotids at its base. Three conodont collections with *Epigondolella* and *Norigondolella* species were recovered.

INA (FIG. 5)

This section is 150 m thick, begins at the base of the limestone member, and goes through ~50 m of the breccia member. Collected in 1996, conodonts recovered from five beds in the limestone member and from a clast within the breccia are taxonomically comparable. Samples from about the middle and from the top of the limestone member contain *B. deweveri* Zone radiolarians. A questionable radiolarian assemblage 1 fauna occurs within the breccia sample, which is an important indication that formation of the breccia was an early Rhaetian event. *Monotis* sp. cf. *M. subcircularis* occurs both at the top of the limestone and in clasts from the breccia.

COB, COD (FIG. 5)

This section was sampled twice, in 1982 (COD) and 1996 (COB). The COD section extends up to 140 m from the base of the sandstone member. It is part of the complete section, BPW82-alpha-BPW82-60, collected up to ~776 m from the top of the limestone member through the sandstone member in 1982. Later, the COB section (the lowest 45 m) was resampled beginning at the base of the sandstone member. Conodont data come from seven samples in the lower ~90 m, from an eighth sample near the top of the underlying breccia member, and from a sample higher in the section that may be repeated by a fault. Radiolarians represent both the *moniliformis* and *tozeri* zones, and suggest that the base of 2b is no higher than ~10 m above the base of the member.

COC (FIG. 6)

Collected in 1996, this ~84 m thick section produced the most abundant Rhaetian conodont and radiolarian faunas. The basal ~15 m is transitional from the underlying breccia, but otherwise it is all in the sandstone unit. Six conodont collections and 12 radiolarian faunas include several radiolarian assemblages, including a defined boundary between the *moniliformis* and *tozeri* zones at ~78 m.

INB, INC (FIG. 6)

This section was sampled twice, in 1982 (INC) and 1996 (INB). The INC section extends to 80 m from the base of the sandstone member and is part of the complete section, BPW82-4-BPW82-34, of 180 m, collected from the top of the breccia member through the sandstone member. Later the INB section (the basal ~75 m of the sandstone member) was resampled. This section is unique in providing a fossil age at the base of the sandstone member; both radiolarians and conodonts show it to be Rhaetian, but the radioarians indicate that it is not basal Rhaetian. Twelve conodont collections and 14 diagnostic radiolarian collections spanning both *moniliformis* and *tozeri* zones were recovered.

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TOWARDS A CARBON ISOTOPE REFERENCE CURVE OF THE UPPER TRIASSIC

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The mass extinction at the Triassic-Jurassic (T-J) boundary is one of the "Big Five" in the Phanerozoic. In marine habitats, significantly increased extinction rates at the end of the Triassic are well documented (Tanner et al., 2004). An important number of ammonoid and radiolarian families, the entire phylum of Conodonta and large numbers of species of bivalves, bryozoans, gastropods, brachiopods, echinoids and crinoids became extinct (McRoberts and Newton, 1995; Lethiers, 1998).

The presence and the amplitude of several crises (Krystyn, 2004) before the T-J boundary, however, may lead us to question its relative importance (Hallam, 2002). Strong disturbance in the environment and in the biodiversity record had already occurred at the Lower Carnian-Upper Carnian boundary and at the Lower to Middle Norian boundary with the most dramatic loss (70%) in biodiversity among Late Triassic molluscs (McRoberts and Newton, 1995). Starting in the Upper Norian (Sevatian), the pelagic fauna undergoes successive crises before the final Rhaetian-Hettangian boundary event (Krystyn and Kürschner, 2005). The relative importance of a major extinction event at the T-J boundary could thus be overestimated by the multiplication of crises during the whole Late Triassic. The continental picture is also equivocal. Catastrophic changes among vertebrates and plants have been suggested in the eastern USA (Olsen et al. 2002), but contradictory data are reported from Europe where macrofossils suggest a gradual transition in vegetation (Benton, 1994). A literature survey of palynological data shows that rates of extinctions significantly increased in the continental realm during the Late Triassic. In North America, 40% of all Late Triassic palynomorph taxa show their last appearances at the Carnian–Norian boundary, and 30% during the Norian, whereas only 20% occur at the T-J boundary (McElwain et al., 1999).

It therefore appears that despite new originations, the general decline in biodiversity was punctuated by a series of accelerated steps between the Carnian and the Rhaetian, while the T-J boundary event may have been the final strike. How these changes in the biosphere were related to oceanographic and/or geochemical changes during the known Late Triassic biotic crisis events is a question of primary importance. In order to solve this issue, two principal questions have to be addressed: (1) are these extinctions best explained by a gradual process of environmental change or by (a series of) abrupt or even catastrophic events? and (2) how do Late Triassic patterns of biotic turnover correlate and couple with oceanographic geochemistry? An expansion of a well-calibrated carbon isotope reference curve for the whole Upper Triassic is an important first step to address these questions.

While a comprehensive isotopic data set is available for the T-J boundary (Morante and Hallam, 1996; Guex et al., 2004; Kürschner et al., in press and reference therein; Pàlfy et al., in press; Ward et al., in press; Michalik et al., in press; Williford et al., in press), only a few data are available for the Upper Triassic (see Atudorei, 1999; Gawlick and Böhm, 2000; Hauser et al., 2001; Muttoni et al. 2004; Hornung and Brandner 2005; Korte et al., 2005; Hornung et al., in press for Carnian-Norian and Ward et al., 2001, 2004; Sephton et al., 2002 for the Rhaetian).

To establish a carbon isotope reference curve, several Tethyan and Peritethyan sections were measured in the Austrian Alps, Slovakia, Taurus, Oman and the Indian Himalayas. The Upper Ladinian samples record an increase in $\delta^{13}C_{carb}$ until the Lower Carnian, followed by stable values until the Upper Carnian. This stability is, however, disturbed by some small negative excursions in the isotopic signal near the Reingraben event and the Lower Carnian-Upper Carnian boundary (Spiti, Indian Himalaya; Mayerling, Austrian Alps and several sections in Taurus, this study; but see also Atudorei, 1999; Hauser et al., 2001; Hornung and Brandner, 2005 and Hornung et al, in press).

The Carnian-Norian boundary interval is marked by a minor increase in the C isotope value (less than 1‰; Gawlick and Böhm, 1999; Muttoni et al. 2004; this study). This transition is observed in Pizzo Mondello, Sicily (Muttoni et al., 2004), in Kälberstein Quarry, Austria (Gawlick and Böhm, 2000), in Bölücektasi Tepe and Erenkolu Mezarlick, Turkey, and in Silicka Brezova, Slovakia (this study), with amplitudes between 0.35‰ to 0.8‰. The isotopic values then show an increase until the Middle Norian followed by a decrease as recorded in Oman (this study), in Pizzo Mondello, Sicily (Muttoni et al., 2004) and in Kälberstein Quarry, Austria (Gawlick and Böhm, 2000). In the Upper Norian the isotopic values are relatively stable, and show no shift across the newly proposed Norian/Rhaetian boundary (Steinbergkogel, Austria and Oman, this study) before increasing again through the classical Norian/Rhaetian boundary (Oman and Oyuklu, Turkey, this study but also in British Columbia: Ward et al., 2001, 2004) into the Lower Rhaetian. Instead, Sephton et al. (2002) described a $\delta^{3}C_{org}$ peak in British Columbia at the Norian-Rhaetian boundary, which seems to be absent in the Tethyan $\delta^{13}C_{carb}$ record. The isotopic record then remains constant until the top of the Rhaetian and the famous negative double peak around the Triassic-Jurassic boundary.

The Reingraben event and the Lower Carnian-Upper Carnian boundary are apparently marked by a disturbance of the carbon cycle. The Lower to Middle Norian crisis is marked by a turning point from slowly increasing carbon isotopic values to gradually decreasing values. The Upper Norian (in the classical sense) is marked by a shift from decreasing to increasing isotope values. From an isotopic point of view, only the Reingraben event and Lower Carnian-Upper Carnian boundary can be interpreted as events, whereas other biotic crises of the Late Triassic seem to have occurred during periods of gradual changes in the isotopic composition of the marine seawater.

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DETAILED CARBON ISOTOPE ANALYSIS OF TRIASSIC-JURASSIC KEY SECTIONS IN THE WESTERN TETHYS REALM

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Significant fluctuations in carbon-isotope values of bulk sedimentary organic matter are recognized in key Triassic-Jurassic boundary sections in Europe and North America. Some of these sections (e.g., St. Audrie's Bay and New York Canyon) consistently show two pronounced negative carbon-isotope shifts in the boundary interval, which are also recognized in the sediments of the Eiberg Basin (Tiefengraben section, Austria). This marginal basin formed during Rhaetian time on top of a widespread carbonate platform along the Tethyan passive margin.

New high resolution studies of several proximal to distal Tr-J boundary sections within this large basin do show up to 7‰ excursions of the carbon-isotope signal that may partly correspond to changes in vegetation and fluctuating influx of organic matter. In addition, we show preliminary results of biomarker analyses in order to determine environmental conditions during the deposition of the boundary interval sediments in this basin.

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PATTERNS OF RECOVERY OF AMPHIBIAN DIVERSITY IN THE TRIASSIC

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Late Permian faunal extinction, albeit affecting the land tetrapod communities in a more or less uniform way, resulted in different starting conditions for the subsequent recovery of amphibian and reptilian components. Distinct from reptiles, the diversity of temnospondyl amphibians notably increased by the early Scythian, as compared with the terminal Permian. This was manifested in a rise of 4-5 new widespread temnospondyl families instead of only the two that existed immediately before the extinction event. Like this event *per se*, such a situation was ultimately underlain by overall uplifting of Pangea, which led to increase in aridity on land and dismembering of former lowland biotopes. These factors in turn forced the surviving tetrapod life to concentrate within, and around, local water basins, which initially gave an advantage to aquatic and subaquatic forms, primarily the amphibians.

As a whole, the dynamics of recovery of the Triassic temnospondyl amphibian fauna suffered a distinctive change with time. Basically, two principal consecutive patterns are discernible in the evolution of this fauna, referred to as the epoch of archaic diversity (Induan-earliest Olenekian) and the epoch of conservative development (mostly from late Olenekian to the end of the Triassic). These are linked by some intermediate types.

The archaic diversity pattern indicated the condition of a much disintegrated and impoverished terrestrial biota, whose existence immediately followed the Permian extinction and fell on the peak of aridification. Under this condition, the ecosystem's control over stability of tetrapod body plans was much weakened. Accordingly, the temnospondyl families of that time are mostly characterized by the following: (a) marked morphological diversity, sometimes producing chimeric structural types, and not necessarily combined with high taxonomic diversity; (b) short-term existence; and (c) quick spatial expansion resulting in worldwide, although much uneven, dispersal over the land.

The most ephemeral cosmopolitan groups demonstrating to various degrees this radiation mode are the Induan families Lydekkerinidae and Tupilakosauridae. The former, which originated and much diversified in southern Gondwana, succeeded in penetrating the north of Western Laurasia via nearshore marginal biotopes. Conversely, the tupilakosaurids that arose in Laurasia are known to rapidly have spread southwards into India, South Africa and Antarctica. Their morphology shows a combination of characters that otherwise seem incompatible in terms of standard temnospondyl structural patterns. A somewhat more long-lasting group of this type is the Gondwanan family Rhytidosteidae (latest Permian-late Olenekian), documented in the northern hemisphere by only two Early Olenekian genera from the coastal biotopes of the Eurasian Arctic margin. It demonstrates an especially wide range of both structural and taxonomic diversification, such that some genera combine advanced cranial features with those shared only by the most archaic Permocarboniferous forms.

Some further groups may be regarded (in terms of their diversification mode) as intermediate between the above-surveyed ones and those typifying the conservative development. One of them is the typical (non-lonchorhynchine) Trematosauridae, which originated in Laurasia in the latest Induan-early Olenekian, underwent a wide radiation in lacustrine and brakish-water basins during the Olenekian and rapidly came to decline in the Ladinian-Carnian. A short-term epibole and wide dispersal displayed by these amphibians are combined with a much limited scope of structural diversity, a character typical of the later advanced temnospondyls. Another example of similar kind is provided by the smaller family Brachyopidae, which shows a rather short, continuously documented history (Olenekian-Early Anisian) in combination with structural uniformity and restricted (Gondwanan) population area. The two Triassic taxa from outside this area currently assigned to brachyopids (from the Olenekian of Russia and Anisian of North America) are most likely the offshoots of Laurasian tupilakosaurids and dvinosaurids, respectively. The unquestionable brachyopid expansion to the northern hemisphere has been recorded only for Jurassic relicts.

The "conservative epoch" in the history of recovery and decline of temnospondyl amphibians may be first exemplified by the evolution of the Capitosauroidea, the largest and most diversified temnospondyl group that had spread over all the continents. Known since the very onset of the Triassic, the capitosauroids s.str. become rather common in the late Olenekian and attain their peak of abundance in the Anisian-Ladinan. At first sight, their worldwide expansion and vast taxonomic diversity do not allow for clear-cut discrimination of the mode of their evolution from the "archaic diversity" pattern as outlined above. But this impression actually seems to result from very poor knowledge of capitosauroid taxonomic structure. The conservatism and homogeneity of their morphology, coupled with homoplasy and the scarcity of material available for most taxa, make it extremely difficult to distinguish the principal higher rank subdivisions within the group. As a consequence, the bulk of it looks like the product of a single, much diversified and cosmopolitan Triassic radiation. However, in those cases that enable discernment of the particular capitosauroid families (Stenotosauridae, Cyclotosauridae, Mastodonsauridae), one can see that in fact each of these included only a few members and inhabited strictly limited geographic realms. It seems most likely that, with a more accurate assessment of capitosauroid interrelationships, the same picture will be revealed for the rest of their contained taxa.

A total switch towards conservative patterns in amphibian evolution by the second half of the Triassic is further demonstrated by the other principal temnospondyl groups of this age. Like the capitosauroids, each of these exhibits very restricted scope of modifications in skeletal morphology. The longest persistence is documented for the Plagiosauroidea, which originated in the Scythian and flourished in the Middle-Late Triassic, producing three stable morphological types. Evaluation of its fossil record, which is limited to Europe, the European Arctic shelf and Thailand, leads to the conclusion that the group (along with accompanying cyclotosaurid capitosaurs) inhabited the Laurasian landmasses bordering the Tethys from the north. A basically similar pattern is demonstrated by the Metoposauridae, a family recorded with confidence only in the Late Triassic. Its population area included the southern Tethyan margin (North Africa and India), a part of the northern margin (Europe) and projected far westwards into the North America. Lastly, the Chigutisauridae, known mainly from the Late Triassic (except one Scythian genus, and putting aside late Mesozoic relicts), never expanded outside of Gondwana.

The above generalizations show that evolutionary changes observed among Triassic temnospondyls tended to slow up with time, while the ranges exhibited by particular lineages underwent reduction. It seems obvious that these trends reflected the gradual recovery and integration of the terrestrial biota, which was primarily expressed in diversification of its reptilian component. The growth of ecosystem stability left ever less room for structural variations attainable for large aquatic amphibians, thus returning them to a position they occupied in tetrapod communities right before the Permian extinction.

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TETRAPOD FAUNA OF THE UPPER TRIASSIC (REVUELTIAN) OWL ROCK FORMATION, CHINLE GROUP, ARIZONA

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Abstract—The Owl Rock Formation, upper Chinle Group, crops out in the Four Corners area. In the 1980s, Kirby made an extensive collection of vertebrate fossils from the Owl Rock Formation in the Ward Terrace area, northeastern Arizona. We review the Owl Rock tetrapod fauna and refine the taxonomic assignments provided by previous workers. The Owl Rock Formation tetrapod assemblage thus consists of: metoposaurid amphibians, including the centra of cf. *Buettneria* sp. and *Apachesaurus* sp.; sphenodontids; kuhneosaurids; various indeterminate procolophonids, archosauromorphs and archosaurs; a variety of suchian reptiles, including cf. *Postosuchus*, *Postosuchus* sp., cf. *Poposaurus* sp. and shuvosaurids; the aetosaur *Typothorax coccinarum*; male and female morphs of the phytosaur *Pseudopalatus buceros*; and a coelophysoid. The presence of *P. buceros* and *T. coccinarum* in the fauna confirm the age of the Owl Rock fossil assemblage as Revueltian.

INTRODUCTION

The Owl Rock Formation is part of the upper portion of the Upper Triassic Chinle Group that crops out in northern Arizona, southern Utah and northwestern New Mexico. The tetrapod fauna of the Owl Rock Formation is considerable, but has never been formally published, except in very preliminary form (Kirby, 1989, 1991, 1993), as descriptions of singular taxa (Murry and Kirby, 2002; Fraser et al., 2005; Butler et al., 2006) or in larger review papers (Long and Murry, 1995; Heckert et al., 2005). In addition, these previous works (Kirby's in particular) are in serious need of updating, given the considerable changes in the taxonomy of Late Triassic tetrapods that have taken place since their publication (e.g., Long and Murry, 1995 and ensuing commentary in the literature). The tetrapod fossils discussed here are from localities along Ward Terrace, in the southwest portion of the Navajo Nation Indian Reservation, northeastern Arizona (Fig. 1). These localities provide the principal tetrapod fauna from the Owl Rock Formation. Here, we review previous studies conducted on the Owl Rock tetrapod fauna, provide our own analysis of the fauna and summarize the differences between the interpretation of previous workers and our own. In this paper, MNA refers to the Museum of Northern Arizona, Flagstaff.

PREVIOUS STUDIES

The history of modern study of the tetrapods from the Owl Rock Formation in Arizona is rather brief, due primarily to the majority of previous information deriving from a single worker, Randy E. Kirby. In two short papers (Kirby, 1989, 1993) and an extensive, unpublished master's thesis, Kirby (1991) provided the basis for our study. Later workers began to revise the fauna first documented by Kirby (1991), but only in piecemeal fashion (e.g., Murry and Kirby, 2002; Butler et al., 2002).

Kirby (1989) provided a preliminary summary of the Ward Terrace collecting area, regional stratigraphy, a depositional model and a faunal list. This faunal list included hybodontid sharks; palaeoniscid, colobodontid and coelacanthid fishes; metoposaurid amphibians; sphenodontid?, poposaurid? and sphenosuchian reptiles; the aetosaur *Typothorax*; two taxa of phytosaurs; and theropod and fabrosaurid dinosaurs. Kirby's (1991) thesis provided an expanded discussion of all the material that he listed previously. This thesis was more focused on the vertebrate fauna, presenting the taxonomy of all the specimens from the Owl Rock Formation in the MNA collection, as well as justification of his taxonomic assignments. This remains the only taxonomic discussion of the fauna. Kirby (1993) summarized the Late Triassic basin evolution of the Chinle Group depositional system and discussed faunal replace-

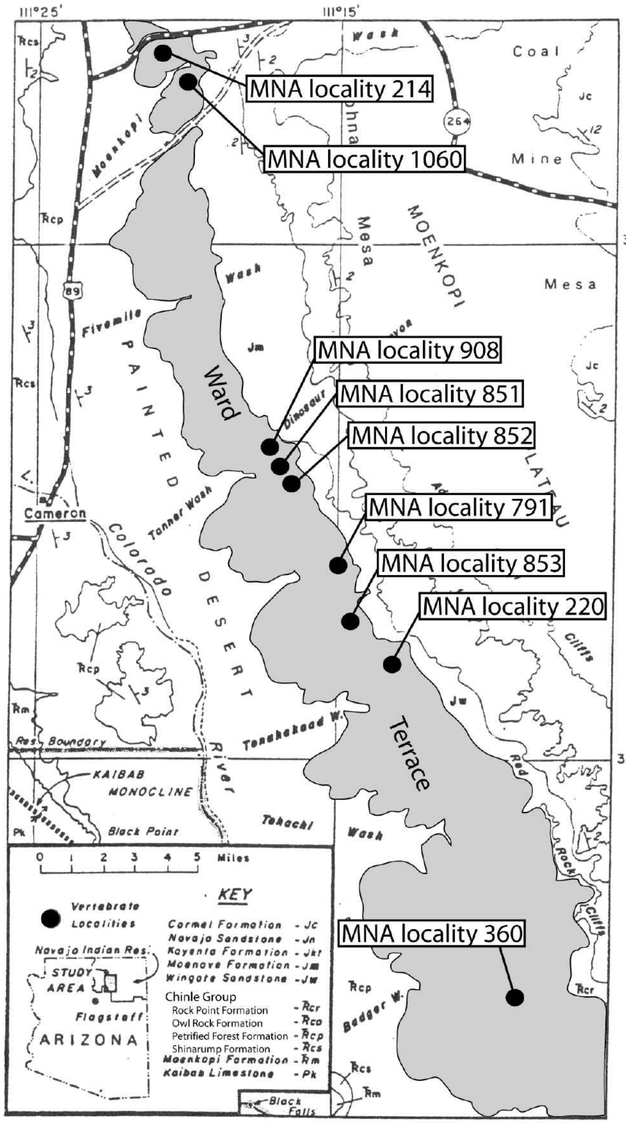

FIGURE 1. Regional map highlighting Owl Rock Formation outcrops (gray) and tetrapod fossil localities in the Ward Terrace collecting area. Modified from Kirby (1989, fig. 1).

ment events in light of this model. He also provided an updated faunal list for the Owl Rock Formation, further revised from Kirby (1991).

Relatively few studies have examined Owl Rock tetrapods since Kirby (1993). Murry and Kirby (2002) described a new genus and species of hybodont shark, *Reticulodus synergus*, from the Owl Rock Formation based on various isolated lateral teeth collected by Kirby during his thesis work. *Reticulodus* is also known from older specimens from stratigraphically lower strata in the Petrified Forest National Park collected by Murry (Murry and Kirby, 2002). Fraser et al. (2005) described a leptopleurine procolophonid, from the unit in the Abajo Mountains of southeastern Utah, based on an incomplete skull; this is the only tetrapod record from the Owl Rock Formation outside of Arizona.

Heckert (2001) briefly re-evaluated some of the putative prosauropod or ornithischian dinosaurs from Kirby's collection. This served as the basis for comparison with an unusual archosauriform tooth from Switzerland that is similar to the Owl Rock form, illustrated by Butler et al. (2006). Heckert et al. (2005) noted that the fauna documented by Kirby (1991) is indicative of a Revueltian age.

SYSTEMATIC PALEONTOLOGY

AMPHIBIA

TEMNOSPONDYLI

METOPOSAURIDAE

Metoposauridae indet.

Kirby (1991) assigned all amphibian material recovered from the Owl Rock Formation at Ward Terrace to cf. *Metoposaurus* sp. This material consists of cranial elements, pectoral girdle elements and various vertebral centra. Much of the material that Kirby (1991) referred to cf. *Metoposaurus* consists of isolated cranial fragments bearing the prominent "waffle-iron" sculpturing that is found on the skull and pectoral girdles of this family of Late Triassic amphibians (Hunt, 1993). Unfortunately, these cranial fragments do not include the lacrimal, a vital bone in order to discriminate genera and species within the Metoposauridae (Hunt, 1993). Thus, all material that we do not discuss separately below is considered Metoposauridae indet.; without the morphology of the lacrimal we cannot provide any finer taxonomic evaluation.

cf. *Buettneria*

MNA V1508 is a set of three relatively large centra (Fig. 2A-F). These centra are discoidal and pertain to a non-*Apachesaurus* metoposaur, most probably *Buettneria* (Hunt, 1993).

Apachesaurus sp.

MNA V5575 is a pair of small, elongate centra (Fig. 2G-L). This elongation of the centra is characteristic of *Apachesaurus* (Hunt, 1993). Thus, these specimens can be confidently assigned to *Apachesaurus* sp.

LEPIDOSAURIA

SPHENODONTIA

SPHENODONTIDAE

Sphenodontidae indet.

An isolated partial dentary (MNA V7056), an incomplete premaxilla? (MNA V7057) and six jaw fragments (MNA V7058-7063) were identified by Kirby (1991) as belonging to sphenodontids. Kirby (1991) found all eight of these specimens generally similar to *Clevosaurus hudsoni*, and he referred to them as "*Glevosaurus* [sic]." Harris et al. (1999) included these specimens in a preliminary analysis of sphenodontian diversity in the Chinle Group, but did not discuss them in detail. All specimens exhibit acrodont tooth implantation, hence Kirby's (1991) interpretation of them as sphenodontian, but they are all fragmentary – few preserve more than one reasonably complete tooth, and none are obviously referable to a known genus.

KUHNEOSAURIDAE

Kuhneosauridae indet.

Kirby (1993, fig. 2) listed abundant kuhneosaurid specimens from a single locality (MNA locality 360) in the Owl Rock Formation. However, specimens of this taxon are not discussed or noted in Kirby (1991)

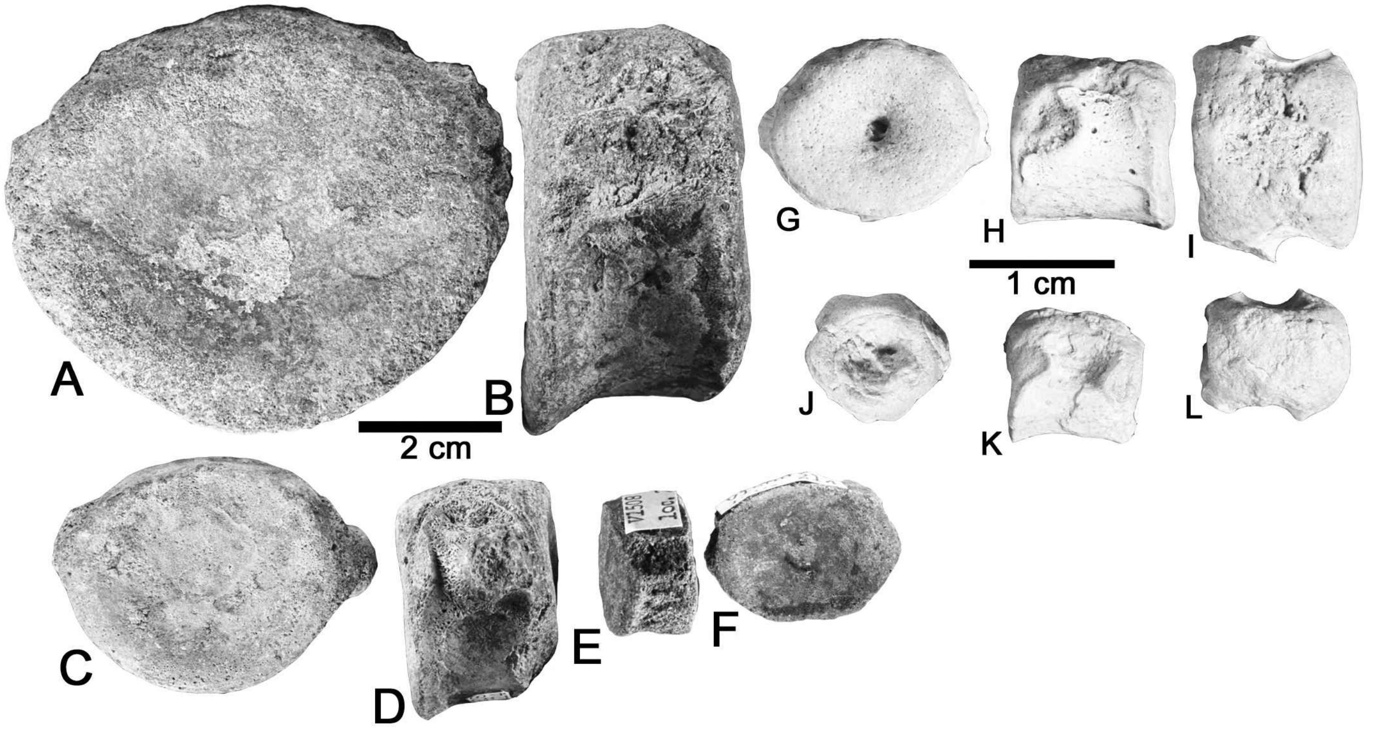

FIGURE 2. **A-F**, MNA V1508, *Buettneria* sp., centra in **A**, **C**, **F**, anterior and **B**, **D**, **E**, lateral views. **G-L**, MNA V5575, *Apachesaurus* sp., centra in **G**, **J**, anterior, **H**, **K**, lateral and **I**, **L**, dorsal views.

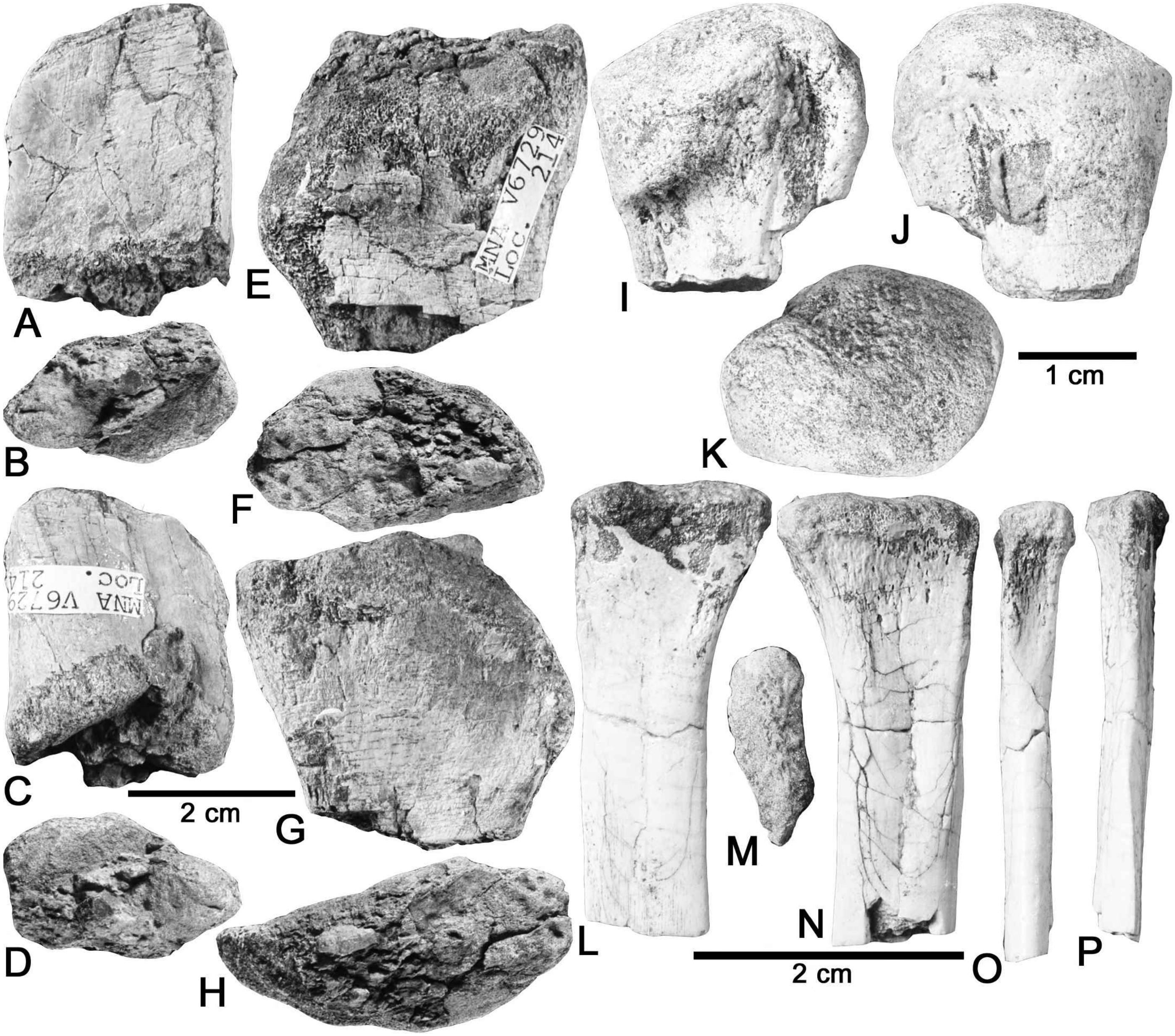

FIGURE 3. **A-D**, MNA V6729 (partim), Archosauromorph indet., bone fragment in **A**, anterior?, **B**, proximal?, **C**, posterior and **D**, distal views. **E-H**, MNA V6729 (partim), Archosauromorph indet., bone fragment in **E**, posterior?, **F**, proximal?, **G**, anterior and **H**, distal views. **I-K**, MNA 7240, Coelophysoidea indet., pathologic proximal right femur fragment in **I**, anterior, **J**, posterior and **K**, proximal views. **L-P**, MNA V7312, Archosauromorph indet., right? femur in **L**, anterior, **M**, proximal, **N**, posterior, **O**, medial and **P**, lateral views.

and were not found during our examination of the MNA collection. As such, there is no discussion, description or photographic documentation of these specimens. Thus, we include them for the sake of completeness but cannot corroborate Kirby's (1993) identification.

ARCHOSAUROMORPHA

Archosauromorpha indet.

Kirby (1993, fig. 2) listed, but did not discuss or illustrate, specimens that he referred to as Ornithischia? indet. from a single locality (MNA locality 853). Some of these were illustrated by Kirby (1991) in his master's thesis. Heckert (2001) described these teeth, noting that they have characteristics of both ornithischians and prosauropods, but are not definitively assignable to either taxon. Butler et al. (2006) demonstrated that at least some of the teeth described by Kirby (1991) are similar to a putative heterodontosaurid from the Upper Triassic of Switzerland that is not referable to Ornithischia and should instead be considered Archosauriformes *incertae sedis*.

During our examination of the MNA collection, we encountered a proximal limb fragment that was labeled as a femur of a Ornithischia? (Fig. 3L-P). This element is very rectangular in proximal view, with a ridge running down the posterior side of the shaft and a rectangular groove along the anterior side of the shaft. When comparing this supposed femur to femora of other basal ornithischians, we noted numerous differences, for example, the femoral head is not twisted as in ornithischians, the shaft is straight not bowed and there is no indication of a fourth trochanter (compare Fig. 3L-P with Norman et al., 2004, fig. 14.5a). Thus, we interpret this element as not pertaining to an ornithischian; and given its rectangular proximal end and straight shaft, we interpret the element as a fibula, not a femur. However, as a fibula it is rather non-descript, so we only identify it as an archosauromorph fibula.

Staurikosaurid? elements were reported, but not discussed, by Kirby (1993, fig. 2). While examining the MNA collection, we encountered two bone fragments, cataloged together, that were identified as Staurikosauridae? indet. (Fig. 3A-H). These appear to be limb elements, with one fragment (Fig. 3A-D) potentially being a distal tibia, given the offset of two surfaces on one end of the fragment (Fig. 3C). The other fragment appears to be a limb element given its elliptical cross-section, but cannot be interpreted further (Fig. 3E-H). Staurikosauridae (Colbert, 1970) is, of course, widely considered a junior subjective synonym of Herrerasauridae (Reig, 1963) (e.g., Langer, 2004). However, given Kirby's (1993) lack of justification for his interpretation and the poor quality of the specimens we assign them to Archosauromorpha indet.

RHYNCHOSAURIA

cf. Rhynchosauridae?

Kirby (1993) includes cf. Rhynchosauridae? in his faunal list of the Owl Rock, but did not discuss, describe or provide specimen numbers for this material. During on examination of the MNA collection, we were not able to identify any material assigned to cf. Rhynchosauridae?, thus, for the sake of completeness, we tentatively include this taxon in our revised faunal list, but cannot corroborate Kirby's (1993) identification of this material.

TRILOPHOSAURIDAE

"*Trilophosaurus*"

Kirby (1991) assigned an isolated incomplete tooth (MNA V7064), five posterior mandible fragments (MNA V7065-7069), two fragmentary quadrate condyles (MNA V7070-7071) and 82 quadrate condyles from bulk samples (MNA V7072-7074) to *Trilophosaurus* cf. *T. buettneri*. Heckert et al. (2006) and Spielmann et al. (2007) considered the isolated tooth to either belong to a procolophonid with similar tooth morphology (e.g., *Tricuspisaurus*) or to be screenwash contamination from previous workers, and thus an unsubstantiated record of *Trilophosaurus*. This interpretation is supported by the fact that this is the only record of *Trilophosaurus* from strata younger than mid-Revueltian and would also be the only Revueltian occurrence of *T. buettneri*, which has a current biostratigraphic range that extends from mid-Otischalkian to mid-Adamanian (Spielmann et al., 2007).

The other cranial material tentatively assigned to *Trilophosaurus* cf. *T. buettneri* includes undiagnostic fragments that, while sharing some features with *T. buettneri*, exhibit the following differences "[the lower jaw] possesses a comparatively deeper ventral border, more constricted cotylus, shallower adductor fossa, and less well-developed retroarticular process. The condyle likewise exhibits greater constriction, and a more attenuated attachment to the quadrate ramus" (Kirby, 1991, p. 246). The only feature that Kirby (1991) noted as a similarity between this material and *T. buettneri* is the quadrate condyle lacking a distinctive external pit. This does not provide a convincing argument to assign this material to *Trilophosaurus buettneri*, though, because there are more differences between this material and *T. buettneri* than similarities. Thus, there is no substantiated record of *Trilophosaurus buettneri* from the Owl Rock Formation. We refer the isolated tooth (MNA V7064) to Procolophonidae indet. and the mandible and quadrate fragments (MNA V7065-7069 and MNA 7070-7074, respectively) to Archosauromorpha indet.

ARCHOSAURIA

Archosauria indet.

MNA V5616 and V5617 are distal femora that Kirby (1991) identified as cf. *Postosuchus* sp. However, the U-shaped groove between the distal condyles indicates that these specimens pertain to either a theropod dinosaur or to a shuvosaurid archosaur, both of which have very similar distal femora. The lack of the crista tibiofibularis makes it difficult to assign these specimens to either group confidently, so we consider them Archosauria indet.

MNA V6731 is a series of three incomplete sacral centra that Kirby (1991) assigned to cf. *Postosuchus* sp. (Fig. 4A-B). Two of the three centra are fused, but, because of their poor preservation, that is all that can be distinguished about them. Three or more fused centra are found in rauisuchians (e.g., *Postosuchus*) and theropod dinosaurs (e.g., *Coelophysis*). With no additional characteristics to distinguish these specimens we refer them to Archosauria indet.

SUCHIA

cf. *Postosuchus* sp.

An extensive list of incomplete cranial and postcranial elements was given by Kirby (1991) as pertaining to cf. *Postosuchus* sp., including numerous elements that can now be assigned to various other related taxa given improvements in rauisuchian taxonomy since Kirby's evaluation (Long and Murry, 1995; Nesbitt and Norell, 2005; Lucas et al., 2007). Any specimens assigned by Kirby (1991) to this taxon that are not discussed elsewhere we still identify as cf. *Postosuchus* sp.

Postosuchus sp.

One specimen, a proximal left tibia fragment (MNA V5604), assigned to cf. *Postosuchus* sp. by Kirby (1991), is identical to the proximal tibia of *Postosuchus kirkpatricki* (Fig. 4U-Y). The proximal articulation of MNA V5604 has a triangular posterior half and a rectangular anterior half, just as in *P. kirkpatricki* (compare Fig 4U with Chatterjee, 1985, fig. 18b). However, the morphology of the tibia is not diagnostic of *P. kirkpatricki*, as interpreted by Chatterjee (1985) or Long and Murry (1995). So, given the close similarity but non-diagnostic nature of this specimen, we tentatively assign it to *Postosuchus* sp.

cf. *Poposaurus* sp.

Kirby (1991) identified a distal tibia (MNA V5605) as belonging to cf. *Postosuchus* sp. (Fig. 4R-T), but this specimen clearly demonstrates a posterior distal condyle that is well below the level of the anterior distal condyle. This feature is present in *Postosuchus*, *Poposaurus* and *Shuvosaurus*, but it is more prominent in *Poposaurus,* as in MNA V5605, so we identify this specimen as cf. *Poposaurus* sp.

SHUVOSAURIDAE

Shuvosauridae indet.

We note that there is no diagnosis of Shuvosauridae that currently encompasses all the specimens assigned to this family, so we use it provisionally to refer to the family of suchian reptiles that include *Shuvosaurus* (=*Effigia*) and *Sillosuchus* (Group X of Nesbitt, 2007). In addition, we follow Lucas et al. (2007) in considering *Shuvosaurus* to be the senior subjective synonym of *Effigia* and recognize that the genus *Shuvosaurus* has two species, *S. inexpectatus* and *S. okeeffeae*.

Two proximal tibia fragments (MNA V5602 and MNA V5603) that Kirby (1991) originally identified as cf. *Postosuchus* sp. are interpreted here as being the proximal tibiae of a shuvosaurid (Fig. 4L-N, Z-DD). The tibiae are subtriangular in proximal view with a proximal groove that overhangs the posterior margin. Overall, the specimens bear a resemblance to *S. okeeffeae* (compare Fig. 4L-N, Z-DD to Nesbitt, 2007, fig. 45), but because the MNA specimens are not identical to *S. okeeffeae*, the Owl Rock specimen having a more D-shaped proximal end and lacking a prominent ridge on its lateral surface, thus, we refer this maerial to Shuvosauridae indet. Indeed, Nesbitt (2007, p. 80) listed shuvosaurid (his Group X) specimens, including tibiae, from the same locality as MNA V5602 and V5603, but he did not provide specimen numbers or additional information.

MNA V5615 is a nearly complete right femur in two fragments (Fig. 4F-K). Kirby (1991) initially identified this specimen as cf. *Postosuchus* sp. However, based on the fibular groove opening at a nearly 90° angle and presence of a fibular condyle that is subangular, we assign this specimen to Shuvosauridae indet. (following Parker and Irmis, 2005).

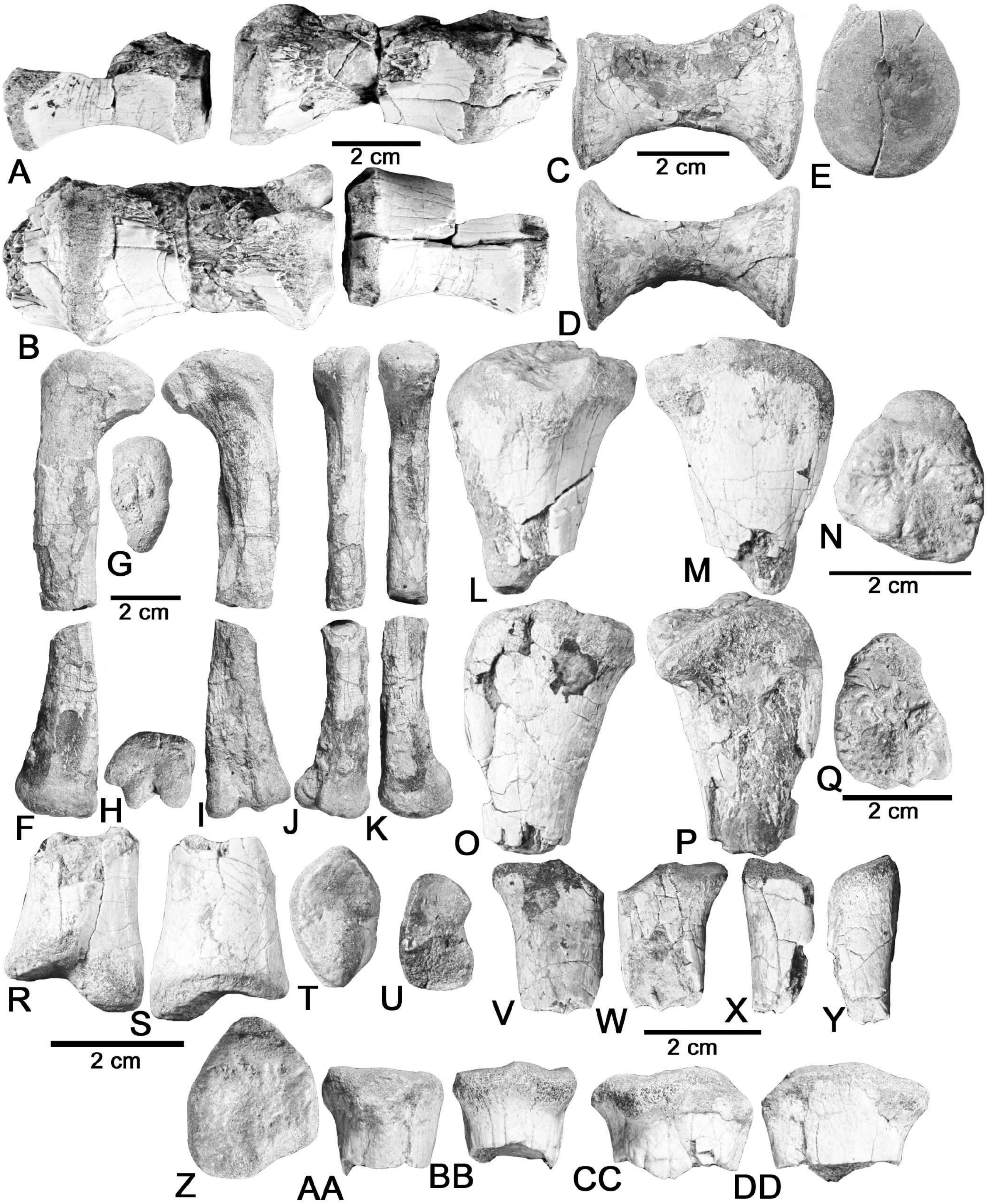

FIGURE 4. **A-B**, MNA V6731, Archosauria indet., three incomplete sacral centra in **A**, lateral and **B**, ventral views. **C-E**, MNA V4763, Parasuchidae indet., anterior caudal centrum in **C**, right lateral, **D**, ventral and **E**, anterior views. **F-K**, MNA V5615, Shuvosauridae indet., nearly complete right femur in two fragments in **F**, anterior, **G**, proximal, **H**, distal, **I**, posterior, **J**, lateral and **K**, medial views. **L-N**, MNA V5602, Shuvosauridae indet., proximal right tibia fragment in **L**, anterior?, **M**, posterior? and **N**, proximal views. **O-Q**, MNA V5601, Archosauromorpha indet., proximal left? tibia fragment in **O**, anterior?, **P**, posterior? and **Q**, proximal views. **R-T**, MNA V5605, cf. *Poposaurus* sp., distal left tibia in **R**, posterior, **S**, anterior and **T**, distal views. **U-Y**, MNA V5604, *Postosuchus* sp., proximal left tibia fragment in **U**, proximal, **V**, medial, **W**, lateral, **X**, anterior and **Y**, posterior views. **Z-DD**, MNA 5603, Shuvosaurid?, proximal left tibia fragment in **Z**, proximal, **AA**, medial?, **BB**, lateral?, **CC**, anterior? and **DD**, posterior? views.

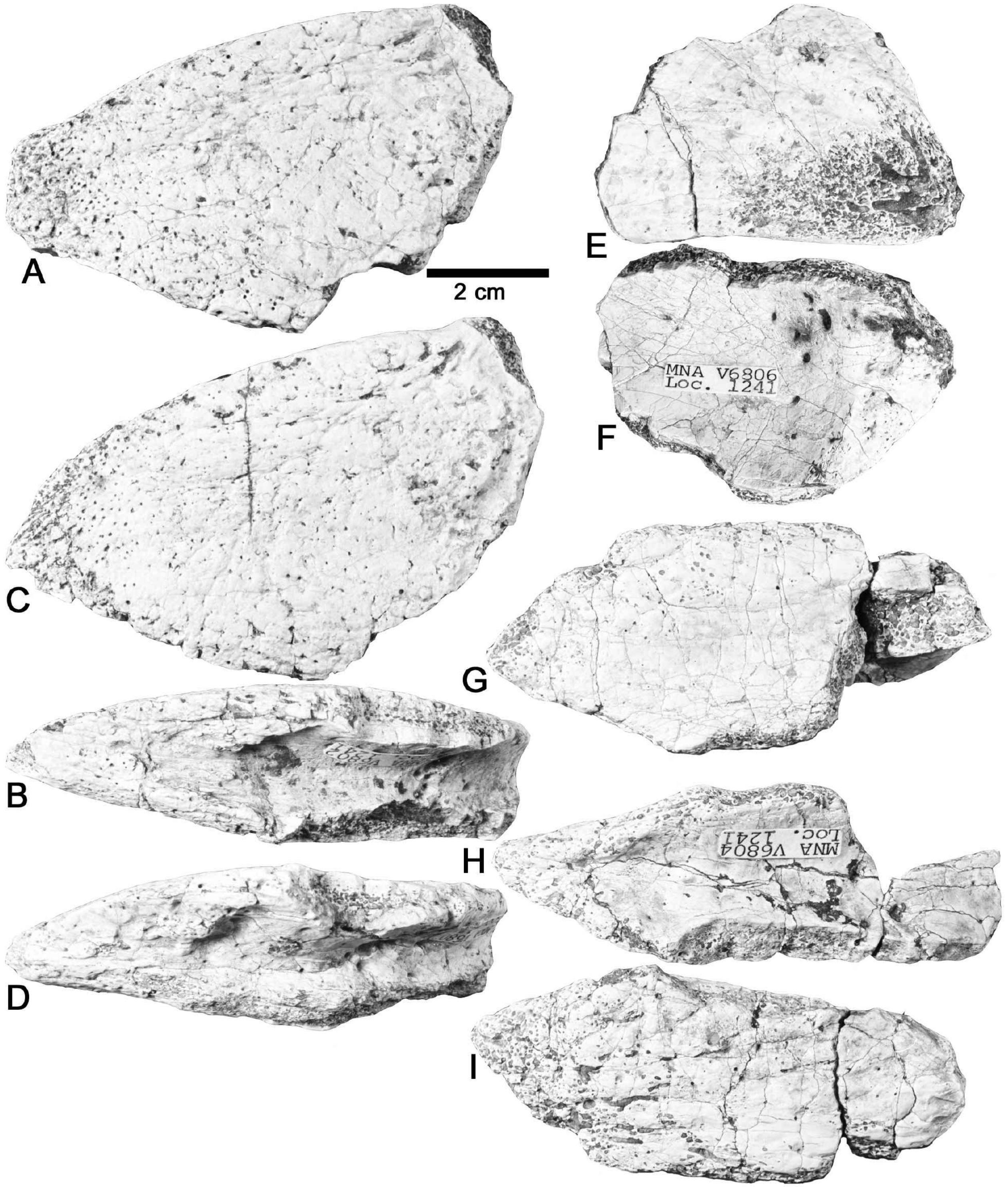

FIGURE 5. **A**-**D**, MNA V6802, *Typothorax coccinarum*, pair of left lateral osteoderms in **A**, **C**, dorsal and **B**, **D**, posterior views. **E**-**F**, MNA V6806, *Typothorax coccinarum*, right lateral osteoderm in **E**, dorsal and **F**, posterior views. **G**-**I**, MNA V6804, *Typothorax coccinarum*, left lateral osteoderm in **G**, dorsal, **H**, posterior and **I**, ventral views.

STAGONOLEPIDIDAE

Typothorax coccinarum

Kirby (1991) assigned numerous osteoderms, a thoracic rib, an incomplete centrum and an incomplete astragalus to the aetosaur *Typothorax coccinarum* based on the osteoderm morphology. Given the slightly arched nature of the paramedian osteoderms and their random, densely pitted ornamentation with prominent transverse ventral keels, along with the dorsoventrally compressed lateral osteoderms (Fig. 5) that are acutely folded into a laterally directed point, we concur. These specimens clearly pertain to *T. coccinarum* and not to *T. antiquum* (Lucas et al., 2002) or to any of the known species of *Redondasuchus* (Hunt and Lucas, 1991; Heckert et al., 1996; Spielmann et al., 2006). These specimens are important in that they corroborate a Revueltian age for the Owl Rock Formation, as first indicated by Lucas (1993; Lucas and Hunt, 1993).

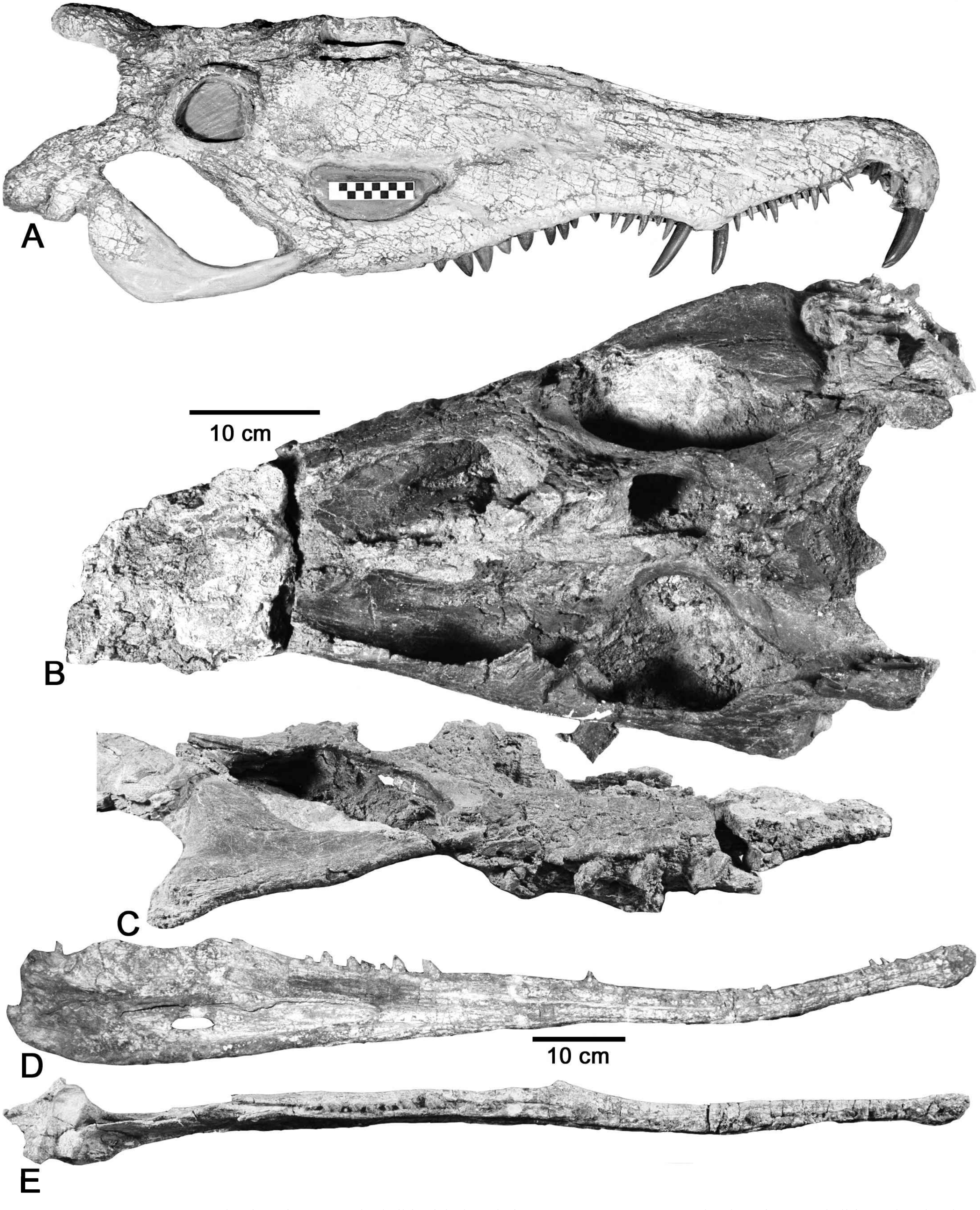

FIGURE 6. **A**, MNA V3478, *Pseudopalatus buceros*, male skull in right lateral view. **B**-**C**, MNA V3478, *Pseudopalatus buceros*, skull in **B**, dorsal and **C**, right lateral views. **D**-**E**, MNA number unknown (on display), *Pseudopalatus buceros*, left lower jaw in **D**, medial and **E**, occlusal views.

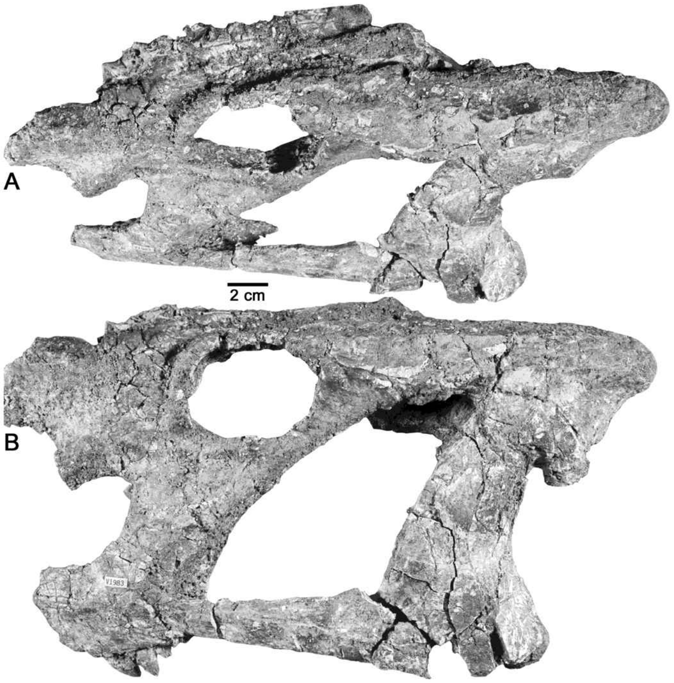

FIGURE 7. **A-B**, MNA V1983, *Pseudopalatus buceros*, posterior skull in **A**, dorsal and **B**, left lateral views.

PARASUCHIDAE

Parasuchidae indet.

Kirby (1991) identified MNA V4763 as a vertebra of cf. *Postosuchus* sp. However, the vertebra is extremely waisted, giving it an hourglass-shape in ventral view, and it lacks the prominent ventral lips on the anterior and posterior articular surfaces of the centra that are seen in *Postosuchus* (compare Fig. 4C-E to Long and Murry, 1995, fig. 130). This morphology more closely resembles an anterior caudal vertebra of a phytosaur than it does *Postosuchus*, so we assign this specimen to Parasuchidae indet.

Pseudopalatus buceros

As noted by Kirby (1991, p. 291), phytosaurs are the "dominant component of [the] Ward Terrace vertebrate [fauna]... at all localities." All of the phytosaur fossils were assigned to either *Pseudopalatus pristinus*, *Pseudopalatus* cf. *P. buceros* or cf. *Pseudopalatus*? sp. by Kirby (1991). We reassign all the phytosaur material from the Ward Terrace localities that is identifiable to the specific level to *Pseudopalatus buceros*. In addition, Kirby (1991) found evidence for five individuals based on cranial material; we revise this assessment, counting at least six individuals from the Ward Terrace sample.

Kirby (1991) identified most of the phytosaur cranial material he examined as *P. pristinus*, with the exception of a complete skull with a rostral crest (MNA V3478) that he identified as *Pseudopalatus* cf. *P. buceros*. Providing no detailed diagnosis for either *P. buceros* or *P. pristinus*, Kirby (1991) simply assigned phytosaur skulls lacking a rostral crest to *P. pristinus* and the one skull possessing a rostral crest (MNA V3478) to *Pseudopalatus* cf. *P. buceros*. The unassociated phytosaur postcrania were assigned to cf. *Pseudopalatus*? sp.

Curiously, a few of the specimens that Kirby (1991) assigned to *P. pristinus* do not have the rostral portion of their skull preserved. For example, MNA V3478, which is not included in Kirby's (1991) list of referred specimens, is a large, incomplete phytosaur skull preserving much of the skull posterior to the anterior margin of the antorbital fenestra (Fig. 6B-C). Unfortunately, the rostral portion of the skull anterior to the antorbital fenestrae is not preserved. This is also the case with MNA V1983, listed as *P. pristinus* in Kirby's (1991) referred specimens; it is the left posterior portion of a skull, and nothing anterior to the nares is preserved (Fig. 7). Again, in MNA V1595, a large fragment of the left posterior portion of the skull, nothing anterior to the orbit is preserved (Fig. 8B).

While a variety of diagnoses exist in the literature for *Pseudopalatus* (Ballew, 1989; Kirby, 1991; Long and Murry, 1995; Hungerbühler, 2002; Zeigler et al., 2002), the features that are generally agreed upon as diagnostic of the genus are: squamosal bars are usually prominently sculptured; supratemporal fenestra are short and narrow in dorsal view with narrow anterior margins; medial expansion of the squamosal bar narrows the transverse diameter of the supratemporal fenestrae; external nares are even with or raised above the level of skull roof; squamosal compressed with no rounded posterior process; supratemporal fenestra partially concealed in dorsal view; no fully crested rostrum; dentition weakly heterodont to homodont; and anterior end of snout is downturned with a constriction just posterior to the anterior margin. All the phytosaur skulls from the Owl Rock Formation clearly possess characteristics of *Pseudopalatus*.

Zeigler et al. (2002, 2003) posited sexual dimorphism in *Pseudopalatus* based on the prominent rostral crest of some specimens being a sexual display device. As explicitly stated by Zeigler et al. (2002, 2003) in their abstracts (though not in the text), the implication of their study is that *Pseudopalatus pristinus*, the "species" lacking the rostral crest, is the probable female morph, and *P. buceros*, possessing a prominent rostral crest, is the likely male morph. Thus, these two species should be synonymized into a single, sexually dimorphic species. Given that *P. buceros* (Cope, 1881) has priority over *P. pristinus* (Mehl, 1928), the result is that *P. pristinus* becomes a junior subjective synonym of *P. buceros*. Thus, all of the phytosaur material from the Owl Rock Formation is assigned to *P. buceros*, with one male skull (MNA V3478) (Fig. 6A), one female skull (MNA V3495) (Fig. 8C-F) and four skulls that are too incomplete to assign to either gender with confidence (MNA V1595, V1983, V3478, V3498) (Figs. 6B-C, 7, 8A-B). This follows figure captions for MNA V3478 and V3495 in Heckert et al. (2005), in which they also identify the skulls as male and female morphs, respectively, of *P. buceros*. The six skulls listed above are represented by distinct elements, most notably the posterior left portion of the skulls, so each represents a single individual. This differs from Kirby's (1991) assessment, which identified only five individuals based on cranial elements, although MNA 3478 is not listed in Kirby's referred specimens, so there is no evidence he saw or was aware of this specimen.

Kirby (1991) briefly described a collection of phytosaur postcrania from the Owl Rock Formation. Most of the specimens in this collection consist of various limb elements (Figs. 9C-F, 11), including paired femora (Fig. 11), as well as some lower jaws (Fig. 6D-E), girdle elements (Figs. 9A-B,10), vertebrae and dermal armor. Phytosaur taxonomy is based almost exclusively on cranial characters (Long and Murry, 1995; Hungerbühler, 2002), so isolated or associated postcrania are rarely assigned to a generic or specific level (but see Camp, 1930; Hunt, 1994). However, given that only *Pseudopalatus buceros* skulls were collected from the Owl Rock localities, we assign the postcrania to *Pseudopalatus buceros* based on their association with more diagnostic material. *Pseudopalatus buceros* is an index taxon of the Revueltian LVF, and is known from older Revueltian strata (e.g., Painted Desert Member of the Petrified Forest Formation) and cements a Revueltian age for the Owl Rock fauna.

SPHENOSUCHIA

Sphenosuchia indet.

Kirby (1991) illustrated and described vertebral centra and isolated teeth that he assigned to sphenosuchidae indet. During our examination of the MNA collection, we did not find, and thus could not examine these centra. However, based on the illustrations of Kirby (1991) these centra do appear waisted as are sphenosuchian centra. Thus, we

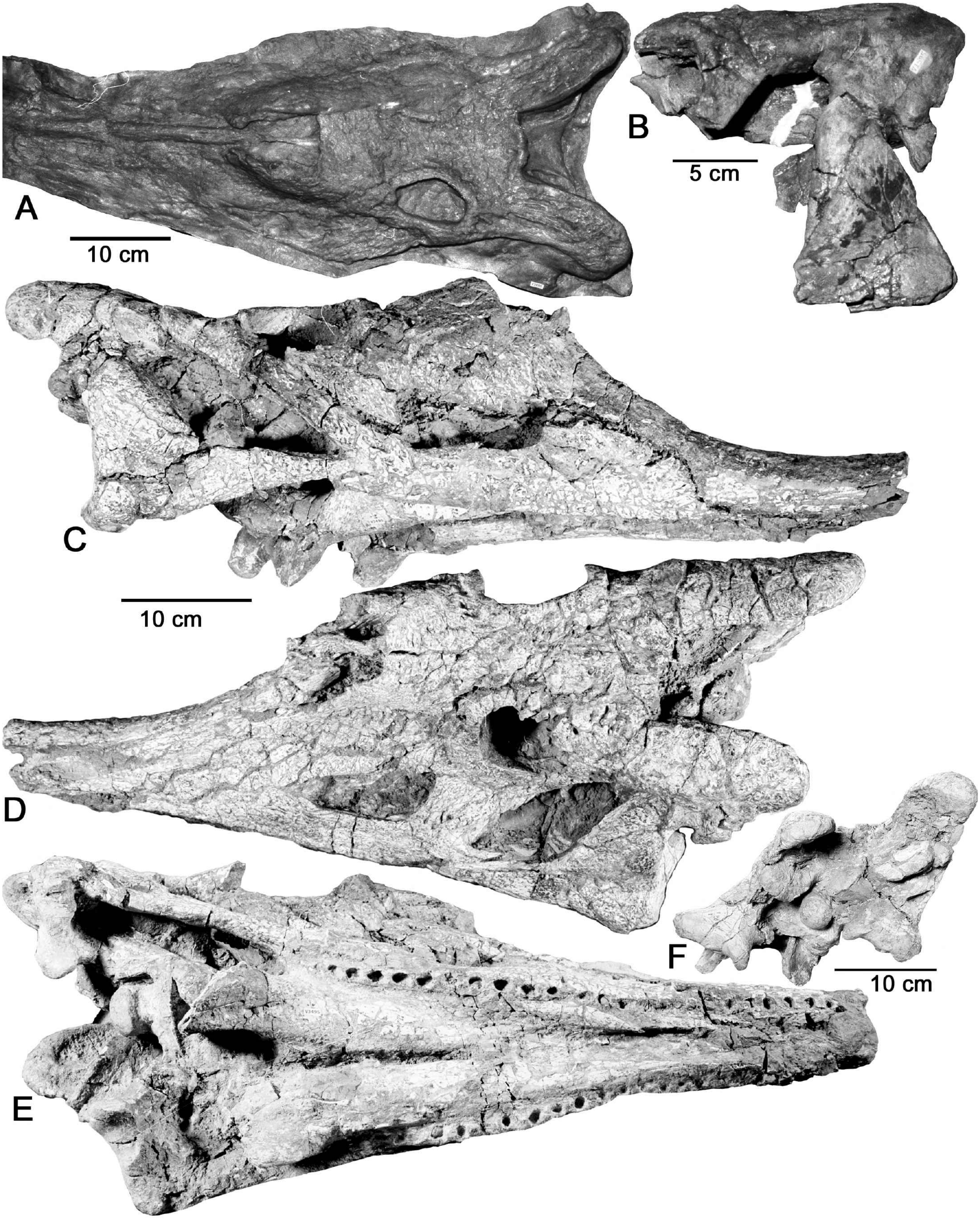

FIGURE 8. **A**, MNA V3498, *Pseudopalatus buceros*, cast of skull in dorsal view. **B**, MNA V1595, *Pseudopalatus buceros*, posterior part of skull in left lateral view. **C**-**E**, MNA V3495, *Pseudopalatus buceros*, female skull in **C**, right lateral, **D**, dorsolateral, **E**, ventral and **F**, posterior views.

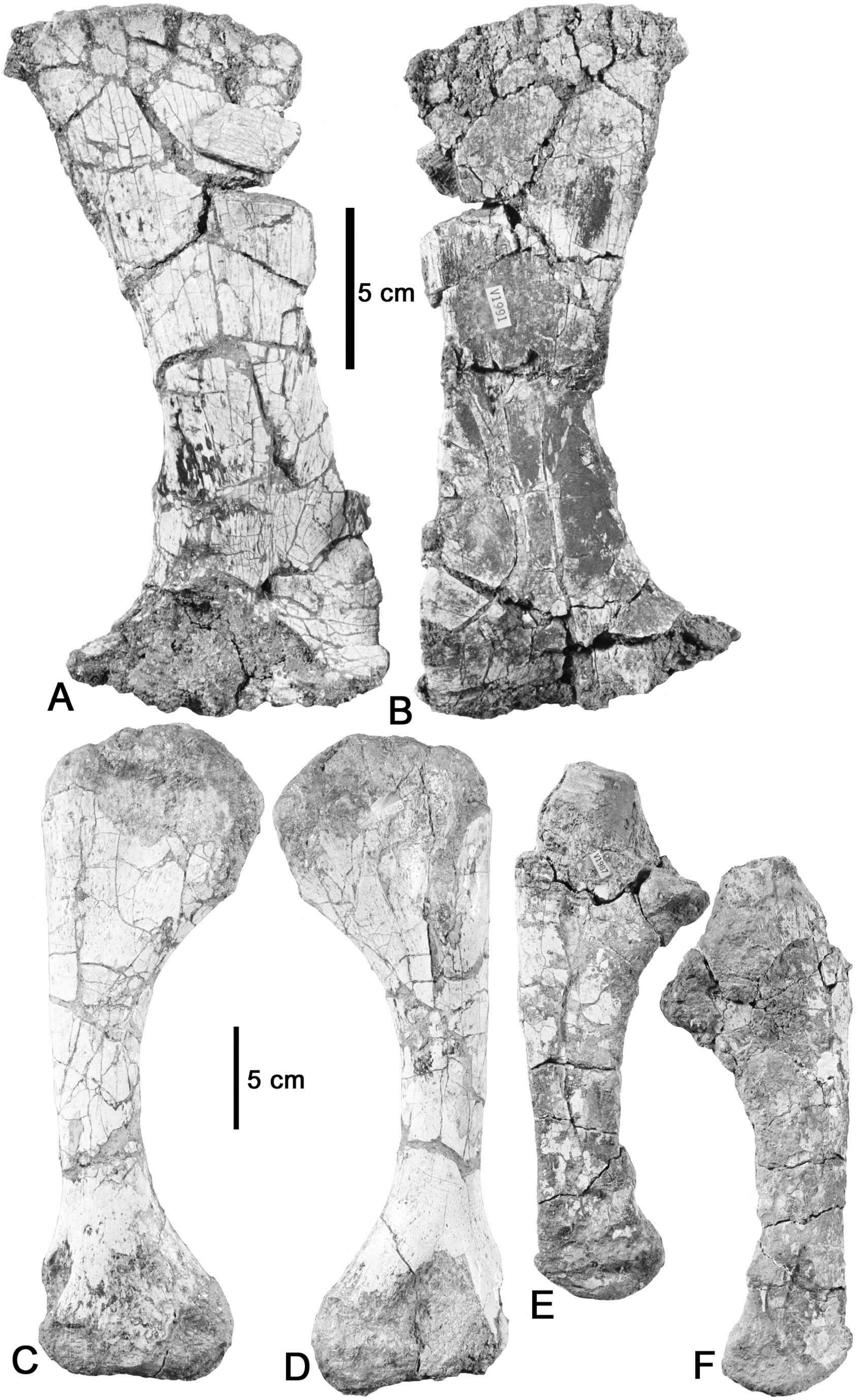

FIGURE 9. **A-B**, MNA V1991, *Pseudopalatus buceros*, right scapula in **A**, lateral and **B**, medial views. **C-D**, MNA V1596, *Pseudopalatus buceros*, left humerus in **C**, anterior and **D**, posterior views. **E-F**, MNA V1987, *Pseudopalatus buceros*, right ulna in **E**, anterior and **F**, posterior views.

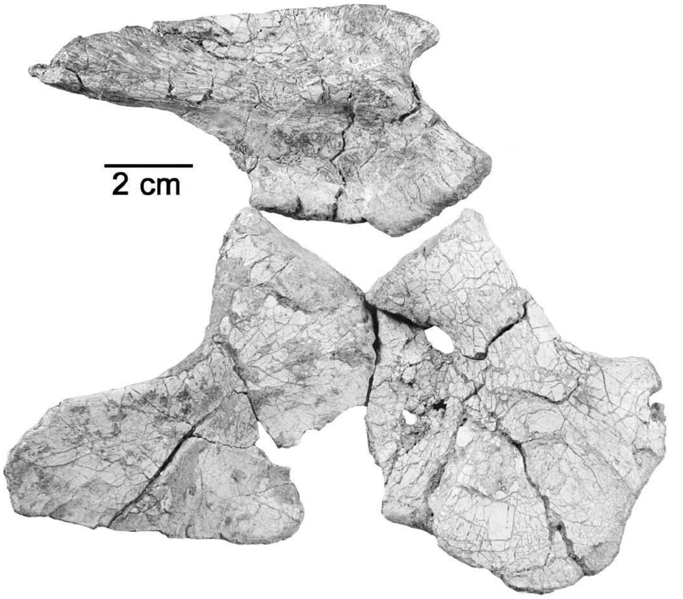

FIGURE 10. Reconstructed right pelvis of *Pseudopalatus buceros*, consisting of MNA V7903, right pubis, MNA V7904, right ischium and MNA V1602, right ilium.

consider this record legitimate. The teeth Kirby (1991) assigned as sphenosuchid are mediolaterally compressed and recurved, but this is a common feature of basal theropods, as well as suchian reptiles, thus these teeth should be considered Archosauromorpha indet.

DINOSAURIA

THEROPODA

Coelophysoidea indet.

A single proximal right femur (MNA V7240) in the MNA collection was labeled as *Coelophysis* sp. (Fig. 3I-K). This specimen is discussed by Kirby (1991) as Ceratosauria?, and Kirby (1993) records putative theropod specimens from the Owl Rock Formation. The femur has a "hooked" femoral head and a prominent trochanteric shelf, characteristic of the Coeolophysoidea. However, the specimen also appears pathologic, given the fine, pustulose bone texture on the trochanteric shelf that is not seen in other coelophysoid specimens and obscures the fine morphology of this feature. Thus, given our inability to further discern this specimen's morphology we assign it to Coelophysoidea indet.

DISCUSSION

Our revision of the Owl Rock tetrapod fauna from the Ward Terrace area provides an update to the previous interpretations of Kirby. As summarized in Table 1, several taxa have been split into additional taxa, some of which were not previously recognized from the Owl Rock Formation, while a few have been collapsed congruent with current taxonomic thinking and nomenclature (e.g., *Pseudopalatus*). The revised Owl Rock faunal list confirms the Revueltian age of the assemblage advocated previously (e.g., Heckert et al., 2005). Thus, the presence of *Pseudopalatus* and *Typothorax coccinarum*, two index taxa of the Revueltian LVF, justify recognition of the Owl Rock tetrapod assemblage as the stratigraphically highest, and thus youngest, Revueltian assemblage in Arizona. Given that the Owl Rock Formation clearly overlies the Black Forest Bed in Petrified Forest National Park (e.g., Heckert and Lucas, 2002) and that the Black Forest Bed has been dated as less than 214 Ma (perhaps as young as 211 Ma) (Riggs et al., 2003), this indicates that the Revueltian extended from well before 214 Ma until well after 210 Ma, because Owl Rock deposition clearly took place over several million years (Tanner, 2000; Tanner and Lucas, 2007).

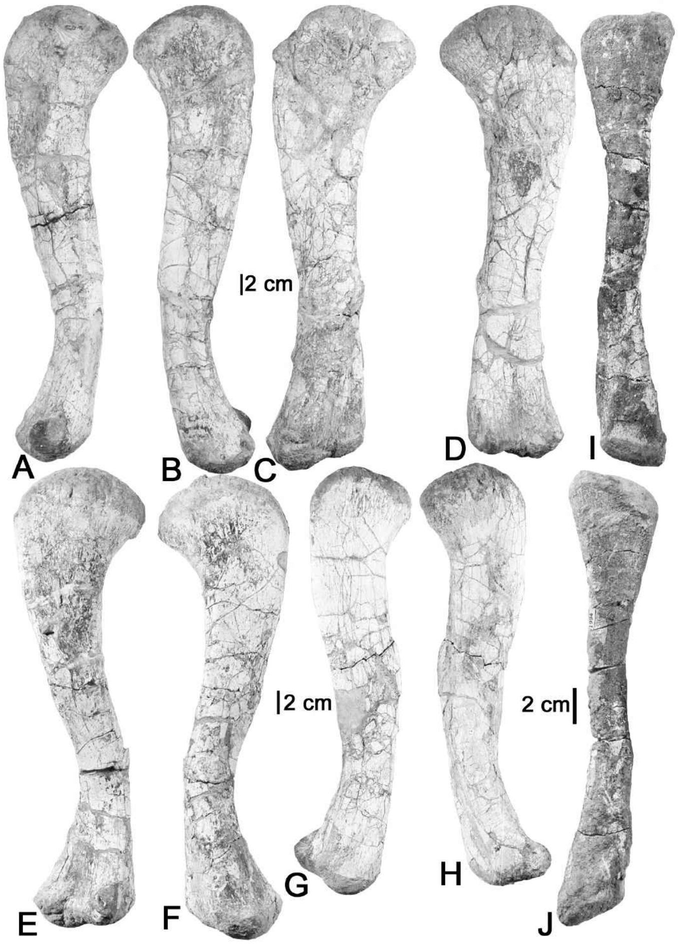

FIGURE 11. **A-B**, MNA V1598, *Pseudopalatus buceros*, left femur in **A**, posterior and **B**, anterior views. **C-D**, MNA 1597, *Pseudopalatus buceros*, right femur in **C**, anterior and **D**, posterior views. **E-F**, MNA V1600, *Pseudopalatus buceros*, left femur in **E**, posterior and **F**, anterior views. **G-H**, MNA 1599, *Pseudopalatus buceros*, left femur in **G**, anterior and **H**, posterior views. **I-J**, MNA V1994, *Pseudopalatus buceros*, left? fibula in **I**, medial and **J**, lateral views.

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TABLE 1. Comparison of the Owl Rock fauna as reported by Kirby (1993) and the revised faunal list advocated here, with principal taxonomic changes noted.

Faunal list of Kirby (1993)	**Principal taxonomic changes**	**Revised faunal list**
Amphibia		**Amphibia**
Metoposauridae		Metoposauridae
cf. *Metoposaurus* sp. A cf. *Metoposaurus* sp. B	cf. *Metoposaurus* sp. A cf. *Metoposaurus* sp. B — Metoposauridae indet. cf. *Buettneria* *Apachesaurus* sp.	Metoposauridae indet. cf. *Buettneria* *Apachesaurus* sp.
Reptilia		**Reptilia**
Procolophonidae		Procolophonidae indet.
Kuhneosauridae		Kuhneosauridae indet.
Sphenodontidae		Sphenodontidae indet.
Trilophosauridae *Trilophosaurus* cf. *buettneri*	*Trilophosaurus* cf. *buettneri* — Procolophonidae indet. Archosauromorpha indet.	
cf. Rhynchosauridae?		cf. Rhynchosauridae?
Poposauridae? cf. *Postosuchus* sp. cf. *Chatterjeea* sp.	cf. *Postosuchus* sp. — cf. *Postosuchus* sp. *Postosuchus* sp. cf. *Poposaurus* sp. Shuvosauridae indet. Parasuchidae indet.	Suchians cf. *Postosuchus* sp. *Postosuchus* sp. cf. *Poposaurus* sp. Shuvosauridae indet.
Stagonolepididae *Typothorax coccinarum*		Stagonolepididae *Typothorax coccinarum*
Phytosauridae		Phytosauridae
Pseudopalatus pristinus *Pseudopalatus* cf. *mccauleyi* cf. *Pseudopalatus*? sp.	*Pseudopalatus pristinus* *Pseudopalatus* cf. *mccauleyi* — *Pseudopalatus buceros* cf. *Pseudopalatus*? sp.	*Pseudopalatus buceros*
Sphenosuchidae?		Sphenosuchidae?
cf. Staurikosauridae?	cf. Staurikosauridae? — Archosauromorpha indet.	
Theropoda	Theropoda — Coelophysoidea indet.	Coelophysoidea indet.
cf. Ornithischia?	cf. Ornithischia? — Archosauromorpha indet.	

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Lucas, S.G. and Spielmann, J.A., eds., 2007, The Global Triassic. New Mexico Museum of Natural History and Science Bulletin 41.

OLDEST RECORDS OF THE LATE TRIASSSIC THEROPOD DINOSAUR *COELOPHYSIS BAURI*

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Abstract— *Coelophysis bauri* is a well-known theropod dinosaur from the Upper Triassic of the southwestern United States. Prior to this study, it was only known from extensive remains from the Whitaker quarry, in the Rock Point Formation, of north-central New Mexico. Here, we document fossils of *C. bauri* from the Upper Triassic Snyder quarry, north-central New Mexico and from the Petrified Forest National Park. Both of these new records are from the Painted Desert Member of the Petrified Forest Formation, stratigraphically below the Rock Point Formation. This extends the biostratigraphic range of *C. bauri* to the early Revueltian (early-middle Norian) through the Apachean (late Norian-?Rhaetian). Thus, *C. bauri* is no longer an index taxon of the Apachean land-vertebrate faunachron.

INTRODUCTION

Coelophysis bauri, one of the best-known Late Triassic dinosaurs, has been known from a single locality, the Whitaker quarry at Ghost Ranch, New Mexico (e.g., Colbert, 1989) (Fig. 1). Here, we describe and photographically illustrate specimens referable to *C. bauri* from the Upper Triassic (Revueltian) Snyder quarry, north-central New Mexico, compare these specimens with another *C. bauri* fossil described from broadly correlative strata in the Petrified Forest National Park of Arizona (Padian, 1986) and summarize the biostratigraphic range of *C. bauri* based on these additional specimens. In this paper, NMMNH = New Mexico Museum of Natural History and Science, Albuquerque and UCMP = University of California Museum of Paleontology, Berkeley.

PREVIOUS STUDIES

Coelophysis bauri is one of the best, if not the best, known Triassic dinosaurs and has been the subject of numerous publications for more than 100 years. In this section we highlight key works that are relevant to our discussion. These include the initial naming of *Coelophysis bauri*, the publication of the Ghost Ranch specimens, the *Rioarribasaurus* vs. *Coelophysis* controversy and the taxonomic relationship of *C. bauri* to *Megapnosaurus* (=“*Syntarsus*”).

In 1881, David Baldwin, while collecting for Edward Drinker Cope, discovered small theropod dinosaur fossils at three localities in the Upper Triassic strata of northern New Mexico; one locality was noted as “Gallina Canyon” and the other two localities as “Arroyo Seco.” After studying these specimens, Cope published two papers on the material. The first (Cope, 1887a) described two new species that Cope assigned to Marsh’s genus *Coelurus*. *C. longicollis*, the larger of the two, was named based on one vertebra from each of the cervical, dorsal and caudal series, plus a femur. The other species, *C. bauri*, was based on a cervical vertebra, a sacrum and a distal femur. The second paper (Cope, 1887b) was a review of North American Triassic vertebrates, in which Cope revised his interpretation of the *C. longicollis* and *C. bauri* material as distinct taxa, instead referring it to the European genus *Tanystropheus* (then perceived as a dinosaur, not a protorosaur). In this same publication, Cope named a third species, *T. willistoni*, that was smaller than the other two. This species was named based on an incomplete acetabular border and a single dorsal centrum. Neither of the two Cope publications included illustrations or locality information, nor were specimen numbers or types designated. In 1889, Cope removed *T. longicollis*, *T. bauri* and *T. willistoni* from the genus *Tanystropheus*, based on the morphology of the neural canals of the centra, and gave these three species the new generic name *Coelophysis* (Cope, 1889).

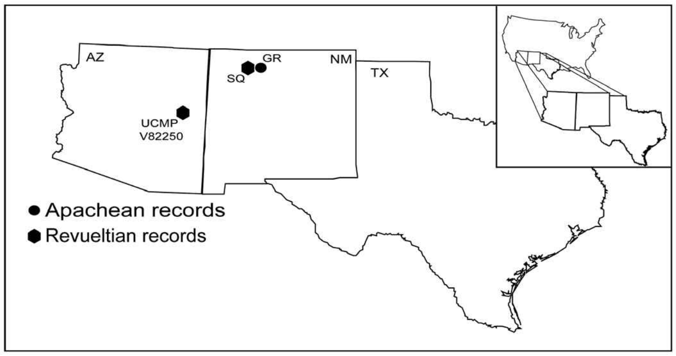

FIGURE 1. Index map showing the distribution of *Coelophysis* fossil localities in Arizona, New Mexico and Texas. Biostratigraphic subdivision after Lucas (1998). Abbreviations: GR – Ghost Ranch and SQ – Snyder quarry.

Later work by Huene (1915) recognized the three species of *Coelophysis*, primarily by size differences, and while he illustrated the material for the first time, he, like Cope, neither provided specimen numbers nor designated any types. It fell to Hay (1930) to designate *Coelophysis bauri* as the type species of *Coelophysis*; *C. bauri* was selected because the other two species were judged to be undiagnostic. The other species were synonymized with *C. bauri* by Colbert (1947).

Colbert (1947) initially described a massive bonebed of complete articulated and disarticulated skeletons of a small theropod from Ghost Ranch, Rio Arriba County, New Mexico. This quarry became known by a variety of names, including the Ghost Ranch quarry, the *Coelophysis* quarry and the Whitaker quarry (after the initial discoverer of the site). Colbert (1947) referred to the theropods from that quarry as *Coelophysis*, but provided no justification for his assignment. Colbert (1964) rediagnosed *Coelophysis bauri* based on the Ghost Ranch material, followed later by a complete osteology (Colbert, 1989). Subsequently, he (Colbert, 1990) described variation in *C. bauri*, again based solely on the Ghost Ranch sample.

In his monographic description of the large, Early Jurassic coelophysoid *Dilophosaurus*, Welles (1984) designated lectotypes for *Coelophysis bauri* and *C. longicollis*, and provided *Longosaurus* as a new generic name for *C. longicollis*, thus creating the binomial *Longosaurus longicollis*. Colbert (1989) also designated a lectotype for *C. bauri*, apparently unaware of the lectotype designation in Welles’

(1984) previous work.

Padian (1986) was the first to point out discrepancies between Cope's holotype material of *Coelophysis* and the Ghost Ranch theropod. Specifically, Padian (1986) noted that of the 24 characters used by Colbert (1964) to diagnosis *Coelophysis bauri*, only eight can be assessed in Cope's syntypes. Hunt and Lucas (1991) expanded upon this line of reasoning by noting that the lectotypes of *C. bauri* and *Longosaurus longicollis* designated by Welles (1984) were ineligible to become lectotypes because the designated material was not part of the original syntypes. Thus, Hunt and Lucas (1991) affirmed the validity of the lectotype for *C. bauri* that Colbert (1989) had proposed. In addition, they designated a lectotype for *C. willistoni*, the only remaining of Cope's species for which a lectotype had not yet been designated. Summarily, Hunt and Lucas (1991) pointed out that none of the lectotypes of Cope's initial three species of *Coelophysis* were in any way diagnostic below the level of Theropoda indet. and that "[n]one of the Whitaker quarry material should ever have been assigned to *Coelophysis*" (p. 195). Thus, they proposed a new generic and specific name for the Whitaker quarry material, *Rioarribasaurus colberti*. In addition, they noted (p. 195) that an attempt to "petition the International Commission on Zoological Nomenclature to conserve the name *Coelophysis bauri*, by designating a neotype, would be met with rejection, simply because the type material of the taxon is extant."

Even though Hunt and Lucas (1991) provided a "by-the-book" argument, frequently citing the International Code of Zoological Nomenclature, which was supplemented by support from Sullivan (1993, 1994, 1995) and Huber (1994), a petition for the designation of a neotype of *Coelophysis bauri* from the Ghost Ranch material was submitted to the International Commission on Zoological Nomenclature (ICZN) by Colbert et al. (1992). They disputed the claim of Hunt and Lucas (1991) that the stratigraphic level of the Ghost Ranch quarry was demonstrably different than the level that yielded the holotype material of *C. bauri*; they also noted that individual bones of the Ghost Ranch material are identical to those of the holotype of *C. bauri* and that the name *Coelophysis bauri* is well entrenched in the literature, both technical and popular, and in the public consciousness. Sullivan et al. (1996) addressed these observations, demonstrating that the Ghost Ranch sample comes from a distinct horizon, with dramatically different preservation than the original material collected by Baldwin. The resultant decision of the ICZN (1996) was to designate a neotype of *C. bauri* from the Ghost Ranch material – this was accomplished by making the holotype of *R. colberti* the neotype of *C. bauri* – rendering *Rioarribasaurus colberti* a junior objective synonym of *Coelophysis bauri*.

Raath (1969) named and described "*Syntarsus*" (=*Megapnosaurus*) *rhodesiensis* based on an incomplete articulated skeleton, lacking the skull and cervical vertebrae, from the Early Jurassic Forest Sandstone Formation near Bulawayo, Zimbabwe (then Rhodesia). Raath (1969) compared "*S.*" *rhodesiensis* to *Coelophysis bauri* and was struck by the similarity between the two taxa. However, he did note a handful of minor differences, mostly confined to the hip and tarsus. Additional work by Raath (1977) provided further description of numerous "*S.*" *rhodesiensis* specimens, and allowed for a better comparison between "*S.*" *rhodesiensis* and *C. bauri*. Raath (1977, table 19) noted further differences between the skulls and forelimbs of the two taxa (reiterated by Colbert [1989]); he subsequently detailed the variation present in the African specimens (Raath, 1990).

In addition, Rowe (1989) and Tykoski (1998) described a new species of "*Syntarsus*," "*S.*" *kayentakatae*, from the Early Jurassic Kayenta Formation of Arizona. Over the years the close taxonomic association between "*Syntarsus*" and *Coelophysis* has only grown closer with numerous differences between the taxa being resolved as more specimens are examined. Paul (1988, 1993) was the first to suggest that "*S.*" *rhodesiensis* and *C. bauri* be placed in the same genus. Downs (2000) further reiterated the synonymy of the two genera based on his analysis of the Ghost Ranch material. Ivie et al. (2001) pointed out that the generic name *Syntarsus* was preoccupied by a beetle and proposed the generic name *Megapnosaurus* ("big dead lizard") for the theropod. Bristowe and Raath (2004) recently placed both species of *"Syntarsus"* in the genus *Coelophysis*, although they remain listed separately in Tykoski and Rowe (2004). Smith and Merrill (2006) found significant morphometric variation between *Coelophysis* and "*Syntarsus*," and argued that the two genera should not be synonymized. In addition, they noted variation within the Whitaker quarry sample, which they interpreted as a result of sexual dimorphism. This assertion thus counters the claim by Smith (1997) that the variation within the Whitaker sample could have systematic significance. The one generally agreed on feature between Bristow and Raath (2004) and Smith and Merrill (2006) is that *Coelophysis bauri* is more closely related to "*S.*" *rhodesiensis* then either is to "*S.*" *kayentakatae*. Thus, *Coelophysis* currently contains two species, *C. bauri* (the type species) and *C. rhodesiensis*; and *Megapnosaurus* (= "*Syntarsus*") *kayentakatae* is a closely related taxon (Tykoski, 2005; Ezcurra, 2006; Ezcurra and Novas, 2006).

Hunt et al. (1998) named a fragmentary coelophysid *Camposaurus arizonensis* (originally described by Lucas et al. [1992]), for ceratosaurian postcrania from the *Placerias* quarry in the Bluewater Creek Formation of east-central Arizona. Some workers (e.g., Long and Murry, 1995; Irmis, 2005) consider this material indistinguishable from *Coelophysis*, whereas others recognize it as a valid, distinct taxon (Tykoski and Rowe, 2004; Heckert et al., 2005), a position we follow here.

Sullivan and Lucas (1999) built upon Sullivan et al. (1996) and described a new theropod, *Eucoelophysis baldwini*, from exposures of the Painted Desert Member of the Petrified Forest Formation in the vicinity of Orphan Mesa. They also referred one of the specimens (a proximal pubis) originally collected by Baldwin to this taxon. Subsequently, Heckert et al. (2000, 2003) referred abundant theropod material from the Snyder quarry, at the same stratigraphic horizon some distance (~2 mi) to the west, to *Eucoelophysis* sp. based on the similar morphology of the tibia and fibula, but refrained from referring them to *E. baldwini*, largely because of differences in the femur. Ezcurra (2006) recently redescribed *Eucoelophysis* as a non-dinosaurian dinosauriform, but agreed that the Snyder material described by Heckert et al. (2000; and thus by extension Heckert et al., 2003) is distinct from *E. baldwini*.

SNYDER QUARRY MATERIAL

The Snyder quarry is a bone bed in the upper part of the Painted Desert Member of the Petrified Forest Formation a few km from Ghost Ranch, in north-central New Mexico (Zeigler et al., 2003) (Fig. 1). Phytosaurs dominate the Snyder quarry assemblage, but theropod fossils also are present.

Heckert et al. (2000, 2003) provided a preliminary discussion of the theropod material from the Snyder Quarry. Here, we expand on their summary and describe additional material that has been prepared since that publication. We agree with Heckert et al. (2000, 2003) that there are two distinct size grades of theropod represented within the Snyder quarry assemblage, one significantly larger than the other. However, we conclude that the material of the smaller theropod is attributable to the theropod dinosaur *Coelophysis bauri*, not *Eucoelophysis baldwini*, which is now considered a non-dinosaurian dinosauriform (Ezcurra, 2006). In addition, Ezcurra (2006) noted that the Snyder quarry material more closely resembles dinosaurs than the dinosauriform *Eucoelophysis*. Specifically, he assigned it to Coelophysoidea indet., cf. Coelophysidae based on the following synapomorphies of the Coelophysoidea: premaxillary body craniocaudally lengthened, heterodont premaxilla, premaxillary nasal process forms more than half of the rostrodorsal narial border, subnarial gap, rostral end of the maxillary alveolar border sharply upturned and cervical vertebrae craniocaudally elongated. Additionally, Ezcurra (2006) noted that the alveolar ridge defining the ventral margin of the antorbital fossa indicates a close relationship of the Snyder quarry small theropod skull to *Liliensternus*, and the square rostral end of the antorbital fossa resembles *Zupaysaurus* (Ezcurra and Novas, 2005) and members of the Coelophysidae (sensu Rauhut, 2003).

Theropoda Indet.

Much of the theropod fossil material recovered from the Snyder quarry consists of isolated ribs, centra and miscellaneous bone fragments. However, only the centra may be identifiable to Theropoda indet. due to neural arch morphology, whereas the rest can only be identified to Reptilia indet., Tetrapoda indet. or Vertebrata indet. Here, we focus only on the more diagnostic elements.

Small Theropod

The smaller of the two theropods initially described by Heckert et al. (2000) is represented by an incomplete skull with associated cervical vertebrae (NMMNH P-30852) (Figs. 2, 3A-D), two incomplete skeletons (NMMNH P-29047 and NMMNH P-31661) (Figs. 3E-F, 4, 6E-I), a set of associated hindlimbs (NMMMH P-29046) (Figs. 5D-M, 6A-D) and several isolated hindlimb elements (NMMNH P-31293, P-54617 through P-54620) (Figs. 5A-C, N-O). These specimens are summarized in Tables 1 and 2, with metrics of each specimen in Appendix. Specimens NMMMNH P-29046, P-29047, P-30852 and P-31661 were all found in close proximity to each other (within ~2m laterally), but repetition of elements (especially left tibiae) indicates the presence of at least three individuals of similar size.

NMMNH P-30852

NMMNH P-30852 is an incomplete skull that includes the left premaxilla, the left maxilla, left lacrimal, left prefrontal, most of both lower jaws and two articulated anterior cervical vertebrae, probably cervicals three and four (Figs. 2, 3A-F). This specimen also provides a rare opportunity to examine the internal surfaces of the various skull elements of *Coelophysis*, as much of the Ghost Ranch material has only the external surfaces of the cranial bones exposed.

The left premaxilla is complete and roughly triangular, with a very thin nasal process projecting posteriorly and a more robust maxillary process. The narial fossa is present where the two processes meet, which also demarcates the anterior margin of the external nares. Four tooth sockets are preserved, the third of which houses an unerupted tooth, whereas the other teeth are incomplete.

The left maxilla is incomplete and is missing its posterior portion. The nearly complete ascending process of the anterior maxilla is triangular. Much of the posterior maxilla is very fragmentary, preserving only the portion directly above the tooth row. Ten teeth, in various states of completeness, are present. The total number of tooth sockets cannot be assessed due to mediolateral crushing of the specimen. The length of the maxilla, as preserved, is ~101 mm.

The left lacrimal (Fig. 3E-F) is complete and has an inverted L-shape. The posterodorsal margin of the element is slightly curved, not linear. A low ridge on the lateral surface of its jugal process extends dorsally, curves and continues anteriorly on the dorsal process of the lacrimal, demarcating the posterodorsal margin of the external antorbital fossa. A small elliptical opening is present on the medial side of the maxillary process. A triangular depression is present on the medial side of the base of the jugal process. Notably, the length of the base of the lacrimal is greater than 30% of the height of the ascending process.

A disarticulated right postorbital is attached to an amalgamation of lower jaw elements, so it can only be seen in lateral view. Overall, it is roughly T-shaped, with the jugal process slanted anteroventrally. A ventrally-projecting triangular process is present on the medial side of the confluence of the frontal, squamosal and jugal processes of the postorbital.

The mandibles are both present, but incomplete. The right jaw preserves more of the tooth row and is more complete posteriorly but is missing its anterior tip. The left lower jaw preserves the anterior tip, but is missing its posterior one-third. Both exhibit little crushing in comparison to the right maxilla.

TABLE 1. *Coelophysis bauri* specimens from the Snyder quarry (NMMNH locality 3845) described in the text.

Specimen Number	Taxon	Description	Note
P-29046	Derived coelophysoid	Partial skeleton – complete left femur, incomplete right femur, complete left tibia and proximal left fibula	Identified as *Eucoelophysis* sp. by Heckert et al. (2000, fig. 3D; 2003, fig. 2D, 3F). Not identified by specimen number by Heckert et al. (2000).
P-29047	Coelophysoidea indet.	Partial skeleton – incomplete right ilium, nearly complete right ischium, proximal left tibia, incomplete left fibula, two complete proximal phalanges, a proximal end of a proximal phalanx, a distal phalanx and an ungual.	Identified as *Eucoelophysis* sp. by Heckert et al. (2000, fig. 3B-C; 2003, fig. 2B-C, 3D-E). Not identified by specimen number by Heckert et al. (2000).
P-30852	*Coelophysis bauri*	Incomplete skull, lower jaws and two cervical vertebrae.	Identified as *Eucoelophysis* sp. by Heckert et al. (2000, fig. 3A; 2003, fig. 2A, 3A-B). Not identified by specimen number by Heckert et al. (2000).
P-31661	Coelophysidae indet.	Partial skeleton – various cervical rib fragments, left scapulocoracoid, right radius, left? metacarpal, manual ungual and partial sacrum.	Identified as *Eucoelophysis* sp. by Heckert et al. (2000, 2003, fig. 3C). Used for scapulocoracoid description by Heckert et al. (2000), but not identified by specimen number.
P-31293	Saurischia indet.	(4) incomplete left tibia and associated cervical rib	
P-54617	Derived coelophysoid	(1) right tibia	Recently prepared; described here for the first time.
P-54618	*Coelophysis* sp.	(1) distal right femur	Recently prepared; described here for the first time.
P-54619	*Coelophysis* sp.	(1) distal right femur	Recently prepared; described here for the first time.
P-54620	*Coelophysis* sp.	(1) large right femur	Recently prepared; described here for the first time.

The left lower jaw preserves an incomplete dentary, portions of the angular, surangular and ?splenial. However, as preserved, it is difficult to discern the sutures between the dentary, angular and surangular. In the left dentary, 20 tooth sockets are preserved, 12 of which bear teeth; portions of the anterior dentary are obscured by the right maxilla, so presumably there are one or two tooth sockets that are not visible.

Anteriorly, the left dentary is relatively short and elliptical in cross-section, with the long axis oriented dorsoventrally, whereas posteriorly the dentary thickens dorsoventrally. All that is preserved of the posterior end of the lower jaws is their ventral margins. An unbroken, slightly curved dorsal margin in this area preserves the ventral margin of the external mandibular fenestra. The ?splenial has been displaced dorsally and is sharply triangular and concave in lateral view.

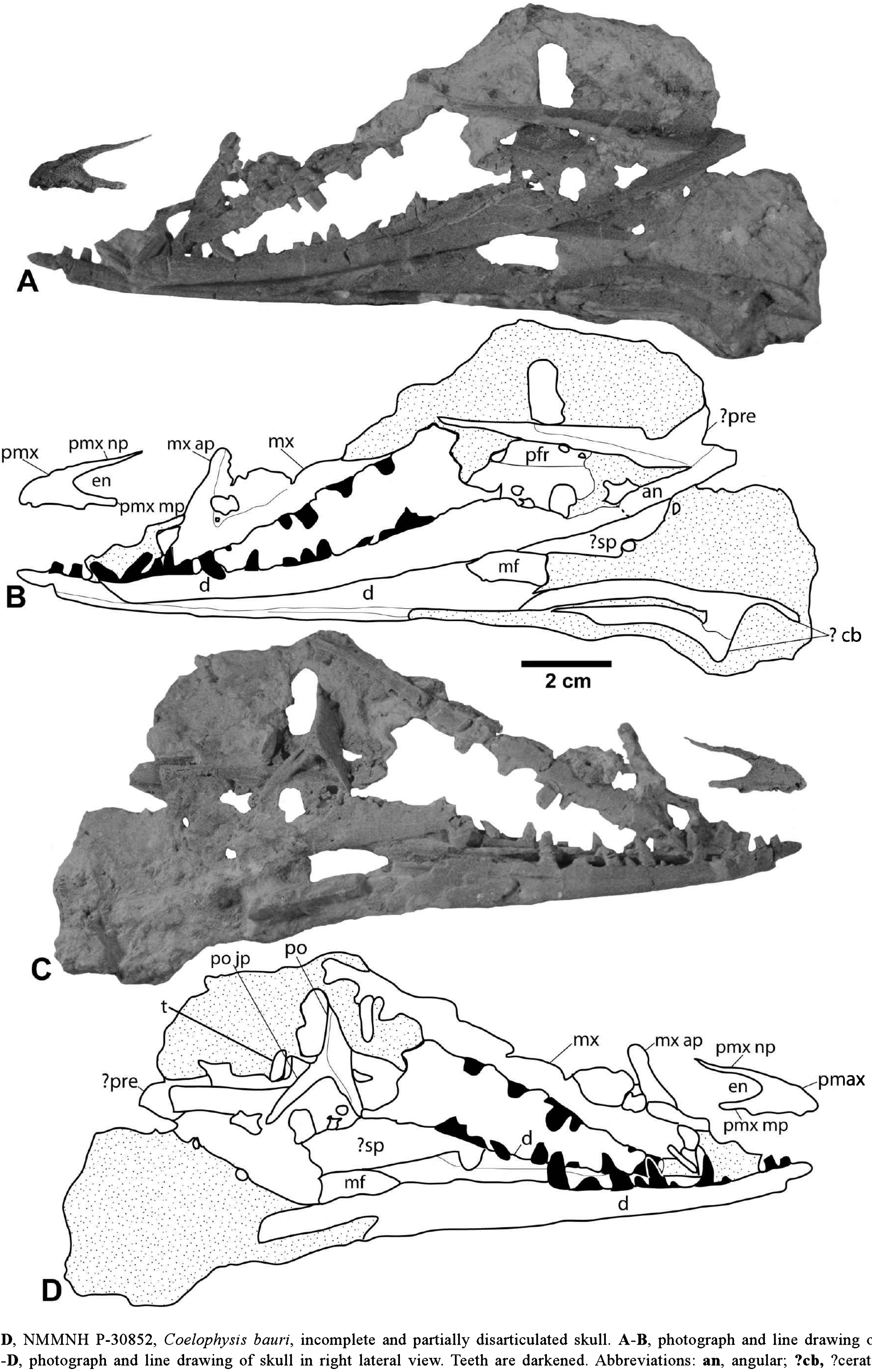

FIGURE 2. **A**-**D**, NMMNH P-30852, *Coelophysis bauri*, incomplete and partially disarticulated skull. **A**-**B**, photograph and line drawing of skull in left lateral view. **C**-**D**, photograph and line drawing of skull in right lateral view. Teeth are darkened. Abbreviations: **an**, angular; **?cb,** ?ceratobranchial; **d**, dentary; **en**, external nares; **mf**, mandibular fenestra; **mx**, maxilla; **mx ap**, ascending process of maxilla; **po**, postorbital; **po jp**, jugal process of postorbital; **pmx**, premaxilla; **pmx mp**, maxillary process of premaxilla; **pmx np**, nasal process of the premaxilla;**?pre**, prearticular; **?sp**, splenial; **t**, isolated tooth.

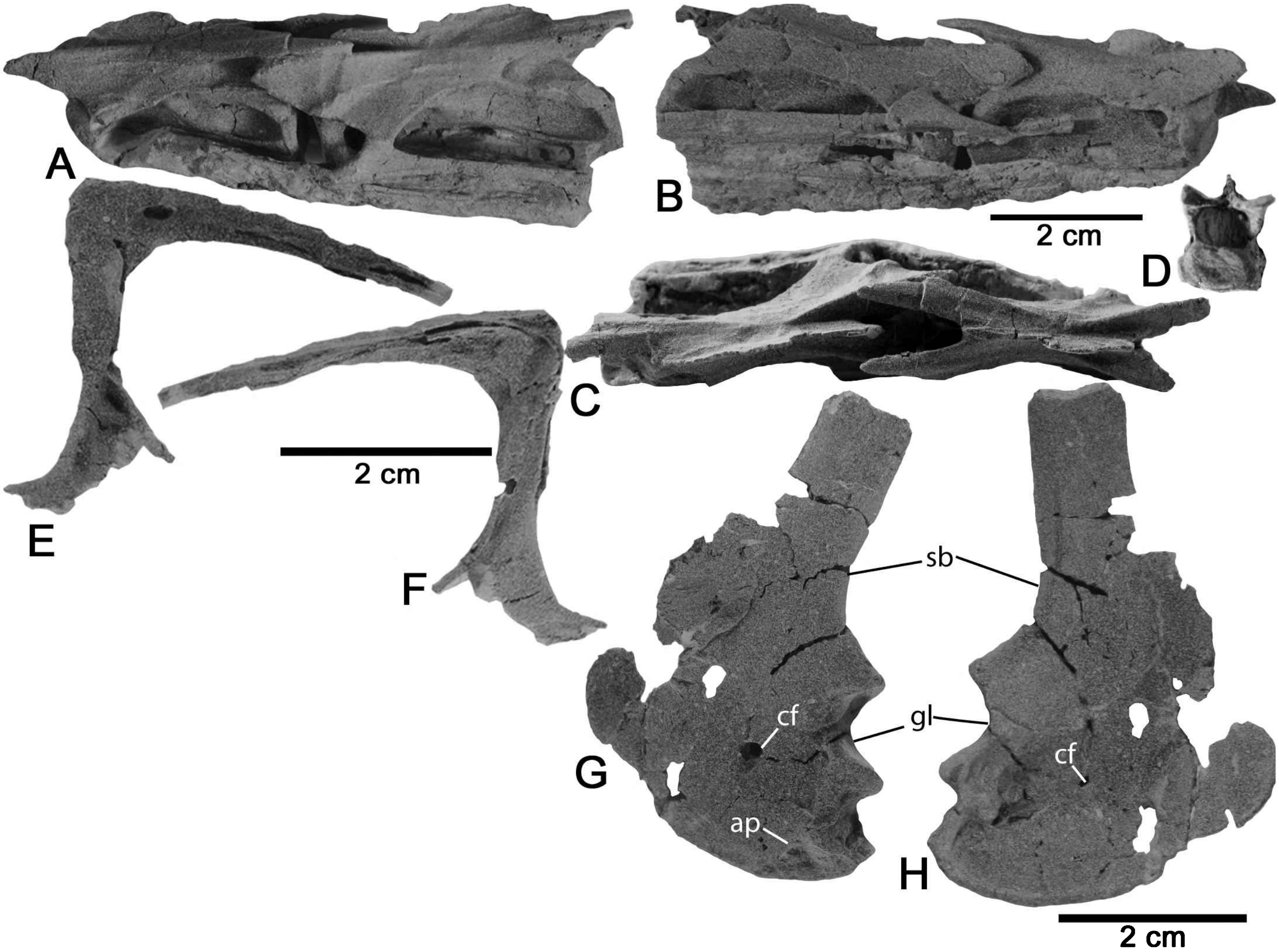

FIGURE 3. **A**-**F**, NMMNH P-30852, *Coelophysis bauri*. **A**-**D**, cervical vertebrae in **A**, left lateral, **B**, right lateral, **C**, dorsal and **D**, anterior views. **E**-**F**, left lacrimal in **E**, medial and **F**, lateral views. **G**-**H**, NMMNH P-31661, *Coelophysis bauri*, left scapulocoracoid in **G**, lateral and **H**, medial views. Abbreviations: **ap**, acromial process; **cf**, coracoid foramen; **gl**, glenoid; **sb**, scapular blade.

The right dentary preserves 17 readily discernable alveoli; some of the posteriormost sockets are not visible. Of the 17 sockets, 10 are tooth-bearing. The anterior dentary is either complete to the symphysis of the lower jaws or nearly so. The posterior portion is missing.

The ?angular is rotated dorsally from its natural position, its medial surface (Fig. 2A-B). The element is triangular with a long pointed process extending anteriorly and a dorsal expansion of the element posteriorly. If correctly interpreted, the relatively smooth edge along the dorsal margin of the ?angular forms the ventral border of the internal mandibular fenestra.

A pair of elongate, mediolaterally compressed elements with slightly expanded posterior ends are present below the lower jaws. Heckert et al. (2003) identified these elements as ?ceratobranchials and we concur with their tentative interpretation, because this pair of elements is positioned where the ceratobranchials would have been in vivo (Colbert, 1989, fig. 47A).

Two cervical vertebrae, associated with the skull, are articulated and nearly complete, missing only their neural spines, the right postzygapophysis of the posterior vertebra and portions of the cervical ribs (Fig. 3A-B). Both are amphicoelous with the anterior articular surfaces angled anteriorly, have elongate triangular pre- and postzygapophyses and elliptical caudal fossa on the lateral sides of the centra that deepen posteriorly. The orientation of laminae (centrodiapophyseal and ventral lamina) in these vertebrae are identical to the morphology of *Coelophysis bauri* and *Liliensternus liliensterni* (Ezcurra and Cuny, 2007, fig. 1). In addition, the posterior vertebra has an accessory canal slightly above and running parallel to the neural canal. This can only be seen in posterior view, because the anterior end of the posterior vertebra is obscured by the articulated postzygapophyses of the vertebra immediately anterior to it. Such accessory canals are also present in the Ghost Ranch sample of *Coelophysis bauri* and were discussed extensively (as "lateral tunnels" by Colbert (1989, p. 78-80)). The cervical ribs are preserved in a block of matrix beneath the centra. The anterior vertebra is missing both the articular ends of the cervical ribs, although an element on the right side of the vertebrae may be a disarticulated anterior cervical rib. The left cervical rib of the posteriormost vertebra has a complete anterior articular surface in articulation. Both cervical ribs are extremely elongate, with those of the anterior vertebra extending posteriorly beyond the posterior vertebra.

NMMNH P-29047

NMMNH P-29047 is an incomplete right pelvis and hindlimb that includes an incomplete right ilium, incomplete right ischium, proximal left tibia, left fibula missing its distal end and five manual and pedal elements (Figs. 4F-J, 6E-I).

The incomplete right ilium (Fig. 4F-H) preserves much of the

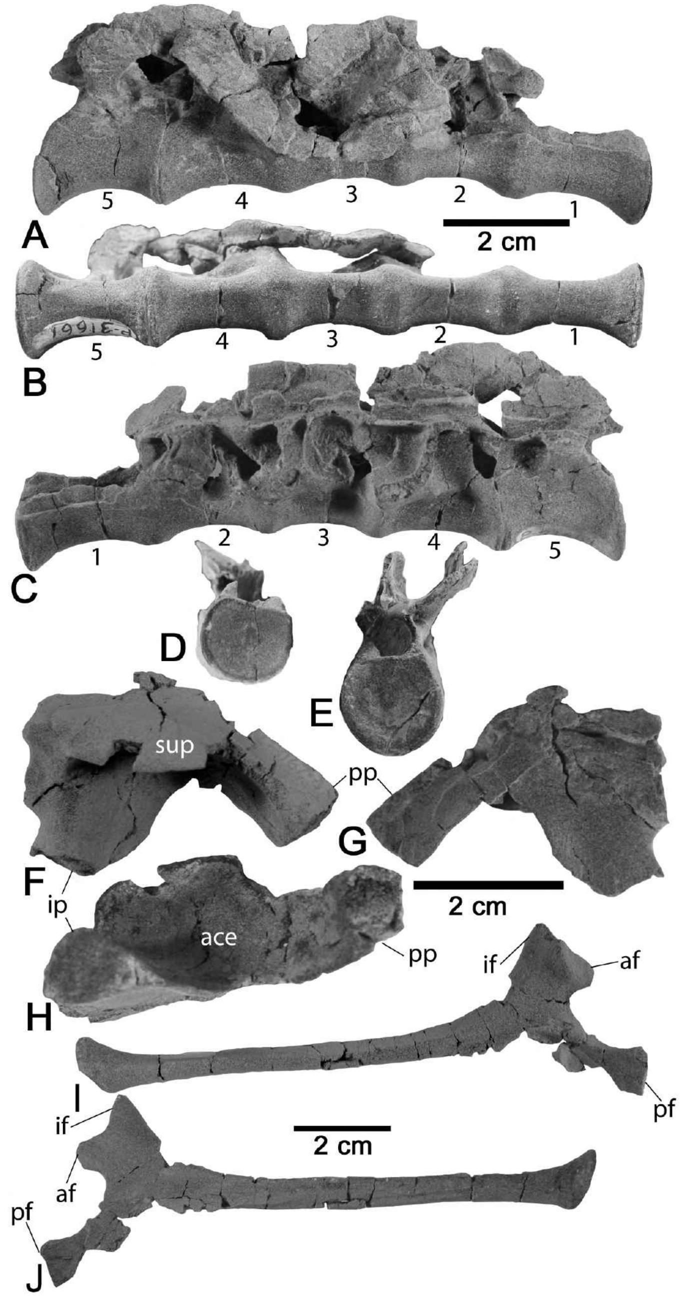

FIGURE 4. **A-E**, NMMNH P-31661, *Coelophysis bauri*, incomplete sacrum in **A**, right lateral, **B**, ventral, **C**, left lateral views, **D**, anterior view of first sacral vertebra and **E**, posterior view of fifth sacral vertebra. **F-J**, NMMNH P-29047, *Coelophysis bauri*. **F-H**, incomplete right ilium in **F**, lateral, **G**, medial and **H**, ventral views. **I-J**, right ischium in **I**, lateral and **J**, medial views. In **A-C**, the vertebrae are numbered. Abbreviations: **ace**, acetabulum; **af**, acetabular facet; **if**, iliac facet; **ip**, ischial peduncle; **pf**, pubic facet; **pp**, pubic peduncle; **sup**, supra-acetabular crest.

acetabular region (both ischial and pubic peduncles and the supra-acetabular crest), but the iliac blade is missing. The anterior margin of the pubic peduncle is also missing, as is the anterior portion of the supra-acetabular crest. The supra-acetabular crest extends from a buttress posterior to the acetabulum to a point relatively low on the pubic peduncle. This creates a dorsal "hood" over the acetabulum, a feature also seen in UCMP 129618 (see below). In ventral view, the acetabulum is suboval; the anterior acetabulum is slightly wider mediolaterally than the posterior portion.

The single right ischium (Fig. 4I-J) is nearly complete except for minor fragments missing from its ventral margin the acetabulum. The iliac articular facet is subtriangular. The acetabular facet (or antitrochanter) is subrectangular and oriented anterodorsally. The pubic facet is triangular. When articulated with the ilium, nearly the entire acetabulum can be delineated: overall, it is elliptical, with the long axis oriented dorsoventrally. The shaft of the ischium is straight, projects posteroventrally and is triangular in cross-section with a circular lateral edge. The rugose medial margin of the ischial shaft demonstrates the articulation of the left and right ischia. The shaft terminates at a small, convex expansion that appears lunate in distal view.

The proximal left tibia (Fig. 6E-G) is broken below the level of the fibular crest. In proximal view, the tibia is subtriangular anteriorly and rectangular posteriorly. There is a slight depression on the medial margin of the proximal tibia; just lateral to this depression is a groove for the reception of the proximal fibula. The cnemial crest is prominent and concave medially, and a distinct groove extends down the shaft from this concavity. A distinct notch is present on the posterior margin of the proximal end of the tibia; an identical notch is present on UCMP 129618 (see below). The fibular crest extends down the proximal quarter of the shaft, and the site of articulation with the fibula extends laterally from the fibular crest as a pyramidal process that is oriented posteriorly. A single nutrient foramen is present just below and posterior to the level of the fibular crest.

The left fibula lacks much of the shaft and its distal end (Fig. 6H-I). In cross section, the proximal fibula is a rounded rectangle that thins anteroposteriorly along the length of the shaft. On the medial side of the fibula is a process extending anteroventrally from the posterior edge of the proximal end that articulates with the fibular crest of the tibia.

The various manual and pedal elements include a complete, elongate metacarpal IV, the distal end of a metatarsal, a complete elongate proximal phalanx, a complete, stout, distal phalanx and a curved terminal manual phalanx. These bones do not differ from the same elements in the Ghost Ranch specimens of *Coelophysis bauri* (Colbert, 1989).

NMMNH P-31661

NMMNH P-31661 comprises parts of a skeleton that consists of numerous cervical rib and rib fragments, a partial left scapulocoracoid, a right radius, an incomplete sacrum, a metacarpal and a terminal pedal phalanx (Figs. 3G-H, 4A-E). These fragments were all collected from a single small jacket, so we consider them associated and to represent a single individual.

Most of the cervical ribs and rib fragments preserve the articular facets and the anterior portions of the rib. Most notable is a prominent anterior expansion of the anterior cervical rib.

The left scapulocoracoid (Fig. 3G-H) is incomplete, missing portions of its anterior margin and most of the scapular blade, though the glenoid is well preserved. In addition, no suture between the scapula and coracoid can be distinguished. The posterior-facing glenoid is saddle shaped, with the ventromedial margin slightly downturned. The pyramidal acromial process lies just ventral to the glenoid, projecting laterally from the element. A ridge runs from the acromial process anteriorly. A moderately-sized coracoid foramen is present, at approximately the level of the ventral margin of the glenoid. In medial view, the coracoid is concave.

The right radius is complete. The proximal radius is elliptical, with the long-axis oriented anteroposteriorly. The radial shaft is also elliptical, though the anteroposterior edges taper to a point. The distal radius is subcircular and has its long axis oriented mediolaterally.

The incomplete sacrum (Fig. 4A-E) includes all five centra expected in a coelophysoid, though in varying degrees of completeness. The first centrum has none of its neural arch preserved. The second centrum includes an incomplete neural arch. The third centrum includes a complete neural arch, the base of the neural spine and portions of the right transverse process. The fourth includes a complete neural arch and the base of the neural spine and the fifth preserves a complete neural

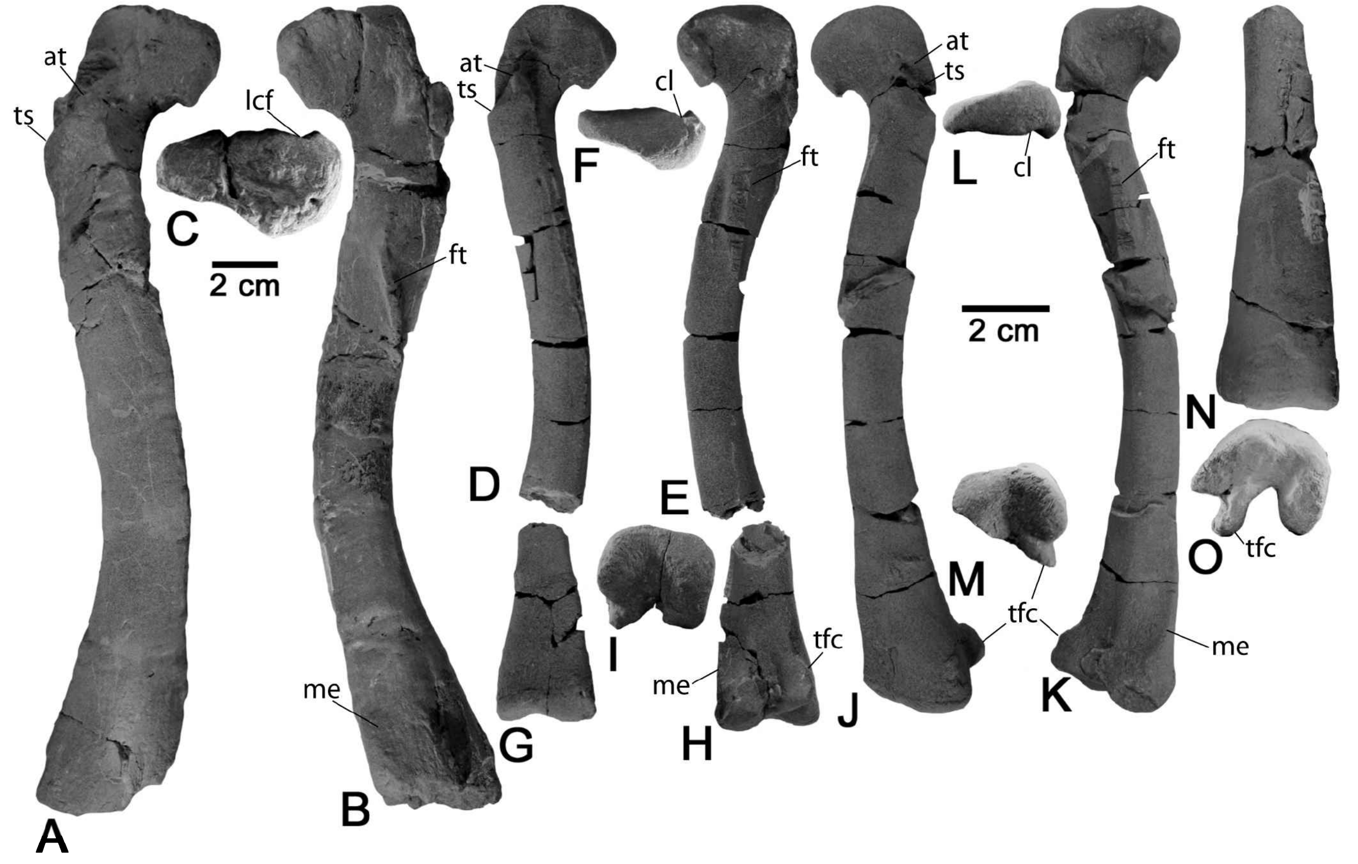

FIGURE 5. **A**-**C**, NMMNH P-54620, *Coelophysis bauri*, large right femur missing distal condyles in **A**, anterior, **B**, posterior and **C**, medial views. **D**-**M**, NMMNH P-29046, *Coelophysis bauri*. **D**-**I**, right femur in **D, G** anterior, **E, H**, posterior, **F**, proximal and **G**, distal views. **J**-**M**, left femur in **J**, anterior, **K**, posterior, **L**, proximal and **M**, distal views. **N**-**O**, NMMNH P-54618, *Coelophysis bauri*, distal right femur in **N**, anterior and **O**, distal views. Abbreviations: **at**, anterior trochanter; **cl**, sulcus for capitular ligament; **ft**, fourth trochanter; **me**, medial epicondyle; **tfc**, tibiofibular crest; **ts**, trochanteric shelf.

arch, the base of the neural spine and a complete right transverse process. All the left transverse processes are missing, whereas the portions of the medial ilium are still adhered to the incomplete right transverse processes of the third through fifth vertebrae. All the centra are nearly rectangular in ventral view and slightly waisted. The anterior articular surface of the first centrum and the posterior articular surface of the fifth centrum are circular and suggest that the sacral vertebrae are amphicoelous. The first through fourth centra are seamlessly fused, whereas the fifth is adhered but demarcated by a distinct line. Colbert (1989) documented this condition in large individuals of *Coelophysis bauri*. Comparison with the NMMNH Whitaker quarry material shows this to be common in small *C. bauri* individuals as well.

The single metacarpal is likely from the right manus, based on the orientation of its distal end. Its proximal end is rectangular and expanded compared to the thinner shaft of the element, which is circular in cross-section. The distal end of the metacarpal has two distinct condyles; the lateral is larger and extends more distally than the medial. The single ungual is not highly curved, as are terminal manual phalanges, so it appears to pertain to the pes. In proximal view, the phalanx is subtriangular. Along either side of the distal two-thirds of the phalanx is a groove just above the ventral surface. These elements are exactly as Colbert (1989) described them in *Coelophysis bauri*.

NMMNH P-29046

Four hindlimb elements – two femora, a left tibia and a proximal left fibula – were found in association, and are proportionate to each other in size, so we consider them to belong to a single individual (Figs. 5D-M, 6A-D). The left femur (Fig. 5J-M) is virtually complete, with a slightly offset break midway along the shaft, and lacking only a portion of the medial distal condyle. The right femur is broken near its distal end, although based on comparisons to the left femur, very little of the element is actually missing. The left tibia is complete, although the shaft is interrupted by two diagenetic fractures that give the element an artificial kinked appearance overall.

The femora are mirror images of each other, but otherwise identical. Each has a prominent greater trochanter that is confluent with the femoral head. The head has a hooked appearance, with a sulcus, visible in proximal view, for the capitular ligament. The hooked appearance of the femoral head differs from the femur illustrated by Colbert (1989, fig. 80), however, many consider Colbert's illustration to be of a non-dinosaurian archosaur (J. Harris, pers. commun.). The anterior ("lesser") trochanter is triangular, robust (compare with Raath, 1977, figs. 15-16) and extends along the anterior surface of the shaft. A trochanteric shelf separates the anterior trochanter and the proximal femoral shaft. This shelf wraps laterally around the shaft to its posterolateral edge. The fourth trochanter, situated on the posterior shaft, begins just below the level of the terminus of the trochanteric shelf and extends distally to above the midpoint of the shaft. Overall, the femoral shaft is subtriangular in cross section. Distally, the tibiofibular crest is subtriangular and extends posteriorly from the lateral condyle. A prominent medial epicondyle is present as a prominent groove running along the distal shaft to meet the distal end of the femur.

The proximal tibia (Fig. 6A-D) is very similar to those described above for NMMNH P-29047, including the cleft along the posterior margin of the proximal end and the flange on the medial side of the proximal shaft for articulation with the fibula. The distal tibia is rhom-

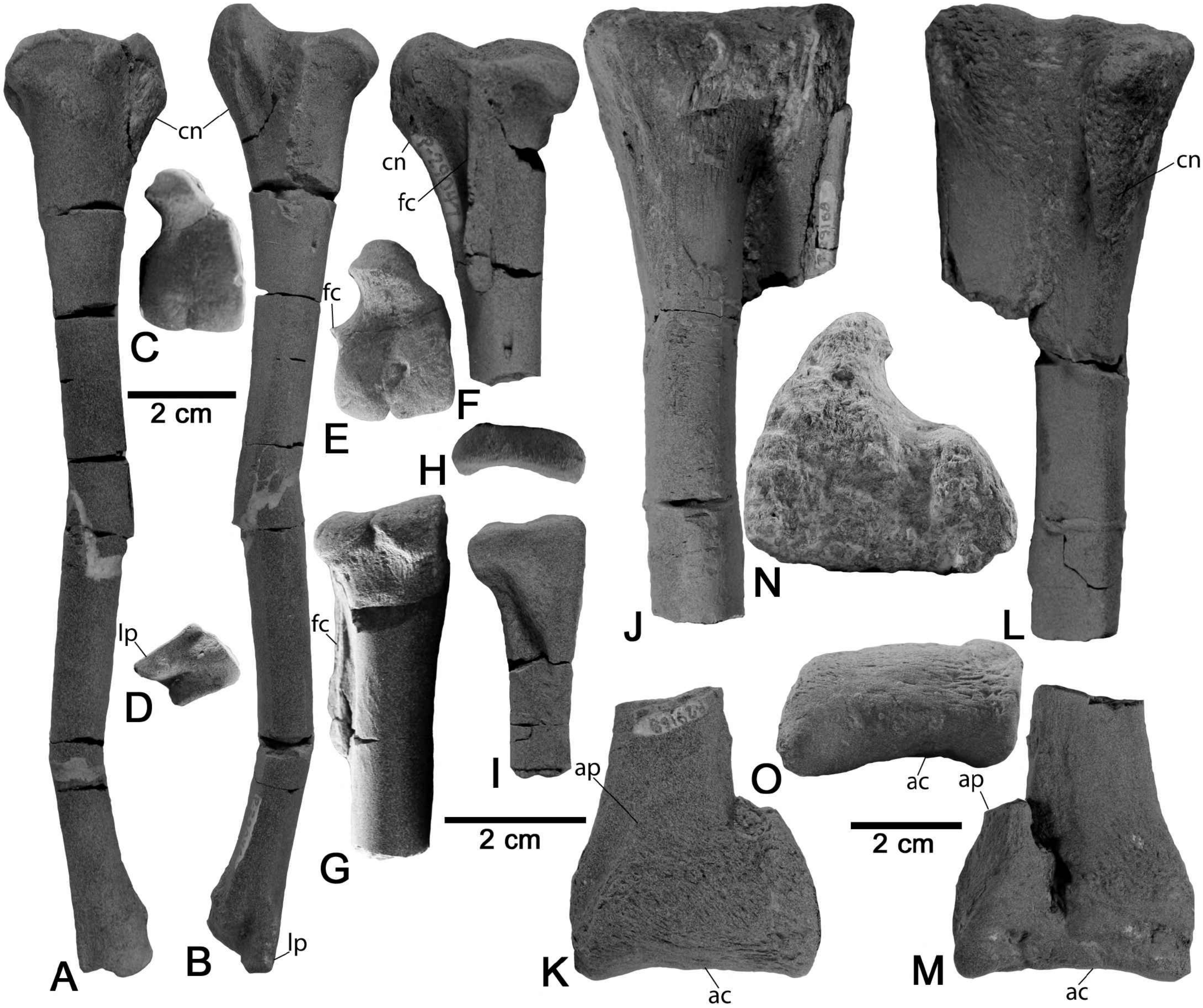

FIGURE 6. **A-D**, NMMNH P-29046, *Coelophysis bauri*, left tibia in **A**, medial, **B**, lateral, **C**, proximal and **D**, distal views. **E-I**, NMMNH P-29047, *Coelophysis bauri*. **E-G**, proximal left tibia in **E**, proximal, **F**, lateral and **G**, posterior views. **H-I**, left fibula in **H**, proximal and **I**, medial views. **J-O**, NMMNH P-29168, large Snyder quarry coelophysoid, fused right tibia/fibula in **J**, **K**, posterior, **L**, **M**, anterior, **N**, proximal and **O**, distal views. Abbreviations: **ac**, astragalocalcaneum; **ap**, ascending process of astragalus; **fc**, fibular crest; **cn**, cnemial crest; **lp**, lateral process of distal tibia.

boidal in distal view. A process on its anterior side for the recepetion of the astragalocalcaneum runs ventrolaterally. A prominent lateral expansion is present, giving the distal tibia a rectangular shape in anterior view. A ridge is also present on the posterior surface. None of the tibiae and fibulae examined in this study are fused to each other; such fusion is variable in *Coelophysis bauri* according to Colbert (1989, p. 107).

The proximal left fibula is morphologically identical to the same element of P-29047 described above, although it is slightly smaller.

Isolated Hindlimb Elements

The other isolated limb elements from the Snyder quarry consist of femora and tibiae in various stages of completeness (Tables 1-2).

Of these, one deserves special mention: NMMNH P-54620, a large right femur missing its distal condyles (Fig. 5A-C). This femur is considerably larger than all the other material referred to the small theropod. The length of this element is 235 mm, as preserved. While this specimen stands out as the largest representative element of the smaller theropod from the Snyder quarry sample, and equivalent in size to UCMP 129618, it is nevertheless slightly smaller than some of the largest *Coelophysis bauri* femora from the Ghost Ranch quarry (the largest of which we are aware is a ~240 mm long femur in the State Museum of Pennsylvania block).

Referral to a Single Taxon

We consider these records to all pertain to a single taxon based on the similarity of like elements, especially the tibiae of NMMNH P-29047 and NMMNH P-29046, the similarity in overall size and the various features that are identical to *Coelophysis bauri* (see below), and fall well within the range of variation others have documented in coelophysoid theropods, including *C. bauri* (Colbert, 1990), *C. rhodesiensis* (Raath, 1990) and *Megapnosaurus kayentakatae* (Tykoski, 1998).

Large Theropod

The larger of the two theropod taxa represented in the quarry, originally noted by Heckert et al. (2000), is represented by a single element, NMMNH P-29168, a fused right tibia and fibula with most of their shafts missing (Fig. 6J-O). The proximal tibia does not have the cleft along the posterior margin as seen in the smaller individual discussed above, but it does have a prominent cnemial crest. The fibula is fused to the lateral condyle of the proximal tibia. The distal tibia and fibula are fused to the astragalocalcaneum. This fusion is extensive: the ascending process of the astragalus is barely discernable on the anterior distal tibia. Just lateral to this process is a prominent groove oriented ventrolaterally. Also, whereas the distal tibia does have a lateral process, it does not extend beyond the level of the shaft, and so is not nearly as extensive as the same feature in the small theropod. We consider this specimen Coelophysoid indet. based on the presence of a deep fossa on the craniolateral surface of the ascending process of the astragalus.

COMPARISON OF THE SNYDER THEROPOD MATERIAL WITH UCMP 129618

Padian (1986) described UCMP 129618, an incomplete skeleton of a theropod dinosaur, from the Painted Desert Member of the Petrified Forest Formation, Chinle Group, of the Petrified Forest National Park, Arizona (UCMP locality V82250). The skeleton includes one dorsal and one anterior caudal centrum, an incomplete right pelvis (Fig. 7), an incomplete left ischium, fragmentary femora (Figs. 8-9), both tibiae (Fig. 10), a left fibula (Fig. 10B-E) and right distal tarsals, metatarsals and phalanges. The specimen was collected in the southwestern portion of the northern half of Petrified Forest National Park, near Lacey Point at a location that subsequently came to be known informally as "Dinosaur Hill." Fossils from Dinosaur Hill come from the uppermost Kachina Point Bed and the fine-grained sediments immediately overlying it (Heckert and Lucas, 2002).

Padian (1986) identified the skeleton as *Coelophysis bauri* based on comparisons to Cope's syntypes of *C. bauri*, not the neotype. When comparing UCMP 129618 to the Ghost Ranch material, Padian (1986, p. 56) noted that "there are differences between the Ghost Ranch and Petrified Forest specimens that may require taxonomic reevaluation when full descriptions of the former are published." With the Ghost Ranch material now serving as the neotype of *C. bauri* it is worth reviewing the comparison to see if Padian's (1986) initial concerns were warranted. Padian (1986) was not the only one to have doubts about the assignment of the UCMP 129618 to *C. bauri*: Long and Murry (1995) also noted that UCMP 129618 is "considerably different from the Ghost Ranch specimens" (p. 187) but did not provide any specific differences. Heckert and Lucas (1998) considered UCMP 129618 an indeterminate ceratosaur. Hunt et al. (1998) noted that the presence of an obturator foramen, a feature that Padian (1986) cited specifically as distinguishing UCMP 129618 from the Ghost Ranch *Coelophysis* material, was in fact shared by both taxa. Thus, while many workers have noted a general difference between the Ghost Ranch *Coelophysis* material and UCMP 129618, no specific differences have been enumerated in the literature. In contrast to these other studies, we find numerous similarities between *Coelophysis* and UCMP 129618.

Fortunately, all the major elements that comprise UCMP 129618 – the incomplete hip, femora, tibiae and fibula – are also represented in the various incomplete skeletons of the small Snyder theropod. The ilia of both animals have prominent supra-acetabular crests that give their acetabula a "hooded" appearance. The proximal femora are identical, sharing a hooked greater trochanter, a triangular anterior trochanter, a trochanteric shelf that wraps laterally around the femoral shaft and a sulcus for the capitular ligament. Likewise, the distal femora are also similar, with prominent, subtriangular tibiofibular crests and prominent medial epicondyles. The tibiae share the following characteristics: a notch along the posterior margin of the proximal tibia, prominent cnemial crest and rhomboid distal tibia with rectangular lateral projection. The fibulae of UCMP 129618 and the small Snyder theropod are also similar. These features shared by both taxa are present in the coelophysoids *Liliensternus liliensterni*, *Coelophysis rhodesiensis* and *Coelophysis bauri*. In addition, given the close temporal and geographic distribution of these taxa, it is most parsimonious to assign both to the same taxon.

COMPARISONS WITH *COELOPHYSIS BAURI*

Utilizing recent phylogenetic analyses of basal theropods (Ezcurra, 2006; Ezcurra and Novas, 2006), examination of *Coelophysis bauri* material from the NMMNH Ghost Ranch quarry block, plus published descriptions of *C. bauri* (Colbert, 1989), we compared the small Snyder theropod and UCMP 129618 to *C. bauri*. Here, we compare these theropods to other Late Triassic basal theropods, based on the diagnoses provided by Ezcurra (2006) and Ezcurra and Novas (2006).

The following characteristics, listed by Ezcurra (2006) and Ezcurra and Novas (2006) as unambiguous apomorphies of coelophysoids are possessed by the Snyder/UCMP theropod: angle between rostral margin and alveolar margin of premaxilla equal or less than 40° (19° in NMMNH P-30852); presence of a ventral process at the caudal end of premaxiallary body (which we refer to above as the maxillary process of the premaxilla); absence of a subnairal foramen; axial diapophysis present; postaxial cervical neural spines dorsoventrally low; articulation facet of pubic penduncle of ilium with pronounced kink and cranial part facing almost entirely cranially. Of note is that the rostral end of the dentary does not appear to be dorsally expanded; a feature that argues against the Snyder/UCMP theropod being a coelophysoid. But, since the dentaries of NMMNH P-30852 are incomplete this is likely the cause of this anomalous feature, especially given the presence of various apomorphies possessed by the Snyder/UCMP theropod that are characteristic of more exclusive clades within Coelophysoidea.

The following characteristics are listed by Ezcurra (2006) and Ezcurra and Novas (2006) as unambiguous apomorphies of the Coelophysidae (consisting of *Coelophysis* and *Megapnosaurus* [= "*Syntarsus*"]) also possessed by the Snyder/UCMP theropod: mediolateral width of anterior end of dentary equal to that of caudal part, caudoventral process of the coracoid tapering and projected beyond the caudal margin of the glenoid fossa, supraacetabular crest and lateral brevis fossa continuous as a well developed ridge, with non-distinct separation between both structures.

The Snyder/UCMP theropod possesses the following characteristics, listed by Ezcurra (2006) and Ezcurra and Novas (2006) as unambiguous apomorphies of *Coelophysis*: absence of promaxillary foramen, rostral process of postorbital at about the same level as or slightly higher than the squamosal process, resulting in a T-shaped postorbital. The angle of the ascending process of the maxilla in NMMNH P-30852 is ~36° as preserved, although the anterior end of the maxilla in NMMNH P-30852 is not visible and thus would increase the length of the maxilla, consequently reducing the angle of the ascending process. This is an important feature since Ezcurra (2006) and Ezcurra and Novas (2006) list an angle of the ascending process of the maxilla less than 35° as an apomorphy of *Coelophysis*.

Bristowe and Raath (2004) used the width of the base of the vertical ramus of the lacrimal, being greater than 30% of its height as a characteristic distinguishing *Coelophysis bauri* from *C. rhodesiensis* (although this feature is also present in *Eoraptor*, *Megapnosaurus* (= "*Syntarsus*") *kayentakatae* and *Zupaysaurus*). The presence of this character in the Snyder/UCMP theropod demonstrates that this material can be identified to *C. bauri*. This is the most logical result given that *C. bauri* is the only coelophysid reported from Upper Triassic strata in North America. In addition to the strict character analysis, side-by-side comparisons of *Coelophysis bauri* and the Snyder/UCMP theropod show that they are identical, as noted throughout the description above.

Table 2 demonstrates that all the material discussed above pertains to basal theropods, while some material (NMMNH P-29046 and P-541671; UCMP 129618) can be identified to the genus *Coelophysis*. Only NMMNH P-30852 can be definitively identified as *Coelophysis bauri*. However, parsimony would dictate that all the basal theropod

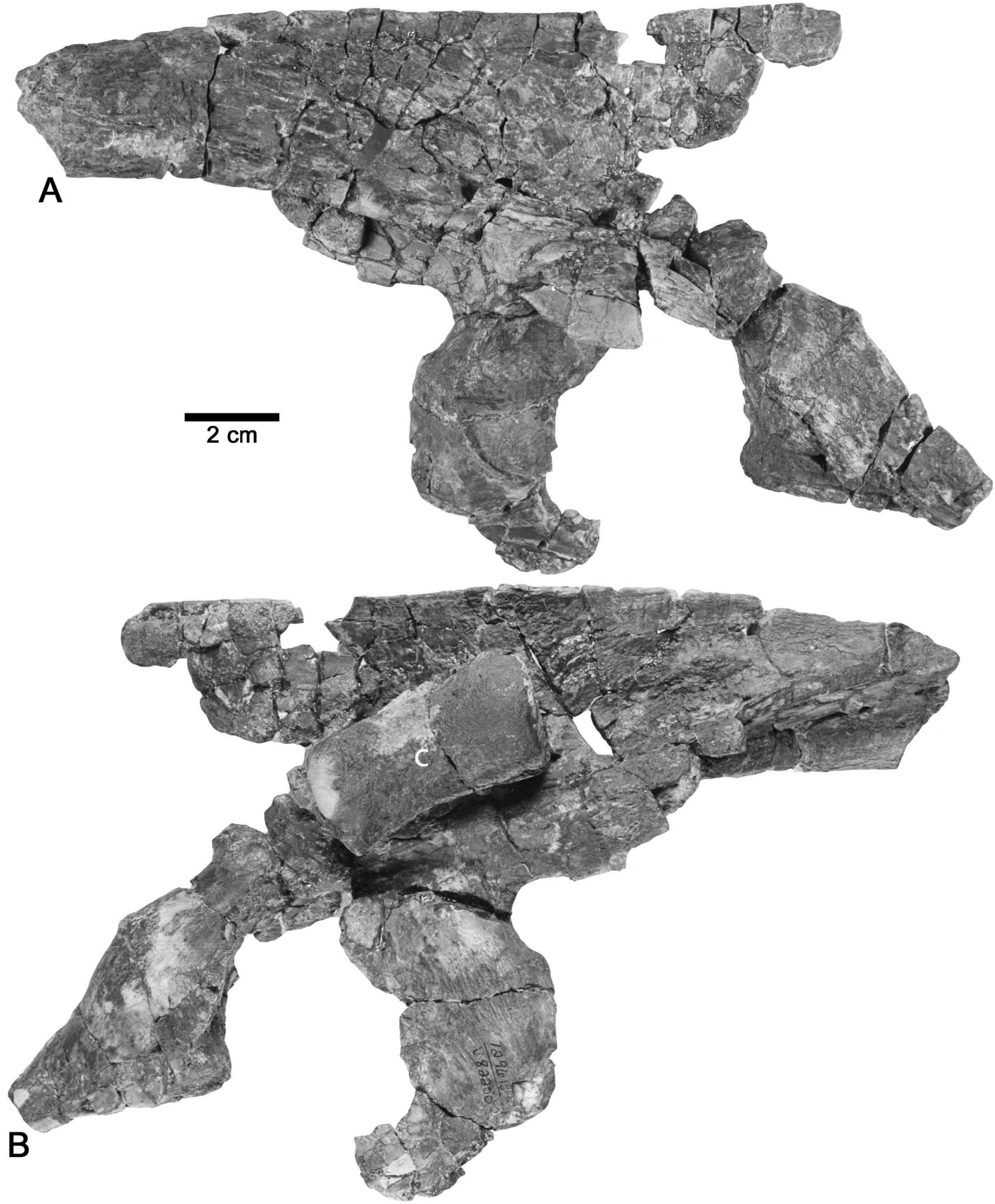

FIGURE 7. **A-B**, UCMP 129618, *Coelophysis bauri*, partial right pelvis in **A**, lateral and **B**, medial view. Note centrum (**c**) adhered to medial ilium.

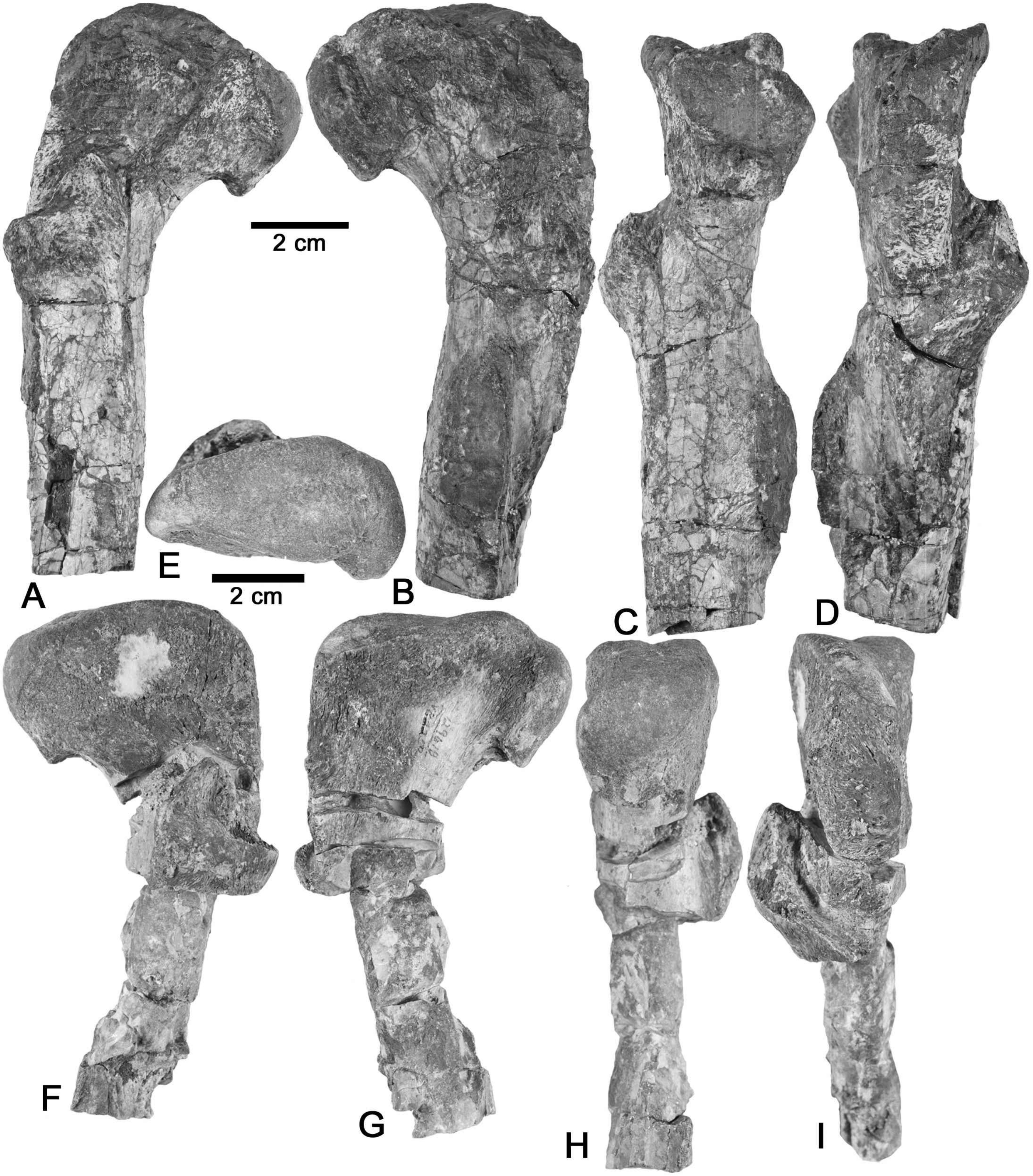

FIGURE 8. **A-I**, UCMP 129618, *Coelophysis bauri*, proximal femora. **A-D**, right proximal femur in **A**, anterior, **B**, posterior, **C**, medial and **D**, lateral views. **E-I**, left proximal femur in **E**, proximal, **F**, anterior, **G**, posterior, **H**, medial and **I**, lateral views.

material from the Snyder quarry is assignable to a single taxon. We believe it is most parsimonious to assign this material to *Coelophysis bauri* because none of the aforementioned taxa, other than *Coelophysis* and *Camposaurus*, existed in the Late Triassic of North America as far as is currently known.

THE BIOSTRATIGRAPHIC RANGE OF *COELOPHYSIS BAURI*

Coleophysis bauri was previously known only from the Ghost Ranch Whitaker quarry, Rio Arriba County, New Mexico, in the Rock Point Formation. The Rock Point Formation is of Apachean age (late

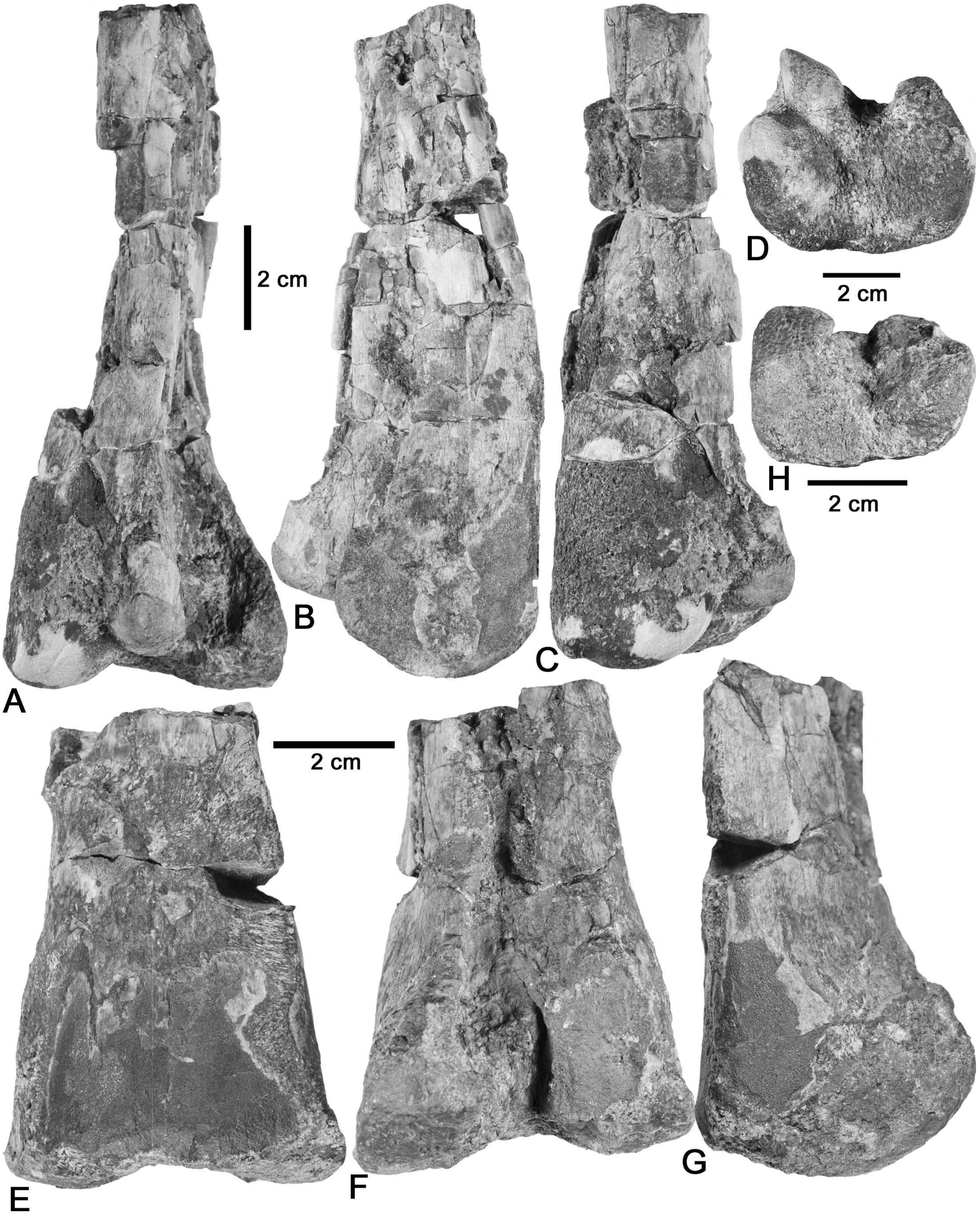

FIGURE 9. **A-H**, UCMP 129618, *Coelophysis bauri*, distal femora. **A-D**, left distal femur in **A**, posterolateral, B, medial, **C**, lateral and **D**, proximal views. **E-H**, right distal femur in **E**, anterior, **F**, posterior, **G**, medial and **H**, distal views.

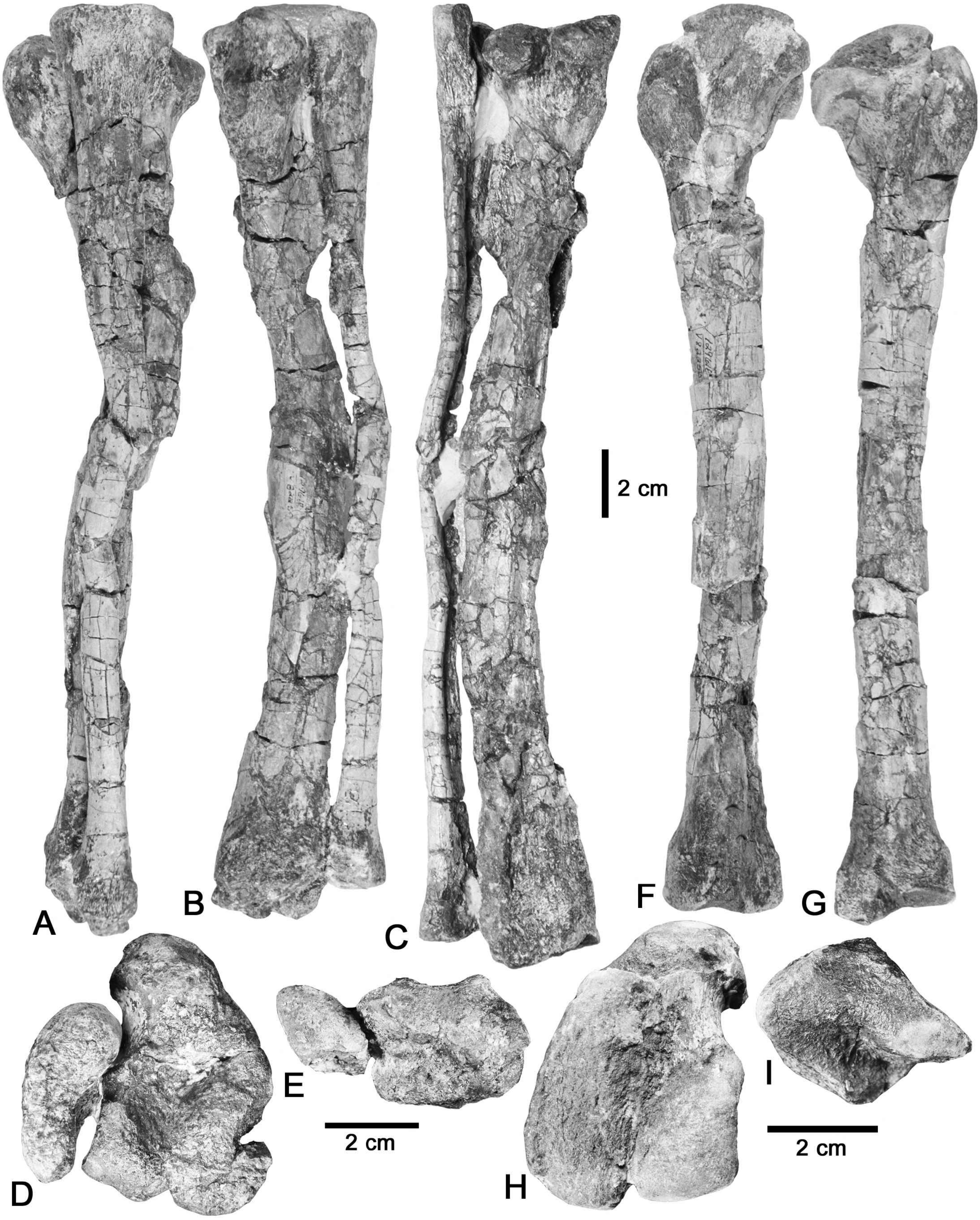

FIGURE 10. **A**-**I**, UCMP 129618, *Coelophysis bauri*, tibiae and fibula. **A**-**E**, left tibia and fibula in **A**, lateral, **B**, anterior, **C**, posterior, **D**, proximal and **E**, distal views. **F**-**I**, right tibia in **F**, medial, **G**, lateral, **H**, proximal and **I**, distal views.

TABLE 2. Specimens discussed in the text, with list of diagnostic characters and taxon to which the individual specimen can be identified.

Specimen Number	Identifiable Taxon	Diagnostic Features
P-29046	Derived coelophysoid	—Anterior trochanter on femur triangular: found only in *Herrerasaurus*, *Coelophysis*, *Liliensternus liliensterni*, and *Dilophosaurus* (Rauhut, 2003, p. 113). —Distal end of femur anteroposteriorly broad and distally flattened: found only in *Eoraptor*, *Herrerasaurus*, *Staurikosaurus*, *Coelophysis* and *Dilophosaurus* (Rauhut, 2003, p. 114-115). —Fibular condyle on proximal tibia confluent with cnemial crest anteriorly in proximal view: found only in *Herrerasaurus*, *Staurikosaurus*, *Coelophysis*, *Gojirasaurus*, *Liliensternus liliensterni*, *Dilophosaurus*, *Segisaurus* and *Elaphrosaurus* (Rauhut, 2003, p. 115). —Lateral process on distal tibia polygonal-shaped: found in all coelophysoids more derived than *Dilophosaurus* (Sereno, 1999).
P-29047	Coelophysoidea indet.	—Dolichoiliac pelvis: found in *Coelophysis* and derived theropods, not found in *Eoraptor*, *Herrarsaurus* and *Staurikosaurus* (Rauhut, 2003, p. 102). —Articular facet of pubic penducle of ilium with pronounced kink and anterior part facing almost entirely anteriorly: found in *Coelophysis*, *Liliensternus liliensterni*, *Lophostropheus airlensis*, *Dilophosaurus* and ornithomimosaurs (Rauhut, 2003, p. 107). —Fibular condyle on proximal tibia confluent with cnemial crest anteriorly in proximal view: found only in *Herrerasaurus*, *Staurikosaurus*, *Coelophysis*, *Gojirasaurus*, *Liliensternus liliensterni*, *Dilophosaurus*, *Segisaurus* and *Elaphrosaurus* (Rauhut, 2003, p. 115).
P-30852	*Coelophysis bauri*	—L-shaped lacrimal: found in all theropods except *Herrerasaurus* (Rauhut, 2003, p. 55). —Lack of promaxillary foramen: diagnostic of *Coelophysis* (Ezcuraa, 2006; Ezcurra and Novas, 2006). —Width of the base of the lacrimal is greater than 30 percent of its height: distinguishable character of *Coelophysis bauri* from *C. rhodesiensis* (Bristowe and Raath, 2004, p. 39).
P-31661	Coelophysidae indet.	—More than three sacral vertebrae: found in all theropods except for *Herrerasaurus*, *Staurikosaurus* and *Eoraptor* (Rauhut, 2003, p. 84-85). —Caudoventral process of the coracoid tapering and projected beyond the caudal margin of the glenoid fossa: diagnostic of the Coelophysidae (Ezcurra, 2006; Ezcurra and Novas, 2006).
P-31293	Saurischia indet.	—Fibular condyle on proximal tibia confluent with cnemial crest anteriorly in proximal view: found only in *Herrerasaurus*, *Staurikosaurus*, *Coelophysis*, *Gojirasaurus*, *Liliensternus liliensterni*, *Dilophosaurus*, *Segisaurus* and *Elaphrosaurus* (Rauhut, 2003, p. 115).
P-54617	Derived coelophysoid	—Lateral process on distal tibia polygonal-shaped: found in all coelophysoids more derived than *Dilophosaurus* (Sereno, 1999).
P-54618	*Coelophysis* sp.	—Distal end of femur anteroposteriorly broad and distally flattened: found only in *Eoraptor*, *Herrerasaurus*, *Staurikosaurus*, *Coelophysis* and *Dilophosaurus* (Rauhut, 2003, p. 114-115). —Proximal surface of femur with transversely extended groove: diagnostic of *Coelophysis* sp. (Ezcurra, 2006; Ezcurra and Novas, 2006).
P-54619	*Coelophysis* sp.	—Distal end of femur anteroposteriorly broad and distally flattened: found only in *Eoraptor*, *Herrerasaurus*, *Staurikosaurus*, *Coelophysis* and *Dilophosaurus* (Rauhut, 2003, p. 114-115). —Proximal surface of femur with transversely extended groove: diagnostic of *Coelophysis* sp. (Ezcurra, 2006; Ezcurra and Novas, 2006).
P-54620	*Coelophysis* sp.	—Anterior trochanter on femur triangular: found only in *Herrerasaurus*, *Coelophysis*, *Liliensternus liliensterni*, and *Dilophosaurus* (Rauhut, 2003, p. 113). —Proximal surface of femur with transversely extended groove: diagnostic of *Coelophysis* sp. (Ezcurra, 2006; Ezcurra and Novas, 2006).
UCMP 129618	Derived coelophysoid	—Dolichoiliac pelvis: found in *Coelophysis* and derived theropods, not found in *Eoraptor*, *Herrarsaurus* and *Staurikosaurus* (Rauhut, 2003, p. 102). —Articular facet of pubic penducle of ilium with pronounced kink and anterior part facing almost entirely anteriorly: found in *Coelophysis*, *Liliensternus liliensterni*, *Lophostropheus airlensis* and ornithomimosaurs (Rauhut, 2003, p. 107). —Anterior trochanter on femur triangular: found only in *Herrerasaurus*, *Coelophysis*, *Liliensternus liliensterni*, and *Dilophosaurus* (Rauhut, 2003, p. 113). —Distal end of femur anteroposteriorly broad and distally flattened: found only in *Eoraptor*, *Herrerasaurus*, *Staurikosaurus*, *Coelophysis* and *Dilophosaurus* (Rauhut, 2003, p. 114-115). —Fibular condyle on proximal tibia confluent with cnemial crest anteriorly in proximal view: found only in *Herrerasaurus*, *Staurikosaurus*, *Coelophysis*, *Gojirasaurus*, *Liliensternus liliensterni*, *Dilophosaurus*, *Segisaurus* and *Elaphrosaurus* (Rauhut, 2003, p. 115). —Lateral process on distal tibia polygonal-shaped: found in all coelophysoids more derived than *Dilophosaurus* (Sereno, 1999).

Norian-Rhaetian?) (Lucas and Tanner, 2007). The presence of the phytosaur *Redondasaurus* in the Whitaker quarry fauna (Rinehart et al., 2004) demonstrates that the assemblage pertains to the Apachean land-vertebrate faunachron (lvf) of Lucas and Hunt (1993).

The Snyder quarry is stratigraphically lower than the Whitaker quarry. It is in the upper part of the Painted Desert Member of the Petrified Forest Formation (Lucas et al., 2003, 2005). The fauna of the Snyder quarry includes the aetosaur *Typothorax coccinarum* and the phytosaur *Pseudopalatus buceros*, both of which indicate a Revueltian (early-middle Norian) age (Heckert et al., 2005).

UCMP 129618 was recovered from strata low in the Painted Desert Member of the Petrified Forest Formation, Petrified Forest National Park, Arizona (Heckert and Lucas, 2002). This record of *Coelophysis bauri*, like the Snyder quarry record, also is Revueltian.

These additional records extend the biostratigraphic range of *Coelophysis bauri* from Apachean to early Revueltian (Fig. 11). This indicates that the temporal range of *C. bauri* encompasses much of Norian time. Thus, the biostratigraphic utility of *C. bauri* is reduced, and it is no longer an index fossil of the Apachean (e.g., Lucas, 1998).

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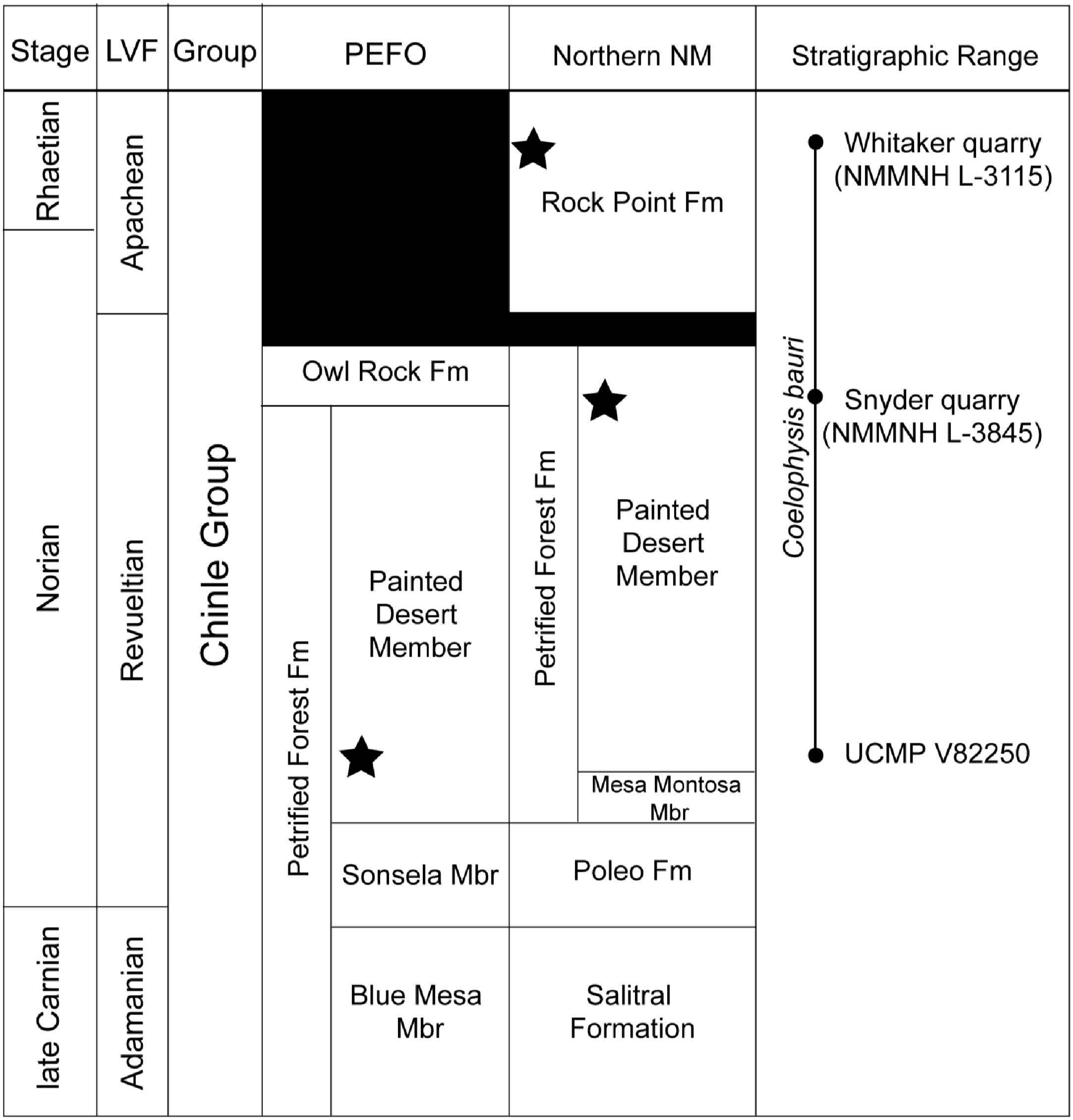

FIGURE 11. Biostratigraphic distribution of *Coelophysis bauri* occurrences in the southwestern USA. See text for discussion.

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APPENDIX

Measurements (in mm) of selected elements from the Snyder quarry *Coelophysis bauri* sample and UCMP 129618. In reference to proximal and distal limb bones, the length is an anteroposterior measurement, whereas the width is a mediolateral measurement. Midshaft diameter is midshaft length/midshaft width. Abbreviations: AP = as preserved; NA = not applicable, indicating a feature is not preserved in a specimen; NM = not measured, the feature is present but due to preservation cannot be measured; * = based on metrics in Padian (1986); ** = measurements of NMMNH C-3086 a cast of the right ilium, proximal and distal femora, both tibiae and left fibula of UCMP 129618.

Skull Metrics

Coelophysis bauri

Specimen Number	Description	Length of left premaxilla	Height of left premaxilla	Length of right maxilla	Length of left lacrimal	Height of left lacrimal
NMMNH P-30852	Incomplete and partially disarticulated	25.9	13.1	98.2 AP	40.7	31.8

		Length of the base of the lacrimal	Length of left lower jaw	Length of right lower jaw	Length of ?cerato-branchials
		17.1	133.9	122.4	54.6/38.2

Vertebrae Metrics

Coelophysis bauri

Specimen Number	Description	Length of articulated vertebrae	Height of articulated vertebrae	Width of articulated vertebrae
NMMNH P-30852	Cervical vertebrae 3 and 4 articulated	78	18.1	13.7

Scapuocoracoid Metrics

Coelophysis bauri

Specimen Number	Left/Right	Description	Length	Height	Glenoid height
NMMNH P-31661	Left	Incomplete	32.7 AP	51.5 AP	11.9

Radius Metrics

Coelophysis bauri

Specimen Number	Left/Right	Description	Length	Midshaft width	Max. proximal length	Max. prox width	Max. distal length	Max. distal width
NMMNH P-31661	Right	Complete	51.8	3.4	7	4.2	4.8	5.9

Ilia Metrics

Coelophysis bauri

Specimen Number	Left/Right	Description	Length	Height	Iliac blade length	Acetabular length	Min. Acetabular height
NMMNH P-29047	Right	Missing iliac blade	41.4 AP	27.7 AP	NA	28.3	8.4
UCMP 129618	Right	Incomplete w/ fused incomplete pubis and ischium	211.4 AP**	117.5 AP**	164.6**	54.7 **	50 AP**

Ischium Metrics

Coelophysis bauri

Specimen Number	Left/Right	Description	Length	Length of ilia articular surface	Width of ilia articular surface
NMMNH P-29047	Right	Complete	115.3	16.6	8.9

Femora Metrics

Coelophysis bauri

Specimen Number	Left/Right	Description	Length	Midshaft width	Max. proximal length	Max. prox width	Max. distal length	Max. distal width
NMMNH P-29046	Left	Complete	155.5	11.7	12.2	25.7	20.5	22.6
NMMNH P-29046	Right	Midshaft break	112.9/47 AP	10.8	12.2	24.7	22.9	23.3
NMMNH P-54618	Right	Distal	89.1 AP	12.9	NA	NA	22.5	26.9
NMMNH P-54619	Right	Distal	100.1	13.7	NA	NA	26.1	27.3 AP
NMMNH P-54620	Right	Missing distal end	235 AP	22.4	23.1	38.7 AP	NA	NA
UCMP 129618	Left	Complete	245*	NM	24.4**	49**	43.9**	49.4**
UCMP 129618	Right	Missing ~10 mm of shaft	235*	NM	24.6**	50.0**	38.0 AP**	51.3**

Tibiae Metrics

Coelophysis bauri

Specimen Number	Left/Right	Description	Length	Midshaft width	Max. proximal length	Max. prox width	Max. distal length	Max. distal width
NMMNH P-29046	Left	Complete	164.0	10.0	27.9	18.5	13.8	17.9
NMMNH P-29047	Left	Proximal	47.6 AP	NA	25.3	16.7	NA	NA
NMMNH P-31293	Left	Midshaft break	115.1/25.5 AP	8.9	21.5	12.7	10.8	14.6
NMMNH P-54617	Right	Missing distal end	149.9 AP	8.3 AP	23.5	16.5	NA	NA
UCMP 129618	Left	Partial fused with left fibula	247**	18.2**	54.3**	35.3**	27.9**	34.9**
UCMP 129618	Right	Complete	261.4**	19.0**	54.3**	36.5**	27.8**	37.2**

Fused Tibia/Fibula Metrics

Snyder quarry large Coelophysid

Specimen Number	Left/Right	Description	Length	Midshaft width	Max. proximal length	Max. prox width	Max. distal length	Max. distal width
NMMNH P-29168	Right	Midshaft break	107.6/50.1 AP	17.5	44.2	46.5	19.4	39.4

Fibulae Metrics

Coelophysis bauri

Specimen Number	Left/Right	Description	Length	Max. proximal length	Max. prox width
NMMNH P-29046	Left	Proximal	34.6 AP	16.7	7.0
NMMNH P-29047	Left	Proximal	36.9 AP	15.0	5.3

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SPONGE-MICROBIAL STROMATOLITES AND CORAL-SPONGE REEF RECOVERY IN THE TRIASSIC OF THE WESTERN TETHYS DOMAIN

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The Lower and Middle Triassic carbonate successions of the Western Tethys domain (Alps, Carpathians, Germanic Basin) comprise very particular sponge-microbial stromatolites that formed within the extremely shallow, perilitoral zone (Szulc, 1997). The stromatolites are capping emergent oolitic bars or form the lining of deep (up to 1.5m) karstic fissures. The stromatolites are composed of interfingered, microbial laminites and small (< 0.5 cm), lenticular sponge bodies. They display a variety of morphology, ranging between mm-thin flat laminites to 50 cm-thick columnar fabrics. Internal structures are relatively poorly preserved, nonetheless the dictyid Hexactinellidea seem to be the main sponge component of the Triassic stromatolites. The aphanitic and peloidal automicrite carbonate fabrics typical of the spongean-microbial association are also recognizable.

The Lower Triassic sponge-microbial stromatolites could be recognized as a "disaster form" enabling survival and recovery of the sponge buildups after the Permian-Triassic extinction. Regarding the paleoecological context of this interval of the Phanerozoic, the stromatolites represent a "Lazarus form." These Lilliputian metazoan-bacterial buildups most likely enabled a survival and recovery of the reef-forming organisms after the P/T mass extinction.

In Middle Triassic times (Pelsonian), the hexactinellid sponges accompanied first by scleractinian corals gave rise to the oldest *in situ* reefs found in the Western Tethys province. The best developed Pelsonian sponge-coral buildups occur in Upper Silesia (Poland) where they form bioherms of some 2-80 meters across and several meters high (Szulc, 2000).

The sponge-coral buildups display a complex vertical succession typical of "catch up reefs" affected by the highstand, shallowing-upward trend in the basin. Generally, the buildup construction began with prostrate colonies of Hexactinellida sponges settled over subequal bioclastic dunes and formed thin (up to 3 cm) veneers perfectly mimicking disposition of the dune surface. The contribution of the sponge component grows upsection and they start to first form biostromal fabrics and afterward bioherms. With the further growth and relative shallowing, other organisms contributed to the reef community: crinoids, other species of sponges, brachiopods, serpulids, encrusting forams and scleractinian branched corals. The sponges and branched corals form domes and knobs clustered together. When the reef crest reached the surf zone, the encrusting corals (*Pamiroseris silesiaca*) became the main reef contributor typical of a highly turbulent environment.

The Silesian reefs developed within the storm wave zone and display a possible zooxanthellate association (Morycowa & Szulc, 2006).

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TECTONIC CONTROLS OF HIGH-FREQUENCY SEDIMENTARY CYCLES IN THE UPPER TRIASSIC DACHSTEIN PLATFORM CARBONATES, NORTHERN CALCAREOUS ALPS

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High-frequency cycles are common features of Triassic platform carbonates from the Western Tethys basins. The 4th and 5th-order cycles have been particularly intensively studied in the Middle Triassic of the Dolomites and in the Upper Triassic of the Dachstein platform. The cycles display both shallowing and deepening upward trends and encompass carbonates formed from subtidal to supratidal environments (Fischer, 1964).

The high-frequency cycles are commonly ascribed to glacio-eustasic mechanisms controlled by astronomical Milankovitch cycles. Recent radiometric data challenged the direct link between the orbital forces and these cycles for the Middle Triassic of the Dolomites (Mundil et al., 2003). Moreover, there is no evidence of Triassic glaciations, hence an alternative genetic model of the cyclicity is needed.

According to field revision of the Upper Triassic Dachstein carbonates, they display common features indicative of synsedimentary tectonic and seismic mobility. Very common are synsedimentary faults, reaching in scale from a few millimeters to meters. Many of the features previously interpreted as karstic fissuring appeared to be tectonic cracks. The brittle faults affected completely lithified carbonates and are commonly accompanied by breccias (e.g., hydraulic breccia) and by flowage of the unconsolidated sediments. The quake motion involved development of cm-sized recumbent folds, flowage deformations and dewatering structures. Particular records of paleoseismic events are *in situ* -deformed stromatolites. The stromatolites show brecciation, cracking and intrastratal liquefaction, obliterating the original laminated fabrics.

Common syndepositionary deformations indicate that the topographic and bathymetric changes of the Triassic carbonate platforms could be controlled by tectonic block movements. Paleoposition of all of the discussed platforms within strike slip zones confirms this presumption.

Considering the cyclic facies succession in terms of syndepositional tectonics, one cycle would reflect the crustal downwarp influencing platform subsidence (deepening trend) that became abruptly arrested and succeeded by rapid uplift during the elastic rebound. Such a course of deformations plausibly explains the direct switch off between the subtidal and subaerial paleoenvironments observed, e.g., in the Lofer cycles. In the opposite case (i.e., under an upwarping regime) one would observe a shallowing upward trend replaced by sudden sinking.

The proposed model of "swinging block" tectonics may be adequately referred to the recent counterparts particularly well recognized in the Chilean and North American western coastal margin. The measured elevation changes in these seismic areas reach rates of several mm/year during strain buildup The crustal swelling lasts for several hundreds to some thousands of years. The coseismic vertical displacement during elastic rebound event may reach values between several centimeters to several meters and takes less than several minutes time and may play havoc against the stroked perilitoral zone.

The radiometrically estimated period of the cycle from the Triassic of the Dolomites is shorter than 3000 years (Mundil et al., 2003). The quake recurrence intervals measured in subrecent examples from plate-boundary belts range between several hundreds and 3000 years. The concordance between the Triassic high-frequency cycles and the recent subsidence-effective earthquakes strongly supports the assumed working model. Also, the remarkable asymmetry of these cycles is plausibly explained in terms of intermittent strain accumulation and release as already postulated by Cisne (1986).

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INTERPRETING THE UPPER TRIASSIC CARBON ISOTOPE RECORD

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Carbon isotope analyses of Upper Triassic marine strata from multiple locations generally record an extended period of stability of the isotopic composition of the ocean atmosphere system during the Late Triassic. Although a minor positive shift may occur at the Carnian-Norian boundary (Muttoni et al., 2004), and a potential positive excursion has been reported from the Norian-Rhaetian boundary (Sephton et al., 2002; Ward et al., 2004), no excursions of significant magnitude or duration are noted in Upper Triassic strata older that latest Rhaetian. Significant negative excursions in the carbon isotope composition of organic matter have been identified in close proximity to the system boundary in a number of marine sections. For example, the sections at St. Audrie's Bay, southwest England (Hesselbo et al., 2002, 2004), Csövár, Hungary (Pálfy et al., 2001), and Tiefengraben, Austria (Kuerschner et al., 2007) display negative δ^{13}C excursions of approximately 2.0 to 3.0‰. Consistently, these excursions begin below the highest occurrence (HO) of conodonts, supporting their correlatability. At the Kennecott Point section in the Queen Charlotte Islands, Canada, a negative δ^{13}C excursion (of approximately 1.5-2.0 ‰) spans the TJB, beginning immediately below the HO of Triassic ammonites and radiolarians, and continuing above the lowest occurrence (LO) of Jurassic radiolarians (Ward et al., 2001, 2004; Williford et al., 2007). In the New York Canyon section of Nevada, USA, a negative δ^{13}C excursion of similar magnitude (about 2.0 ‰) also begins just below the HO of conodonts, Triassic ammonites (*Choristoceras crickmayi* and *Arcestes* spp.) and Triassic bivalves (Guex et al., 2004). Additionally, a similar trend has been claimed for several other sections based on the carbon-isotope composition of carbonate deposited in more proximal environments (e.g., Galli et al., 2005, 2007).

A negative δ^{13}C excursion for organic carbon in terrestrial environments also has been claimed for nonmarine strata encompassing the Triassic-Jurassic boundary (TJB), but these data are problematic (McElwain et al., 1999; Hesselbo et al., 2002). The presumption is that the marine excursion resulted from a drastic alteration of the δ^{13}C of the global CO_2 reservoir that similarly was recorded by vascular plants. However, published isotope analyses of plant macrofossils for TJB sections in Scania fail to exhibit this excursion in any fashion (McElwain et al., 1999). Data from Greenland display an apparent trend that appears to correlate with the marine data, although there is significant intersample δ^{13}C variability and therefore a lack of the consistency that is displayed in the marine record (McElwain et al., 1999; Hesselbo et al., 2002). Notably, terrestrial organic matter displays significant interspecific variations in isotopic composition due to variations in the organic composition. Furthermore, variations in the isotopic composition of plants may result from environmental factors other than the δ^{13}C of the atmosphere.

The widespread nature of the negative isotope excursion draws comparisons to other major paleontologic boundaries in which negative carbon isotope excursions are prominent features, such as the end-Permian (Holser and Magaritz, 1992; Magaritz et al., 1992), the end-Cretaceous (Kump, 1991) and the late Paleocene (Koch et al., 1992; Norris and Röhl, 1999), although these various isotopic events vary in their magnitude and duration. The significance and causes of most of these isotopic events are not yet fully understood, however, although diverse mechanisms have been proposed and various attempts have been made to explain them through mass-balance modeling (Kump and Arthur, 1999; Beerling and Berner, 2002; Berner, 2002; Dickens, 2003). Major changes in the carbon isotope composition of both organic matter and carbonate suggest a disruption of the carbon cycle of global extent; such a disruption may result from a variety of causes. Diagenesis can be ruled out where δ^{13}C displays parallel trends for both carbonate and organic matter becδuse diagenesis has little effect on the isotopic composition of organic matter (Kump and Arthur, 1999). The introduction of large volumes of isotopically light carbon into the global carbon reservoir will produce this parallel trend, but there are multiple sources of light carbon. Sudden decreases in primary productivity may result in a rapid buildup of light carbon in the carbon reservoir, and this mechanism has been offered to explain the shifts at the K-T boundary (Kump, 1991) and the end-Permian (Holser and Magaritz, 1992; Magaritz et al., 1992). However, Beerling and Berner (2002) and Berner (2002) have pointed out that the loss of primary productivity alone can account for no more than one-half of the observed isotopic shift. The rapid release of dissolved CO_2 derived from organic decomposition during ocean overturn may also introduce substantial volumes of light carbon; this process has been suggested to explain the end-Permian isotopic excursion (Knoll et al., 1996). Such an overturn should be recorded by deposition of anoxic ocean sediments, but widespread anoxia is not recognized at the TJB (Pálfy et al., 2001).

The dissociation of methane hydrates in ocean-floor sediments is now regarded widely as a likely source for the rapid introduction of large volumes of very light carbon (δ^{13}C = –60 to -65 ‰) to the ocean-atmosphere system (Dickens et al., 1995, 1997). In theory, once the release of sea-floor methane is triggered, ocean warming and dropping of the thermocline may result in continued dissociation and a "runaway greenhouse" effect (Dickens et al., 1995). The isotopic shifts at the end-Paleocene clearly coincide with a warming event of 5-7°C, the late Paleocene thermal maximum (LPTM). This event is now explained as the result of methane release, possibly triggered by a change in oceanic thermohaline circulation (Dickens et al., 1995). Additionally, methane release has been proposed to explain other isotopic excursions in the stratigraphic record, particularly, the end-Permian (Krull and Retallack, 2000; Wignall, 2001; Berner, 2002). Pálfy et al. (2001) proposed that CAMP eruptive activity in some way triggered methane release that led to biotic extinction at the system boundary. However, mass balance calculation of the volume of methane required to effect a significant isotopic shift in the ocean carbon reservoir raises questions regarding the potential to store sufficient quantities of methane in the warm ocean of the Late Triassic.

The eruption of large igneous provinces is, perhaps, not coincidentally, associated with the isotopic excursion events associated with some paleontologic boundaries, including the end-Permian (the Siberian traps eruption), the end-Triassic (CAMP), the end-Cretaceous (Deccan Traps), and the LPTM (the North Atlantic Igneous Province; Wignall, 2001). Although McElwain et al. (1999) initially suggested a major role of CAMP degassing of isotopically light CO_2 in driving the isotopic shift, subsequent authors have discounted this hypothesis on the basis that unreasonably large volumes of mantle-derived CO_2 with δ^{13}C = -5 to -6 ‰ are required to effect the observed shift. Notably, these calculations assume a deep mantle origin for CAMP magmas, an assumption not clearly supported by petrologic constraints. Wignall (2001) pointed out that much lighter CO_2 (δ^{13}C = -20 ‰) may be derived from the carbon in recycled lithosphere at subduction boundaries. Current understanding of the source of the CAMP magmas does not dictate against such recycling. Consequently, I propose an alternative to the currently popular *deus ex machina* of methane release; the consequences of the voluminous CAMP eruptions included the release of well over 1000 Gt of isotopically depleted C as CO_2. Moreover, the environmental consequences of the eruptions, including atmospheric opacity and acid fallout, forced a significant decline in primary productivity. Together, these effects produced the observed change in the isotopic composition of carbon in the ocean-atmosphere system and forced the biotic turnover that marks the system boundary.

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UPPER TRIASSIC CARBON ISOTOPE STRATIGRAPHY OF THE LAGRONEGRO SUCCESSION, SOUTHERN APENNINES, ITALY

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Abstract—We present a new carbon isotope stratigraphy for the Upper Triassic (Norian) to lowermost Jurassic (Hettangian) strata of the Lagronegro succession in the southern Apennines. Previously published data for these strata, the upper *Calcari con Selce* and lower *Scisti Silicei* formations, displayed evidence (covariance of δ^{13}C and δ^{18}O) of diagenetic alteration of the isotopic signature. The new data, from a section on Monte Sirino, appear to record the primary isotopic signature of the carbonate. These data are most notable for the lack of evidence of an isotopic excursion at the Norian-Rhaetian stage boundary. However, the sampling density does not allow close interpretation of the isotopic record at the system boundary.

INTRODUCTION

The decline in diversity during the Late Triassic is now recognized as the result of progressive and prolonged extinction, rather than as a single mass-extinction "event" (Hallam, 2002; Tanner et al., 2004; Lucas and Tanner, 2004). Examination of the stratigraphic record reveals that extinctions took place in a step-wise fashion through the Late Triassic. For example, the more than 150 ammonite genera and subgenera that existed during the Carnian were reduced to 90 in the Norian, and reduced again to 6 or 7 during the Rhaetian (Teichert, 1988). This indicates that the most significant ammonite extinctions were during or at the end of the Norian. Inspection of the Late Triassic bivalve record also suggests that extinctions for this group were distributed episodically throughout this interval. Most significant was the extinction of the cosmopolitan and abundant pectinacean *Monotis* at the end-Norian (Dagys and Dagys, 1994; Hallam and Wignall, 1997) Furthermore, conodonts suffered high rates of extinction throughout the Triassic (e.g., Clark, 1983; Sweet, 1988; Aldridge and Smith, 1993), and the largest drop in conodont diversity took place at the end of the Norian.

Various explanations have been offered for these extinctions, including both gradualistic and catastrophic mechanisms. Regression during the Rhaetian, with consequent habitat loss, is compatible with the disappearance of some marine faunal groups, but may be regional, not global in scale. Gradual, widespread aridification of the Pangaean supercontinent could explain a decline in diversity of terrestrial fauna during the Late Triassic, but suggests little about the marine realm. The presence of multiple impact structures with Late Triassic ages suggests the possibility of bolide impact-induced environmental degradation as a catastrophic forcing mechanism. Widespread eruptions of flood basalts of the Central Atlantic Magmatic Province (CAMP) apparently were synchronous with or slightly preceded the system boundary; emissions of CO_2 and SO_2 during these eruptions were substantial, but the specific environmental effects of outgassing of these lavas remains to be determined.

In several marine Upper Triassic-Lower Jurassic sections, significant negative excursions in the isotopic composition of organic matter have been noted near the system boundary (Hesselbo et al., 2002, 2004). At the New York Canyon section of Nevada, USA, for example, the negative δ^{13}C excursion (about 2.0 ‰) begins just below the highest occurrence (HO) of conodonts, Triassic ammonites (*Choristoceras crickmayi* and *Arcestes* spp.) and Triassic bivalves (Guex et al., 2004). Similarly, at the Kennecott Point section in the Queen Charlotte Islands, Canada, a pronounced negative δ^{13}C excursion (of approximately 1.5 – 2.0 ‰) begins slightly below the HO of Triassic ammonites and radiolarians, and extends to a level above the lowest occurrence (LO) of Jurassic radiolarians (Ward et al., 2001, 2004; Williford et al., 2007). Moreover, several European sections display significant negative δ^{13}C excursions, as at St. Audrie's Bay, southwest England (2.0 ‰; Hesselbo et al., 2002, 2004), Csövár, Hungary (2.0 ‰ Pálfy et al., 2001), and Tiefengraben, Austria (3.0 ‰; Kuerschner et al., 2007). Notably, in all of these sections, the excursion begins below the HO of conodonts and is succeeded by an interval of strata in which the isotopic composition of the organic matter returns to previous values, or is enriched. This positive excursion is succeeded, in turn, by an interval again displaying depleted isotopic values. Several examples have been offered of a similar trend in the carbon-isotope composition of carbonate (e.g., Pálfy et al., 2001; Galli et al., 2005, 2007).

In contrast to the negative excursion now associated with the system boundary, the extinctions at the Norian-Rhaetian boundary have been linked to a positive δ^{13}C excursion (Sephton et al., 2002; Ward et al., 2004). Increases in δ^{13}C are commonly regarded as a product of an increased rate of burial of organic carbon, which should produce parallel increases in the composition of both carbonate and organic carbon (Kump and Arthur, 1999). Sephton et al. (2002) suggested that ocean anoxia at the Norian-Rhaetian boundary resulted from conditions of a stratified ocean, sluggish circulation, and a low latitudinal gradient. These authors also presented nitrogen isotope evidence in support of this interpretation. More recently, Ward et al. (2004) have critiqued this work, noting that the section analyzed by Sephton et al. (2002) is severely condensed, as the entire Rhaetian is represented by only 10 m of section. Ward et al. (2004) also described a positive excursion in the isotopic composition of organic matter near the Norian-Rhaetian boundary at the Kennecott Point section in the Queen Charlotte Islands, also in British Columbia. Further, they noted that the excursion coincides closely with a severe reduction in *Monotis* in the section and a lithologic change from bioturbated to thinly laminated facies. Again, increased ocean anoxia is cited as the cause of the isotope enrichment. Of particular note, however, is that while the data of Sephton et al. (2002) suggest a pronounced excursion that is maintained over a (condensed) stratigraphic interval that corresponds to most of the Rhaetian stage, the data of Ward et al. (2004), from a greatly expanded section, display great complexity, with substantial variation in isotopic values over short intervals.

In a continuing attempt to increase understanding of the relationship between ocean chemistry and biotic events, we examined the carbon isotope stratigraphy of the Upper Triassic-Lower Jurassic section in the Lagronegro basin, southern Apennines, at Monte Sirino (Fig. 1). Tanner et al. (2006) previously examined the carbon isotope (from carbonate) stratigraphy of uppermost Triassic strata at a section near Pignola. In their study of 50+ m of strata encompassing the uppermost Norian and

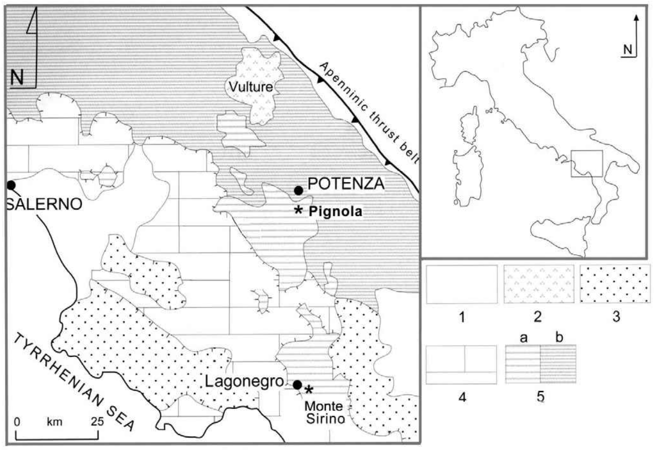

FIGURE 1. Geologic map of the southern Apennines with locations described in the text (adapted from Bazzucchi et al., 2005). Units on map as follow: 1) mostly Recent sediments; 2) Quaternary volcanics; 3) Cilento units; 4) Mesozoic platform carbonates; 5) units of the Lagronegro succession of Permian to Early Cretaceous age (5a) and Early Cretaceous to Miocene (5b).

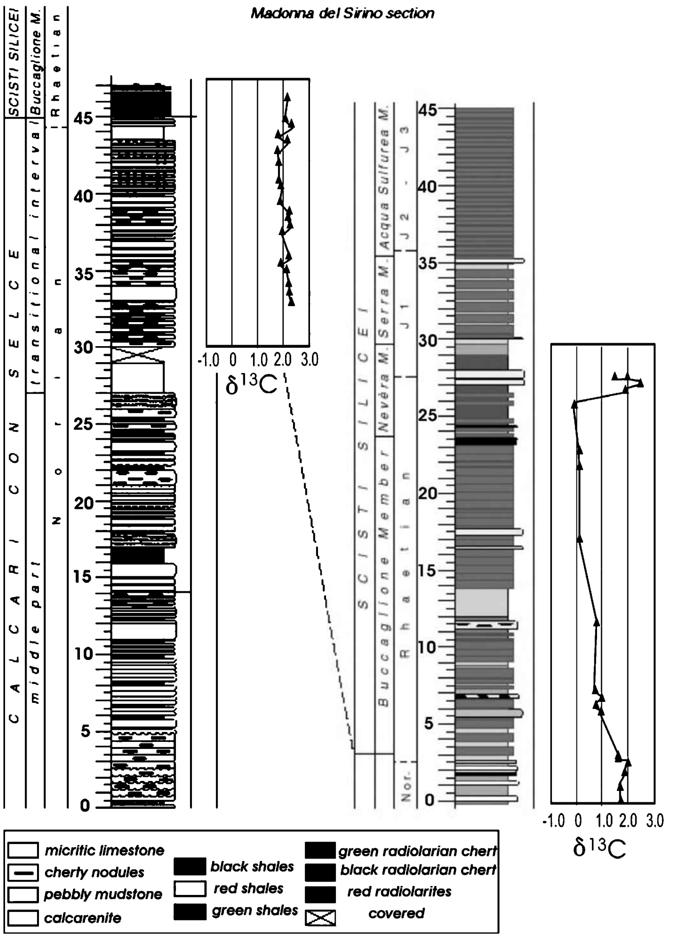

FIGURE 2. Lithostratigraphy and carbon isotope stratigraphy for the Monte Sirino section.

most of the Rhaetian, they found several negative excursions of $\delta^{13}C$ of significant magnitude. The largest, occurs slightly above the LO of *Misikella posthernsteini*, a conodont that marks the base of the Rhaetian stage (*sensu* Kozur and Mock, 1991). We note that Dagys and Dagys (1994) instead define the base Rhaetian by the LO of *M. hernsteini*, but these condonts co-occur at this stratigraphic interval (H. Kozur, pers. comm.). Another excursion, below the last *in situ* Triassic conodont, *M. ultima*, is consistent with the multiple short-duration carbon isotope excursions below the system boundary in other sections. Notably, however, the carbon and oxygen isotopes from the section Tanner et al. studied display some covariance, suggesting at least partial recrystallization of the carbonate from isotopically light formation waters. The section at Pignola analyzed by Tanner et al. (2006) occupied a medial position within the Lagronegro basin, and was located considerably more proximal than the Monte Sirino section studied here.

SETTING AND STRATIGRAPHY

Mesozoic through Cenozoic units of the Lagronegro basin comprise a substantial portion of the orogenic wedge of the southern Apennines (Fig. 1; Passeri et al., 2005; Cirapica, 2007). During the Mesozoic, the basin, a part of the Ionian Tethys, was located adjacent to one or more shallow carbonate platforms (e.g., the Apenninic and possibly the Apulian platforms; Ciarapica and Passeri, 2002; Finetti, 2004, 2005; Ciarapica and Passeri, 2005). The early Mesozoic succession in this basin records deepening as the shallow-water siliciclastics and limestones of the lowermost *Monte Facito* Formation (Lower to Middle Triassic) are succeeded by deeper water radiolarite facies deposited in the Ladinian (uppermost Monte Facito Formation) and are followed by the Upper Triassic and Jurassic *Calcari con Selce* and *Scisti Silicei* formations, possibly a consequence of transtensional tectonics due to the rifting of the Ionian Ocean (Ciarapica and Passeri, 2000; 2005).

The Upper Triassic-Jurassic Lagronegro succession is well exposed on the western flank of Monte Sirino, near the town of Lagonegro (Fig. 1). Nearly continuous outcrop occurs along a trail that connects the Madonna del Brusco Sanctuary to the Madonna del Sirino Sanctuary (Reggiani et al., 2005). The succession is composed of primarily cherty limestones and siliceous shales and radiolarites. The former characterize the *Calcari con Selce* Formation, and the latter the *Scisti Silicei* Formation. The transitional interval between these two formations is gradual and features interbedded lithologies characteristic of both formations, such as micritic limestones, radiolarian cherts and siliceous shales (Miconnet, 1983; Amodeo and Baumgartner, 1994; Amodeo, 1996; 1999). The prevalence of deeper water facies in this sequence indicates deposition of the succession in a distal part of the basin (Scandone, 1967; Reggiani et al., 2005).

The Monte Sirino section exposes 45 m of continuous section of the upper *Calcari con Selce* Formation, most of which consists of well-bedded micritic limestones, commonly with chert nodules. The uppermost 18 m are bracketed between two siliceous red shales horizons and are informally designated the “transitional interval” (Fig. 2). This interval differs from the major part of the *Calcari con Selce* by the greater component of siliceous shale and the presence of scattered radiolarites, and is correlatable to many other sections within the Lagronegro basin (Passeri et al., 2005). The red shale beds allow for precise correlation of the section between outcrops across switchback turns in the trail. The upper part of the *Calcari con Selce* has been well-dated with conodonts, including such upper Norian forms as *Epigondolella bidentata*, *E. postera* and *E. matthewi* (Reggiani et al., 2005). The Norian-Rhaetian stage boundary is placed within the upper red shale bed near the top of the transition zone based on the LO of *M. hernsteini* at this level in correlative sections (Dagys and Dagys, 1994; Bertinelli et al., 2005).

The overlying *Scisti Silicei* Formation is characterized by the absence of micritic limestone beds, consisting primarily of radiolarian-bearing siliceous shales and cherts with minor calcarenites. The lowermost member of the *Scisti Silicei*, the *Buccaglione* Member, comprises 21 m of thin-bedded red siliceous shales, black shales with green and black radiolarian chert layers, silicified calcarenites with cherty nodules, and a single 1-m thick calcirudite bed (Reggiani et al., 2005). Siliceous shales in the lower *Buccaglione* Member have yielded a well-preserved

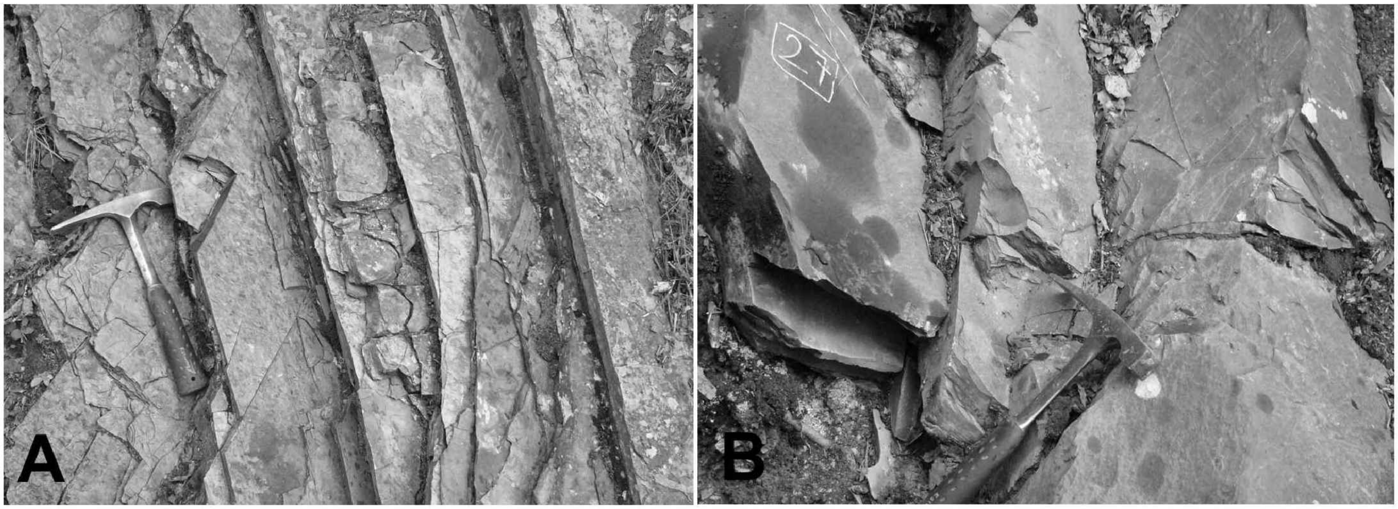

FIGURE 3. Outcrop views of the *Nevèra* Member, *Scisti Silicei* Formation, at Monte Sirino. A) Black shales in the uppermost Rhaetian section about 3 m below the system boundary; B) The lower of two calcarenite beds in the upper *Nevèra* Member. The system boundary is placed at the top of this bed (to the upper right).

and robust radiolarian assemblage referable to the early Rhaetian. Assemblages from the upper part of this member are referred to the uppermost part of the Rhaetian due to the presence of *Globolaxtorum tozeri* (Reggiani, et al., 2005).

The overlying *Nevèra* Member consists of ~6 m of black and green shales (Fig. 3A) with minor very fine-grained, partially to wholly silicified calcarenites (Fig. 3B). The shales of the *Nevèra* Member are barren, but the calcarenites yield pyritized radiolarians that probably are Triassic specimens with twisted spines, and potentially some primitive Jurassic spumellarians (Reggiani et al., 2005). The succeeding *Serra* Member, which consists mainly of red siliceous shales and thin red radiolarites, was not sampled for this study. Radiolarians in the lower part of this member include spumellarians referable to the Lower Jurassic (Reggiani et al., 2005). Based on this biostratigraphy, the system boundary occurs within the *Nevèra* Member between two calcarenite beds just below the base of the *Scisti Silicei* (Figs. 2, 3B; Reggiani et al., 2005).

METHODS

We analyzed the carbon and oxygen isotope composition of carbonate in 40 samples, representing 42 m of section (Fig. 2) from the upper *Calcari con Selce* (transitional interval) and lower *Scisti Silicei* (*Buccaglione* and *Nevèra* members). Sampling of the section included a repeat of about 2 m where the outcrop was correlated across a turn in the trail (i.e. the section is discontinuous). The analyses were conducted in the Stable Isotope Laboratory of the Department of Earth and Planetary Sciences at the University of New Mexico. Carbonate carbon and oxygen isotope ratios were measured by conventional phosphoric acid digestion methods using elemental analyzer continuous flow isotope ratio mass spectrometry with a Carlo Erba Elemental Analyzer coupled to a Finnigan Mat Delta Plus mass spectrometer. Results are reported in parts per thousand (‰) relative to the Vienna Pee Dee Belemnite standard (VPDB).

RESULTS

The isotopic composition of the carbonate demonstrates substantial consistency throughout the section (Figs. 2,4), falling within the range of +2.47 ‰ maximum and -0.02 ‰ minimum, maintaining an average $\delta^{13}C$ of +1.56 ‰. Values of $\delta^{18}O$ range from -3.58 ‰ to -6.2 ‰, with an average of -4.35 ‰ (Fig. 4). Several trends are discernable within these results. First, the lack of correlation (covariance) between $\delta^{13}C$ and $\delta^{18}O$ (Fig. 4), as well as the limited range of $\delta^{18}O$ values, suggests limited or no alteration of the carbonate by isotopically depleted pore waters. Thus, we are relatively confident that the carbon isotope values reported here represent the primary signature of the carbonate as originally precipitated from marine waters. By comparison, the data reported for the approximately correlative section at Pignola display a greater range of values of $\delta^{18}O$ and covariance of $\delta^{13}C$ and $\delta^{18}O$ at a significant level (see Tanner et al., 2006, fig. 6). Furthermore, the range of $\delta^{13}C$ values at Monte Sirino is substantially smaller than at Pignola, where the minimum value of $\delta^{13}C$ = -3.5 ‰. We conclude, therefore, that re-equilibration of the isotopic signature of the carbonate in this section was minimal and that the carbon isotope record at Monte Sirino represents a record of the primary (original) isotopic composition of the carbonate sediments. Conversely, the data reported from Pignola likely represent carbonate in which the isotopic composition possibly has been altered by diagenesis.

The significance of these new data is most apparent when combined with biostratigraphic constraints on the age of the strata. Sample density is greatest in the uppermost Norian and basal Rhaetian portion of the section (transitional interval and basal *Buccaglione* Member), due to the greater abundance of limestone beds (Fig. 2). Through this section, from 33 to 46.5 m before the break in the section at the turn in the trail, and 0 to 3 m after the section break, $\delta^{13}C$ values display very consistent values between a minimum of +1.6 ‰ to a maximum of 2.3 ‰. However, the sample density is considerably lower through most of the Rhaetian section (the remainder of the *Buccaglione* and lower *Nevèra* members) due to the substantially lower frequency of carbonate beds. Nevertheless, it is notable that $\delta^{13}C$ values decrease higher in the section and maintain values near 0 ‰ until the system boundary (within the *Nevèra* Member), where $\delta^{13}C$ recovers to values near and exceeding 2.0 ‰ (Fig. 2).

DISCUSSION

Sephton et al. (2002) first drew attention to the perceived positive (organic) carbon isotope excursion at the Norian-Rhaetian boundary, although as pointed out by Ward et al. (2004), the section studied by Sephton was condensed, and therefore the stratigraphic placement of the reported excursion is suspect. Ward et al. (2004), as described earlier, also reported a positive carbon isotope excursion at the Norian-Rhaetian boundary although their data across this boundary display a series of short-lived fluctuations, rather than a single, pronounced excursion. In particular, Ward et al. (2004) related these isotopic fluctuations to the disappearance of *Monotis*. Significantly, Williford et al. (2007) re-analyzed the section studied by Ward. They also documented a complex

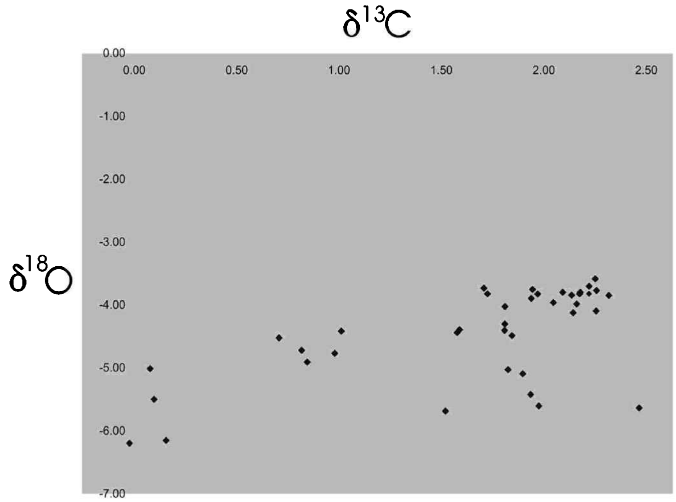

FIGURE 4. Bivariate plot of $\delta^{13}C$ and $\delta^{18}O$ for carbonate from the Monte Sirino section.

sequence of variation in $\delta^{13}C_{org}$, but, conspicuously, these data do not indicate any significant excursion in the vicinity of the stage boundary, nor did these authors describe one. Although our data are derived from analysis of carbonate, rather than organic carbon, our $\delta^{13}C_{carb}$ values appear to represent the primary carbon isotope signature. The $\delta^{13}C$ values we obtained are consistent across the Norian-Rhaetian boundary, indicating neither positive nor negative excursions. Thus we find little convincing evidence for a disruption of the global carbon cycle associated with the extinction event at this boundary.

In regard to the system (Triassic-Jurassic) boundary, our data offer less information. Due to the lower carbonate content of the Rhaetian strata, sample frequency was significantly lower (< 1 sample per two meters of section) than in the underlying Norian section (approximately 2 samples per meter of section). Notably, the data display consistently depleted carbon through the Rhaetian section, as compared to the underlying Norian section. This differs from the carbonate carbon isotope data published for most other sections. We suggest two tentative explanations for this difference. One possibility is that the much lighter organic carbon influences (or contaminates) the analyses in samples with a low carbonate yield, resulting in lower isotopic values. An alternative explanation is that some fractionation or bias toward depleted carbon operates under conditions of minimal carbonate precipitation or preservation, such as deeper marine environments where the sediment interface is near or below the CCD. We note, for example, that the $\delta^{13}C_{carb}$ reported from the deep-water section at Kennecott Point (Ward et al., 2004) is also considerably depleted compared to the values reported from marine sections on or marginal to carbonate platforms (e.g., Palfy et al., 2001; Galli et al., 2007). In this view, the lower $\delta^{13}C_{carb}$ values exhibited in the Rhaetian section are environmentally biased and do not represent the ocean carbon isotope composition of this time. Given this uncertainty about the Rhaetian isotope record at Monte Sirino, we cannot interpret the nature of the abrupt change to heavier $\delta^{13}C_{carb}$ values at the system boundary. These appear to represent normal values for carbonate derived from an adjacent platform, but given the lack of sample resolution, it is impossible to say if these values represent the ocean carbon composition immediately prior to the end-Triassic excursion, or the recovery of the carbon cycle following the initial negative excursion observed at most other sections.

CONCLUSIONS

The carbon isotope stratigraphy for both carbonate and organic carbon now has been published for numerous Upper Triassic-Lower Jurassic sections, including settings ranging from shallow platform to basinal, in both Tethyan and North American Cordilleran realms. A consensus has emerged from these studies that a distinct, short-lived negative isotope excursion occurred shortly before the end of the Triassic. Beyond this, however, there is little than can be agreed upon. Earlier reports of a positive isotope excursion at the Norian-Rhaetian stage boundary are not supported by the results of the present study (or other recent studies). Indeed, detailed carbon isotope records for extended stratigraphic intervals document considerable noise; the isotope stratigraphy records frequent, and sometimes pronounced shifts of short duration, rather than extended intervals of uniform isotopic composition. Serious questions remain regarding the causes and extent of variation of these variations in the isotopic record, and their relation to biotic events.

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NEW DATA ON THE LATE TRIASSIC (NORIAN-RHAETIAN) FORAMINIFERANS OF THE WESTERN PRECAUCASUS (RUSSIA)

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The Upper Triassic successions of the Western Precaucasus are very interesting because it occupies a key geographic and geological position between the Caucasus, Central Asia and Europe (Fig. 1.). The uppermost part of the Upper Triassic in the Western Precaucasus is the limestone-clay unit in the Regional Stratigraphical Scheme of the Western Precaucasus and Caucasus (Oleynikov and Rostovtsev, 1979). It correlates to the Upper Norian (Upper Triassic). These deposits lie with unconformity on Paleozoic or Triassic deposits (Ladinian-Carnian, Chelbasskaya Formation) and are unconformably overlain by Jurassic or Lower Cretaceous rocks. Bivalves (*Monotis salinaria* (Schloth.) and others) and brachiopods (*Oxycolpella*) occur in the limestone-clay unit. Besides this unit, there are deposits in several wells of the Western Precaucasus, which correspond to the Upper Triassic or Upper Triassic/Lower Jurassic. In some unpublished reports there are some references to the Late Triassic and Late Triassic/Early Jurassic foraminiferal assemblages. The first paper with references to foraminiferans from the different areas of the Western Precaucasus and levels of the Triassic was published by Bigun and Pinchuk (2003), but some data in this paper are not complete.

In the framework of this research, diverse foraminiferal assemblages were found in three wells of the Western Precaucasus: Severo-Nekrasovskaya N 1, Chernigovskaya N 1 and Molodezhninskaya N 4. In the Severo-Nekrasovskaya area, well N 1 (depth 3555-3560 m), I have found a foraminiferal assemblage from the Triassic- Jurassic stratigraphical interval. This level is represented by limestone and clay beds. Foraminiferans were studied in thin-sections from limestones. This assemblage consists of *Cornuspira*? sp., *Cornulocilina* ex gr. *C. orbiculare* (Burbach), *Ophthalmidium lucidum* (Trifonova), *Quinqueloculina*? ex gr. *Q. kunaensis* Antonova, *Dentalina subsiliqua* Franke, *Nodosaria* ex gr. *N. nitidana* Brand, *N.* spp., *Frondicularia* ex gr. *F. xiphoidea*, *F.* sp., *Lenticulina subquadrata* (Terquem), *L.* sp. and *Astacolus* sp. From the Chernigovskaya area, well N 1, foraminiferal assemblages were studied in thin-sections from two limestone levels (depths 3484-3490 m and 3514-3519 m). Bigun and Pinchuk (2003) correlate these levels to the Norian. *Permodiscus* ex gr. *P. pragsoides* Oberhauser, *Semiinvoluta clari* Kristan, *S. violae* Blau, *Trocholina turris* Frentzen, *Sigmoilina*? sp., *Nodosaria* spp., *Pseudonodosaria vulgata multicamerata* Kristan-Tollmann and *Frondicularia*? sp. were found in the first limestone level, and the second level contain *Semiinvoluta clari* Kristan, *S. violae* Blau, *Trocholina turris* Frentzen, *Piriniella blindi* Blau, *Sigmoilina*? sp., *Nodosaria* spp., *Pseudonodosaria* sp. and *Lenticulina* sp. The genera and species composition of these two assemblages are very similar. In the Molodezhninskaya area, well N 4 (depth 2409-2414 m), there are diverse foraminiferal assemblages, which were studied in thin-sections from one limestone level. Bigun and Pinchuk (2003) correlate these rocks to the Middle Triassic and list only three foraminiferal genera. This assemblage consists of *Auloconus permodiscoides* (Oberhauser), *Triasina*? sp. (*T.* ex gr. *T. oberhauseri* Koehn-Zaninetti et Broennimann), *Coronipora austriaca* Kristan, *C. etrusca* (Pirini), *Trocholina turris* Frentzen, *Ophthalmidium lucidum* (Trifonova), *Quinqueloculina nucleiformis* Kristan-Tollmann, *Sigmoilina schaeferae* Zaninetti, Altiner, Dager et Ducret, *Lenticulina varians typica* Franke and *Duostomina*? ex gr. *D. rotundata* Kristan-Tollmann.

The assemblage from the Severo-Nekrasovskaya N 1 has many species that occur in the Lower Jurassic and Upper Triassic of Europe (Antonova and Pinchuk, 1991; Efimova, 1991; Kristan-Tollmann, 1964; Salaj et al., 1983). Therefore, the above mentioned beds with this assemblage can be correlated to the Lower Jurassic and Upper Triassic. The assemblage of the Chernigovskaya N 1 consists of forminiferans that are more characteristic of the Upper Triassic and has some Early Jurassic species (Antonova and Pinchuk, 1991; Blau, 1987a, 1987b; Efimova, 1991; Kristan-Tollmann, 1964; Salaj et al, 1983; Vuks, 2000). So, this assemblage can correspond to coeval assemblages from the Lower Jurassic and Upper Triassic of Europe. In the Molodezhninskaya N 4 well, foraminiferans are more typical of the Upper Triassic (Norian-Rhaetian) (Kristan-Tollmann, 1964; Salaj et al, 1983; Efimova, 1991; Vuks, 2000). *Triasina*? sp. (*T.* ex gr. *T. oberhauseri* Koehn-Zaninetti et Broennimann) and *Duostomina*? ex gr. *D. rotundata* Kristan-Tollmann are the most important species for the definition of age, but they are not well preserved. Nevertheless, this assemblage is similar to the Norian-Rhaetian assemblages from the Western Caucasus and other regions of Europe, and it can be correlated to the Norian-Rhaetian.

FIGURE 1. Studied area of the Late Triassic of the Western Precaucasus.

The studied deposits correspond to different stratigraphic levels of the Triassic and Triassic-Jurassic according to these results. The studied rocks from well N 1 of the Severo-Nekrasovskaya area and well N 1 of the Chernigovskaya area correspond with the Upper Triassic and Lower Jurassic. First, the Norian-Rhaetian foraminiferal assemblage is found in well N 4 of the Molodezhninskaya area. Two of the above–mentioned levels with foraminiferans are very good correlative levels for interregional correlation of the described beds from the Upper Triassic and Upper Triassic/Lower Jurassic of the Western Precaucasus. The generic compositions of the presented foraminiferal assemblages are similar to the composition of the assemblages from the Upper Triassic of the Western Caucasus, Western Carpathians, and Alps.

So, the present research demonstrates more completed lists of foraminiferans and more precise correlation than were presented by Bigun and Pinchuk (2003).

In the general picture of Triassic foraminiferal evolution in the world there are several points of radiations and development of rich foraminiferal communitues. Among them there is one point in the Norian-Rhaetian, which has a place in the Western Precaucasus, too, according to the results of this research. Besides, data of this study partly confirm the results of previous researchers, which are in unpublished reports. The existence of similar foraminiferal assemblages from the Caucasus and Precaucasus to Alps and Carpathians allows us to mark the possibility of migration of the benthic foraminiferans between these paleobasins. Finally, in the territory under consideration there are diverse foraminiferal communities, which indicate a good paleoenvironmental situation for the development of the benthic fauna. So, the results of this study allow us to obtain more detail data about the distribution of foraminiferans in the Triassic and Triassic/Jurassic of the Western Precaucasus. Thus, these data are a new contribution to the creation of a more complete picture of biotic evolution in this territory.

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UPPER TRIASSIC RADIOLARIA AND CONODONTS FROM SAN HIPÓLITO FORMATION, BAJA CALIFORNA SUR, MEXICO

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Late Triassic (late Norian-Rhaetian) conodonts and radiolarians are reported from three members of the San Hipólito Formation, part of the Vizcaino terrane. This formation consists of 2400 m of marine sedimentary rocks that overlie pillow basalts of the La Costa Ophiolite. It is divided into four informal members: from the base, chert, limestone, breccia and sandstone. These members range in age from Late Triassic (?Carnian/Norian) to Early Jurassic (late Pliensbachian). The composition of these volcanic and tuffaceous rocks indicates that the San Hipólito Formation was deposited adjacent to an active oceanic volcanic arc.

The conodont and radiolarian faunas of the San Hipólito Formation are intercalibrated utilizing the Rhaetian radiolarian zonation from Queen Charlotte Islands (QCI), British Columbia, Canada, and both European and North American conodont zonations. Collectively, they show that the limestone member is late Norian based on conodonts of the *bidentata* Zone, and sparse radiolarian fauna of the *Betraccium deweveri* Zone. The overlying breccia member includes re-worked upper Norian limestone and questionably includes basal Rhaetian radiolarians.

The upper sandstone member is Rhaetian, but neither the conodonts nor the radiolarians indicate latest Rhaetian: it includes common and variably preserved representatives of the *Proparvicingula moniliformis* Zone (lower to middle Rhaetian), and abundant and well preserved faunas assigned to the *Globolaxtorum tozeri* Zone (upper Rhaetian). This fauna is dominated by species of *Canoptum*, *Citriduma*, *Fontinella*, *Globolaxtorum*, *Haeckelicyrtium*, *Laxtorum* and *Livarella.* Conodont faunas from the sandstone member include species of *Epigondolella* that are well known in the Rhaetian of North America, accompanied by elements of *Misikella*, *Oncodella*, and *Zieglericonus* that are better known from low latitude Eurasian Tethys but which are rare in North America.

The radiolarians from the sandstone member compare closely with the Rhaetian faunas from the Sandilands Formation of QCI, but there is minor variation in the range of a few species, and other taxa occur that characterize low latitude regions of Tethys, i.e. the Philippines, central Japan and Turkey, but are unknown in QCI. Biogeographically and/or paleoecologically, the Baja faunas appear to be intermediate between those of eastern Panthalassa and Tethys. Understanding the affinity between Baja radiolarian and conodont faunas and those of more Tethyan regions may help to determine the position of the Vizcaíno terrane during the Late Triassic-Early Jurassic.

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THE PERMO-TRIASSIC CRISIS IS PROLONGED, AND THE PTB MASS EXTINCTION IS MULTI-PHASE

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The end-Guadalupian and the Permian-Triassic boundary (PTB) extinctions constitute two phases of a biotic crisis. Following the end-Guadalupian extinction phase, the Paleozoic biota underwent a steady decline through the Lopingian (Late Permian), resulting in their decimation at the PTB level. This trend coincided with the integration of Pangea and related global changes, including the palaeomagnetic shift from a stable reversed superchron to the Permo-Triassic Mixed Superchron (PTMS), double-phase volcanism (Emeishan and Siberia Traps) and the greatest Phanerozoic regression. The extinction at the end of the Guadalupian and that marking the end of the Permian are thus related. The subsequent recovery of the biota occupied the whole of the Early Triassic. Several phases of perturbations in $\delta^{13}C_{carb}$ occurred through a similar period, from the Late Wuchiapingian to the end of the Early Triassic. Therefore, the Permian-Triassic crisis was protracted, and spanned Late Permian and Early Triassic time.

The mass extinction at the Permian-Triassic Boundary (PTB) is said to have been abrupt (at the base of bed 25) and probably caused by an extraterrestrial impact. However, evidence from the Global Stratotype Section and Point (GSSP) of the base of the Induan at Meishan, China, shows that the biotic crisis began prior to bed 25 at which the postulated impact event occurred. Evidence of such a prelude occurs in other sections in South China, and in central and western Tethyan regions. This event is characterized by the extinction of a range of faunas, including corals, deep-water radiolarians, most fusulinids and pseudotirolitid ammonoids, and many Permian brachiopods. In all sections, this extinction level is usually a few decimeters to meters below that of the main mass extinction in the event beds (25 and 26) at Meishan, and their correlatives elsewhere.

Research advances related to the biotic crisis, molecular fossils and volcanism show that there is a second PTB extinction at bed 28 and its equivalents in South China and Tethys. This is the epilogue of the PTB extinction. Hence, the extinction associated with the PTB occurred in two episodes, the main act (accompanied with the prelude) and the epilogue. The prelude commenced at bed 24, prior to beds 25 and 26 at Meishan and coincided with the end-Permian regression. The main act happened in beds 25 and 26 at Meishan. The epilogue occurred in the late Griesbachian bed 28. The temporal distribution of these episodes constrains the interpretation of mechanisms responsible for the greatest Phanerozoic mass extinction, particularly consideration of the significance of a postulated bolide impact that may have occurred about 25,000 years after the prelude.

The prolonged and multi-phase nature of the Permo-Triassic crisis favors mechanisms of Earth's intrinsic evolution rather than an extraterrestrial catastrophy . The most significant regression in the Phanerozoic, the paleomagnetic disturbance of the PTMS, widespread extensive volcanism, and other events, may all be related, through deep-seated processes that occurred during the integration of Pangea. These combined processes could be responsible for the profound changes in marine, terrestrial and atmospheric environments that resulted in the end-Permian mass extinction. Bolide impact is possible but is neither an adequate nor a necessary explanation of these changes.

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SEDIMENTARY FRAMEWORK OF THE LOWER BLACK BEAR RIDGE SECTION, BRITISH COLUMBIA: A POTENTIAL CARNIAN-NORIAN BOUNDARY GSSP

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The upper Ludington and lower Pardonet formations at Black Bear Ridge, northeastern British Columbia, Canada, represent a continuously exposed succession through the upper Carnian and lower Norian (Upper Triassic). These strata were deposited in a deep marine setting (distally steepened carbonate ramp/medial to distal slope) on the northwestern margin of the Pangean supercontinent. The Black Bear Ridge section is apparently continuous, with no evidence for either subaerial exposure or submarine erosion. The absence of erosional scours in the study interval confirms emplacement of these strata below both fairweather and storm wave base.

The Carnian-Norian boundary interval at Black Bear Ridge is dominated by event beds, particularly those resulting from sediment gravity flows. Upper Carnian strata, primarily assigned to the Ludington Formation at Black Bear Ridge, record an upward transition from moderate-scale, olistolith-bearing debris flow deposits (debrites) to medium/thin-bedded turbidites remobilized as small-scale sediment slump/slides. The Carnian-Norian boundary interval and the lower Norian succession is dominated by medium- to thin-bedded calcareous turbidites and lesser hemipelagic suspension deposits.

Diverse and abundant fossil assemblages, particularly conodonts and bivalves, occur within the study interval. Despite post-depositional sediment remobilization conodont faunal successions indicate that the Black Bear Ridge section represents a complete, continuous Carnian-Norian boundary succession. Rapid and relatively continuous sedimentation is attested to by the thickness of the section, the abundance of calcareous turbidites and the thin nature of intercalated hemipelagic beds.

Abundant fossils, evidence of continuous and rapid sedimentation and minimal alteration by tectonic disturbances, metamorphism or diagenesis make Black Bear Ridge an excellent candidate Global Stratotype Section and Point (GSSP) for the Carnian-Norian boundary.