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New Mexico Museum of Natural History & Science

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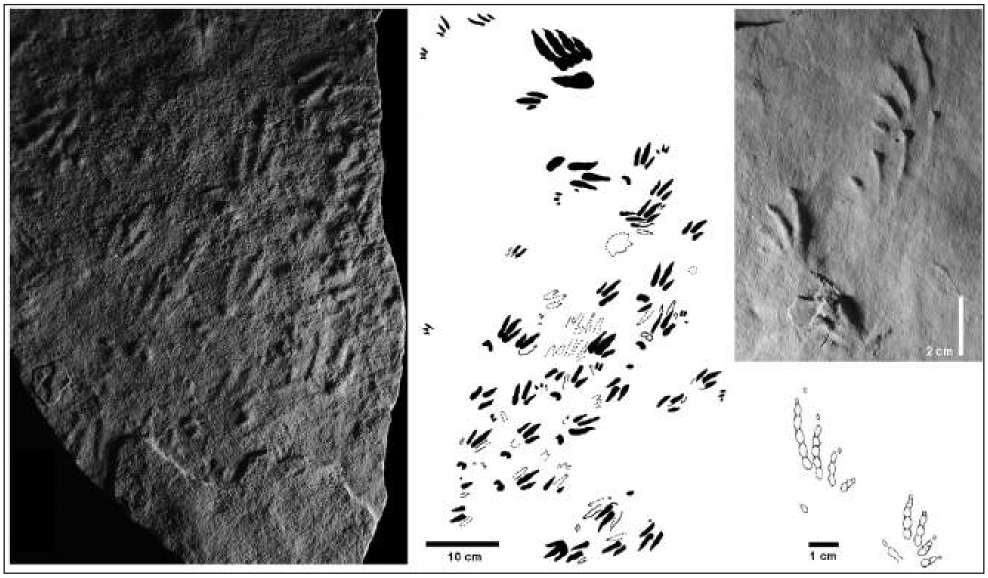
THE TRIASSIC TETRAPOD FOOTPRINT RECORD



by

HENDRIK KLEIN AND SPENCER G. LUCAS

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Cover illustration: Middle Triassic (Anisian) footprint assemblages. **Left and center:** Slab with juvenile specimens of *Chirotherium ferox* co-occurring with *Rhynchosauroides* isp. and *Synaptichnium pseudosuchoides* (top) from Eschenbach Formation, Germany. **Right (top and bottom):** *Rhynchosauroides tirolicus* from Middle Triassic of Northern Italy. From Haubold and Klein (2002), Klein and Lucas (2018), Avanzini and Renesto (2002).

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THE TRIASSIC TETRAPOD FOOTPRINT RECORD

HENDRIK KLEIN AND SPENCER G. LUCAS

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THE TRIASSIC TETRAPOD FOOTPRINT RECORD

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Abstract—Triassic tetrapod footprints have been studied since the 1830s and are now known from all of the World's continents. An ichnotaxonomic revision of all Triassic tetrapod ichnogenera recognizes 34 valid ichnogenera: *Anshunpes, Apatopus, Atreipus, Banisterobates, Batrachichnus, Batrachopus, Brachychirotherium, Brasilichnium, Capitosauroides, Characichnos, Chelonipus, Chirotherium, Dicynodontipus, Dikoposichnus, Dolomitipes, Eoanomoepus, Eosauropus, Eubrontes, Evazoum, Grallator, Gwyneddichnium, Isochirotherium, Pengxianpus, Pentasauropus, Procolophonichnium, Protochirotherium, Protorodactylus, Pseudotetrasauropus, Rhynchosauroides, Rotodactylus, Synaptichnium, Tetrasauropus, Therapsipus and Trisauropodiscus.* A comprehensive, ichnospecies-level ichnotaxonomic revision of chirotheriid footprints recognizes the following ichnospecies as valid: *Brachychirotherium hassfurtense, B. thuringiacum, B. parvum, Chirotherium barthii, C. ferox, C. ladinicum, C. postchirotherioides, C. ischigualastianum, C. rex, C. sickleri, Isochirotherium soergeli, I. herculis, I. coltoni, I. lomasi, I. marshalli, I. coureli, I. felenci, Protochirotherium wolfhagense, P. hauboldi, Synaptichnium pseudosuchoides, S. diabloense, S. cameronense* and *S. kotanskii*. A comprehensive review of the geographic and stratigraphic distribution of Triassic footprints identifies five tetrapod biochrons of Triassic age, mostly based on archosaur footprint ichnotaxa: (1) Earliest Triassic dicynodont footprints of Lootsbergian (= latest Changshingian-Induan) age; (2) *Protochirotherium* in strata of Nonesian age (=Olenekian); (3) The appearance of *Chirotherium barthii* and *C. sickleri*, *Rotodactylus*, *Isochirotherium* and *Synaptichnium* ("*Brachychirotherium*") roughly demarcates the Nonesian-Perovkan (late Olenekian-Anisian) transition; (4) The appearance of tridactyl footprints and quadrupedal to bipedal trackways of the *Atreipus*-*Grallator* type ("*Coelurosaurichnus*") demarcates the late Perovkan-Berdyankian (= late Anisian-Ladinian); and (5) *Brachychirotherium* (*sensu stricto*) appears at the beginning of the Otischalkian (= early Carnian) and is a characteristic ichnotaxon of the Late Triassic. Triassic tetrapod footprint assemblages can be assigned to the five archetypal tetrapod footprint ichnofacies (*Batrachichnus, Brontopodus, Grallator, Chelichnus* and *Characichnos*) and encompass diverse ichnocoenoses. An ichnological perspective based on footprints on Triassic tetrapod evolution reaches the following conclusions: (1) the tetrapod-footprint record lends no support to identification of a mass extinction of tetrapods across the Permo-Triassic boundary; (2) the upright gait originated during the Permian but was employed by diverse taxa, many bipedal, during the Triassic; (3) dicynodont therapsids diminished during the Triassic from abundant in the Early Triassic, to extinct late in the Triassic, whereas cynodonts were much more abundant and diverse during the Triassic; (4) the oldest turtle fossils are Early Triassic footprints, which significantly predate the oldest turtle body fossils, which are of Late Triassic (Carnian) age; (5) the oldest dinosaur body fossils are of Late Triassic (Carnian) age, but some footprints of Middle Triassic age were plausibly made by dinosaurs; and (6) both the body fossil and footprint record indicate a prolonged interval of high extinction rates and low origination rates of tetrapods across the Triassic-Jurassic boundary, not a single mass extinction of tetrapods.

INTRODUCTION

In 1834, German mining geologist Friedrich August von Alberti coined the term Trias, and Triassic won rapid acceptance as the name of a time period in the geological timescale.

Only one year later, in 1835, German zoologist J. J. Kaup applied binomial nomenclature to Triassic tetrapod footprints from Germany, naming them *Chirotherium barthii* and *C. sickleri*. Thus, Triassic tetrapod footprints have been studied since at least the inception of the chronostratigraphic concept of the Triassic.

We have long known that the Triassic world was a Pangean world, in which the vast supercontinent stretched nearly from pole to pole, surrounded by the great ocean Panthalassa, which had a huge embayment into eastern Pangea that we call the Tethyan seaway, or simply Tethys. Across Triassic Pangea, depositional settings conducive to the preservation of Triassic footprints as fossils were widespread (Figs. 1-2). These were primarily the sites of deposition of siliciclastic red beds by fluvial and lacustrine depositional systems. However, they also include carbonate systems in paralic settings near large lakes and the sea, especially the shorelines of Tethys and its epeiric embayments into parts of Pangea. Indeed, in some Triassic strata, tetrapod footprints are among the most common fossils found and often the only fossils to document the former presence of particular kinds of tetrapods. Triassic tetrapod footprints have thus proven to be scientifically valuable as paleobiogeographic records and as biostratigraphic datums.

In the long history of tetrapod evolution, the Triassic stands out as a critical juncture. After the extinctions of the middle and late Permian, the tetrapod fauna was transformed from synapsid dominated to archosaur dominated—changes that were spread out through much of Triassic time. These changes were also accompanied by the origination of several significant tetrapod groups on land, notably the turtles, crocodylomorphs, dinosaurs and mammaliaforms. Particularly significant were substantial innovations in tetrapod locomotory style—posture and gait—especially the evolution of the upright posture of dinosaurs and active flight in pterosaurs. Triassic tetrapod footprints provide prima facie understanding of these changes that enhances our appreciation of them based on the body-fossil record.

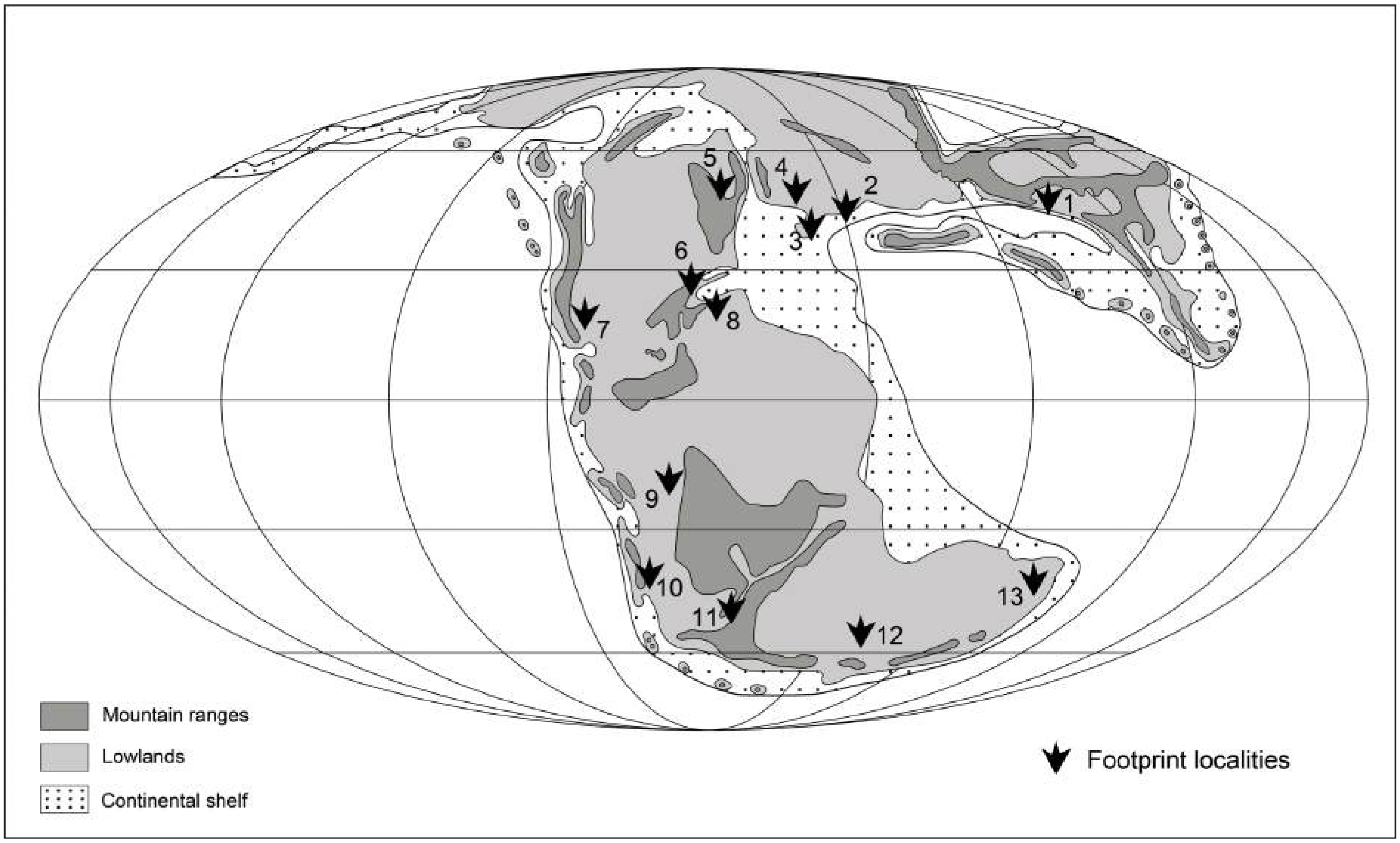


FIGURE 1. Paleogeography of the Triassic with distribution of main tetrapod footprint localities. 1 = China; 2 = Italy; 3 = Spain; 4 = western Europe; 5 = Greenland; 6 = Newark Basin, eastern North America; 7 = Chinle Basin, western North America; 8 = Argana Basin, Morocco, northern Africa; 9 = Brazil; 10 = Argentina; 11 = southern Africa; 12 = Antarctica; 13 = Sydney Basin, Australia. Base map after Wing and Sues (1992).

The study of Triassic tetrapod footprints has been a large amount of diverse research over nearly two centuries. As a result, we now know of Triassic tetrapod footprints from all of the World's continents and from all the substantial subdivisions of Triassic time. The fossil record of Triassic footprints is thus extensive and complex, and it has been the source of much ichnotaxonomic, paleobiogeographic, biochronologic and functional morphologic analysis.

Thus, it seems timely to present a comprehensive evaluation of the Triassic record of tetrapod tracks. This encompasses a critical review of Triassic tetrapod footprint ichnotaxonomy and the establishment, as precisely as possible, of the geographic and stratigraphic (temporal) distribution of the valid ichnotaxa of Triassic tetrapod footprints. Within this framework, we can analyze the Triassic track record in terms of its paleobiogeographic, biochronologic and evolutionary significance. The correlation of footprint and body fossil records is largely possible, even if being based rather on "grades" and evolutionary developments of the locomotor apparatus, than on a comparison of distinct taxa.

HISTORY OF STUDY

Early Years

The scientific description and naming of tetrapod footprints started with Triassic material from Germany. In 1835, J. J. Kaup, a zoologist from Darmstadt, introduced *Chirotherium barthii* and *C. sickleri* as the first binominally named ichnotaxa based on trackways from surfaces in the Middle Buntsandstein of the Solling Formation (Middle Triassic) near Hildburghausen in southern Thuringia (Kaup, 1835a, b). These had been discovered in 1833 by F.K.L. Sickler (see also Sickler, 1834, 1836; Bornemann, 1887; Walther, 1917; Willruth, 1917). Because of its excellently preserved footprints, the Hildburghausen material is still a reference for comparisons with other Triassic ichnofaunas from the global record.

In later studies, following Kaup's pioneering work, Triassic footprints, especially chirotherians, underwent a different classification. This was due to new discoveries, in particular in Great Britain. Assemblages widely co-eval with those from Germany contained a similar ichnofauna with *Chirotherium barthii* and *C. sickleri* as well as footprints of different sizes, overall shapes and digit proportions (Egerton, 1839; Morton, 1863, 1891; Beasley 1895, 1904, 1905, 1907, 1908, 1909; Woodward, 1902; Maidwell, 1911,1914; Nopcsa, 1923). A first detailed analysis of chirotherians and their producers followed (Soergel, 1925). Further ichnotaxonomic work came from Kirchner (1927) and Rühle v. Lilienstern (1939).

Later Studies

A comprehensive study of Triassic footprints and pioneering ichnotaxonomy was published by Peabody in 1948. This influential paper can be considered the basis of modern ichnotaxonomic work that was subsequently carried on by Baird (1954, 1957). More recent studies of Triassic footprints of great importance for ichnotaxonomy are those of Haubold (1967, 1971a, b) and Demathieu (1970, 1971, 1985, 1989), Demathieu and Haubold (1972, 1974), and Demathieu and Demathieu (2004). Many ichnotaxa established by these authors and their classifications of footprints are still valid and widely in use.

A large number of new Triassic ichnotaxa were introduced by Ellenberger (1970, 1972, 1974) based on material from Lesotho in southern Africa. However, many of them are *nomina dubia* or are considered to be junior synonyms of other known ichnotaxa from North America and Europe (see

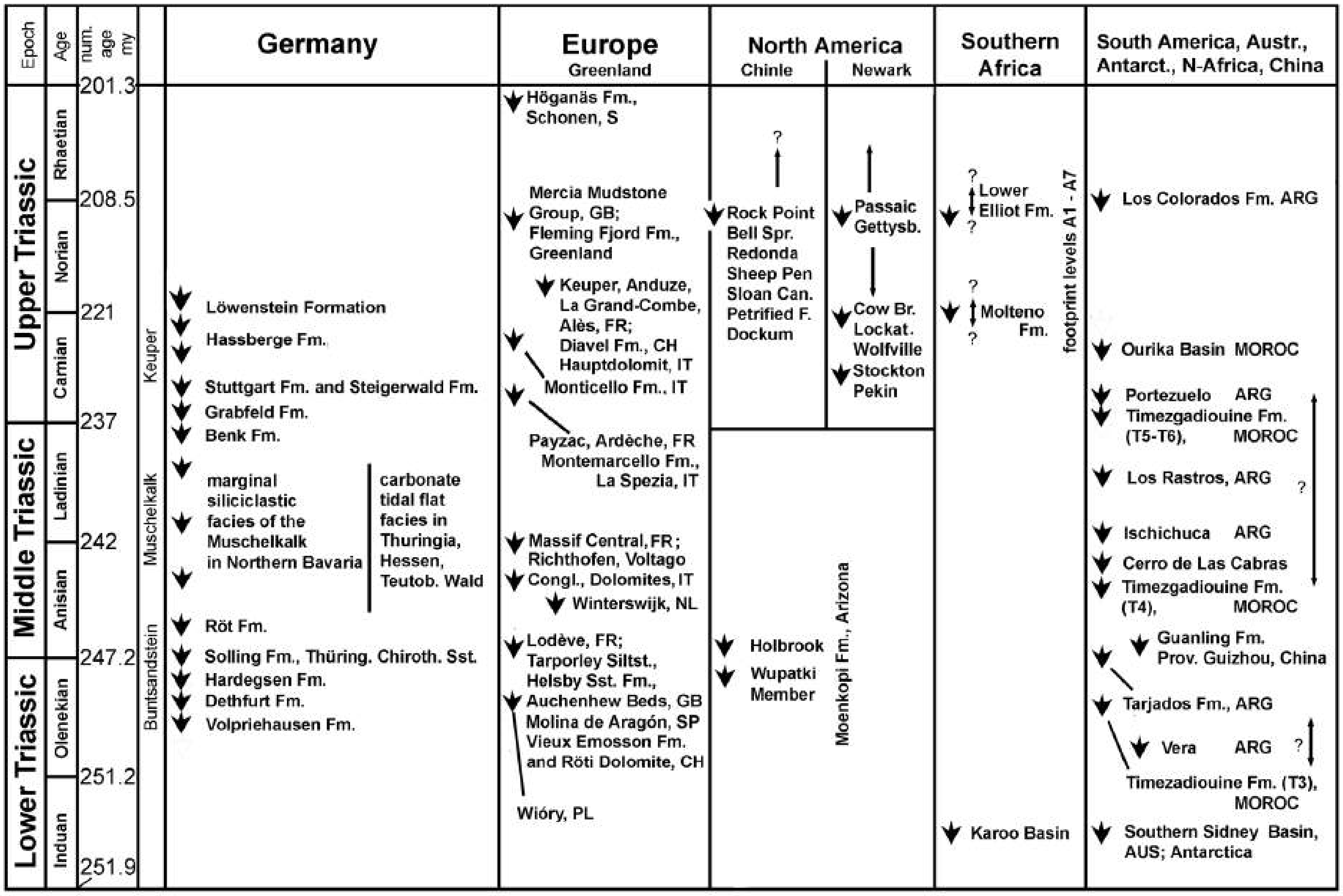


FIGURE 2. Principal Triassic tetrapod footprint horizons and localities. German section and numerical age after Menning & German Stratigraphic Commission (2002) and Bachmann and Kozur (2004), updated.

below). Indeed, the influence of the substrate on footprint shape (extramorphology) was not adequately considered in the studies of Ellenberger. Nevertheless, his famous documentary work contributed widely to our knowledge of Triassic tetrapod footprints. Further ichnotaxonomic papers of major importance are those of Beurlen (1950), Kuhn (1958a, b, 1963) and Sarjeant (1967, 1970, 1996).

Contemporary studies and papers on Triassic footprint ichnotaxonomy have been published in recent years on the tetrapod ichnofaunas from all over the globe. These are based on material from: **(1) North America** (Olsen and Baird, 1986; Weems, 1987, 1992;, Fraser and Olsen, 1996; Klein et al., 2006; Hunt and Lucas, 2007a; Lucas et al. 2010; Klein and Lucas, 2010b; Lockley and Lucas, 2013), **(2) Greenland** (Klein et al. 2013c; Lallensack et al. 2017), **(3) South America** (Melchor and De Valais, 2006), **(4) Europe** with Italy (Mietto, 1987; Leonardi and Lockley, 1995; Avanzini and Leonardi, 2002; Nicosia and Loi, 2003; Avanzini and Wachtler, 2012), Poland (Fuglewicz et al., 1990; Ptaszyński 2000; Niedźwiedzki and Ptaszynski, 2007; Klein and Niedźwiedzki, 2012), Germany (Karl and Haubold, 1998; Haubold and Klein, 2000, 2002; Klein and Haubold, 2003, 2004; Fichter and Kunz, 2004, 2011; Klein and Lucas, 2018), France Courel and Demathieu, 2000; Demathieu and Demathieu, 2004; Gand and Demathieu, 2005; Gand et al., 2000, 2005), Switzerland (Cavin et al., 2012; Klein et al., 2016), Great Britain (King et al., 2005; Clark and Corrance, 2009), **(5) Southern Africa** (Olsen and Galton, 1984; D'Orazi Porchetti and Nicosia, 2007; Marchetti et al., 2019b, 2020), **(6) North Africa** (Klein et al., 2010, 2011), and **(7) China** (Lockley et al., 2013; Xing et al., 2013a; Xing and Klein, 2019). Reviews of the systematics of global ichnotaxa have been given by Lockley et al. (2006a, b), Klein and Lucas (2013), Klein et al. (2013b, 2015b) and Lucas et al. (2014). Studies on ichnofacies and biostratigraphy have been published by Lucas (2005), Hunt and Lucas (2007c, d), Klein and Haubold (2007) and Klein and Lucas (2010a).

Recent Studies and Methods

In recent years, the phenomenon of extramorphological variation and its influence on footprint shape has been generally recognized but not followed by all authors (Milàn, 2006; Milàn and Bromley, 2006, 2008; Falkingham and Gatesy, 2014; Marchetti et al. 2019c). "Splitters" and "lumpers" are still debating different Triassic tetrapod ichnotaxa and classification criteria.

Several neoichnological studies of extant reptiles and birds (e.g., Milàn and Bromley, 2006, 2008; Milàn and Falkingham, 2016) enhanced our knowledge of the influence of substrate consistencies on footprint shape. Other authors emphasized that the ichnotaxobase of footprints should include only unequivocally diagnosed anatomical features, and presented synapomorphy-based criteria that identify common derived characters of footprints and foot skeletons (Olsen, 1986; Haubold and Klein, 2001, 2002, Farlow et al., 2014; Lallensack et al., 2017). Nevertheless, some ichnologists still use statistical methods to differentiate footprint morphologies, not considering that their results might reflect different preservation (e.g. Gand and Demathieu, 2005; Gand et al., 2005).

Other methods used in recent studies for ichnotaxomomic differentiation are morphometric or landmark analyses (Rasskin-

Gutman et al., 1997; Karl and Haubold, 1998; Klein and Haubold, 2003; Lallensack, 2016). However, these methods are limited by the small number of stable (anatomically controlled) landmarks that can be identified in footprints and are useful at best for a distinction at the ichnogenus level. Three D laser scanning and photogrammetry methods have contributed to a more objective documentation of footprints independent of the subjective evaluation of footprint shape reflected in outline drawings (Mathews et al., 2016; Falkingham, 2012, 2016; Falkingham and Gatesy, 2014; Falkingham et al., 2018; Manning, 2004; Petty et al., 2008; Belvedere et al., 2017). Nevertheless, 3D models as well as original specimens have to be interpreted, thus creating some subjectivity, even if some programs generate "automated" outlines. Basically, photogrammetry is a measuring tool, including the determination of different depths of digits, claws, palm etc. We believe that a combination of all these approaches will help to develop stable ichnotaxobases for Triassic tetrapod-footprint ichnotaxonomy.

Tetrapod footprints not only reflect the anatomy of the trackmaker's foot, but their morphology is also the result of two other factors: (1) the dynamics of the foot; and (2) the conditions of the substrate. Their interaction controls the depth of footprints and the degree of preservation of anatomical details (Belvedere and Farlow, 2016; Falkingham et al., 2020; Szewczyk et al., 2020; Turner et al., 2020) such as digital pads and skin texture, but also, to some extent, other ichnotaxonomically important features such as length/width ratio, and even digit proportions (Klein and Haubold, 2004; Klein and Lucas, 2018). Recently, definition of terms like "formation" and "preservation" of footprints have been discussed in Gatesy and Falkingham (2018) and Marchetti et al. (2019c). Gatesy and Falkingham (2018) proposed that "formation" should essentially define foot movement and interaction of the foot with the substrate, whereas "preservation" describes influences taking place after the footprint was made, such as diagenetic processes and erosion. Following this approach, a deeply impressed footprint with poorly preserved anatomical details nevertheless could be classified as well-preserved, because it provides much information about foot movements of the trackmaker. However, in practice when examining a slab with footprints, both "formation" and "preservation" may be difficult to distinguish. Marchetti et al. (2019c, 2020) proposed to use "registration" instead of "formation" to designate the process when the foot actively leaves a print. The latter authors also introduced a "morphological preservation" scale to determine the quality of preservation, based on the presence of original anatomical details (see also Belvedere and Farlow, 2016, for a similar classification).

Due to extramorphological overprinting and deformation resulting from differing substrates, footprint assemblages can present a false ichnotaxonomic diversity. Oversplit ichnotaxonomy was a common practice in tetrapod ichnology for decades and continues to the present day (e.g., Ellenberger, 1970, 1972). Most of these "phantom taxa," as defined by Haubold (2000), and "taphotaxa" (Lucas, 2001), were based on extramorphological features and not on anatomical characters. The latter, however, should be the rule when introducing new ichnotaxa.

This study is based strictly on anatomical features and synapomorphy-based approaches from foot skeletons, which means anatomical details from the latter have to be identified in the footprints. The authors thus are ichnotaxonomic "lumpers" rather than "splitters."

SYSTEMATIC ICHNOLOGY—TRIDACTYL FOOTPRINTS

Atreipus–Grallator–Anchisauripus–Eubrontes–Plexus
Figures 3-8

Here, we follow common practice and use the term "grallatorid footprints" for any tridactyl mesaxonic pes tracks of this plexus, including those of the ichnofamilies Grallatoridae, Anchisauripodidae and Eubrontidae (*sensu* Lull, 1904a).

Anchisauripus Lull, 1904
Figure 3P

1841	*Ornithichnites* (in part): E. Hitchcock, p. 486, pl. 37, fig. 21
1843	*Ornithichnites* (in part): E. Hitchcock, p. 255-256
1845	*Eubrontes* (in part): E. Hitchcock, p. 23
1847	*Brontozoum* (in part): E. Hitchcock, p. 49-50
1904a	*Anchisauripus* Lull, p. 288
1904a	*Brontozoum* (in part): Lull, p. 486
1915	*Brontozoum* (in part): Lull, p. 181
1915	*Anchisauripus*: Lull, p. 181
1953	*Brontozoum* (in part): Lull, p. 166
1953	*Anchisauripus*: Lull, p. 168
1992	*Grallator* (*Anchisauripus*): Olsen et al., p. 507, fig. 12B
1998	*Anchisauripus*: Olsen et al., p. 592, figs. 6-8

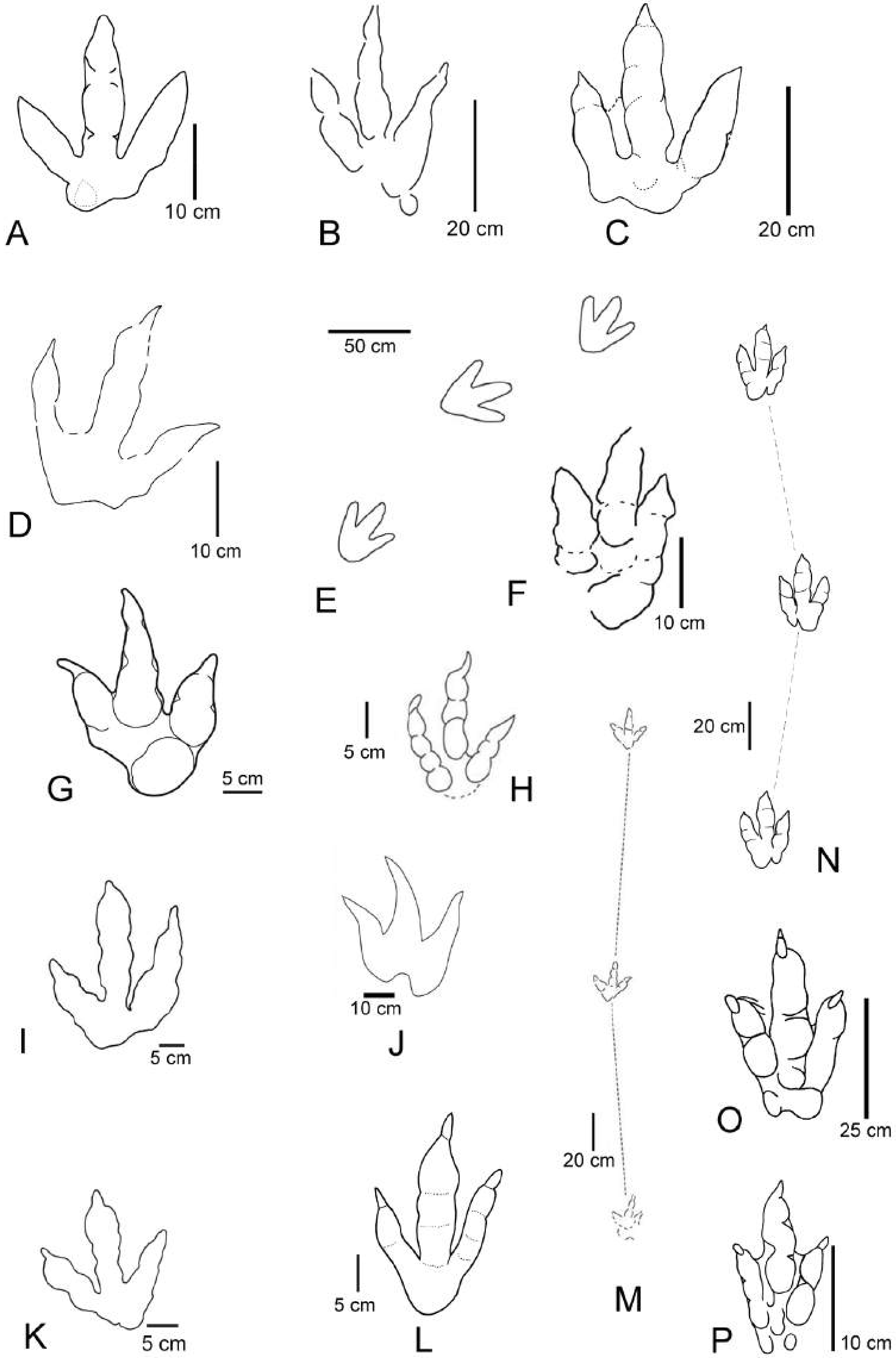
Type ichnospecies: *Anchisauripus sillimani* (E. Hitchcock, 1843) (Fig. 3P).

Included ichnospecies: Presently only the type ichnospecies is considered as valid by us. Thus far a convincing ichnotaxonomy and discrimination of Triassic tridactyl grallatorid footprints have failed. These footprints are principally of similar morphology and can be discriminated only by very few details (e.g., pad impressions) that may be obscured by extramorphological (substrate-related) factors. Therefore, we prefer a conservative approach, assigning all Triassic *Anchisauripus* to the type ichnospecies. Future comprehensive studies of these tracks might possibly solve this problem more satisfyingly.

Distribution: *Anchisauripus* is well known from Late Triassic tracksites of the Newark Supergroup in eastern North America and from the Ørsted Dal Formation of the Fleming Fjord Group of East Greenland (Norian-Rhaetian), but rare elsewhere. It may also be present in the Molteno and Lower Elliot formations (Carnian-Rhaetian) of southern Africa, under various synonymous names (Ellenberger, 1970, 1972), as well as in other Upper Triassic units of France, Sweden and Slovakia.

Diagnosis (from Olsen et al., 1998): Medium-sized (~ 20 cm long), functionally tridactyl ichnite in which the digit III projection ratio averages about 1.4, and the length-to-width ratio is about 2.0. Digit II tends to project more than IV along the axis

FIGURE 3. (facing page) Large theropod footprints from the Triassic as sketches. **A,** *Pengxianpus cifengensis* from Xujiahe Fm. (Upper Triassic) of Sichuan Province, China. B-O. *Anchisauripus-Eubrontes.* **B,** From Lower Elliot Fm. (Norian) of Lesotho, Southern Africa. **C,** From Höganäs Fm. (Upper Triassic, Rhaetian) of southern Sweden. **D,** From Lower Elliot Fm. (Norian) of Lesotho, Southern Africa. **E,** From Upper Triassic of Australia. **F,** From Timezgadiouine Fm. (T5, Carnian) of the Argana Basin, Morocco. **G,** From Upper Triassic (Carnian) of the Southern Alps. **H,** From Upper Triassic (Norian) of southern France. **I,** From Tomanová Fm. (?Late Norian-Rhaetian) of Slovakia. **J,** From Caturrita Fm. (Upper Triassic) of Brazil. **K,** From Tomanová Fm. (?Late Norian Rhaetian) of Slovakia. **L,** From Lower Jurassic (Hettangian) of northern Bavaria, Germany. **M,** From Upper Triassic (Norian) of southern France. **N-O,** *Eubrontes giganteus* from Lower Jurassic of Newark Supergroup, North America (O = type). **P,** *Anchisauripus sillimani* (type) from Lower Jurassic of Newark Supergroup, North America. Sketches from Ellenberger et al. (1970), Haubold (1971b, 1984), Gierliński and Ahlberg (1994), Olsen et al. (1998), Gand et al. (2000), Lucas et al. (2006), Klein and Haubold (2007), Niedźwiedzki (2011, Lagnaoui et al. (2012), Silva et al. (2012), Bernardi et al. (2013) and Xing et al. (2013).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of digit III. Divarication of outer digits averages 27°

Description: Trackway of a biped with medium-sized (~ 15-25 cm long) tridactyl pes impressions with slender digits and tapering claws. Digit III significantly longer than digits II and IV, which are of subequal length, thus differing from the pattern in tridactyl versions of the chirotheroid type. Phalangeal pads are often well preserved. Trackway pattern with high pace angulation (up to 175°).

Discussion: As discussed below under *Grallator*, Olsen et al. (1998) recognized three ichnogenera of Late Triassic-Early Jurassic tridactyl theropod dinosaur tracks that are size classes (of pes lengths) across a continuum: *Grallator* <150 mm long, *Anchisauripus* 150-250 mm long and *Eubrontes* > 250 mm long. Some workers (most recently Rainforth, 2005) argue that *Grallator*, *Anchisauripus* and *Eubrontes* should be one ichnogenus. While we agree in principle with this conclusion, we continue to use the three ichnogeneric names as useful terms to identify theropod tracks of different sizes (see below; also see Lucas et al., 2006b).

"*Anchisauripus*" has been identified in Middle Triassic deposits of France (Demathieu, 1989; Demathieu and Demathieu, 2004; Gand and Demathieu, 2005), together with footprints assigned to "*Coelurosaurichnus*." However, Haubold and Klein (2000, 2002) included these trackways of facultative bipeds from the Middle-Upper Triassic in the *Atreipus–Grallator* plexus.

Trackmaker: *Anchisauripus* (sensu stricto) is widely regarded as the footprint of a "medium-sized" Late Triassic theropod dinosaur based on characteristic anatomical features reflected in these tracks (see Farlow and Lockley, 1993; Smith and Farlow, 2003; Lucas et al., 2006a).

Atreipus Olsen and Baird, 1986
Figures 4-6

1952 *Gigandipus* (?*Anchisauripus*): Bock, p. 403, 406-407, pl. 43, fig. 3, pl. 44
1952 *Coelurosaurichnus*: Heller, p. 135, pl. 9, figs. 2-3
1957 *Grallator*: Baird, p. 453, fig. 1, pl. 1
1981 *Tridactylus*: Biron and Dutuit, p. 404-406, fig. 1, pl. 2A-E, J
1986 *Atreipus* Olsen and Baird, p. 62, figs. 6.3-6.10
2000 *Coelurosaurichnus*: Courel and Demathieu, p. 39-40, figs. 2-3, p. 43, fig. 5
2000 *Atreipus–Grallator*: Haubold and Klein, p. 68, fig. 4, p. 69, fig. 5D-F, H-I, p. 71, fig. 7, p. 72, fig. 8, p. 73, fig. 9A-F, p. 74, fig. 10, p.75, fig. 11C
2002 *Atreipus–Grallator*: Haubold and Klein, p. 11, fig. 8B-C
2003 *Atreipus*: Szajna and Hartline, p. 266, fig. 16.3A, C
2006 *Atreipus*: Lucas and Sullivan, p. 252, fig. 5
2008 *Atreipus*: D'Orazi-Porchetti et al., p. 281, figs. 6-7
2012 *Atreipus-Grallator*: Lagnaoui et al., p. 244, fig. 5A-B,
2016 *Atreipus-Grallator*: Lagnaoui et al., p. 6, fig. 5A, p. 8, fig. 7B

Type ichnospecies: *Atreipus milfordensis* (Bock, 1952) (Fig. 4H).

Included ichnospecies: The type ichnospecies and *A. metzneri* (Heller, 1952), *A. sulcatus* (Baird, 1957) and *A. acadianus* Olsen and Baird, 1986.

Distribution: Lockatong and Passaic formations of the Newark Supergroup (lithostratigraphy of Weems et al., 2016), in the Newark, Gettysburg, Dan River and Fundy basins of eastern North America; Rock Point Formation, Chinle Group of the western USA (Lucas et al., 2006a); Steigerwald and Hassberge formations (Keuper, Carnian-Norian) of Germany (Haubold and Klein, 2002); Carnian of Ardèche region, France (Courel and Demathieu, 2000); Travenanzes Formation (Carnian) of northern Italy (D'Orazi-Porchetti et al., 2008); and Timezgadiouine Formation (T5-T6, Upper Triassic, Carnian) of the Argana Basin, Morocco (Lagnaoui et al., 2012, 2016). Depending on differing evaluations of the ichnotaxonomy, some researchers identify *Atreipus-Grallator* plexus footprints as early as the Middle Triassic (Anisian-Ladinian) in different formations of Germany and France (Haubold and Klein, 2002).

Diagnosis (after Olsen and Baird, 1986): Small (9-14 cm long), tulip-shaped pes impression with metatarsal-phalangeal pads of digits II and IV that are oval to circular and often impressed. Distal phalangeal pads often more indistinct than more proximal pads. Hallux impression absent. Relative proportions of pes very similar to *Grallator*. Manus much smaller than pes, with digit III longest, followed in length by II, IV and I.

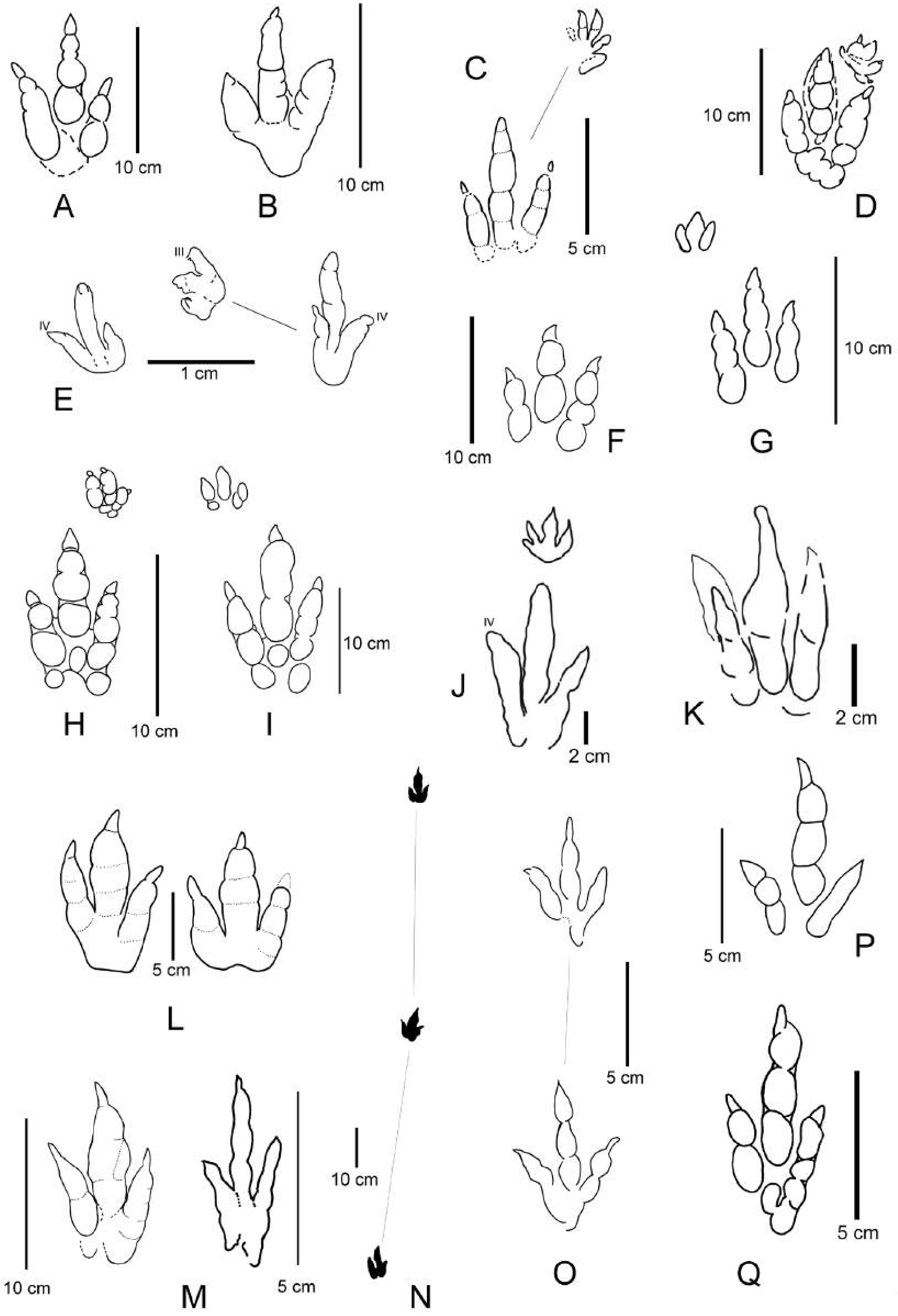
Description: Trackway of a quadruped with a relatively small (9-14 cm long), tridactyl, tulip-shaped pes in which digit III is longest and the digits are thick, with oval metatarsophalangeal pads. The manus impression is small, tridactyl or tetradactyl-pentadactyl and digitigrade, with digit IV relatively short and laterally spread.

Discussion: Without the manus impression, the pes impression of *Atreipus* would readily be assigned to *Grallator* (cf. Baird, 1957). However, the manus is of chirothere morphology–small and transverse with relatively short, blunt digit tips. Haubold and Klein (2000, 2002) described footprints from the Middle Triassic (Ladinian) Benk Formation, formerly assigned to "*Coelurosaurichnus,*" as *Atreipus* and proposed the plexus *Atreipus-Grallator* for trackways of facultative bipeds from this unit. The ichnogenus has a broad geographic distribution in North America in strata of Carnian-Norian age (Olsen and Baird, 1986; Lucas et al., 2006a).

Trackmaker: Olsen and Baird (1986) provided a lengthy discussion of the trackmaker of *Atreipus* to conclude that it was most likely made by an early ornithischian dinosaur, a conclusion also advocated by Szajna and Hartline (2003) and Lucas and Sullivan (2006). However, tracks of *Atreipus* have been attributed to a theropod dinosaur (e.g., Thulborn 1990), and Haubold and Klein (2000) attributed them to a dinosauromorph foot form that is a precursor to the theropod foot form of *Grallator*. Indeed, Lucas and Sullivan (2006) noted that a dinosauriform such as *Silesaurus* (see Dzik, 2003) could have been the *Atreipus* trackmaker. Probably, a dinosaur or a tetrapod close to a dinosaur (dinosauriform or dinosauromorph) made the track called *Atreipus*, even if stem-crocodylian archosaurs such as *Poposaurus* were able to produce tridactyl pes imprints similar to *Atreipus* (Farlow et al., 2014). However, *Poposaurus* was a habitual biped and thus left no manus impressions.

Indeed, it is possible that both dinosauromorphs and dinosaurs made these tracks. Given the absence of dinosauromorphs as body fossils after the Carnian, and the arguments of Olsen and

FIGURE 4. (facing page) *Atreipus–Grallator* plexus tetrapod footprints from the Triassic as sketches. **A-B,** From Middle Triassic (Anisian-Ladinian) of France. **C,** From Benk Fm. (Ladinian) of Germany. **D,** From Middle Triassic (Anisian-Ladinian) of France. **E,** From Timezgadiouine Fm. (T4, Anisian) of the Argana Basin, Morocco. **F-G,** From Upper Triassic (Carnian) of France. **H,** From Upper Triassic of Newark Supergroup, North America. **I,** From Steigerwald Fm. (Carnian) of Germany. **J-K,** From Bigoudine and Timezgadiouine formations (T6, T5, Carnian-Norian) of the Argana Basin, Morocco. **L,** From Hassberge Fm. (Carnian) of Germany. **M,** From Hassberge Fm. (Carnian) of Germany. **N,** From Redonda Fm. (Chinle Group, Norian-Rhaetian) of New Mexico. **O-P,** From Chinle Group, North America. **Q,** *Grallator cursorius* composite drawing from type trackway, Lower Jurassic of Newark Supergroup, North America. Sketches from Courel and Demathieu (2000), Haubold and Klein (2000, 2002), Gand et al. (2005), Klein and Lucas (2010a), Klein et al. (2011) and Lagnaoui et al. (2012).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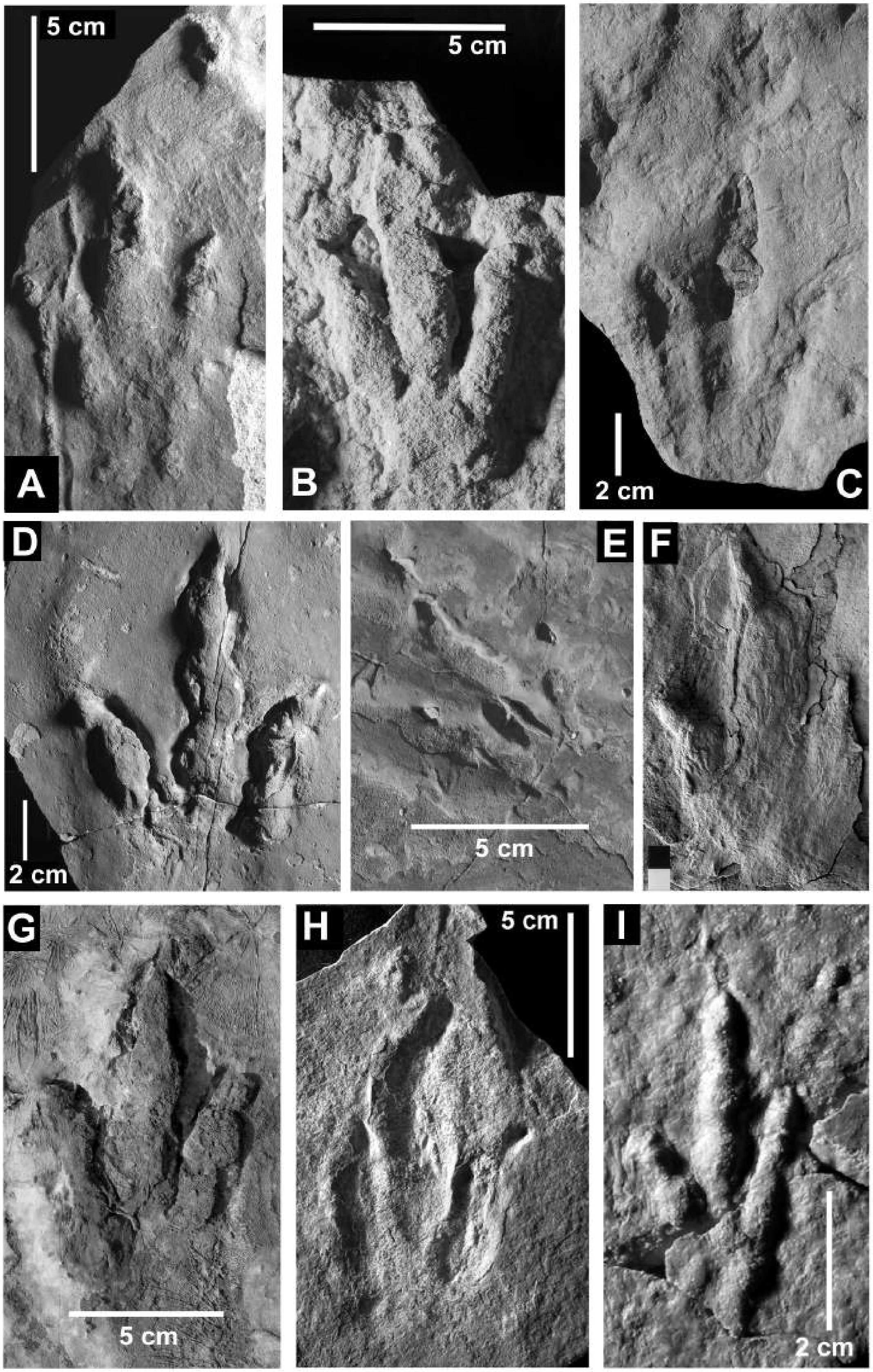


FIGURE 5. *Atreipus–Grallator* plexus tetrapod footprints from the Triassic as photographs. **A,** Hassberge Fm., Coburger Sandstein (Carnian), Germany. **B,** Steigerwald Fm., Ansbacher Sandstein (Carnian), Germany. **C,** Bigoudine Fm. (T6, ?Norian), Argana Basin, Morocco. **D-G,** Redonda Fm., Chinle Group (Norian-Rhaetian), New Mexico. **H-I,** Hassberge Fm., Coburger Sandstein (Carnian) Germany.

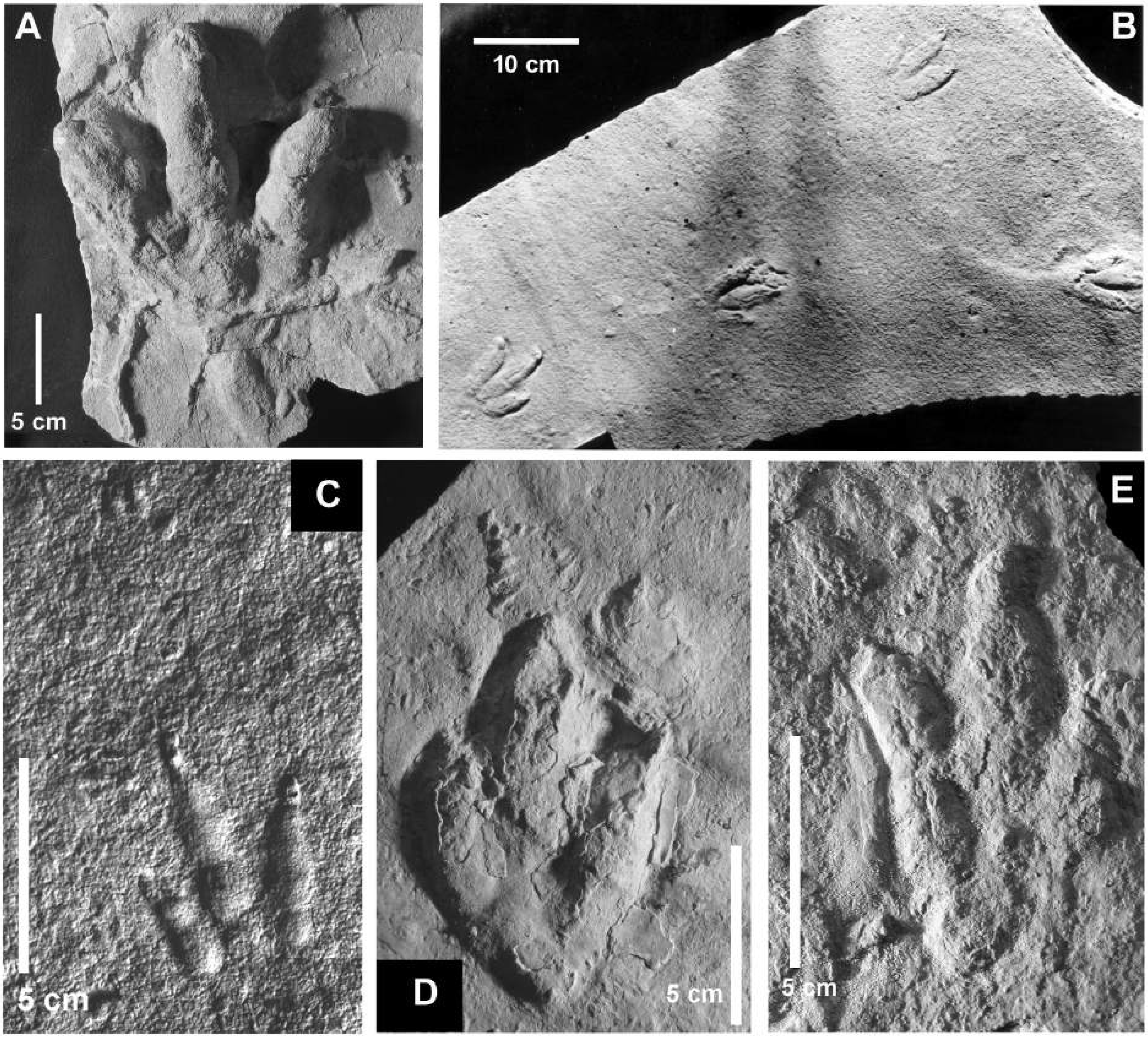


FIGURE 6. Functionally tridactyl footprints from the Middle to Late Triassic of Europe. **A,** *Chirotherium* (“*Parachirotherium*”) *postchirotherioides* from Benk Fm. (Ladinian) of Germany. **B-C,** *Atreipus-Grallator* from same unit. **D-E,** *Atreipus-Grallator* from the Middle Triassic (Anisian-Ladinian) of France.

Baird (1986), it cannot be excluded that the *Atreipus* trackmaker in the Norian of Pennsylvania documented by Lucas and Sullivan (2006) was an ornithischian dinosaur. If this is correct, then ornithischians were locally abundant during Norian time in what is now the Newark basin, refuting the suggestion of Parker et al. (2005) and Nesbitt et al. (2007), based on a reappraisal of the bone record, that there were no Triassic ornithischians in North America.

Banisterobates Fraser and Olsen 1996
Figure 7

1996 *Banisterobates*: Fraser and Olsen, p. 7, fig. 2
1997 *Banisterobates*: Fraser and Grimaldi, p. 192, fig. 2
2000 *Banisterobates*: Haubold and Klein, p. 69, fig. 5 J
2006 *Banisterobates*: Fraser, p. 230, fig. 11.7.

Type ichnospecies: *Banisterobates boisseaui* Fraser and Olsen, 1996

Included ichnospecies: Only the type ichnospecies.

Distribution: Dry Fork Formation (Upper Triassic, Carnian) of Dan River Group, Virgina, USA. Thus far this is the only occurrence of the ichnotaxon.

Diagnosis (after Fraser and Olsen, 1996): Ichnite of quadruped with tetradactyl pes but with digit I very much reduced so that the pes is essentially mesaxonic. Digit III markedly longer than II and IV and digit II slightly longer than IV. Manus poorly defined but with three very short digit impressions.

Description: Trackway with three successive pes imprints and associated manus imprints of a very small individual (pes length 1.8-2.5 cm). The stride length is 12.2 cm, and the pace angulation is 146°. Imprints are rotated moderately outward relative to the midline.

Discussion: The combination of a grallatorid pes with a manus impression resembles the ichnogenus *Atreipus* (see above), however, the latter shows no digit I impression. The presence of a distinct hallux trace justifies keeping *Banisterobates* as a valid ichnogenus, even if its morphological peculiarities are related to the very small size and ontogenetic growth stage of the trackmaker, and it is possible that *Banisterobates* represents a juvenile *Atreipus*.

Trackmaker: A small dinosauromorph or dinosauriform, either a juvenile individual or representative of a small adult species, can be considered as the most likely trackmaker. Ornithischian dinosaurs are less likely, but cannot be excluded for the same considerations discussed above for *Atreipus*.

Eubrontes E. Hitchcock, 1845

Figures 3, 8

1836 *Ornithichnites*: Hitchcock, p. 317, fig. 21
1841 *Ornithoidichnites*: Hitchcock, p. 484, pl. 36, fig.18
1845 *Eubrontes*: E. Hitchcock, p. 23.
1847 *Brontozoum*: Hitchcock, p. 57
1848 *Brontozoum*: Hitchcock, 169, pl. 1., fig.1
1858 *Brontozoum*: E. Hitchcock 1858, p. 64, pl. 57, fig. 1
1994 *Grallator* (*Eubrontes*): Gierliński and Ahlberg, p. 101, fig. 3,
1998 *Eubrontes*: Olsen et al., p. 590, fig. 4, p. 592, fig. 5
2006 *Eubrontes*: Lucas et al., p. 87, fig. 3, p. 88, fig. 4, p. 89, fig. 5
2011 *Eubrontes*: Niedźwiedzki, p. 296, fig. 5
2012 *Eubrontes*: Lagnaoui et al., p. 244, fig. 5C
2018 *Eubrontes*: Zouheir et al., p. 8, fig. 7F-H

Type ichnospecies: *Eubrontes giganteus* E. Hitchcock, 1845 (Fig. 3O).

Included ichnospecies: Presently only the type ichnospecies is considered as valid by us. Thus far a convincing ichnotaxonomy and discrimination of Triassic tridactyl grallatorid footprints have failed (see explanations in *Anchisauripus* above). Therefore we prefer a conservative approach, assigning all Triassic *Eubrontes* to the type ichnospecies. Future comprehensive studies of these tracks might possibly solve this problem in a more convincing fashion. These could include the trackway pattern and details of preserved phalangeal pads. Actual methods and photogrammetric re-documentation of the best preserved trackways will be very useful here.

Distribution: *Eubrontes* tracks are well known from Lower Jurassic strata, especially in southern Africa, western Europe, eastern North America and the American Southwest, and some have advocated that the lowest occurrence (LO) of *Eubrontes* corresponds to the Triassic-Jurassic boundary (e.g., Olsen et al., 2002). However, the LO of *Eubrontes* in the Newark Supergroup of eastern North America, long considered to be equivalent to the base of the Jurassic, is demonstrably of Late Triassic age (Lucas and Tanner 2007, 2015). There are well documented Late Triassic records of *Eubrontes* in Australia, southern Africa, western Europe, Greenland and North America. Thus, Triassic *Eubrontes* localities are: Striped Bacon Coal Seam at Rhonda Colliery in the Sydney basin of eastern Australia (Staines and Woods, 1964; Hill et al., 1965; Bartholomai, 1966; Molnar, 1991; Thulborn, 1998, 2003); Lower Elliot Formation, South Africa (Ellenberger (1970, 1972, 1974; Olsen and Galton, 1984; Bordy et al., 2017); Irohalene Member (T5) of Timezgadiouine Formation, Argana Basin, Morocco, North Africa (Lagnaoui et al., 2012, 2016; Zouheir et al., 2018); Mercia Mudstone Group (Norian-Rhaetian), coastal exposures of Wales (Thomas, 1879; Sollas, 1879; Bassett and Owens, 1974; Tucker and Burchette, 1977; Lockley et al., 1996); Hauptdolomit Group (Norian) of the Graubünden Canton in the Swiss Alps (Furrer, 1993; Lockley and Meyer, 2000; Meyer et al., 2013, 2019); Keuper strata of d'Anduze (Norian) of southern France (Ellenberger, 1965; Ellenberger et al., 1970); Norian strata of Grand-Combe, southwestern France; possibly in western France at Vendée (Lapparent and Montenat, 1967); Carnian deposits of Northern Italy (Bernardi et al., 2013); "Rhätolias" strata of northern Bavaria (Kuhn, 1958); Tomanová Formation in the Tatra Mountains of Poland and Slovakia (Michalik and Kundrat, 1998; Gierliński and Sabath, 2005); Bjuv Member of the Höganäs Formation in northwestern Scania, Sweden (Bölau, 1952; Haubold, 1971, 1986; Gierliński and Ahlberg, 1994); Ørsted Dal Formation of the Fleming Fjord Group (Norian) of Jameson Land in east Greenland (Jenkins et al., 1994; Gatesy et al., 1999); the LO of *Eubrontes* in the Newark basin of New Jersey-Pennsylvania, USA, is just below the lowest basalt sheet of the Newark extrusive zone; Balls Bluff Siltstone (Norian) at the Culpeper Crushed Stone Quarry in the Culpeper Basin of Virginia (Weems, 1987, 2018); possibly the Blue Mesa Member of the Petrified Forest Formation (upper Carnian) in the Petrified Forest National Park, Arizona (Martin and Hasiotis, 1998); and Sloan Canyon Formation of northeastern New Mexico (Lockley and Hunt, 1993).

Diagnosis (from Olsen et al., 1998): Large (> 30 cm long), functionally tridactyl ichnite in which the digit III projection ratio is about 2.2, and the length-to-width ratio is about 1.4 to 1.5. Projection of digits II and IV along the axis of digit III about equal. Divarication of outer digits 30°-40°.

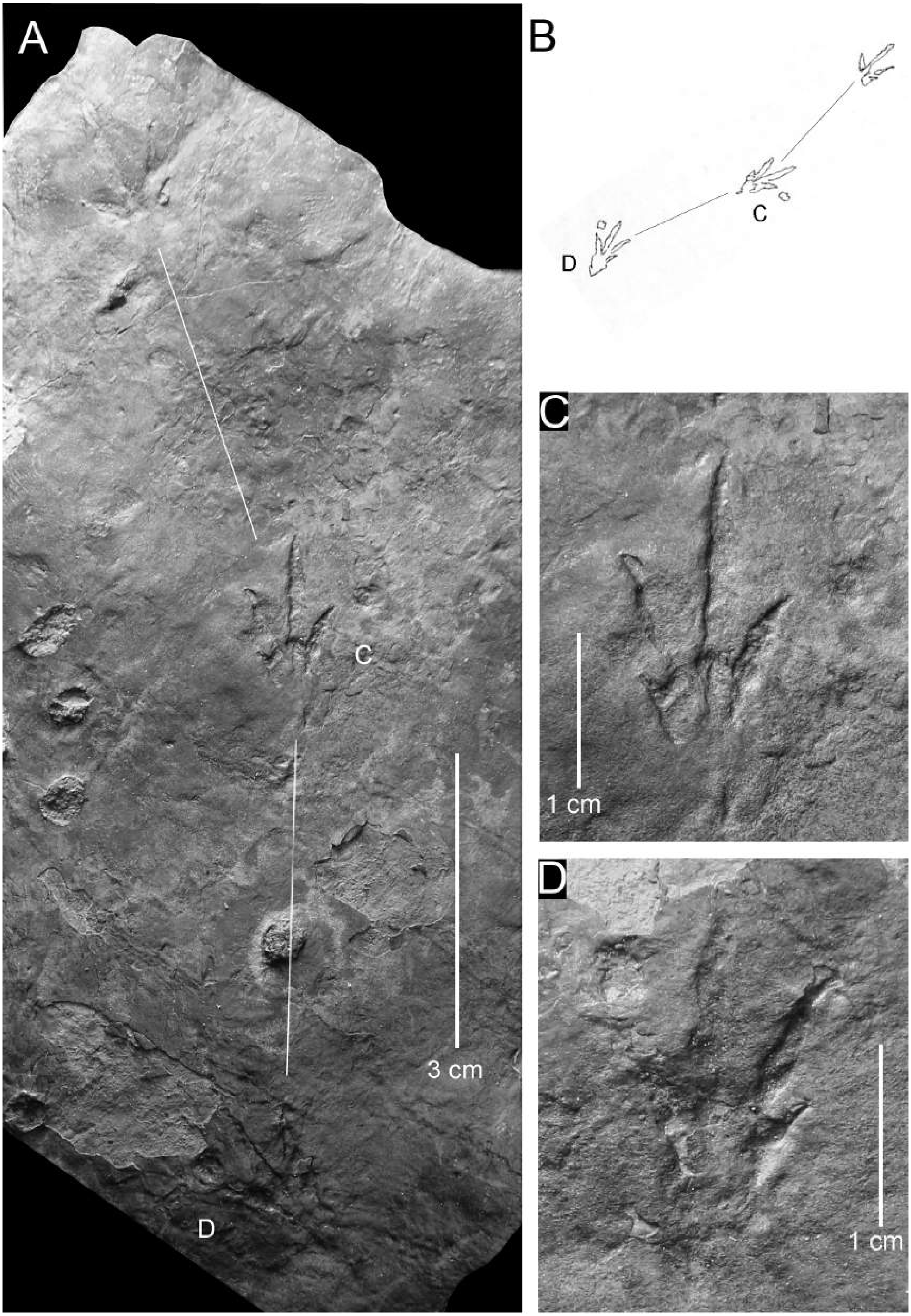
Description: Trackway of a biped of relatively large size (pes >25 cm long). The pes impression is broad and tridactyl with a relatively short digit III (low mesaxony) if compared to *Grallator*, and a hallux which is rarely, if ever, impressed. Divarication of outer digits averages 25° to 40°.

Discussion: As also noted under *Anchisauripus* and *Grallator*, several authors have argued (most recently Rainforth, 2005) that *Eubrontes* and the smaller *Grallator* should be the same ichnogenus, as they are only reliably distinguished on the basis of size. However, we stress that, besides their overall similarity, there are some morphological differences that make it reasonable to retain their status as distinct ichnogenera. We still use *Eubrontes* here also because of the biostratigraphic significance that has been attached to this ichnogenus, understood as a *Grallator*-like pes imprint larger than 25 cm long.

As noted by Olsen (1980), Lockley (1999, 2009) and Milner et al. (2006), *Grallator* tracks are generally more elongate, with a greater anterior projection of digit III, than *Eubrontes*. This is what Weems (1992) refers to as "toe extension." Placing *Grallator* in the same ichnogenus as *Eubrontes*, as suggested by Rainforth (2005), requires an allometric argument that implies "lumping" or synonymy. Such an approach explicitly allows the synonymy of two morphologies that represent end members of a *Grallator-Anchisauripus-Eubrontes* plexus, originally proposed by Olsen (1980) under the double barreled "sub-ichnogenus" labels *Grallator* (*Grallator*), *Grallator* (*Anchisauripus*) and *Grallator* (*Eubrontes*). This scheme has been accepted by some authors and discussed by others (Gierliński, 1991; Gierliński and Ahlberg, 1994; Weems, 1992; Lockley 2000).

Note that Olsen et al. (1998), who undertook the most recent and thorough investigation of the problem, still maintain the *Grallator-Eubrontes* distinction, which moves away from the implied synonymy of the original allometric plexus argument of Olsen (1980). Like Lucas et al. (2006), we follow this more recent position (Olsen et al., 1998) in maintaining the *Grallator-Eubrontes* distinction. *Eubrontes* as used here also encompasses other large grallatorid ichnotaxa from the Triassic-Lower Jurassic, such as *Kayentapus*, *Dilophosauripus* and *Gigandipus*, considered by some authors as distinct from *Eubrontes* as well

FIGURE 7. (facing page) *Banisterobates boisseaui* from Dry Fork Fm. (Upper Triassic, Carnian) of Dan River Group, Virgina, USA. **A-B,** Trackway as photograph and sketch. **C-D,** Details corresponding to position in A-B. Photographs by Alex Hastings, Virginia Museum of Natural History. Sketch in B from Fraser and Olsen (1996).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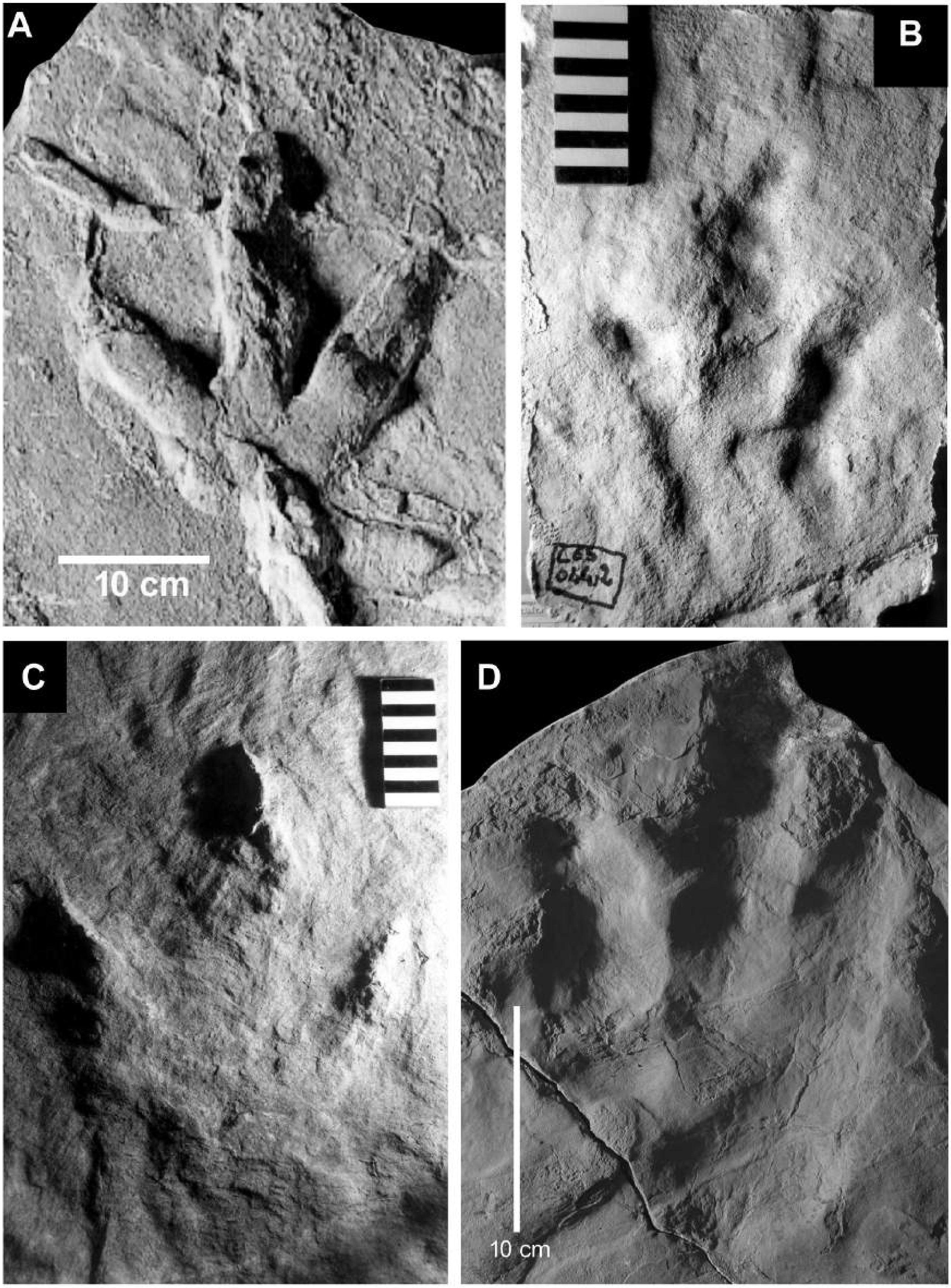


FIGURE 8. *Eubrontes* and similar large theropod footprints from the Late Triassic. **A,** *Pengxianpus cifengensis* from Xujiahe Fm. of Sichuan Province, China. **B-C,** *Eubrontes* from the lower Elliot Fm. of Lesotho, southern Africa. **D,** *Eubrontes* from Timezgadiouine Fm. (T5, Carnian) of the Argana Basin, Morocco.

as several forms described under separate names from the Elliot Formation of South Africa (Ellenberger 1970, 1972, 1974). Full agreement on the synonymy of these ichnogenera has not been reached,

Trackmaker: There is virtually universal agreement that the *Eubrontes* trackmaker was a relatively large, early Mesozoic theropod dinosaur, such as the ceratosaur *Dilophosaurus*. Weems (2003, 2019) argued that a *Plateosaurus*-like prosauropod was the *Eubrontes* trackmaker, but the disparity between prosauropod foot structure and *Eubrontes* tracks is so great that we dismiss Weems's contention, as have others (e. g., Lucas et al., 2006a; Farlow et al., 2018).

Grallator E. Hitchcock, 1858
Figures 4-5

1847 *Brontozoum* (in part): E. Hitchcock, p. 44, figs. 1, 2a
1848 *Brontozoum* (in part): E. Hitchcock, p. 44, pl. 3, fig. 4
1858 *Grallator* (in part) E. Hitchcock, p. 72, pl. 13, fig. 3; pl. 33, fig. 5
1904 *Grallator*: Lull, p. 494, fig. 12
1915 *Grallator*: Lull, p. 200, fig. 53
1953 *Grallator*: Lull, figs. 26-27
1998 *Grallator*: Olsen et al., p. 595, figs. 9-15
2000 *Grallator*: Gand et al., p. 613, fig. 9
2003 *Grallator*: Gaston et al., p. 154-156, figs. 2-6
2010 *Grallator*: Lucas et al., p. 46-47, figs. 37-38

Type ichnospecies: *Grallator cursorius* E. Hitchcock, 1858 (Fig. 4Q).

Included ichnospecies: Presently only the type ichnospecies is considered as valid by us. As for *Eubrontes,* we note that thus far a convincing ichnotaxonomy and discrimination of Triassic tridactyl grallatorid footprints have failed and, therefore, we prefer a conservative approach, assigning all Triassic *Grallator* to the type ichnospecies. Future comprehensive studies of these tracks might resolve this problem (see above).

Distribution: *Grallator* is almost ubiquitous in Late Triassic tracksites of the upper Chinle Group in the western USA, of the Newark Supergroup in eastern North America and in western Europe (e.g., Conrad et al., 1987, Lockley and Hunt, 1993, 1995, 1999; Lockley et al., 1993, 1996; Gand et al., 2000, 2005; Haubold and Klein, 2000; Szajna and Hartline, 2003; Gaston et al., 2003; Lockley and Eisenberg, 2006; Lucas et al., 2006b; Hunt and Lucas, 2007). It is also present in Carnian deposits of the Timezgadiouine Formation of the Argana Basin, Morocco, North Africa (Lagnaoui et al., 2012, 2016; Zouheir et al., 2018).

Furthermore, *Grallator* is present in the Lower Elliot Formation (Norian) of southern Africa (Ellenberger, 1970, 1972; Olsen and Galton, 1984) and in the Ørsted Dal Formation of the Fleming Fjord Group (Norian) of Jameson Land in East Greenland (Gatesy et al., 1999)

Diagnosis (from Olsen et al., 1998): Small (<150 mm long), bipedal, functionally tridactyl ichnite. Digit III projects relatively farther anteriorly, and the foot is more narrow than in *Eubrontes* and *Anchisauripus* (length/width ratio close to or greater than 2). Hallux rarely impressed. Divarication of outer digits 10° to 30°.

Description: Trackway of a biped with small- to medium-sized (4-15 cm long) tridactyl pes impressions with slender digits and tapering claws. Digit III significantly longer than digits II and IV, which are of subequal length, thus differing from the pattern in tridactyl versions of the chirotheroid type. Phalangeal pads are often well preserved. Trackway pattern with high pace angulation (up to 175°) and stride lengths up to 117 cm in specimens of 8-9 cm pes length.

Discussion: Hitchcock (1858) gave the name *Grallator parallelus* to small, strongly mesaxonic tridactyl footprints from the Lower Jurassic strata of the Newark Supergroup. Olsen et al. (1998), who studied the complicated historical background and ichnotaxonomy of the types of *Grallator* in the Newark Supergroup, identified *G. parallelus* as the type species. However, Rainforth (2005, p. 76-77) pointed out that *G. cursorius* is the proper name for the type species of *Grallator*.

Olsen et al. (1998) recognized three ichnogenera of Late Triassic-Early Jurassic tridactyl theropod dinosaur tracks that are size classes (of pes lengths) across a continuum: *Grallator* <150 mm long, *Anchisauripus* 150-250 mm long and *Eubrontes* > 250 mm long.

Other supposed diagnostic differences between these ichnogenera – relative length (projection) of digit III and relative width of the pes – are variable extramorphologically, so they do not consistently separate the three ichnogenera, as do pes lengths. Of course, using size alone to separate ichnogenera is questionable; for example, tracks referred to *Grallator* may merely be tracks made by the juvenile of the adult trackmaker that impressed *Eubrontes* tracks. This had led some workers (most recently Rainforth, 2005) to argue that *Grallator*, *Anchisauripus* and *Eubrontes* should be one ichnogenus. While we agree in principle with this conclusion, we continue to use the three ichnogeneric names as useful terms to identify theropod tracks of different sizes (also see Lucas et al., 2006b). Ichnotaxonomically, the synonymization of *Anchisauripus* and *Eubrontes* with *Grallator* might be a reasonable step. However, because of the wide use of these names in the literature, we propose to keep the traditional treatment, and for reasons of morphological similarity group them in the *Grallator-Anchisauripus-Eubrontes* (GAE) plexus.

Trackmaker: *Grallator* is widely regarded as the footprint of a relatively small theropod dinosaur.

Pengxianpus Yang and Yang (1987)
Figures 3A, 8A

Type ichnospecies: *Pengxianpus cifengensis* Yang and Yang 1987.

Included ichnospecies: Only the type ichnospecies is known.

Distribution: Xujiahe Formation (Norian-Rhaetian) of Sichuan Provice, China.

Diagnosis (after Xing et al., 2013): Large (>25 cm length), tridactyl, mesaxonic pes imprints of a biped showing a wide digit II-IV divarication angle (up to 69°). Digits of long and slender shape with rounded pads, digit III the longest, followed by II and IV. Small, but pronounced circular metatarsal-phalangeal pad on digit IV.

Description: The holotype is an incomplete trackway consisting of two successive pes imprints that shows a narrow pattern, moderate pace length and orientation of imprints parallel to the midline. Pes imprints are mesaxonic and nearly symmetrical along digit III. Digit III is longest, and digit IV is slightly shorter than digit II. Digits are long and slender with moderately preserved pad traces and tapering distal ends, indicating the presence of claws. The posterior margin shows rounded metatarsal-phalangeal pad traces with that of digit IV being most distinct and separated by a sharp notch along the lateral outline.

Discussion: The original material was described by Yang and Yang (1987) from the Xuijahe Formation of Sichuan Province, China. Lockley and Matsukawa (2009) and Xing et al. (2013) illustrated and re-described these tracks, which include details such as skin impressions. The large pes imprints (over 25 cm pes length) are of typical theropod shape and co-occur on the surface with small, mammal-like tracks. Even if the size and general shape is similar to *Eubrontes*, the morphology is different. This is revealed by the pad configuration and the larger digit divarication that resembles a morphotype often described under the ichnogenus *Kayentapus,* well known from the Lower

Jurassic and here attributed to *Eubrontes*. Presently, based on the known material, a synonymization of *Pengxianpus* with *Kayentapus* or *Eubrontes* is not possible, and we tentatively consider *Pengxianpus* a valid ichnotaxon, following Lockley et al. (2013).

Trackmaker: Most likely a relatively large Late Triassic theropod dinosaur similar to the trackmaker of *Eubrontes*.

SYSTEMATIC ICHNOLOGY—CHIROTHERIID FOOTPRINTS

Figures 9-34

Brachychirotherium Beurlen 1950

Figures 9-14, 31C, 32E

1936 *Chirotherium*: Kuhn, p. 92-93, pl. XIII, fig. 3
1937 aff. *Otozoum*: Kuhn, p. 320, fig. 3
1952 *Chirotherium*: Bock, pl. 41-43 (1)
1957 *Chirotherium*: Baird, p. 475, fig. 5, pl. 1, fig. 2, pl. 2
1970 *Sauropodopus* [*nomen nudum*] Ellenberger, p. 345, fig. 40
1970 *Pseudotetrasauropus* [*nomen nudum*] Ellenberger, p. 345, figs. 10, 28-34
1971a *Chirotherium*: Haubold, fig. 24e-k
1971b *Brachychirotherium*: Haubold, fig. 35 (5-10)
1972 *Pseudotetrasauropus* Ellenberger, fig. 31; pl. IX upper left
1972 *Paratetrasauropus*: Ellenberger, fig. 37, pl. IX, upper right
1972 *Sauropodopus*: Ellenberger, fig. 40; pl. 7
1972 *Deuterosauropodopus*: Ellenberger, figs. 50-5; pl. XIII, upper left, lower right
1984 *Brachychirotherium*: Olsen and Galton, p. 96, fig. 3 C
1984 *Brachychirotherium*: Haubold, fig. 95 (10-11)
1984 *Sauropodopus*: Haubold, p. 47, 170, fig. 116.4
1990 "Chirotherian footprints": Leonardi and De Oliveira, p. 221, pl. V D-F
1992 *Brachychirotherium*: Lockley et al., p. 388, fig. 7
1993 "New taxon A": Silvestri and Szajna, p. 441, fig. 3 A
1994 *Chirotherium*: Leonardi, pl. II, figs. 4-6
1996 *Brachychirotherium*: Szajna and Silvestri, p. 278, fig. 3
1998 *Brachychirotherium*: Karl and Haubold, figs. 5-9, pl. 1-6
2000 *Pseudotetrasauropus*: Lockley et al., p. 11, fig. 3, partim
2001 *Brachychirotherium*: Olsen and Rainforth, p. 101, fig. 24 B-C, p. 139, fig. 51 B-C
2001 *Brachychirotherium*: Lucas et al., p. 178, figs. 2 B, 3 C-E, 4 A, C
2001 *Pseudotetrasauropus*: Lucas et al., p. 179, fig. 4 A, C
2003 *Brachychirotherium*: Szajna and Hartline, p. 269, fig. 16.5 B
2004 *Brachychirotherium*: Lockley et al., p. 99, fig. 17
2006 *Brachychirotherium*: Klein et al., figs. 3-4, 5A, 7
2006 cf. *Brachychirotherium*: Melchor and De Valais, p. 362, fig. 4B-C
2007 *Paratetrasauropus*: D'Orazi Porchetti and Nicosia, p. 239, figs. 18-19
2007 *Sauropodopus*: D'Orazi Porchetti and Nicosia, p. 240, fig. 20
2007 cf. *Brachychirotherium*: D'Orazi Porchetti and Nicosia, p. 241, fig. 21
2010 *Brachychirotherium*: Lucas et al., figs. 21A-J, 22 A, 23-24, 25B, 27-28, 30 B-C
2013 *Brachychirotherium*: Hminna et al., fig. 3
2016 *Brachychirotherium*: Lagnaoui et al., p. 6, fig. 5B, p. 7, fig. 6A
2018 *Brachychirotherium*: Zouheir et al., figs 5-6
2019 *Brachychirotherium*: Hminna et al., figs. 4-6

Type ichnospecies: *Brachychirotherium hassfurtense* Beurlen, 1950 (Fig. 9A, 10A).

Included ichnospecies: *B. thuringiacum, B. parvum.*

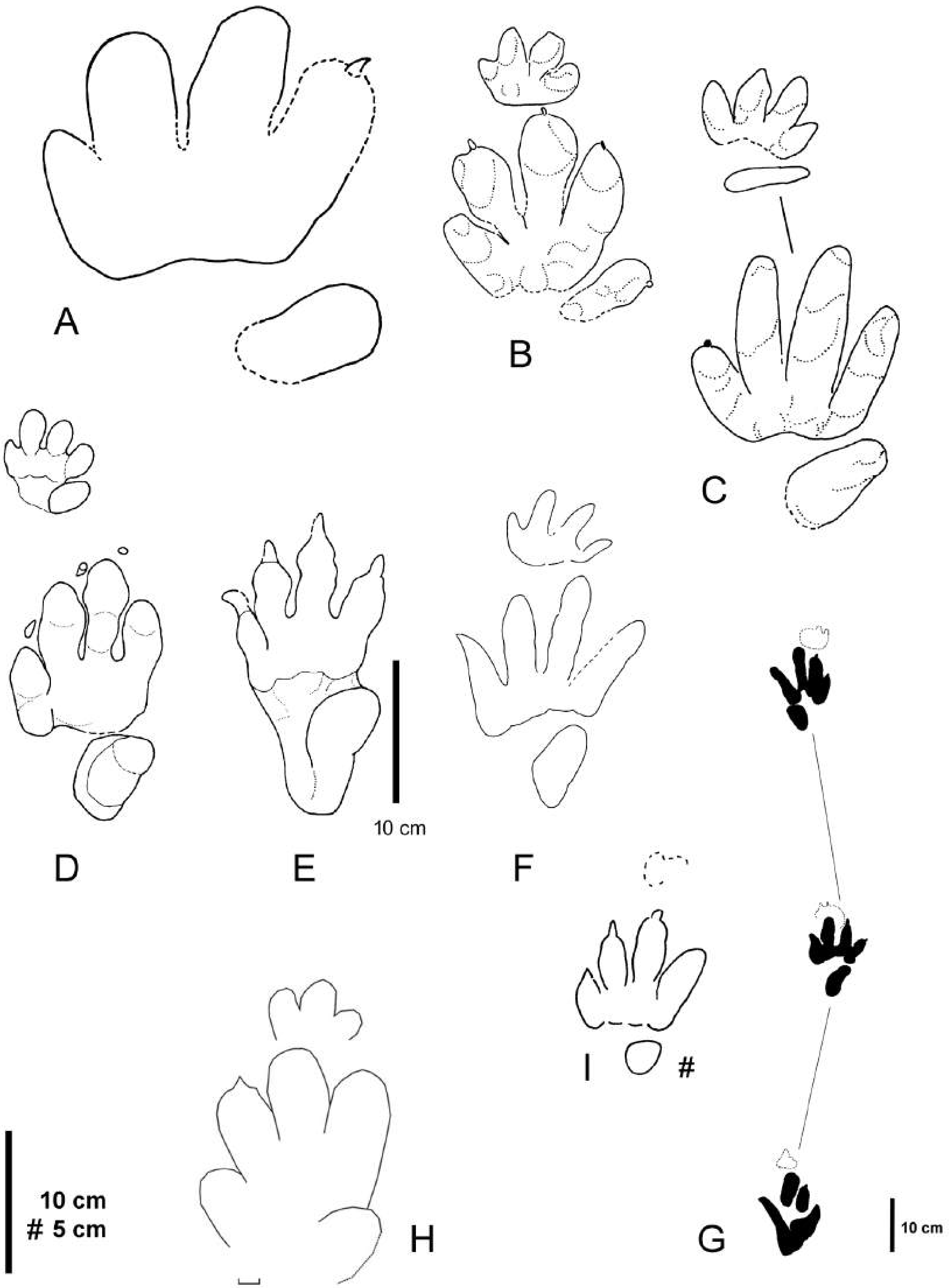
Distribution: Upper Triassic (Keuper, Carnian-Norian) of Germany, Upper Triassic (Carnian) of Italy; Upper Triassic (Timezgadiouine and Oue Oum Er Rbiaa formations, Carnian-Norian) of Morocco; Upper Triassic (Lower Elliot Formation, Norian-Rhaetian) of southern Africa; Ørsted Dal Formation of Fleming Fjord Group (Norian-Rhaetian) of Greenland; Chinle Group and Newark Supergroup of the USA and eastern Canada; Upper Triassic (Norian) of Argentina, South America.

Diagnosis (after Karl and Haubold, 1998): Chirotheriid trackways of a quadruped with plantigrade to semidigitigrade posture of the pes and manus. Pentadactyl pes imprint with rounded to oval shape and broad plantar surface. Pedal digit group I–IV nearly as wide as long and with an overall divarication of more than 40°. Digits moderately spread, relatively short and broad with robust, rounded pads and narrow claws, digits III and II longest, digit IV always preserved. Pedal digit V lacks a separated phalangeal segment or shows an indistinct trace of it, which is anteriorly oriented, but never recurved. In comparison with the pes, the manus imprint is much smaller, and manual digit group I–IV is mostly wider than long, but otherwise of a shape similar to the pes. Trackways with narrow pattern and relatively high pace angulation (160°), moderate outward rotation of the pes and stronger outward rotation of the manus.

Description: Pentadactyl, broad pes imprints with short, blunt digits and thin claws. Digit proportions of anterior digit group are III > II > IV > I. Digit V is preserved only as an oval basal pad posterolateral to the anterior digit group and laterally divergent in the type ichnospecies but on the axis of digit IV in stratigraphically younger forms. Creases between rounded phalangeal and metatarsophalangeal pads are indistinct. The manus is much smaller and of similar shape. Digits I and V in the imprints can be missing. Remarkable is the occurrence of tridactyl versions due to different substrate conditions. Rare trackways from the Chinle Group of North America show a narrow pattern with pes imprints slightly rotated outward.

Discussion: The ichnogenus *Brachychirotherium* was introduced by Beurlen in 1950 based on material from the Coburger Sandstein of the Hassberge Formation in Germany (Upper Triassic, Carnian). Subsequently, the name was used informally by Baird (1957) and Haubold (1967, 1971a) in their classifications of chirotheriids as the term "Brachychirotherian Group" for forms with a broad sole surface and short, clumsy digits. Haubold (1971b) confirmed the validity of the ichnogenus and additionally added small footprints from the Lower-Upper Triassic such as *Brachychirotherium praeparvum*, *B. harrassense*, *B. lorteti*, *B. circaparvum*, *B. tintanti*, *B. hessei*, *B. parvum*, *B. eyermani* and *B. thuringiacum* as new combinations. Several other ichnospecies were described from the Lower-Middle Triassic (Demathieu, 1967; Demathieu and Gand, 1973; Demathieu and Haubold, 1982; Demathieu and Leitz, 1982; Demathieu and Oosterink, 1983; Demathieu and Demathieu, 2004; Ptaszyński, 2000; Niedźwiedzki and Ptaszyński, 2007). Karl and Haubold (1998), in their revision of the type material from the German Upper Triassic, recognized problems when applying the diagnosis of *Brachychirotherium* to Lower-Middle Triassic forms. Thus, Klein and Haubold

FIGURE 9. (facing page) *Brachychirotherium* from the Upper Triassic as sketches. **A,** *B. hassfurtense*, lectotype from Hassberge Fm. (Carnian) of Germany. **B,** *B. thuringiacum* from same unit. **C,** *B. thuringiacum*, holotype from same unit. **D,** *B. parvum* from Passaic Fm. of North America. **E,** *B. eyermani* from same unit. **F-G,** *B. parvum* from Redonda Fm. of North America. **H,** *B. parvum* from Oued Oum Er Rbiaa Fm. of Morocco. **I,** *Brachychirotherium* isp. from Los Colorados Fm., Upper Triassic of Argentina. Sketches from Karl and Haubold (1998), Haubold (1971b), Klein and Lucas (2010a), Lucas et al. (2010) and Hminna et al. (2013).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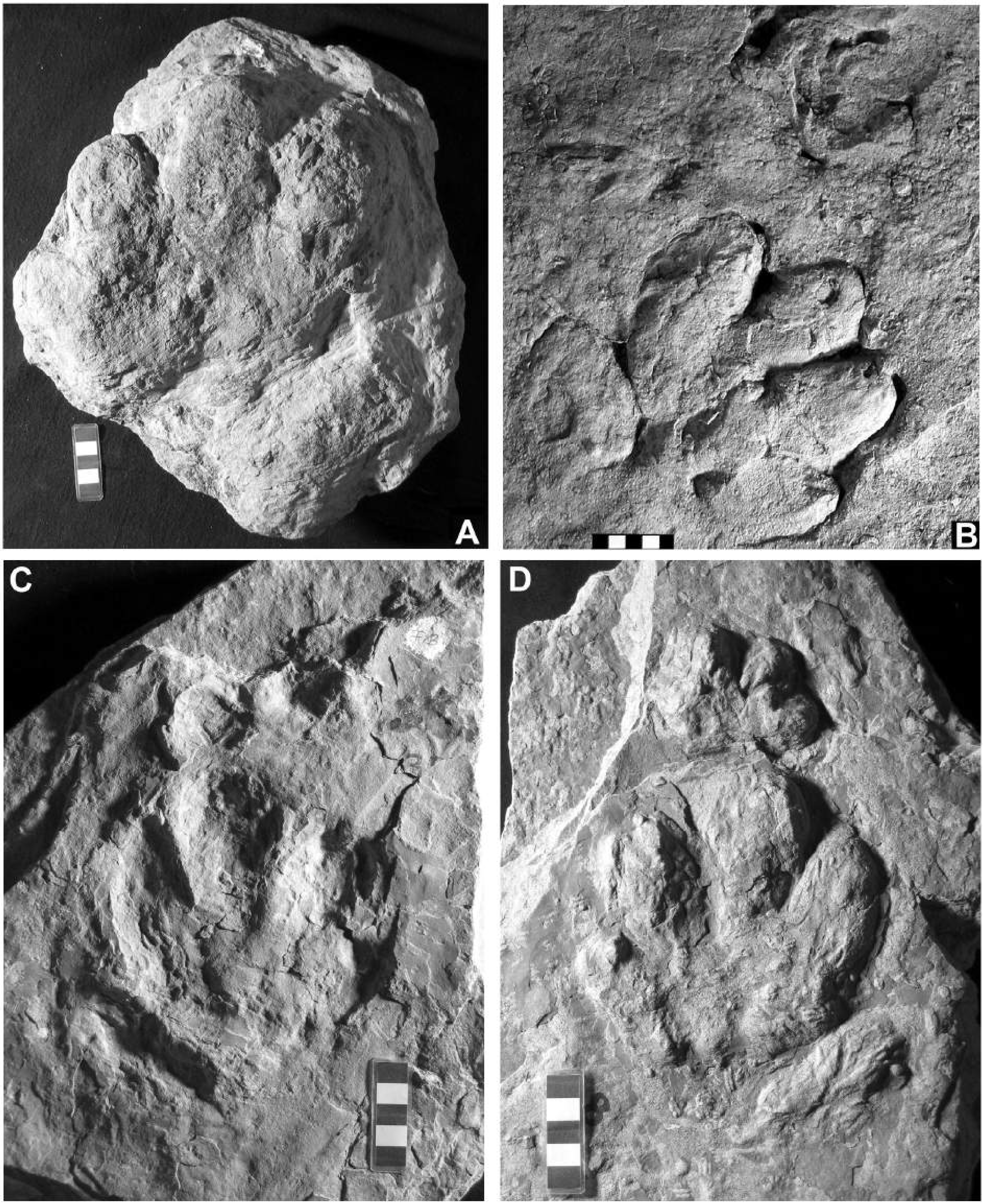


FIGURE 10. Photographs of *Brachychirotherium* from the Upper Triassic Hassberge Fm. (Coburger Sandstein, Carnian) of Germany. **A,** *B. hassfurtense* lectotype. **B-D,** *B. thuringiacum*. C-D are concave epirelief and convex counterslab.

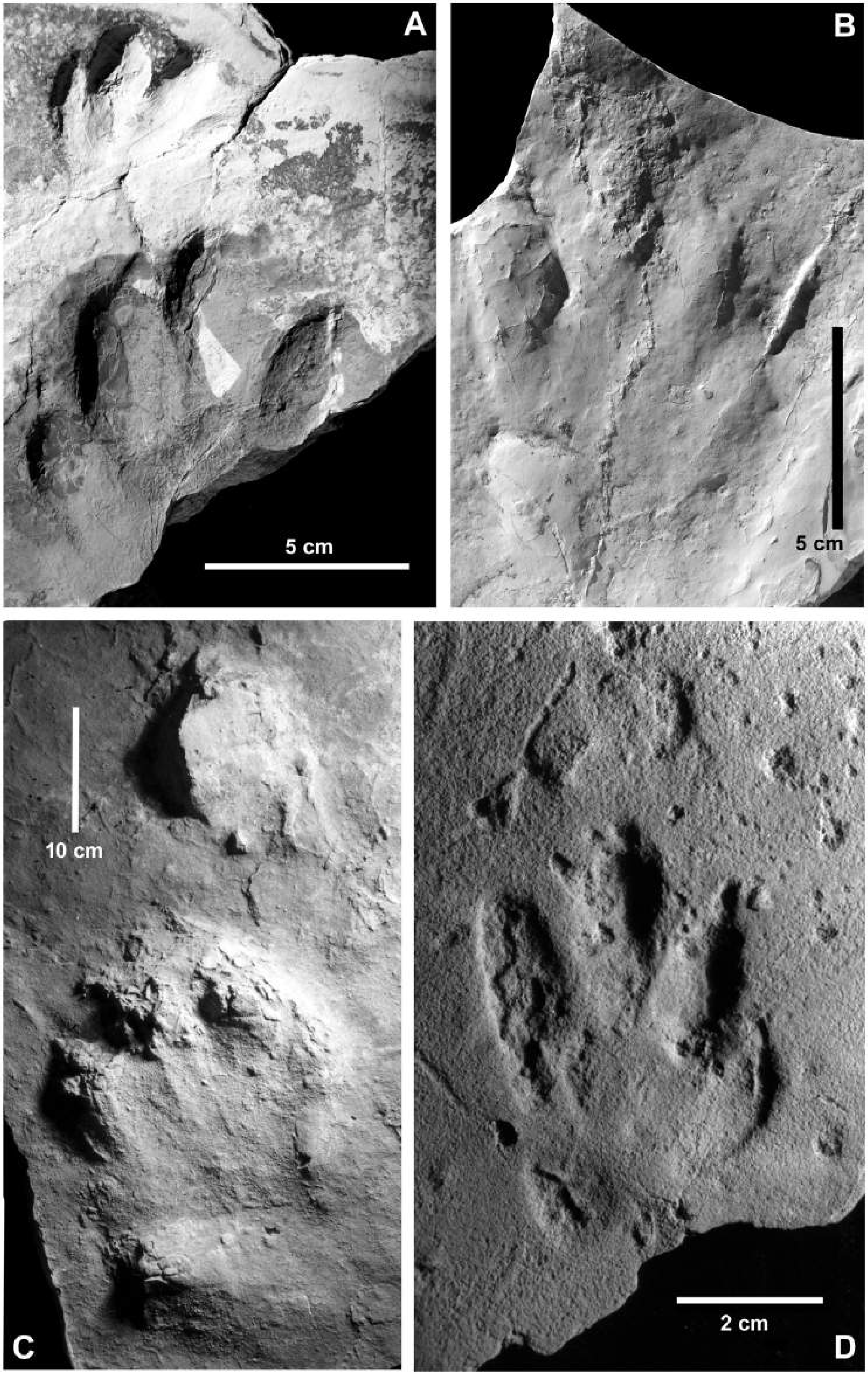


FIGURE 11. Photographs of *Brachychirotherium* from different localities. **A-B,** *B. parvum* from Oued Oum Er Rbiaa Fm. of Morocco. **C,** *B*. isp. ("*Deuterosauropodopus minor*") from lower Elliot Fm. of Lesotho, southern Africa. **D,** *B*. isp. from Los Colorados Fm., Argentina.

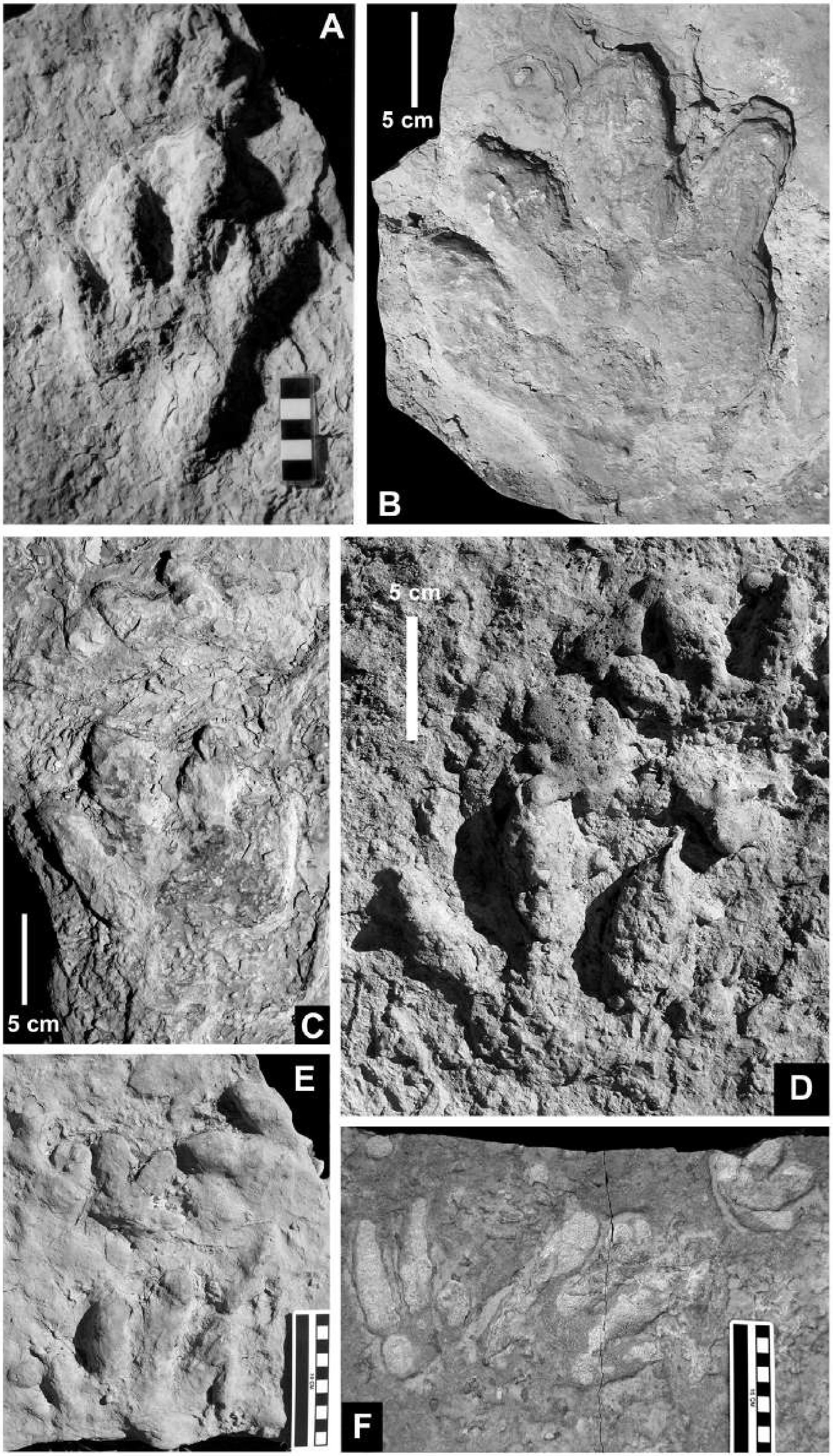


FIGURE 12. Photographs of *Brachychirotherium parvum* from Redonda Fm. (Norian-Rhaetian) of New Mexico. Note associated *Evazoum* in F.

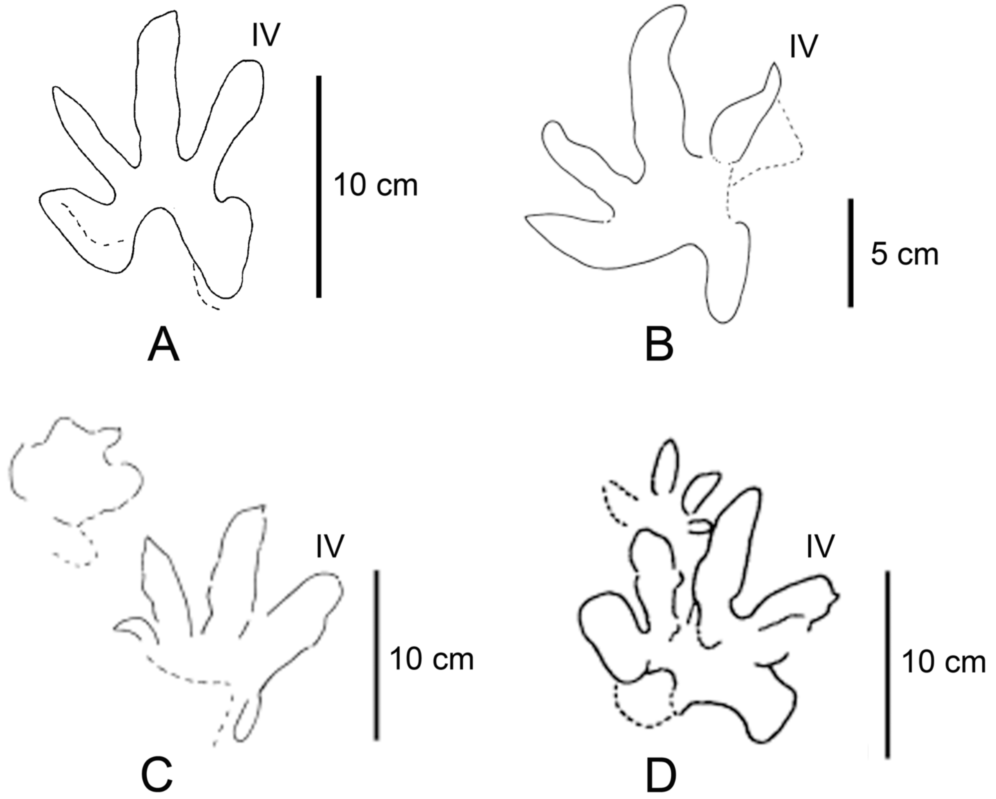


FIGURE 13. Sketches of extramorphological variations of *Brachychirotherium parvum* from Redonda Fm. (Norian-Rhaetian) of New Mexico. From Lucas et al. (2010).

(2004) demonstrated that due to the wide extramorphological variation of footprints of the ichnogenus *Synaptichnium* from Middle Triassic deposits of Germany, some footprints show a transition to a very brachychirothere-like shape. They concluded that *Brachychirotherium* should be restricted to the Upper Triassic material only, and that "*Brachychirotherium*" from stratigraphically older strata likely represents other ichnogenera, including *Synaptichnium*.

Klein and Niedźwiedzki (2012) revised the Lower Triassic ichnofauna from Wióry, Poland, re-assigning several footprints formerly assigned to *Brachychirotherium* to the ichnogenus *Protochirotherium*. We follow these interpretations and emphasize that the stratigraphic range of the ichnotaxon *Brachychirotherium* is restricted to the Upper Triassic (see below). Hunt and Lucas (2007a, b) referred all *Brachychirotherium* material from the Upper Triassic to the ichnospecies *B. parvum*. Presently, we recognize the valid ichnospecies as *B. hassfurtense* (type ichnospecies) and *B. thuringiacum* from the Carnian-Norian of Germany, and *B. parvum* from the Newark Supergroup and Chinle Group (Carnian-Norian) of North America.

Trackmaker: *Brachychirotherium* has been attributed to crocodylian stem and crocodylomorph archosaurs. Especially aetosaurs, such as *Typothorax coccinarum* (Lucas and Heckert, 2011), but also rauisuchians such as *Postosuchus* and even sphenosuchids, have been discussed (Karl and Haubold, 1998; Lucas and Heckert, 2011; Klein et al., 2006; Avanzini et al., 2010; Lucas et al., 2010). The narrow trackway pattern of *Brachychirotherium*, one of the most plausible arguments against an aetosaur interpretation, has been partly refuted by demonstrating a possible narrow gauge of the aetosaur *Typothorax* derived from skeletal anatomy (Heckert et al., 2010; Lucas and Heckert, 2011).

Chirotherium Kaup 1835
Figures 15-21, 31A, 32F-K

1835a *Chirotherium*: Kaup, p. 327-328
1835b *Chirotherium*: Kaup, p. 246-249
1906 *Chirosaurus*: Navas, p. 208, figs. 2-3
1906 *Chirotherium*: Navas, p. 213, figs. 2-3
1931 *Rigalites*: v. Huene, pl. 1
1950 *Dinosaurichnium*: Rehnelt, p. 37, fig. 1-2, pl.1
1958 *Parachirotherium*: Kuhn, pl. VI(1)
?1961 *Chirotherium*: Reig, p. 81
1963 *Chirotherium*: Kuhn, p. 71
1966 *Sphingopus*: Demathieu, p. 485, fig. 2
1971a Chirotheriidae indet.: Haubold, p. 486
1971b Chirotheriidae indet.: Haubold, p. 58
1981 *Anomoepus*: Biron and Dutuit, p. 406-407, fig. 3A, pl. 2F, L
1981 *Quadridigitus*: Biron and Dutuit, p. 406-407, fig. 3B, pl. 2K
2002 *Sphingopus*: Haubold and Klein, p. 9-10, fig. 6-7, p. 12, fig. 9
2012 *Sphingopus*: Avanzini and Wachtler, p. 65, fig. 2
2012 *Parachirotherium*: Lagnaoui et al., p. 244, fig. 5D
2012 *Chirotherium*: Díaz-Martínez and García, p. 146
2015 *Chirotherium*: Díaz-Martínez et al., p. 8-10, 12-15, figs. 4-7, 8J-L
2016 *Parachirotherium*: Lagnaoui et al., p. 4, fig. 3, p. 5, fig. 4, p. 8, fig. 7A
2018 *"Sphingopus"*: Klein and Lucas, figs. 7-8, 9(A-C)
non 1967 *Chirotherium*: Haubold, p. 36, fig. 14, p. 38, fig. 15 left, p. 39, figs. 16-17

Older names: *Chirosaurus* Kaup, 1835, *Cheirotherium* Sickler, 1836, *Cheirotherion* Kessler and Sickler, 1836,

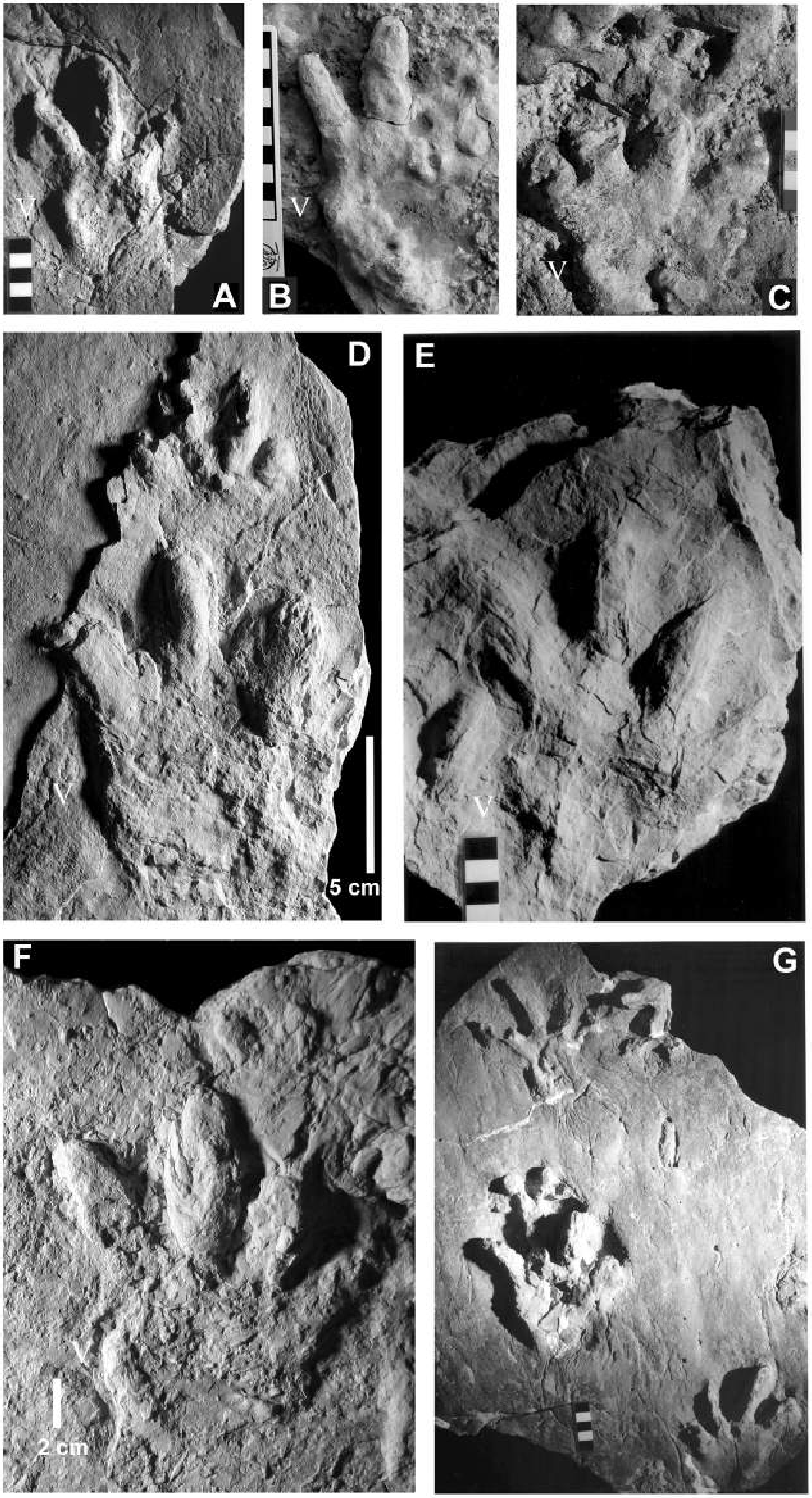


FIGURE 14. Photographs of extramorphological variations of *Brachychirotherium parvum* from Redonda Fm. (Norian-Rhaetian) of New Mexico. From Lucas et al. (2010).

Krocodilipus Nopcsa, 1923, *Saurichnites* Geinitz, 1861.

Type ichnospecies: *Chirotherium barthii* Kaup, 1835 (Fig. 15H).

Included ichnospecies: *C. sickleri*, *C. rex*, *C. ferox*, *C. ladinicus*, C. *postchirotherioides*, and *C. ischigualastianus.*

Distribution: Lower-Middle Triassic (Middle-Upper Buntsandstein and Muschelkalk, Anisian-Ladinian) of Germany; Middle Triassic, Anisian-Ladinian of Poland, Great Britain, Spain and Italy; Middle-Upper Triassic, Anisian-Carnian (Timezgadiouine Formation, T4-T5) of Morocco; Lower-Middle Triassic (Olenekian-Anisian), Moenkopi Group of the USA; and Middle Triassic (Anisian) Guanling Formation of China.

Diagnosis (emended after Haubold, 1971a, b): Trackways of quadrupeds or facultative bipeds with pentadactyl pes and manus imprints. Pes imprint with functionally tridactyl, pronounced digit group II– IV; digit III longest; digit I reduced and thinner; pedal digit V positioned slightly laterally behind the digit group I–IV; ratio of manus:pes area in completely preserved specimens = 1:2, up to 3.5. Pace angulation mostly 160°-170°.

Description: Slender pes imprints with pronounced digit group II-IV in which digit III is longest. Digit I is strongly reduced and thinner; digit V often but not always curved backward, with rounded circular or elongate oval basal pad and mostly with a distinct phalangeal portion.

Discussion: The ichnogenus *Chirotherium* is the oldest named tetrapod ichnotaxon, originally based on a scientific description of material from the Thüringischer Chirotheriensandstein (Middle Buntsandstein) of southern Thuringia, Germany. Kaup (1835) established *Chirotherium,* naming two different ichnospecies, *C. barthii* and *C. sickleri,* from the type locality Hildburghausen (Kaup, 1835a, b). *Chirotherium* is different from all other chirotheriid ichnogenera by the pronounced (“grallatorid”) pedal digit group II–IV, with digit III being longest, tending to a functionally tridactyl pattern, and by the thinner and short digit I that (except in *C. sickleri*) is shifted backward relative to II–IV.

Trackmaker: *Chirotherium* shows the most advanced chirotheriid pes morphology and evolution towards reduction to a functionally tridactyl foot (Haubold and Klein, 2002; Klein et al., in press). This suggests that the trackmakers were early avemetatarsalians (dinosaur-bird-line) and/or crocodylian-stem archosaurs that developed a similar pes structure as seen, for example, in some poposauroids (Farlow et al., 2014).

Chirotherium barthii Kaup 1835
Figures 15H, 16-17, 31A, 32H

1835a *Chirotherium barthii*: Kaup, p. 327-328
1835b *Chirotherium barthii*: Kaup, p. 246-249
1906 *Chirosaurus ibericus*: Navas, p. 208, figs. 2-3
1906 *Chirotherium ibericum*: Navas, p. 213, figs. 2-3
1941 *Chirotherium angustum*: Huene, p. 5, pl. I
1948 *Chirotherium barthi*: Peabody, p. 364-374, fig. 25, pl. 39-40
1955 *Chirotherium barthii*: Peabody, p. 239-240
?1961 *Chirotherium bairdi*: Reig, p. 81
1963 *Chirotherium ibericum*: Kuhn, p. 71
1969 *Chirotherium barthii*: Haubold, p. 837-839, figs. 1-3
1971a Chirotheriidae indet. (for *Chirosaurus ibericus*): Haubold, p. 486.
1971a *Chirotherium barthii*: Haubold, p. 441-450, figs. 13-15, pl. 9-14
1971b *Chirotherium barthii*: Haubold, p. 54-55, fig. 33 (2-4)
1971b Chirotheriidae indet. (for *Chirotherium ibericum*): Haubold, p. 58
1975b *Chirotherium* sp. : Gand, pl. 2D
1984 *Chirotherium barthii*: Haubold, p. 143, fig. 94 (9)
1986 *Chirotherium barthii*: Demathieu and Gand, p.26, fig. 4C-D, p. 28, pl. I C
1991 *Chirotherium mediterraneum*: Demathieu and Durand, p.120, fig. 3., pl. 1 (1-2)
1994 *Chirotherium barthii*: Leonardi, pl. II, fig. 1
1999 Possible *Chirotherium barthii*: Nesbitt, p. 27, fig. 5
2003 *Chirotherium* sp.: Lucas et al., p. 133, fig. 3B
2004 *Chirotherium mediterraneum*: Dematthieu and Demathieu, p. 85, fig. 7
2005 “chirotheroid type”: Marsicano and Barredo, p.326, fig 9A-B.
2006 *Chirotherium storetonense*: King et al., p. 247, figs. 3-4
2005 *Chirotherium barthii*: King et al., p. 249, figs. 5-6
2005 *Chirotherium vorbachi*: King et al., p. 252, fig. 7
2005 *Chirotherium barthii*: Gand and Demathieu, fig 4 (5)
2005 *Chirotherium mediterraneum*: Gand and Demathieu, fig. 4 (6)
2006 *Chirotherium barthii*: Haubold, 2006, figs. 1-49
2006 *Chirotherium barthii*: Melchor and De Valais, p. 362, fig. 4D, F
2009 *Isochirotherium* sp.: Avanzini and Cavin, fig. 3
2010b *Chirotherium barthii*: Klein and Lucas, p. 29, 31, figs. 26C, 31-37
2011 *Chirotherium barthii*: Klein et al., p. 220-221, fig. 3
2011 *Chirotherium* cf. *barthii*: Cavin et al., figs. 2d, 4
2012 *Chirotherium barthii*: Díaz-Martínez and García, p. 146
2013 *Chirotherium barthii*: Xing et al., p. 102-105, figs. 3-8
2015 *Chirotherium barthii*: Díaz-Martínez et al., p. 8-10, 12-15, figs. 4-7, 8J-L
2016 *Chirotherium barthii*: Klein et al., p. 306, fig. 8a-b

Older synonyms. *C. majus* Sickler 1836, *C. storetonense* Morton 1863, *C. vorbachi* Kirchner 1927, *Saurichnites auraensis* Kirchner, 1927, *S. gambachensis* Schuster 1936, *C. higuerensis* Rusconi 1952. King et al. (2005) revived *C. vorbachi* and *C. storetonense* based on purported differences from *C. barthii* such as the relative size of the manus and the more slender shape. These features are considered here to be extramorphological, and these ichnospecies are thus synonyms of *C. barthii*.

Distribution. Solling Formation (Middle-Upper Buntsandstein, Middle Triassic, Anisian) of Germany; Middle Triassic (Anisian-Ladinian) deposits of France, northern Italy and Poland; Helsby Sandstone and Tarporley Siltstone formations of Great Britain; Timezgadiouine Formation (T4, Middle Triassic) of the Argana Basin, Morocco; Holbrook and Anton Chico members of the Moenkopi Formation of Arizona-New Mexico, USA; Cerro de Las Cabras Formation, Argentina; Guanling Formation of Guizhou Province, southern China.

Diagnosis (emended after Haubold, 1971a, b): Trackways of quadrupeds with low trackway width, pace angulation ~170°, but relatively short stride length, Stride:pes length ratio = 5:1; compared with the pes, manus turned more strongly outward. Digit group I–IV relatively long and slender compared with other chirotheriids. Pes imprint with pronounced and symmetrical anterior digit group II–IV in which digit III is longest, and digits II and IV are subequal in length. Digit I reduced, thinner and shifted slightly posteriorly relative to digit group II–IV. Digit V with large basal pad behind the metatarsophalangeal pad IV and with a distinct, thinner phalangeal portion that is often curved backward. Robust and rounded phalangeal and metatarsophalangeal pads visible, the bases of digits II and III being formed by the amalgamated metatarsophalangeal pads II and III. Manus pentadactyl, short, with digit III longest, digits I and V reduced, and IV relatively short and often laterally abducted. Claws in the pes and manus triangular.

Description: The larger form *Chirotherium barthii* (pes lengths = 13-27 cm ; Haubold, 1971a) is characterized by a pentadactyl pes imprint showing a compact and nearly symmetrical anterior digit group II–IV, with digit III being longest. Digit I is thinner than the other digits and shifted

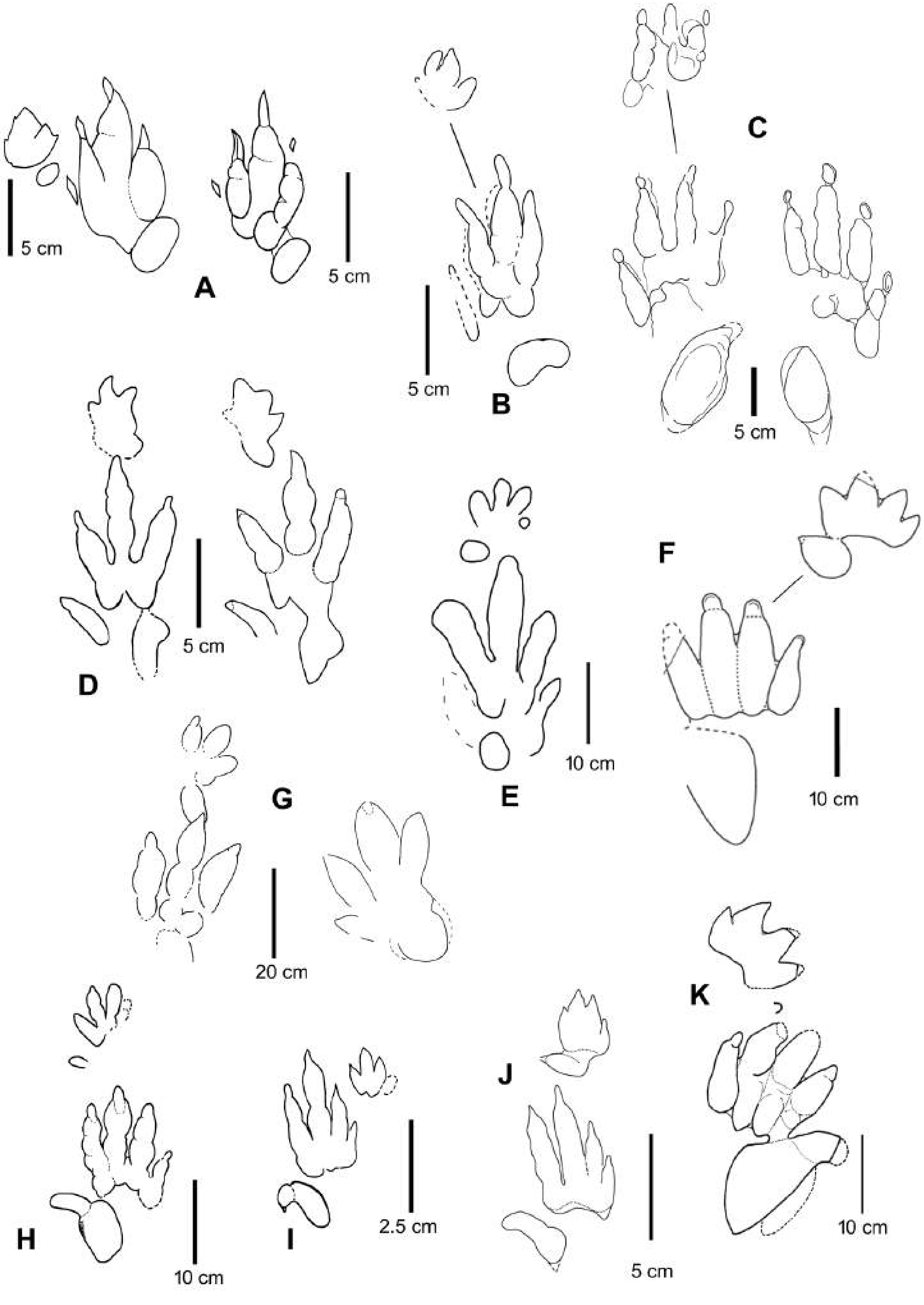


FIGURE 15. Sketches of chirotheriid footprints assigned to the ichnogenus *Chirotherium* in this paper. **A,** *Chirotherium* ("*Sphingopus*") *ferox* comb. nov. (holotype right) from the Middle Triassic of France. **B,** *C. ferox* comb nov. from Eschenbach Fm. (Middle Triassic, Anisian) of Germany. **C,** *C. ladinicum* comb nov. from the Middle Triassic of the Dolomites, northern Italy. **D,** *C*. ("*Parachirotherium*") *postchirotherioides* comb. nov. from Benk Fm. of Germany. **E,** *Chirotherium* cf. *C. postchirotherioides* from Timezgadiouine Fm. (T5) of the Argana Basin, Morocco. **F,** *C. rex* from Holbrook Fm. of Moenkopi Group, Arizona. **G,** *C. ischigualastianum* nov. comb. from Los Rastros Fm. (Ladinian-?Carnian) of Argentina. **H,** *C. barthii* from Solling Fm. of Germany. **I-J,** *C. sickleri* from Solling Fm. (Anisian) of Germany (H-I) and from Wupatki Member of Moenkopi Fm. (Olenekian) of Arizona (J). **K,** *C. rex* from Wupatki Member of Moenkopi Fm., Arizona. Sketches from Haubold (1971b), Haubold and Klein (2000, 2002), Klein and Lucas (2010a, b), Lagnaoui et al. (2012) and Avanzini and Wachtler (2012).

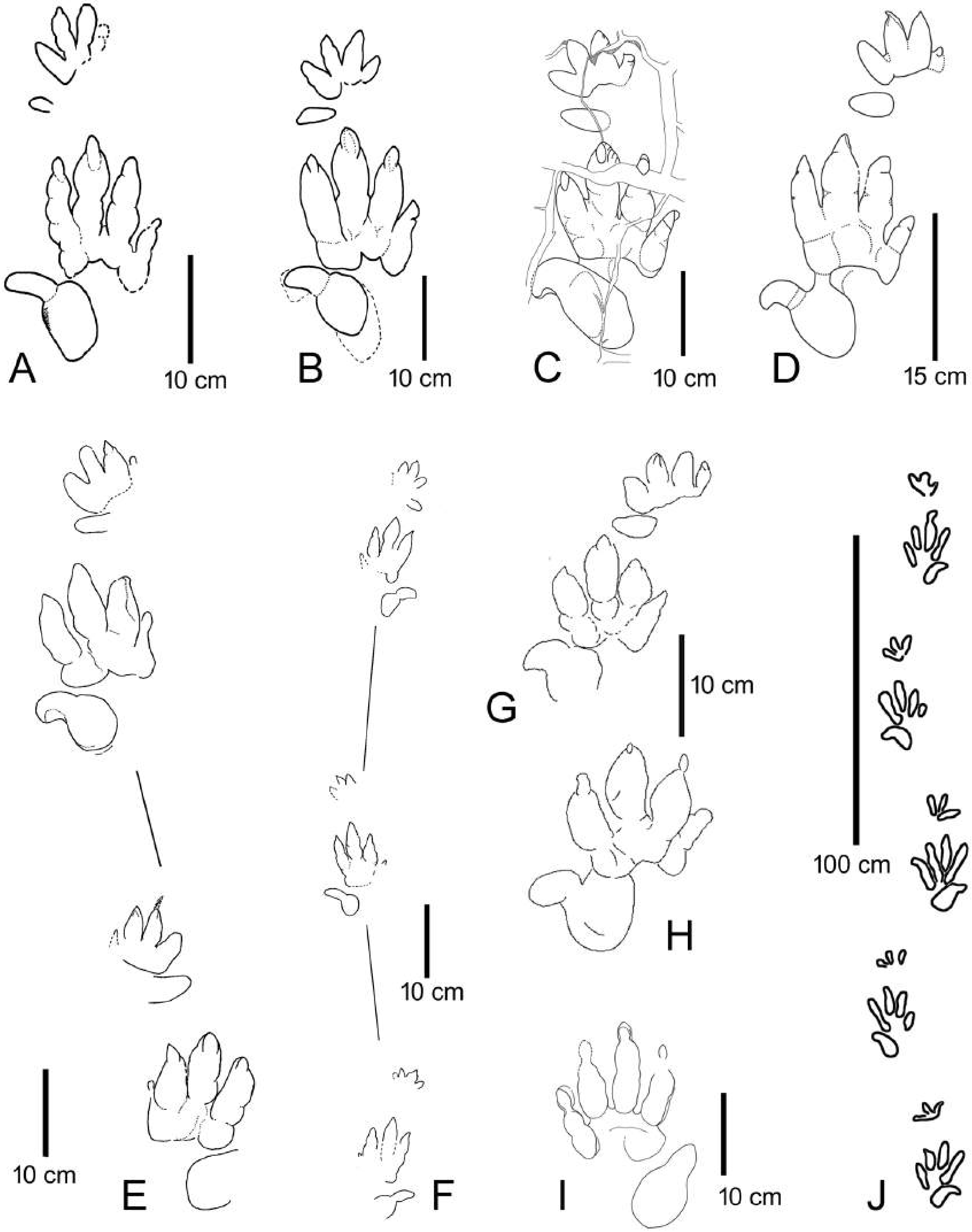


FIGURE 16. *Chirotherium barthii* from different localities. **A-B,** From type surface in Solling Fm. (Anisian) of Germany. **C-F,** From Holbrook Member of Moenkopi Fm. (Anisian) of Arizona. **G-H,** From Timezgadiouine Fm. (T4, Anisian) of Argana Basin, Morocco. **I,** From Middle Triassic of northern Italy. **J,** From Guanling Fm. (Anisian) of Guizhou Province, China. Sketches from Haubold (1971a, b), Klein and Lucas (2010b), Klein et al. (2011), Avanzini and Wachtler (2012), Xing et al. (2013).

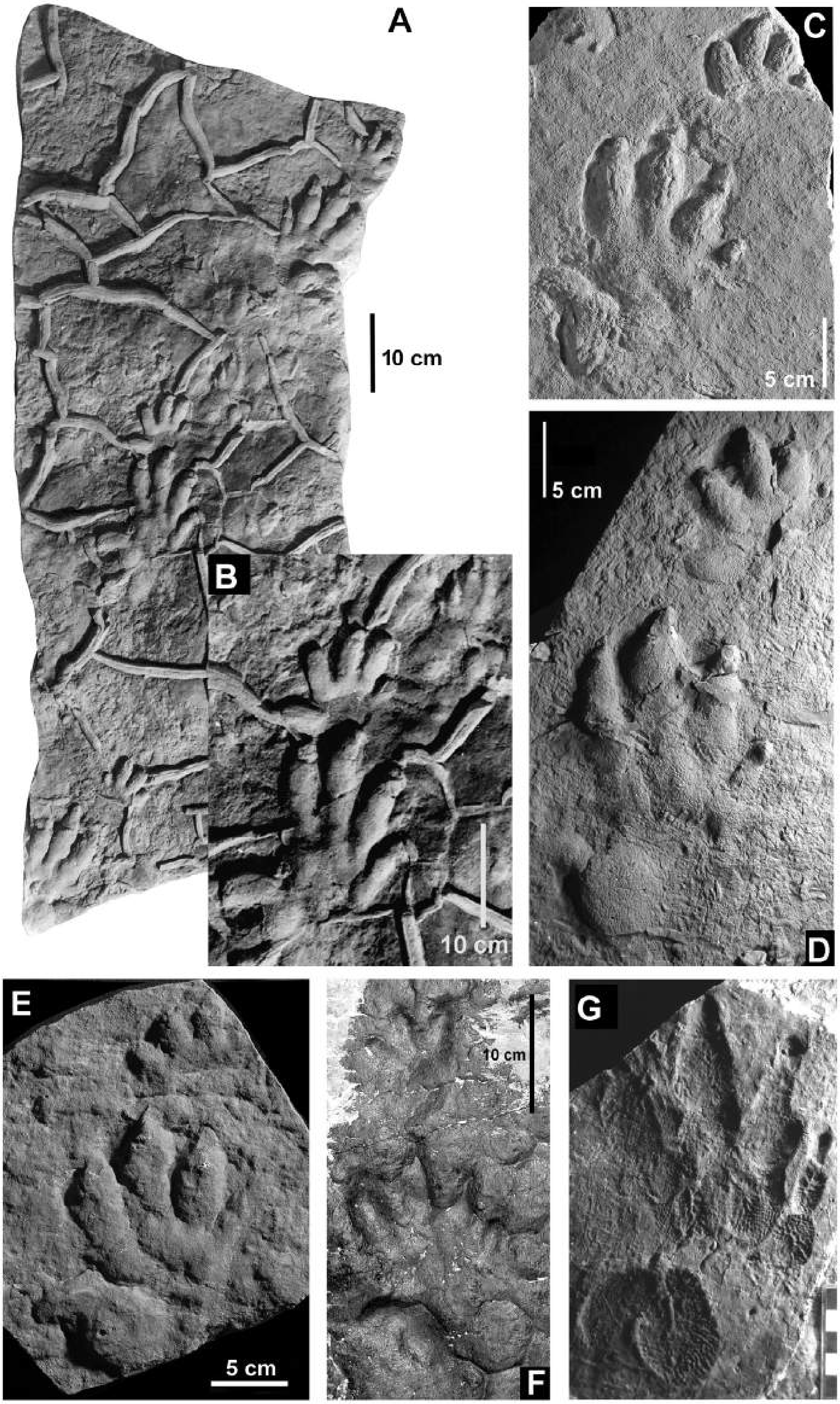


FIGURE 17. Photographs of *Chirotherium barthii*. **A-B,** From type surface in Solling Fm. (Anisian) of Germany. **C,** From Solling Fm. (Anisian) of Germany. **D,** From Holbrook Member of Moenkopi Fm. (Anisian) of Arizona. **E,** From Timezgadiouine Fm. (T4, Anisian) of Argana Basin, Morocco. **F,** From Guanling Fm. (Anisian) of Guizhou Province, China. **G,** From Cerro de las Cabras Fm. (Anisian) of Argentina. Photos in A-B by D. Hildebrand, in C by Michael Hielscher, Jena.

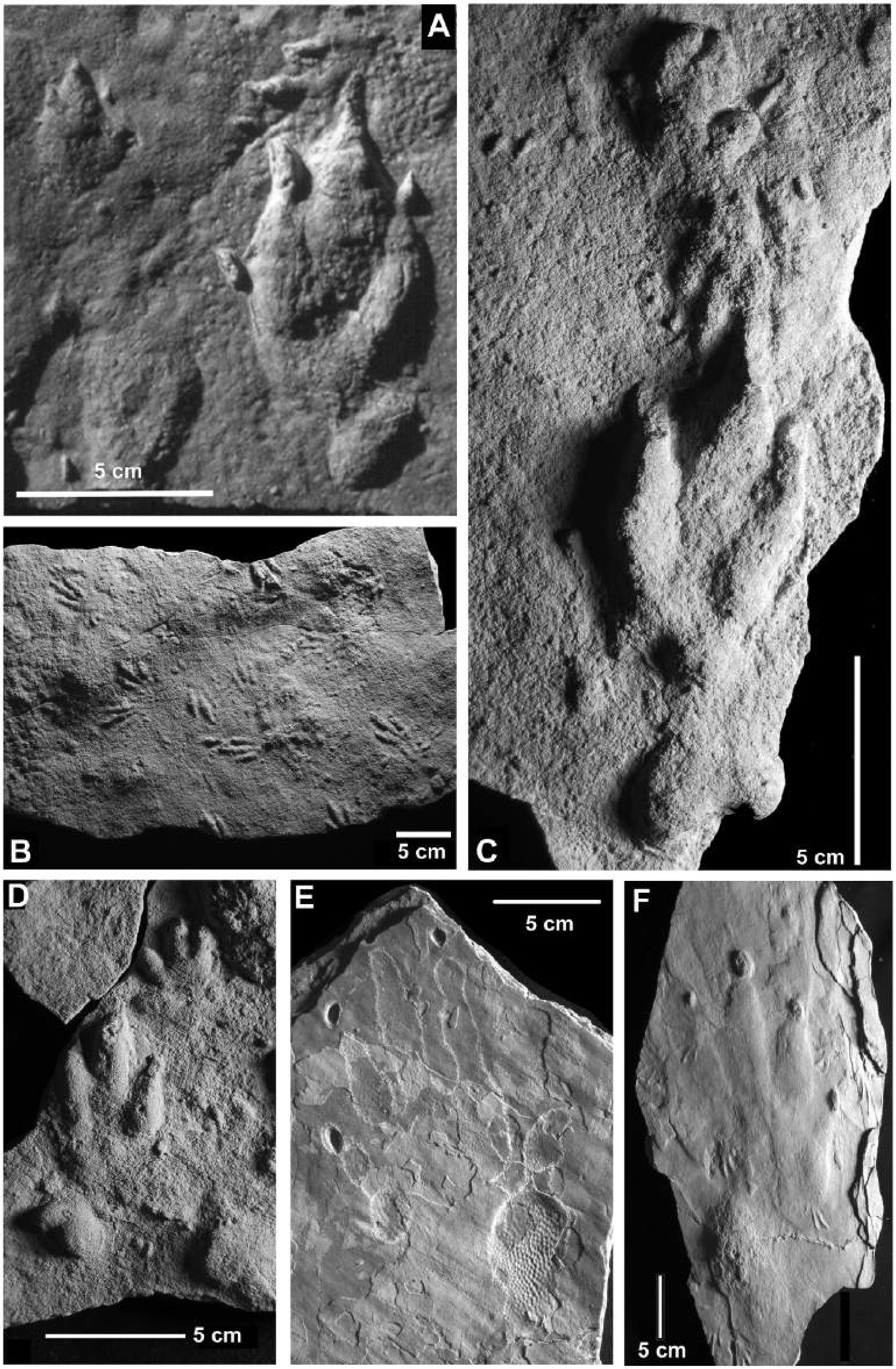


FIGURE 18. A-D, *Chirotherium ferox* comb. nov. **A,** Holotype from Middle Triassic of France. **B-D,** Small, probably juvenile and adult forms from Eschenbach Fm. (Middle Triassic, Anisian) of Germany. **E-F,** *C. ladinicum* comb. nov. from the Middle Triassic of northern Italy.

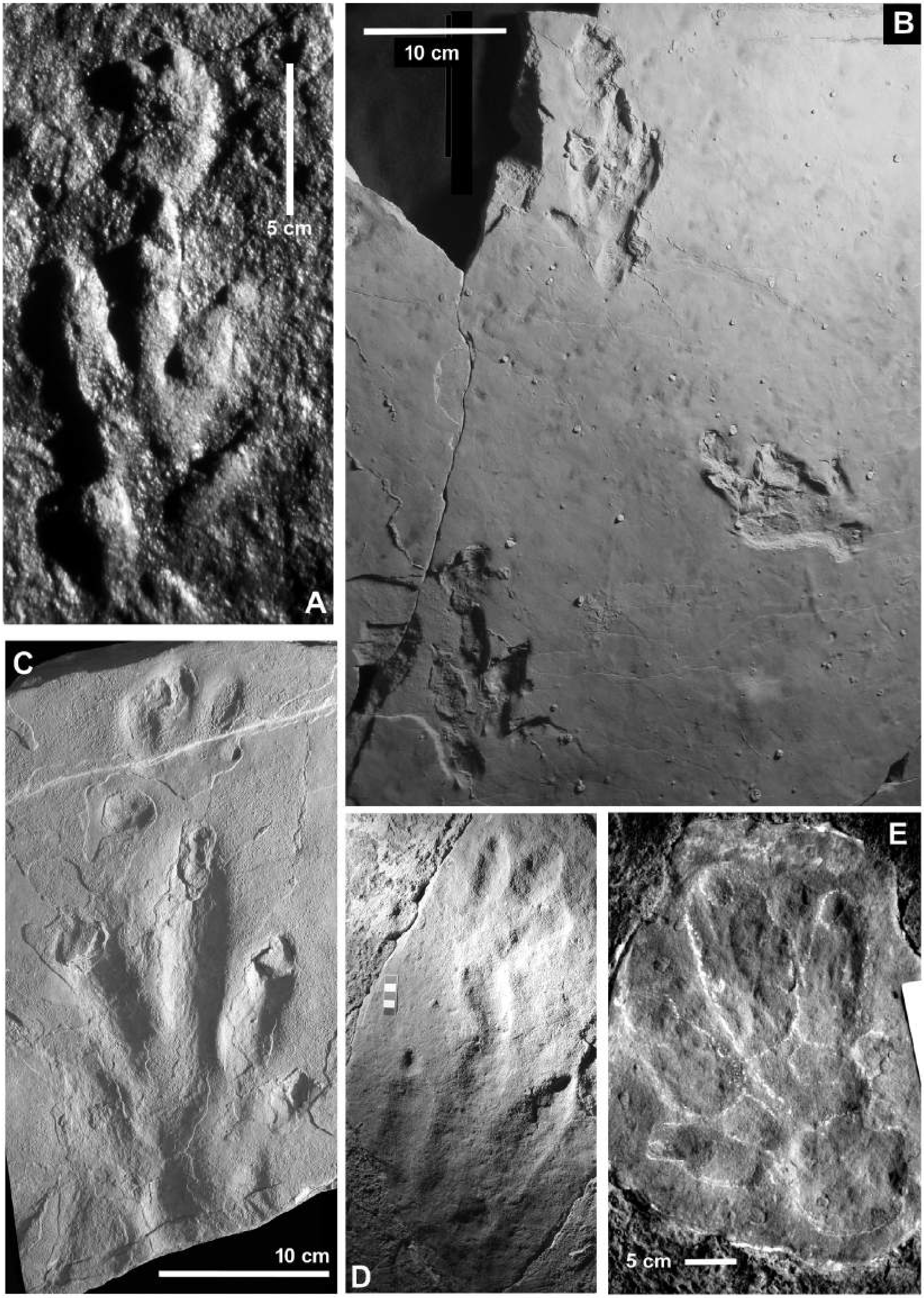


FIGURE 19. A-C, *Chirotherium postchirotherioides* comb. nov. **A,** Holotype from Benk Fm. (Middle Triassic, Ladinian) of Germany. **B,** Slab with two crossing trackways from Benk Formation (Middle Triassic, Ladinian) of Germany. **C,** From Timezgadiouine Fm. (T5, Carnian) of Morocco. **D-E,** *Chirotherium ischigualastianum* comb. nov., plaster casts of pes and manus imprints from Los Rastros Fm. (Ladinian-?Carnian) of Argentina.

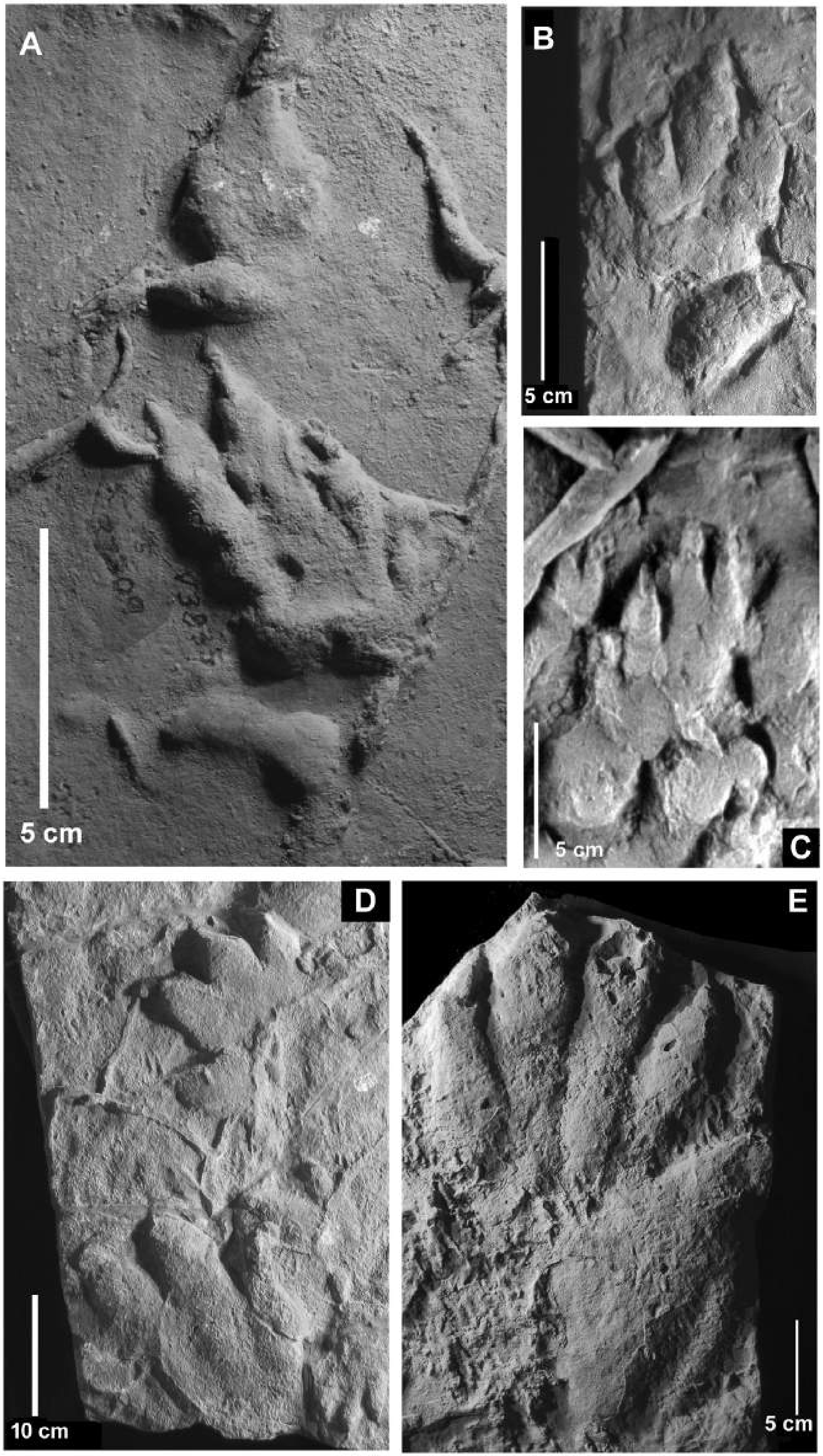


FIGURE 20. **A-C,** *Chirotherium sickleri* from Wupatki Member of Moenkopi Fm. (Anisian) of Arizona (A-B) and from Solling Fm. (Anisian) of Germany. **D-E,** *C. rex* from Holbrook Member of Moenkopi Fm. (Anisian) of Arizona (D, holotype) and from Wupatki Member of Moenkopi Fm. (Olenekian) of Arizona (E).

slightly posteriorly. The posterolaterally positioned digit V has a massive circular to oval basal pad and a thinner phalangeal portion that is often curved backward. The claw traces are robust, acuminate and triangular in shape. The smaller manus impression is pentadactyl, digit III is longest, and digits IV and V are relatively short and laterally divergent. The claws in the manus are small and terminal. In the manus and in the pes the impressions of digits I and V may be absent due to the substrate conditions and/or posture of the autopodia. Trackways show a narrow pattern with stride lengths of up to 145 cm and a pace angulation of 140-170°. The pes is slightly, and the manus is more strongly, rotated outward relative to the midline. The manus is positioned anteriorly or anteromedially to the pes or may be overstepped by the latter due to the velocity of the trackmaker.

Discussion: *Chirotherium barthii* is the type ichnospecies that has the most characteristic shape and generally can most easily be identified among Triassic chirotheriids. This concerns the functionally tridactyl pes imprint with the posteriorly shifted and thinner digit I, the recurved phalangeal part of digit V, and the manus, in which digits IV and V are reduced and laterally abducted. It is known from excellently preserved trackways with imprints that partly show details such as phalangeal pads and skin texture. In particular, the material from the classical Hildburghausen locality is a reference for chirotheriid trackways and their pattern, reflecting the characteristic narrow archosaurian parasagittal gait (Haubold, 1971a, b, 1984, 2006).

Trackmaker: Early avemetatarsalians (dinosaur-bird-line) and/or crocodylian-stem archosaurs.

Chirotherium ferox (Demathieu, 1966) comb. nov.
Figures 15A-B, 18A-D, 32J

1962 Empreintes de Dinosaurien: Lorenz and Demathieu, pl. II, fig. 2
1966 *Sphingopus ferox* ichnogen. nov. ichnosp. nov.: Demathieu, p. 485, fig. 2
1969 *Chirotherium sickleri*: Haubold, 1969, p. 840, fig. 4 J
1971 *Sphingopus*: Gand, pl. III
1974b *Sphingopus*: Gand, pl. 8
1974c *Sphingopus*: Gand, fig. 2 B
1975b *Sphingopus*: Gand, pl. 3G, 4G
1976 *Sphingopus*: Courel and Demathieu, p. 208, fig. 6, pl. 3, fig. 2
1977b *Sphingopus*: Gand, p. 38, pl. 11
1979a *Sphingopus*: Gand, p. 16, pl. 3
1981a *Sphingopus*: Demathieu and Gand, p. 15, pl. IV, figs. 18-19
1981b *Sphingopus*: Demathieu and Gand, p. 24, pl. VIII, fig. 10
1986 *Sphingopus*: Demathieu and Gand, p. 27, fig. 5A-E, p. 29, pl. II D
2002 *Sphingopus* isp.: Haubold and Klein, p. 9-10, fig. 6-7, p. 12, fig. 9
2005 *Sphingopus*: Gand and Demathieu, fig. 5 (1-2)
2018 *"Sphingopus" ferox*: Klein and Lucas, figs. 7-8, 9(A-C)

Distribution: Gres Lyonnais (Middle Triassic, Anisian-Ladinian) of France, Eschenbach Formation (Lower Muschelkalk, Anisian) of Germany, Middle Triassic of Southern Alps, Northern Italy.

Diagnosis (emended): Trackways of a quadruped with slender, functionally tridactyl pes impressions with subparallel digits I–IV; digit III longest, digits II and IV shorter, digit I short, thin and posteriorly shifted, often impressed only by the tip of the claw; digit V reduced to an oval basal pad, and, in more complete imprints, with a backwardly curved phalangeal portion; manus much smaller, pentadactyl, often impressed with only three digits (II, III, IV), digit III is longest, digit IV laterally abducted and short; trackways with stronger outward rotation of the pes relative to the midline, manus less rotated outward.

Description: Pentadactyl pes and manus imprints. The pes imprint shows a pronounced anterior digit group II–IV, with digit III being longest, and having a mostly parallel and narrow configuration. Digit I is shifted backward and strongly reduced, often preserved only by a claw impression. Digit V is mostly present as an oval impression. The claw traces are robust and relatively large and sharp. Manus imprints show relatively short and laterally divergent digits IV and V; digit III is longest. Traces of digits I and V can be missing in both the pes and the manus. Trackways have a stride length of up to 108 cm and a pace angulation of up to 165°. Manus imprints show a stronger outward rotation when compared with the pes.

Discussion: *Sphingopus ferox* was described by Demathieu (1966) based on material from the French Middle Triassic. The diagnostic features listed by Demathieu (1966, 1970) mostly match general characteristics of the ichnogenus *Chirotherium*. Others are related to substrate conditions and extramorphological variation, such as the elongated claw traces. The holotype also shows relatively broad digit impressions, suggesting extramorphological deformation. Well-preserved specimens from the Eschenbach Formation of Germany (Klein and Lucas, 2018) show strong similarities to the ichnogenus *Chirotherium*. Features such as the pronounced digit group II– IV, the short and backward shifted digit I and the strongly reduced digit V, which, in some imprints, displays a recurved distal end, convinces us to reassign the type ichnospecies of *Sphingopus* to *Chirotherium* and propose here the new combination *Chirotherium ferox*. Thus, we regard *Sphingopus* as a junior subjective synonym of *Chirotherium*.

Chirotherium ferox is similar to *C. postchirotherioides* and *C. barthii* in the reduced and backward shifted digit I and in the morphology of the manus with short and laterally spread digits IV and V. However, it differs in the more slender overall shape of the pes imprint with an almost parallel orientation of digits II–IV, and by the punctiform claw trace of digit I, mostly lacking the remainder of the digit impression.

Trackmaker: Early avemetatarsalians (dinosaur-bird-line) and/or crocodylian-stem archosaurs.

Chirotherium ladinicum (Avanzini and Wachtler, 2012) nov. comb.
Figures 15C, 18E-F

2012 *Sphingopus ladinicus*: Avanzini and Wachtler, ichnosp. nov., p. 65, fig. 2

Distribution: Richthofen Conglomerate (Anisian) of northern Italy.

Diagnosis (from Avanzini and Wachtler, 2012): Pes long and slender, pentadactyl (III>IV>II>I>V) with anteriorly directed, subparallel digits II-IV, a small and proximally positioned digit I and a marked proximal pad V. Manus tracks are tridactyl and rounded (pronounced heteropody -- manus/pes ratio = 0.4) and placed in front of the hind foot. Narrow trackway, with a slightly outward rotation of the manus impressions from the midline.

Description: Similar to "*Sphingopus*" *ferox* in the slender overall morphology and parallel orientation of digits II–IV and the backward shifted digit I, but relatively large, with a complete and robust impression of digit I and a massive basal pad of digit V.

Discussion: Avanzini and Wachter (2012) described *Sphingopus ladinicus* based on material from the Richthofen Conglomerate unit of the Dolomites in northern Italy. They correctly identified strong similarities with "*Sphingopus*" *ferox* from the Middle Triassic of France (Demathieu, 1966) but also noticed differences from the latter. Here, we consider the ichnospecies as valid, but, because of the morphological congruence with the ichnogenus *Chirotherium*, we propose the new combination *Chirotherium ladinicum*. The assignment of the formerly separate ichnogenera *Parachirotherium* and

Sphingopus to the ichnogenus *Chirotherium* makes sense, as a distinction from similar forms such as *C. barthii* is often difficult, and many track surfaces from Germany and Italy show transitional morphs (Haubold and Klein, 2002; Avanzini and Wachtler, 2012; Klein and Lucas, 2018). Also, *Chirotherium* is well diagnosed and can be more easily distinguished from the other chirotheriids such as *Brachychirotherium*, *Isochirotherium*, *Synaptichnium* and *Protochirotherium* (Fig. 31).

Trackmaker: Early avemetatarsalians (dinosaur-bird-line) and/or crocodylian-stem archosaurs.

***Chirotherium postchirotherioides* (Rehnelt, 1950) comb. nov.**
Figures 6A, 15D-E, 19A-C, 32K

1950 *Dinosaurichnium postchirotherioides*: Rehnelt, fig. 1-2
1950 *Dinosaurichnium schlehenbergense*: Rehnelt, fig. 3
1952 "*Dinosauripus* spec.": Rehnelt, p. 40, fig. 1
1958a *Parachirotherium postchirotherioides*: Kuhn, pl. VI, fig. 1a-b
1958a ?*Coelurosaurichnus schlehenbergensis*: Kuhn, pl. VI, fig. 2
1958a "*Dinosauripus*" (*Coelurosaurichnus*) sp.: Kuhn, pl. IX, fig. 6
1959 *Dinosaurichnium postchirotherioides*: Rehnelt, pl. II, fig 1
1959 *Coelurosaurichnus schlehenbergensis*: Rehnelt, pl. I, fig. 2, pl. III, figs. 1-2
1959 *Coelurosaurichnus kronbergeri*: Rehnelt, p. 101, fig. 1, p. 102, fig. 2, pl. III, figs. 1-2
1960 *Parachirotherium postchirotherioides*: Rehnelt, p. 73-74, figs. 3-4
1983 *Coelurosaurichnus arntzeniusi*: Rehnelt, p. 48, fig. 1
1963 *Parachirotherium postchirotherioides*: Kuhn, pl. 5, Fig. 22
1976 Unspecified tracks: Weiss, 1976, p. 1, fig. 1, p. 2, fig. 2, p. 5, fig 4
1981 *Anomoepus*: Biron and Dutuit, p. 406-407, fig. 3A, pl. 2F, L
1981 *Quadridigitus*: Biron and Dutuit, p. 406-407, fig. 3B, pl. 2K
1999 non *Parachirotherium* isp.: Avanzini, p. 202, fig. 1
1999 *Parachirotherium* isp.: Avanzini, p. 202, fig. 2
2012 *Parachirotherium* cf. *P. postchirotherioides*: Lagnaoui et al., p. 244, fig. 5D
2016 *Parachirotherium* isp.: Lagnaoui et al., p. 8, fig. 7A
2018 *Parachirotherium* isp.: Zouheir et al., p. 4-5, figs. 3-4

Distribution: Benk Formation (Keuper, Middle Triassic, Ladinian) of northern Bavaria, Germany; Timezgadiouine Formation (T5, Upper Triassic, Carnian) of the Argana Basin, Morocco.

Diagnosis (emended after Haubold, 1971b, Haubold and Klein, 2000): Trackways of a facultative biped with a 66 cm stride length and a pace angulation of 169°. Pes slightly, and manus more strongly, turned outward. Pes imprint pentadactyl, functionally tridactyl and digitigrade to semiplantigrade. Digit III longest, digits II and IV shorter and subequal. Digits I and V strongly reduced and shifted backward, isolated from digits II–IV; digit I much thinner than other digits; digit V mostly reduced to an oval impression, only present in some specimens with short recurved distal portion. Manus imprint pentadactyl, digit III longest, digits IV and V short, and laterally and posterolaterally divergent, respectively. Imprints of digits I and V can be absent in both the pes and the manus.

Description: Relatively small (14 cm in length, 7 cm in width) pentadactyl pes imprints with a pronounced, nearly symmetrical digit group II–IV in which digit III is longest and IV is slightly longer than II. Digit I is short, thin and strongly shifted posteriorly, and digit V is posterolaterally positioned and strongly reduced to an elongate oval or slightly outward curved impression. Claws on digits I–IV are elongate, triangular and sharp. The manus is small, and, if completely preserved, pentadactyl with digit III longest, IV and V strongly reduced and laterally spread, and I short and thin; all digits have small, acuminate claws. Trackways have a stride length of 66 cm and a pace angulation of 169°. Manus imprints are more strongly turned outward compared with the pes imprints and relative to the midline.

Discussion: The ichnospecies was erected based on material from the Middle Triassic Benk Formation of Germany by Rehnelt (1950) and originally described as *Dinosaurichnium postchirotherioides*. Kuhn (1958) referred it to his new ichnogenus *Parachirotherium*. Haubold and Klein (2000, 2002) considered *Parachirotherium* as valid, but demonstrated that in complete trackways, these imprints show variation between pentadactyl and tridactyl (grallatorid) morphology as well as an occasional lack of the manus impression, indicating facultative bipedality of the trackmaker.

The general morphology of the pes and manus imprints matches the diagnosis of the ichnogenus *Chirotherium* in the pronounced pedal digit group II–IV, with digit III being longest and a strongly reduced and thinner digit I. There are other congruent features, especially with *C. barthii*, such as the backward shift of pedal digit I and the short and laterally spread digits IV and V in the manus. Morphologically, a transition from *C. barthii* to *Sphingopus* and *Parachirotherium* morphotype imprints, sometimes being indistinguishable, has been documented from Middle Triassic deposits of Germany and Italy (Klein and Haubold, 2000, 2002; Avanzini and Wachtler, 2012).

Therefore, we regard *Parachirotherium* as a junior subjective synonym of *Chirotherium* and propose the new combination *Chirotherium postchirotherioides*, which is placed within the ichnofamily Chirotheriidae based on described common features of chirotheriids. *Chirotherium postchirotherioides* is considered here as a valid ichnospecies. It is different from *C. barthii* in the more strongly reduced pedal digits I and V and in the more backward shifted digit I. From *C. ferox* it is distinguished by the larger divarication of pedal digits I–IV and by the complete impression of pedal digit V, which, in the former, is preserved with only the distal end.

Trackmaker: Early avemetatarsalians (dinosaur-bird-line) and/or crocodylian-stem archosaurs

***Chirotherium ischigualastianum* (Huene, 1931) nov. comb.**
Figures 15G, 19D-E, 32I

1931 *Rigalites ischigualastianus*: Huene, p. 112, pl. 9
1971b *Rigalites ischigualastianus*: Haubold, p. 61, fig. 37 (1)
1990 *Rigalites ischigualastianus*: Leonardi and De Oliveira, p. 219, pl. III G
1994 *Rigalites ischigualastianus*: Leonardi, pl II, fig. 2, pl XVI, figs. 5-7
2004 *Rigalites ischigualastianus:* Marsicano et al., p. 177, fig. 6A-B
2006 *Rigalites ischigualastianus*: Melchor and De Valais, p. 369, fig. 7A

Distribution: Los Rastros Formation (?Middle-Upper Triassic, Ladinian-Carnian) of Argentina.

Diagnosis (emended after Haubold, 1971b and Melchor and De Valais, 2006): Narrow trackway of a quadruped with relatively long stride length (Stride:pes length = 6 :1 up to 8:1), with a pace angulation of more than 160° and in which the manus can be proximally overstepped by the pes. Pes imprints parallel or slightly directed outward relative to the midline, manus imprints more strongly directed outward with digit V often directed backward. Pes tetradactyl to pentadactyl and functionally tridactyl with digit III being longest, digit I being reduced, thin and posteriorly shifted relative to II–IV, and digit V preserved as a circular to oval pad lacking a phalangeal portion. Digits I–IV with robust, elongate, triangular and pointed claws. Manus smaller and pentadactyl, occasionally lacking impressions of digits I and V, with pointed claws on digits I–IV.

Description: Large imprints with the pes showing a length of 35 cm. Pedal digits often broadly impressed with rounded and robust phalangeal pads; well-preserved specimens with more slender digits. The metatarsophalangeal area is extensive, about half the length of the free digits, with amalgamated pads III and IV. For other features see the diagnosis above.

Discussion: Huene (1931) described *Rigalites ischigualastianus* based on several trackways from the Los Rastros Formation (?Ladinian) of northwestern Argentina. Regarding the potential trackmaker, Huene considered ornithischian dinosaurs, whereas Haubold (1971b) listed *Rigalites* under Crocodylia.

Indeed, these tracks show some similarity with crocodylian tracks such as *Batrachopus*, especially in the manus imprint being strongly rotated outward. However, *Batrachopus* is functionally tetradactyl and has a robust pedal digit I, whereas the tracks from South America are functionally tridactyl, with digit I being more strongly reduced, thin and in a backward shifted position, similar to the conditions seen in characteristic representatives of the ichnogenus *Chirotherium* such as *C. barthii*, *C. postchirotherioides* and *C. spherox* (see above). Also, the strong reduction of pedal digit V, the more lateral orientation of the manus relative to the pes, the reduction of digits IV and V in the manus, and the narrow trackways, etc., are similar to the pattern known from chirotheriid imprints described from the Middle-Upper Triassic of central Europe, North Africa, North America, South America and China (e. g., Peabody, 1948; Haubold, 1971a, b, 2006; Haubold and Klein, 2000, 2002; Melchor and De Valais, 2006; Klein and Lucas, 2010c; Avanzini and Wachtler, 2012; Lagnaoui et al., 2012; Xing et al., 2013). Thus far, no affinities to chirotheriids have been discussed. However, our examination of the *Rigalites ischigualastianus* material in the collections of Tucuman, Argentina, and the comparison with co-eval trackways from different localities in this country (Melchor and De Valais, 2006; Marsicano et al., 2006, 2010) confirmed our earlier suggestions (Klein and Lucas, 2010a; Lagnaoui et al., 2016) that this ichnogenus should be considered a junior subjective synonym of *Chirotherium*.

Trackmaker: Early avemetatarsalians (dinosaur-bird-line) and/or crocodylian-stem archosaurs.

Chirotherium rex Peabody 1948
Figures 15F, K, 20D-E, 21

1948 *Chirotherium moquiensis*: Peabody, p. 376, fig. 26, pl. 41, 42D
1948 *Chirotherium rex*: Peabody, p. 381, fig. 28, pl. 43 (in part)
1956 *Chirotherium moquinense*: Peabody, pl. 78, fig. 3, pl. 80, fig. 2
1971a *Chirotherium moquinense*: Haubold, p. 462, fig. 19b
1971a *Chirotherium rex*: Haubold, p. 462, fig. 19c
1971b *Chirotherium moquinense*, p. 54, fig. 33(1)
1971b *Chirotherium rex*, p. 54, fig. 33(6)
2010b *Chirotherium rex*: Klein and Lucas, p. 45, fig. 45 (in part), p. 47, fig. 46 (in part), p. 48, fig. 47, p. 49, fig. 48, p. 50, fig. 49, p. 51, fig. 50, p. 52, fig. 51

Distribution: Wupatki, Holbrook, and upper red members/formations (OlenekianAnisian) of the Moenkopi Formation/Group of Arizona, USA. Peres Formation–Richthofen Conglomerate (Anisian) of the Dolomites (northern Italy).

Diagnosis (emended after Peabody, 1948): Footprints of large chirotheriids with a pes length of more than 33 cm. Digits I–IV with proportions III > II > IV > I, coalesced along 2/3 of their proximal length, forming a flat sole surface in which phalangeal and metatarsophalangeal pads are indistinct and have a straight posterior margin. Digit V as long as digit III and represented by a massive basal pad that runs into an elongate “heel” and lacks a distinct phalangeal portion. Claw impressions on pes digits I–IV rounded or spatulate-like; manus hooflike with wide and short, stubby digits tapering at their distal ends and indicating the presence of acuminate claws.

Description: Large pentadactyl pes and manus imprints (more than 33 cm pes length). Pes imprint semi-plantigrade, showing robust, relatively broad digits that are moderately spread out. Anterior digit group with proportions III > II > IV > I and distinct posterior margin. In their proximal portion, digits overlap and amalgamate along 2/3 of their length. The posterolaterally positioned digit V is as long as digit III and represented by a massive, elongate basal pad that often runs into a distinct “heel.” The overall shape is characterized by a flattened sole surface in which pads are only indistinctly visible. Claws are present on digits I–IV and have a spatulate shape. The pentadactyl manus imprint is wider than long and has short, broad digits showing traces of small, pointed claws

Discussion: Peabody (1948) erected a new ichnospecies based on large chirotheriid tracks preserved on the lower surface of a sandstone block from the Holbrook Member of the Moenkopi Formation of Arizona. These co-occur with imprints of *Chirotherium barthii* that, besides their smaller size, can be distinguished from *C. rex* by the digit proportions in the pes being III > II = IV > I, digit V with a less extensive basal pad and distinct recurved phalangeal portion, a posteriorly concave proximal margin of the anterior digit group I–IV and the more triangular shape of the claw. Another large chirotheriid from the Wupatki Member of the Moenkopi Formation was also described by Peabody (1948) as *C. moquinense* but was referred to *C. rex* in a revision of the Moenkopi ichnofauna by Klein and Lucas (2010). The shape of the pes imprints partly resembles that of *Isochirotherium*, in particular *I. herculis* (see also King et al., 2006; Klein and Lucas, 2010b). However, the manus imprint is larger. Therefore, we choose the more conservative way and keep *C. rex* here as a valid *Chirotherium* ichnospecies. Nevertheless, we cannot exclude that future studies might find it in a combination with *Isochirotherium*, possibly even in synonymy with *I. herculis* which would have priority.

Trackmaker: Non-archosaurian archosauriforms or crocodylian-stem archosaurs.

Chirotherium sickleri Kaup, 1835
Figures 15I-J, 20A-C, 32F-G

1835b *Chirotherium*: Kaup, p. 248.
1948 *Chirotherium minus*: Peabody, p. 326, fig. 16, p. 327, fig. 17, p. 359, fig. 23, pls. 37, 38
1954 *Chirotherium minus*: Baird, p. 171, fig. 1D
1967 *Chirotherium sickleri*: Haubold, p. 28, figs. 9-10
1969 *Chirotherium sickleri*: Haubold, p. 840, fig. 4 A-H
non 1969 *Chirotherium sickleri*: Haubold, p. 840, fig 4 J
1971a *Chirotherium sickleri*: Haubold, p. 453, fig. 16(a-h), p. 454, fig. 17, pls. XIII, XIV, XV, XVI, XXXII, XXXIV, XXXV
1971b *Chirotherium sickleri*: Haubold, p. 53, fig. 32(10-11), p. 54, fig. 33(5)
1989 *Chirotherium sickleri*: Demathieu and Fichter, p. 145, pl. 1, fig. 2
2010b *Chirotherium sickleri*: Klein and Lucas, p. 11, fig. 9C, p. 39-44, figs. 38-43

Older synonyms: *Chirotherium bipes* Berthold, 1835, *C. minus* Sickler, 1836, *C. bornemanni* Willruth, 1917, *C. beasleyi* Nopcsa, 1923, *Krokodilipus minus* Nopcsa, 1923, *C. pfeifferi* Soergel, 1925.

Distribution: Solling Formation (Middle-Upper Buntsandstein, Middle Triassic, Anisian) of Germany; ?Emosson Formation (Olenekian-Anisian) Switzerland; Helsby Sandstone and Tarporeley Siltstone formations (Anisian) of Great Britain; Wupatki Member of the Moenkopi Formation (Lower Triassic, Olenekian) of Arizona, USA.

Diagnosis (after Haubold, 1971a, b): Digit IV in the pes slightly shorter than III but much longer than II. Digit I thin and short but with minor posterior shift compared with other *Chirotherium* ichnospecies. Digit V with slender, recurved phalangeal portion and slightly enlarged basal pad. Trackway narrow with long strides, pace angulation 160°.

Description: The smaller form *Chirotherium sickleri* is similar to *C. barthii* in the pronounced anterior pedal digit group II–IV with digit III being longest, and in the thin, short digit I and the posterolaterally positioned and recurved digit V. It is different from the latter in: (1) the pedal digit group II–IV being less symmetrical and digit IV being relatively long compared with digit III; (2) pedal digit I lacking a posterior shift relative to II–IV; (3) a relatively long manual digit IV; and (4) the trackway pattern with a smaller pace angulation, and the pes imprints showing stronger rotation outward relative to the pes.

Discussion: *Chirotherium sickleri* is the second chirotheriid originally described from the Hildburghausen type locality (Kaup, 1835), its footprints being smaller than those of *Chirotherium barthii*. That these tracks represent a juvenile trackmaker of *C. barthii,* thus reflecting allometric growth (see discussions in King et al., 2005 and Díaz-Martínez et al., 2015), can be excluded because *C. sickleri* and *C. barthii* are morphologically different, and specimens of similar size show the same differences as large representatives (Klein and Haubold (2003). Compared with other *Chirotherium* ichnospecies, *C. sickleri* is the most conservative form, with both pes and manus imprints showing a relatively long digit IV, and the trackways having the pes more outwardly rotated when compared with the manus. In these features, *C. sickleri* slightly resembles the ichnogenus *Synaptichnium*.

Trackmaker: Probably a crocodylian-stem or non-crown group archosaur. Despite the narrow trackway pattern, this morphotype appears slightly more conservative than *C. barthii*, in the longer digit IV in the manus and pes imprints and a pes imprint that is outward rotated relative to the manus imprint (vise versa in *C. barthii*). These features suggest a non-avemetatarsalian archosaur.

Isochirotherium Haubold, 1971
Figures 22-23, 31B, 32D

1948 *Chirotherium*: Peabody, p. 386, fig. 30, p. 392, fig. 32A, pl. 44
1954 *Chirotherium* (*C. lomasi*): Baird, p. 174
1967 *Chirotherium*: Haubold, p. 31, fig. 12, p. 33, fig. 13
1971a *Chirotherium*: Haubold, p. 466, fig. 20, p. 470, fig. 21, p. 474, fig. 22, p. 483, fig. 24d, pls. XVII, XVIII, XIX, XX, XXI, XXII, XXIV
1971b *Isochirotherium*: Haubold, p. 54, fig. 33(8-9), p. 56, fig. 34, p. 60, fig. 36(2)
1974 *Isochirotherium*: Gand, pl. 2 B
1974c *Isochirotherium*: Gand, fig. 2 C
1976 *Isochirotherium*: Courel and Demathieu, p. 200, fig. 3, p. 205, fig. 4, pl. 1, fig. 2-3, pl. 2, figs. 2-3
1977b *Isochirotherium*: Gand, p. 31, pl. 8
1979b *Isochirotherium*: Gand, p. 22-25, pls. I-IV
1981a *Isochirotherium*: Gand, p. 12, pl. III, figs. 7-8, 10
1981b *Isochirotherium*: Demathieu and Gand, p. 22, pl. VII, fig. 5, p. 24, pl. VIII, fig. 8
non 1982 *Isochirotherium*: Demathieu and Haubold, p. 98, “photo 1”, p. 100, “photo 2”, p. 106, fig. 1b
1986 *Isochirotherium*: Demathieu and Gand, p. 26, fig. 4 F-L, p. 28, pl. I D, p. 29, pl. IIA
non 1990 *Isochirotherium*: Fuglewicz et al., p. 124, fig. 7(1-5, 7), pls. 4(3-4), 5(3-4), 10(2), 11
non 2000 *Isochirotherium*: Ptaszyński, p. 164, fig. 9B-C, p. 165, fig. 10B-E, p. 166, fig. 11, p. 167, fig. 12, p. 168, fig. 13A-C.
2005 *Isochirotherium*: Gand and Demathieu, fig. 4 (12-17)
2010b *Isochirotherium*: Klein and Lucas, p. 55, fig. 53, p. 56, fig. 54, p. 57, fig. 55

Type ichnospecies: *Isochirotherium soergeli* (Haubold, 1967) (Fig. 22A).

Included ichnospecies: *I. herculis*, *I. coltoni*, *I. lomasi*, *I. marshalli*, *I. coureli*, *I. felenci.*

Distribution: Middle-?Upper Triassic (Buntsandstein, Muschelkalk, ?Keuper, Anisian-?Norian) of Germany; Middle Triassic (Anisian) of Great Britain, Spain and Italy; Middle Triassic (Timezgadiouine Formation, T4, Anisian) of Morocco; Lower-Middle Triassic (Moenkopi Group, Olenekian-Anisian) of the USA.

Diagnosis (after Haubold, 1971b): Narrow trackways of a quadruped with a pace angulation of ~165° and relatively strong outward rotation of the pentadactyl pes and manus imprints (20°-30° on average). Pedal digits II and III are longest, and digit IV is mostly as long as digit I and distinctly divergent from digit III. Basal pad of digit V close behind metatarsophalangeal area I–IV, and, in larger forms, progressively amalgamated with these. Distal phalangeal segment of digit V only weakly loaded. Very small manus-ratio of manus:pes area = 1:4.5-6.8. Digit III in the manus is longest.

Description: The digit proportions of the pes are significant, with the dominance of digits II and III. Either digit II or III can be the longest in different ichnospecies, whereas digits I and IV are short and subequal. The rounded manus is positioned anterior to the pes or located slightly inward; it has the smallest size relative to the pes compared to other chirotheriids. The combination of low trackway width with a strong outward rotation of the imprints is characteristic. Isolated pes imprints of some ichnospecies, especially *Isochirotherium soergeli* from the German Buntsandstein, might be confused with other chirotheriid ichnotaxa such as *Chirotherium barthii*. However, *I. soergeli* has a shorter digit IV in the pes, and the manus imprint is much smaller when compared to the pes.

Extramorphological variation and deformation can therefore make a distinction difficult.

Discussion: The ichnogenus *Isochirotherium* was introduced by Haubold (1971b) based on material with the characteristic digit proportions and trackway pattern from the German Buntsandstein (Middle Triassic, Anisian). *I. soergeli*, which is the type ichnospecies, as well as *I. herculis,* are typical representatives of the ichnogenus in the Buntsandstein and have also been identified in the Middle Triassic (Anisian) of Great Britain. *I. herculis* is the largest form and was described from Great Britain under *Chirotherium herculis* by Egerton (1839).

Interestingly, the shape of the pes is similar to that in large chirotheriids from the American Moenkopi Group (Lower-Middle Triassic, Olenekian-Anisian) that have been described as *Chirotherium rex* and “*Chirotherium moquinense*” by Peabody (1948; see also revision of *C. rex* by Klein and Lucas, 2010b). The overall shape and digit proportions of the pes are similar, but *C. rex* has a larger manus. Therefore, the latter was considered a valid ichnotaxon by Klein and Lucas (2010).

Peabody (1948) classified chirotheriids in “small manus” and “large manus” groups based on the relative size of manus and pes imprints. The former are chirotheriids that were later referred to the new ichnogenus *Isochirotherium* (Haubold, 1971b), while the latter included, for example, *Chirotherium barthii*, *C. sickleri* (“*C. minus*”) and footprints now assigned to *Synaptichnium* (“*C. diabloense*,” “*C. cameronense*”). Haubold (1971a, b) gave values for the manus/pes size ratios of different chirotheriids: about 1:3 for large manus group and about 1:5 or more for small manus group members. The different relative size of autopodia reflects the different shift of the center of body mass (COM) posteriorly or anteriorly, and tendencies towards bipedality and quadrupedality, respectively.

Small forms known as *Isochirotherium delicatum* are from the Middle Triassic of France and northern Italy (Gand, 1974a, b, 1975, 1978, 1979; Courel and Demathieu, 1976; Demathieu and Gand, 1981a, b, 1986, Avanzini and Lockley, 2002; Todesco et al., 2008). Juvenile tracks of *I. soergeli* are also known from Germany (Haubold, 1967). Other occurrences and ichnospecies have been described from Lower-Middle Triassic localities in Germany, Poland, France, Italy, Spain, Great Britain, Morocco and the western USA (Gand, 1974a, b, 1975, 1978, 1979; Courel and Demathieu, 1976; Demathieu and Gand, 1981a, b, 1986; Avanzini and Leonardi, 2002; Demathieu and Demathieu, 2004; Ptaszyński, 2000; Diedrich, 2008, 2009, 2012, 2015; King et al., 2005; Klein and Lucas, 2010b, 2018; Klein et al., 2011; Fortuny et al., 2011). Purported *Isochirotherium* from the Lower Triassic of Wióry, Poland (Ptaszyński, 2000) was re-assigned to *Protochirotherium* by Klein and Niedźwiedzki (2012). An isolated pes with an associated very small manus from the Upper Triassic Löwenstein Formation (Norian) of Germany (Haderer, 1991) shows similarities with *Isochirotherium* and, together with some finds from Morocco (see below), is possibly the only record of the ichnogenus from the Upper Triassic. *Isochirotherium* ichnospecies considered as valid by us are: *I. soergeli* (type ichnospecies), *I. herculis*, *I. coltoni*, *I. marshalli*, *I. lomasi*, *I. coureli* and *I. delicatum*.

Trackmaker: Crocodylian-stem archosaurs or non-crown-group archosauriforms are possible trackmaker candidates. However, presently there is no exact match between *Isochirotherium* footprints and distinctive archosaur-pes skeletons.

***Protochirotherium* Fichter and Kunz, 2004**
Figures 24-25, 31D, 32A

1982 *Isochirotherium*: Demathieu and Haubold, 1982, p. 98, “photo 1”, p. 100, “photo 2”, p. 106, fig. 1
1990 *Chritherium* [sic]: Fuglewicz et al., p. 119.
1990 *Chirotherium*: Fuglewicz et al., figs. 5 (1–6), 6 (1–2, 4, 9), 7 (6); pls. 2 (1–3), 3 (1–4), 4 (1–2), 11, 13 (2).
1990 *Isochirotherium*: Fuglewicz et al., fig. 7 (1–2, 3–5, 7); pls. 4 (3–4), 10 (2), 11.
1990 *Brachychirotherium*: Fuglewicz et al., fig. 8 (1–4); pls. 5 (1–4), 6 (1), 10 (3).
1990 Chirotheriidae indet.: Fuglewicz et al., fig. 5 (3, 5–8); pl. 12 (3).
1990 *Synaptichnium*: Fuglewicz et al., fig. 8 (5–7); pl. 6 (2–4).
1997 *Isochirotherium*: Fichter and Lepper, figs. 2–4.
1999 “chirothere”: Lockley and Meyer, fig. 3.14 (top).
2000 *Brachychirotherium*: Ptaszyński, figs. 5a–c, 6a–c, 7a–c, 8a–c, 9a, 10a.
2000 *Isochirotherium*: Ptaszyński, figs. 9b–c, 10b–e, 11a–c, 12a–b, 13a–c.
2000 *Synaptichnium*: Ptaszyński, figs. 13d–f, 14a–d.
2004 *Protochirotherium* ichnogen. n.: Fichter and Kunz, figs. 3a–b, 5a–b, 6.
2007 *Isochirotherium*: Niedzwiedzki and Ptaszyński, fig. 7b, d.
2007 *Synaptichnium*: Niedzwiedzki and Ptaszyński, fig. 7c.
2007 *Brachychirotherium*: Niedzwiedzki and Ptaszyński, fig. 7e–f.
2007 *Synaptichnium*: Klein and Haubold, fig. 2b (left).
2007 *Protochirotherium*: Klein and Haubold, fig. 2d–e.
2009 *Chirotherium* sp.: Gümbel, figs. 3–5, 7, 9, 12–13.
2010 *Protochirotherium-Synaptichnium*: Klein et al., figs. 2c–d, f, 5c–d, f–g, j.
2010 *Protochirotherium*: Klein et al., figs. 4C, 5a–b.
2010 *Protochirotherium*: Klein and Lucas, fig. 3b–c.
2010a *Synaptichnium*: Klein and Lucas, fig. 3d (left).
2010 *Brachychirotherium*: Tourani et al., figs. 2a, c–d, f, l, 3a, f–g, i–j.
2010 *Isochirotherium*: Tourani et al., figs. 2g, j, 3c, l.
2010 *Chirotherium*: Tourani et al., figs. 2i, m, 3b, k.
2011 *Protochirotherium*: El Hachimi et al., p. 171, fig. 2.
2011 *Brachychirotherium*: El Hachimi et al., p. 171, fig. 2.
2011 *Isochirotherium*: El Hachimi et al., p. 171, fig. 2.
2011 *Chirotherium*: El Hachimi et al., p. 171, fig. 2.
2011 *Brachychirotherium*: Brusatte et al., p. 2, figs. S2, S4 (supplementary material).
2011 *Brachychirotherium*: Brusatte et al., p. 3, figs. S2, S4 (supplementary material).
2011 *Isochirotherium*: Brusatte et al., p. 3, fig. S2 (supplementary material).
2011 *Synaptichnium*: Brusatte et al., p. 3, fig. S2, S4 (supplementary material).
2011 *Protochirotherium*: Fichter and Kunz, p. 8, fig. 6a–c, p. 9, figs. 1–3, p. 14, fig. 14.
2011 *Palaeochirotherium*: Fichter and Kunz, p.10, figs. 1–2, p. 11, fig. 7a–b, p. 13, fig. 12e.
2012 *Chirotherium barthii:* Lovelace and Lovelace, p. 649, fig. 10A, p. 650, fig. 11.
2012 aff. *Protochirotherium*: Krainer et al., p. 208, fig. 2A-B
2014 aff. *Protochirotherium*: Thomson et al., p. 131, fig. 2
2015 *Protochirotherium*: Fichter and Kunz, p. 256, fig. 4A-B
2015 *Palaeochirotherium*: Fichter and Kunz, p. 256, fig. 4C-E

Type ichnospecies: *Protochirotherium wolfhagense* Fichter and Kunz, 2004 (Fig. 24A-B).

Included ichnospecies: The type ichnospecies and *Protochirotherium hauboldi*.

Distribution: Lower Triassic (Buntsandstein, Olenekian) of Germany; Lower Triassic (Olenekian) of Austria; Lower Triassic (Wióry Formation, Olenekian) of Poland; Lower Triassic (Timezgadiouine Formation, T3) of the Argana Basin, Morocco, North Africa; Lower Triassic (Olenekian) of Niger, North Africa; Lower Triassic (Moenkopi Group, Olenekian) of USA.

Diagnosis (emended after Fichter and Kunz, 2004): Chirotheriids with plantigrade to semiplantigrade pes and manus imprints. Anterior digit group I–IV with digit III longest and digit IV being only slightly shorter. Digit V in the pes with massive oval basal pad, often strongly elongated proximally and with a separate thinner phalangeal part that is nearly straight or slightly curved outward.

Description: In their relatively long digits IV and V, the imprints of *Protochirotherium* resemble the ichnogenus *Synaptichnium* (see above), and, on some track surfaces, the two ichnogenera are difficult to distinguish. However, imprints of *Protochirotherium* are broader in overall shape, and digit IV is slightly shorter, whereas in *Synaptichnium* digit IV is longest or subequal to III. *Protochirotherium* also shows a more massive oval basal pad of pedal digit V that can be extended posteriorly into an elongated “heel.” Some ichnospecies are characterized by the different imprint depth, showing an emphasis on digits I–III, whereas digit IV is more faintly impressed and laterally divergent (Klein and Niedźwiedzki, 2012). In well preserved specimens, circular to oval phalangeal and metatarsophalangeal pads as well as impressions of the skin texture can be observed. Robust triangular claws with acuminate to slightly rounded tips are present on digits I–IV. One trackway from Wióry, Poland, with pes imprints of 11.7 cm length, shows an average stride length of 63.5 cm and a (maximum) pace angulation of the pes of 163°. Other trackways have much lower values of pace angulation, for example 119°-145°, which is relatively low for chirotheriids in general. The same is true for the relatively large trackway width. Both pes and manus imprints are turned strongly outward. In some rare cases, tail traces have been observed (Klein and Niedźwiedzki, 2012).

FIGURE 21. Photograph of *Chirotherium rex* pes-manus set with skin impressions from the Middle Triassic (Anisian) of northern Italy. Original specimen from Brandner (1973).

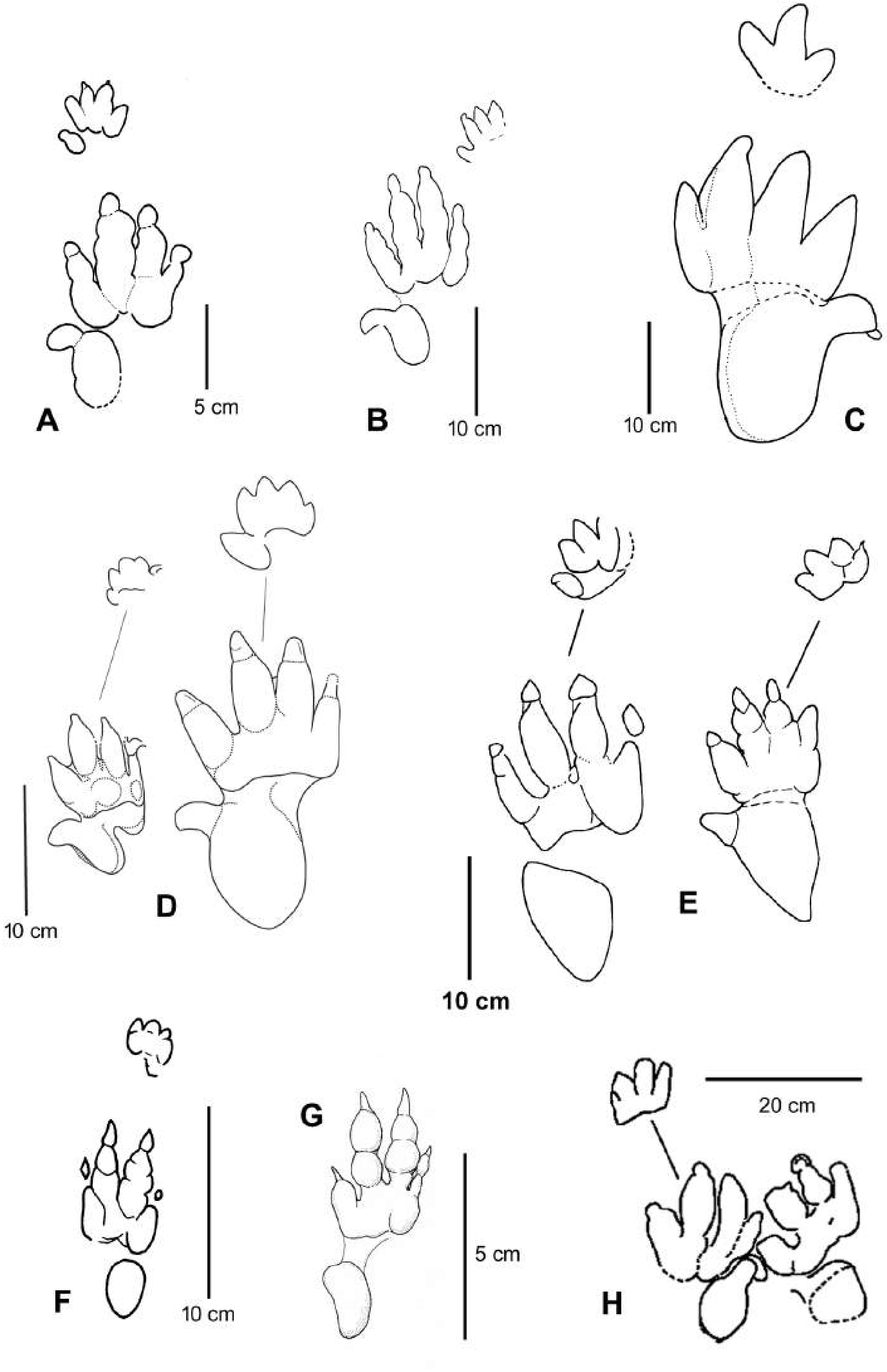


FIGURE 22. Sketches of *Isochirotherium* from different localities. **A,** *I. soergeli* holotype from Solling Fm. of Germany. **B,** *I. lomasi* from Middle Triassic (Anisian) of Great Britain. **C,** *I. herculis* from Solling Fm. (Anisian) of Germany. **D,** *I. coltoni* and *I. marshalli* from Wupatki and Holbrook members of Moenkopi Fm. of Arizona. **E,** *I. coureli* and *I. felenci* from Middle Triassic of France. **F-G,** *I. delicatum* from Middle Triassic of France and Italy. **H,** *I. coureli* from Timezgadiouine Fm. (T4, Anisian) of Argana Basin, Morocco. Sketches from Haubold (1971a, b), Demathieu (1970), Avanzini and Lockley (2002) and Klein et al. (2011).

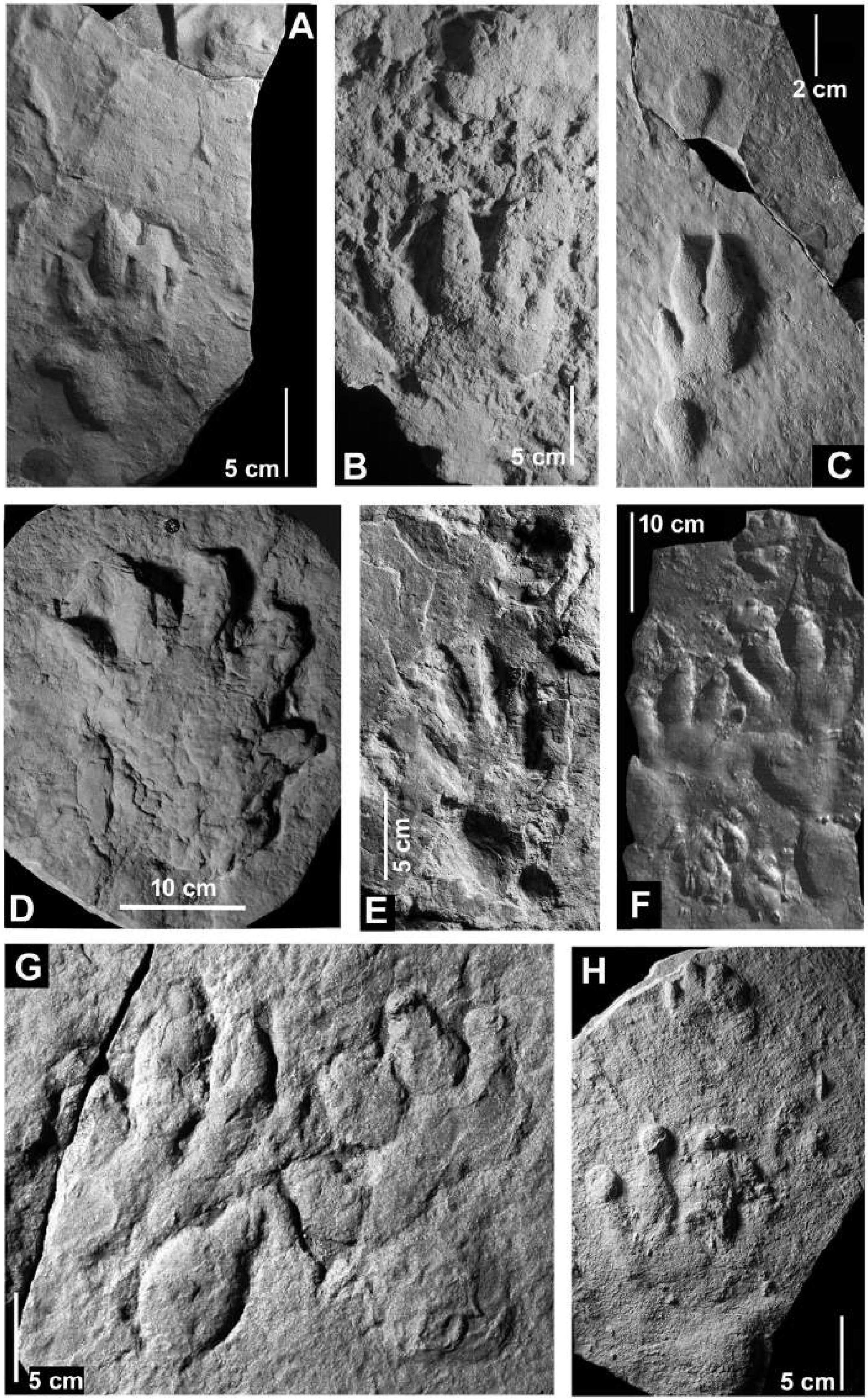


FIGURE 23. Photographs of *Isochirotherium* from different localities. **A,** *I. coltoni* from Wupatki Member of Moenkopi Fm. (Olenekian) of Arizona. **B,** *I. marshalli* from Holbrook Member of Moenkopi Fm. (Anisian) of Arizona. **C,** *I. delicatum* from Middle Triassic of Southern Alps, northern Italy. **D,** *I. herculis* from Solling Fm. (Anisian) of Germany. **E,** *I. soergeli* from same unit. **F,** *I. coureli* (center) co-occurring with *Chirotherium ferox* (bottom) from Middle Triassic of France. **G,** *I. coureli* from Timezgadiouine Fm. (T4, Anisian) of Argana Basin, Morocco. **H,** *I. coureli* from Eschenbach Fm. (Anisian) of Germany.

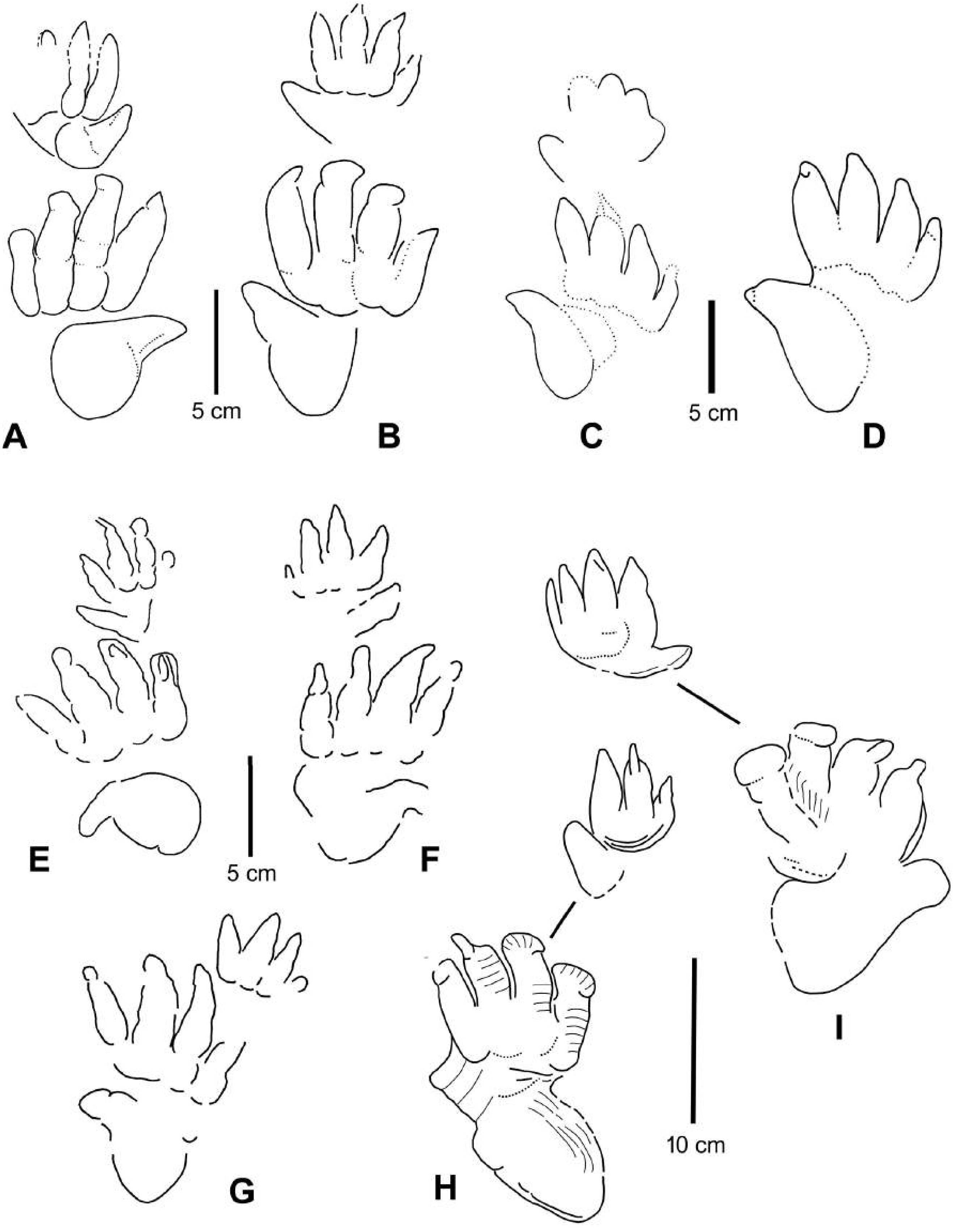


FIGURE 24. Sketches of *Protochirotherium* pes and manus imprints from different localities. **A-B,** *P. wolfhagense* from Detfurth Fm. (Olenekian) of Germany. **C-G,** *P. hauboldi* from Wióry Fm. (Olenekian) of Poland. **H-I,** *Protochirotherium-Synaptichnium* plexus footprints from Timezgadiouine Fm. (T3, Olenekian) of the Argana Basin, Morocco. Sketches from Klein et al. (2010, 2013b) and Klein and Niedźwiedzki (2012).

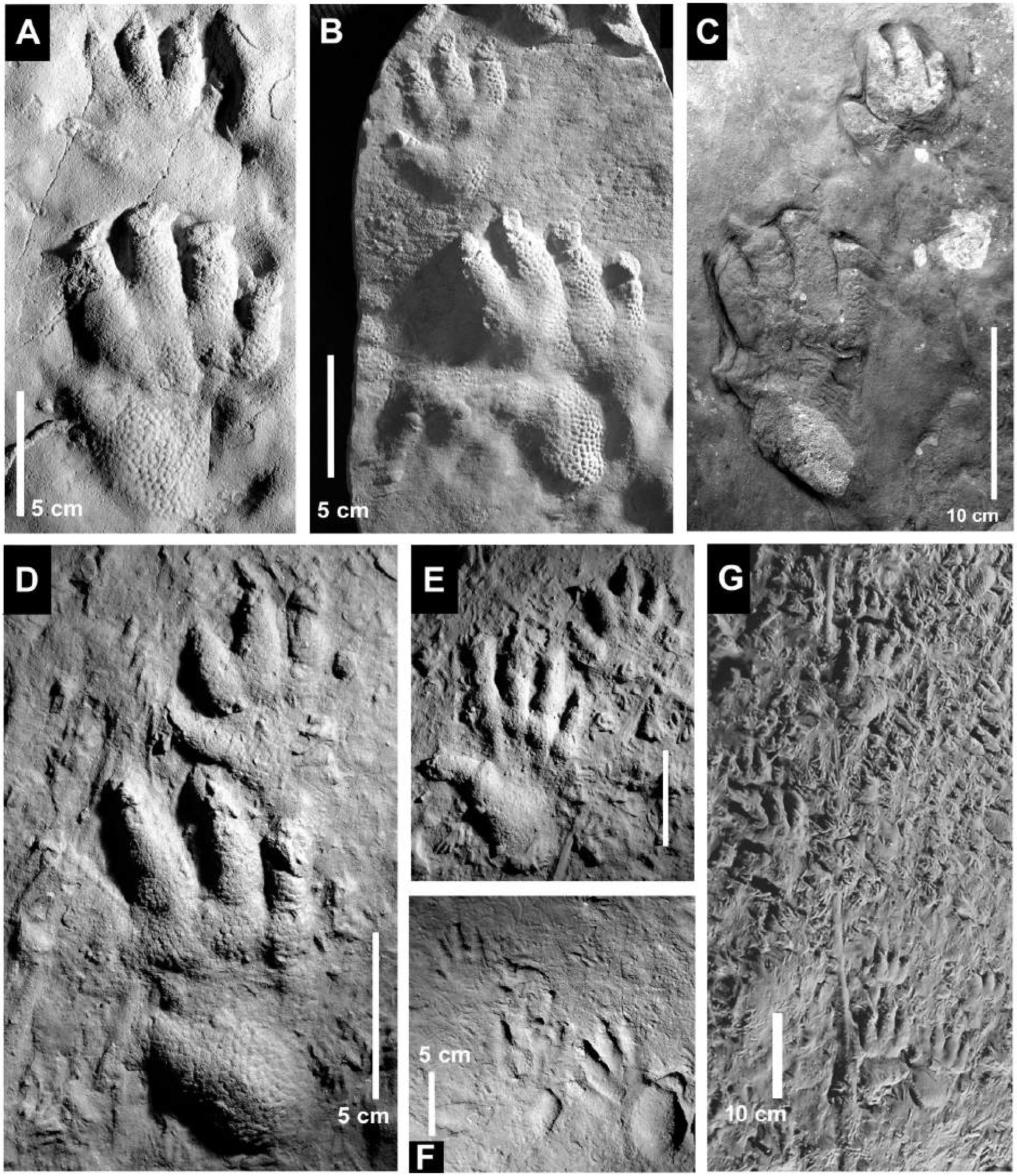


FIGURE 25. Photographs of *Protochirotherium* from different localities. **A-B,** *P. wolfhagense* from Detfurth Fm. (Olenekian) of Germany (artificial casts, holotype at left). **C,** *Protochirotherium-Synaptichnium* plexus footprints from Timezgadiouine Fm. (T3, Olenekian) of Argana Basin, Morocco. **D-G,** *P. hauboldi* from Wióry Fm. (Olenekian) of Poland with trackway showing tail trace (G).

Discussion: Fichter and Kunz (2004) erected the ichnogenus *Protochirotherium* based on footprints from the Detfurth Formation (Middle Buntsandstein, Lower Triassic, Olenekian) of northern Hesse, Germany. This appeared to be a characteristic morphotype of the Lower Triassic that subsequently was documented from different localites in Germany, Poland and Morocco (Klein and Haubold, 2007, Klein and Lucas, 2010b; Klein and Niedźwiedzki, 2012; Klein et al., 2011, 2013; Fichter and Kunz, 2011). Morphologically and temporally, *Protochirotherium* precedes typical *Chirotherium barthii* and "modern" chirotheriid track assemblages in the Middle Triassic, giving it an importance for biostratigraphic and biochronologic analyses (see below). It is one of the best known tetrapod ichnotaxa of the Triassic and documented by many excellently preserved trackways and hundreds of imprints.

Trackmaker: Non-crown group Archosauriformes or crocodylian-stem archosaurs (Klein and Niedźwiedzki, 2012, Klein et al., 2013, Bernardi et al., 2015). This is suggested by the pes imprints with digit III longest. The relatively narrow trackway pattern excludes nonarchosauriform archosauromorphs, proterosuchids and erythrosuchids.

***Synaptichnium* Nopcsa, 1923**
Figures 26-28, 31E, 32B-C

1923 *Synaptichnium* Nopsca, p. 142, pl. VI, fig. 4
1948 *Chirotherium*: Peabody, p. 351, fig. 22, pls. 33-36,
1954 *Chirotherium*: Baird, p. 171, fig. 1B-C
1954 *Synaptichnium*: Baird, p. 171, fig. 1E
1971a *Chirotherium*: Haubold, p. 456, fig. 18
1971b *Chirotherium*: Haubold, p. 53, fig. 32(1-5)
1974b *Synaptichnium*: Gand, pl. 2 A-B
1977b *Synaptichnium*: Gand, p. 28, pl. 7
1981a *Synaptichnium*: Gand, p. 7, figs. 3, 6
1981b *Synaptichnium*: Demathieu and Gand, p. 22, pl. VII, figs. 1-2, 6
1982 *Synaptichnium*: Demathieu and Haubold, 1982, p. 98, "photo 1", p. 100, "photo 2", p. 101, "photo 3" top, p. 103, "photo 4", p. 106, figs. 1-2.
1986 *Synaptichnium*: Demathieu and Gand, p. 26, fig. 4, O-Q, p. 29, pl. II B
1990 non *Synaptichnium*: Fuglewicz et al., p. 128, fig. 8 (5-7), pl. 6(2-4)
2000 *Synaptichnium*: Ptaszyński, p. 172-176, figs. 15, 16 A-D, 17A-B, 18A-F, 19A
2000 non *Synaptichnium*: Ptaszyński, p. 168, fig. 13D-F, p. 171, 14A-D
2004 *Synaptichnium*: Klein and Haubold, p. 9-10, figs. 3-4
2005 *Synaptichnium*: Gand and Demathieu, fig. 4 (1-4)
2005 *Synaptichnium*: King et al., p. 54, fig. 8
2007 non *Synaptichnium*: Niedźwiedzki and Ptaszyński, p. 328-329, figs. 2-3
2010b *Synaptichnium*: Klein and Lucas, p. 23-32, figs. 21-30
2012 *Synaptichnium*: Klein and Niedźwiedzki, p. 8, fig. 6H, p. 9, fig. 7J, p. 12, fig. 11-12 (in part), p. 14-17, figs. 13C-E, 14-16 (in part), p. 30, fig. 31, p. 35-37, figs. 36-38(C-I) 2018 *Synaptichnium*: Klein and Lucas, p. 164-167, figs. 2-5

Type ichnospecies: *Synaptichnium pseudosuchoides* Nopcsa, 1923 (Fig. 26H).

Included ichnospecies: The type ichnospecies and *Synaptichnium diabloense*, *S. cameronense*, *S. kotanskii*.

Distribution: Lower-Middle Triassic (Buntsandstein and Muschelkalk, OlenekianAnisian) of Germany; Lower Triassic (Wióry Formation, Olenekian) of Poland; Middle Triassic (Anisian-Ladinian) of France, The Netherlands, Great Britain, Spain and Italy; Middle-Upper Triassic (Timezgadiouine Formation, T4-T5, Anisian-Carnian) of the Argana Basin, Morocco; Lower-Middle Triassic (Moenkopi Group, Olenekian-Anisian) of the USA.

Diagnosis (after Haubold, 1971b; King et al., 2005): Moderately narrow trackways of a quadruped with a pace angulation that is only slightly larger than 160° (140° on average); imprints pentadactyl with strong outward rotation of the pes. Pes imprints with digits I–IV increasing in length and digit IV being longest or subequal with III; digit V more laterally than proximally positioned behind front digits, slender, elongate and straight or slightly curved outward and with oval basal pad. Manus more rounded, with digit III being longest. Ratio of manus:pes area relatively large for chirotheriids = 1:1.8, up to 1:3.7. (1:2.5 on average). Sharp claws on digits I–IV in both the pes and manus. Distinct rounded phalangeal and metatarsophalangeal pad traces.

Description: Pes imprints are long, slender and ectaxonic, with straight or slightly inward curved digits increasing in length from I to IV. The digit V impression is posteriorly elongated into a short "heel." The smaller manus is positioned anterior to the pes or is laterally overstepped by the latter. Digit III of the manus longest. Trackways seem to show a large extramorphological variability in stride length, pace angulation and trackway width due to differing gait and velocity of movement.

Discussion: The ichnogenus *Synaptichnium* was erected based on material from Staffordshire, Great Britain, by Nopcsa (1923). The latter was originally described as "*Rhynchosaurus*" (Woodward, 1902), and form "D3" and "*Rhynchosauroides*" by Beasley (1905) and Maidwell (1911), respectively. Unfortunately, the holotype of the type ichnospecies of *S. pseudosuchoides* was lost, but parts of the holotype slab were re-located and proposed by King et al. (2005) as the lectotype.

The different *Synaptichnium* ichnospecies introduced by Peabody (1948) based on material from the Moenkopi Formation of Arizona and referred to *Chirotherium* (Peabody, 1948; Haubold, 1971a) were later assigned to *Synaptichnium* (Haubold, 1971b; Klein and Lucas, 2010b). Additional *Synaptichnium* material was described from France (Demathieu, 1970), Italy (Avanzini 1999, 2000; Avanzini and Neri, 1998), Germany (Klein and Haubold, 2004; Klein and Lucas, 2018), Poland (Ptaszyński, 2000; Klein and Lucas, 2012) and Morocco (Klein et al., 2011; Lagnaoui et al., 2012). Several trackways and imprints described under "*Brachychirotherium*" from Lower-Middle Triassic deposits by different authors were reassigned to *Synaptichnium* by Klein and Haubold (2004) based on observed extramorphological variations of *Synaptichnium* tracks that resemble *Brachychirotherium*; others might represent new ichnogenera that will be the subject of a different study (Figs. 29-30; see below). The stratigraphic range of *Brachychirotherium* is restricted to the Upper Triassic.

Trackmaker: Non-crown group Archosauriformes. The pes imprint would nearly match the pes skeleton of proterosuchids, with digit IV being longest, however, proterosuchids have a relatively broad gait, whereas *Synaptichnium*, in particular *S. cameronense*, has a very narrow trackway pattern (Bernardi et al., 2015; Klein and Lucas, 2017).

Chirotheriidae indet. Figures 29-30

"*Brachychirotherium*"
Figures 29-30

1925 *Chirotherium*: Soergel, p. 15, fig. 12
1967 *Chirotherium*: Haubold, p. 34-42, figs. 14-18D
1970 *Chirotherium*: Demathieu, p.139-144, figs. 49-50
1971a *Chirotherium*: Haubold, p. 477-479, fig. 23, p. 483, fig. 24a-c, 1
1971b *Brachychirotherium*: Haubold, figs. 32 (6-8), 35 (1-3), 36 (3)
1971 *Brachychirotherium*: Gand, p. 8, pl. 3, 2F
1973 *Brachychirotherium*: Demathieu and Gand, p. 11-18, pl. 1-2, fig. 1

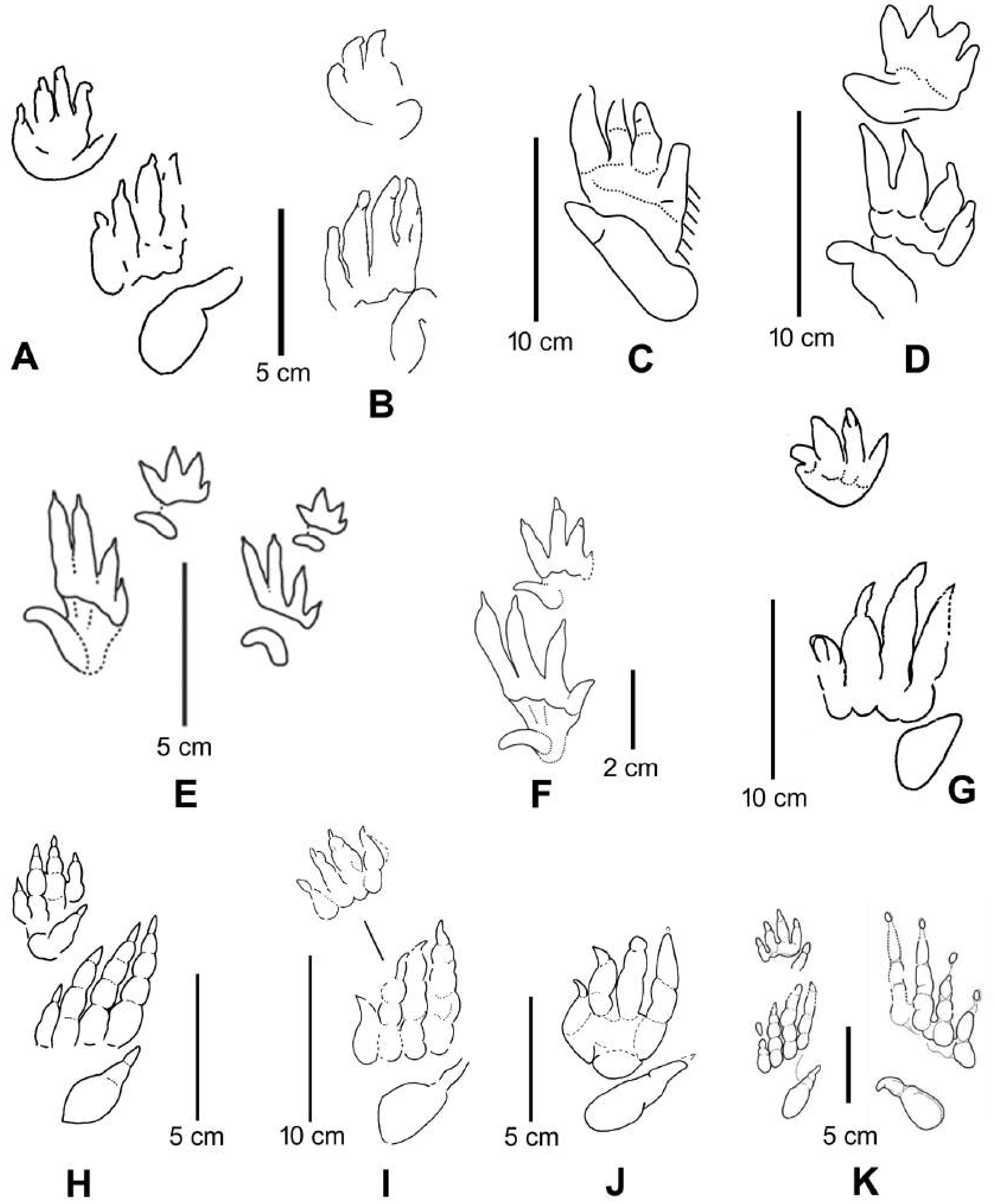


FIGURE 26. Sketches of *Synaptichnium* footprints from different localities. **A-B,** *S. kotanskii* from Wióry Fm. (Olenekian) of Poland. **C-D,** *Protochirotherium-Synaptichnium* plexus footprints from Timezgadiouine Fm. (T3, Olenekian) of the Argana Basin, Morocco. **E,** *S. diabloense* from Wupatki Member of Moenkopi Fm. (Olenekian) of Arizona. **F,** *S. cameronense* from Holbrook Member of Moenkopi Fm. (Anisian) of Arizona. **G,** *S.* isp. from undesignated member of Moenkopi Fm. of Arizona. **H,** *S. pseudosuchoides* from Middle Triassic of Great Britain. **I,** *S. pseudosuchoides* from Eschenbach Fm. (Anisian) of Germany. **J,** *S. priscum* from Middle Triassic of France. **K,** *S. pseudosuchoides* and *S.* isp. from Middle Triassic of the southern Alps, northern Italy. Sketches from Haubold (1971b), Klein and Haubold (2004), Avanzini and Mietto (2008a), Klein and Lucas (2010a, b), Klein et al. (2010) and Klein and Niedźwiedzki (2012).

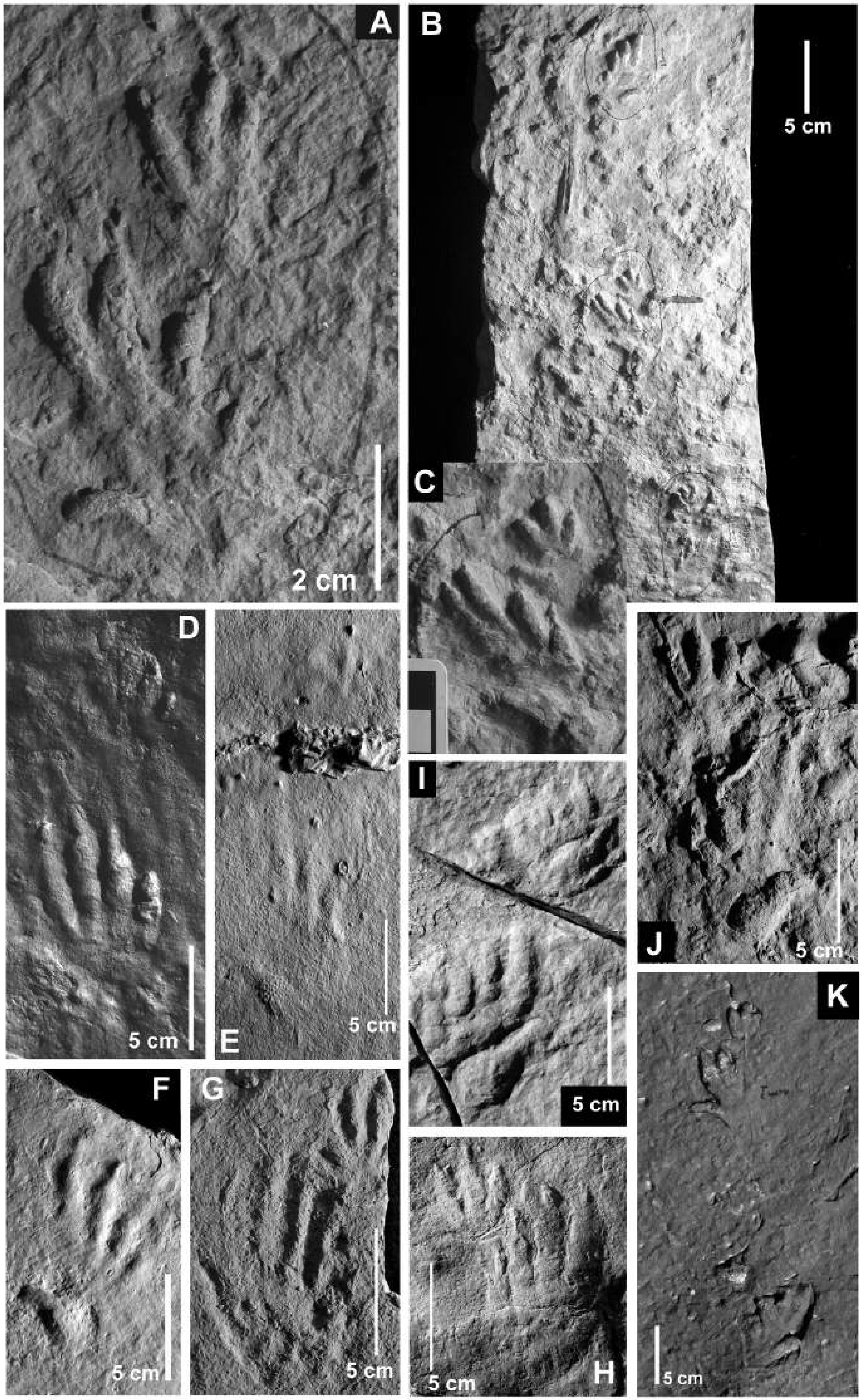


FIGURE 27. Photographs of *Synaptichnium* footprints from different localities. **A,** *S. cameronense* from Holbrook Member of Moenkopi Fm. (Anisian) of Arizona. **B-C,** *S. diabloense* from Wupatki Member of Moenkopi Fm. (Olenekian) of Arizona. **D,** *S.* isp. from undesignated member of Moenkopi Fm. of Arizona. **E-F,** *S.* isp. and *S. cameronense* from the Middle Triassic of the Southern Alps, northern Italy. **G-H,** *S.* isp. from the Middle Triassic of France. **I,** *S.* isp. from Timezgadiouine Fm. (T4, Anisian) of the Argana Basin, Morocco. **J,** *S. kotanskii* from Wióry Fm. (Olenekian) of Poland. **K,** *Protochirotherium-Synaptichnium* plexus footprints from Timezgadiouine Fm. (T3, Olenekian) of the Argana Basin, Morocco.

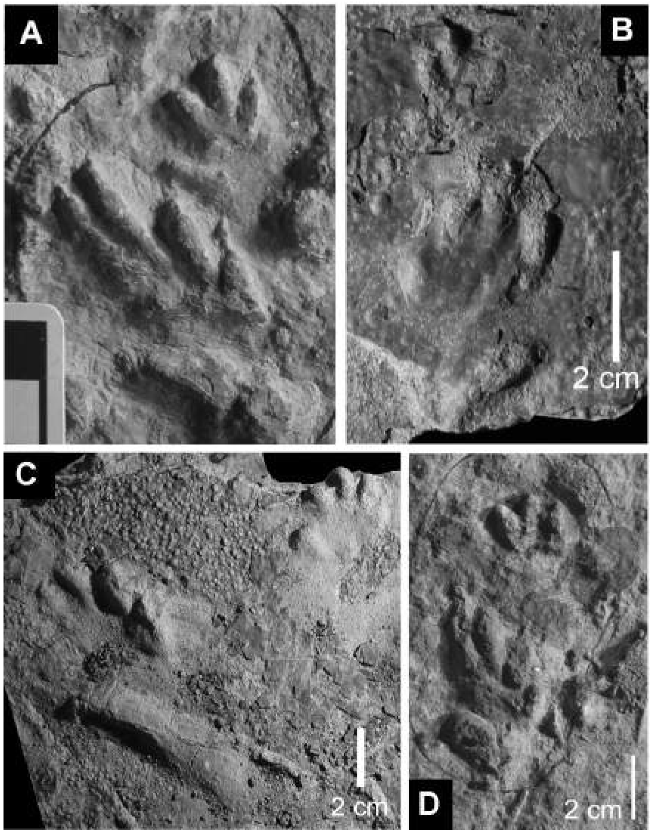


FIGURE 28. Photographs of *Synaptichnium* footprints from different localities. **A,** *S. diabloense* from Wupatki Member of Moenkopi Fm. (Olenekian) of Arizona. **B-C,** *S.* ("*Brachychirotherium*") isp. from Solling Formation (Anisian) of Germany. **D,** *S. diabloense* from Wupatki Member of Moenkopi Fm. (Olenekian) of Arizona.

1974 *Brachychirotherium*: Demathieu, p. 6-7, fig. 1
1974b *Brachychirotherium*: Gand, p. 15, pl. 4, fig. 1A-B, fig. 2B-C, pl. 5A-F
1974c *Brachychirotherium*: Gand, p.18, fig. 2A, p. 19, fig. 3F, I
1975a *Brachychirotherium*: Gand, p. 11-18, pl. 1-4
1975b *Brachychirotherium*: Gand, p. 38-43, pl. 2A-C, E, pl. 5A, D-F
1976 *Brachychirotherium*: Courel and Demathieu, p. 206-208, fig. 5, pl. 2, fig. 4, pl. 3, fig. 1
1978a *Brachychirotherium*: Gand, p. 15-16, pl. 3
1978b *Brachychirotherium*: Gand, p. 33-35, pl. 9
1979a *Brachychirotherium*: Gand, p. 15, pl.2, p. 17, pl. 4
1981a *Brachychirotherium*: Demathieu and Gand, p. 10-11, p. 15, pl. 4
1982 *Brachychirotherium*: Demathieu and Haubold, p. 103-104, fig. 4, p. 106-107, fig. 2d
1982 *Brachychirotherium*: Demathieu and Leitz, p. 73-80, figs. 5-6
1983 *Brachychirotherium*: Demathieu and Oosterink, p. 16-17, figs. 13, p. 48, fig. 54
1984 *Brachychirotherium*: Haubold, figs. 95 (1-9)
1986 *Brachychirotherium*: Demathieu and Gand, p. 11-12, 26, fig. 4, p. 29, pl. 2C
1988 *Brachychirotherium*: Demathieu and Oosterink, p. 6-9, fig. 4
2004 *Brachychirotherium*: Demathieu and Demathieu, p. 83-85, fig. 8a-b
2005 *Brachychirotherium*: Gand and Demathieu, p. 729, fig. 4 (9-10)
2006 *Brachychirotherium*: Melchor and De Valais, p. 359-361, fig. 4A

Distribution: Middle Triassic (Buntsandstein, Anisian) of Germany; Middle Triassic (Anisian-Ladinian) of The Netherlands, France, Spain and Italy; ?Middle–Upper Triassic Ipaguazú Formation, Bolivia.

Description: Chirotheriids that show relatively wide pes imprints with broad, rounded digits. In the pes, digit III is longest, digit IV sometimes, but not always shorter than digit II. Digit V proximo-medially elongated with large basal pad often elongated into a massive heel. Manus imprints short, rounded with digits II and III longest and subequal in length. Trackways narrow, with outwardly rotated pes and manus imprints

Discussion: In particular, trackways from the French Middle Triassic, but also from the Lower-Middle Triassic of Germany, Poland and The Netherlands have been described as *Brachychirotherium* (see citations above and discussion under this ichnogenus). Based on several differences from the diagnosis of the ichnogenus (see above), originally described from the Upper Triassic (Beurlen, 1950; Karl and Haubold, 1998), we consider all Middle Triassic specimens to belong to a different (probably new) chirotheriid ichnogenus.

Differences from Upper Triassic *Brachychirotherium* concern the digit proportions of the pes, with pedal digit IV sometimes subequal to or longer than digit II, and the more massive, posteriorly elongated pedal digit V. Some material from Germany shows an extramorphological transition of "*Brachychirotherium*" to *Synaptichnium* (Klein and Haubold, 2004; Klein and Lucas, 2018). Lower Triassic "*Brachychirotherium*" from Olenekian deposits of Poland (Fuglewicz et al., 1990; Ptaszyński, 2000) has proven to be *Protochirotherium* (Klein and Niedźwiedzki, 2012; see above). This can only be cleared up by a future comprehensive study of the Middle Triassic material, in particular from France.

Trackmaker: Stem-crocodylian or non-crowngroup archosauriform

"Brachychirotherium tintanti" Demathieu, 1971

1971 *Brachychirotherium*: Demathieu, p. 814, fig. 67 1971b
1971 *Brachychirotherium*: Haubold, p. 57, fig. 35 (3)
1984 *Brachychirotherium*: Haubold, p. 144, fig. 95 (9)
2005 *Brachychirotherium*: Gand and Demathieu, p. 729, fig. 4 (7)

Distribution: Grés des Lyonnais (Middle Triassic, Anisian-Ladinian)

Description: An isolated, relatively broad and short pentadactyl impression with broad, short digits. Associated are the distal digits of a pes imprint.

Discussion: Based on the short imprint and associated distal portions of a larger footprint, *Brachychirotherium tintanti* is probably a manus impression and not a pes. The ichnotaxon was obviously introduced based on an incomplete set. Therefore, we re-assign this ichnotaxon to "Chirotheriidae indet."

Trackmaker: Typical chirotheriid manus imprint with postero-laterally positioned, laterally abducted digit V. Because of the fragmentary specimen, only a general attribution to archosauriform tetrapods can be given.

"Chirotherium atlensis" Biron and Dutuit, 1981

Distribution: Upper Triassic (Carnian), Ourika Basin, Morocco.

Description: Partial trackways of a quadruped with pentadactyl pes and manus imprints (15-20 cm pes length), suggesting a narrow trackway width and relatively strong rotation outward. Digit proportions in the pes show digits II and III dominating in length, whereas digits I and IV are shorter. Digit V preserved as an elongate triangular pad. The specimens on the slab illustrated by Biron and Dutuit (1981, pl. IV, B-C)

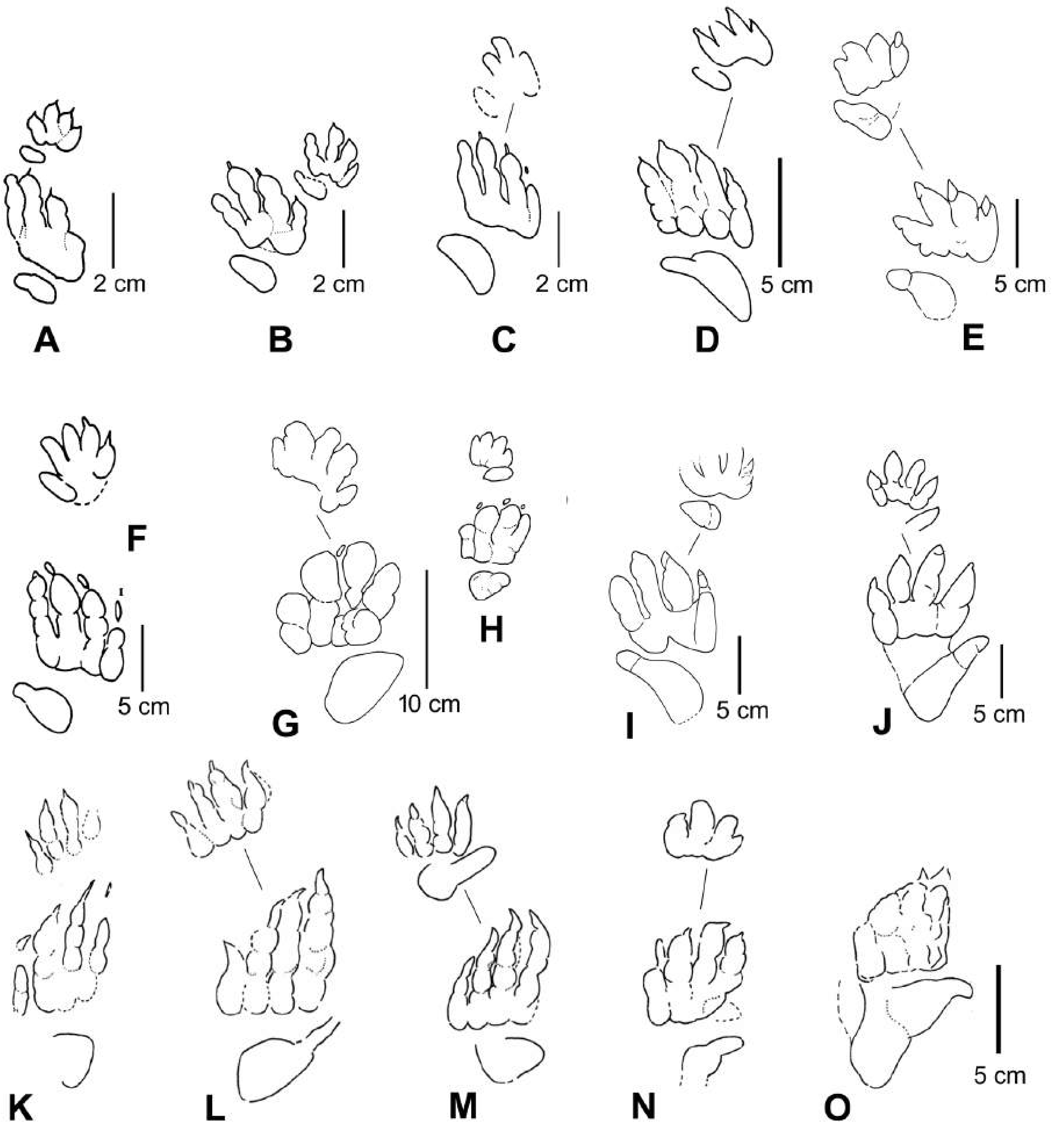


FIGURE 29. Sketches of pre-Late Triassic "*Brachychirotherium*" and *Synaptichnium* footprints (A-J) with extramorphological variation of *Synaptichnium* and transition to "*Brachychirotherium*-like" imprints (K-O). **A,** "*B.*" *harrasense*. **B,** "*B.*" *praeparvum*. **C,** "B." *hessei*. **D,** "*B.*" *paenaparvum*. **E,** "*B.*" *kuhni*. **F,** "*B.*" *paraparvum*. **G,** "*B.*" *pachydactylum*. **I,** "*B.*" *lorteti*. **J,** "*B.*" *gallicum*. **K-O,** *Synaptichnium pseudosuchoides*. A-E. From Solling and Roet formations (Anisian) of Germany. F. From Vossenveld Formation (Anisian) of The Netherlands. G-J. From the Middle Triassic (AnisianLadinian) of France. K-O. From Eschenbach Formation (Anisian) of Germany. Sketches from Haubold (1971b, 1984), Demathieu and Oosterink (1988) and Klein and Haubold (2004).

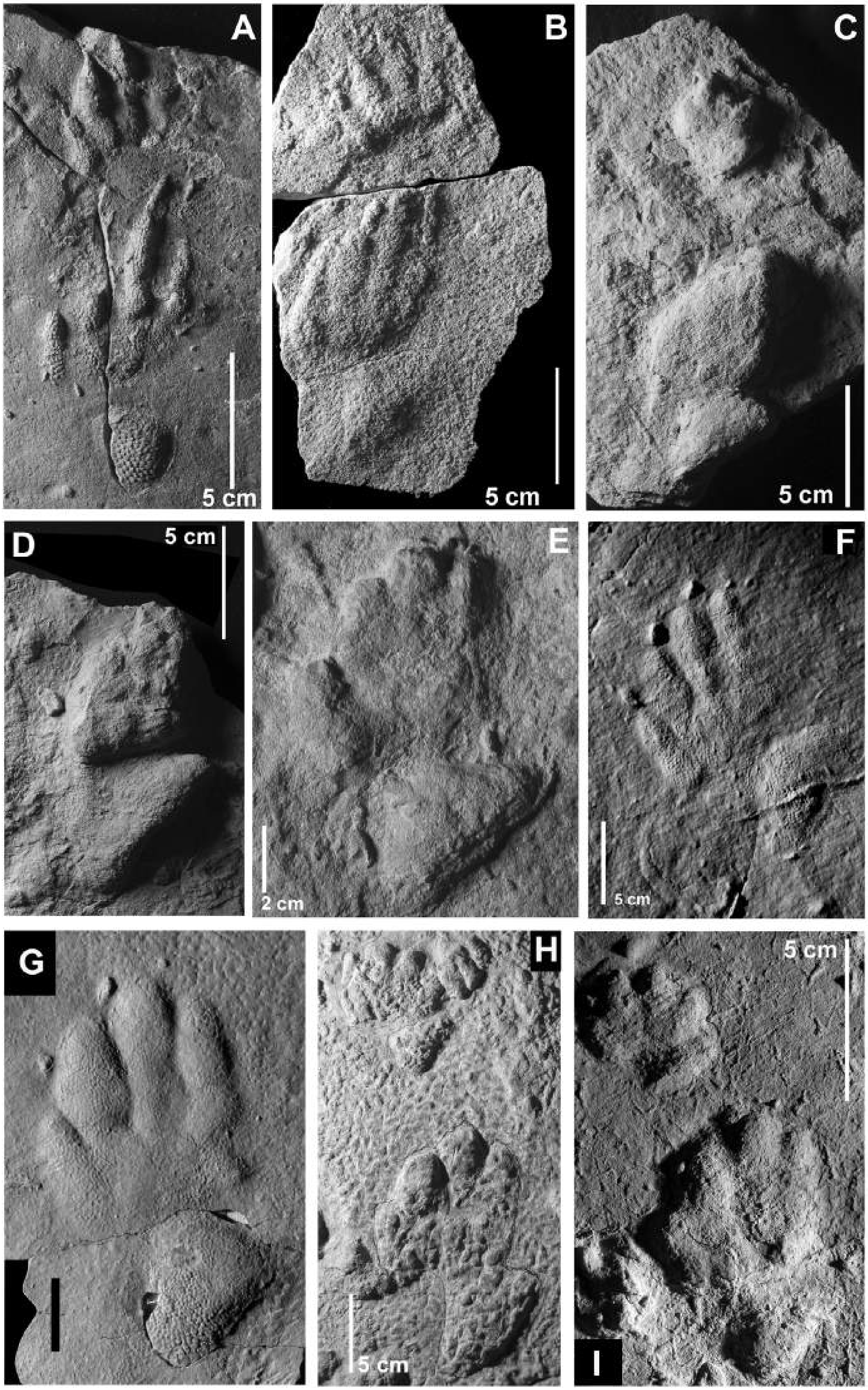


FIGURE 30. Photographs showing *Synaptichnium* and "*Brachychirotherium*-like" footprints from the Middle Triassic. **A-E,** *Synaptichnium pseudosuchoides* from Eschenbach Fm. (Anisian) of Germany. **F,** "*Brachychirotherium*" *paraparvum* from Vossenveld Fm. (Anisian) of The Netherlands. **G,** "*B.*" aff. *parvum*" from the Middle Triassic of the Dolomites, northern Italy. **H-I,** "*B*". *pachydactylum* and "*B.*". *circaparvum* from the Middle Triassic of France. Scale in G = 2 cm.

are preserved with skin texture.

Discussion: The footprints from Morocco are different from *Chirotherium* in their digit proportions. Whereas the latter is characterized by a pes imprint with a compact digit group II-IV and digit I being thinner and strongly reduced (see above), the pes tracks from Morocco show pronounced digits II and III with shorter and subequal digits I and IV. This morphology is similar to *Isochirotherium,* and the combination of a narrow trackway pattern with strongly outward rotated imprints also resembles this ichnogenus. However, thus far *Isochirotherium* is known from Middle Triassic deposits except for a single possible record from the Norian Löwenstein Formation of Germany (Haderer, 1991; see above). It cannot be excluded that the stratigraphic range of *Isochirotherium* footprints extended to the Upper Triassic. However, presently we prefer a more tentative assignment to chirotheriid indet. pending more material from the locality in Morocco.

Trackmaker: The overall-shape of the imprints, with the pes imprint being functionally pentadactyl, excludes these tracks from being produced by Avemetatarsalia. Stem-crocodylian archosaurs are the most likely producers.

"*Chirotherium catalaunicum*" Casanovas-Cladellas et al., 1980

1980 *Chirotherium*: Casanovas-Cladellas et al., p. 41, pl. 1
2011 nomen dubium: Fortuny et al., p. 69
2012 nomen dubium: Díaz-Martínez et al., p. 146
2015 nomen dubium: Díaz-Martínez and García, p. 3

Distribution: Buntsandstein (Middle Triassic) of the Catalonian Basin.

Description: Isolated fragmentary pes track lacking the posterior portion with digit V. Digits I-IV are preserved with broad digits. Digit III appears to be longest, digit I is shortest and thinner than other digits.

Discussion: This is poorly preserved, incomplete material. According to Fortuny et al. (2011), the holotype is now lost. Therefore, we assign *C. catalaunicum* to Chirotheriidae indet.

Trackmaker: Too poorly preserved and fragmentary to suggest any closer attribution. Because it is definitely a chirotheriid footprint, an archosauriform tetrapod can be considered as the producer.

"*Chirotherium* (*Brachychirotherium*) *gallicum*" Willruth, 1917 (Bornemann ms.)
Figure 29J

1917 *Chirotherium*: Willruth, p. 426-427, fig. 4
1925 *Chirotherium*: Soergel, p. 14, fig. 11
1948 *Chirotherium*: Peabody, p. 346
1959 *Chirotherium*: Leonardi, p. 236, 243, pl. 35
1971a *Chirotherium*: Haubold, p. 443, 449
1971b *Chirotherium*: Haubold, p. 55
1974 *Chirotherium*: Demathieu, p. 8-10, fig. 2
1984 *Chirotherium*: Haubold, p. 143, fig. 94 (10)
2004 *Brachychirotherium*: Demathieu and Demathieu, p. 84-85, fig. 8c
2005 *Brachychirotherium*: Gand and Demathieu, p.729, fig.4 (8)

Distribution: Middle Triassic, France and Spain.

Description: Medium-sized pentadactyl pes and manus imprints. Pes imprints show a compact anterior digit group I-IV and a posterolaterally positioned, massive, straight or slightly outward curved digit V that is extended posteriorly into a "heel." Digit proportions of anterior digit group are III > IV > II > I. Manus short and rounded with digits II and III being longest.

Discussion: Willruth (1917) erected the ichnospecies *Chirotherium gallicum* based on material from the Middle Triassic of Lodève, France. The name, itself, however, was mentioned earlier in a manuscript of J.G. Bornemann. Subsequently, *Chirotherium gallicum* and the new combination *Brachychirotherium gallicum* were identified in different Middle Triassic units of France and Spain (Leonardi, 1959; Demathieu, 1974; Pérez López, 1993; Demathieu and Demathieu, 2004; Gand et al., 2010). Haubold (1971b) considered *C. gallicum* to be a junior synonym of *C. barthii*. Footprints from the Middle Triassic of Spain illustrated in Gand et al. (2010) under *Brachychirotherium gallicum* are clearly *C. barthii*.

Others documented in Pérez López (1993) and also assigned to *B. gallicum* show the typical digit proportions and trackway pattern of *Isochirotherium* and can possibly be assigned to that ichnogenus. Some imprints described under *C. gallicum* (Demathieu, 1974) also show some similarities with *Chirotherium rex* from the Moenkopi Formation of Arizona (Peabody, 1948; Klein and Lucas, 2010b). We thus conclude that *Chirotherium* (*Brachychirotherium*) *gallicum* is a wastebasket taxon for chirotheriid footprints of different ichnogeneric affinities. Ichnotaxonomic problems related to this ichnotaxon also comprise those of the ichnogenus *Brachychirotherium* in general and its identification in deposits of pre-Late Triassic age (see above).

Trackmaker: As in other functionally tetradactyl-pentadactyl, chirotheriid imprints, stem-crocodylian or non-crowngoup archosaurs are the most likely producers.

"*Chirotherium* (?) *huberi*" Bock, 1952

1952 *Chirotherium*: Bock, p. 416-417, pl. 47, fig. 1
1963 *Chirotherium* (?): Kuhn, p. 71
1971a Chirotheriidae indet.: Haubold, p. 486
1971b Chirotheriidae indet.: Haubold, p.58

Distribution: Lower Lockatong Formation (Carnian), Newark Supergroup, Pennsylvania.

Description: Large pes impression showing four digits, probably representing digits IIV. Digits are separated from each other, with slender appearance, except digit ?II, which is more broad. At their distal ends, digits show sharp terminations.

Discussion: Based on the illustration of Bock (1952, pl. 47, fig. 1), this is an isolated, incomplete pes imprint. His photograph shows three clearly defined digits and another one at bottom right that is probably the distal end of the innermost digit I. Bock (1952) mentions a pad impression of digit V right behind digit IV. Indeed, this impression is visible in the photograph, but it cannot be confirmed that it truly represents digit V. The slender digits with sharp ends and their proportions resemble the ichnogenus *Evazoum* (see below), however, Bock (1952) mentions an associated manus track in identical specimens from the site that unfortunately could not be collected. *Evazoum* is the trackway of a biped, therefore, we think that this is instead a poorly preserved *Brachychirotherium*, but this cannot be confirmed. Here we assign *Chirotherium huberi* to Chirotheriidae indet.

Trackmaker: Probably a stem-crocodylian archosaur, but the incomplete chirotheriid specimen illustrated by Bock (1952) does not allow a closer attribution.

"*Chirotherium*" *lulli* Bock, 1952
Figures 32L, 33D-E

1952 *Chirotherium*: Bock, p. 415-416, pl. 49, fig. 7
1954 *Chirotherium*: Baird, p. 167-176, p. 177, fig. 2A, p. 179, fig. 3, pl. 1, pl. 2, fig. 1
1958 *Chirotherium*: Kuhn, p. 21
1971a *Chirotherium*: Haubold, p. 463-465, p. 456, fig. 18c
1971b *Chirotherium*: Haubold, p. 53, fig. 32 (9), p. 55
1980 *Chirotherium*: Olsen, p. 44-45, fig. 3.4.M
1984 *Chirotherium*: Haubold, p. 143, fig. 94 (16), p. 158, fig. 105 (5), p. 160
2003 *Chirotherium*: Szajna and Hartline, p. 268-269, fig. 16.5A
2018 *Chirotherium*: Hunt et al., p. 452, fig. 12.3 E, 454-455

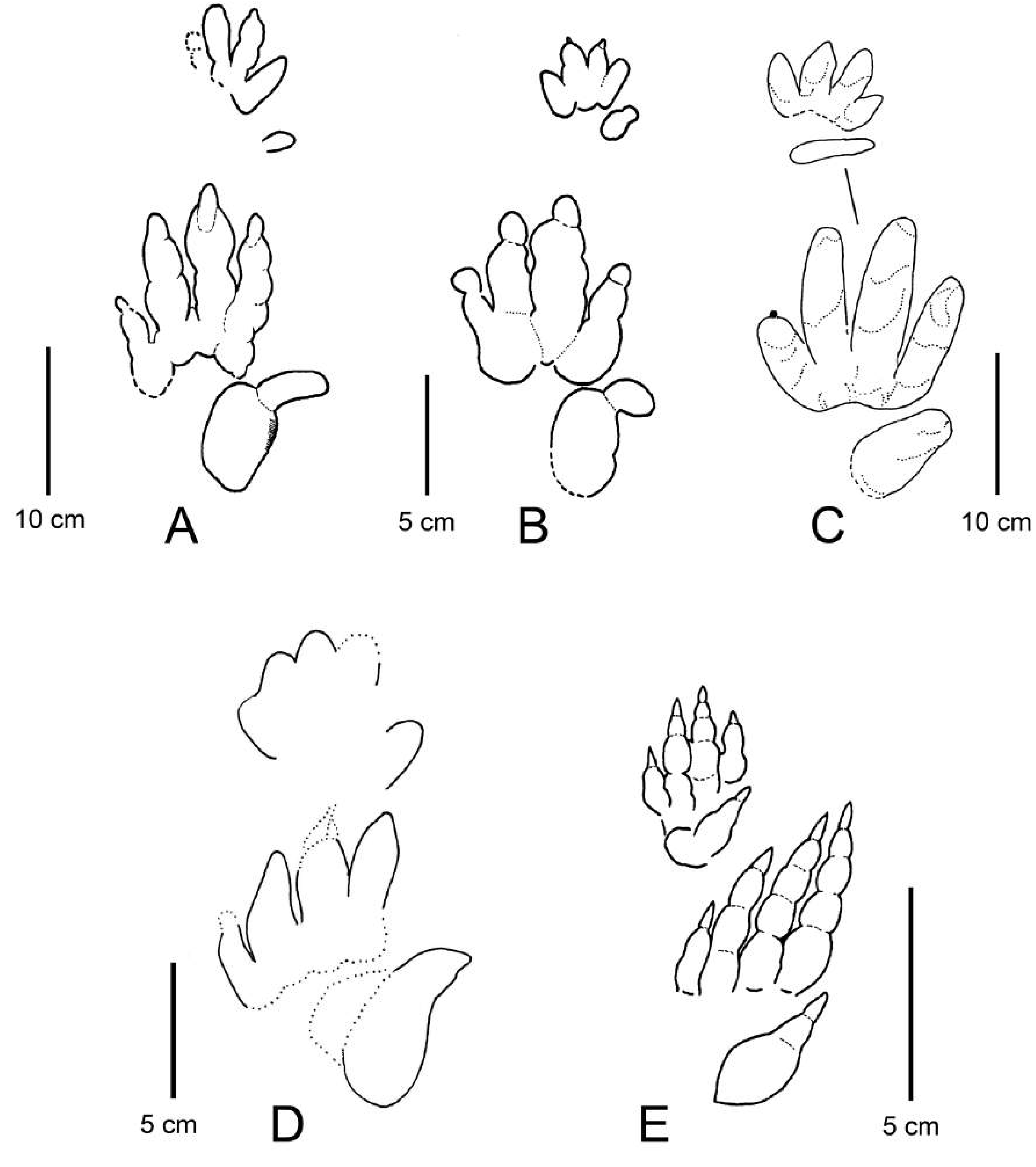


FIGURE 31. Overview of chirotheriid ichnogenera as sketches. **A,** *Chirotherium*. **B,** *Isochirotherium*. **C,** *Brachychirotherium*. **D,** *Protochirotherium*. **E,** *Synaptichnium*. Sketches from Haubold (1971b) and Klein and Niedźwiedzki (2012).

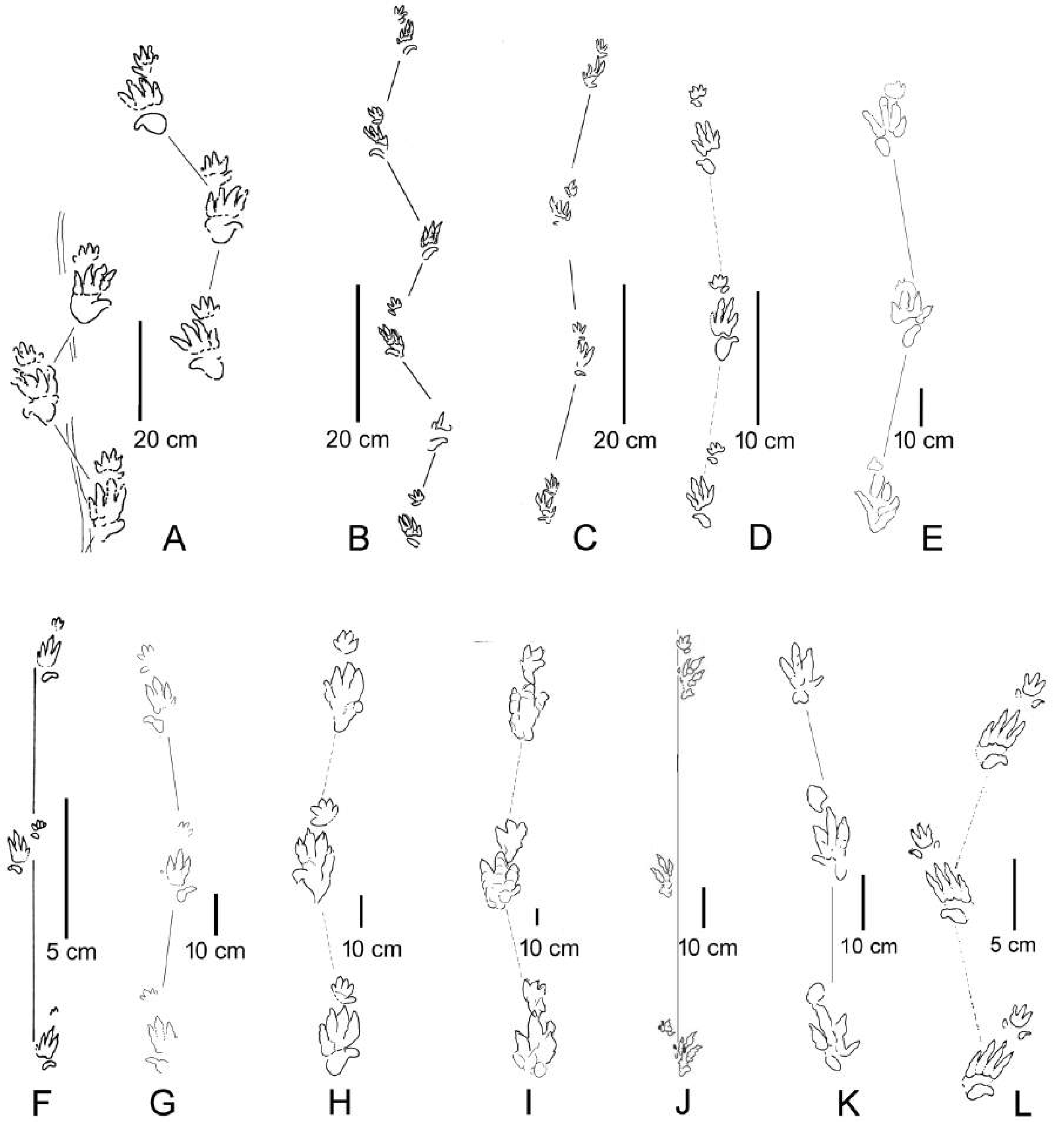


FIGURE 32. Trackways of chirotheriid ichnotaxa as sketches. **A,** *Protochirotherium hauboldi*. **B,** *Synaptichnium diabloense*. **C,** *S. cameronense*. **D,** *Isochirotherium soergeli*. **E,** *Brachychirotherium parvum*. **F,** *Chirotherium sickleri*. **G-H,** *C. barthii*. **I,** *Chirotherium ischigualastianum*. **J,** *C. ferox*. **K,** *C. postchirotherioides*. **L,** "*C.*" *lulli*. Sketches from Klein et al. (in press).

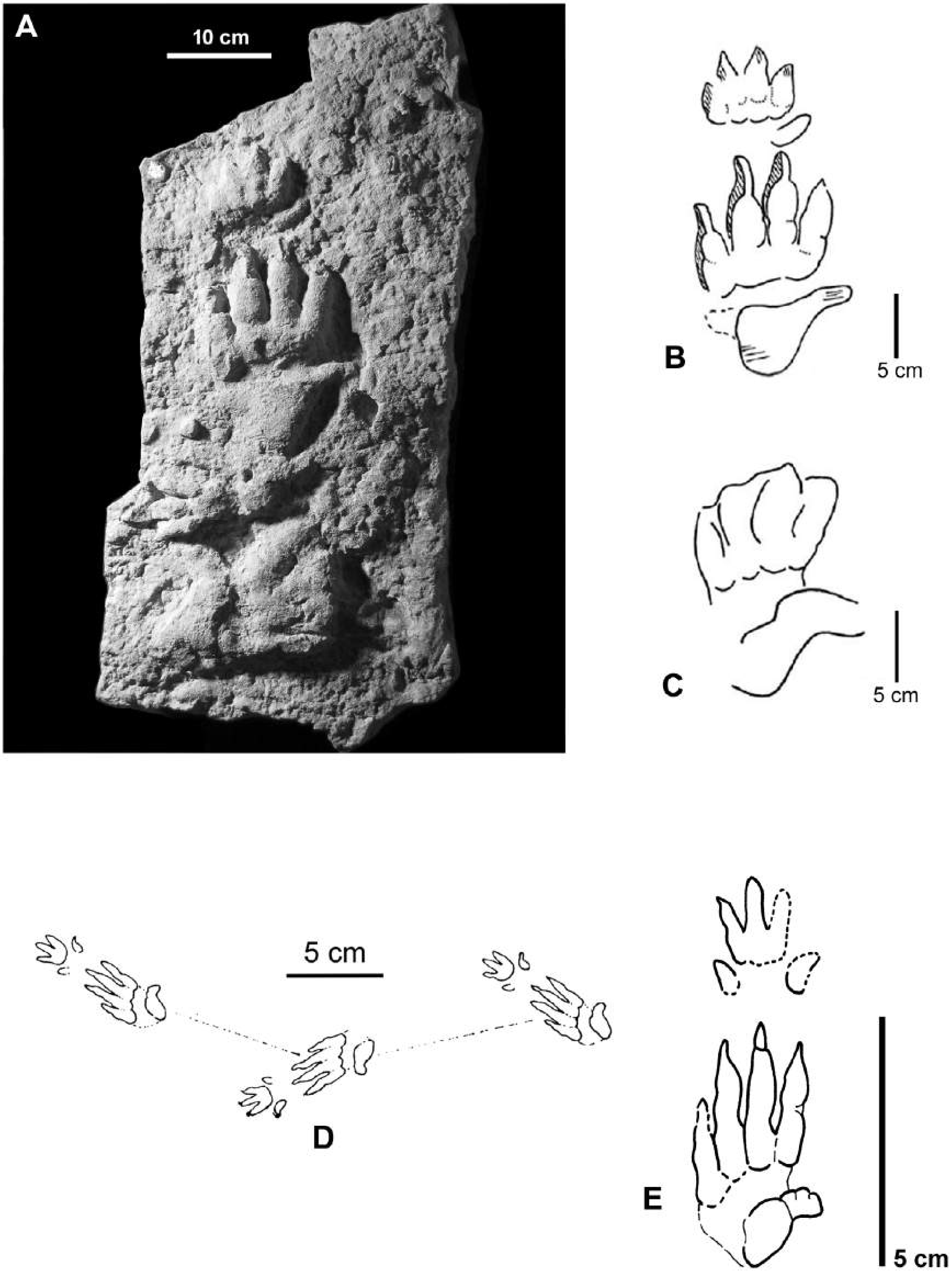


FIGURE 33. Chirotheriid footprints of indeterminate affinity. **A,** "*Chirotherium*" *wondrai* from Steigerwald Formation (Ansbacher Sandstein, Carnian) of Germany. **B-C,** Sketches of "*C.*" *wondrai*. **D,** "*C.*" *lulli* from Passaic Fm. (Norian) of North America. **E,** Detail of D. Note associated *Atreipus metzneri* footprints in A. Sketches from Haubold (1984) and Klein and Haubold (2003, 2004).

Distribution: Newark Supergroup, Passaic Formation (Norian) of eastern North America; Chinle Group of southeastern Utah, southwestern North America.

Description: Trackways with small pentadactyl pes (length 4.4 cm) and manus imprints of chirotheriid shape. The stride length is 23.2 cm, and the pace angulation is 150°. Pes and manus imprints are turned outward by 29° relative to the midline. Pes imprints long and slender. The anterior digit group shows the digit proportions III > IV > II > I and an oblique cross axis angle of 68° (values from Baird, 1957). Digit V is positioned posterolaterally. It has an oval basal pad and a restricted phalangeal portion that is curved backward. Acuminate claws are visible on digits I–IV. The overall shape of the pes imprint is long and slender. Phalangeal and metatarsophalangeal pads are distinct. The rounded manus, which is positioned anterior to the pes, is indistinct, but digit III seems to be the longest.

Discussion: *Chirotherium lulli* was introduced by Baird (1957) based on footprints from the Passaic Formation of the Newark Supergroup at Milford, New Jersey. The assignment of the ichnospecies to *Chirotherium* was followed by Haubold (1971a, b). However, our re-definition of the ichnogenus *Chirotherium,* based strictly on features observed in the type species, requires the removal of *C. lulli* from the ichnogenus and determination as chirotheriid inc. sed.

The functionally tetradactyl anterior digit group with a robust digit I and the oblique cross axis and the strongly outward rotated orientation in the trackway are different from all other ichnospecies of *Chirotherium*. There is a slight similarity with conservative forms from the Lower-Middle Triassic such as *Synaptichnium diabloense,* and it cannot be excluded that some *Synaptichnium*-like forms range into the Upper Triassic. This is indicated also by some isolated material from the Upper Triassic Timezgadiouine Formation of Morocco (Lagnaoui et al., 2012). Further study is needed, so we assign these tracks tentatively to “Chirotheriidae indet.”

Trackmaker: The oblique cross-axis and outward rotation of the pes and manus imprints suggest a non-avemetatarsalian trackmaker, probably a stem-crocodylian archosaur.

“Chirotherium” wondrai Heller, 1952
Figures 33A-C

1952 *Chirotherium*: Heller, p. 131-135, pl 9, fig. 1
1971a *Chirotherium*: Haubold, p. 461-463, fig. 19d
1971b *Chirotherium*: Haubold, p. 54-55, fig. 33 (7)
1984 *Chirotherium*: Haubold, p. 143, fig. 94 15, p. 154
2000 *Chirotherium: Haubold and Klein, p. 66, 74, fig. 10a*
2004 *Chirotherium*: Klein and Haubold, p. 7-8, 12-13, figs. 7, 8p, p. 14
2018 *Chirotherium*: Hunt et al, p. 452, fig. 12.3 F, p. 455

Distribution: Ansbacher Sandstein, Stuttgart Formation (Upper Triassic, Carnian), Germany.

Description: These are pentadactyl pes (up to 20 cm in length) and manus imprints of typical chirotheriid shape. In the pes, digit III is longest, followed by digits II, IV and I. Digit V has a massive oval basal pad that is extended into a broad posterior end of the track, and a thinner, slightly recurved phalangeal portion. Anterior digits I–IV are robust with rounded pads and elongate triangular claws. The posterior margin of the digit group I–IV is sharp and straight. The manus is rounded, showing short digits with tapering distal ends. No trackways are known.

Discussion: *Chirotherium wondrai* was described by Heller (1952) from the Ansbacher Sandstein of the Stuttgart Formation (Upper Triassic, Carnian) of Germany. It is the only occurrence thus far. Following Heller, Haubold (1971a, b) also assigned these footprints to *Chirotherium*, but our review of the ichnogenus supports a determination as chirotheriid inc. sed. This is based on the functionally tetradactyl anterior portion of the pes with a robust digit I, whereas in *Chirotherium* the anterior pes is functionally tridactyl, and digit I is thinner than the other digits.

Trackmaker: The functionally tetradactyl-pentadactyl pes imprint suggests a stem-crocodylian or non-archosaurian archosauriform.

“Dahutherium” Montenat, 1968

1968 *Dahutherium*: Montenat, p. 373, pls. 1, 4, 2.8-9
1972 *Dahutherium* - “Parachirotheriidae”: Demathieu and Haubold, p. 805, 818, 820, fig. 5 (8)
1974b *Dahutherium* - “Batrachopodidae”: Gand, p. 9-10, p. 19, pl. 8A-D
1974c *Dahutherium*: Gand, p. 18, fig. 2G
1984 *Dahutherium*: Haubold, p. 150, 152, fig. 102 (7)

Distribution: Grés de Lyonnais **(**Middle Triassic, Anisian-Ladinian) of France.

Description: Tetradactyl pes imprints, about 10 cm long. Digits II-IV robust, distally tapering, sometimes with a distinct acuminate claw. Digit III is longest, followed by digit IV, II and digit I, which is very short, thinner than the other digits and posteriorly shifted.

Occasionally a small tri- to tetradactyl manus imprint is visible anterior to the pes.

Discussion: No formal description or designation of a holotype and type ichnospecies was given by Montenat (1968). Therefore, *Dahutherium* is a *nomen nudum*. These tracks resemble incomplete chirotheriids such as *Chirotherium ferox*. The proportionately long digit III and the thin and short digit I suggest this. However, the material is so incomplete that we assign the *nomen nudum* “*Dahutherium*” here to “Chirotheriidae indet.”

Trackmaker: Footprints are too fragmentary and poorly preserved to support an attribution closer than “Archosauriformes.”

“Large manus chirotheriid”

2018 Chirotheriid footprints indet.: Klein and Lucas, p. 169, p. 172, fig. 10C-E.

Distribution: Eschenbach Fm. (Middle Triassic, Anisian) of Germany.

Description: Klein and Lucas (2018) describe this material from a diverse assemblage discovered in the siliciclastic marginal facies of the Muschelkalk (Middle Triassic, Anisian) of southern Germany. These are medium-sized (pes length = 16 cm), isolated pentadactyl pes and manus imprints with robust digits preserved as natural casts. Pedal digit III is longest, digit IV shorter; digit V shows a massive oval basal pad. The manus is very large relative to the pes (low heteropody, 1:1.4 vs. 1:1.8.-3.7 in *Synaptichnium*) but more rounded than the pes; digit III in the manus is longest, and digit IV is short and laterally everted. Skin impressions are preserved in some portions.

Discussion: A chirotheriid with such extreme low heteropody is unknown thus far. *Synaptichnium* shows the lowest heteropody of all chirotheriids but does not reach comparable values. Possibly this is a new ichnotaxon, but more complete material, including trackways, is needed to evaluate this.

Trackmaker: Stem-crocodylian or non-archosaurian archosauriform: The functionally tetradactyl-pentadactyl pes imprints and the very large manus point to a non-avemetatarsalian archosaur.

“Parasynaptichnium” Mietto, 1987

1987 *Parasynaptichnium*: Mietto, p. 39-42, figs. 2-3
2003 *Parasynaptichnium*: Avanzini, p. 177-178, fig. 1 (5)
2008 *Parasynaptichnium*: Avanzini and Mietto, p. 4, 7-9, fig. 2C
2011 *Parasynaptichnium*: Avanzini et al., p. 596-597, fig. 3I

Distribution: Middle Triassic Anisian (Pelsonian) deposits of the Dolomites in northern Italy.

Description: Pentadactyl, functionally tridactyl pes and manus imprints. The type material is incomplete, most of the posterior portion of the pes is missing. Only the paratype shows the distal part of digit V. Digit III is longest, followed by digits IV and II, and digit I is shortest. Digits are relatively slender and curved inward, terminating in small, triangular claws. The manus is much smaller with digit III slightly longer than digits II and IV; digits I and V are short, the latter being postero-laterally positioned, without backward curvature.

Discussion: This ichnotaxon is only known from the Middle Triassic of the Dolomites region in Northern Italy. It comprises a single ichnospecies, *Parasynaptichnium gracilis*.

Mietto (1987) and subsequent authors (Avanzini, 2003; Avanzini and Mietto, 2008; Avanzini, 2011) illustrated a composite reconstruction of the pes imprint, in which digit V is not adequately illustrated. Based on the paratype (Mietto, 1987) and a specimen illustrated in Avanzini and Mietto (2008, fig. 2C) it seems most likely that these are incomplete, functionally tridactyl chirotheriid imprints, similar to *Chirotherium ferox*, *C. postchirotherioides* or *C. barthii* (see above). Nevertheless, because the known specimens are incomplete, we avoid here a concrete ichnospecific assignment.

Trackmaker: Stem-crocodylian or avemetatarsalian archosaur. Based on the incomplete material, no closer attribution is possible.

"Pentichnus" Biron and Dutuit, 1981
Figure 34C

1981 *Pentichnus* Biron and Dutuit, p. 410, fig. 7, pl. 2H-I

Distribution: Timezgadiouine Formation (T5, Upper Triassic, Carnian) of the Argana Basin, Morocco.

Description: Isolated large, (28 cm long, 31 cm width) pentadactyl imprints with robust digits and triangular claws. Digits II and III are longest, digits I and IV are shorter, digit V is in a postero-lateral position relative to other digits.

Discussion: *Pentichnus largus* is one of numerous ichnotaxa that were introduced by Biron and Dutuit (1981) from the Triassic of the Argana and Ourika basins in Morocco, North Africa. Based on their morphology with the postero-laterally positioned digit V, these large footprints are probably chirotheriid. Their short and broad shape suggests manus imprints of very large forms. There is also some resemblance with the tracks of dicynodonts such as *Therapsipus* (Hunt et al., 1993), especially in the short and broad shape with a concave posterior margin and digit proportions. More complete material is needed, so our assignment to Chirotheriidae indet. is tentative.

Trackmakers: Based on the isolated material illustrated by Biron and Dutuit (1981), large tetrapods, either archosaurs or dicynodont synapsids.

"*Pseudochirotherium*" Biron and Dutuit, 1981
Figure 34D

1981 *Pseudochirotherium*: Biron and Dutuit, p. 409, fig. 6, pl 2M

Distribution: Upper Triassic (Carnian), Ourika Basin, Morocco.

Description: Isolated semi-plantigrade to plantigrade tetradactyl imprint (18 cm pes length) showing digits II-V. Digits are robust and relatively short, straight, and ending in indistinct claws. Digits III and IV are longest, II is shorter, digit I is missing. Digit V consists of a large oval basal pad and a thinner, distally rounded ?phalangeal part, which is not recurved.

Discussion: Biron and Dutuit (1981) described these tracks as *Pseudochirotherium oukaimedensis*. Based on morphology, this is a chirotheriid of indeterminate affinity.

Trackmaker: The chirotheriid shape suggests an archosauriform tetrapod. Based on the incomplete and isolated material, no detailed correlation with a distinct archosaur group is possible.

"*Swinnertonichnus*" Sarjeant, 1967

1967 *Swinnertonichnus*: Sarjeant, p. 332-334, fig. 3, pl. 14
1971b *Swinnertonichnus*: Haubold, p. 68-69, fig. 42 (14)
1984 *Swinnertonichnus*: Haubold, p. 47, 150
1995 *Chirotherium*: King and Benton, p. 218-222, figs. 5-6
2005 *Chirotherium*: King et al., p. 266-268

Distribution: Middle Triassic Sneinton Formation (Anisian) of Mapperley Park, Nottingham, Great Britain.

Description: Isolated tridactyl pes imprint with robust digits. Digit III is longest, outer digits II and IV are shorter. Digits end with rounded margins lacking claw impressions.

Discussion: The ichnotaxon *Swinnertonichnus mapperleyensis* (monotypic) was introduced based on poorly preserved material from Great Britain and interpreted as a tridactyl dinosaur footprint (Sarjeant, 1967). King and Benton (1996) and King et al. (2005) re-evaluated the holotype and argued that it is an incomplete *Chirotherium* pes track. We agree with these authors that it is a chirotheriid, but because of the fragmentary type specimen, we assign it to Chirotheriidae indet.

Trackmaker: Archosauriform tetrapod. Too fragmentary for closer attribution.

SYSTEMATIC ICHNOLOGY—OTHER FOOTPRINTS

Anshunpes Xing et al., 2020
Figure 35

Type ichnospecies: *Anshunpes aquacursor* Xing et al., 2020.

Included ichnospecies: Monotypic.

Distribution: Songzikan Member (Member I) of Guanling Formation (Middle Triassic, Anisian-Ladinian) of Yunnan Province, southwestern China

Diagnosis (from Xing et al., 2020): Plantigrade to semi-plantigrade tetradactyl imprints, averaging 15 cm in length and 9 cm in width, with outwardly curved, blunt or slightly tapering robust digits and broad sole area. Two medial digits II and III longest, outer digits IV and V shorter, with the lateral one being in a more posterior position relative to all others. Posterior margin of the sole often extended to a bi- or trilobed "heel." Trackways broad, with Tw = 45.8 cm on average. Imprints positioned opposite to each other and outwardly rotated relative to the midline. Different from 1) *Characichnos* by complete semiplantigrade-plantigrade foot impressions with defined digits, vs. scratch-like digit traces in the latter, 2) *Chelonipus* by longer foot and blunt digit impressions vs. very short and broad foot imprints with sharp digit and claw traces in the latter, and 3) *Chirotherium* by the less compact anterior digit group II–IV and the relatively long digit V.

Description: These are broad trackways with small-medium-sized (pes length = 15 cm, pes width = 9 cm) plantigrade to semi-plantigrade tetradactyl imprints that are rotated outward. Left and right imprints are arranged symmetrically relative to the midline. Imprints show blunt, thick and outwardly curved digits and a broad sole. The two middle digit traces are longest and subequal in length, and the medial and lateral digit traces are shorter. The lateral one shows a posterior shift relative to other digits. Digit and sole traces can be posteriorly dragged and elongated, forming a bilobed "heel." Extramorphological and incomplete imprint variations can show a bean-shape or consist of elongated scratches.

Discussion: Xing et al. (2020) described a large surface from the Guanling Formation (Anisian-Ladinian) of Guizhou Province, southwestern China. It shows abundant trackways and isolated foot impressions of buoyant tetrapods, subaqueously moving and punting across the bottom of shallow lagoons. From

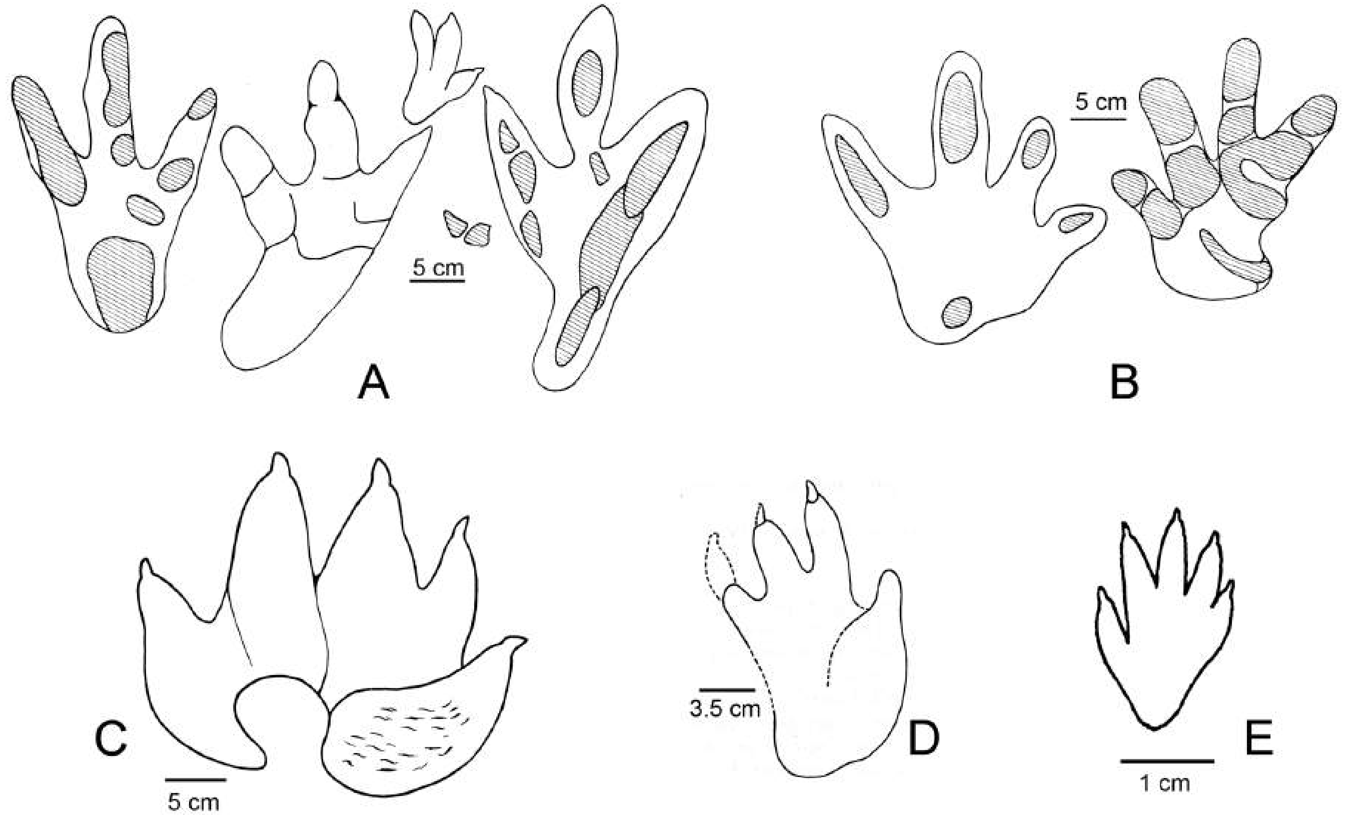


FIGURE 34. Sketches of chirotheriid and other imprints from the Upper Triassic of Morocco, after Biron and Dutuit (1981). **A,** "*Tridactylus machouensis*." **B,** "*Anomoepus moghrebensis*." **C,** "*Pentichnus largus*." **D,** "*Pseudochirotherium oukaimedensis*." **E,** "*Enigmatopus atlensis*". A-C. From the Timezgadiouine Fm. (T5, Carnian) of the Argana Basin. D-E. From ?Carnian deposits of the Ourika Basin.

this site, Xing et al. (2020) introduced the new ichnogenus and ichnospecies *Anshunpes aquacursor* for tetradactyl traces of synchroneously swimming tetrapods. These are different from the ichnotaxon *Dikoposichnus lupingensis,* co-occurring on the same surface and formerly described by Zhang et al. (2014) from the Guanling Formation of Yunnan Province as foraging trackways of nothosaurs. In contrast to *D. luopingensis,* which has half moon- to crescent-shaped imprints with sharp, laterally directed digit traces (see below), *Anshunpes aquacursor* has complete foot impressions, with distinct digit and palm impressions, similar to terrestrially walking tetrapods. They are interpreted as manus tracks with digits II, III, IV and V (Xing et al., 2020).

Trackmaker: The broad manus-only trackways and the symmetrically positioned left and right imprints pointing antero-laterally, indicate swimming or "punting" behaviour of tetrapods, where trackmakers are moving their limbs synchroneously, touching the bottom with their forefeet. This subaqueous progression is characteristic of some marine reptiles that were abundantly discovered in the Guanling Formation (Anisian-Ladinian) and in the overlying Falang Formation (Ladinian-Carnian), such as placodonts, and saurosphargids. These marine diapsids were of broad body shape and probably used their robust forelimbs while moving and foraging on the bottom of shallow marine habitats along the coast of the Eastern Tethys. The presence of robust, blunt digits lacking sharp claw traces and similar proportions in both manus skeletons and footprints, also support this.

Apatopus Baird, 1957
Figures 36-37

1952 *Otozoum*(?): Bock, pl. 48, fig. 1
1957 *Apatopus*: Baird, p. 488, fig. 7, p. 491, fig. 8, pl. 3-4
1971 *Apatopus*: Haubold, p. 60, fig. 36(7)
1981 *Rectilinetopus* ichnogen. nov.: Biron and Dutuit, p. 408, fig. 5, pl. III, E
1981 *Apatopus*: Biron and Dutuit, p. 412, fig. 9, pl. IV, A
1986 *Apatopus*: Baird, p. 140-141, figs. 10-11
1987 *Apatopus*: Conrad et al., p. 131, figs. 4 (below right), 6B
1996 "thecodont tracks:" Dalla Vecchia, p. 6-12, figs. 1–5
1998 *Apatopus lineatus*: Olsen and Huber, p. 82, fig. 6C-E, 7
2000 *Apatopus*: Foster et al., p. 175, fig. 7, p. 176, fig. 8
2003 *Apatopus*: Foster et al., p.166, figs. 1-2
2007 *Apatopus*: Rainforth, p.57, fig. 7
2007 "aetosaur trackway:" Avanzini et al., p. 469, fig. 3A-C
2007 *Apatopus*: Hunt and Lucas, p. 2017, fig. 2E
2009 archosaur trackway: Le Loeuff et al., p. 247, fig. 2
2012 *Apatopus*: Lagnaoui et al., p. 243, fig. 4
2013 *Apatopus*: Klein and Lucas, p. 315-320, figs. 2-8
2016 *Apatopus*: Lagnaoui et al., p. 7, fig. 6B
2017 *Apatopus*: Hunt et al., p. 470, fig. 12.6(g, j), 451-452, figs. 12.2(f), 12.3(q-r)

Type ichnospecies: *Apatopus lineatus* (Bock, 1952).

Included ichnospecies: Known only from the type ichnospecies.

Distribution: *Apatopus lineatus* has been described from Adamanian, Revueltian and Apachean (Carnian-Norian) strata in North America (New Jersey, Pennsylvania, Utah) (Baird, 1957, 1956; Foster et al., 2000, 2003; Klein and Lucas, 2013; Weems, 2018), central Europe (Germany, Poland) (Sulej et al., 2011; Klein and Lucas, 2013), northern Italy (Dalla Vecchia, 1996; Avanzini et al., 2007; Bernardi et al., 2010), North Africa (Argana Basin, Morocco) (Lagnaoui et al., 2013) and southeast Asia (Thailand) (LeLoeff et al., 2009).

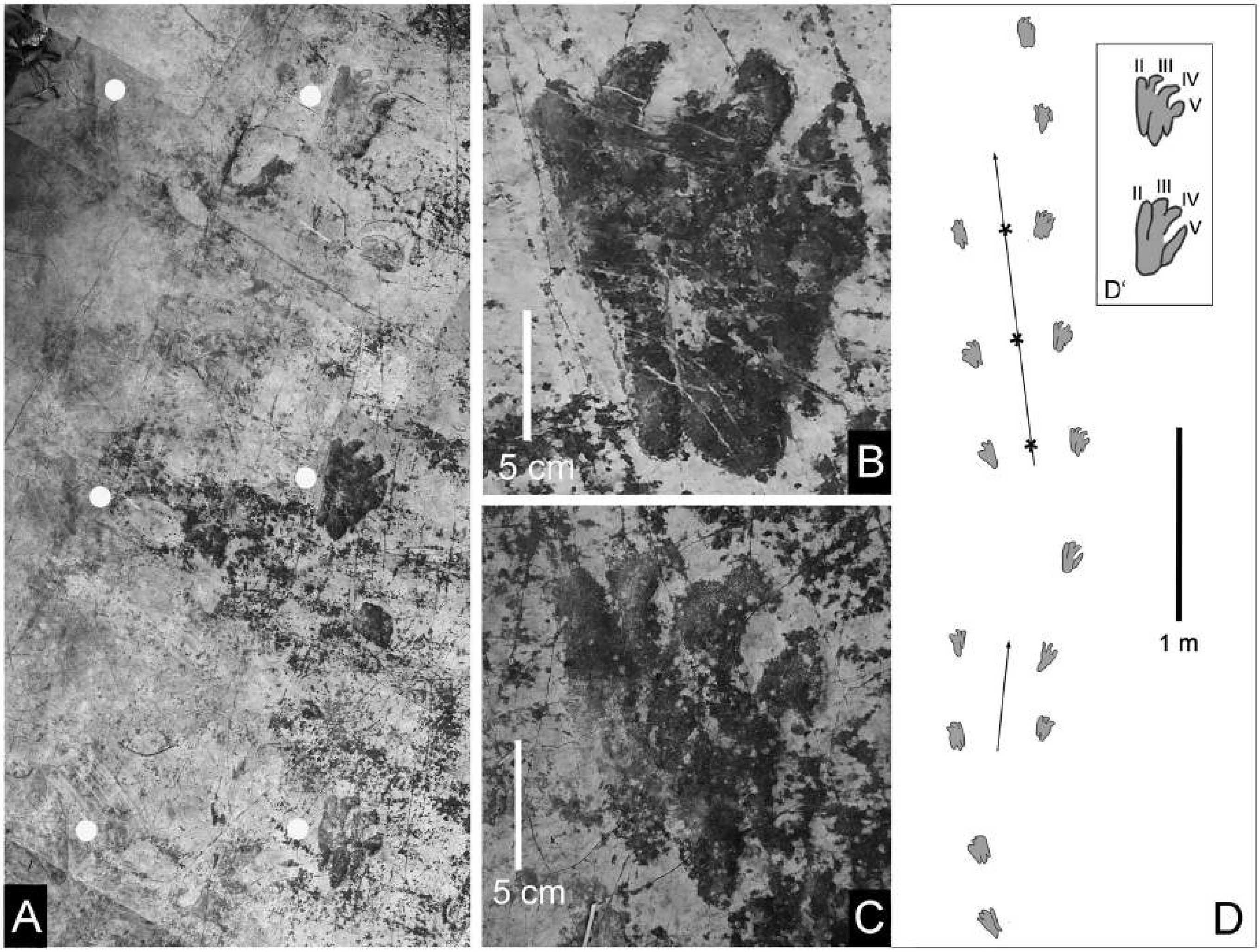


FIGURE 35. *Anshunpes aquacursor,* holotype trackway from Guanling Formation (Middle Triassic, Anisian-Ladinian) of Guizhou Province, southwestern China. **A,** Trackway; white dots demarcate position of imprints, probably of the manus. **B-C,** Details with tetradactyl imprints. **D-D',** Interpretive outline drawing of trackway and detail. From Xing et al. (2020).

Diagnosis (from Klein and Lucas, 2013, emended after Baird, 1957): Trackways of a quadruped with pace angulation of the pes ranging from 108° to 120°. Pes, but not manus, toed out. Pes long and narrow, semiplantigrade to plantigrade, pentadactyl with slender digits increasing in length from I to IV. Digit IV often very faintly impressed or missing; digit V straight, antero-laterally oriented and with posteriorly-elongated "heel." Digits with well-developed articular swellings and sharp claws. Manus pentadactyl, semiplantigrade, short, rounded and symmetrical around digit III, which is longest; manus positioned in the trackway anterior to or slightly medial to the pes.

Description: Small to medium-sized pentadactyl pes and manus imprints, mostly showing faintly impressed, indistinct phalangeal pads. Digits with sharp claws, often distally extended into scratches and furrows, indicating a transition to swim tracks. A few specimens with skin texture are known (Klein and Lucas, 2013). Klein and Lucas (2013) presented descriptions and illustrations of most of the known *Apatopus* specimens.

Discussion: Klein and Lucas (2013) presented a detailed review and revision of *Apatopus* that justifies the synonymy listed above. The ichnogenus *Apatopus* was introduced by Baird (1957), with the type species *A. lineatus*. It was based on material from the Passaic Formation of New Jersey originally described by Bock (1952) as *Otozoum lineatum*. Baird (1957) recognized the distinctive morphology in which the pes has digits that increase in length from I to IV and a long, straight and anterolaterally directed digit V. He also drew attention to the crocodylian-like overall shape of the imprints and webbing between the digits. The webbing, however, could not be confirmed during the re-examination of the type material and the revision of the ichnogenus (Klein and Lucas, 2013). Such structures are likely extramorphological due to substrate conditions rather than anatomically based features.

Klein and Lucas (2013) also stressed the crocodylian-like overall shape of *Apatopus*, recognizing a relationship with the semi-aquatic lifestyle of the trackmakers, which were phytosaurs. A distinct similarity with the shape of some chirotherian footprints (*Synaptichnium*) from the Lower-Middle Triassic was documented by these authors, who concluded that evolutionary developments reflect a change in adaptation from a terrestrial to a semi-aquatic lifestyle within Phytosauria, similar to later changes that took place among the crocodylians (cf. Klein and Lucas, 2015 and later discussion).

Trackmaker: *Apatopus* footprints were produced by phytosaurs. This was posited by Baird (1957) and convincingly demonstrated by Padian and Pchelnikova (2010; also see Klein and Lucas, 2013). Phytosaurs, similar to modern crocodylians, had a semi-aquatic lifestyle (e.g., Hunt, 1989). This explains also the rare occurence of *Apatopus* in the Triassic tetrapod footprint record, which is obviously due to the limited preservation potential of complete, well-preserved footprints in subaqueous environments.

Batrachichnus Woodworth, 1900
Figure 38

2010b Tetrapod footprints indet.: Klein and Lucas, p. 59, fig. 57

Type ichnospecies: *Batrachichnus salamandroides* (Geinitz, 1861).

Included ichnospecies: See Voigt (2005) for synonyms of the type ichnospecies, which is generally regarded as the only valid ichnospecies.

Distribution: Lower Carboniferous (Mississipian) to Early or Middle Triassic. The single Triassic occurrence is in the Moenkopi Group of Pat's Hole, Moffat County, Colorado; the precise stratigraphic position is unknown.

Revised diagnosis (from Fillmore et al., 2012): Small (up to 20 mm long) footprints of a quadruped with four and five digits on manus and pes, respectively. Pes plantigrade to semiplantigrade and length less than 20 mm long (typically 10-15 mm). Pes digits I to III closely grouped together with increasing length, digit IV longest and somewhat separate from the others; digit V set somewhat posterior and laterally directed. Manus semiplantigrade, smaller than pes; increasing lengths of digits from I to III, digit IV diverging outward from the grouping of I-III. Narrow quadrupedal trackways, common alternating manus-pes sets, small divergence of manus and pes axes, pace angulation rarely exceeds 90°. Tail/body drag may be present (based primarily on Gilmore, 1928; Haubold 1971b, 1996; and Melchor and Sarjeant, 2004).

Description (from Klein and Lucas, 2010b): A single slab from the Moenkopi Group in Colorado has a sequence of 3-5? consecutive sets with small pes and manus impressions as well as isolated imprints and scratch marks. The pes is faintly impressed, digitigrade and pentadactyl, with straight and slender digits, in some cases with bifurcated or knob-like distal ends, reflecting rotation during movement, about 1.6 cm long. Digit proportions are digits II-V increasing in length, digit IV subequal to III, and digit V as long as I and laterally spread. Manus smaller, about 1.1 cm long and tetradactyl. Identification of digits difficult, either I-IV or II-V are present. The two central digits are longest and subequal in length, and the others are short, with the lateral one slightly spread, as in the pes, with bifurcate or knob-like distal ends. Trackway broad, with a pace angulation of 90°-105° and a stride length of about 8.3 cm. Pes parallel to the midline (along digit III), and manus anterior to the pes with more or less inward rotation, dependent on the identification of digit III. Thin tail traces are associated with the trackways.

Discussion: The overall morphology and size of the imprints and digit proportions, the manus imprint being distinctly tetradactyl and symmetrical along a median axis, and the occurrence of a tail trace is characteristic of the amphibian ichnogenus *Batrachichnus* Woodworth, 1900. Originally, Klein and Lucas (2010b) tentatively assigned the specimen to indeterminate footprints, but we refer it to *Batrachichnus* isp. This is the first Mesozoic record of the ichnogenus, an extension of the stratigraphic range of this typical late Paleozoic morphotype.

Trackmaker: Amphibians, most likely small temnospondyls (e. g., Haubold, 1971b; Melchor and Sarjeant, 2004; Voigt, 2005).

Batrachopus Hitchcock, 1845
Figure 39

1845 *Batrachopus* Hitchcock, p. 45 (see Olsen and Padian, 1986, p. 261 for additional synonymy of the names Hitchcock introduced for this footprint morphology)
1986 *Batrachopus*: Olsen and Padian, p. 260, fig.20.1, p. 261, fig. 20.2., p. 264, fig. 20.3., p. 265, figs. 20.4-20.6., p. 266, figs. 20.7-20.8., p. 267, figs. 20.9.-20.10.
1993 New taxon A: Silvestri and Szajna, p. 443, fig. 3A
1993 New taxon B: Silvestri and Szajna, p. 443, fig. 3B
1993 *Batrachopus*: Silvestri and Szajna, p. 443, table 1.
1996 New taxon A: Szajna and Silvestri, p. 280, fig. 5A
2003 New taxon A: Szajna and Hartline, p. 270, fig. 16.6 A
2010 *Batrachopus*: Klein and Lucas, p. 55.

Type ichnospecies: *Batrachopus deweyi* (Hitchcock, 1843).

Included ichnospecies: Besides the type ichnospecies, *Batrachopus deweyi*, several other ichnospecies have been described from Lower Jurassic strata: *B. bellus*, *B. gracilior*, *B. gracilis*, *B. parvulus* and *B. dispar*, all from the Newark Supergroup (Hitchcock, 1845, 1858; Lull, 1904, 1953). Olsen and Padian (1986) synonymized *B. bellus, B. gracilior* and *B. gracilis* with *B. deweyi.* Rainforth (2005) rejected this, and Rainforth (2007) synonymized *B. gracilior* with *B. gracilis,* and *B. parvulus* with *B. deweyi*. Additional ichnotaxa synonymized with *Batrachopus* by Rainforth (2007) are: *Shepardia palmipes* Hitchcock, 1858 with *B. gracilis* and *Comptichnus obesus* Hitchcock, 1865 with *B. bellus*; *Arachichnus* and *Cheirotheroides* were also partially synonymized with *Batrachopus*. Rainforth (2007b) distinguished two groups of *Batrachopus*: (1) imprints with long and slender digits that do not contact each other, and (2) imprints with short and broad digits that contact each other.

Haubold (1971b) also synonymized *Comptichnus* with *Batrachopus*. Lockley et al. (2004b) considered *Batrachopus* and *Selenichnus* to be related forms. Rainforth (2007) rejected this and noted that, unlike *Batrachopus*, the holotype of *Selenichnus* is the trackway of a biped. Several *Batrachopus*-like footprints were described from the Upper Stormberg Group (Lower Jurassic) of Lesotho (southern Africa) by Ellenberger (1970, 1974) under the ichnogeneric names *Plateotetrapodiscus*, *Suchopus*, *Molapopentapodiscus* and *Synaptichnium* and need to be re-evaluated (see Olsen and Galton, 1984).

Here, we consider only *Batrachopus* as a valid ichnogenus. Others are nomina dubia or synonyms of *Batrachopus*. Furthermore, as long as the different ichnospecies cannot be unequivocally differentiated, we propose the type ichnospecies *B. deweyi* as the single valid species.

Distribution: Upper Triassic-Lower Jurassic of Newark Supergroup and Glen Canyon Group, North America, ?Lower Cretaceous of southeast Asia (Thailand) (Olsen and Padian, 1986; LeLoeuff et al., 2009; Klein and Lucas, 2010b). Even if known from rare occurrences in the Upper Triassic (Lucas and Klein, 2010b), it is a characteristic and common Lower Jurassic ichnotaxon with some biochronological potential.

Diagnosis: Trackways of a quadruped with relatively low pace angulation. Pes imprints are functionally tetradactyl and digitigrade, with moderately spread digits. Digit III is longest, and digit I shortest. Digit V is reduced to an oval pad posterior to and nearly in line with digit III. The manus is pentadactyl and shows a wide digit divarication. It is strongly rotated outward relative to the pes, with digit V pointing backward.

Description: Pes imprints are slightly similar to *Brachychirotherium* with digits I–IV forming a compact group and showing well-rounded pads and small claws. Digits are straight, their proportions in the pes imprint being I < II ≤ IV < III.

Discussion: *Batrachopus* is a well known ichnogenus long considered to have been made by crocodylomorph trackmakers (see Klein and Lucas, 2010c and references therein). The ichnotaxon was established by Hitchcock (1845) on material from the Lower Jurassic of the Newark Supergroup. *Batrachopus* refers to trackways of a small quadruped, consisting of imprints of a functionally tetradactyl pes and a smaller, pentadactyl manus. The overall morphology of *Batrachopus* is similar to that of chirotheres in the relatively compact anterior digit group

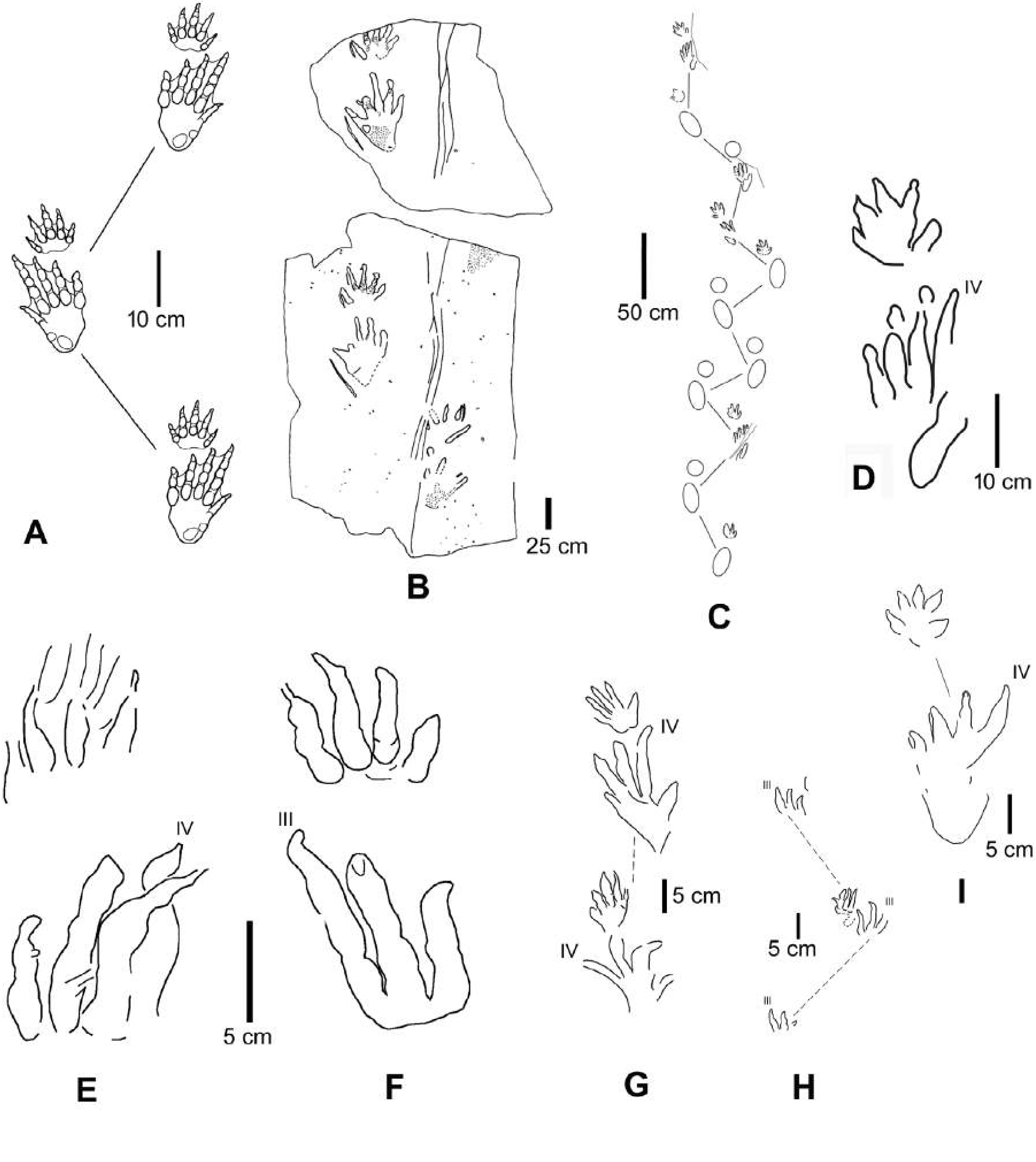


FIGURE 36. Sketches of *Apatopus lineatus* from different localities. **A,** From Passaic Fm. (Norian) of New Jersey (trackway reconstruction). **B,** From Chinle Group (Norian) of Utah. **C-D,** From Timezgadiouine Fm. (T5, Carnian) of the Argana Basin, Morocco. **E-F,** From holotype trackway, Passaic Fm., New Jersey. **G-H,** From Hassberge Fm. (Carnian) of Germany. **I,** From Steigerwald Fm. (Carnian) of Germany. Sketches from Baird (1957), Foster et al. (2003), Lagnaoui et al. (2012) and Klein and Lucas (2013).

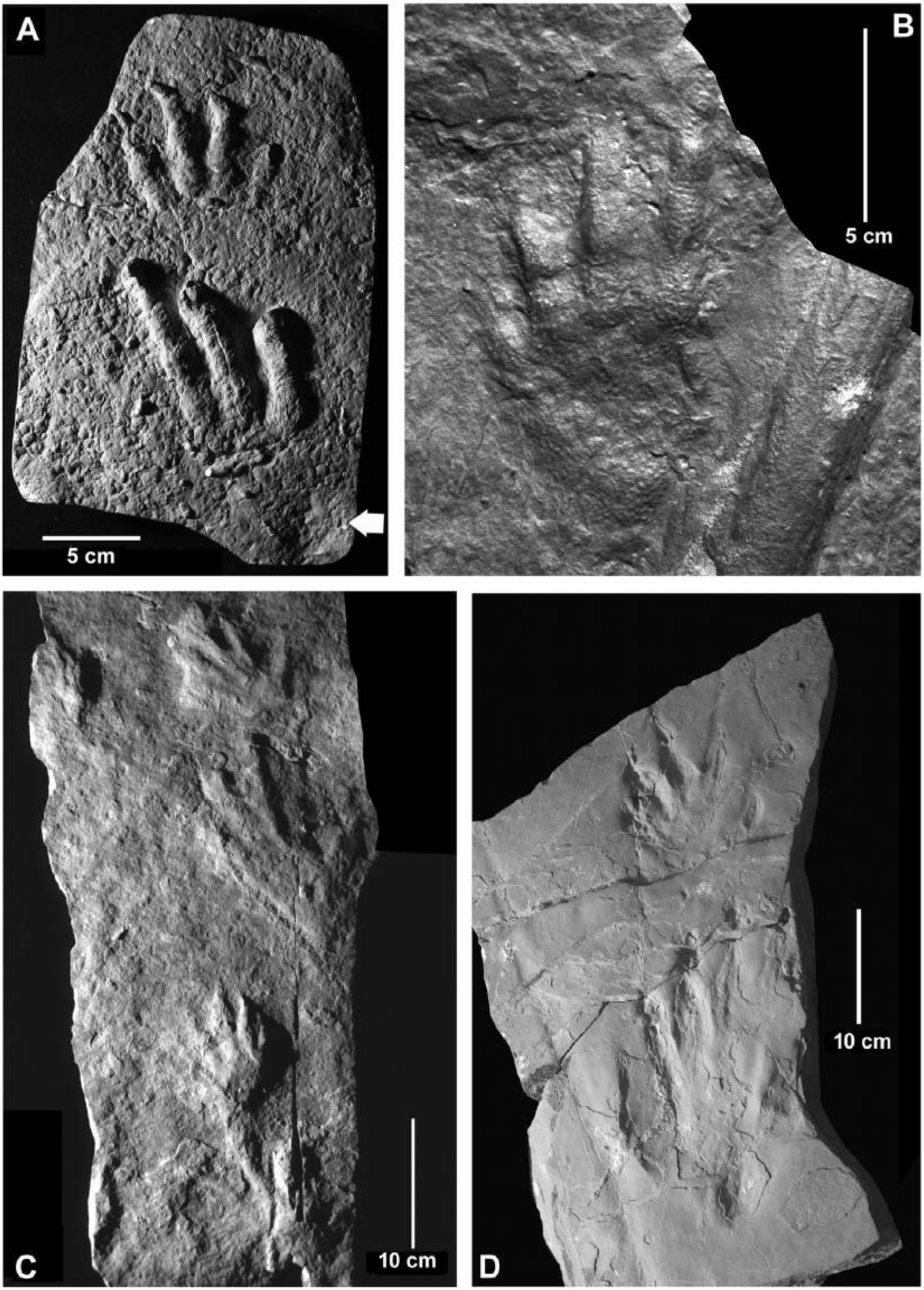


FIGURE 37. Photographs of *Apatopus lineatus* from different localities. **A,** Holotype from Passaic Fm. (Norian) of New Jersey. **B,** From Passaic Fm. of Pennsylvania. **C,** From Hassberge Fm. (Coburger Sandstein, Carnian) of Germany. **D,** From Timezgadiouine Fm. (T5, Carnian) of the Argana Basin, Morocco.

FIGURE 38. Slab with *Batrachichnus* isp. footprints from undesignated member of Moenkopi Group, Colorado.

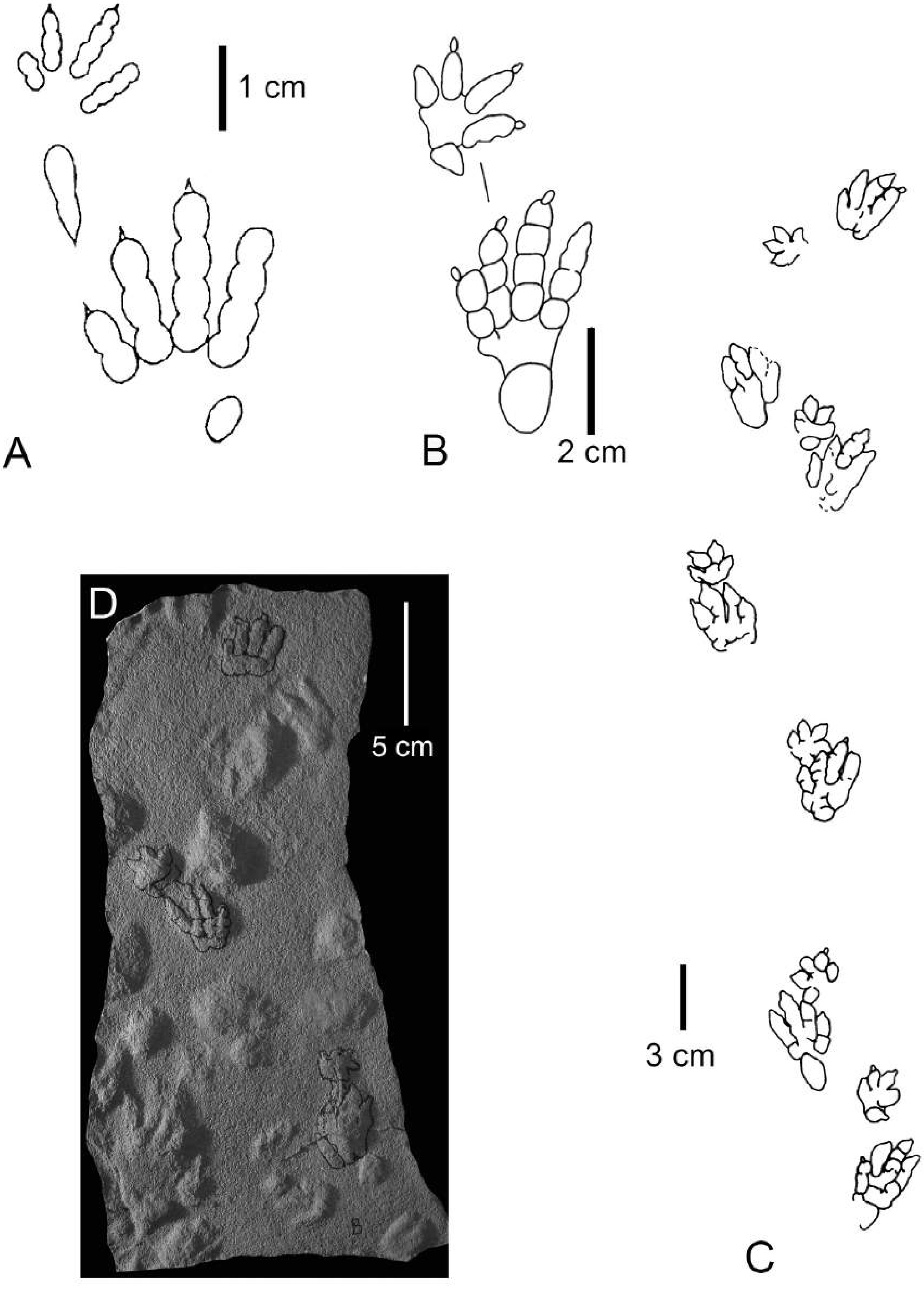

A
1 cm
B
2 cm
C
3 cm
D
5 cm

FIGURE 39. (facing page) *Batrachopus* and similar footprints from North America. **A,** ?*Batrachopus* isp. from Passaic Fm., Pennsylvania. **B,** *B. deweyi* composite of Lower Jurassic Newark Supergroup material. **C,** *B. deweyi* neotype from East Berlin Fm. (Lower Jurassic, Newark Supergroup) of Massachusetts. **D,** *B.* isp. from Moenave Fm. (Lower Jurassic of Arizona). Sketches from Olsen and Padian (1986) and Szajna and Hartline (1996).

I-IV in the pes. In contrast to chirotheres, however, pedal digit V is mostly absent or strongly reduced. Furthermore, the manus shows a larger outward rotation.

Thus far, the Triassic record of this ichnogenus is restricted to specimens from the Newark Supergroup of eastern North America (Olsen and Padian, 1986). Thus, in the Newark basin of Pennsylvania, Silvestri and Szajna (1993), Szajna and Silvestri (1996) and Szajna and Hartline (2003) recognized *Batrachopus*-like footprints in strata of latest Triassic age, a few meters below the stratigraphically lowest Newark basalt (Lucas and Tanner, 2007, 2015). They were determined by these authors as new taxa A and B, "*Batrachopus*" and small *Brachychirotherium*. Olsen et al. (2002) also indicated that the range of the ichnogenus *Batrachopus* goes back to the Late Triassic interval of the Newark Supergroup. Purported occurrences of *Batrachopus* in the Middle-Upper Triassic of Europe and South America have been referred to *Brachychirotherium* or have been re-dated to a younger stratigraphic level (Klein and Lucas, 2010b).

Trackmaker: For Triassic *Batrachopus*, small terrestrial sphenosuchian crocodylomorphs, similar to *Terrestrisuchus* and *Hesperosuchus*, which have skeletons known from Upper Triassic deposits of Europe and North America, are the most likely trackmakers (Klein and Lucas, 2010b).

Brasilichnium Leonardi 1981
Figures 40-41

1981 *Brasilichnium* Leonardi, p. 794, fig. 2, p. 795, fig. 3, p. 796, fig. 4, p. 800, fig. 5, p. 801, fig. 6
2004 Synapsid trackway: Lockley et al., p. 96, figs. 13-14
2004 Small mammal or mammal like trackway: Lockley et al., p. 97, fig. 15.
2006 Undetermined (?synapsid) trackway: Klein et al., p. 249, fig. 11B-C
2006 Isolated (?synapsid) imprint: Klein et al., p. 249, fig. 11C
2010 *Brasilichnium*: Lucas et al., p. 38, figs. 34, 35A-C

Type ichnospecies: *Brasilichnium elusivum* Leonardi, 1981.

Included ichnospecies: The type ichnospecies; *B. anaiti* D'Orazi Porchetti, Bertini and Langer, 2017; *B. saltatorum* Buck et al., 2017.

Distribution: Upper Triassic-Lower Jurassic of North America (Chinle Group, Wingate, Moenave and Navajo formations) and southern Africa? (Elliot Formation, Stormberg Group), Lower Cretaceous (Botucatu Formation) of Brazil.

Diagnosis (after Fernandes and Carvalho, 2008; Buck et al., 2017): Trackway of a small quadruped with mean glenoacetabular distance of 7.5 cm. Manus significantly smaller than pes; manus-pes distance increases when the walking speed decreases. Pace angulation relatively high for a quadruped. Heteropody is directly proportional to the positive rotation of the longitudinal axis of the pes (values> 75º). Longitudinal axis of the pes parallel to the trackway axis and with pace angulation > 125º, and does not show heteropody. Pes impressions are elliptical with a nearly transverse major axis and anteroposterior axis slightly directed into the trackways; short digits, usually rounded, with possible phalangeal formula 2-3-3-3-3; the posterior autopodium is ectaxonic and tetradactyl (digits II, III, IV and V) in a semiplantigrade condition. There is a greater hypex of digit V in slight abduction. Anterior autopodium has at least four digits with claws; claws present or absent due to preservation. Tail impressions/drag marks absent.

Description: Small footprints of a quadrupedal tetrapod that show a distinctive size difference between the smaller manus and the larger pes impressions. Imprints are tetradactyl.

The pes is semiplantigrade, wider than long and ectaxonic. Digits are short and rounded, digit V of the pes being laterally separated from the other digits.

Discussion: The ichnogenus *Brasilichnium* was originally described from the Lower Cretaceous Botucatu Formation of the Paraná Basin, Brazil, by Leonardi (1981) and has more recently been revised by Fernandes and Carvalho (2008). It remains best known from the Botucatu Formation (D'Orazi Porchetti et al., 2017; Buck et al., 2017), and there are also well described records from the Lower Jurassic Navajo Sandstone in the western USA (e.g., Lockley, 2011).

The only confirmed Triassic records of *Brasilichnium* are from the Redonda Formation of the Chinle Group and Wingate Formation of New Mexico and Colorado, respectively (Klein et al., 2006; Lockley et al., 2004; Lucas et al., 2010). Other Late Triassic *Brasilichnium* records may be partly hidden in the material of Ellenberger (1972, 1974, 1975) from the Stormberg Group of southern Africa.

Trackmaker: All workers agree that *Brasilichnium* is the footprint of a small, nonmammalian and/or basal mammalian synapsid (e.g., Fernandes and Carvalho, 2008; Lockley et al., 2004; Lucas et al., 2010).

Capitosauroides Haubold 1971
Figures 42

1971a *Capitosauroides*: Haubold, p. 413-414, figs. 4-5, p. 545, pl. I-II
1971b *Capitosauroides*: Haubold, p. 16, fig. 12(2)
1984 *Capitosauroides*: Haubold, p. 149, fig. 100(2)
2019a *Capitosauroides*: Marchetti, p. 751, p. 752, fig. 3C-G, p. 769, fig. 14B

Type ichnospecies: *Capitosauroides bernburgensis* Haubold 1971.

Included ichnospecies: The type ichnospecies is the only valid ichnospecies.

Distribution: Middle Permian, Abrahamskraal-Teekloof formations, Beaufort Group, South Africa; upper Permian, Val Gardena Formation, northern Italy; ?Wióry Formation, Lower Triassic, Poland; Lower-Middle Triassic, Solling Formation (Buntsandstein), Germany.

Diagnosis (after Haubold, 1971a): Moderately wide trackways of a quadruped. Pace angulation of pes ~100°. Pes and manus imprints pentadactyl, semiplantigrade, clumsy, without distinct proximal termination of the sole surface or specialized metatarso-/metacarpophalangeal area. Digits with broad, rounded distal ends lacking claw traces.

Description: Imprints with widely spread digits. Manus slightly smaller than pes and impressed anterior to the latter. Axes of imprints with strong outward rotation.

Discussion: The type locality near Bernburg, Sachsen-Anhalt, Germany, has yielded the best preserved specimens with complete trackways (Haubold, 1971a, b). From the Lower Triassic of Wióry in the Holy Cross Mountains of Poland, possible *Capitosauroides* has been identified with a distinct ichnospecies (Ptaszyński, 2000; Klein and Niedźwiedzki, 2012).

Trackmaker: *Capitosauroides* was attributed to temnospondyl amphibians by Haubold (1971a, b). Klein and Niedźwiedzki (2012) doubted this interpretation, considering a non-amphibian tetrapod or reptiliomorph based on the five-toed manus impression. In temnospondyl amphibians, the number of digits in the manus is generally reduced to four. However, Watson (1958) described the skeleton of the temnospondyl

Paracyclotosaurus davidi from the Middle Triassic of New South Wales, Australia. In his description, this author mentions five digits of the manus essentially based on the number of preserved metacarpalia. The reconstruction also shows five manual digits (Watson, 1958). Teschner and Konietzko-Meier (2015) and Konietzko-Meier et al. (2020) mention five metacarpalia in *Metoposaurus krasiejowensis* from the Upper Triassic of Poland. Recently, *Capitosauroides* has been attributed to therocephalian synapsids (Marchetti et al., 2019). Nevertheless, the attribution of *Capitosauroides* to a distinct tetrapod group still remains uncertain.

Characichnos Whyte and Romano, 2001
Figure 43

2001 *Characichnos*: Whyte and Romano, p. 230, figs. 4, 6, 8B1-B6
2006 Swim tracks: Lockley and Milner, p. 257, figs. 3-8
2006 *Eubrontes*-type swim tracks: Milner et al., p. 315, figs. 7-8
2006 *Grallator*-type swim tracks: Milner et al., p. 315, figs. 5E, 6
2006 *Characichnos*: Milner et al., p. 321
2010 *Characichnos*: Lucas et al., p. 40, fig. 35D-E
2014 Swim tracks: Thomson and Lovelace, p. 103, figs.3, 5, 7, 10, 14

Type ichnospecies: *Characichnos tridactylus* Whyte and Romano, 2001.

Included ichnospecies: Only the type ichnospecies.

Distribution: Common in the North American Moenkopi and Chinle groups (Lockley and Milner, 2006; Milner et al., 2006; Lucas et al., 2010; Lovelace and Lovelace, 2012; Thomson and Lovelace, 2014).

Diagnosis (from Whyte and Romano, 2001): Two to four elongate, parallel hypichnial ridges (or epichnial grooves) that may be straight, gently curved or slightly sinuous. The termination of the ridges (or grooves) may be straight or slightly flexed.

Description: Long, thin, slightly arcuate scratch marks of variable size and interdigital space, two, three or four in parallel series.

Discussion: The ichnotaxonomic status of tetrapod "swim traces" or "swim tracks" is problematic. Indeed, referring to such traces as swim tracks is somewhat questionable, as a swimming tetrapod generally would leave no traces. The term swim trace/track thus is based on the perception that these are digit scratch marks left by a partially buoyant tetrapod, much as *Undichna* is perceived to be the scratch marks left by the fin(s) of a fish swimming just above (but also touching) the sediment-water interface. Some recent papers use the term "punting" for traces left by tetrapods while drifting and touching the bottom with their fore- or hind feet (see Xing et al., 2020 and references therein).

Lockley and Foster (2006) discussed the ichnotaxonomy of tetrapod swim tracks, noting that there are five named ichnogenera for these traces: *Chelonichnium*, *Saltosauripus*, *Hatcherichnus*, *Characichnos* and *Albertasuchipes* (Bernier et al., 1982, 1984; Thulborn, 1990; Foster and Lockley, 1997; Whyte and Romano, 2001; McCrea et al., 2004). Of these, *Characichnos* is most common in being two to four long, thin, well-spaced scratch marks. Lockley et al. (2014) differentiated turtle, crocodylomorph and pterosaur swim tracks based on morphological features.

However, vertebrate swim tracks have also been assigned to an ichnogenus of walking track, if a clear association can be established. Thus, for example, Lockley (2006) identified swim tracks and walking tracks of *Gwyneddichnium*, and Milner et al. (2006) assigned swim tracks to *Characichnos* but established their clear association with *Grallator* and *Eubrontes*. Indeed, if tetrapod footprint ichnotaxa are intended to correspond to biotaxa (e.g., Lucas, 2005), why should a nomenclature exist for the extramorphological variants called swim tracks? Shouldn't the swim tracks be assigned to the associated "walking track" ichnogenus, as was done by Lockley (2006) with *Gwyneddichnium*? Lockley et al. (2014) describe pterosaur swim tracks, which they connect to *Pteraichnus* without mentioning a swim track label. Clearly, this is a problem created by the presence of a common extramorphological variant (swim track) and the degree of confidence with which it can be associated with a walking track ichnogenus.

Lucas et al. (2010) proposed a solution to this problem as follows: recognize the ichnogeneric names of swim tracks as form ichnogenera, use these names where appropriate (i.e., where the swim tracks fit into the morphological definition of the swim track ichnogenus) and attempt, if possible, to establish the association of the swim tracks with a walking track ichnogenus. This is what was done by Milner et al. (2006) and Lockley et al. (2014), and is followed here.

Chelonipus Rühle von Lilienstern 1939
Figure 44

1838a [footprints]: Plieninger, p. 132, fig.
1838b [footprints]: Plieninger, p. 563
1844 [footprints]: Von Meyer and Plieninger, p. 79, pl. 1, figs. 1-3, pl. 2 1932 Coelurosaurier-Fährten: Huene, p. 345, figs. 38-39.
1939 *Chelonipus*: Rühle von Lilienstern, p. 329, 336, figs. 10, 12, pl. 6, figs 4-15, pl. 7, figs. 3-12.
1956 *Chelonipus*: Huene, p. 222
1958 *Chelonipus*: Kuhn, p. 19, pl. 5, figs. 5-6
1959 *Chelonipus*: Schmidt, p. 20, 33, 92, 97, 117, figs. 37.11, 39g
1963 *Chelonipus*: Kuhn, p. 60
1968 *Chelonipus*: Kuhn, p. 41
1971a *Chelonipus*: Haubold, p. 417, figs. 6-7, pl. 4
1971b *Chelonipus*: Haubold, p. 89, fig. 56
2012 cf. *Chelonipus*: Lovelace and Lovelace, p. 636, fig. 3
2012 *Chelonipus*: Lovelace and Lovelace, p. 647, fig. 8
2014 cf. *Chelonipus*: Thomson and Lovelace, p. 124, tables 1, 3, fig. 11,
2017 *Chelonipus*: Lichtig et al., p.1115-1119, figs. 3-8

Type ichnospecies: *Chelonipus torquatus* Rühle von Lilienstern, 1939 (= *C. cuneiformis* Rühle von Lilienstern, 1939; = *C. plieningeri* Haubold, 1971a).

Included ichnospecies: Known only from the type ichnospecies.

Distribution: Known from the Early Triassic of Wyoming and Utah (USA), from the Middle and Late Triassic of Germany and possibly the Late Triassic of Spain (Lichtig et al., 2017).

Diagnosis (after Haubold, 1971a, b): Tracks of a quadruped in which trackway width is almost as long as stride length; manus and pes tracks are in parallel rows and preserve 3 to 5 digits; the manus is broad and arched, with digit III or IV longest; and the pes often has a rounded plantar surface and relatively longer digits compared to the manus.

Description: Tracks of a quadruped that are always nearly in parallel rows with the manus and pes tracks of one side of the body forming nearly straight lines, one following the other in an understep ranging from an extreme, full understep by which the fore foot is overstepped by the hind foot of the next cycle of steps, to a more standard understep walk in which the hind foot is placed just behind the fore foot of the same series of steps. The broad, arched manus has the longest digit being digit III or IV, and the pes often has a rounded plantar surface and relatively longer digits compared to the manus.

Discussion: The extreme understep walk of turtles is likely the basis for the variation in turtle tracks given the name

Chelonipus plieningeri (Haubold 1971a). Thus, Lichtig et al. (2017) considered *C. plieningeri* a synonym of *C. torquatus* based on extramorphological and/or gait variation.

In *Chelonipus,* the correct identification of pes and manus imprints has been debated. While Rühle von Lilienstern (1939), in his first description of *C. torquatus,* considered the anterior imprint of a set as the pes overstepping the manus, this was questioned and reinterpreted by Haubold (1971a, b) as a reverse arrangement, with the manus in a set being continuously positioned anterior to the pes. In contrast, Avanzini et al. (2005) followed Rühle von Lilienstern (1939) based on experiments with recent forms, and Lichtig et al. (2017) endorsed the conclusion that the *C. torquatus* type trackway shows the pes overstepping the manus.

Lichtig et al. (2017) recently revised and reviewed *Chelonipus*. Rühle von Lilienstern (1939) originally described *Chelonipus torquatus* and *C. cuneiformis* based on material from a single surface in the uppermost Middle Buntsandstein (Solling Formation) of southern Thuringia, Germany (late Olenekian-Anisian: Lucas and Schoch, 2002). Haubold (1971a) synonymized both ichnospecies under *C. torquatus* and introduced another ichnospecies, *C. plieningeri*, based on a trackway from the Upper Triassic Middle Keuper (Stuttgart Formation) of Feuerbacher Heide near Stuttgart in southwestern Germany. The latter was originally described by Plieninger (1838) and Meyer and Plieninger (1844). It was incorectly attributed to a coelurosaurian dinosaur by Huene (1932). Another Triassic record comes from the Keuper (Upper Triassic) of Spain (Márquez-Aliaga, 1999). This is a single track and of uncertain origin, but we agree with Avanzini et al. (2005) that a turtle was the most likely trackmaker.

Lovelace and Lovelace (2012) illustrated a trackway with scratch marks from the Lower Triassic Red Peak Formation of central Wyoming, USA, which they attributed to turtles. These tracks appear to be *Chelonipus*, as they include the minimal divarication of 3-4 digits with digit III longest and a narrow sole posterior to all of the digits. Furthermore, the parallel tracks are what would be expected of a turtle trackway. The tracks illustrated in Lovelace and Lovelace (2012, figs. 8C, E) are nearly identical to the type material of *Chelonipus* described by Rühle von Lilienstern (1939). Thomson and Lovelace (2014) described several tracks from the base of the Virgin Formation of the Thaynes Group and Torrey Formation of the Moenkopi Group, Utah, which they assigned to *Chelonipus*. Reolid et al. (2018) describe turtle tracks from Carnian deposits of the Iberian Range in eastern Spain. Both tracks and trackways of swimming/bottom walking and terrestrially walking individuals are described. The manus imprints are arched, characteristic of turtle manus tracks, with digit impressions often showing robust scratches with curved and sharp ends.

Trackmaker: A *Proganochelys*-like turtle (Lichtig et al., 2017).

Ichnogenus *Dicynodontipus* Rühle v. Lilienstern, 1944
Figures 45-46

1876 *Chirotherium*: Hornstein, p. 923-924
1902 *Chirotherium*: Hornstein, p. 119-121, fig. 1
1944 *Dicynodontipus*: Rühle v. Lilienstern, p. 371, fig. 1, p. 383, fig. 7, pl. 22-23
1964 *Calibarichnus*: Casamiquela, p. 145-147, pl. 17, fig. 2
1964 *Gallegosichnus*: Casamiquela, p. 154-158, pl. 15, fig. 1, pl. 16, fig. 2, pl. 19, fig. 1-2
1964 *Palaciosichnus*: Casamiquela, p. 150-154, pl. 18, fig. 1-2,
1966 *Chelichnus*: Haubold, figs. 3-9
1971a *Dicynodontipus*: Haubold, p. 500-508, figs. 30-32, pl. 27-28
1971b *Dicynodontipus*: Haubold, p. 41-42, fig. 26 (1-6)
1971b *Gallegosichnus*: Haubold, p. 42, fig. 26(8)
1971b *Palaciosichnus*: Haubold, 1971b, p. 42, fig. 26(9)
1971b *Calibarichnus*: Haubold, p. 42, fig. 26(10)
1975 *Calibarichnus*: Casamiquela, p. 563-564, p. 578, pl. 4, fig. 2
1975 *Stipanicichnus*: Casamiquela, p. 569-571, p. 580, pl. 6
1975 *Gallegosichnus*: Casamiquela, p. 565-566, p. 576, pl. 2-3
1975 *Palaciosichnus*: Casamiquela, p. 566-569, p. 579, pl. 5
1984 *Dicynodontipus*: Haubold, p. 140- 141, figs. 91 (2a-c), 92
1989 *Dicynodontipus*: Demathieu and Fichter, p. 147, pl. 2, figs. 2-4, p. 149, pl. 3, p. 151, pl. 4, figs. 1-3
1990 *Gallegosichnu*s, *Calibarichnus*, *Palaciosichnus*, *Rogerbaletichnus*: Leonardi and De Oliveira, pl. II , III, VI-VIII.
1994 cf. *Dicynodontipus*: Leonardi, pl. II, fig. 9
1994 *Gallegosichnus*: Leonardi, pl. II, fig. 11, pl. XVI, figs. 1-3
1994 *Calibarichnus*: Leonardi, pl. XVI, fig. 4
1994 *Palaciosichnus*: Leonardi, pl. XVI, fig. 9
2004 "Types Q1 and Q2": Marsicano and Barredo, p. 324-325, figs. 7-8.
2004 "*Dicynodontipus*": Marsicano et al., p. 176, fig. 5
2006 *Dicynodontipus*: Melchor and De Valais, p. 365, fig. 5
2006 Morphotype C ("*Calibarichnus*"): Domnanovich and Marsicano, p. 59-60, fig. 5
2006 Morphotype E ("*Palaciosichnus*"): Domnanovich and Marsicano, p. 62-63, fig. 7
2006 Morphotype F ("*Gallegosichnus*"): Domnanovich and Marsicano, p. 63-65, figs. 8-9
2006 Morphotype G ("*Stipanicichnus*"): Domnanovich and Marsicano, p. 65-67, fig. 10
2008 *Calibarichnus*: Domnanovich et al., fig. 3
2008 *Gallegosichnus*: Domnanovich et al., fig. 4
2008 *Palaciosichnus*: Domnanovich et al., fig. 5
2019a *Dicynodontipus*: Marchetti et al., p. 752, p. 753, fig. 4, p. 769, fig. 14C

Type ichnospecies: *Dicynodontipus geinitzi* (Hornstein, 1876).

Included ichnospecies: Only the type ichnospecies is valid.

Distribution: Upper Permian, Val Gardena Sandstone Formation, Dolomites, Northern Italy; Lower Triassic (Palingkloof Member of Balfour Formation, Induan) of South Africa; Lower-Middle Triassic (Buntsandstein, Solling Formation, Olenekian-Anisian) of Germany; Wióry Formation (Olenekian) of Poland; Middle Triassic (Anisian) of Northern Italy; Upper Triassic (Vera Formation, ?Lower Triassic) of Argentina.

Diagnosis (after Haubold, 1971a, b): Relatively narrow trackways, pace angulation not below 100° at normal gait. Manus imprints positioned anterior to pes imprints, but in trackways of fast moving individuals widely overstepped by the latter. Pes and manus imprints of the same morphology--plantigrade, pentadactyl with short, forward-pointing digits, digit IV longest, and digit V shifted slightly posteriorly.

Description: Small (up to 55 cm long) pentadactyl pes and manus imprints. Manus imprints only slightly smaller than pes imprints. Digits subequal in length and straight with small claw traces. Large plantar and palmar surfaces, often separated from digits by a distinct groove. Trackways with relatively large pace angulation (160°) and occasional lateral overstep of the manus by the pes, depending on the velocity of progression.

Discussion: The ichnogenus *Dicynodontipus* was introduced in 1944 based on material from the German Buntsandstein (Olenekian-Anisian) (Rühle v. Lilienstern, 1939, 1944). The type ichnospecies, *D. geinitzi,* was originally described under a different combination, *Chelichnus geinitzi* (Hornstein, 1876). Subsequently, *Dicynodontipus* was identified in different middle Permian-Late Triassic deposits (DeKlerk, 2002; Melchor and De Valais, 2005; Silva, 2008a; Marchetti et al., 2019a). Thus far, only the type ichnospecies can be considered valid.

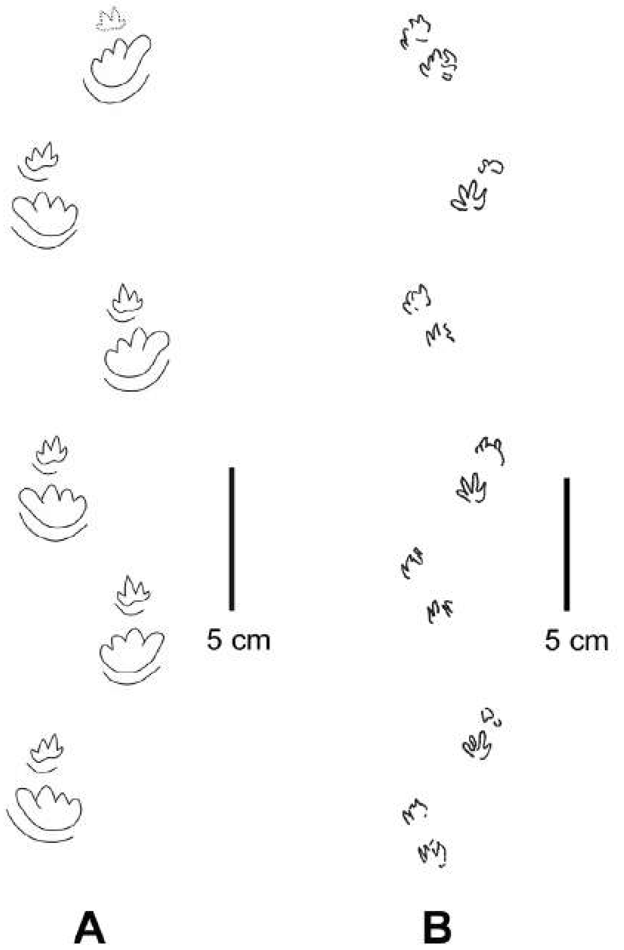


FIGURE 40. *Brasilichnium* and similar footprints. **A,** *Brasilichnium elusivum* trackway from Botucatu Fm. (Lower Cretaceous) of Brazil. **B,** ?*Brasilichnium* isp. from Wingate Fm. (Rhaetian) of western Colorado. Sketches from Lockley et al. (2004) and Fernandes and Carvalho (2008).

Trackmaker: Therapsid synapsids; while the name implies dicynodonts, cynodonts were most likely the trackmakers (Marchetti et al., 2019a).

Dikoposichnus Zhang et al., 2014
Figure 47

Type ichnospecies: *Dikoposichnus luopingensis* Zhang et al., 2014, monotypic

Distribution: Shizishan Member (Member II, Luoping Biota) of the Guanling Formation (Middle Triassic, Anisian) of Yunnan Province, China.

Diagnosis (from Zhang et al., 2014): Double row of imprints, preserved as concave epireliefs (bed) or convex hyporeliefs (sole). Each imprint is a narrow, V-shaped, slot-like depression, with a mound of sediment behind. Individual imprints may be elliptical to sigmoid-shaped in plan view, sometimes with an anterior sweep at the medial edge. Individual imprints are transverse to the direction of travel, spaced widely apart and with variable pace length. When preserved as trackways, prints generally occur in matching pairs, suggesting the limbs moved in concert, but they may be offset, produced by alternate left-right pacing. Overall trackway width is 30-70 cm, and individual prints are 5-20 cm along their longest axis, transverse to the direction of movement. Occasionally comprises a single trackway of prints.

Description: Imprints are half-moon to crescent-shaped and much wider than long, posteriorly with a rim of backwardly pushed sediment. Laterally, 3-4 digit traces with sharp terminations are visible, often continuing in elongated scratches. Trackways are very broad, and impressions are arranged opposite to each other (left-right) along the trackway midline.

Discussion: Zhang et al. (2014) introduced this ichnotaxon from shallow marine deposits of the Guanling Formation in Yunnan Province, China. They occur as numerous long trackways in argillaceous dolostones of this unit and were obviously left by marine reptiles when touching the bottom with their forefeet. More recently, Klein et al. (2019) reported a further occurrence of *Dikoposichnus luopingensis* from the Songzikan Member (Member I) of the Guanling Formation in adjacent Guizhou Province. Here, they are associated with subaqueous trackways of other marine diapsids, probably placodonts or saurosphargids (Xing et al., 2020).

Trackmaker: According to Zhang et al. (2014), nothosaurs are the most likely makers of *Dikoposichnus luopingensis*.

Ichnogenus *Dolomitipes* Marchetti et al., 2019
Figure 48

Type ichnospecies: *Dolomitipes accordii* (Ceoloni et al., 1988)

Referred ichnospecies: *Dolomitipes icelsi* (De Klerk, 2002)

Distribution: Val Gardena Sandstone Formation (late Permian), Northern Italy, Balfour Formation; late Permian (Wuchiapingian)–Early Triassic (Induan), of the Karoo Basin, South Africa.

Diagnosis (from Marchetti et al., 2019): Trackway of a quadrupedal tetrapod with pentadactyl, semiplantigrade (manus) to plantigrade (pes) footprints. Pentadactyl manus different from *Limnopus*. Digit impressions straight to distally inwards bent (manus), terminating in enlarged tips showing a sub-circular shape and an arcuate arrangement. Median digits of the pes distinctly longer than the outer digits and subequal in length (mesaxony), different from *Ichniotherium*, *Limnopus*, and *Dimetropus*. Manus weakly ectaxonic. Manual imprint about one third wider than long and more deeply impressed than the pes. Both features different from *Dimetropus* and *Dicynodontipus*. Well-impressed palm with concave proximal margin and large, rounded metacarpal-phalangeal pads of all digits. Pads of digits II-V not present in *Ichniotherium* and *Limnopus*. Pedal imprint shallower and about as wide as long, of size similar to the manus. Digits I–IV about 1/3 of the pes length, with rounded metatarsalphalangeal pads clearly separated from the proximal-lateral, elliptical heel. Sole structure different from *Ichniotherium*, *Limnopus* and *Dicynodontipus*. Digit V short and proximally- and laterally-positioned, different from *Dimetropus*. Trackways consisting of alternating sets of manus-pes imprints with inwardly rotated manus and forward-directed pes, relatively high gait and no tail or body trace preserved.

Description: Trackways are broad to moderately broad with pentadactyl pes and manus imprints of nearly equal size that show a distinct palm/sole and digits with pad impressions. Imprints are mostly mesaxonic, the manus is slightly ectaxonic. Imprints of Triassic specimens from South Africa are up to 14 cm in length and 12.5 cm in width. The manus imprints are oriented parallel to the midline or are slightly inward rotated, while the pes is oriented parallel to the midline.

Discussion: The ichnogenus *Dolomitipes* was originally introduced by Marchetti et al. (2019a) based on material from the Val Gardena Sandstone Formation (Permian, Lopingian) of the Dolomites (Northern Italy). Subsequently it was identified

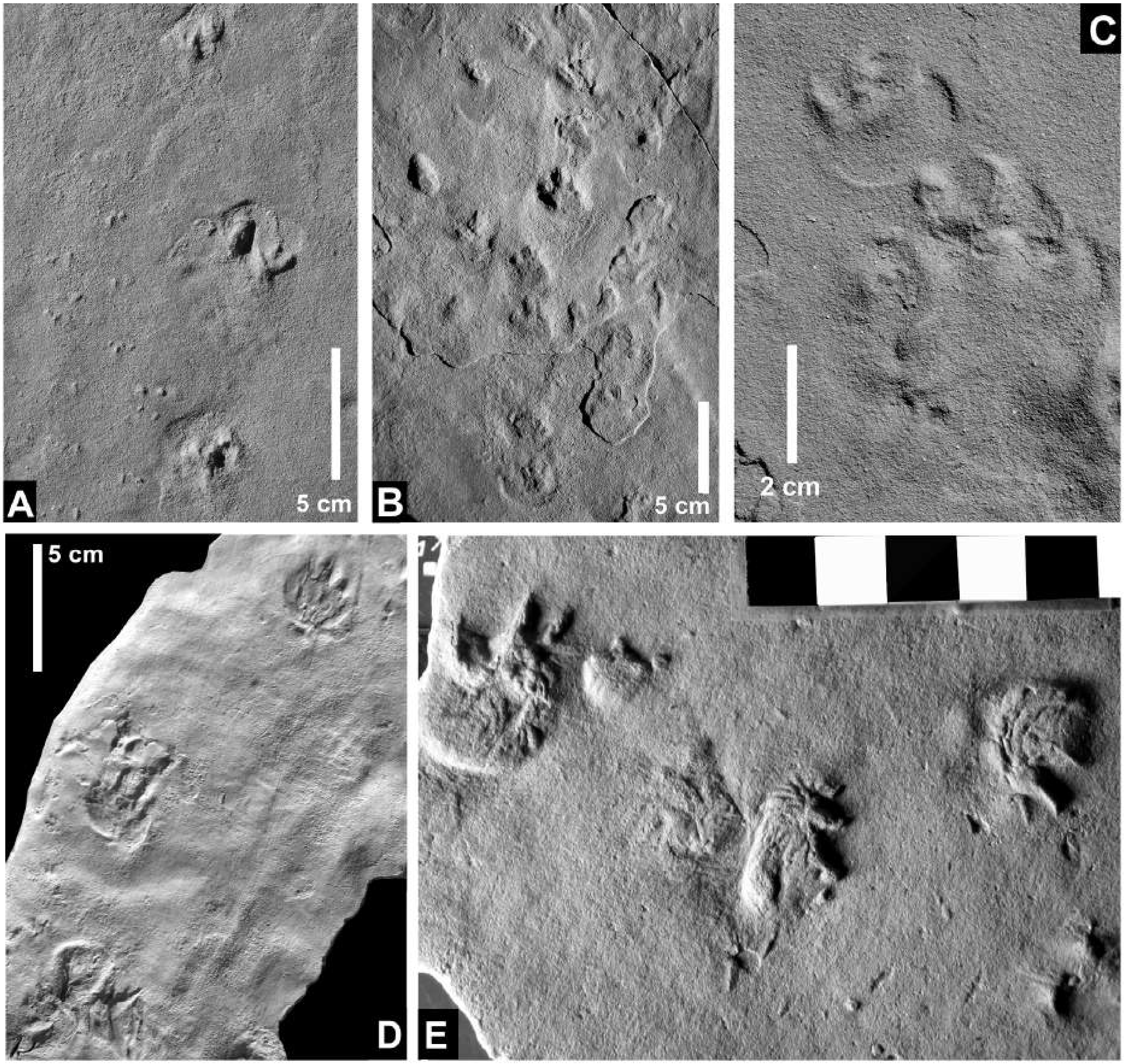


FIGURE 41. *Brasilichnium elusivum* trackways from Redonda Fm. (Chinle Group) of New Mexico. From Lucas et al. (2010).

also in the Balfour Formation (late Permian, Wuchiapingian–Early Triassic, Induan) of the Karoo Basin in South Africa (Marchetti et al., 2019b). Some of the South African material comes from strata in the *Lystrosaurus* zone, probably above the P-T boundary and most likely is of earliest Triassic age. Morphologically, *Dolomitipes* is different from all other known Late Paleozoic Mesozoic tetrapod ichnogenera (see diagnosis above; Marchetti et al., 2019a, b) and therefore is considered here a valid ichnotaxon.

Trackmaker: Small to medium-sized dicynodont synapsids (Marchetti et al., 2019a, b).

Eoanomoepus Lockley et al., 2018

Type ichnospecies: *Eoanomoepus latus* Lockley et al., 2018.

Included ichnospecies: Only the type ichnospecies.

Distribution: Chinle Group near Moab, southeastern Utah.

Diagnosis (after Lockley et al., 2018): Transverse tridactyl tracks only two thirds as long as wide, hence more transverse than typical *Anomoepus* with digit traces little connected, and digit divarication wide but variable. Step short, trackway very wide, with low pace angulation, and outward rotation of pes. *Eoanomoepus* differs from *Anomoepus* in length/width ratio (0.60-0.70 vs. ~1.08) and lack of obvious inward rotation characteristic of the latter, well-known ichnogenus. The trackway width of *Eoanomoepus* differs from *Anomoepus* in being unusually wide, also with usually an irregular step and stride dimensions. *Eoanomoepus* also differs from *Anomoepus* in lacking evidence of a hallux (digit I) trace and being more digitigrade.

Description (after Lockley et al., 2018): These are small (mean length 9.0-9.6 cm; mean width 13.4–15.0 cm) tridactyl,

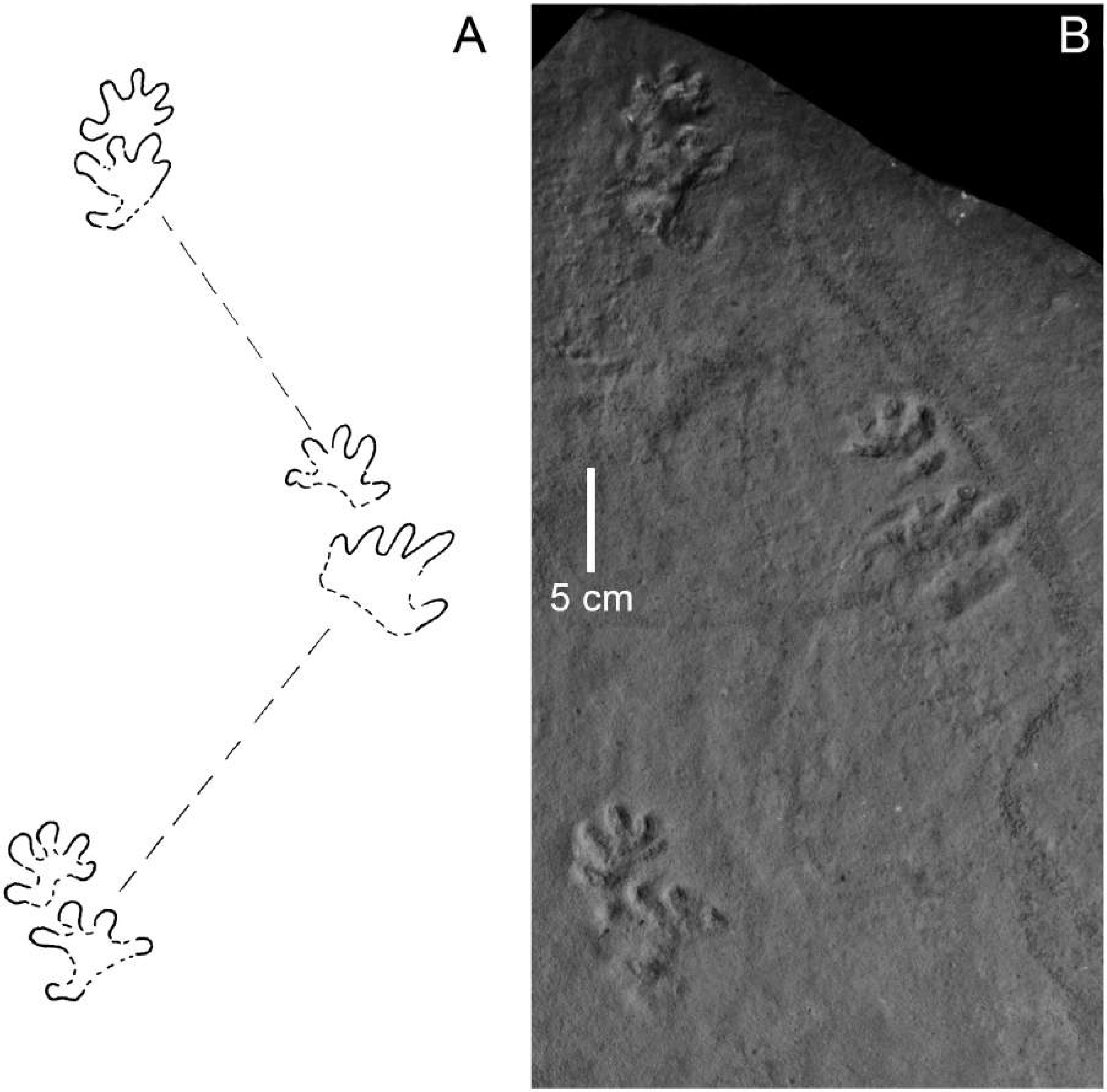
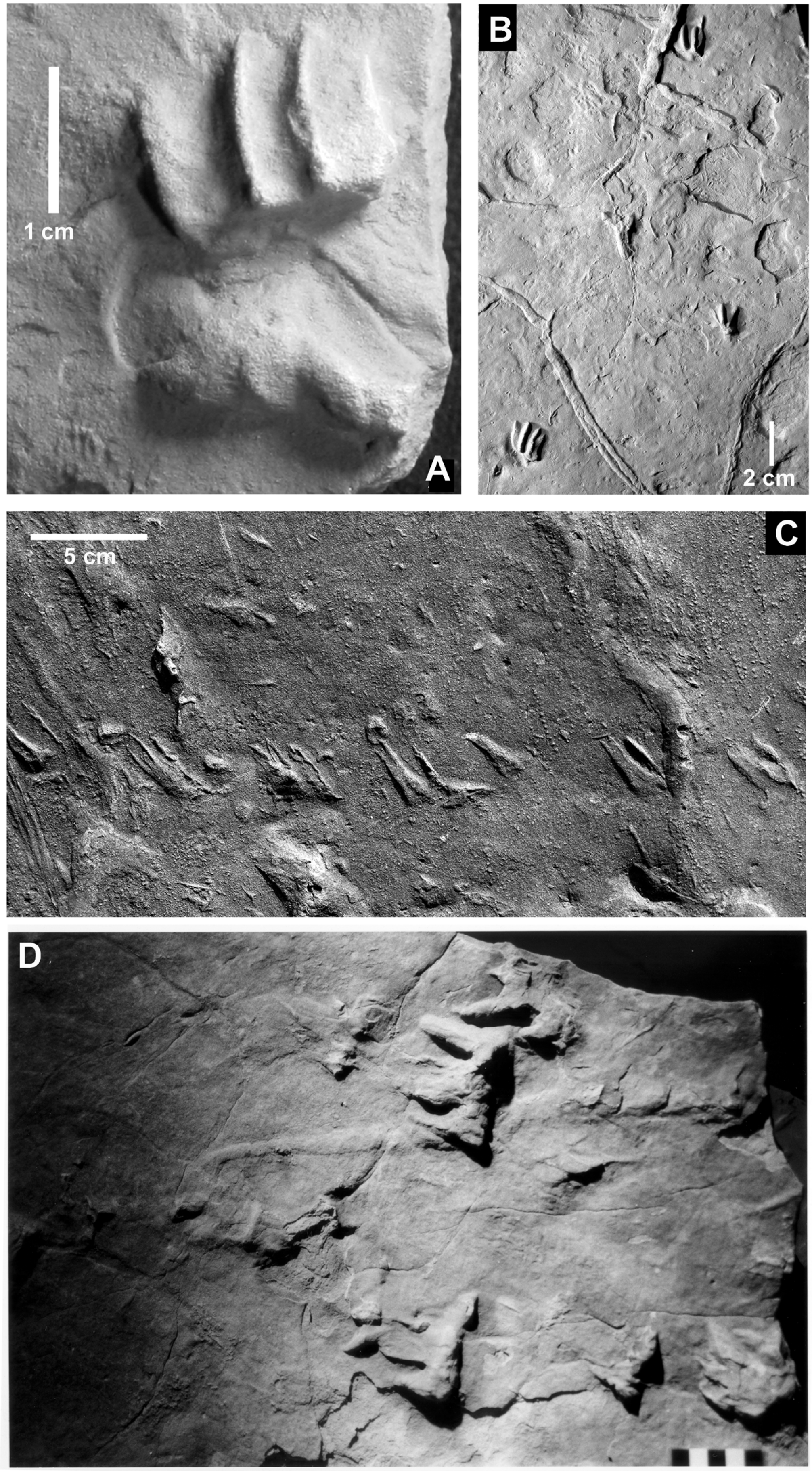


FIGURE 42. *Capitosauroides bernburgensis* holotype from Solling Fm. (Thüringischer Chirotheriensandstein, Anisian) of Germany. **A,** Sketch. **B,** Photograph. Sketch from Haubold (1971a).

FIGURE 43. (facing page) *Characichnos* swim tracks and trackways. **A,** From Moenkopi Fm. (?Anisian) of Utah. **B,** From Moenkopi Fm. (?Anisian) of Arizona. **C,** From Wióry Fm. (Olenekian) of Poland. **D,** *Barrancapus cresapi* trackway from holotype slab for comparison. From Klein and Lucas (2010b) and Klein and Niedźwiedzki (2012).


1 cm
A
B
2 cm
C
5 cm
D

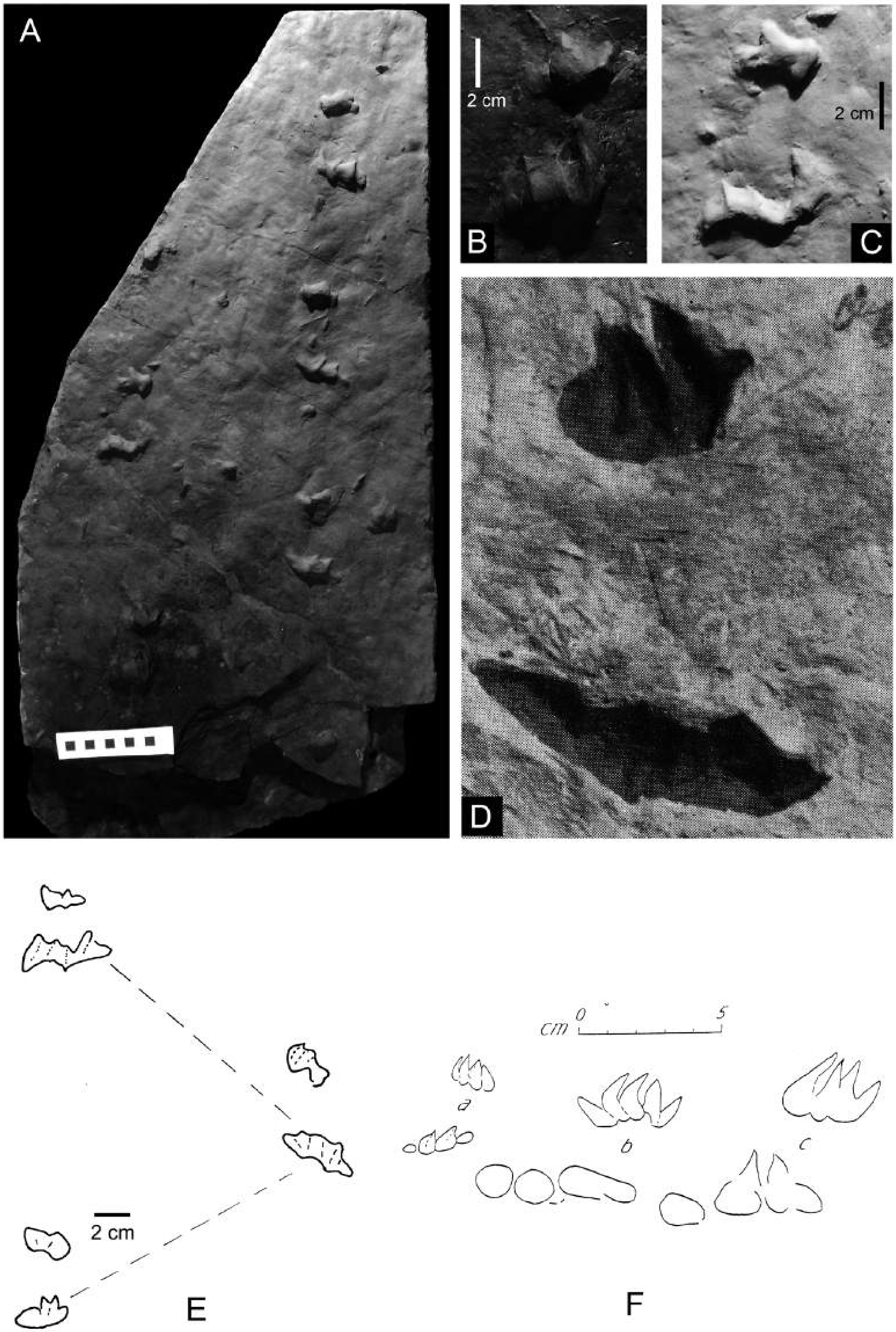


FIGURE 44. *Chelonipus torquatus* turtle trackways. **A,** From Stuttgart Fm. (Schilfsandstein, Carnian) of Germany. **B-C,** Details. **D,** From Solling Fm. (Thüringischer Chirotheriensandstein, Anisian) of Germany. **E,** Sketch of trackway from Stuttgart Fm. **F,** Sketches of imprints from Solling Fm. A-C. Photos by Frank-Otto Haderer, from Lichtig et al. (2018). D. From Rühle v. Lilienstern (1939). E-F. From Haubold (1971a).

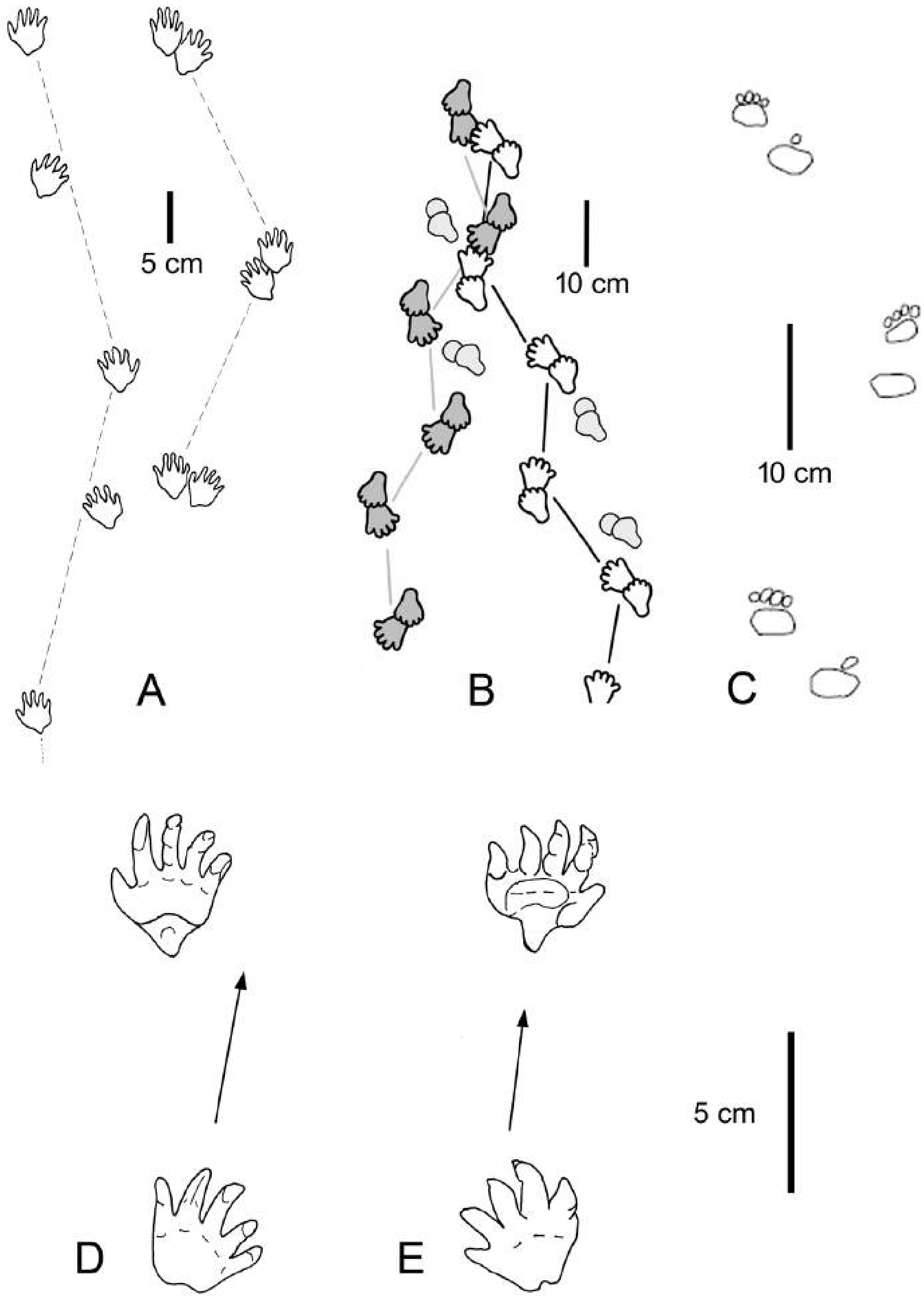


FIGURE 45. **A-B, D-E,** *Dicynodontipus geinitzi* tracks and trackways from Solling Fm. of Germany. **C,** Therapsid trackway ?*Pentasauropus argentinae* from Portezuelo Fm. (Middle-?Upper Triassic) of Argentina for comparison. Sketches A, B, D, E from Haubold (1971a) and Demathieu and Fichter (1989), sketch in C from Marsicano and Barredo (2004).

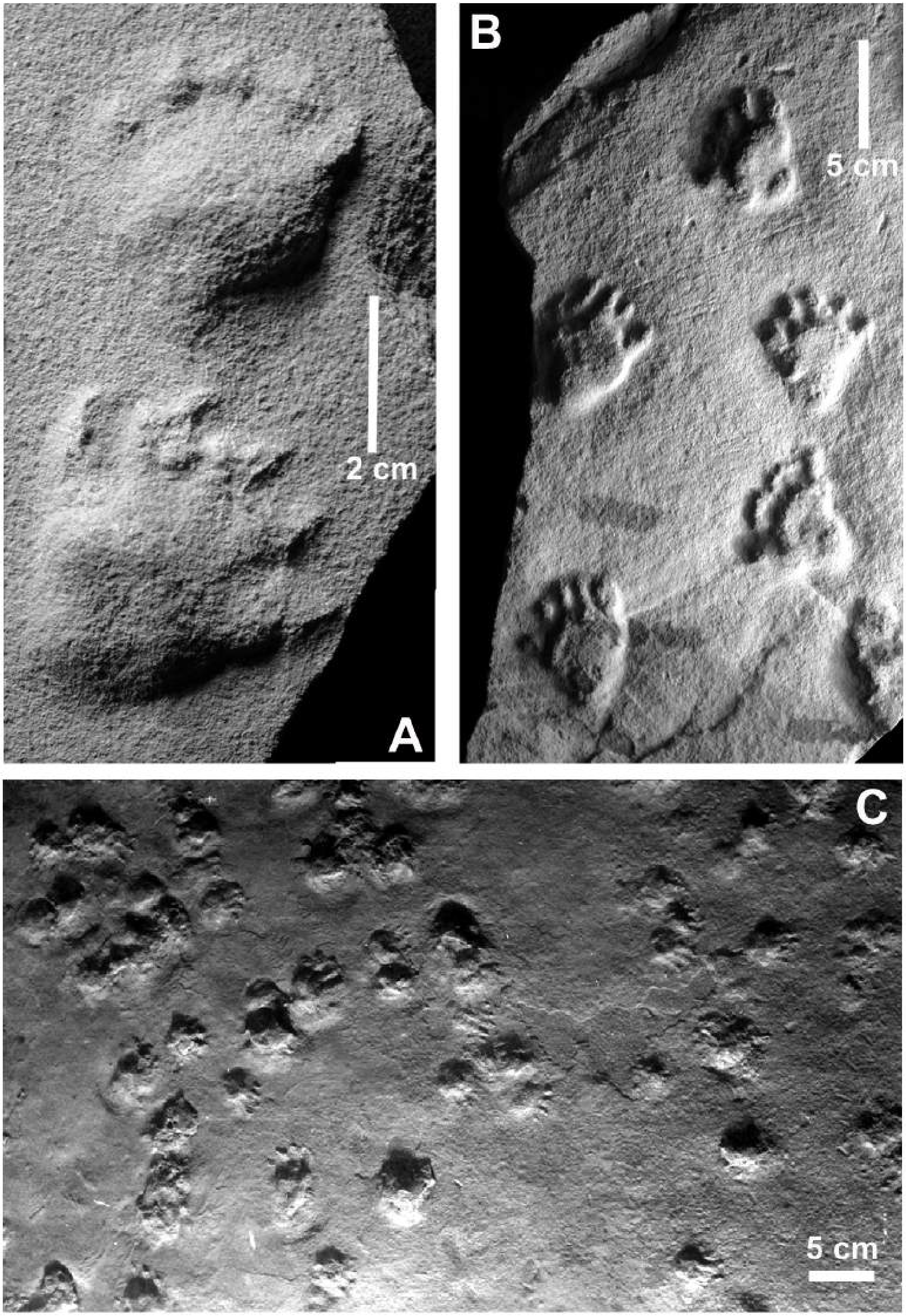


FIGURE 46. *Dicynodontipus* tracks and trackways from the ?Lower-Middle Triassic. **A,** "*Calibarichnus*." **B,** "*Gallegosichnus*." **C,** *Dicynodontipus geinitzi*. A-B. From Vera Fm. (?Lower Triassic) of Argentina. C. From Solling Fm. (Olenekian-Anisian) of Germany.

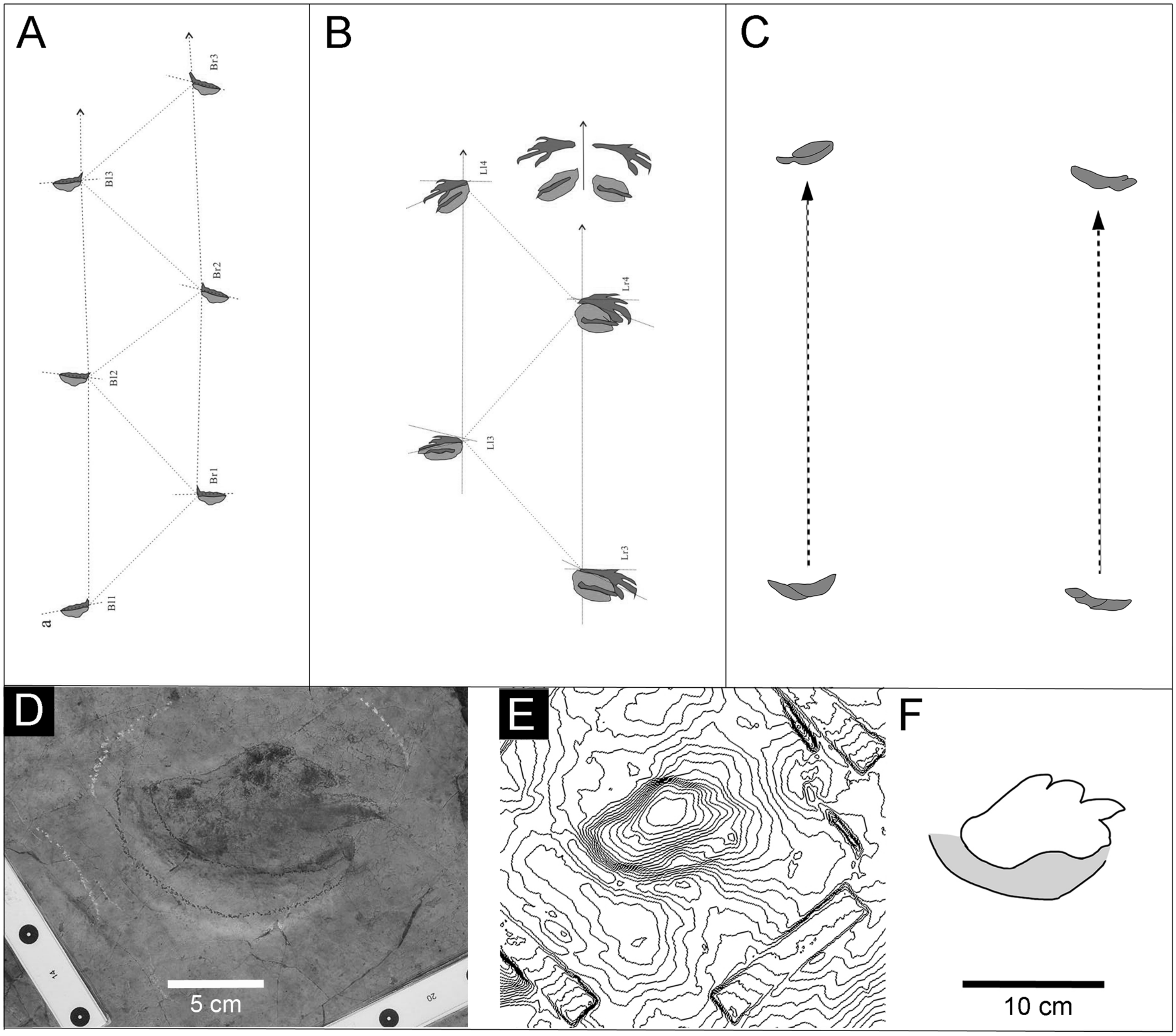


FIGURE 47. *Dikoposichnus luopingensis* from Guanling Formation (Middle Triassic, Anisian-Ladinian) of southwestern China as interpretive outline drawings (A-C, F), photograph (D) and contour map (E). **A-B,** Trackways from type surface in Yunnan Province. **C-F,** Trackway and isolated imprint showing lateral digit traces and posterior push-back sediment rim (gray) from Guizhou Province. A-B. From Zhang et al. (2014). C-F. From Xing et al. (2020).

wider than long pes imprints with very slender digits that show a large divarication angle (II–IV up to 109°). Digit traces are little connected, and phalangeal and metatarso-phalangeal pads are absent. Trackways show relatively short steps (averaging 41 cm) and low pace angulation between 99–127°. Footprints are rotated outward relative to the trackway midline.

Discussion: The ichnogenus *Eoanomoepus* was introduced based on material from the Chinle Group near Moab, southeastern Utah, USA, by Lockley et al. (2018). The latter authors distinguished *Eoanomoepus* from the Jurassic ornithischian track *Anomoepus* by several features, such as the wider than long pes imprints, being longer than wide in *Anomoepus*, the lack of hallux and metatarsal impressions, being occasionally present in *Anomoepus*, and by the outward rotation of the pes imprints, vs. the inward rotation in *Anomoepus*. In overall-shape, with their wide digit divarication, and the slender digit impressions lacking pad traces, these tracks slightly resemble the bird-like ichnogenus *Trisauropodiscus*, originally described from the Late Triassic-Lower Jurassic of the Stormberg Group, southern Africa (Ellenberger, 1970; see below). However, *Trisauropodiscus* occasionally shows traces of the hallux, which has not been observed in *Eoanomoepus*. Therefore, *Eoanomoepus* is here considered a valid ichnogenus. Comprehensive future studies of early Mesozoic "bird-like" tracks from the Triassic should revise this. Other material from the Rhaetian Tomanova Formation of Slovakia (Niedźwiedzki, 2011), also assigned to *Eoanomoepus* by Lockley et al. (2018), is too poorly preserved to be referred to this ichnogenus with confidence.

Trackmaker: Lockley et al. (2018) suggest a trackmaker with long legs and short wide feet, possibly an ornithischian dinosaur.

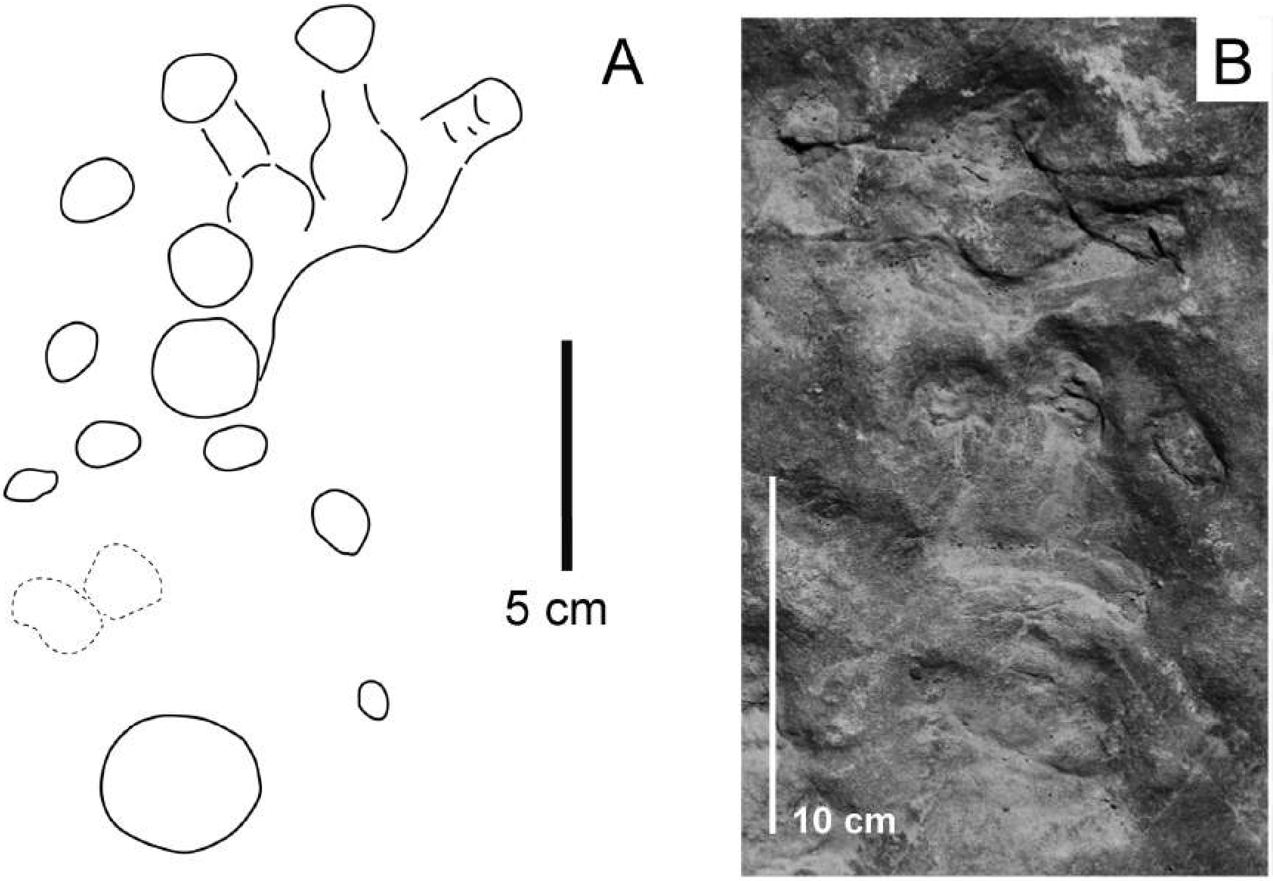


FIGURE 48. *Dolomitipes accordii*. **A,** Interpretive outline drawing of pes-manus set from upper Permian (Lopingian) Val Gardena Sandstone Formation of northern Italy. **B,** Photograph of pes-manus set from Palingkloof Member of Balfour Formation (*Lystrosaurus* Assemblage Zone, Induan) of South Africa. A. From Marchetti et al. (2019a). B. From Marchetti et al. (2019b).

Eosauropus Lockley, Lucas and Hunt, 2006
Figures 49-50

1986 unnamed track: Lockley, fig. 16, pl. I (top left)
1987 *Chirotherium* sp.: Conrad et al., figs. 4, 5B p. 132
1987 unnamed phytosaur tracks: Lockley, fig. 3
1992 ?*Chirotherium* sp., phytosaur trackways: Lockley et al., figs. 5, 7
1993 ?*Tetrasauropus*: Lockley and Hunt, figs. 2-3
1995 ?*Tetrasauropus*: Lockley and Hunt, p. 85-91, figs. 3.13, 3.24
1995 "trackway of a wide-bodied animal": Lockley and Hunt, 1995, fig. 4.4
1996 *Tetrasauropus*: Hunt et al., fig. 7.2
1996 cf. *Tetrasauropus* or cf. *Chirotherium*: Lockley et al., p. 31, fig. 8 left, second from left, p. 33, fig. 10, p. 36, fig. 12 center
2000 *Tetrasauropus*: Lockley et al., p. 11, fig. 4
2000 *Tetrasauropus*-like track: Lockley and Meyer, figs. 4.6, 4.8, 4.14
2001 *Tetrasauropus*: Lockley et al., p. 184, figs. 2B, 3A-B, p. 185, figs 4-5, figs. 1-8
2002 *Tetrasauropus*: Lockley and Peterson 2002, p. 51, inside front cover illustration
2003 unnamed trackway: Nicosia and Loi, figs. 5-6
2005a *Tetrasauropus*: Wilson, fig. 5A, B
2005b *Tetrasauropus*: Wilson, fig 1.12A
2005 *Tetrasauropus*: Wright, fig. 9A-C, G-I
2006a *Eosauropus* Lockley et al., p. 193, figs. 1-6
2006 *Eosauropus*: Lucas et al., p. 115, figs. 5B-C, 8D, 9A
2011 *Eosauropus*: Lockley et al., p. 338-342, figs. 3-9
2017 *Eosauropus* sp.: Lallensack et al., p. 836-837, figs. 2-3

Type ichnospecies: *Eosauropus cimarronensis* Lockley et al., 2006.

Included ichnospecies: Known only from the type ichnospecies.

Distribution: Revueltian-Apachean (Norian) of western USA (New Mexico, Arizona, Colorado, Utah) (Lucas et al., 2006; Lockley et al., 2001, 2006; McClure et al., 2021), Greenland (Jenkins et al., 1994; Sulej et al., 1994; Niedźwiedski et al., 2014; Lallensack et al., 2017), China? (Xing et al., 2018), Italy (Nicosia and Loi, 2003), and United Kingdom (Wales) (Lockley et al., 1996, 2006; Lockley and Meyer, 2000).

Diagnosis: (after Lockley et al., 2006): Narrow-gauge trackway of large quadruped with strong heteropody (pes larger than manus) and short step and stride. Pes elongate, oval, tetradactyl to pentadactyl, with long axis and prominent distal claw impressions rotated outward. Manus transverse, tetradactyl to pentadactyl with outwardly-rotated digit impressions and concave posterior margins.

Description: Narrow-gauge trackway of large quadruped with strong heteropody (pes much larger than manus) and short step and stride. Pes elongate, oval tetradactyl to pentadactyl with long axis and distal claw impressions outwardly rotated. Pes length averages 21.7 cm long and 19.7 cm wide in the holotype trackway. Manus transverse, tetradactyl to pentadactyl,

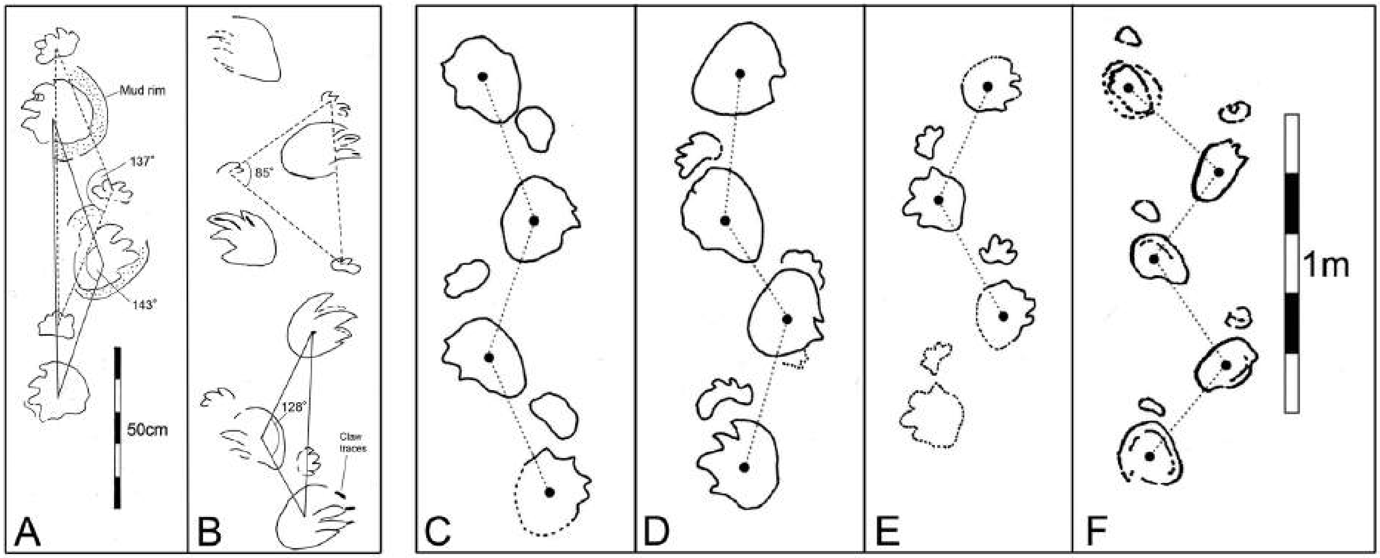


FIGURE 49. *Eosauropus cimarronensis* trackways from different localities in the Chinle Group of North America as sketches. From Lockley et al. (2006).

with outwardly rotated digit impressions and concave posterior margins. Manus averages 7.7 cm long and 12.7 cm wide in holotype trackway. Step and stride short, averaging 46 and 87 cm, respectively, for pes, and 46 and 87 for manus in holotype. Pace angulation 143^{o} and 137^{o}, respectively, for manus and pes in holotype.

Discussion: Moderately-large, problematic tetrapod footprints, made by a large quadruped, from the upper part of the Upper Triassic Chinle Group in western North America, long presented ichnotaxonomic problems and uncertainty about the identity of the trackmaker. In the 1980s they were first tentatively considered to be of chirotherian affinity on the basis of manus morphology, and provisionally labeled *Chirotherium* sp. (Conrad et al., 1987), but from the outset the pes impression was recognized as resembling that of a small sauropod (Lockley et al., 2001, 2006).

In the 1990s the *Chirotherium* label was abandoned, and the South African ichnogenus *Tetrapodosaurus* was tentatively adopted, implying a sauropodomorph affinity for the trackmaker (Lockley and Hunt, 1995; Lockley and Meyer, 2000). However, due to problems surrounding the ichnotaxonomy of this ichnogenus the label was never formally applied or considered satisfactory. Moreover, in the 1990s there were no sauropods known from the Late Triassic, and body fossil evidence diagnostic of sauropodomorphs was sparse or absent in the Chinle Group. In the 2000s, however, Late Triassic sauropod body fossils were documented from southeast Asia (e. g., Buffetaut et al., 2000, 2002), which led to a re-evaluation of the type material of *Tetrasauropus*. The result was that North American "*Tetrasauropus*" (informally referred to by some authors in quotation marks) was the basis of a new ichnogenus named *Eosauropus* (Lockley et al., 2006a). Subsequently, *Eosauropus* has been identified from additional Upper Triassic localities of the USA (Lockley et al., 2011), Greenland (Lallensack et al., 2017), Europe (Lockley et al., 2006a) and China (Xing et al., 2018) (see also Hunt et al., 2018 for overview).

Trackmaker: There is general consensus that sauropodomorphs were the trackmakers of *Eosauropus* (Wilson, 2005b; Wright, 2005; Lockley et al., 2006a; Lallensack et al., 2017; Xing et al., 2018). Wright (2005, p. 262-264,) discussed the trackways later named *Eosauropus* and suggested that despite these Triassic trackways having "been met with a certain amount of skepticism ….These trackways fit the sauropod diagnostic criteria and are most likely to have been made by Late Triassic sauropods [and that] these Triassic sauropod trackways seem not to have been made by basal sauropods such as *Vulcanodon*, but by eusauropods." In a synapomorphy-based analysis of *Eosauropus* trackways from the Upper Triassic of Greenland, Lallensack et al. (2017) showed that features such as the entaxonic semi-digitigrade pes with laterally deflected unguals suggest a sauropodiform, probably eusauropod trackmaker. This supports the early (pre-Jurassic) occurrence of sauropods, which has been confirmed by the discovery of Late Triassic sauropod body fossils (e. g. Buffetaut et al., 2000, 2002).

Evazoum Nicosia and Loi, 2003
Figures 51-52

1992 *Pseudotetrasauropus*: Lockley et al., fig. 2B
1993 *Pseudotetrasauropus*: Lockley and Hunt, 1993, p. 283
1993 *Pseudotetrasauropus*: Hunt et al., p. 201, fig. 3A
1993 *Pseudotetrasauropus* : Farlow and Lockley, fig 5
1996 *Pseudotetrasauropus*?: Lockley et al., fig. 7 (left and center)
1998 *Pseudotetrasauropus*: Cotton et al., p. 145, fig. 4
2000 *Pseudotetrasauropus*: Hunt et al., fig. 1
2000 *Kalosauropus* (cf. *Pseudotetrasauropus*): Lockley and Meyer, fig 4.9
2000 *Pseudotetrasauropus*: Lockley et al., figs. 2, 3 and 5
2001 *Pseudotetrasauropus*: Lucas et al., p. 179, figs. 2D-E, 4A,-C
2001 *Pseudotetrasauropus*: Lockley et al., fig. 2A.
2002 *Pseudotetrasauropus*: Lockley and Peterson, p. 51.
2003 *Pseudotetrasauropus*-like tracks: Gaston et al., fig.8.
2003 *Evazoum* Nicosia and Loi, p. 182, figs. 5-9
2003 *Pseudotetrasauropus*: Rainforth, pl. 1, figs 4-5
2006 *Brachychirotherium* (in part): Klein et al., p. 242, figs. 4F-H, 5B-L, 6, 8
2007 *Pseudotetrasauropus*: D'Orazi Porchetti and Nicosia, fig,. 22b-d
2010 *Evazoum*: Lucas et al., p. 41, figs. 21E-F, H, 22B-F, H-L, 25A, 26

Type ichnospecies: *Evazoum sirigui* Nicosia and Loi, 2003.

Included ichnospecies: The type ichnospecies and *E. gatewayensis* Lockley and Lucas, 2013.

Distribution: Montemarcello Formation (Carnian) of La Spezia (Italy) (Nicosia and Loi, 2003); Chinle Group (Norian-Rhaetian) of western USA (Lockley et al., 2006b; Lucas et al., 2010; Lockley and Lucas, 2013); Hassberge Formation

FIGURE 50. *Eosauropus cimarronensis* holotype from Sloan Canyon Formation (Chinle Group, Upper Triassic) of New Mexico. **A,** Original surface. **B,** Replica of three consecutive pes-manus sets. From Lockley et al. (2006).

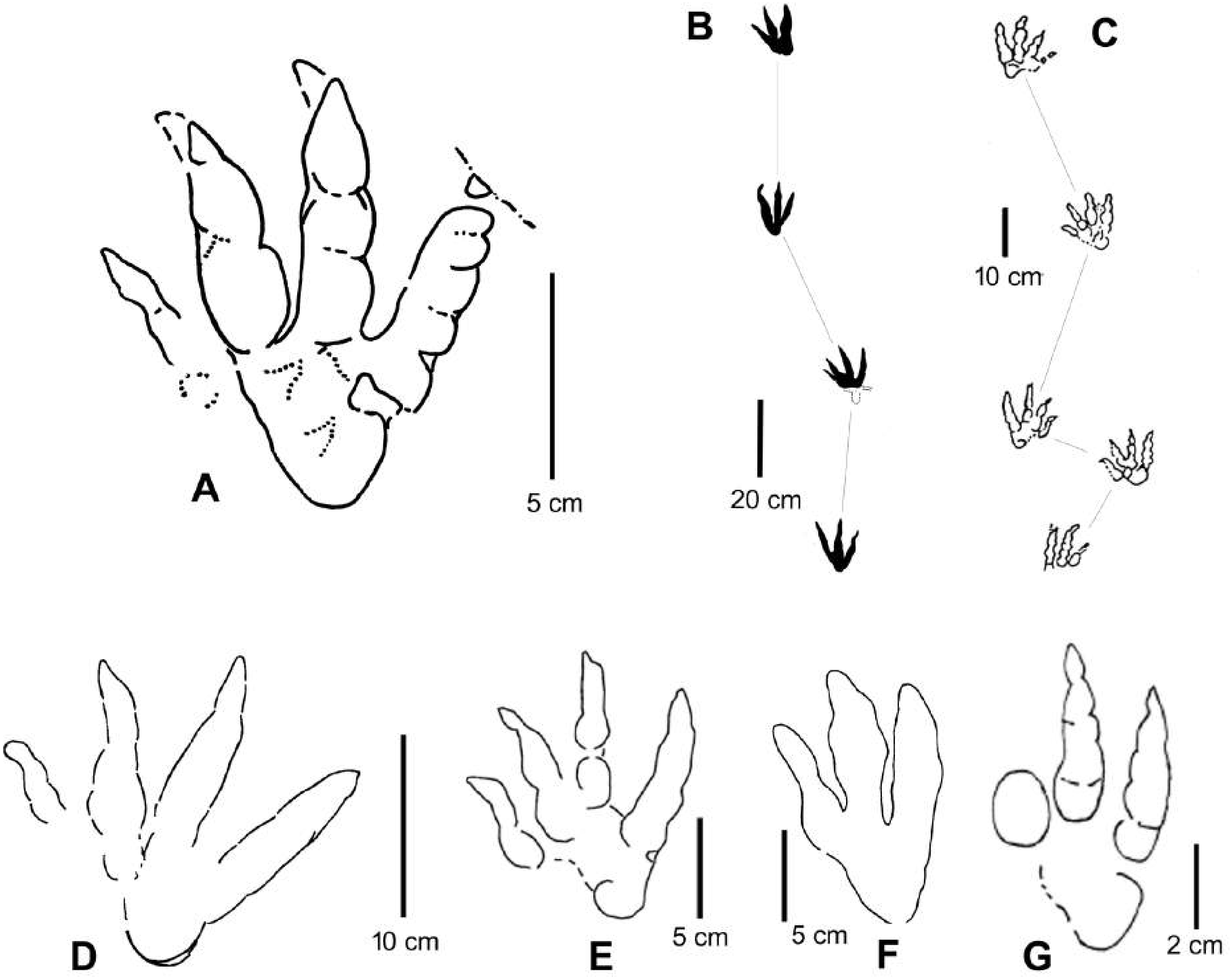


FIGURE 51. Sketches of *Evazoum* tracks and trackways. **A,** *Evazoum sirigui* holotype from Montemarcello Fm. (Carnian) of Italy. **B-F,** From Redonda Fm. (Norian Rhaetian) of New Mexico. **G,** Chinle Group of Colorado. Sketches from Nicosia and Loi (2003), Gaston et al. (2003), Lockley et al. (2006) and Lucas et al. (2010).

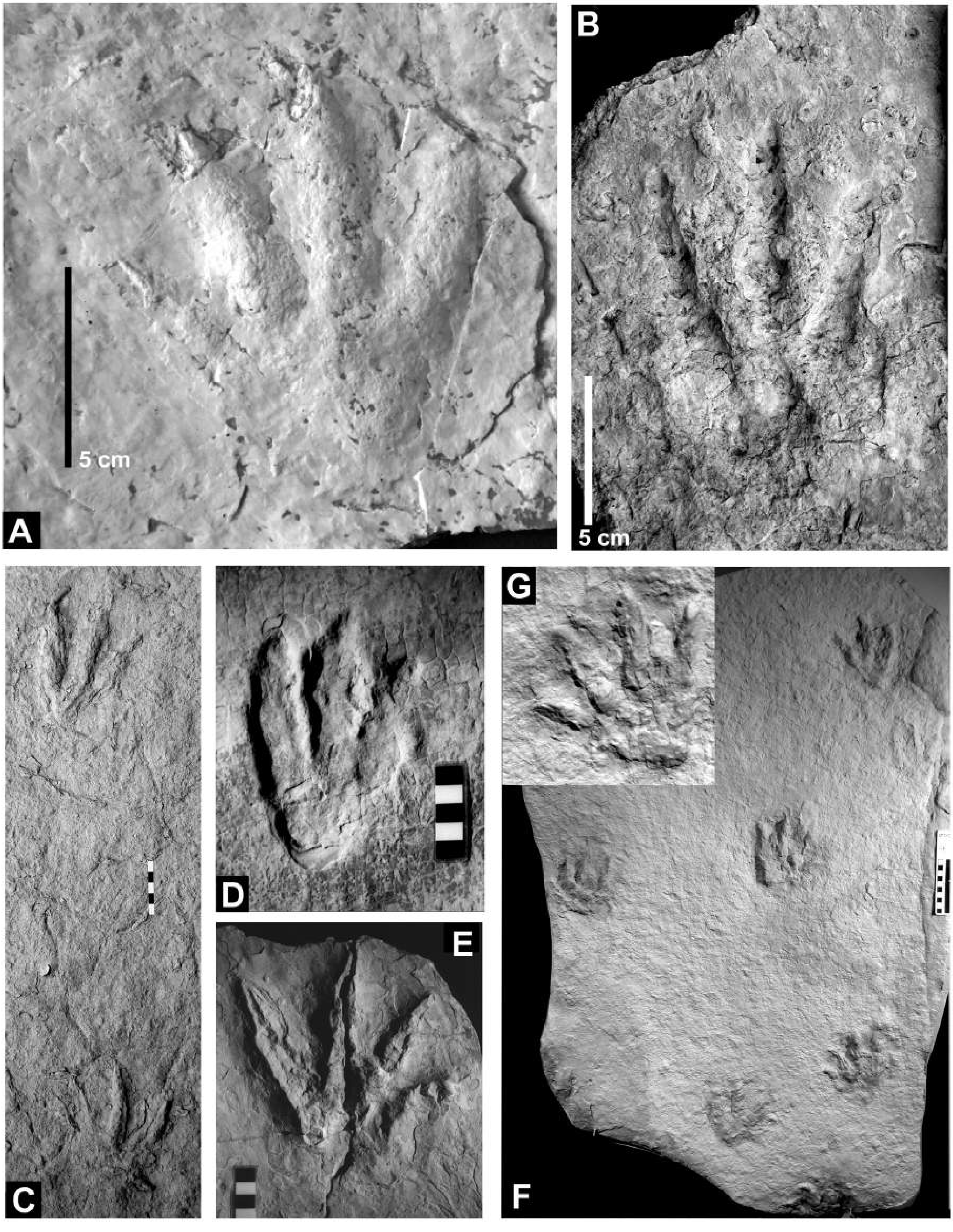


FIGURE 52. Photographs of *Evazoum* tracks and trackways. **A,** *E. sirigui* replica of holotype from Montemarcello Fm. (Carnian) of Italy at Earth Science Department, University of Rome. **B-G,** From Redonda Fm. (Norian-Rhaetian) of New Mexico. **F,** Replica of trackway from Redonda Fm. (Norian-Rhaetian) of New Mexico at Mesalands Dinosaur Museum, Tucumcari, NM. **G,** Detail. B-G. From Lucas et al. (2010).

(Kieselsandstein, Carnian) of southern Germany (Haderer, 2015); Ørsted Dal Formation of Fleming Fjord Group (Norian-Rhaetian) of East Greenland (Lallensack et al., 2017).

Diagnosis (from Nicosia and Loi, 2003): Medium-sized bipedal tetradactyl footprints, ectaxonic to mesaxonic, functionally tridactyl, nearly as wide as long. First digit oriented forward. Digits evenly splayed, giving an overall fan-shaped impression. Rounded metapodial pad below digits III and IV. Second and fourth digits are sub-equal in length, while the third is the longest. Relatively fleshy digits showing well developed pads. Triangular, slightly smooth, long, claw marks on all digits. Trackways variable but with quite wide pace angulation ranging between 140° and 170°.

Description: Trackways with small to medium-sized tri- and tetradactyl pes imprints (functionally tridactyl) with digit III being longest, II and IV being shorter and subequal in length or IV slightly longer than II but longer relative to digit III compared with *Grallator*. Sharp claw marks are present on all digits. Digits II–IV are straight, and digit I is often curved inward. All digits show variably developed phalangeal pads. A distinct metatarso-phalangeal pad is present behind digits II and IV. Trackways have relatively large pace angulations, ranging between 140° and 170°.

Remarks: Nicosia and Loi (2003) described the ichnogenus *Evazoum* based on material from the Upper Triassic (Carnian) of La Lerici, Italy. These are tetradactyl imprints of a biped or facultative biped. Lockley et al. (2006b) re-assigned tri- to pentadactyl imprints and trackways of a biped from the Redonda Formation of the Chinle Group in east-central New Mexico to this ichnogenus. The footprints from New Mexico were formerly assigned to *Pseudotetrasauropus* (see Lockley et al. 2006b; Lucas et al. 2010), an ichnogenus known from the Upper Triassic of southern Africa (Ellenberger 1970, 1972; D'Orazi Porchetti and Nicosia 2007). *Pseudotetrasauropus* are tetra-pentadactyl large imprints of chirothere-like shape. Trackways lack manus imprints. The trackmaker was therefore generally considered as a biped. In contrast with these interpretations, Klein et al. (2006) considered the tracks assigned to *Evazoum* from New Mexico as extramorphological variants of *Brachychirotherium*, because in some cases a transition from typical *Brachychirotherium* to *Evazoum* can be observed. For discussion of ichnotaxonomic problems resulting from these footprints and a justification of the validity of *Evazoum* see Lucas et al. (2010).

Trackmaker: *Evazoum* is generally considered to be the footprint of a prosauropod dinosaur (Lockley et al. 2006b; Lucas et al. 2010), but see D'Orazi-Porchetti et al. (2008) for alternative interpretations.

Gwyneddichnium Bock, 1952
Figures 53-54

1952 *Gwyneddichnium* Bock, p. 417-429, pl. 49, figs. 1-5, pl. 50, fig. 1
1958 *Gwyneddichnium:* Kuhn, p. 20, pl. 11, fig. 10
1963 *Gwyneddichnium*: Kuhn, p. 65
1971 *Gwyneddichnium*: Haubold, p. 48, figs. 29.5-29.6
1986 *Gwyneddichnium*: Baird, p. 134, fig. 7A
1989 *Gwyneddichium*: Olsen and Flynn, p. 31, fig. 20.
1989 *Gwyneddichnium*: Olsen et al., fig. 5.13C
1991 *Gwyneddichium*: Lockley et al., p. 9, figs. 3, 5
1992b *Gwyneddichnium*: Lockley et al., p. 86, figs 1-3
1993 *Gwyneddichnium*: Silvestri and Szajna, p. 140, fig. 3
1995 *Gwyneddichnium*: Lockley and Hunt, p. 95, figs. 3.21-3.22
1996 new ichnotaxon: Cotton et al., p. 56.
2000 *Gwyneddichnium*?: Foster et al., p. 175, fig. 9A-C
2001 *Rhynchosauroides* sp.: Lucas et al., p. 178, fig 3A-B
2001 ?*Gwyneddichnium*: Foster et al., p. 8, fig. 7
2003 *Gwyneddichnium*?: Foster et al., p. 165
2006 *Gwyneddichnium*: Lockley, fig. 4.
2007a *Gwyneddichnium* Hunt and Lucas, p. 216, fig. 2A
2007b *Apachepus* Hunt and Lucas, p. 71, figs. 2-4
2010 *Gwyneddichnium*: Lucas et al., p. 45, figs. 41-43
2014 *Gwyneddichnium*: Lucas et al., p. 138, figs. 2-16
2018 *Gwyneddichnium*: Klein and Lucas, fig. 12E-G

Type ichnospecies: *Gwyneddichnium majore* Bock, 1952 (= *G. elongatum* Bock, 1952; = *G. minore* Bock, 1952; = *Apachepus cottonorum* Hunt and Lucas, 2007b).

Included ichnospecies: Only known from the type ichnospecies.

Distribution: Middle Triassic of Germany; Upper Triassic strata of the Newark Supergroup in the eastern USA (Pennsylvania and New Jersey) and the Chinle Group in the western USA (New Mexico, Colorado and Utah).

Diagnosis (from Lucas et al., 2014): Footprints of a quadruped in which the manus and pes are pentadactyl and mesaxonic, the pes is substantially larger than the manus, digits are thin, long, straight to slightly curved, have nodular phalangeal pad impressions and terminate in claws. Differs from the most similar, lacertoid ichnogenus *Rhynchosauroides* in the digit proportions, with digits III > II ≥ IV > I in *Gwyneddichnium*, whereas in *Rhynchosauroides* the proportions are IV > III > II > I. Also, the digits in *Rhynchosauroides* are thicker and display a greater curvature, whereas the digits of *Gwyneddichnium* are nearly straight or only slightly curved. Digit V in *Rhynchosauroides* is strongly recurved laterally, whereas in *Gwyneddichnium* digit V is often nearly parallel to digit IV.

Description: Lucas et al. (2014) described and illustrated most of the known material of *Gwyneddichnium*, obviating the need for a description here.

Remarks: The distinctiveness of *Gwyneddichnium* as an ichnogenus has never been questioned. The most similar, co-eval ichnogenus, *Rhynchosauroides,* is ectaxonic rather than mesaxonic, and differs in several features, as noted above. A peculiarity of *Gwyneddichnium* appears to be the nodular shape of the phalangeal pads in a relatively widely separated arrangement with thin interpad spaces.

Lucas et al. (2014) revised *Gwyneddichnium,* recognizing one ichnospecies (*G. majore*) as valid. Lockley et al. (1991) drew a distinction between what they considered to be walking and swimming traces of *Gwyneddichnium*. This is the distinction between trackways indicating quadrupedal progression, with separated digits and bipedal (pes only) tracks with interdigital webbing. Lockley (2006, p. 172) claimed that this webbing is "suggestive of an aquatic track maker." Certainly, it suggests an aquatic or amphibious habitus for the trackmaker, but it is possible to question whether the tracks were made while swimming and should be called "swim tracks." The imprint of interdigital webbing could also be left by pressing on the substrate while walking or reflect an incomplete trackway, as only the pes impressions appear to be preserved.

The ichnogenus *Gwyneddichnium* is mostly confined to Upper Triassic strata of the Newark Supergroup (eastern USA) and the Chinle Group (American Southwest). It is widely recognized as a characteristic ichnotaxon of Late Triassic tetrapod footprint ichnoassemblages (e.g., Lucas, 2007). A single occurrence in the Germanic Basin of Germany extends its temporal range back to the Middle Triassic (Lucas et al., 2014; Klein and Lucas, 2018). This is in congruence with the occurrence of tanystropheids, the best candidate trackmaker known from body fossils from Middle and Upper Triassic deposits (see below).

Trackmaker: Originally, Bock (1952, p. 418) inferred that *Gwyneddichnium* was likely made by a trackmaker that was "probably close to the small pseudosuchians." Haubold (1986) adopted a similar, rather generalized position, inferring

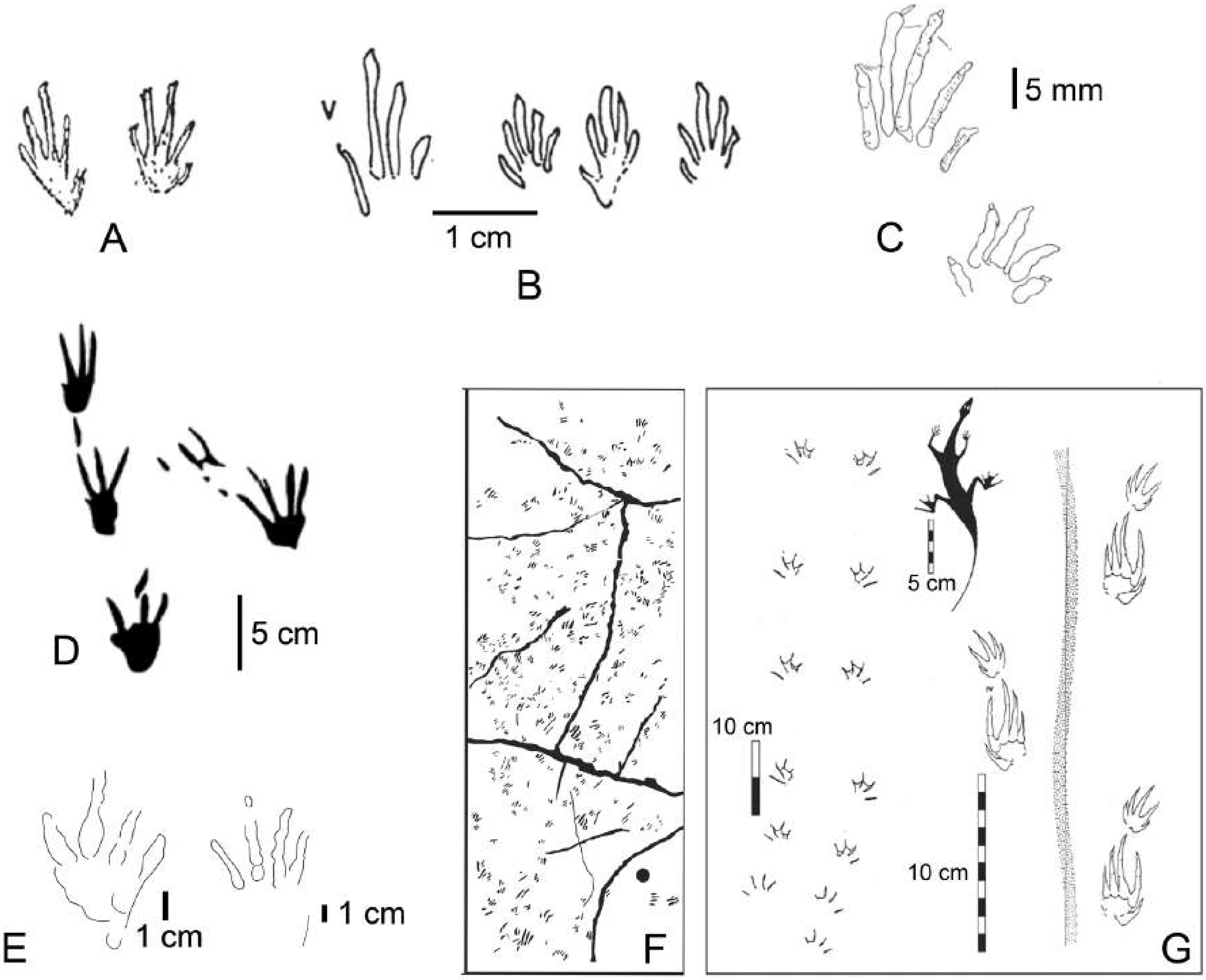


FIGURE 53. Sketches of *Gwyneddichnium majore* tracks and trackways. **A-C,** From Lockatong Fm. of Newark Supergroup, eastern North America. **D,** From Redonda Fm. (Chinle Group, Norian-Rhaetian) of New Mexico. **E,** From Eschenbach Fm. (Middle Triassic, Anisian) of Germany. **F,** Surface with *G. majore* from Lockatong Fm. of Pennsylvania. **G,** Trackway of "swimming" *G. majore* trackmaker (left) vs. trackway of walking individual from Rock Point Fm., Chinle Group of Colorado. All illustrations from Lucas et al. (2014).

that the trackmaker was an undifferentiated pseudosuchian or ornithosuchian. Description of "*Tanytrachelos*" (a synonym of *Gwyneddosaurus*) from the Newark Supergroup by Olsen (1979) based on extensive and articulated material, provided a plausible trackmaker for *Gwyneddichnium*. As Olsen and Flynn (1989) argued, the morphology of the feet of "*Tanytrachelos*" is an excellent match for the footprints assigned to *Gwyneddichnium*.

Lockley (2006) noted that Colbert and Olsen (2001) had implied that drepanosaurs could be possible trackmakers of *Gwyneddichnium* because the body fossils of this group are more common than those of "*Tanytrachelos*." However, given an extensive review of drepanosaur anatomy by Renesto et al. (2010), this suggestion now seems unlikely. A tanystropheid trackmaker is most plausible, even if the question remains, why the extensive footprint record from the marginal marine Middle Triassic Winterswijk locality has no *Gwyneddichnium*, despite the presence of *Tanystropheus* in the bone record (Wild and Oosterink, 1984).

Ichnogenus *Pentasauropus* Ellenberger 1972
Figure 55

1970 *Pentasauropus* [*nomen nudum*] Ellenberger, p. 345, figs. 5, 39, 52-53
1972 *Pentasauropus*, Ellenberger, p. 32, fig. 5, 39, 52-53, pls. 2, 10, 14
1984 *Pentasauropus*, Olsen and Galton, p. 96, fig. 3 G
1995 *Pentasauropus*: Lockley and Hunt, p. 80, fig. 3.10 top
2007 *Pentasauropus*: D'Orazi Porchetti and Nicosia, p. 235, fig. 14, p. 236, figs. 15-17
2019 *Pentasauropus*: Lagnaoui et al., p. 45, p. 48-50, figs. 5-7

Type ichnospecies: *Pentasauropus incredibilis* Ellenberger, 1972

Included ichnospecies: *Pentasauropus argentinae* Lagnaoui et al., 2019.

Distribution: Lower Elliot Formation (Upper Triassic), Lesotho, southern Africa; Cerro de las Cabras Formation, Middle Triassic, Argentina.

Diagnosis (from D'Orazi Porchetti and Nicosia, 2007): *Pentasauropus* is the trackway of a quadruped, with very low

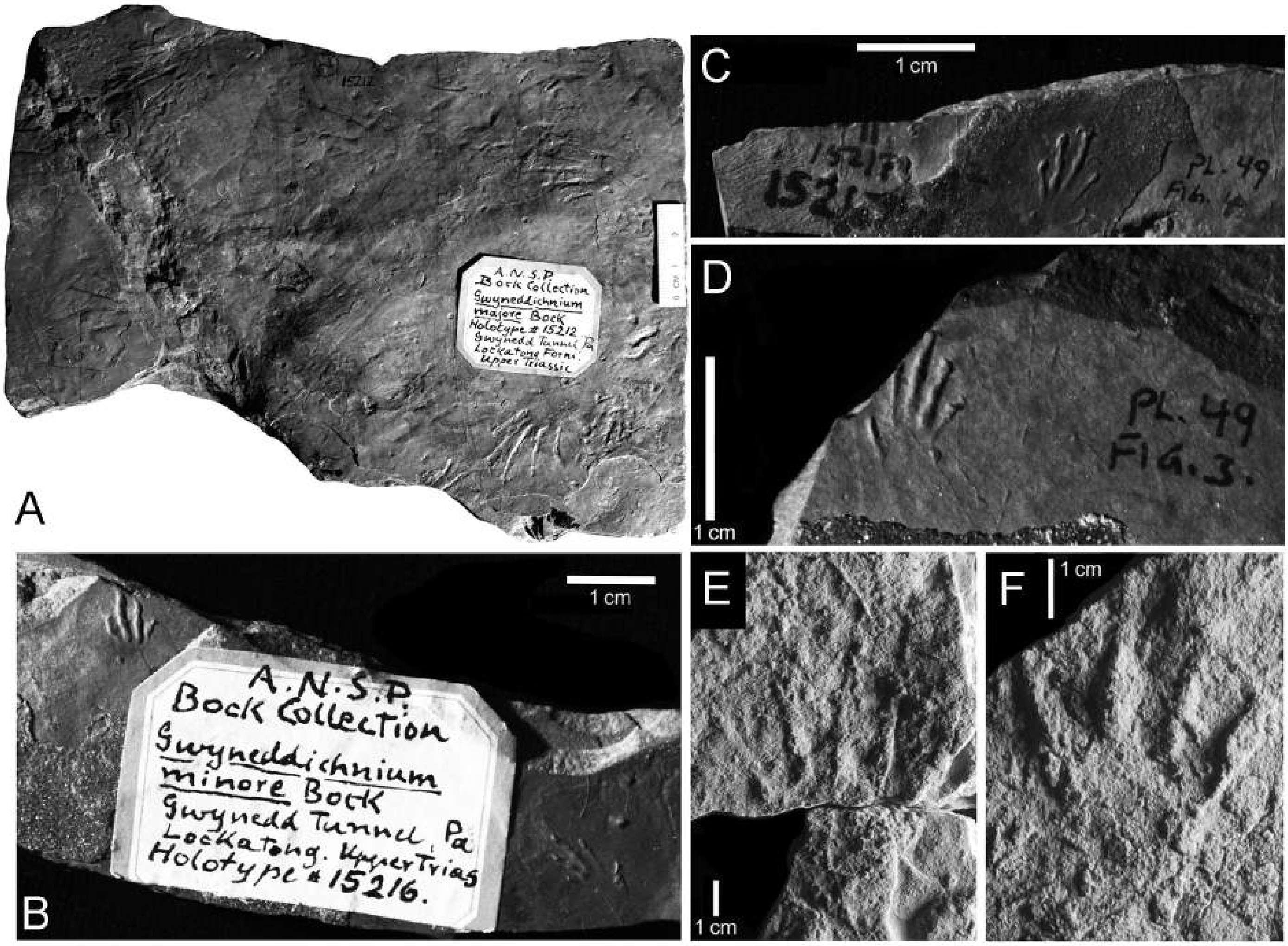


FIGURE 54. Photographs of *Gwyneddichnium majore* tracks and trackways. **A,** Slab with syntypes (lectotype at lower right). **B-D,** holotype and paratypes of *Gwyneddichnium* "*minore*" here considered a synonym of *G. majore*. from Lockatong Formation of Pennsylvania. **E-F,** From Eschenbach Fm. (Middle Triassic, Anisian) of Germany. Photographs from Lucas et al. (2014) and Klein and Lucas (2018).

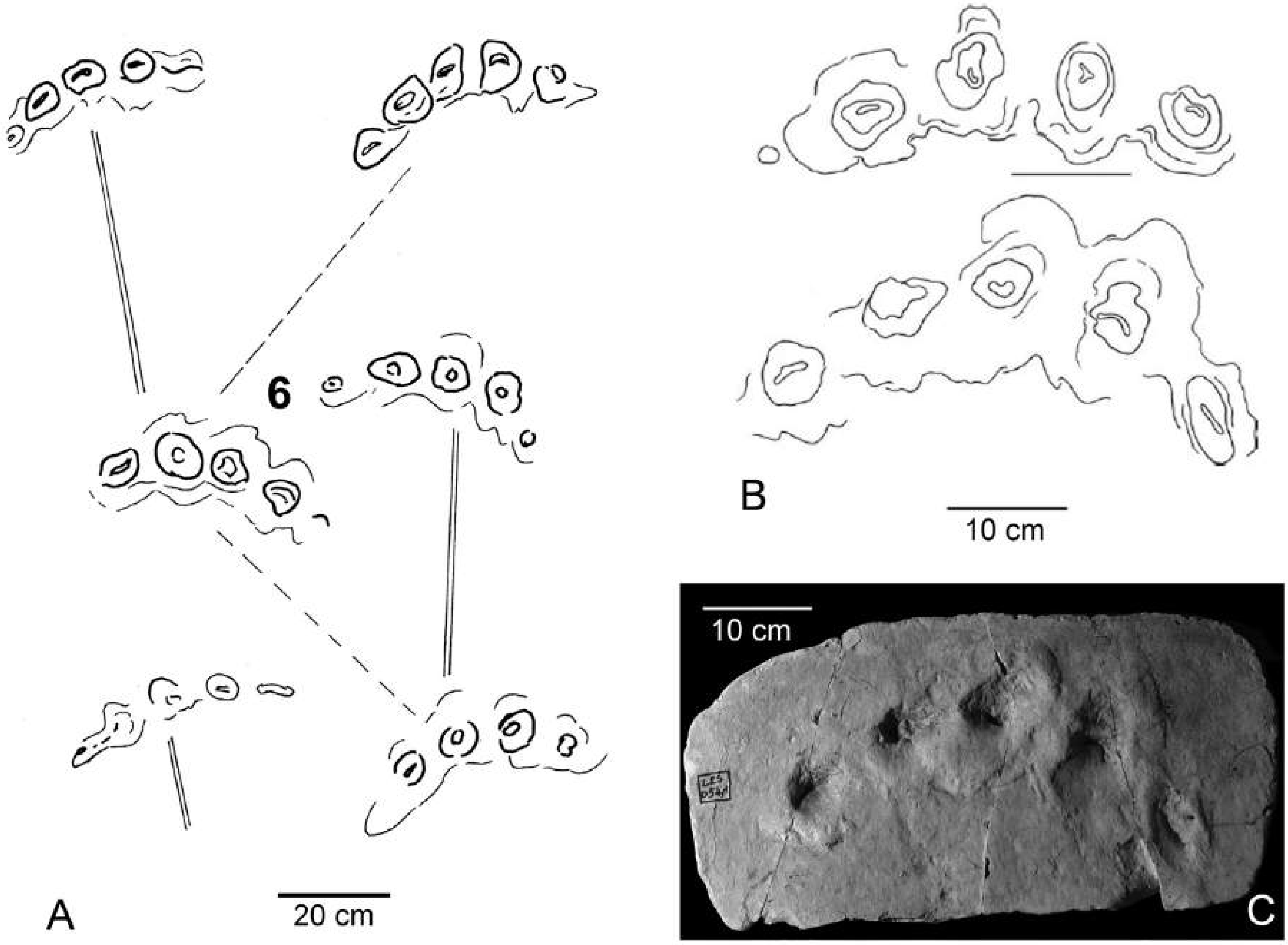


FIGURE 55. *Pentasauropus incredibilis* from lower Elliot Fm. of Lesotho, Southern Africa. **A,** Holotype trackway after Ellenberger (1970, 1972). **B,** Sketch of holotype from D'Orazi Porchetti and Nicosia (2004). **C,** Photograph of holotype courtesy of Simone D'Orazi Porchetti.

heteropody. The track is usually wide, with a reduced pace angulation, and manus and pes axes face forward, or inward. When present the pes sole is rounded. No tail traces are noticed. The main characters shown by this ichnotaxon are five equally spaced traces of digits forming a broad, arcuate pattern that is convex anteriorly.

Description: Trackways of large tetrapods showing low heteropody and short steps. Pentadactyl pes and manus imprints preserved only by distal ends of digits that are arranged in an arc-like pattern.

Discussion: *Pentasauropus* is only known from trackways with pes and manus imprints showing round distal ends of digits and occasionally a faint impression of the sole. It has never been found with complete imprints.

Trackmaker: Ellenberger (1970, 1972) and other authors considered prosauropod sauropodomorphs as the trackmakers of *Pentasauropus*. In recent years, dicynodont therapsids have been discussed, and these seem the most likely producers (D'Orazi Porchetti and Nicosia, 2007; Kammerer, 2018; Lagnaoui et al., 2018).

Ichnogenus *Procolophonichnium* Nopcsa 1923
Figures 56-57

1904 *Procolophon*: Seeley, p. 287–289, fig. 1 A–C
1923 *Procolophonichnium*: Nopcsa, p. 138, pl. VI, fig. 6
1954 non "*Procolophonichnium*"?: Müller, p. 190, fig. 1, pl. 16 (1, 2), tab. 1.
1958 non *Procolophonichnium* (?): Kuhn, p. 34, pl. III, fig. 21 2556
1962 non *Procolophonichnium*: Müller, p. 22, pl. V-VII.
1955 *Procolophonichnium*: Lessertisseur, p. 105, fig. 58e
1958 *Procolophonichnium*: Kuhn, p. 46, pl. IX, fig. 2
1963 *Procolophonichnium*: Kuhn, p. 145, pl. 1, fig. 7, p. 147, pl. 2, fig. 5, p. 155, pl. 6, fig. 36
1970 *Rhynchosauroides*: Holst et al., figs. 2, 7, pl. I, fig. 3, pl. II, figs. 4–6
1971a *Procolophonichnium*: Haubold, pl. III
1971b *Procolophonichnium*: Haubold, p. 30, fig. 19.1.(7)
1977 *Procolophonichnium*: Demathieu, p. 357, fig. 3, pl. 2 (2)
1977 *Circapalmichnus*: Gand, p. 20, 22, pl. D, figs. 1–2, pls. 3–4
1978 *Procolophonichnium*: Demathieu and Müller, p. 157–163, figs. 2–4
1983 *Procolophonichnium*: Demathieu and Oosterink, p. 13, 39, 41–42, 44–46, figs. 8, 33–50
1983 *Phenacopus*: Demathieu and Oosterink, p. 15, fig. 10, p. 16, fig. 12, p. 47, figs. 51–53
1984 *Rhynchosauroides*: Haubold, p. 147, fig. 98 (13)
1984 *Procolophonipus*: Haubold, p. 149, fig. 100(5)
1984 *Circapalmichnus*: Haubold, p. 149, fig. 100(6)

1986 *Procolophonichnium*: Baird, p. 133, figs. 5–6B.
1988 *Procolophonichnium*: Demathieu and Oosterink, p. 13, fig. 6
1988 *Phenacopus*: Demathieu and Oosterink, p. 14, fig. 7A–B
1990 *Rhynchosauroides*: Fuglewicz et al., figs. 9(5–8), 10(1), pls. 8(1–4), 10(1)
2000 *Procolophonichnium*: Ptaszyński, p. 178, fig. 20
2000 *Procolophonichnium*: Diedrich, p. 385, fig.6A–D
2002a *Procolophonichnium*: Diedrich, p. 82, fig. 3D, p. 85, fig. 4
2002b *Procolophonichnium*: Diedrich, p. 45, figs. 8–9
2002c *Procolophonichnium*: Diedrich, pl. II, fig. 9, fig. 7,
2007 *Procolophonichnium*: Valdiserri and Avanzini, p. 113, figs. 8–9
2007 *Circapalmichnus*: Gand et al., p. 16, fig. 6T, pl. 2O
2008 *Dicynodontipus*: Silva et al., p. 102, fig. 3, p. 103, fig. 4, p. 104, fig. 5, p. 105, fig. 6
2010b *Procolophonichnium*: Klein and Lucas, p. 5–6, p. 11, fig. 9A–C
2010 *Procolophonichnium*: Todesco and Bernardi, p. 207, pl. 1
2011 *Procolophonichnium*: Klein et al., p. 227, 9A–D
2012 *Procolophonichnium*: Klein and Niedźwiezki, p. 51, fig. 50C, F, I–J
2015b *Procolophonichnium*: Klein et al., p. 158, figs. 1-9, 10-14, tables 1-3

Type ichnospecies: *Procolophonichnium nopcsai* Kuhn, 1963.

Included ichnospecies: *P. haarmuehlensis, P. nectouxi, P. lockleyi.*

Distribution: Early Triassic Palingkloof Member, Balfour Formation, South Africa; Lower Triassic Wióry Formation, Poland; Middle-Upper Triassic Buntsandstein, Muschelkalk and Keuper, Germanic Basin; Upper Triassic Timezgadiouine Formation (T4) of Morocco; Middle Triassic Holbrook Member of Moenkopi Formation, Arizona; Upper Triassic Passaic Formation, New Jersey.

Diagnosis (after Haubold, 1971a, b, Klein et al., 2015b): Pentadactyl and semiplantigrade to plantigrade asymmetrical footprints of small quadrupeds with digits increasing in length from I–IV; digit IV subequal in length to digit III; digit V subequal in length to digit II. Manus similar in shape but smaller than pes and positioned anterior to or being slightly overstepped by the latter posteriorly. Differs from the most similar tracks of other ichnogenera in the following features: (1) from *Rhynchosauroides* and *Dromopus* by digit proportions, with minor differences of length and relatively longer digit V, and (2) from *Rhynchosauroides*, *Dromopus* and *Varanopus* by proportionately shorter and stouter digits, by (mostly) straight to outward curved digits vs. the strong inward curvature of digits in the latter, and by semi-plantigrade to plantigrade imprints vs. digitigrade to semi-plantigrade imprints observed in these latter ichnotaxa.

Description: Small pentadactyl pes and manus imprints with straight, relatively robust digits and small claws; pes imprints display a short sole that is about 1/3 of total footprint length. Manus imprints slightly smaller than pes imprints. Digits have the proportions IV = III > II = V> I. Trackways are relatively narrow, with imprints of different ichnospecies variously oriented parallel to the trackway midline, or pointing inwardly or outwardly.

Discussion: The ichnogenus *Procolophonichnium* was introduced by Nopcsa (1923), with the type ichnospecies *P. nopcsai* based on material from?Lower Triassic deposits of South Africa. The isolated pes-manus set was originally described by Seeley (1904, 1905).

Unfortunately, the holotype specimen of *P. nopcsai* was destroyed in the Bavarian State Collection of Paleontology, Munich, during World War II. Only a plaster cast is preserved in the Museum of Natural History, London, which was designated as the "plasto-holotype" (Klein et al., 2015b). Other important Triassic occurrences are from the Buntsandstein of Germany (Demathieu and Müller, 1978) and the Muschelkalk (Anisian-Ladinian) of The Netherlands, Germany and France (Gand, 1977, Demathieu and Oosterink, 1983, 1988; Diedrich, 2000, 2002a, b, c). Klein et al. (2015b) revised the ichnogenus, considering four ichnospecies as valid: *P. nopcsai, P. haarmuehlensis, P. nectouxi and P. lockleyi*. The latter was introduced by these authors based on complete trackways from the Hassberge Formation (Coburger Sandstein, Carnian) of Germany. In their revision, Klein et al. (2015b) were aware of some morphological differences that possibly indicate a further ichnotaxonomic differentiation, even at the ichnogenus level. Therefore, it cannot be excluded that future studies will find these four ichnospecies under different new combinations. Against the background that there was limited access and/or loss of some holotype specimens, Klein et al. (2015b) preferred the more conservative approach, assigning all to *Procolophonichnium*.

Trackmaker: Procolophonid parareptiles and/or therapsids (Klein et al., 2015b; Marchetti et al., 2017, 2019b).

Ichnogenus *Prorotodactylus* Ptaszyński 2000

Figures 58-59

2000 *Prorotodactylus*: Ptaszyński, figs. 16 C (in parte), 23D, 27A-B, 28A-E, 29A-D, 30A-D.
2011 *Prorotodactylus*: Brusatte et al., figs. 2f-k, 3a-b.
2013 *Prorotodactylus*: Niedźwiedzki et al., figs. 4-12
2012 *Prorotodactylus*: Fichter and Kunz, figs. 3-6.
2015 *Prorotodactylus*: Fichter and Kunz, p. 259-260, fig. 8.

Type ichnospecies: *Prorotodactylus mirus* Ptaszyński, 2000.

Included ichnospecies: Only the type ichnospecies.

Distribution: Wióry Formation (Olenekian) of Wióry, Poland, Middle Buntsandstein (Detfurth Formation, Olenekian) of Germany (Ptaszyński, 2000; Klein and Niedżwiedzki, 2012; Fichter and Kunz, 2015).

Diagnosis (from Klein and Niedźwiedzki, 2012): Long striding trackways with small, lacertoid, pentadactyl pes and manus imprints. Manus overstepped laterally by the pes. Pes rotated outward and manus rotated inward with respect to the midline. Digitigrade pes with digits I-IV increasing in length, II-IV subparallel and tightly "bunched" with low divarication angle between digits II and IV (≤ 10°). Distinct, straight metatarsal-phalangeal axis forming posterior end of digits II-IV. Digit I everted. Digit V rarely impressed, if present, in a posterolateral postion relative to digits I-IV. Manus semiplantigrade, of chirotheroid shape, compact and rounded with postero-laterally positioned digit V mostly impressed. Digit III always longest, followed by digits IV, II and I, which is shortest.

Description: *Prorotodactylus* has pentadactyl pes and manus imprints with long and slender digits. In the pes imprints, digits increase in length from I–IV; in the manus imprints, digit III is longest, and digit IV is shorter than digit III. Digit V is positioned postero-laterally to I–IV and short. In particular, digits I–IV form a tightly bunched group. Pes imprints are digitigrade, manus imprints are semi-plantigrade to plantigrade and smaller. Trackways show lateral overstep of the manus by the pes.

Discussion: *Prorotodactylus* was first described by Ptaszyński (2000) from the Wiòry Formation (Olenekian) of Poland, where the ichnogenus occurs on the surfaces in mass accumulations, together with numerous chirotheriid footprints. By its overall-shape and by the trackway pattern with the lateral overstep of the manus by the pes, it is similar to *Rhynchosauroides* and *Rotodactylus*. It is different from *Rhynchosauroides*, however, by the short manual digit IV, which is longest in the latter. From *Rotodactylus* it is differentiated by the position of

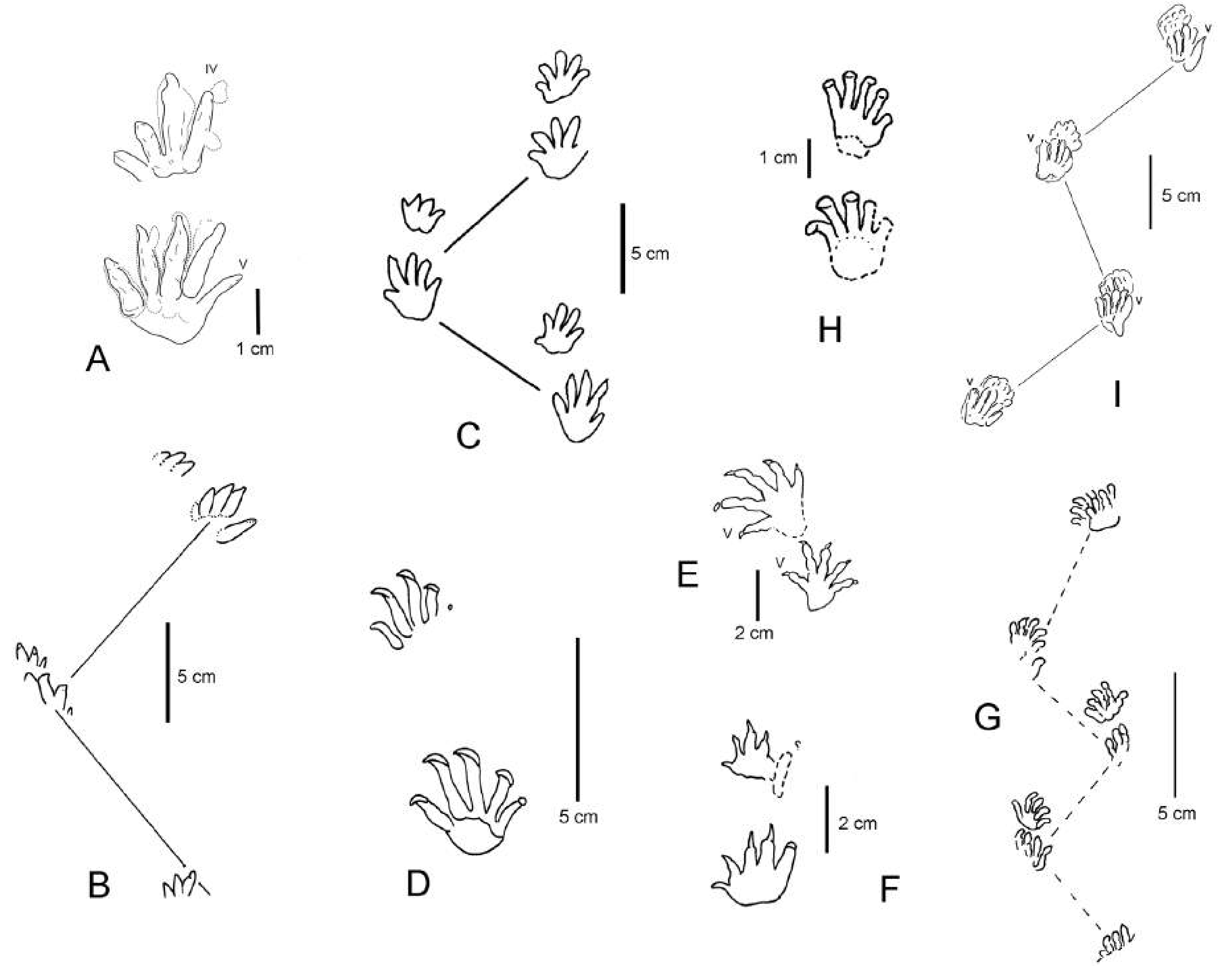
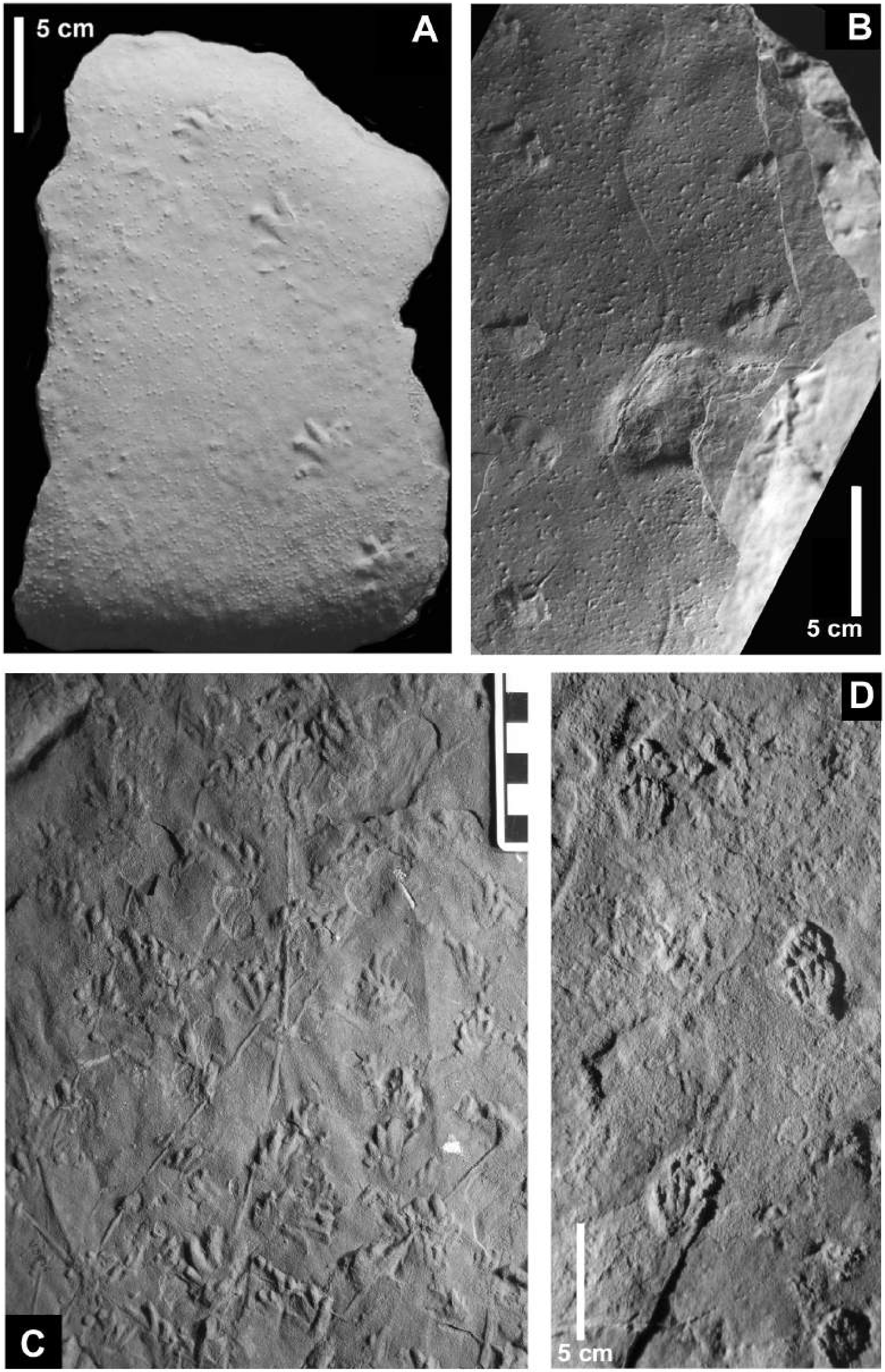


FIGURE 56. *Procolophonichnium* tracks and trackways from different Lower-Upper Triassic localities. **A,** *P. nopcsai* after "plastotype" from Balfour Fm. (Lower Triassic), South Africa. **B,** *P. polonicum* holotype trackway from Wióry Fm. (Lower Triassic), Poland. **C-F,** *P. haarmuehlensis* (E = holotype) from the Lower-Middle Triassic of Germany (C, E) and The Netherlands (D, F). **G,** *P. nectouxi* holotype trackway from Middle Triassic of France. **H,** *P*. isp. from Passaic Fm. (Upper Triassic of New Jersey. **I,** *P. lockleyi* holotype trackway from Hassberge Fm. (Upper Triassic, Carnian) of Germany. Sketches from Klein et al. (2015b).

FIGURE 57. (facing page) Photographs of *Procolophonichnium* trackways. **A-B,** *P. haarmuehlensis* from Vossenveld Fm. (Anisian) of Winterswijk, The Netherlands. **C,** *P. haarmuehlensis* from Wupatki Member of Moenkopi Fm. of Arizona. **D,** *P. lockleyi* from Hassberge Fm. (Carnian) of Germany. Photos in A-B by Henk W. Oosterink.


5 cm
A
B
5 cm
C
D
5 cm

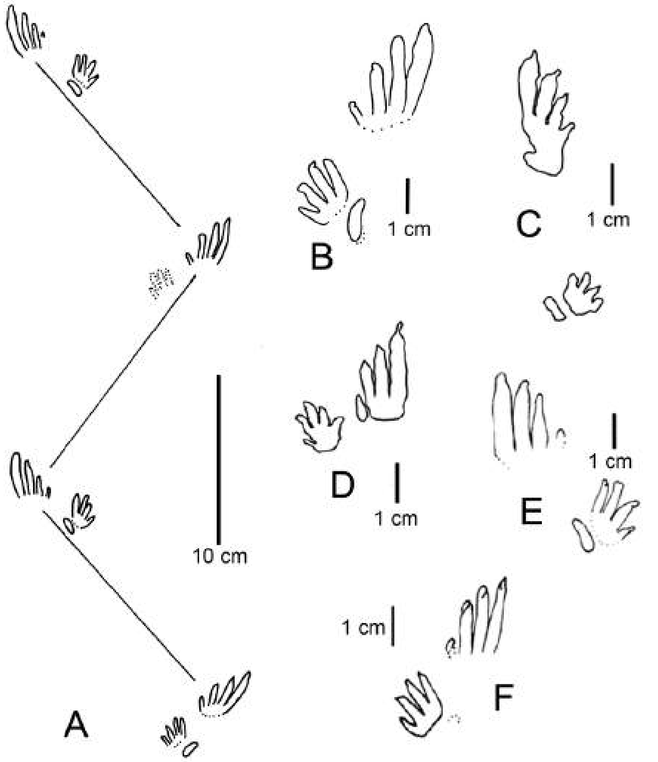


FIGURE 58. *Prorotodactylus mirus* pes and manus imprints from Wióry Fm. (Olenekian) of Poland as sketches. From Klein and Niedźwiedzki (2012).

digit V relative to digit group I–IV, which is at a distance of four times digit IV length in *Rotodactylus*, but relatively short in *Prorotodactylus*, similar to *Rhynchosauroides*.

Trackmaker: Brusatte et al. (2011) and Niedżwiedzki et al. (2013) attributed *Prorotodactylus* to dinosauromorph trackmakers similar to the trackmaker of *Rotodactylus* (Haubold, 1999). However, archosauromorph and even lepidosauromorph trackmakers cannot be excluded (see also discussion in Klein and Niedżwiedzki, 2012). Indeed, given the great similarity of *Protorodactylus* and *Rhynchosauroides* (one of us SGL, considers both genera to be likely synonyms), a lepidosauromorph trackmaker seems most likely.

Pseudotetrasauropus Ellenberger, 1972
Figure 60

1958 Pistes bipe`des te´tradactyles: Ellenberger and Ellenberger, p. 67, fig. K
1964 Pistes d'un animal bipe`de: Ellenberger et al., p. 317, fig. H
1969 Bipedal broad tracks: Ellenberger et al., p. 339, fig. 2G
1970 Pistes apparemment bipe`des: Ellenberger et al., p. 154, fig. 2g
1970 *Pseudotetrasauropus* Ellenberger, p. 345, pl. II, fig. 28
1970 *Pseudotetrasauropus:* Ellenberger, p. 345, pl. II, fig. 34
1971 *Otozoum* sp.: Haubold, p. 85, fig. 52(2)
1972 *Pseudotetrasauropus:* Ellenberger, p. 58, pl. II, fig. 28; pls. V, VII (lower left)
1972 *Pseudotetrasauropus:* Ellenberger, p. 65, pl. (dessins) II, fig. 34; pls. X, XI (upper)
1974 Dinosaurier: Haubold, p. 134, Abb. 84 K.
1984 *Pseudotetrasauropus*: Haubold, p. 172, Abb. 116 1 (second from the upper left)
1984 *Brachychirotherium* sp.: Olsen and Galton, fig. 3A, p. 109
1996 *Pseudotetrasauropus*: Lockley et al., p. 30, fig. 7 (lower right)
2000 *Pseudotetrasauropus*: Lockley and Meyer, p. 81, 87, fig. 4.2 (lower), fig. 4.7
2000 ?*Otozoum*: Lockley and Meyer, p. 87, fig. 4.7
2001 *Pseudotetrasauropus:* Lockley, et al., p. 183, fig. 1F, H-I
2003 *Pseudotetrasauropus:* Rainforth, p. 825, fig. 2
2007 *Pseudotetrasauropus*: D'Orazi Porchetti and Nicosia, p. 227, figs. 7-13

Type ichnospecies: *Pseudotetrasauropus bipedoida* Ellenberger, 1972.

Included ichnospecies: The type ichnospecies *Pseudotetrasauropus bipedoida* Ellenberger, 1972, and *P. grandcombensis* (Gand et al., 2000), and "*P. lehmani*" Ellenberger, 1970.

Distribution: Lower Elliot Formation (Upper Triassic), Lesotho, southern Africa; ?Upper Triassic, southwestern France; ?Upper Triassic Hauptdolomit and Kössen formations of Switzerland.

Diagnosis (after D'Orazi Porchetti and Nicosia, 2007): Trackway of a biped of large dimensions, digitigrade. Four straight digits impressions anteriorly oriented. A clear basal pad, related to the presence of a fifth digit, always present on the rear margin, slightly on the external border. Digits almost completely separated along their length. Foot axis orientation slightly variable, ranging from inward to outward.

Description: Large tetradactyl-pentadactyl footprints of a biped showing straight, anteriorly oriented digits with rounded distal ends. Digit V, if present, preserved with a basal pad only, and positioned in line with digit IV. In the anterior digit group, Digit III is longest, followed by II, IV and I, which is shortest. Claws are indistinct, if preserved at all. Trackways with pes imprints that are rotated inward or outward and with relatively short steps.

Discussion: Ellenberger (1972) originally described *Pseudotetrasauropus* from the Lower Elliot Formation of Lesotho (southern Africa). The ichnogenus was also identified from the Chinle Group (Late Triassic) of New Mexico (see Lockley et al., 2006 and Lucas et al., 2010 for ichnotaxonomic overview), however, specimens from this latter region were later referred to *Evazoum* (see above). Other possible occurrences are in the Upper Triassic of southwestern France (Ellenberger 1965; Ellenberger et al. 1970; Gand et al. 2000; see also Rainforth 2003). Olsen and Galton (1984) considered *Pseudotetrasauropus* as a bipedal *Brachychirotherium*. The similarity of pes imprints to *Brachychirotherium* based on the digit proportions is remarkable, however, *Brachychirotherium* is clearly the footprints of a quadruped. D'Orazi-Porchetti and Nicosia (2007) confirmed *Pseudotetrasauropus* as a valid ichnogenus. Because of morphological similarities of *Pseudotetrasauropus* and other ichnogenera such as *Otozoum*, *Evazoum* and *Kalosauropus* Lockley et al. (2006b) proposed to include these tracks in the so-called OPEK plexus.

Trackmaker: *Pseudotetrasauropus* is mostly interpreted as a sauropodomorph (footprint Lockley and Hunt, 1995; Lockley and Meyer, 2000), which, for example, could have been made by prosauropods such as plateosaurids.

Rhynchosauroides Maidwell, 1911
Figures 61-63

1911 *Rhynchosauroides*: Maidwell, p. 141, 143, pls. 4, 6, fig. 1
1915 *Ichnites*: Fucini, p. 60, pl. 10, fig. 16
1923 *Pontopus*: Nopsca, p. 141
1941 *Rhynchocephalichnus*: Huene, pl. VI, fig. 4, pl. VII
1942 *Eurichnus* Lull, p. 50, fig. 2, pl. 1, fig. 3B
1957 *Rhynchosauroides*: Baird, p. 494
1958 *Rhynchosauroides*: Kuhn, p. 19
1958 *Eurichnus*: Kuhn, p. 14
1963 *Eurichnus*: Kuhn, p. 25

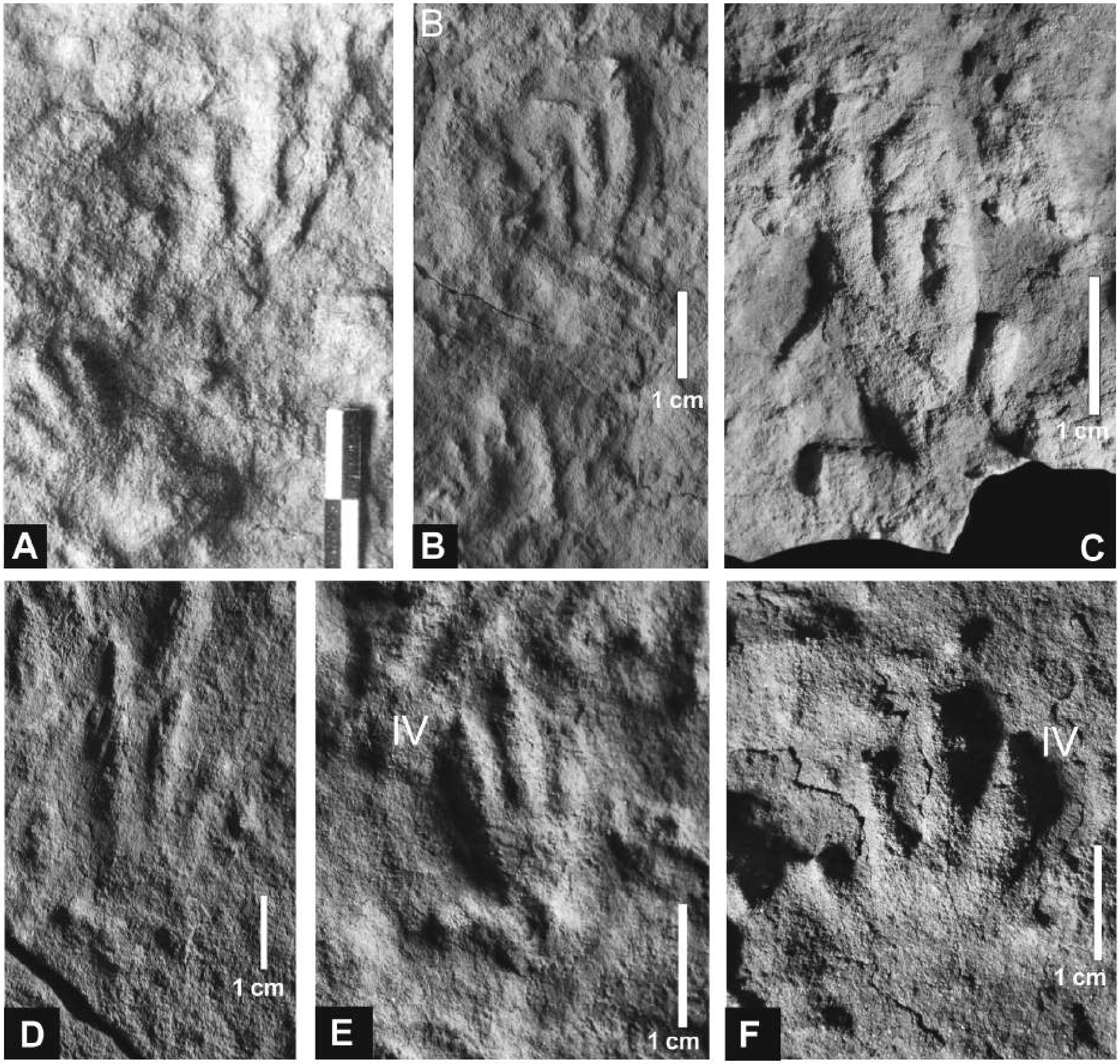


FIGURE 59. Photographs of *Prorotodactylus mirus* footprints from Wióry Fm. (Olenekian) of Poland. From Klein and Niedźwiedzki (2012).

1963 *Rhynchosauroides*: Kuhn, p. 61
1971 *Rhynchosauroides*: Haubold, p. 45-46
1994 *Rhynchosauroides*: Lucas, p. 105, fig. 2B-C
2001 *Rhynchosauroides*: Lucas et al., p. 178, fig. 2A.
2001 non *Rhynchosauroides*: Lucas et al., p. 2001, fig. 3A-B
2006 *Rhynchosauroides*: Klein et al., p. 246, fig. 11A
2007 *Rhynchosauroides*: Hunt and Lucas, p. 216, fig. 2B, table 1
2010 *Rhynchosauroides*: Lucas et al., p. 45, figs. 44-46
2018 *Rhynchosauroides*: Klein and Lucas, p. 173, fig. 11
2019b *Rhynchosauroides*: Marchetti et al., p. 155, fig. 7C-D

Type ichnospecies: *Rhynchosauroides rectipes* Maidwell, 1911.

Included ichnospecies: *R. pallini*, *R. schochardti*, *R. tirolicus*, *R. hyperbates*

Distribution: Upper Permian, Triassic, Upper Jurassic of Europe; Triassic of North America, South America (Argentina, Brazil), North Africa (Morocco), Palingkloof Member, Balfour Formation (Induan) of South Africa.

Diagnosis: Lacertoid ectaxonic footpints of a quadruped; broad trackways with lateral overstep of the manus by the pes. Pace angulation 70°-125°, depending on the velocity. Manus medially positioned relative to the pes. Pes slender and digitigrade; the smaller manus is more stout and more plantigrade. Length of digits increases from I to IV; digit V much shorter. Digits I-IV usually curved inward.

Description: Relatively broad trackways of a small quadruped with low pace angulation (70°–130°). In most cases, the pes oversteps the manus laterally, however, the position of the manus anterior to the pes is also known from some trackways. This variability of the trackway pattern is obviously controlled

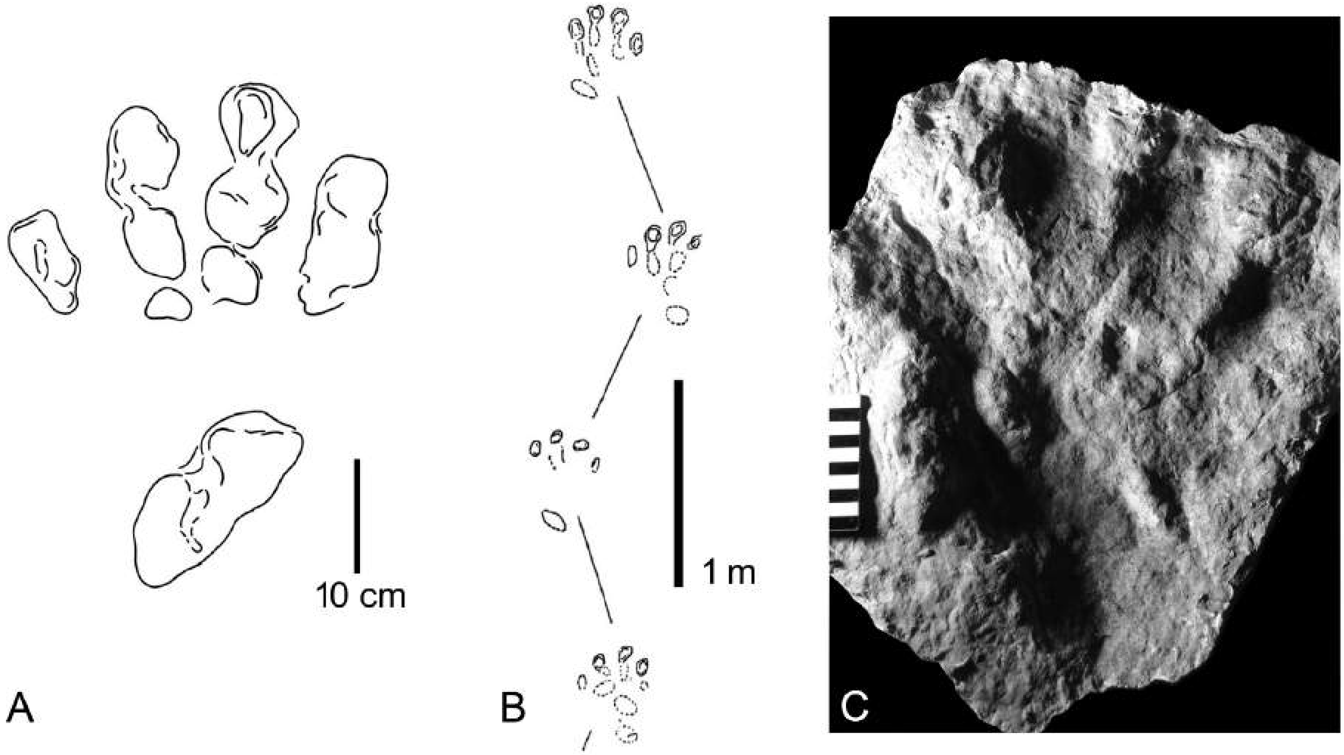


FIGURE 60. *Pseudotetrasauropus bipedoida* holotype from lower Elliot Fm. (Upper Triassic, Norian) of Lesotho, Southern Africa. **A,** Sketch of pes imprint. **B,** Trackway. **C,** Photograph of pes imprint. Sketches from D'Orazi Porchetti and Nicosia (2004).

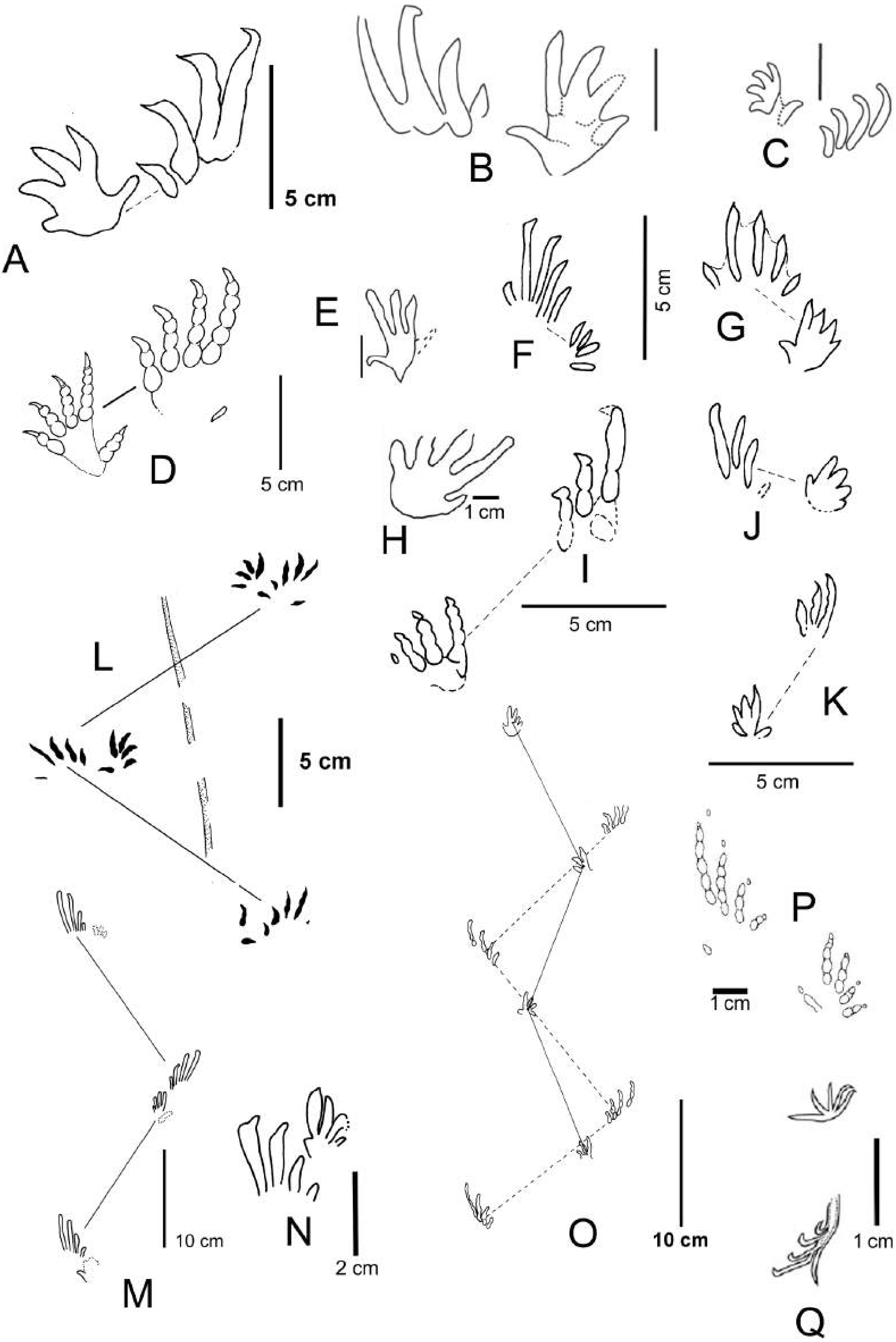
by the velocity of movement. The pentadactyl pes imprints are digitigrade. They show long and very slender digits that increase in length from I through IV, with digit IV being the longest. Digits are often curved inward. Tiny, sharp claws are present on all digits. Digit V, if preserved, is positioned posterolateral to the other digits and short. The manus is similar in shape, but shorter and rather semi-plantigrade or plantigrade. Well-preserved specimens show rounded pads and impressions of the scales. Occasionally, tail drag marks are preserved (Haubold, 1966, 1971a, b; Klein and Niedźwiedzki, 2012).

Discussion: *Rhynchosauroides* has long been a form genus for Triassic lacertoid tracks (e.g., Baird, 1957, p. 498). Currently, there are numerous named Triassic ichnospecies of *Rhynchosauroides*, many of these of doubtful validity, and the ichnogenus is in dire need of revision. *Rhynchosauroides* tracks also are known from the upper Permian and Lower Jurassic (e.g., Cassinis and Santi, 2005; Valentini et al., 2007; Avanzini et al., 2010; Marchetti et al., 2019a). Triassic records are from North America, South America and Europe (e.g., Baird, 1957, 1964; Haubold, 1971a, b, 1984; Lucas and Sullivan, 2006; Avanzini and Renesto, 2002; Melchor and De Valais, 2006). *Rhynchosauroides* is usually attributed to Beasley in Maidwell (1911), with the type ichnospecies identified as *Rhynchosauroides rectipes* (see above). However, Owen (1842) first referred to tracks of this morphology using the osteological binomen *Rhynchosaurus articeps*. Also, Pohlig (1893) used the footprint binomen *Protritonichnites sublacertoides* for Triassic lacertoid tracks, although he had previously used this ichnogenus to apply to Permian lacertoid tracks now assigned to *Dromopus*. Therefore, there may be some question as to the proper name and authorship of the ichnotaxon normally referred to as *Rhynchosauroides rectipes*.

Pending a much-needed revision of all the ichnospecies of *Rhynchosauroides,* we reiterate some of the observations of Hunt and Lucas (2007). There are different sizes of *Rhynchosauroides* ichnospecies, some with pes lengths greater than 50 mm and smaller representatives, several less than 30 mm. The larger Triassic ichnospecies 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 few specimens from the Brunswick Formation of New Jersey. This ichnotaxon is now known from exquisitely preserved specimens (e.g., Olsen, 1988, fig. 8-8), and, together with *R. tirolicus* and *R. peabodyi*, these are the best known of the *Rhynchosauroides* ichnospecies.

FIGURE 61. Sketches of *Rhynchosauroides* footprints from different localities and units. **A-B,** *R. schochardti* from Solling Fm. (Middle Triassic, Anisian) of Germany and from Holbrook Member of Moenkopi Fm. (Anisian) of Arizona. **C,** From Wupatki Member of Moenkopi Fm. of Arizona. **D,** *R. peabodyi* from Vossenveld Fm. (Anisian) of The Netherlands. E., *R.* isp. from Timezgadiouine Fm. (T5, Carnian) of the Argana Basin, Morocco. **F-G,** *R. rectipes* from Middle Triassic (Anisian) of Great Britain. **H,** *R.* isp. from Timezgadiouine Fm. (T5, Carnian) of the Argana Basin, Morocco. **I,** *R. hyperbates* from Passaic Fm. (Norian) of Eastern North America. **J,** *R. franconicus* from Keuper (Upper Triassic) of Germany. **K,** *R. petri* from Middle Triassic of France. **L,** *R. palmatus* from Red Peak Fm. (Olenekian) of Wyoming. **M,** *R. rdzaneki* from Wióry Fm. (Olenekian) of Poland. **N,** *R. brevidigitatus* from Wióry Fm. (Olenekian) of Poland. **O-P,** *R. tirolicus* from Middle Triassic of the Southern Alps, northern Italy. **Q,** *R. retroversipes* from Santa Maria Formation (Upper Triassic) of Brazil. Sketches from Baird (1964), Haubold (1971a, 1984), Avanzini and Renesto (2002), Silva et al. (2008), Klein and Lucas (2010b), Klein and Niedźwiedzki (2012) and Lagnaoui et al. (2012).


A
5 cm
B
C
E
F
5 cm
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D
5 cm
H
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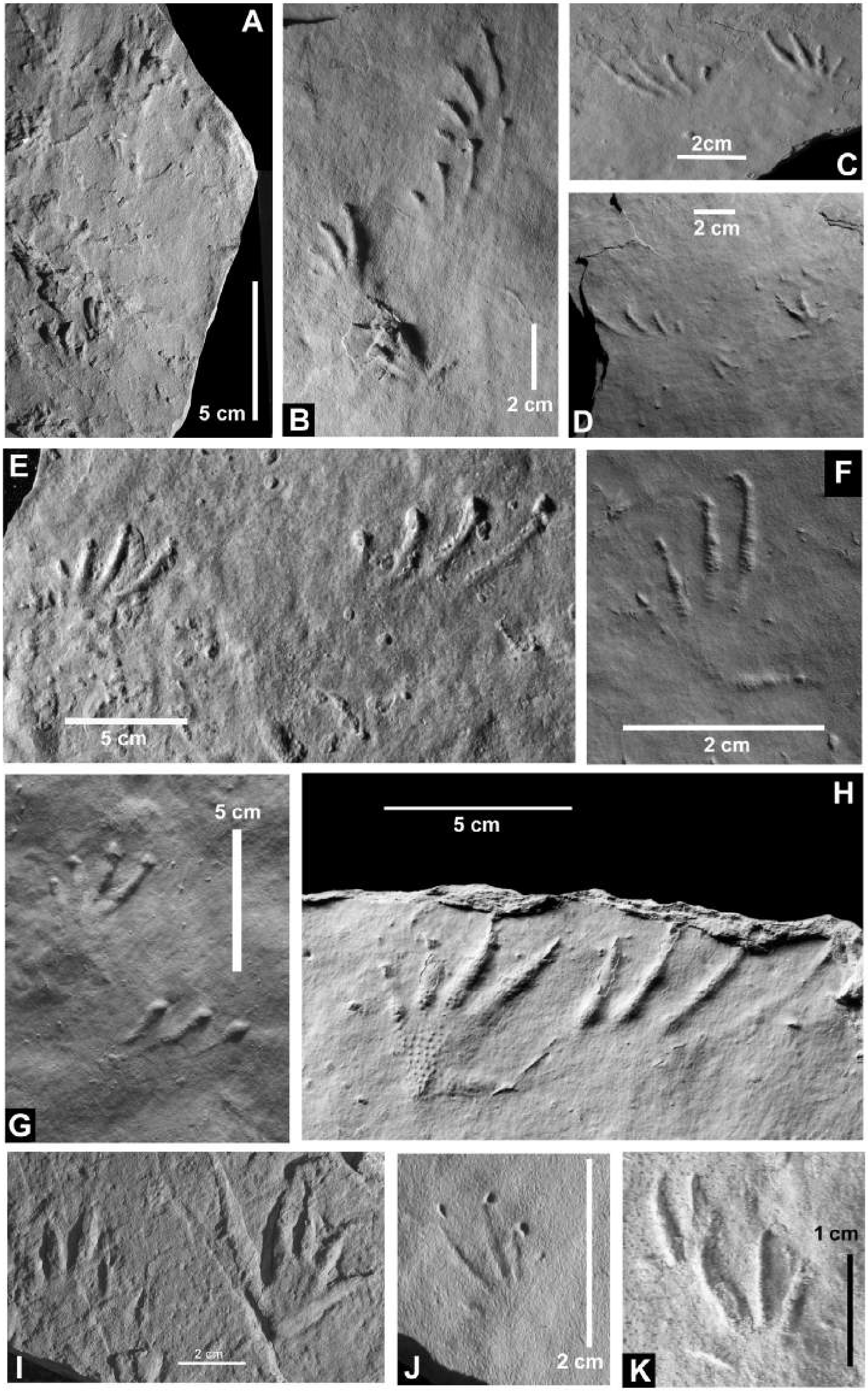

FIGURE 62. Photographs of *Rhynchosauroides* footprints from different localities and units. **A,** *R. brevidigitatus* from Wióry Fm. (Olenekian) of Poland. **B-G,** *R. tirolicus* from Middle Triassic of the Southern Alps, Northern Italy. **H,** *R. peabodyi* from Vossenveld Fm. (Anisian) of The Netherlands. **I,** *R.* isp. from Timezgadiouine Fm. (T5, Carnian) of the Argana Basin, Morocco. **J-K,** R. isp. from Redonda Fm. (Chinle Group, Norian-Rhaetian) of New Mexico.

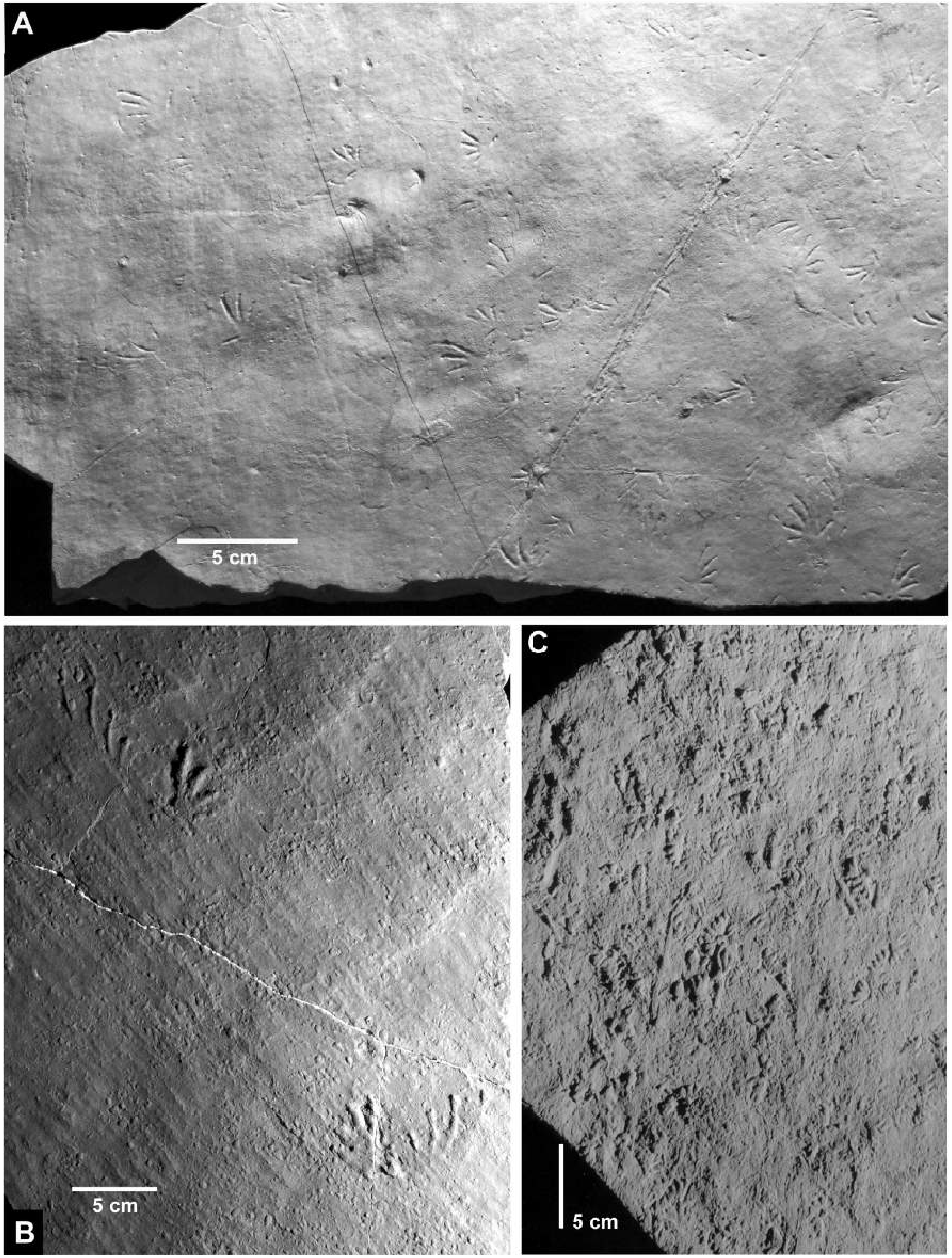

FIGURE 63. Photographs of *Rhynchosauroides* footprints from different localities and units. **A-B,** *R. tirolicus* from the Middle Triassic of the Southern Alps, Northern Italy. **C,** *R.* isp. from Benk Fm. (Ladinian) of Germany.

Rhynchosauroides specimens demonstrate a wide range of extramorphological variation including differences in overall size, relative position and orientation of the manus and pes imprints, divarication of the digit impessions (particularly the digit V impression) and curvature of the digit impressions (Baird, 1964). In many trackways the manus impressions are weakly imprinted or unrecognizable, and drag marks extend the length of the digit impressions (Baird, 1964). Silva et al. (2008) describe a new ichnospecies *R. retroversipes*, based on trackways with a backward-oriented pes imprint, from the Upper Triassic Santa Maria Formation of Brazil. Based on this wide range of variation, it is likely that many named ichnospecies of *Rhynchosauroides* are actually synonymous, for example the large Middle Triassic ichnospecies *R. tirolicus* Abel, 1926, *R. peabodyi* (Faber, 1958) and *R. moenkopiensis* Haubold, 1971a from Europe and North America. Avanzini and Renesto (2002), however, 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 digit impression V. Nevertheless, we believe that these two characters are subject to extramorphological variation. Other ichnotaxonomically important characters in *Rhynchosauroides* include the size of the manus imprint relative to the pes (i.e., heteropody; for example, *R. rectipes* has a relatively small manus and *R. hyperbates* has a relatively large one).

Clearly, there is a need for much more ichnotaxonomic work on *Rhynchosauroides*. Thus, we take the very conservative course here of referring all small Triassic lacertoid tracks to *Rhynchosauroides* ichnosp. and do not attempt to make further ichnotaxonomic distinctions.

Rhynchosauroides footprints often occur on trampled surfaces in mass accumulations, together with scratch marks of the same trackmaker. They have been documented from the majority of Triassic footprint assemblages in the global record, often associated with archosaur footprints such as chirotheres or grallatorids. In some marginal marine associations, for example, in the Middle Triassic tidal flat deposits of the Muschelkalk (Anisian-Ladinian) of the Germanic Basin, they are the dominant tetrapod footprints (Demathieu and Oosterink 1983; Diedrich 2008). However, in the Late Triassic they are less abundant, only occasionally being frequent, for example at some Newark Supergroup and Chinle Group localities.

Trackmaker: Contrary to the name given by Maidwell (1911), *Rhynchosauroides* cannot be attributed to rhynchosaurs, instead being the footprints of lepidosauromorph and/or archosauromorph trackmakers (Avanzini and Renesto, 2002). Their long stratigraphic range, with the oldest record known from the late Permian of northern Italy (Conti et al., 1977; Marchetti et al., 2019a), and the youngest from the Late Jurassic of Spain (Avanzini et al., 2010), suggests different trackmakers with similar foot morphologies.

Ichnogenus *Rotodactylus* Peabody 1948
Figures 64-65

1948 *Rotodactylus*: Peabody, p. 325, p. 328, fig. 18, p. 335, fig. 19, pl. 30-32
1967 *Rotodactylus*: Haubold, p. 21, figs. 3-4
1973 *Rotodactylus*: Demathieu and Gand, pl. III-V
1974b *Rotodactylus*: Gand, pl. 6-7
1974 *Rotodactylus*: Demathieu and Gand, figs. 1-8
1975a *Rotodactylus*: Gand, pl. 3-4
1975b *Rotodactylus*: Gand, pl. 3D-F
1976b *Rotodactylus*: Gand, pl. 4D-H
1977b *Rotodactylus*: Gand, p. 36, pl. 10
1981a *Rotodactylus*: Demathieu and Gand, p. 15, pl. IV, fig. 20
1981b *Rotodactylus*: Demathieu and Gand, p. 24, pl. VIII, fig. 14
1986 *Rotodactylus*: Demathieu and Gand, p. 27, fig. 5I-J, R,U
2004 *Rotodactylus*: Kotański et al., p.91, fig. 2, p. 93, fig. 4, p. 94, fig. 5
2005 *Rotodactylus*: Gand and Demathieu, p. 728, fig. 3 (8-11)
2010b *Rotodactylus*: Klein and Lucas, p. 14-22, figs. 12-20

Type ichnospecies: *Rotodactylus cursorius* Peabody 1948.

Included ichnospecies: *R. matthesi*, *R. bradyi.*

Distribution: Lower-Middle Triassic of Arizona and Utah (Moenkopi Formation/Group); Germany (Detfurth, Solling, Eschenbach formations); Grés des Lyonnais of France; Poland (Wióry Formation),; Morocco (Timezgadiouine Formation, T4, AnisianLadinian), Algeria (Haizer-Akouker unit, Middle Triassic).

Diagnosis (after Peabody, 1948; Haubold, 1971a; Klein and Lucas, 2010b; Klein and Niedźwiedzki, 2012): Moderately narrow trackways. Pes digitigrade with dominance of digit group II-IV and an extreme, posteriorly positioned, small, punctiform mark that constitutes the impression of digit V. Manus similar to pes, but much smaller. The digit proportions are I<II<III<IV, in the manus of some ichnospecies I<II<IV<III. 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.

Description: Digits I–IV are mostly straight and show a parallel orientation, with a compact, tightly bunched digit group II–IV, in which digit IV in the pes is longest. Digit V is only preserved with a small rounded mark behind digit group I–IV and in line with digit IV, at a distance of about four times digit IV length.

Discussion: In some cases, *Rotodactylus* can be confused with *Rhynchosauroides*. Both ichnogenera are lacertoid, ectaxonic, small tracks with trackways showing lateral overstep of the manus by the pes. However, *Rhynchosauroides* footprints have digits that are more spread out, when compared with those of *Rotodactylus*. Also, in the former, digit V is positioned closer to the anterior digit group I–IV, whereas in *Rotodactylus* it lies far posterior.

Trackmaker: Haubold (1999) presented a convincing correlation of *Rotodactylus* with the feet of *Lagerpeton*-like dinosauromorphs.

Ichnogenus *Tetrasauropus* Ellenberger 1972
Figures 66-67

1970 *Tetrasauropus* [*nomen nudum*] Ellenberger, p. 345, figs. 35-38
1972 *Tetrasauropus* Ellenberger, p. 67, fig. 35-38, pls. 6, 7, 8
1984 *Tetrasauropus*: Olsen and Galton, p. 96, fig. 3E
1996 *Tetrasauropus*: Lockley et al., p. 36, fig. 12 left
2001 *Tetrasauropus*: Lockley et al., p. 183, fig. 1 A

Type ichnospecies: *Tetrasauropus unguiferus* Ellenberger 1972.

Included ichnospecies: Only the type ichnospecies is valid.

Distribution: Lower Elliot Formation (Late Triassic) Lesotho, southern Africa and ?Hauptdolomit-Kössen formations (Late Triassic) of Switzerland.

Diagnosis (from D'Orazi Porchetti and Nicosia, 2007): Large-sized quadrupedal track, plantigrade, with a tetradactyl pes showing strong ectaxony, and with the foot axis almost parallel to the midline of the trackway. Strong claws in the pes bend inward; manus smaller than the pes (about 2/3) with four digits. Manus regularly placed in front of, and external to, the pes.

Description: Large tetradactyl pes and manus imprints with digits pointing inwards towards the trackway midline and extended to sharp claw marks. Manus imprint slightly smaller than pes imprint and positioned anterior to the latter. Trackways moderately broad, with short steps.

Discussion: *Tetrasauropus* was originally described by

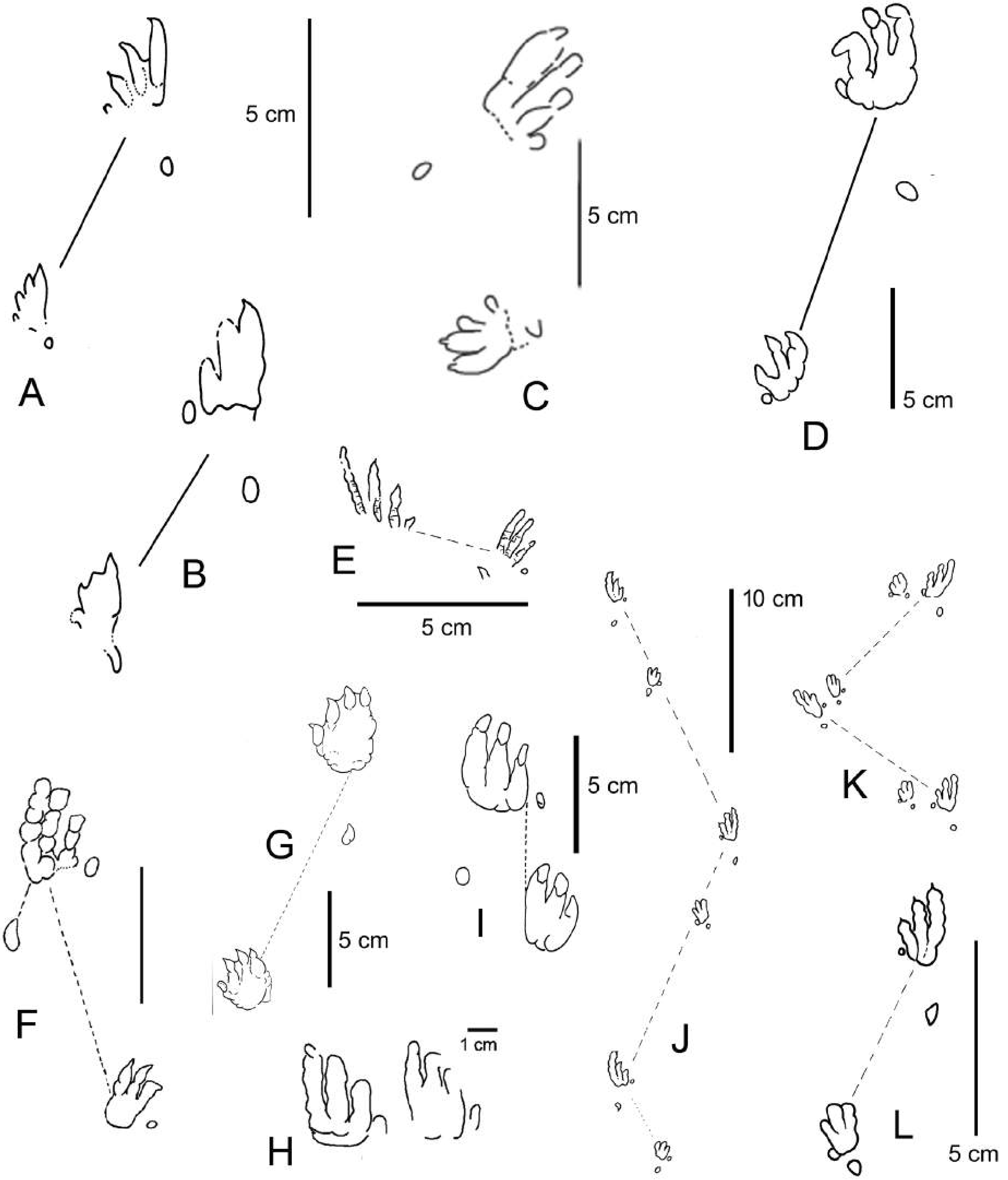

FIGURE 64. *Rotodactylus* footprints from different localities and units as sketches. **A-B, E,** *R.cursorius* from Moenkopi Fm. of Arizona and Utah. **C,** *R. bradyi* from Holbrook Member of Moenkopi Fm., Arizona. **D,** *R. lucasi* from the Middle Triassic of France. **F,** *R*. isp. from the Middle Triassic of France. **G,** *R. velox* from the Middle Triassic of France. **H,** *R*. isp. from Timezgadiouine Fm. (T4, Anisian) of the Argana Basin, Morocco. **I,** *R. rati* from the Middle Triassic of France. **J-L,** *R. matthesi* from Solling Fm. (Anisian) of Germany. Scale in F = 5 cm. Sketches from Haubold (1971a, b, 1984), Gand (1977b), Klein and Lucas (2010b) and Klein et al. (2011).

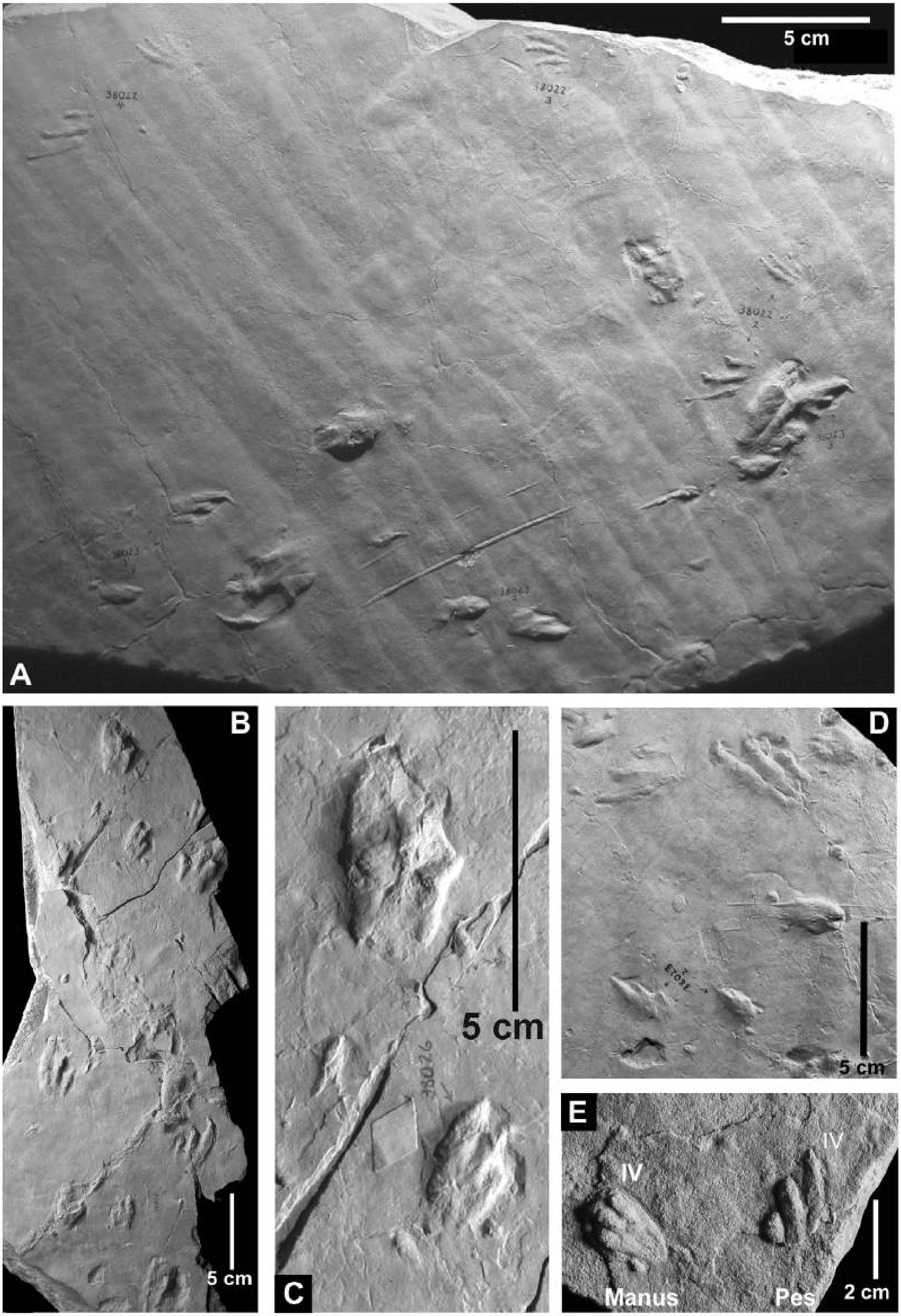

FIGURE 65. Photographs of *Rotodactylus* footprints. **A-D,** *R. cursorius* from Moenkopi Fm. (Olenekian-Anisian) of Utah and Arizona. **E,** *R. matthesi* from Solling Fm. (Anisian) of Germany. From Klein and Lucas (2010b) and Puff and Klein (2011).

FIGURE 66. *Tetrasauropus unguiferus* holotype from lower Elliot Fm. (Norian) of Lesotho, Southern Africa. **A,** Pes-manus set. **B,** Trackway. Sketches from D'Orazi Porchetti and Nicosia (2007).

Ellenberger (1970, 1972) from the Lower Elliot Formation (Norian-Rhaetian) of Lesotho in southern Africa. Subsequently, it was identified also at other Triassic locations in Switzerland (Meyer and Lockley, 2000; Meyer et al., 2013, 2018, 2019), Great Britain (Lockley et al., 1996; Meyer and Lockley, 2000), Greenland (Meyer and Lockley, 2000), the USA (Lockley and Hunt, 1995; Lockley et al., 2001) and Argentina (Melchor and De Valais, 2006). The Argentinian occurrences can be referred to indeterminate tetrapod footprints; some of them were re-evaluated and proven to be Eocene in age (Melchor et al., 2013a). The material from Great Britain, Greenland and USA was recently re-assigned to the ichnogenus *Eosauropus* (Lockley et al., 2006a; Lallensack et al., 2017). Here we consider *Tetrasauropus* a valid ichnogenus based on the type material from southern Africa and probable further occurrences in Upper Triassic deposits of Switzerland (see above). *Tetrasauropus* is different from *Eosauropus* mainly by the more parallel or slight outward orientation of the imprints relative to the midline (strongly outward in *Eosauropus*) and the inward curved digit traces (outward in *Eosauropus*).

Trackmaker: Prosauropod sauropodomorphs are widely accepted as the trackmakers (e.g. Haubold, 1984; Thulborn, 1990; Lockley et al., 1996; Lockley and Hunt, 1995; Lockley and Meyer, 2000; D'Orazi-Porchetti and Nicosia, 2007; and references therein).

Therapsipus Hunt, Santucci, Lockley and Olson, 1993
Figure 68

1993 *Therapsipus* Hunt et al., p. 213, figs. 3-4
2003 *Therapsipus*: Lucas et al., p. 242, figs. 2C, 3E
2012 cf. *Therapsipus*: Klein and Niedźwiedzki, p. 49, figs. 51, 52F-G, 53
2015 *Therapsipus*: Hunt and Lucas, p. 14

Type ichnospecies: *Therapsipus cumminsi* Hunt, Santucci, Lockley and Olson, 1993.

Included ichnospecies: Only known from the type ichnospecies.

Distribution: Middle Triassic interval of Moenkopi Formation, Arizona-New Mexico, USA (Hunt et al., 1993; Lucas et al., 2003); possibly Early Triassic of the Holy Cross Mountains, Poland (Klein and Niedźwiedzki, 2012).

Diagnosis (after Hunt et al., 1993): Large (pes length ~ 230-260 mm) footprints of a quadruped in which both pes and manus are pentadactyl, digit I is poorly impressed and have concave posterior margins; pace angulation ~ 85^{o}.

Description: Pentadactyl pes (25 cm long, 22 cm wide) and manus imprints (21 cm long and 22 cm wide). In the pes, digit III is longest, whereas outer/inner digits decrease in length. In the manus, digits III and IV are longest and subequal in length, whereas digits II and V are shorter and subequal in length. Digit I is short and often absent. Trackways relatively broad, with low pace angulation and short steps; the manus is positioned anterior to the pes; pes imprints are rotated outwards by 45°, manus imprints rotated outward by 60° relative to the trackway midline.

Discussion: *Therapsipus* differs from *Dicynodontipu*s in that the latter is much smaller, with elongate manus and pes impressions and a narrower trackway width (Hunt et al., 1993). Definite records of *Therapsipus* are restricted to the uppermost Moenkopi strata in Arizona-New Mexico, USA. The only other possible published record is by Klein and Niedźwiedzki (2012), who reported isolated tracks possibly referable to this ichnogenus from the Early Triassic strata of the Holy Cross Mountains in Poland.

Trackmaker: All authors agree a relatively large dicynodont was the trackmaker of *Therapsipus* (e. g., Hunt et al., 1993; Nesbitt and Angielczyk, 2002)

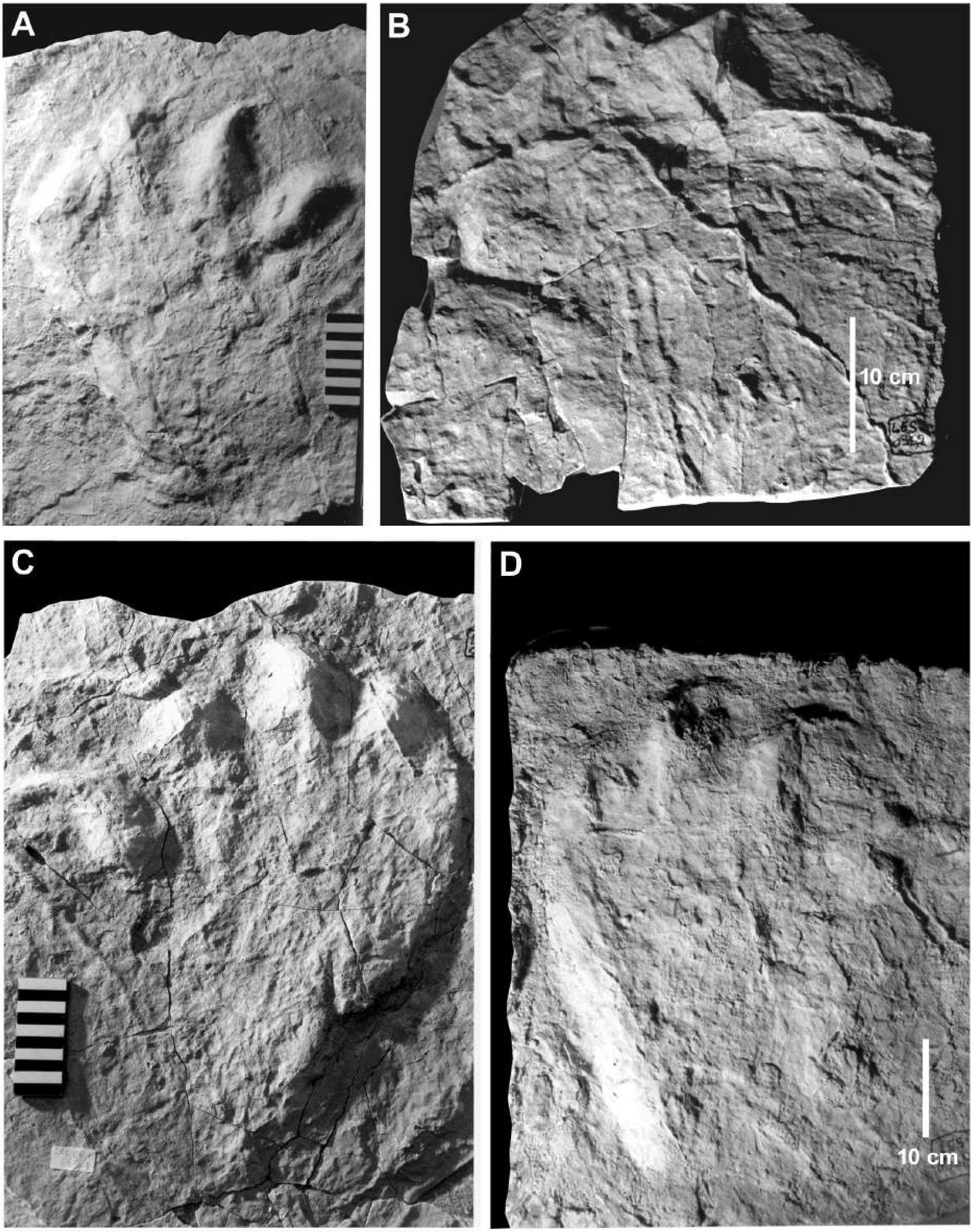

FIGURE 67. Photographs of *Tetrasauropus unguiferus* plaster casts in the collection of Paul Ellenberger in the University of Montpellier, France. All pes imprints except B, which is a manus imprint.

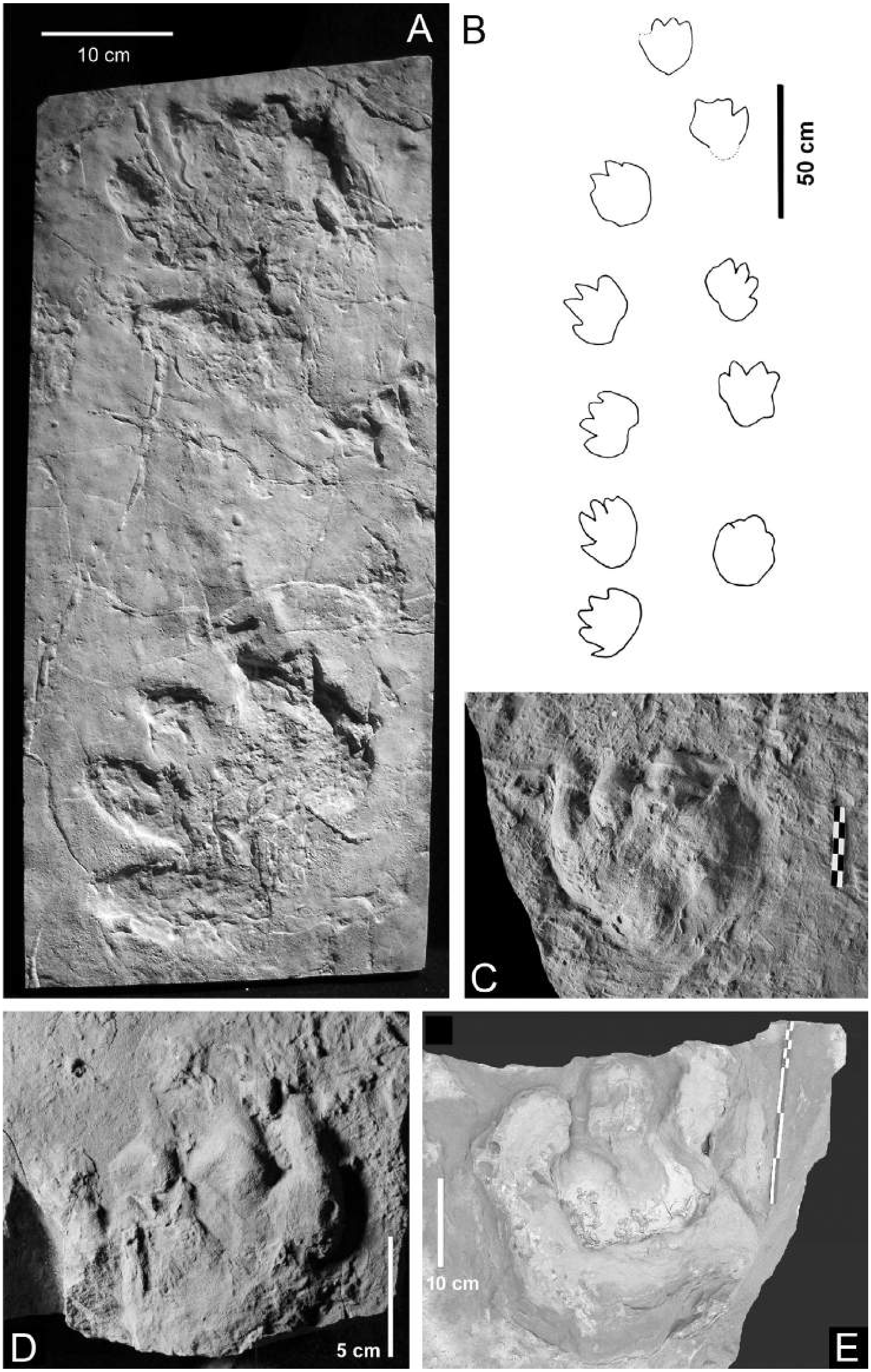

FIGURE 68. Photographs and sketch of *Therapsipus* footprints. **A,** Replica of pes-manus set from holotype trackway in the Moenkopi Fm. (Holbrook Member, Anisian) of Arizona. B**,** Sketch of holotype trackway. **C-E,** cf. *Therapsipus* from Wióry Fm. **(**Olenekian) of Poland. Photograph in A courtesy Martin Lockley. Sketch in B from Hunt et al. (1993). Photographs in C-E from Klein and Niedźwiedzki (2012).

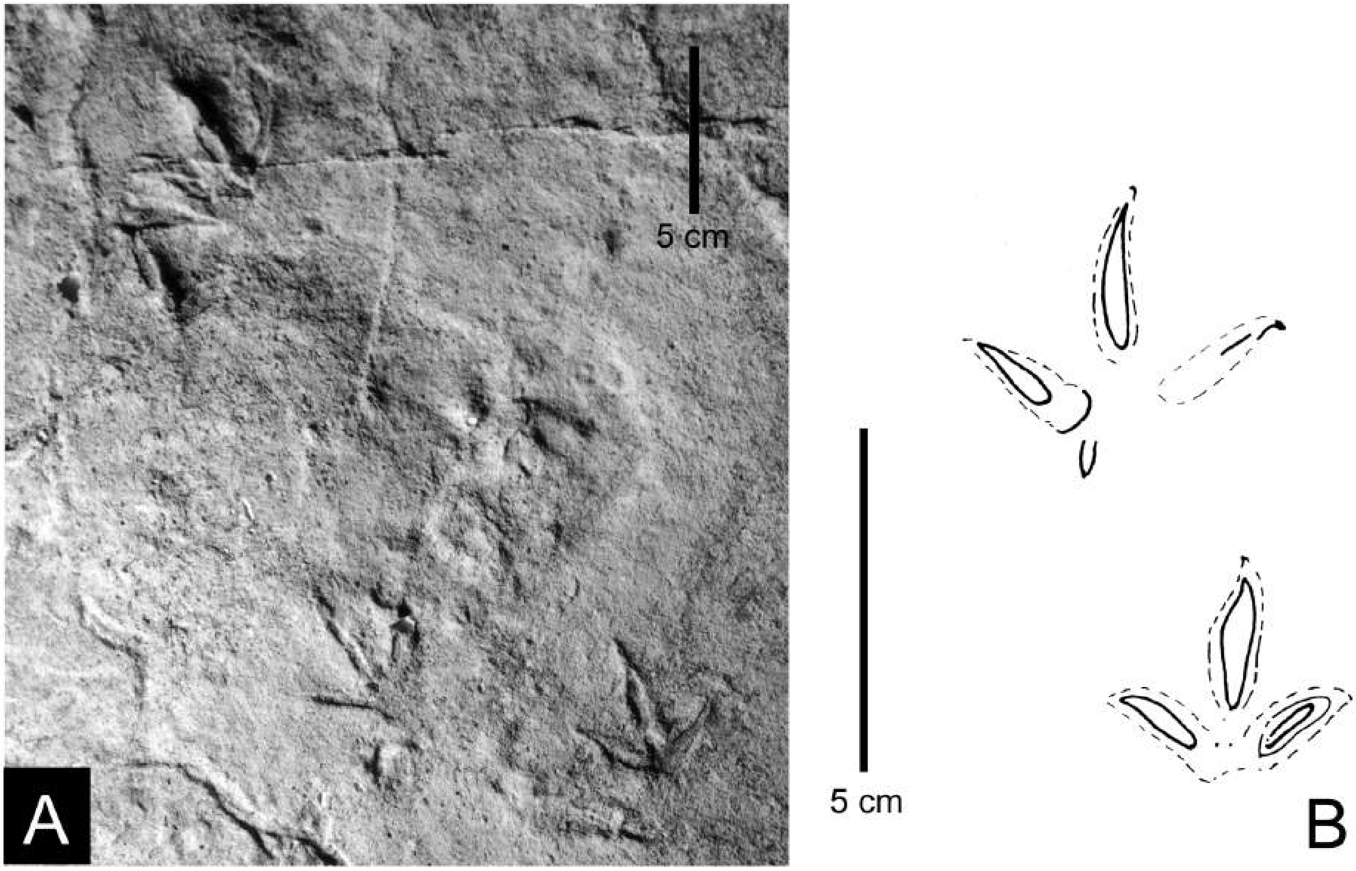

FIGURE 69. *Trisauropodiscus aviforma* footprints from lower Elliot Fm. (Norian) of Lesotho, southern Africa. **A,** Plaster cast in the collection of Paul Ellenberger in the University of Montpellier, France. **B,** Sketch from Ellenberger (1972).

Trisauropodiscus Ellenberger, 1970
Figure 69

1970 *Trisauropodiscus* [*nomen nudum*] Ellenberger, p. 346, figs. 47-48, 55-56
1972 *Trisauropodiscus* Ellenberger, p. 98, figs. 55-56, pls. 15, 16, 17
1984 Indeterminate: Olsen and Galton, p. 109, 110
1984 *Trisauropodiscus* Haubold, p. 49, 173, fig. 118.4

Type ichnospecies: *Trisauropodiscus aviforma* Ellenberger, 1970.

Included ichnospecies: Only the type ichnospecies is valid.

Distribution: Lower-Upper Elliot Formation (Upper Triassic-Lower Jurassic), Lesotho, southern Africa; Imilchil Formation (Middle Jurassic, Bajocian-Bathonian) of Morocco.

Diagnosis: Functionally tridactyl (with main digit group II-IV) footprints of small- to medium-sized bipeds with occasional presence of a trace of the reversed semi-functional hallux. Footprints mesaxonic–symmetrical with digit III being longest and lateral digits that are subequal in length. Tracks lack metatarsophalangeal pads of digits II and IV, while that of digit III is occasionally present, but not clearly separated from the phalangeal portion of digit III. Digits are very narrow and widely divaricated (> 90°).

Description: Small, tridactyl-tetradactyl (I–IV) bird-like pes imprints. Digits II–IV symmetrical, with digit III much the longest and widely divaricated. Digit I (hallux), if present, short and often posteriorly oriented.

Discussion: Ellenberger (1970) erected the ichnogenus based on material from the Lower Elliot Formation of Lesotho in southern Africa. Three ichnospecies were described by this author: *Trisauropodiscus aviforma* Ellenberger , 1970 (type ichnospecies), *T. galliforma* Ellenberger, 1972 and *T. superaviforma* Ellenberger, 1972. Based on their strong morphological similarities, we consider the latter two as synonymous with the type ichnospecies. Several authors (e.g., Lockley and Harris, 2010) have doubted the validity of *Trisauropodiscus* and assigned these footprints to the ornithischian ichnogenus *Anomoepu*s. The latter often has a similar shape, with wide digit divarication and an occasional hallux trace. Gierliński et al. (2017) confirmed the validity of the ichnogenus *Trisauropodiscus* based on new material from the Middle Jurassic of Morocco.

Trackmaker: *Trisauropodiscus* has commonly been considered the track of avian or non-avian theropods with a bird-like pes (Haubold, 1984; Gierliński et al. (2017). Given the known temporal distribution of avian body fossils (none are older than Late Jurassic), a non-avian trackmaker seems highly likely.

Nomina Dubia Based On Triassic Material

Ellenberger's (1970, 1972, 1974) Ichnotaxonomy

Ellenberger (1970, 1972, 1974) published a highly problematic ichnotaxonomy of Triassic-Jurassic footprints from southern Africa. Thus, Ellenberger (1970) began by introducing 28 ichnogeneric names for Triassic footprints (and about as many for Jurassic footprints, but these are not reviewed here) by simply listing names and presenting line figures of the ichnotaxa. These names are thus *nomina nuda* by ICZN rules. Then, Ellenberger (1972, 1974) made these *nomina nuda* into available names by meeting Article 13 of the ICZN, especially in publishing clear intent to name new ichnotaxa with diagnoses and holotype designations for ichnospecies, though not all the type ichnospecies of the ichnogenera were made clear.

The many ichnogenera named by Ellenberger (1972, 1974) have never been comprehensively reviewed. They are based on type material only represented by replicas or material that was left in the field. Demathieu and Weidmann (1982; also see Avanzini and Cavin, 2009) used a few of Ellenberger's ichnogenera. Haubold (1984) listed most of Ellenberger's ichnogenera, even redrawing some of his illustrations. He referred to the theropod footprint ichnogenera of Ellenberger as "South African equivalents" (Haubold, 1984, p. 173) of ichnogeneric names used in North America (*Grallator*, *Anchisaurpus*, *Eubrontes*).

However, Olsen and Galton (1984) provided a very different evaluation of Ellenberger's ichnogenera, proclaiming most of them indeterminate. They considered Ellenberger's ichnogenera *Prototrisauropus* and *Qemetrisauropus* junior synonyms of *Grallator*, and *Deuterosauropodopus* a junior synonym of *Brachychirotherium*. Nevertheless, other than listing these conclusions, Olsen and Galton (1984) provided no detailed evaluation of Ellenberger's ichnotaxa to support their ichnotaxonomic conclusions.

D'Orazi Porchetti and Nicosia (2007) validated five of Ellenberger's ichnogenera—*Paratetrasauropus*, *Pentasauropus*, *Pseudotetrasauropus*, *Sauropodopus* and *Tetrasauropus*. We regard *Pentasauropus, Pseudotetrasauropus* and *Tetrasauropus* as valid, and we also recognize *Trisauropodiscus* as valid.

Here, we present as comprehensive of a review as possible of the Triassic ichnogenera named by Ellenberger, proclaiming most of them *nomina dubia*. Our review is mostly literature based; we have not had the opportunity to examine Ellenberger's type material of his ichnotaxa, except study of some plaster casts in the University of Montpellier, France, and a few original tracks during the stay of HK in South Africa in 2017. Hence, we are conservative in our conclusions, not proposing formal synonymy of most of these ichnogenera (even though assignment of several to *Grallator* or *Eubrontes* seems almost certain).

Agrestipus Weems, 1987

1987 *Agrestipus* Weems, p. 13, fig. 4, pl. 1F.
1989 possible *Grallator* spp.: Smoot and Olsen, p. 62, fig. 4.4F

Distribution: Upper Triassic, Virginia, USA.

Discussion: *Agrestipus* is the undertrack of a small tridactyl footprint in which separate digits may be discernable from the shape of the outline of the footprint (Weems, 1987, fig. 4). This is likely an extramorphological variant of *Grallator* but too poorly preserved to be determined (also see Smoot and Olsen, 1989). Thus, we consider *Agrestipus* to be a *nomen dubium*.

Anatrisauropus Ellenberger, 1972

1970 *Anatrisauropus* [*nomen nudum*] Ellenberger, p. 344, fig. 8A-B
1972 *Anatrisauropus* Ellenberger, p. 35, fig. 8A-B, pl. 2
1984 Indeterminate: Olsen and Galton, p. 109
1984 *Anatrisauropus*: Haubold, p. 48, 155, fig. 115.2

Distribution: Lower Elliot Formation, Upper Triassic, Lesotho, southern Africa.

Discussion: Ellenberger (1972) named two ichnospecies of *Anatrisauropus* from his zone A/2, *A. ginsbergi* and *A. hereroensis.* We designate *A. ginsbergi* as the type ichnospecies of *Anatrisauropus.* The ichnogenus is for tridactyl footprints of a theropod dinosaur in which pes length = 220-250 mm and a likely synonym of *Anchisauripus*.

Barrancapus Hunt, Lockley and Lucas, 1993
Figure 70A-B

1993 *Barrancapus* Hunt et al., p. 200, fig. 2A-B.

Lectotype: Designated here, trackway in the lower left of Hunt et al. (1993, fig. 2A), bottom left of our Figure 70A with detail in Fig. 70B, NMMNH P-4782.

Horizon and locality of lectotype: Bull Canyon Formation, Chinle Group, Barranca Creek, New Mexico, NMMNH locality 55.

Discussion: Hunt et al. (1993) named *Barrancapus cresapi* (new ichnogenus and ichnospecies) for a "trackway" found in the Upper Triassic (Norian/Revueltian) Bull Canyon Formation in eastern New Mexico, USA. They published an outline drawing of the entire rock slab, calling it the holotype, even though more than one trackway is present on the slab, and they published an outline drawing of a detail of a manus/pes pair (Hunt et al., 1993, figs. 2AB). According to Hunt et al. (1993), the holotype slab was not collected, but a "plastotype" was made and catalogued as NMMNH P-4782. Subsequently, Lucas and A. B. Heckert collected the slab, and it is now at NMMNH catalogued as P-4782 (Fig. 70A-B). According to Hunt et al. (1993, p., 200), *Barrancapus cresapi* is diagnosed "by the combination of a pentadactyl pes print with a manus print that has a medially extended digit I impression, short digit II, III and IV impressions and an elongate, anteriorly oriented digit V impression." They suggested it is the trackway of an archosaur, and compared it to *Navahopus*, which they regarded as a prosauropod track, but stated that the number of digits precludes a prosauropod trackmaker for *Barrancapus*. Hunt et al. (1993) also mentioned that two parallel trackways are present on the holotype slab and took this as either the paleotopographically-forced parallel progression of two animals or as evidence of social behavior. However, they did not clarify which of the trackways is the holotype of *B. cresapi*.

The holotype slab of *Barrancapus cresapi*, NMMNH P-4782, is a thick block of ripple laminar, grayish red and color mottled sandstone that preserves two trackways and two isolated tracks in convex hyporelief. There are two slightly curved ridges on the same surface as the trackways, and we regard them as tool marks. The trackway (here, trackway A) in the lower right of the slab (Fig 70; lower left of the Hunt et al., 1993, fig. 2A, which is a drawing of the cast of the tracks in concave epirelief) is three unambiguous manus-pes pairs. These tracks are interpreted by us as larger pes overstepping smaller manus. The pes has a maximum length of 65 mm and maximum width of 45 mm, and the manus has a maximum length of 55 mm and maximum width of 45 mm. The pes is wider than long and preserves four straight, anteriorly direct digit impressions that are joined posteriorly along a transverse ridge that likely represents the phalangeal-metatarsal joint. The manus is longer than wide and preserves four slightly curved digit impressions with pointed tips. Presumably manus and pes are pentadactyl, but only three or four digit impressions are preserved.

The second trackway (here, trackway B) is in the upper left of the slab (Fig. 70), and is the upper right trackway of Hunt et al. (1993, fig. 2A). This trackway has two certain manus-pes couples and two other likely pes tracks. It is not overstepped. All of these tracks are slightly smaller than the tracks in trackway A and vary much in morphology because they very variably preserve or don't preserve digits. There are two other isolated tracks on the periphery of the slab that resemble the other tracks.

We fix the lectotype of *Barrancapus cresapi* as trackway A of the holotype slab, because it is generally better preserved. Hunt et al. (1993) refer to a diagnostic feature of a medially directed manual digit I, which is illustrated as a detail from trackway A in their Figure 2B.

Hunt et al. (1993) claimed that the holotype of *Barrancapus cresapi* has a pentadactyl pes, though this is not clear from any of the pes impressions on NMMNH P-4722. What they claim is a medially directed digit I of the manus is also not certain, given how incompletely the manual digits are preserved. Instead, this projection is most likely part of a transverse ridge that represents the metapodial-phalangeal joint. We thus view the lectotype of *B. cresapi* as a poorly preserved trackway that reveals much extramorphology, particularly in the variable preservation and presence/absence of digit impressions. *B. cresapi* bears some resemblance to swim traces of buoyant or bottom walking tetrapods or some Triassic turtle tracks (cf. Lovelace and Lovelace, 2012, fig. 8; Thomson and Lovelace, 2014, figs. 10-11; Lichtig et al., 2018, fig. 8), so it could be argued that *Barrancapus* is a synonym of *Chelonipus*. However, the lectotype of *B. cresapi* is not complete enough or well enough preserved to allow definite ichnotaxonomic conclusions, so we regard *B. cresapi* as a *nomen dubium*.

Batrachopodiscus Ellenberger, 1972

1970 *Batrachopodiscus* [*nomen nudum*] Ellenberger, p. 345, figs. 42-43
1972 *Batrachopodiscus* Ellenberger, p. 76, figs. 42-43, pl. 9
1984 Indeterminate: Olsen and Galton, p. 109
1984 *Batrachopodiscus*: Haubold , p. 37

Distribution: Upper Triassic-Lower Jurassic, southern Africa.

Discussion: Ellenberger (1972) named four ichnospecies of *Batrachopodiscus*, *B. tsantalani* and *B. curvus* from his zone A/3, and *B. qurthingensis* and *B. likoerensis* from his Jurassic zone B/5. There is no clear type ichnospecies of the ichnogenus in Ellenberger (1972), so we designate *B. tsantalani* as the type ichnospecies of *Batrachopodiscus* because it has the most completely preserved holotype. The four ichnospecies are based on small footprints (pes length = 6-10 mm) that are preserved as little more than digit impressions. Indeed, *B. curvus* is just pairs of disorganized, curved scratch marks, and we are not even certain these are vertebrate trace fossils. Ellenberger (1972) interpreted *Batrachopodiscus* as the footprints of amphibians, but they could also be the footprints of a small therapsid or mammal. The footprints of *Batrachopodiscus* are too poorly preserved to evaluate, so the ichnogenus is best considered a *nomen dubium*.

Bifidichnium Demathieu and Weidmann, 1982

1982 *Bifidichnium* Demathieu and Weidmann, p. 751, figs. 13D, 14C.
2016 Chirotheriidae indet.: Klein et al., p. 310.

Distribution: Vieux Emosson Formation, Early-Middle Triassic (Olenekian-Anisian), Switzerland.

Discussion: Based on two connected, oval impressions, *Bifidichnium ambiguum* is based on material too poorly preserved for it to serve as a valid ichnotaxon. Klein et al. (2016) considered it to be an indeterminate chirothere.

Bosiutrisauropus Ellenberger,1972

1970 *Bosiutrisauropus* [*nomen nudum*] Ellenberger, p. 345, figs. 23-24.
1972 *Bosiutrisauropus* Ellenberger, p. 52, figs. 23-24, pls. 10, 12.
1984 Indeterminate: Olsen and Galton, p. 109
1984 *Bosiutrisauropus*: Haubold , p. 48, fig. 115.5

Distribution: Upper Triassic, southern Africa.

Discussion: Ellenberger (1972) named *Bosiutrisauropus phuthiatsani* for small tridactyl footprints of a biped with a pes length of 200 mm from his zone A/3. He identified two "varieties" (subspecies?), *B. p. minor* and *B. p. major*, though the size difference between the two is insignificant. *Bosiutrisauropus* is almost certainly a synonym of *Grallator*.

Chelone? Morton, 1897

1897 *Chelone*? Morton, p. 299
1971 *Chelone*?: Haubold, p. 41
1997 *Chelone*?: Tresise and Sarjeant, p. 14, 93-94, fig. 11.7F

Distribution: Middle Triassic, Anisian, Great Britain.

Discussion: *Chelone*? *subrotundum* was based on a single footprint with a round sole impression and four short, round digit impressions. We do not have access to Morton (1897), so base our evaluation on the information in Tresise and Sarjeant (1997). Clearly, both Beasley (1895) and Morton (1897) thought this was a turtle track, whereas Haubold (1971b) regarded it as a therapsid track. It bears comparison to therapsid footprints such as *Dicynodontipus*, but is too poorly known to be confirmed as a valid ichnotaxon.

Chelonichnium Schimper, 1850

1850 *Chelonichnium* Schimper, p. 10, table IV, fig. B
1928 *Chelonichnium:* Schmidt, p. 414, fig. 1163.
1955 *Chelonichnium:* Lessertisseur, p. 107.
1958 *Chelonichnium:* Kuhn, p. 19, pl. 9.17.
1959 *Chelonichnium:* Schmidt, p. 92.
1963 *Chelonichnium:* Kuhn, p. 59.
1971b *Chelonichnium:* Haubold, p. 99, fig. 62.7.

Distribution: Middle Buntsandstein, Lower Triassic, France.

Discussion: *Chelonichnium* is based on a paraxonic, tetradactyl-tridactyl footprint with a broad and rounded heel. It was originally thought to have been made by a turtle but is more likely a chirothere undertrack. Like Haubold (1971), we regard the type material as indeterminate, so we consider *Chelonichnium* to be a nomen dubium.

Comptichnus Ellenberger, 1972

1970 *Comptichnus* [*nomen nudum*] Ellenberger, p. 346, fig. 40
1972 *Comptichnus* Ellenberger, p. 95, fig. 46, pl. 16

Distribution: Lower Elliot Formation, Upper Triassic, Lesotho, southern Africa.

Discussion: *Comptichnus moorosii* is based on a single footprint from zone A/4 of Ellenberger (1972) that is tetradactyl, wider than long and has a length of 95 mm. The digits are short and have rounded tips. This may be a chirothere manus impression, but provides too few data upon which to base an ichnogenus. Therefore, we regard *Comptichnus* as a *nomen dubium*.

Cryptobranchichnus Huene, 1941

1941 *Cryptobranchichnus* Huene, p. 1, pl. 8, figs. 3-4.
1955 *Cryptobranchichnus*: Lessertisseur, p. 10, fig. 56C.
1958 *Cryptobranchichnus*: Kuhn, p. 17, pl. 11.6a.
1963 *Cryptobranchichnus*: Kuhn, p. 49.
1971b *Cryptobranchichnus*: Haubold, p. 99.

Distribution: Middle Triassic (Ladinian), northern Italy.

Discussion: These are very small ?tetrapod tracks (up to 12 mm long). They slightly resemble *Batrachichnus*, but the type material of *Cryptobranchichnus* is too poorly preserved to allow a definitive ichnotaxonomic judgment, so we regard the ichnogenus as a *nomen dubium*.

Cynodontipus Ellenberger, 1976

1976 *Cynodontipus* Ellenberger, p. 772, figs. 1-3, 6-7, 10
1984 *Cynodontipus*?: Haubold, p. 56

Distribution: Middle Triassic, France.

Discussion: Ellenberger (1976) named *Cynodontipus polythrix* for an incomplete footprint from a horizon he regarded as Middle Triassic just below the *Chirotherium* sandstone at Fozières (Hèrault) in France. This incomplete footprint is a large (estimated footprint length = 180-200 mm according to Ellenberger, width of the three preserved digits is 225 mm), tridactyl impression in which the digits are broadly triangular in outline, blunt to round tipped and separated by distinct notches. This appears to us to be an incomplete impression of digits II-IV of a chirothere pes, not the footprint of a diademodontid therapsid, as claimed by Ellenberger (1976). Therefore, we regard *Cynodontipus* as a *nomen dubium* based on a tridactyl remnant of a chirothere footprint.

Thin, wavy ridges cover the incomplete footprint of *Cynodontipus* and some of the surrounding matrix. Ellenberger (1976) concluded these ridges are hair impressions. He illustrated modern mammal footprints with hair impressions for comparison, but these bear far more closely spaced, finer ridges confined to the footprint impression and thus not present on surrounding matrix. Therefore, we conclude that these ridges are likely a diagenetic/weathering feature or a microbially-induced sedimentary structure, not hair impressions.

Delairichnus Haubold 1971b

1970 Unnamed: Delair, p. 178, figs. 1-2.
1971b *Delairichnus* Haubold, p. 96, figs. 26.7, 26.11.

Distribution: Triassic, Great Britain.

Discussion: Haubold (1971b) named *Delairichnus* for what he considered cynodont tracks, originally described in open nomenclature by Delair (1970). These are small tracks (L x W = 15 x 20 mm) in which an arc of circular digit imprints is separated from the round sole imprint. They slightly resemble *Dicynodontipus*. This ichnotaxon needs to be re-evaluated together with numerous similar, small tracks named by Ellenberger (1970, 1972, 1974). Given the overall poor preservation of its type material, we regard *Delairichnus* as a *nomen dubium*.

Deuterotetrapous Nopcsa, 1923

1910 "Type P": Beasley, p. 152, fig. 1, pl. 3, figs. 1-2.
1923 *Deuterotetrapous* Nopsca, p. 199.
1958 *Deuterotetrapous*: Kuhn, p. 23.
1963 *Deuterotetrapous*: Kuhn, p. 88, pl. 5.9
1967 *Deuterotetrapous*: Sarjeant, p. 335, fig. 4a, pl. 15
1971b *Deuterotetrapous*: Haubold, p. 95, fig. 59.3, 59.4

Distribution: Middle-Upper Triassic, Europe, southern Africa.

Discussion: This ichnogenus is the tracks of a quadruped with angular, forward-pointing digits, digitigrade digits II-IV, digit V reduced, pes up to 5 cm long and the manus much smaller than the pes and wider than long. These poorly preserved tracks are possibly those of chirotheres but are not well enough preserved for a definite assessment. Therefore, we regard *Deuterotetrapous* as a *nomen dubium*.

Deuterotrisauropus Ellenberger, 1972

1970 *Deuterotrisauropus* [*nomen nudum*] Ellenberger, p. 75, fig. 44, 50-51
1972 *Deuterotrisauropus* Ellenberger, p. 345, fig. 44, pls. 13, 16
1984 *Deuterotrisauropus*: Haubold , p. 48, 173, fig. 115.7

Distribution: Lower Elliot Formation, Upper Triassic, Lesotho, southern Africa.

Discussion: *Deuterotrisauropus socialis* is the tridactyl footprint of a theropod dinosaur from Ellenberger's horizon A/2. Pes length = 200 mm. It is likely a synonym of *Anchisauripus* or *Grallator*.

Dijaquesopus Ellenberger, 1972

1970 *Dijaquesopus* [*nomen nudum*] Ellenberger, p. 344, fig. 12
1972 *Dijaquesopus* Ellenberger, p. 43, fig. 12
1984 Indeterminate: Olsen and Galton, p. 109

Distribution: Late Triassic, southern Africa

Discussion: Ellenberger (1972) based *Dijaquesopus obliquus* on a trackway from his A/2 horizon. Ellenberger identifies 5 digits in these footprints, but his illustrations show only bean-shaped impressions that are wider than long and up to 70 mm long, arranged in a broad trackway. Ellenberger (1972) thought this to be the trackway of a crocodile or turtle, but all we see are likely incomplete sole impressions that are indeterminate. Therefore, we regard *Dijaquesopus* as a *nomen dubium.*

Enigmatopus Biron and Dutuit, 1981

Fig. 34E

1981 *Enigmatopus* Biron and Dutuit, p. 415, fig. 12

Distribution: Upper Triassic (Carnian), Ourika Basin, Morocco.

Discussion: Biron and Dutuit (1981) proposed *Enigmatopus atlensis* (type ichnospecies by monotypy) for a single, small lacertoid footprint, Only illustrated by a line drawing, this footprint is 50 mm long, 30 mm wide, pentadactyl and plantigrade. Digit I is slightly divergent and digit V>IV>III>II>I. Biron and Dutuit (1981) attributed this footprint to a small reptile or a mammal. *Enigmatopus* bears some resemblance to *Rhynchosauroides*- or *Procolophonichnium*-like lacertoid forms, but is too little characterized to represent a valid ichnotaxon, so we regard it as a *nomen dubium*.

Furcapes Demathieu, 1977

Fig. 71A

1977 *Furcapes*: Demathieu, p. 352, fig. 1, pl. 1.1
1984 *Furcapes*: Haubold, p. 149, fig. 100.9

Distribution: Middle Triassic (Anisian-Ladinian), France.

Discussion: *Furcapes nanus* was based on the trackway of a small quadruped (pes length up to 13 mm) consisting of five successive pes-manus sets. Pes tridactyl, probably representing digits II-IV. Digits are slender and straight or slightly inward curved. They increase in length from II to IV, with digit IV being longest. Trackway relatively broad, with low pace angulation (up to 80°). Pes imprints directed parallel to the midline. The smaller manus imprint is similar to the pes imprint in shape and positioned anteromedial to the latter. Its orientation along digit III is also parallel to the midline (measurements from Demathieu, 1977).

Furcapes is somewhat similar in shape, size and relative position of the imprints to *Minutipes,* known from the same unit (see below). However, the orientation of the imprints relative to the midline is different. Whereas in the former these are directed parallel to the midline, in the latter they are rotated outward (pes) and inward (manus). There are some similarities to the ichnogenus *Rhynchosauroides* in the shape of the imprints, but the trackway pattern is different. Presently the assignment and validity of *Furcapes* is uncertain, so we list this ichnotaxon here under *nomina dubia*.

Gregaripus Weems, 1987

1987 *Gregaripus* Weems, p. 18, fig. 4, pl. 2.
1989 possible *Grallator* spp.: Smoot and Olsen, p. 62, fig. 4.4E.

Distribution: Upper Triassic, Virginia, USA.

Discussion: Like *Agrestipus* (see above), *Gregaripus* is the undertrack of a small tridactyl footprint in which the three digits are only distinct at their distal tips. Likely an extramorphological variant of *Grallator* (also see Smoot and Olsen, 1989), the type material of *Gregaripus* is too poorly preserved to be diagnostic, so it is a *nomen dubium*.

Huenepus Kuhn, 1958

1935 Pseudosuchian: Huene, p. 290, fig. 2.
1958 *Huenepus* Kuhn, p. 20, pl. 7, fig. 10.
1963 *Huenepus*: Kuhn, p. 65
1971b *Huenepus*: Haubold, p. 97, fig. 62.4.

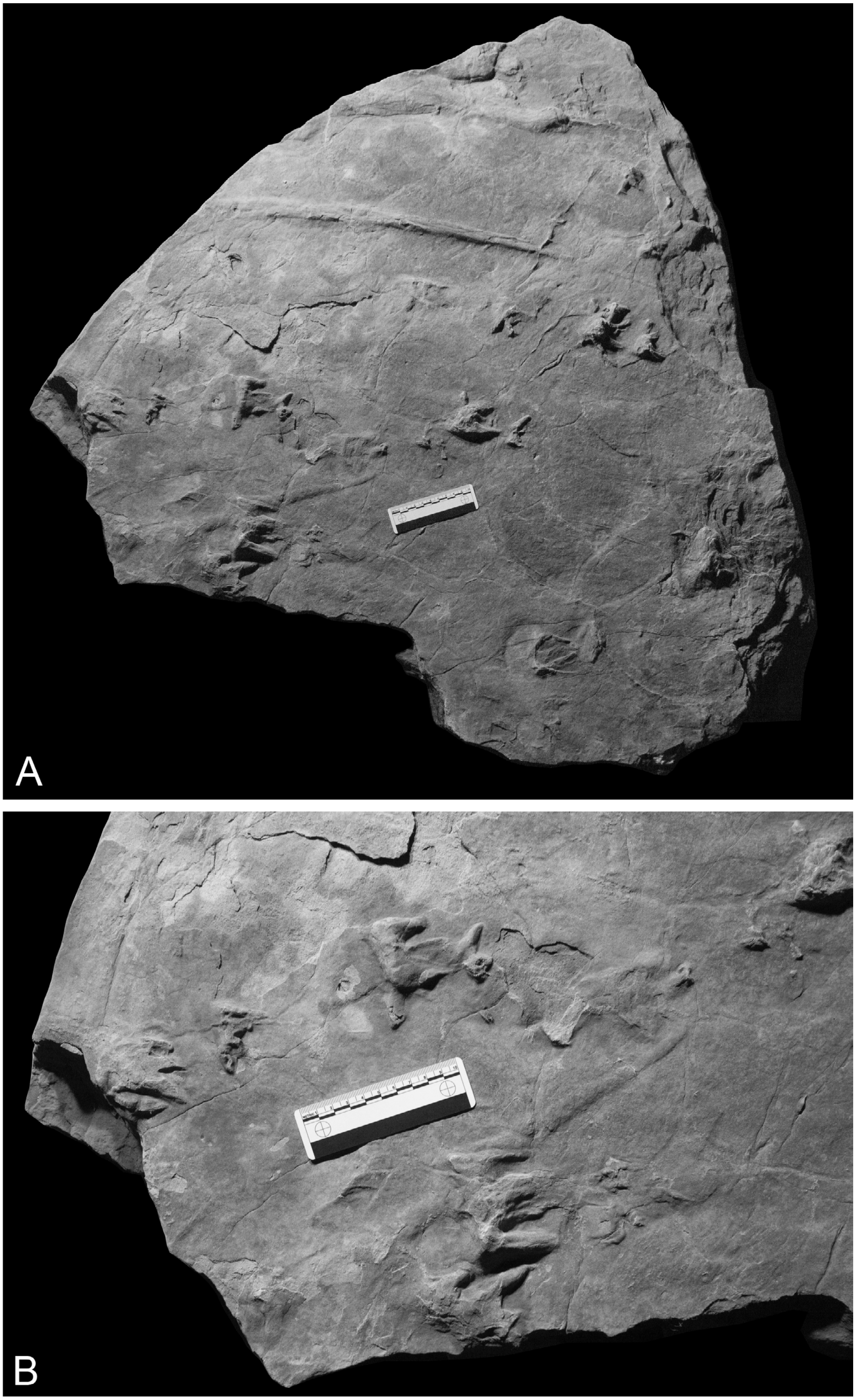

FIGURE 70. *Barrancapus cresapi*. Slab with holotype trackway from Bull Canyon Fm. (Norian) of New Mexico. **A,** Overview. **B,** Detail.

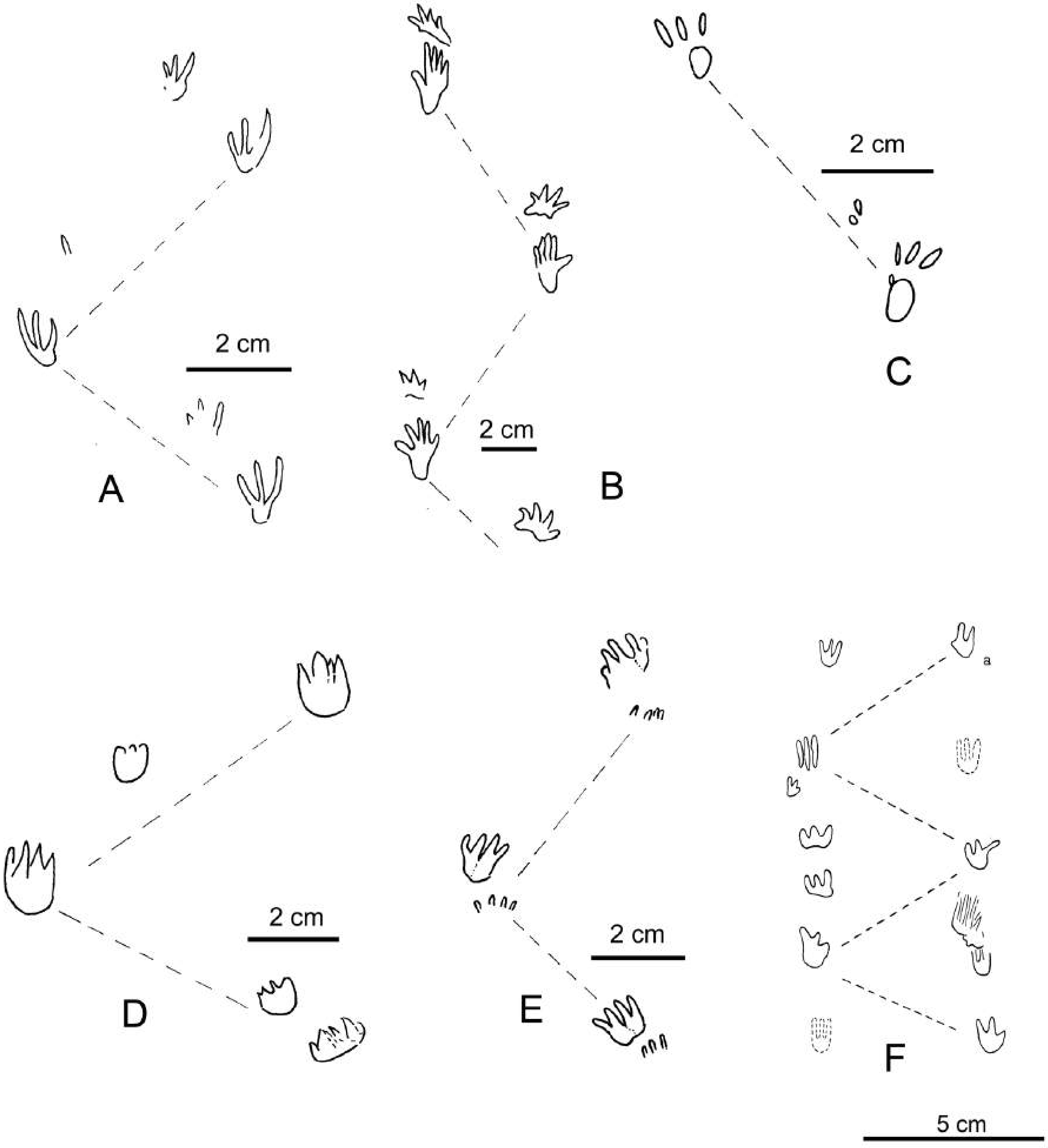

FIGURE 71. Sketches of selected tetrapod footprints identified here as *nomina dubia*. **A,** *Furcapes nanus*. **B,** *Longipes planus*. **C,** *Minutipes gracilis*. **D,** *Procolophonipus acutus*. **E,** *Procolophonipus muelleri*. **F,** *Rueckliniсhnium tridactylum*. A-C from the Middle Triassic of France. D-F from Buntsandstein (Olenekian-Anisian) of Germany. Sketches from Demathieu (1970, 1977) and Haubold (1971a).

Distribution: Stubensandstein, Löwenstein Formation (Upper Triassic, Norian), southern Germany.

Description: Relatively broad trackways with small, plantigrade, lacertoid pes imprints (pes length 3.3 cm) lacking a manus impression. The pace angulation is 90°, and the imprints are rotated slightly toward the midline. Digits I-IV are curved inward and increase in length so that IV is longest. The posterolaterally positioned digit V is curved outward. Remarkable is the presence of a tail trace (measurements from Huene, 1935 and Haubold, 1971b).

Discussion: The purported bipedality of the trackmaker is uncertain, as the lack of a manus imprint could be an extramorphological feature or the result of the manus being overstepped by the pes. The archosaurian (pseudosuchian) origin (Huene, 1935) is doubtful, and the overall morphology rather points to a lacertoid or procolophonoid trackmaker. There is some similarity to the ichnogenus *Procolophonichnium* in the shape of the imprints and the trackway pattern. However, a concrete assignment is difficult, and the validity of the ichnogenus remains doubtful. Therefore, we regard *Huenepus* as a *nomen dubium*.

Ichnites Hitchcock, 1837

1837 *Ichnites* Hitchcock, p. 175 (see Rainforth, 2005 for a review of Hitchcock's diverse uses of this term/name).
1886 *Ichnites*: Tommasi, p. 219-220, pl. XIII, fig. 24a-f
1915 *Ichnites*: Fucini, p. 60, pl. 10, fig. 16

Distribution: Quarziti di Monte Serra Formation (?Middle-Upper Triassic, Carnian) of Tuscany, northern Italy.

Discussion: The name was given to material later re-assigned to "*Rhynchocephalichnus*" (*Rhynchosauroides*) and "*Thecodontichnus*" (Huene, 1941).

Ingenierichnus Casamiquela, 1964

1964 *Ingenierichnus*: Casamiquela, p. 142, pls. 17, 19.
2006 "dubious assignation:" Melchor and De Valais, p. 371, text-fig. 9D.

Distribution: Upper Triassic (Carnian), Argentina.

Discussion: This name was applied to a tail/body drag impression flanked by a few indistinct footprints. It lacks useful morphological detail, so we regard *Ingenierichnus* as a *nomen dubium*, as did Melchor and De Valais (2006).

Lacertoidipus Ellenberger, 1972

1970 *Lacertoidipus* [*nomen nudum*] Ellenberger, p. 345, fig. 41
1972 *Lacertoidipus* Ellenberger, p. 74, fig. 41, pl. 9
1984 Indeterminate: Olsen and Galton, p. 109
1984 *Lacertoidipus*: Haubold, p. 42

Distribution: Upper Triassic of southern Africa.

Discussion: *Lacertoidipus socialis* was based on a manus-pes pair and associated slightly sinusoidal tail (body) drag mark from Ellenberger's zone A/3. The pes is 78 mm long, and the manus is 65 mm long. Both are pentadactyl and bear some resemblance to *Gwyneddichnium*. However, the type material is too incomplete to permit a confident assessment.

Longipes Demathieu, 1977
Figure 71B

1977 *Longipes*: Demathieu, p. 354, fig. 2, pl. 2.1.1
1984 *Longipes*: Haubold, p. 149, fig. 100.8

Distribution: Middle Triassic (Anisian-Ladinian), France.

Description: Trackway of a small quadruped (pes length up to 3.2 cm) with pentadactyl, plantigrade, elongate slender pes imprints showing an increase of digit lengths from I-IV, with digit IV being longest or subequal to III. Digit V is in a posterolateral position, straight and anterolaterally directed. The posterior end of the pes imprint is elongated into a "heel" impression that is nearly half the length of the total imprint. The manus imprint is tetradactyl to pentadactyl and relatively large (1.2 cm long, 1.7 cm wide). The trackway is relatively broad and has a pace angulation between 120° and 160°. The oriention of the pes imprints is parallel to the midline, and that of the manus imprints is strongly directed outward.

Discussion: The overall shape of the pes imprints slightly resembles those of chirotheriids and also the ichnogenus *Gwyneddichnium*, but in the latter pedal digit IV is shorter than or subequal to digit II. Based on its distinctive features, *Longipes* might be justified as a valid ichnogenus, however, more material is needed to evaluate this hypothesis.

Mafatrisauropus Ellenberger, 1972

1970 *Mafatrisauropus* [*nomen nudum*] Ellenberger, p. 353, fig. 45
1972 *Mafatrisauropus* Ellenberger, p. 80, fig. 45, pl. 16
1984 Indeterminate: Olsen and Galton, p. 109
1984 *Mafatrisauropus*: Haubold , p. 48, 155, fig. 115.8

Distribution: Lower Elliot Formation, Upper Triassic, Lesotho, southern Africa.

Discussion: *Mafatrisauropus errans* is from Ellenberger's zone A/5. It is the tridactyl footprint of a bipedal theropod dinosaur with a pes length of 160 mm. *Mafatrisauropus* is almost certainly a synonym of *Grallator*.

Marpurgichnium Schindewolf, 1928

1928 *Marpurgichnium*: Schindewolf, p. 42, figs. 13-14
1935 *Marpurgichnium:* Abel, p. 124, fig. 103
1955 *Marpurgichnium:* Lessertisseur, p. 102
1958 *Marpurgichnium:* Kuhn, p. 17, pl. 9.7
1959 *Marpurgichnium:* Schmidt, p. 29, 87, 92
1963 *Marpurgichnium:* Kuhn, p. 49, pls. 6.2, 7.16
1971a *Marpurgichnium*: Haubold: p. 512-514, fig. 34b
1971b *Marpurgichnium:* Haubold, p. 99, fig. 62.8

Distribution: Lower Buntsandstein (Lower Triassic), Germany.

Description: Poorly preserved tetradactyl to pentadactyl rounded imprints (3 cm long) showing distinct heteropody, probably representing traces of the pes and manus. Digits are indistinct, forming broad and short, triangular impressions.

Discussion: *Marpurgichnium knetschi* is poorly preserved isolated footprints inferred to be plantigrade. Abel (1935) interpreted them as the footprints of an amphibian. However, given their poor preservation and isolated nature, no concrete attribution is possible.

Microtetrapodiscus Ellenberger, 1972

1970 *Microtetrapodiscus* [*nomen nudum*] Ellenberger, p. 347, fig. 60-61.
1972 *Microtetrapodiscus* Ellenberger, p. 102, fig. 60.
1984 Indeterminate: Olsen and Galton, p. 110
1984 *Microtetrapodiscus*: Haubold , p. 56

Distribution: Lower Elliot Formation, Upper Triassic, Lesotho, southern Africa.

Discussion: *Microtetrapodiscus longiforma* was based by Ellenberger (1972) on a manus-pes pair from his zone A/7. These small footprints are pentadactyl, digitigrade and longer than wide. Ellenberger estimated the manus length as 22 mm and pes length as 30 mm.

The footprints show some similarity to *Gwynnedichium* but are too incomplete to allow a definite assessment.

Minutipes Demathieu, 1970
Figure 71C

1970 *Minutipes* Demathieu, p. 102, fig. 35, pl. 2.3
1971b *Minutipes*: Haubold, p. 41, fig. 26.11

1984 *Minutipes*: Haubold, p. 149, fig. 100.7

Distribution: Middle Triassic (Anisian-Ladinian) of France.

Description: Relatively broad trackways of a small quadruped showing pes imprints with a length of 1.5 cm and indistinct traces of a small manus. The pace angulation is 87°, and the stride length is 8.4 cm. Pes functionally tridactyl (digits ?II-?IV) with slender digit traces and a circular posterior "heel" impression, rotated outward relative to the midline. Manus traces closer to the midline and anteromedial to the pes or slightly overstepped laterally by the latter, rotated inward (Demathieu, 1970).

Discussion: *Minutipes gracilis* is based on tridactyl pes impressions and manus impressions that are little more than short scratch marks. The preservation does not allow a distinct assignment, and the validity of this ichnotaxon is doubtful. Demathieu (1970) regarded *Minutipes* as a lacertoid footprint, but Haubold (1971) suggested it is more likely a therapsid footprint. It could be based on poorly preserved specimens of *Rhynchosauroides* or another lacertoid ichnotaxon, but is too poorly preserved to allow definite interpretation.

Moltenotetrapodiscus Ellenberger, 1972

1970 *Moltenotetrapodiscus* [*nomen nudum*] Ellenberger, p. 344, fig. 11
1972 *Moltenotetrapodiscus* Ellenberger, p. 42, fig. 11, pl. 2
1984 Indeterminate: Olsen and Galton, p. 109
1984 *Moltenotetrapodiscus*: Haubold , p. 59, 170

Distribution: Lower Elliot Formation, Upper Triassic, Lesotho, southern Africa.

Discussion: *Moltenotetrapodiscus vetus* from Ellenberger's zone A/2 was based on a small, overstepped manus and pes. These footprints may be plantigrade and pentadactyl with short blunt digits, but the drawing of Ellenberger (1972) does not well distinguish their morphology. According to Ellenberger (1972), the pes is either 30 or 50 mm long, depending on how one interprets the sole impression. Ellenberger considered *Moltenotetrapodiscus* the footprints of a "proto-mammal," and it does somewhat resemble small therapsid footprints such as *Brasilichnium*. However, the type material of *M. vetus* is too poorly preserved and incomplete to allow definite conclusions.

Nothosauripus Kuhn, 1958

1935 Sauropterygier: Huene, p. 293, fig. 3.
1958 *Nothosauripus* Kuhn, p. 25, pl. 7.12 1963 *Nothosauripus*: Kuhn, p. 98.
1971b *Nothosauripus*: Haubold, p. 99, fig. 62.3.

Distribution: Middle Triassic (Ladinian), northern Italy.

Discussion: The type material is a small (~ 30 mm long), isolated pentadactyl footprint. Huene (1935) considered it to be the manus track of a sauropterygian. Kuhn (1958) named it as a nothosaur track. Instead, it could be the track of a small temnospondyl, such as *Batrachichnus*, but is not sufficient to diagnose, so we consider *Nothosauripus* a *nomen dubium*. We also note that it is very different from what appear to be bona fide nothosaur tracks (Zhang et al., 2014).

Onkichnium Kuhn, 1963

1923 *Onkichnium* Nopsca, p. 140.
1955 *Onkichnium*: Lessertisseur, p. 106.
1958 *Onkichnium*: Kuhn, p. 15, 19.
1963 *Onkichnium*: Kuhn, p. 59.
1971b *Dicynodontipus*: Haubold, p.41

Discussion: Nopsca (1923) proposed the ichnogenus name *Onkichnium* for material described in open nomenclature by Beasley (1904, 1907). However, there was no ichnospecies name (and thus no type ichnospecies for the ichnogenus) proposed by Nopsca with *Onkichnium*, so the name was not then available by ICZN rules. Nevertheless, Kuhn (1953) proposed the binomen *O. beasleyi* as the genotypic ichnospecies, which made the name available, dating its proper proposal from Kuhn (1963). Haubold (1971) regarded *Onkichnium* as a junior synonym of *Dicynodontipus,* but we regard it as a *nomen dubium* based on inadequate type material.

Onychopoides Kuhn, 1958

1939 *Onychopus*: Rühle von Lillienstern, p. 349, fig. 15.
1958 *Onychopoides*: Kuhn, p. 20, pl. 5, fig. 7.
1971a *Onychopoides*: Haubold , p. 513-514, fig. 34c
1971b *Onychopoides*: Haubold, p. 99-100, fig. 62.11

Distribution: Thüringischer Chirotheriensandstein (Solling Formation, Middle Triassic, Anisian), Germany.

Description: Poorly preserved paired imprints with elongate shape but otherwise indistinct morphology up to 2.5 cm in length arranged in a trackway-like pattern.

Discussion: Kuhn (1958) introduced the new ichnogeneric name *Onychopoides* to replace the preoccupied ichnogeneric name *Onychopus* Rühle von Lillienstern, 1939. This ichnogenus is represented by tracks that are four impressions—two comma or narrow, wedge-shaped impressions followed? by two round impressions. Clearly, this is an undertrack, and its lack of morphological detail prevents a full ichnotaxonomic assessment. Therefore, we regard *Onychopoides* as a *nomen dubium*.

Pachysaurichnium Demathieu and Weidmann 1982

1982 *Pachysaurichnium* Demathieu and Weidmann, p. 749, figs. 13C, 14B.
2016 Chirotheriidae indet.: Klein et al., p. 310.

Distribution: Vieux Emosson Formation, Early-Middle Triassic, Switzerland.

Discussion: Based on a tridactyl impression, *Pachysaurichnium emossonense* is based on material too poorly preserved for it to serve as a valid ichnotaxon. Klein et al. (2016) considered it to be an indeterminate chirothere.

Paraophidichnium Demathieu, 1977

1977 *Paraophidichnium*: Demathieu, p. 358-359, pl. 1, figs.2-3

Distribution: Middle Triassic, France.

Discussion: Demathieu (1977) illustrated sinuous, ribbon-like traces (7-8 mm in width) consisting of three parallel furrows and introduced the new ichnogenus and ichnospecies *Paraophidichnium triassicum.* No autopodial impressions are visible. This might be a body and/or tail trace of an unknown tetrapod. Demathieu (1977) considered a limbless tracemaker, and Haubold (1984, p. 42) listed *Paraophidichnium* under tracks of limbless (snake-like) tetrapods. However, the material is very incomplete, so we consider *P. triassicum* a *nomen dubium*.

Paratrisauropus Ellenberger, 1972

1970 *Paratrisauropus* [*nomen nudum*] Ellenberger, p. 345, figs. 26-27, 53D.
1972 *Paratrisauropus* Ellenberger, p. 55, figs. 26-27.
1982 *Paratrisauropus*: Demathieu and Weidmann, p. 736, figs. 6c, 7c, 7d, 8b
1984 Indeterminate: Olsen and Galton, p. 109
1984 *Paratrisauropus*: Haubold , p. 51, 154, 170, fig. 115.6
2009 *Paratrisauropus*: Avanzini and Cavin, figs. 5a-c
2016 Chirotheriidae indet.: Klein et al., p. 310 (for the specimens of Demathieu and Weidmann, 1982 and Avanzini and Cavin, 2009)

Distribution: Lower Elliot Formation, Upper Triassic, Lesotho, southern Africa.

Discussion: *Paratrisauropus mendrezi* is a tridactyl footprint of a biped with pes length = 180 mm. We designate this the type ichnospecies of *Paratrisauropus*, as Ellenberger (1972) named two other ichnospecies of the ichnogenus: *P. lifofanensis* and *P. equester*. *P. mendrezi* and *P. lifofanensis* are from Ellenberger's zone A/3, whereas *P. equester* is from his zone A/4. These are the footprints of a small theropod dinosaur that should likely be assigned to *Grallator*.

Plesiothornipos Harkness, 1850

1850 *Plesiothornipos* Harkness, p. 442.
1959 *Plesiothornipos*: Huene, p. 57
1963 *Plesiothornipos*: Kuhn, p. 85-86.
1971b *Plesiothornipos*: Haubold, p. 99, fig. 62.5

Distribution: Lower Triassic, Great Britain.

Discussion: The name is for small, isolated tridactyl footprints. Haubold (1971) judged the type material to not be diagnostic, and we concur, considering *Plesiothornipos* to be a *nomen dubium*.

Procolophonipus Rühle von Lilienstern, 1939
Figure 71D-E

1939 *Procolophonipus*: Rühle von Lilienstern, p. 341, figs. 13-14.
1952 *Procolophonipus*: Bock, p. 49, pl. 6, fig. 3
1958 *Procolophonipus*: Kuhn, p. 18, pl. 5, figs. 2, 12-13; pl. 11, fig,. 4.
1971a *Procolophonipus*: Haubold, p. 508-511, fig. 33a-b
1971b *Procolophonichnium*: Haubold, p. 31.
1984 *Procolophonichnium*: Haubold, p. 149, fig. 100.5

Distribution: Thüringischer Chirotheriensandstein (Solling Formation, Middle Triassic, Anisian), Germany.

Description: Broad trackways with low pace angulation and small (2-3 cm long) pes and manus imprints. Manus smaller than pes. Orientation of imprints rotated towards the trackway midline.

Discussion: *Procolophonipus triadicus* and *P. acutus* were described from the Buntsandstein (Olenekian-Anisian) of Germany by Rühle v. Lilienstern (1939). *Procolophonipus muelleri* was established as a new ichnospecies based on material from the same unit by Haubold (1971a). All three ichnotaxa are tetradactyl. This may be a preservational feature or anatomically based. However, it is constantly present in all imprints of these trackways. Haubold (1971b) reassigned them to *Procolophonichnium* and "Diverse Trias indet.," respectively, together with *Procolophonipus italicus* originally described by v. Huene (1941) from the Upper Triassic of Italy (Haubold, 1971b, p. 31, p. 100, fig. 62).

Haubold (1984) again listed all these ichnotaxa under *Procolophonipu*s (Haubold, 1984, p. 149, fig. 100 [3–4]). *Procolophonipus vonhuenei,* described by Bock from the Newark Supergroup (Upper Triassic) of New Jersey (Bock 1952, pl. 46, fig. 3), encompasses groups of (up to four) elongated marks or scratches that can be interpreted as swim traces. They are otherwise indeterminate. Some of the trackways described by Rühle v. Lilienstern (1939) and Haubold (1971a, b, 1984) under *Procolophonipus* may be referable to *Procolophonichnium* (see also Klein et al., 2015).

Prototrisauropodiscus Ellenberger, 1972

1970 *Prototrisauropodiscus* [*nomen nudum*] Ellenberger, p. 353, fig. 13.
1972 *Prototrisauropodiscus* Ellenberger, p. 49, fig. 13, 10.
1984 Indeterminate: Olsen and Galton, p. 109
1984 *Prototrisauropodiscus*: Haubold , p. 49, 173, fig. 115.3

Distribution: Lower Elliot Formation, Upper Triassic, Lesotho, southern Africa.

Discussion: *Prototrisauropodiscus minimus* is based on a trackway of small tridactyl footprints of a biped from Ellenberger's zone A/3. Pes length = 67 mm, and there is a "dew claw" impression. These are the footprints of a small theropod dinosaur like *Grallator*.

Prototrisauropus Ellenberger, 1972

1970 *Prototrisauropus* [*nomen nudum*] Ellenberger, p. 345, figs. 13-20
1972 *Prototrisauropus* Ellenberger, p. 45, figs. 13-20
1982 *Prototrisauropus*: Demathieu and Weidmann, p. 744, fig. 11
1984 *Grallator*: Olsen and Galton, p. 96, fig. 3Ha,c,e
1984 *Prototrisauropus*: Haubold , p. 49, 154
2016 Chirotheriidae indet.: Klein et al., p. 310 (for the specimens of Demathieu and Weidmann, 1982)

Distribution: Lower Elliot Formation, Upper Triassic, Lesotho, southern Africa.

Discussion: Ellenberger (1972) named *Prototrisauropus* for footprints from his zone A/3 as four ichnospecies: *P. crassidigitus*, *P. angustidigitus*, *P. graciosus* and *P. rectilineus*. He recognized two varieties (subspecies?) of *P. crassidigitus* and three varieties of *P. rectilineus*. We designate *P. crassidigitus* as the type ichnospecies of *Prototrisauropus.* The four ichnospecies of *Prototrisauropus* are based on tridactyl footprints of a bipedal theropod dinosaur that range in pes length from 150 to 250 mm. The differences between the ichnospecies are subtle features of extramorphology and pay ample testament to the degree to which Ellenberger oversplit the ichontaxonomy. Furthermore, *Protrisauropus* is almost certainly a synonym of *Grallator*.

Pseudotrisauropus Ellenberger, 1972

1970 *Pseudotrisauropus* [*nomen nudum*] Ellenberger, p. 344, figs. 9-10, 25A
1972 *Pseudotrisauropus* Ellenberger, p. 38, figs. 9-10, pls. 2, 12, 13
1984 Indeterminate: Olsen and Galton, p. 109
1984 *Pseudotrisauropus*: Haubold , p. 49, 173, fig. 115.10

Distribution: Lower Elliot Formation, Upper Triassic, Lesotho, southern Africa.

Discussion: *Pseudotrisauropus* is another Ellenberger name for tridactyl footprints of a bipedal theropod dinosaur and a likely synonym of *Grallator*. He named five ichnospecies: *P. humilis* and *P. minusculus* from his Zone A/2, *P. molekoi* from zone A/3 and *P. dieterleni* and *P. masserui* from zone A/4. We designate *P. humilis* as the type ichnospecies. *P. molekoi* may have five digits, so its assignment to the ichnogenus is puzzling. Pes lengths are: *P. humilis* (120 mm), *P. minusculus* (73 mm), *P. molekoi* (120 mm), *P. dieterleni* (150 mm) and *P. maserui* (290 mm).

Psilotrisauropus Ellenberger, 1972

1972 *Psilotrisauropus* Ellenberger, p. 85, fig. 49A, pl. 12
1984 *Psilotrisauropus*: Haubold , p. 51, 179, fig. 115.9

Distribution: Lower Elliot Formation, Upper Triassic, Lesotho, southern Africa.

Discussion: Ellenberger named *Psilotrisauropus subengensis* for a tridactyl impression flanked by two much smaller digit? impressions from his horizon A/4. He raised the possibility that this might be a tridactyl undertrack of a pentadactyl foot impression, but nonetheless categorized *Psilotrisauropus* as a "tridactyl with a reduced median digit." The tridactyl impression is 125 mm long and possibly is a chirothere undertrack. However, the impression is not complete enough to support a firm conclusion, so we regard *Psilotrisauropus* as a *nomen dubium*.

Qemetrisauropus Ellenberger, 1972

1970 *Qemetrisauropus* [*nomen nudum*] Ellenberger, p. 344,

figs. 6-7
1972 *Qemetrisauropus* Ellenberger, p. 33, figs. 6-7, pl. 2
1984 *Grallator*: Olsen and Galton, p. 96, fig. 3Hb,b
1984 *Qemetrisauropus*: Haubold , p. 49, 173, fig. 115.1

Distribution: Lower Elliot Formation, Upper Triassic, Lesotho, southern Africa.

Discussion: Ellenberger (1976) named two ichnospecies of *Qemetrisauropus* from his zone A/2, *Q. princeps* and *Q. minor*. We designate *Q. princeps* as the type ichnospecies of *Qemetrisauropus*. This ichnogenus is based on tridactyl footprints of a bipedal theropod dinosaur. The pes length of *Q. princeps* is 350 mm, well within the size range of *Eubrontes* as recognized here. Thus, this is another Late Triassic record of *Eubrontes*.

Rogerbaletichnus Casamiquela 1964

1964 *Rogerbaletichnus*: Casamiquela, p. 147-148, pl. XVII, fig. 3
1971b *Rogerbaletichnus*: Haubold, p. 41
2006 “Tracks of dubious assignation”: Melchor and De Valais, p. 372, fig. 9C
2006 “Morphotype D”: Domnanovich and Marsicano, p. 60-61. fig. 6

Distribution: Vera Formation (Upper Triassic, Carnian) of Argentina.

Discussion: The holotype is a trackway consisting of three successive, small, pes-manus sets accompanied by a sinuous drag mark. No morphological details are preserved. Therefore, we consider *Rogerbaletichnus* as a *nomen dubium*.

Rotodactylopus Ellenberger, 1983

1970 *Rotodactylopus* [*nomen nudum*] Ellenberger, p. 343, fig. 1.
1972 *Rotodactylopus* Ellenberger, p. 26, fig. 1.
1984 *Rotodactylopus*: Haubold , p. 47, 150

Distribution: Upper Beaufort Group, Early Triassic?, Lesotho, southern Africa.

Discussion: *Rotodactylopus archaeus* is based on an impression of the distal portions of four digits and possibly part of a sole that could represent a 250-mm-long footprint.

However, we regard this footprint as too incompletely preserved to be identified.

Ruecklinichnium Kuhn, 1958
Figure 71F

1958 *Ruecklinichnium* Kuhn, pl. 17, pl. 9.8.
1963 *Ruecklinichnium*: Kuhn, p. 49-50.
1971a *Ruecklinichnium*: Haubold, p. 513-514, fig. 34a
1971b *Ruecklinichium*: Haubold, p. 99, fig. 62.10.

Distribution: Upper Buntsandstein (Middle Triassic, Anisian), southwestern Germany.

Description: Broad trackways with small, plantigrade, tridactyl imprints (0.5-3.0 cm length) representing traces of the pes and manus. Digits anteriorly directed. Pace angulation very low.

Discussion: The trackway pattern, size and imprint morphology somewhat resemble those of small temnospondyls (*Batrachichnus*). However, the type material is clearly undertracks and thus does not provide sufficient morphological detail to support a definitive ichnotaxonomic judgment. Therefore, we consider *Ruecklinichnium* to be a *nomen dubium*.

Saurichnium Gürich, 1926

1926 *Saurichnium* Gürich, p. 113, pl. 2, fig. 1.
1963 “*Saurichnium*”: Kuhn, p. 87, pl. 3.4, 3.5, 3.7, 3.8
1971 *Saurichnium*: Haubold, p. 82

Distribution: Upper Triassic, Stormberg Group, southern Africa.

Discussion: Gürich (1926) named four ichnospecies of *Saurichnium* for isolated footprints of a tridactyl biped. These poorly preserved theropod footprints are insufficient material upon which to base an ichnogenus.

Saurischichnus Huene, 1941

1941 *Saurischichnus* Huene, p. 121, plate on page 140.
1958 *Saurischichnus*: Kuhn, p. 23, pl. 12.24.
1959 *Saurischichnus*: Schmidt, p. 103-104.
1963 *Saurischichnus*: Kuhn, p. 88.
1971 *Saurischichnus*: Haubold, p. 96, fig. 59.5.

Distribution: Stubensandstein, Upper Triassic (Norian), Germany.

Discussion: The poorly preserved type material represents the tracks of a quadruped, with pes length up to 75 mm and substantial overstepping. *Saurischichnus* has been consided a prosauropod track by most. However, the type material is too poorly preserved for a definite ichnotaxonomic judgment, so we regard *Saurischichnus* as a *nomen dubium*.

Seakatrisauropus Ellenberger, 1972

1970 *Seakatrisauropus* [*nomen nudum*] Ellenberger, p. 345, figs. 21-22
1972 *Seakatrisauropus* Ellenberger, p. 50, figs. 21-22
1984 Indeterminate: Olsen and Galton, p. 109
1984 *Seakatrisauropus*: Haubold , p. 49, fig. 115.4

Distribution: Lower Elliot Formation, Upper Triassic, Lesotho, southern Africa.

Discussion: *Seakatrisauropus divergens* from horizon A/3 of Ellenberger is based on the tridactyl footprint of a theropod dinosaur, similar to *Grallator*, in which pes length = 180 mm. Digit III is relatively much longer than digits II and IV.

Senqutrisauropus Ellenberger, 1972

1970 *Senqutrisauropus* [*nomen nudum*]: Ellenberger, p. 344, fig. 4
1972 *Senqutrisauropus*: Ellenberger, p. 31, fig. 4, pl. 2
1984 *Sequentisauropus* [*lapsus calami*]: Haubold , p. 51

Distribution: Lower Elliot Formation, Upper Triassic, Lesotho, southern Africa.

Discussion: *Senqutrisauropus priscus* from Ellenberger’s zone A/2 is another ichnotaxon he based on tridactyl footprints of a bipedal theropod dinosaur. Pes length = 102 mm. Ellenberger (1976, fig. 4) illustrates two rather different footprints under this ichnogenus, one with nearly equal digit lengths and another in which digit III is long relative to digits II and IV. *Senqutrisauropus* is a likely synonym of *Grallator*.

Shimmelia Casamiquela, 1964

1964 *Shimmelia* Casamiquela, p. 139, pls. 15-16.
1971 *Shimmelia*: Haubold, p. 101.
2006 “nomen nudum:” Melchor and De Valais, p. 371, text-fig. 9A.

Distribution: Upper Triassic (Carnian), Argentina)

Discussion: Melchor and De Valais (2006) regarded the type material of *Shimmelia* as indeterminate chirothere tracks, and we agree. However, they called the ichnotaxon a nomen nudum, which is not technically correct, as Casamiquela’s (1964) introduction of the name did make it available. Instead, a *nomen dubium* based on undiagnostic type material is the correct label for *Shimmelia*.

Tetrapodichnus Haubold, 1971

1971a *Tetrapodichnus* Haubold, p. 510-512, figs. 33c, pl. XXX
1971b *Tetrapodichnus*: Haubold, p. 104, fig. 64.

Distribution: Middle Buntsandstein (Lower Triassic), Germany.

Discussion: Haubold (1971a) introduced the ichnogeneric name *Tetrapodichnus* for rather amorphous, round to oval tracks in relatively broad trackways with small pes and manus imprints lacking a distinct morphology. He included in the ichnogenus some material previously termed *Chelichnus* as well as the type ichnospecies of *Amblyopus* and *Venatoripes* (cf. Gilmore, 1927; Frenguelli, 1950; Schmidt, 1959). Most of these are Permian records, but the type ichnospecies of *Tetrapodichnus* is *T. poerthensis* Haubold, 1971, from the German Triassic Middle Buntsandstein.

The type material of *Tetrapodichnus poerthensis* lacks sufficient details, particularly of digit morphology, to be evaluated ichnotaxonomically. Therefore, we regard *Tetrapodichnus* as a *nomen dubium*.

Thecodontichnus Huene, 1941

1941 *Thecodontichnus* Huene, p. 5-14, fig. 1, pl 1, fig. 2-6, pl. 2, fig. 1-2, pl. 3-5, fig. 12, pl. 6, fig. 1-2
1971a *Thecodontichnus*: Haubold, p. 488
1971b *Thecodontichnus*: Haubold, p. 64
1984 *Thecodontichnus*: Haubold, p. 46, 114, 154, 213

Distribution: Middle Triassic (Ladinian), Verrucano, northern Italy.

Description: The footprints are tetradactyl-pentadactyl pes and manus tracks, some constituting trackways that partially show tail traces. Digit III is longest, followed by IV and II. Digits I and V are strongly reduced and short in both pes and manus tracks. Pes tracks posteriorly elongated, while the smaller manus tracks are short and rounded.

Discussion: Huene (1941) described several ichnotaxa based on mostly poorly preserved material from the Triassic of Tuscany, Northern Italy. He introduced the ichnogenus *Thecodontichnus* with two ichnospecies, *T. fucinii* and *T. verrucae*.

T. fucinii was assigned to indeterminate chirotheriids and *T. verrucae* to Parachirotheriidae by Haubold (1971b, 1984). Unfortunately, only interpretive drawings were given of these ichnotaxa by Huene (1941). *Thecodontichnus* was subsequently identified also from Permian strata by Conti et al. (1977), but the latter material was referred to *Rhynchosauroides* by Marchetti et al. (2019a). Because we could not study Huene's material directly, we regard his Triassic ichnotaxon from Tuscany as a *nomen dubium*.

Tikoepentapodiscus Ellenberger, 1972

1970 *Tikoepentapodiscus* [*nomen nudum*] Ellenberger, p. 343, fig. 3
1972 *Tikoepentapodiscus* Ellenberger, p. 28, fig. 3
1984 *Tikoepentapodiscus*: Haubold , p. 56, 150

Distribution: Late Permian or Early Triassic of southern Africa.

Discussion: *Tikoepentapodiscus fabri* was based on a single footprint from either the *Cistecephalus* zone (late Permian) or *Lystrosaurus* (Early Triassic) zone. This 62-mm-long footprint is illustrated as tetradactyl but said by Ellenberger to be pentadactyl. It is too incomplete for a definite ichnotaxonomic assignment.

Trichristolophus Ellenberger, 1972

1970 *Trichristolophus* [*nomen nudum*] Ellenberger, p. 346, fig. 2
1972 *Trichristolophus* Ellenberger, p. 24, fig. 2
1984 *Trichristolophus*: Haubold , p. 47, 150

Distribution: Lower Triassic? (*Cynognathus* zone?) of southern Africa.

Discussion: *Trichristolophus dubius* is based on scratch marks of a 210 mm-long pes? impression. The footprint is stated by Ellenberger (1972, p. 24) to have come from a stratigraphic level "4 meters above a conglomerate with bones ('*Euparkeria*,' etc.)." Although Ellenberger considered this a Middle Triassic record, it is more likely Early Triassic. The footprint, nevertheless, is inadequate as a basis for ichnotaxonomic assignment.

Tritotrisauropus Ellenberger, 1972

1970 *Tritotrisauropus* [*nomen nudum*] Ellenberger, p. 346, fig. 54.
1972 *Tritotrisauropus* Ellenberger, p. 97, fig. 54.
1984 Indeterminate: Olsen and Galton, p. 109
1984 *Tritotrisauropus*: Haubold , p. 49, 173

Distribution: Lower Elliot Formation, Upper Triassic, Lesotho, southern Africa .

Discussion: *Tritotrisauropus medius* from Ellenberger's zone A/5 is the tridactyl footprint of a bipedal dinosaur. This pes impression is 170 mm long and shows relatively narrow digit divarication and a digit III significantly longer than digits II and IV. *Tritotrisauropus* is almost certainly a synonym of *Grallator.*

Tetrapod footprints indet.

Trackway of a quadruped
Figure 72

2010b Tetrapod footprints indet.: Klein and Lucas, p. 54-58, fig.56

Distribution: Upper Red Formation of Moenkopi Group, Capitol Reef National Monument, Utah.

Discussion: Peabody (1956) first published this trackway of a quadruped with 15 semi-plantigrade consecutive sets (Fig. 72). It belongs to a small quadruped (4 cm pes length) with five blunt digits. Peabody (1956) considered an amphibian as the trackmaker. Probably this is the trackway of a therapsid. There is some similarity to *Capitosauroides bernburgensis* in imprint morphology. This concerns the blunt digits, digit proportions and the posterolaterally positioned digit V. *Capitosauroides* has recently been attributed to therocephalian therapsids (Marchetti et al., 2019b).

"*Coelurosaurichnus*"

1988 *Coelurosaurichnus*: Demathieu and Oosterink, p. 10-11, fig. 5 A-D

Distribution: Vossenfeld Formation (Middle Triassic, Anisian), Winterswijk, The Netherlands.

Discussion: Demathieu and Oosterink (1988) illustrated three fragmentary pes-manus sets and an isolated manus. The manus is pentadactyl and relatively large (up to 132 mm in length and 175 mm in width). The pes is only preserved by the distal ends of three digits.

Robust, oval to triangular claws are present. Demathieu and Oosterink (1988) assigned this material to a new ichnospecies *Coelurosaurichnus ratumensis*. However, it might instead represent an incomplete chirotheriid.

"*Sustenodactylus*"

1988 *Sustenodactylus*: Demathieu and Oosterink, p. 15, fig. 8 A

Distribution: Vossenfeld Formation (Middle Triassic, Anisian), Winterswijk, The Netherlands.

Discussion: This trackway of a small quadruped (pes length ~ 1cm) with pentadactyl pes and manus imprints shows a broad gait and low pace angulation. Pes imprints show a more extensive, oval plantar impression. Probably, the trackway can

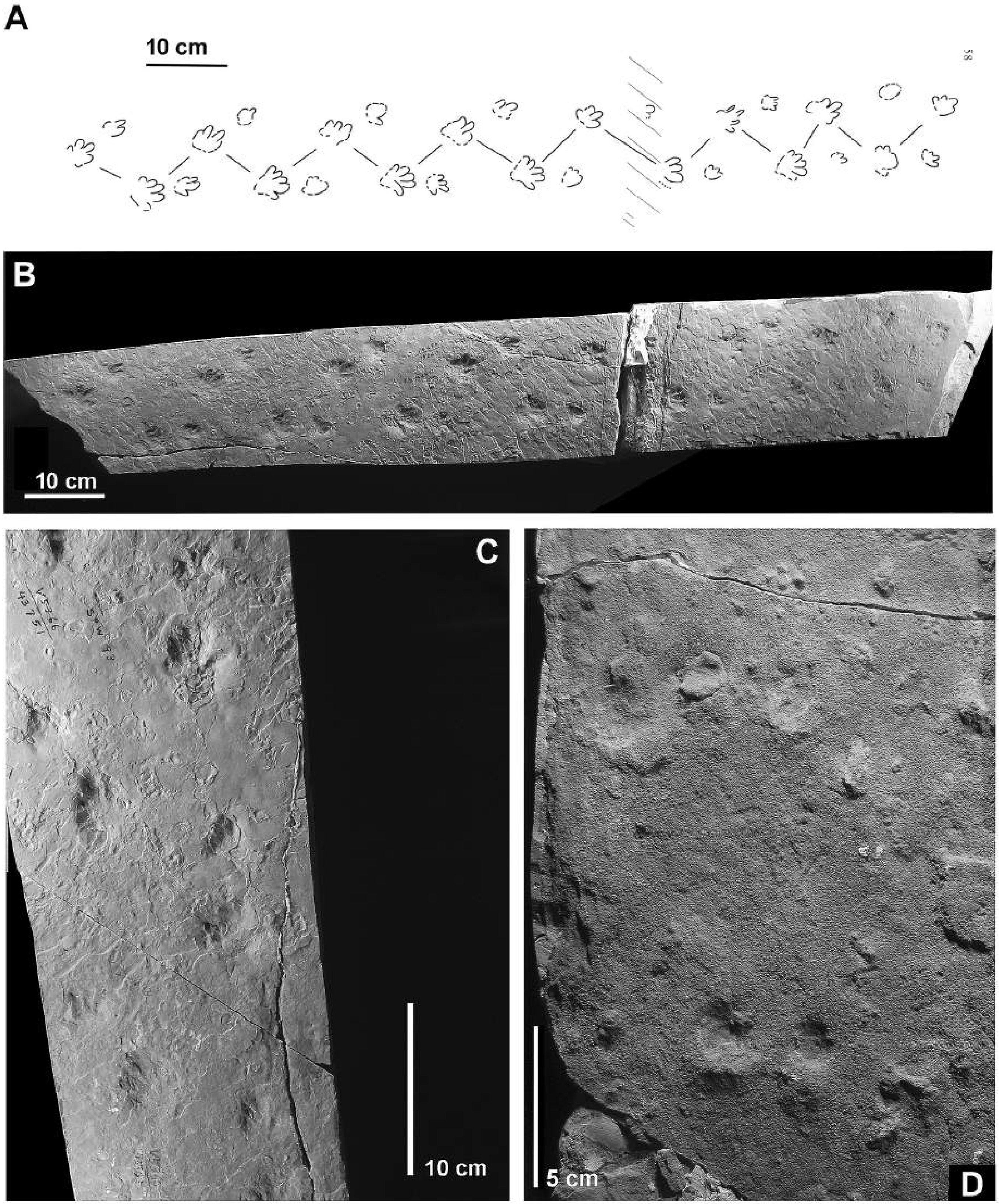

FIGURE 72. A-C. Slab with trackway of a quadruped from ?upper red formation (Anisian) of Moenkopi Group, Capitol Reef National Monument, Utah, assigned to tetrapod footprints indet. **A-B,** Overview as interpretive drawing and photograph. **C,** Detail. **D,** Indeterminate imprints, probably pes and manus with round digit traces arranged in a half-circular pattern, from Wupatki Member (Olenekian) of Moenkopi Fm., Arizona. These might be referred to *Pentasauropus* or similar therapsid tracks. From Klein and Lucas (2010b).

be attributed to a therapsid trackmaker.

“*Capitosauroides*”

1988 *Capitosauroides*: Demathieu and Oosterink, p. 15, fig. 8 B

Distribution: Vossenfeld Formation (Middle Triassic, Anisian), Winterswijk, The Netherlands.

Discussion: The trackway a small quadruped with mesaxonic pentadactyl pes and manus imprints and associated sinuous tail trace are of poor preservation and therefore cannot be assigned to a distinct ichnotaxon. Demathieu and Oosterink (1988) referred this material to the ichnogenus *Capitosauroides*, but there is no morphological congruence. A slight resemblance to turtle tracks is probably an extramorphological rather than an anatomical feature.

“Capitosaurid footprints”

1948 Capitosaurid footprints: Peabody, fig. 9A-B, pl 27A-B, fig. 58
2010b “Capitosaurid footprints”: Klein and Lucas, p. 57, p. 60, fig. 58

Distribution: Wupatki Member of Moenkopi Formation in northern Arizona.

Discussion: These are round digit impressions, placed in couples of semi-circular arrangements, obviously representing pes and manus imprints**.** The footprints resemble *Pentasauropus* from the Middle-Late Triassic of Southern Africa and Argentina. However, the material is poorly preserved and incomplete and possibly represents undertracks (Klein and Haubold, 2010b).

“Vertebrate trace incertae sedis”

1988 “Vertebrate trace incertae sedis”: Demathieu and Oosterink, p. 15, fig. 8 C

Distribution: Vossenfeld Formation (Middle Triassic, Anisian), Winterswijk, The Netherlands.

Discussion: The poorly preserved trackway of a small quadruped with strongly inverted pes imprints and associated tail/?body trace cannot be assigned to any ichnotaxon.

Further material is needed.

“*Dicynodontipus*”

1996 *Dicynodontipus*: Retallack, p. 303, fig. 2, p. 304, fig. 3, p. 306, fig. 4

Distribution: ?Upper Permian-Lower Triassic of the southern Sidney Basin, Australia.

Discussion: A trackway consisting of three successive pes-manus sets (pes- manus ~8 cm long) and isolated tracks, all displaying low heteropody, were published by Retallack (1996). He assigned the material to the cynodont ichnogenus *Dicynodontipus* and introduced a new ichnospecies, *D. bellambieri*. The general morphology of the pentadactyl imprints with long tapering digits and a more extensive plantar/palmar surface slightly resembles *Procolophonichnium nopcsai* from South Africa (Klein et al., 2015), however a distinct assignment is not possible.

“New genus 1”

2001 ?saurischian dinosaurian track “new genus 1”: Olsen and Rainforth, p. 139, fig. 51 E

Distribution: Passaic Formation (Upper Triassic, Norian) at Lyndhurst, New Jersey.

Discussion: Some isolated (~10 cm long) tridactyl-tetradactyl imprints were announced as a possible new ichnogenus by Olsen and Rainforth (2001). They slightly resemble *Evazoum* in the relatively low mesaxony and can probably be attributed to this ichnogenus. More complete material is needed from this locality to confirm this.

“*Dicynodontipus*”

2008a *Dicynodontipus*: Silva et al., figs. 3-6, 8

Distribution: Santa Maria Formation (Upper Triassic) of Brazil.

Discussion: Silva et al. (2008a) introduced the new ichnospecies *Dicynodontipus protherioides* for trackways of a small quadruped with plantigrade, pentadactyl feet and a distinct tail trace. The assignment to the ichnogenus cannot be confirmed here. Digit proportions, the shape of the plantar/palmar surface and the presence of a tail trace are different. More material is needed, so we assign these trackways to tetrapod footprints indet.

GEOGRAPHIC AND STRATIGRAPHIC DISTRIBUTION

North America

Triassic tetrapod footprints are known from three lithosomes in North America: (1) Moenkopi Group/Formation of the western USA; (2) Chinle Group and lower part of Glen Canyon Group in the western USA; and (3) Newark Supergroup of the eastern USA and eastern Canada. These units produce some of the most important Triassic footprints sites and have been the subject of diverse research.

Moenkopi Group/Formation

Longwell (1928) first reported tetrapod tracks from the Moenkopi lithosome, mentioning “small reptilian tracks” in the Valley of Fire near Overton, Nevada. To our knowledge, this record has never been fully documented. Subsequently, Brady (1935) first identified *Chirotherium* tracks in Moenkopi Formation strata along the Little Colorado River of northern Arizona.

In 1948 and 1956, F. E. Peabody published comprehensive studies of the Moenkopi footprints from northern Arizona and southern Utah (see above). Untermann and Untermann (1949, table 1) listed reptile tracks from the Moenkopi Formation in Dinosaur National Monument, Utah. Kinney (1955, p. 60) reported reptile tracks (“possible *Chirotherium*”) from the Moenkopi Formation near Vernal in northeastern Utah. McKee (1954, p. 70-72) reviewed the Moenkopi tetrapod footprint record listing localities in Arizona and Utah, in large part based on Brady (1935) and Peabody (1948). Stewart et al. (1972, p. 69-70) also reviewed the Moenkopi track record, based largely on Peabody (1948, 1956).

At present, the Moenkopi track record is from Wyoming, Utah, Colorado, Arizona and New Mexico in sites that range from Nonesian to Perovkan (Olenekian to Anisian) in age.

Wyoming

In Wyoming, Lower Triassic strata of the Red Peak Formation (Chugwater Group) are part of the same red-bed lithosome as the Moenkopi Group/Formation and should be included in the Moenkopi Group. They have yielded a growing tetrapod footprint record first documented by Lull (1942; also see Branson, 1946, 1947). Thus, footprints from the Red Peak Formation just north of Lysite in the Wind River Basin were named *Colletosaurus palmatus* and *Eurichnus jenseni* by Lull (1942), but were reassigned to *Akropus* by Branson (1947), Peabody (1948) and Colbert (1957) and then to *Rhynchosauroides* by Haubold (1971a, 1984) (also see Lucas, 1994; Fig. 73).

Boyd and Loope (1984) reported tetrapod “swim traces” from the Red Peak Formation, and Thomson and Lovelace (2014) reviewed these and other swim track records in Moenkopi Group strata in Wyoming. They identified five swim track localities in the Red Peak Formation, three of which (Wolf Point, Pine Hill and Rex Lake) were sites discussed by Boyd and Loope (1984). The other two sites, Baker Cabin Road and Trampled by Turtles,

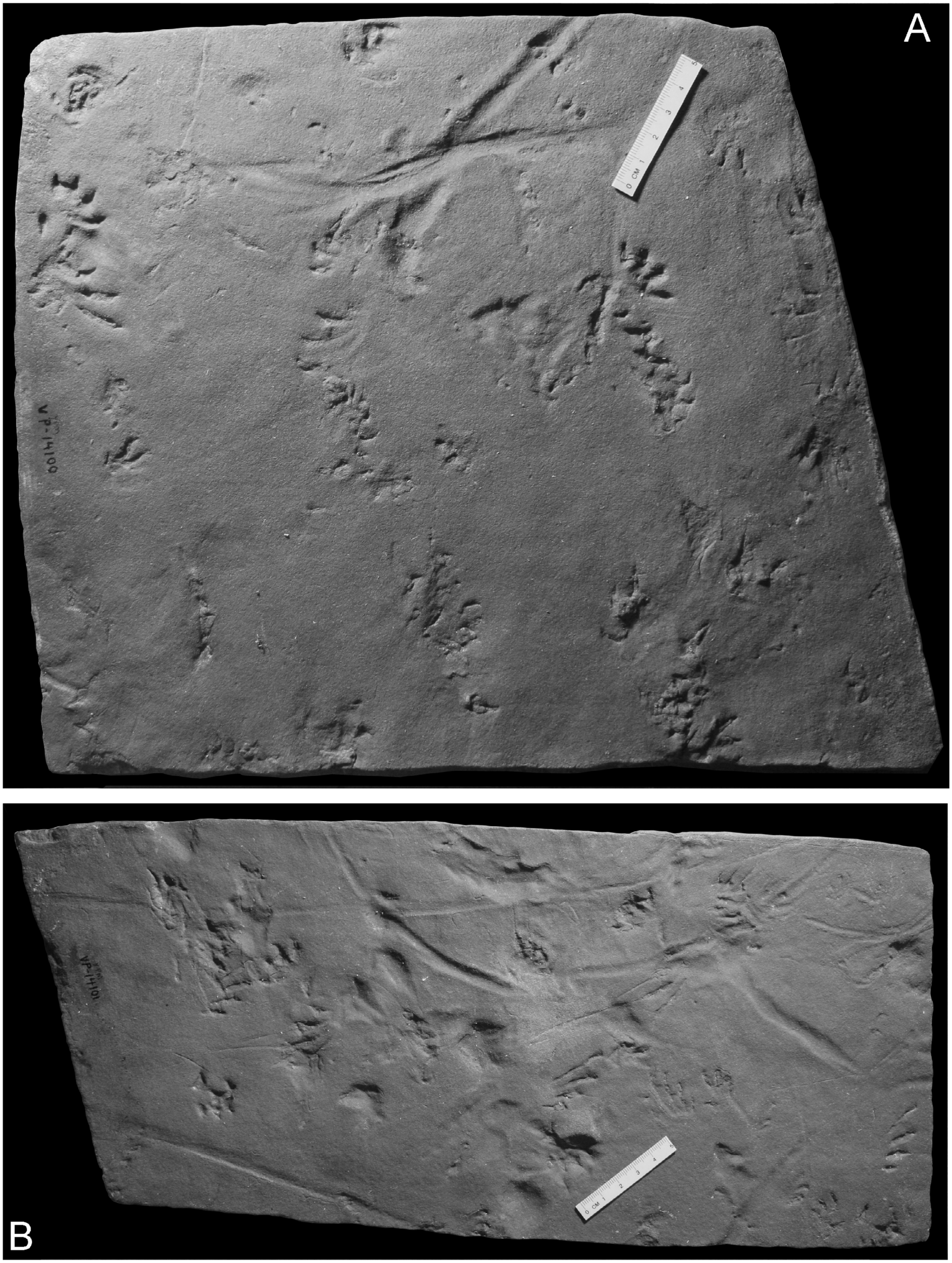

FIGURE 73. Holotype specimens of Triassic footprint ichnotaxa named by Lull (1942). **A,** *Eurichnus jenseni*. **B,** *Colletosaurus palmatus*. Both from Red Peak Fm. (Olenekian), Moenkopi Group, of Wyoming and assigned now to *Rhynchosauroides*.

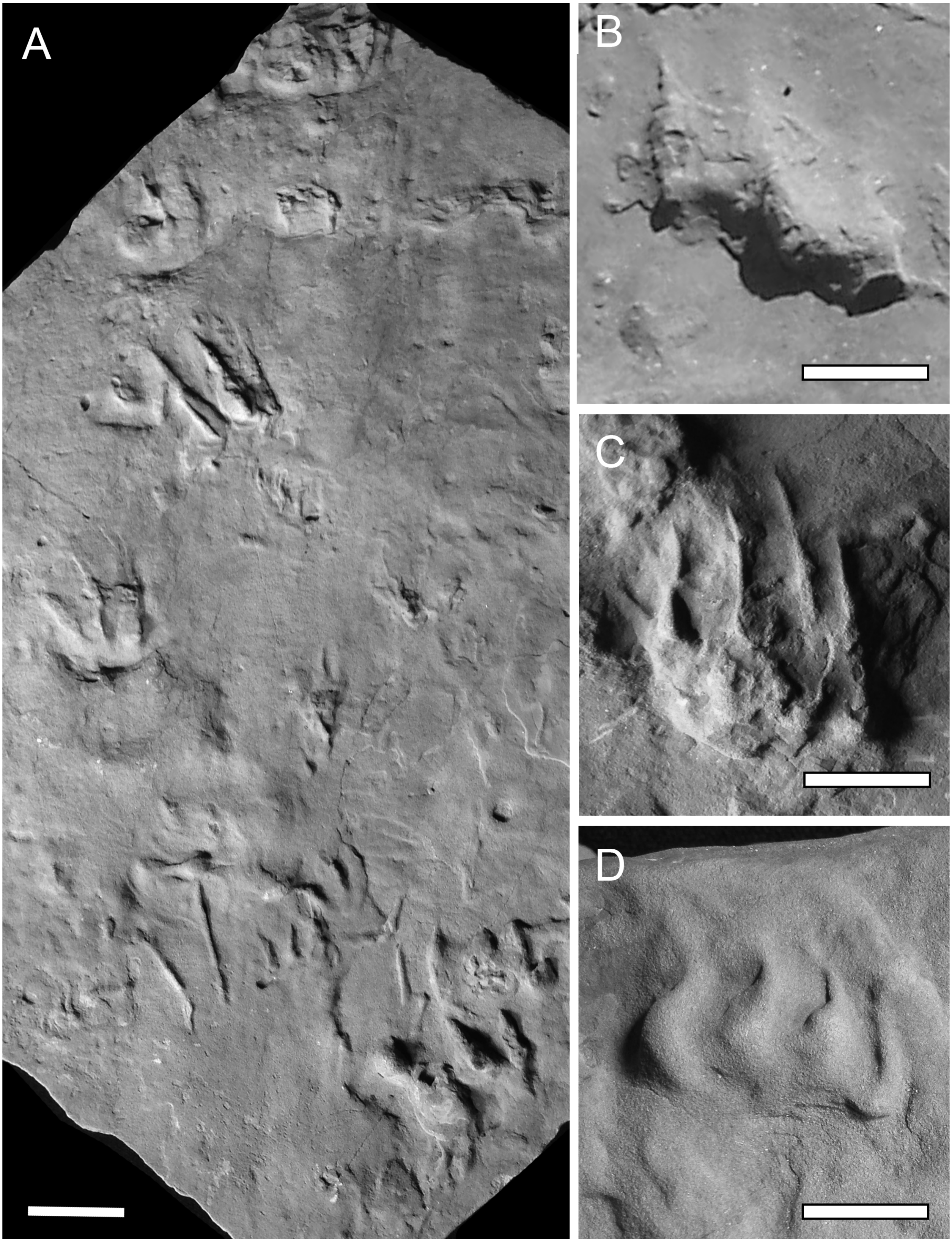
A
B
C
D

FIGURE 74. (facing page) Footprints of stem-turtles *Chelonipus* isp. from Red Peak Fm. (Olenekian), Moenkopi Group, of Wyoming. From Lichtig et al. (2018). Scale bar 1 cm.

produce tracks assigned to *Chelonipus* (also see Lichtig et al., 2017; Fig. 74).

Lovelace (2011) mentions a footprint assemblage from the Middle Triassic Crow Mountain Formation of central Wyoming comprising cf. *Rotodactylus*, *Chirotherium barthii*, *Rhynchosauroides* isp. and cf. *Chelonipus*. Lovelace and Lovelace (2012) described the tetrapod tracks from two other Red Peak Formation localities—Red Wall in Natrona County and Red Hole in Hot Springs County. The collective tetrapod ichnoassemblage from these sites was assigned *to Rotodactylus, Rhynchosauroides, Chirotherium barthii* and *Chelonipus*.

Utah

The stratigraphy and distribution of the Moenkopi Group and footprint localities in Utah are shown in Figures 75 and 76. Several track horizons are known.

Stewart et al. (1972) reported (but did not document) *Chirotherium* tracks from 12 m below the top of the Moenkopi Formation in the Orange Cliffs area of Garfield County, Utah.

Lockley et al. (1998, p. 186, fig. 5; also see Schultz et al., 1995, fig. 1) briefly reported on two Moenkopi tracksites in the Glen Canyon National Recreation Area of southern Utah. They assigned the traces from these tracksites to limulids, *Rhynchosauroides* and tetrapod swim traces.

Mickelson et al. (2006a; also see Mickelson, 2003 and Mickelson et al., 2000, 2001, 2005, 2008) reported tetrapod footprints assigned to *Chirotherium*, *Rotodactylus* and *Rhynchosauroides*, as well as *Undichna* and "swim tracks," from the Torrey Formation of the Moenkopi Group in southeastern Utah (San Rafael Swell, Capitol Reef and Glen Canyon National Recreation area). Mickelson et al. (2006b) documented footprints from the lower red formation of the Moenkopi Group in Zion National Park, Utah, that they identified as *Rhynchosauroides, Chirotherium* and swim tracks. Zeilstra and Lohrengel (2001) reported small reptile footprints from a probable tidal flat environment in the Timpoweap (= Sinbad) Formation of Washington County, Utah.

Thomson et al. (2014) document footprints similar to *Protochirotherium* and *Synaptichnium* as well as swim tracks from the Moenkopi Group near Dinosaur National Monument.

Thomson and Lovelace (2014) list 12 localities in the Moenkopi Group in Utah that yield "swim tracks." These are: (1) Red Fleet, Moenkopi Group formation undetermined; (2) Dinosaur National Monument, which also yielded the chirothere tracks documented by Thomson et al. (2014); (3) Thistle Dam, strata of the Mahogany Formation produce swim track morphotypes I and II of Thomson and Lovelace (2014); (4) Tomsich Butte; (5) Temple Mountain; (6) Capitol Reef National Park; (7) Hite; (8) Rainbow Canyon, where strata of the Torrey Formation yield swim track morphotypes I, II and II; (9) Circle Cliffs; (10) Cedar City, Virgin Formation of the Thaynes Group; (11) Kolob 1, where the lower red formation of the Moenkopi Group contains tracks assigned to swim track morphotypes I and II as well as ?*Chirotherium*, *Rhynchosauroides* and cf. *Chelonipus* (Mickelson et al., 2006b); and (12) St. George. Additionally, *Procolophonichnium* has been mentioned from the Shnabkaib Formation of the Moenkopi Group in southwestern Utah by Thomson and Milner (2012).

Thomson and Droser (2015) (see also Davis and Eves, 2020 describing the same material), based primarily on the "swim track" record of the Lower Triassic Moenkopi Group in the western USA, claimed that it indicated low ichnodiversity and slow recovery after the tetrapod mass extinctions at the end of the Permian. Not only is a tetrapod mass extinction at the end of the Permian questionable, but the idea of delayed recovery after such an extinction has largely been rejected (e.g., Lucas, 2017). Furthermore, the compilation of swim track records of Thomson and Droser (2015, fig. 1) does not concur with our observations that there are abundant "swim tracks" in Late Triassic strata in the western USA (e.g., Milner et al., 2006; Lucas et al., 2010). Finally, the abundance of "swim tracks" in the Moenkopi Group should be considered in light of the depositional facies, which are mostly shallow water deposits on a vast coastal plain, where such "swim tracks" would be preferentially preserved. Thus, the conclusions of Thomson and Droser (2015) regarding Early Triassic swim tracks appear to be based on questionable assumptions, incomplete data and a failure to analyze the track record within its facies context.

Colorado

A fieldnote by C. L. Camp (1946, p. 3164) mentions a single Moenkopi footprint locality at Pat's hole (UCMP locality V 4622) in Moffat County, Colorado, as the source of material in the UCMP collection (cf. Klein and Lucas, 2010b). No designation of the exact stratigraphic position is given. The former Fruita Museum in western Colorado (now Chamber of Commerce building) displays a footprint slab with trackways of *Procolophonichnium* isp. and an indeterminate form, cf. *Capitosauroides*. These have recently been identified by Lockley et al. (2021). The exact provenance and stratigraphic position is unknown, however, the lithology of the slab and the presence of two ichnogenera known to be common in Middle Triassic strata, suggest the Moenkopi Group as the most probable origin.

Arizona

Peabody (1948, p. 304-308) documented the geological context of the Moenkopi tetrapod tracksites in northern Arizona. In northern Arizona, Peabody (1948) followed Welles (1947) in dividing the Moenkopi Formation into three informal units: Lower (pregyspum), middle (gypsum) and upper (postgypsum) members. McKee (1954) used formal nomenclature for these units, the Wupatki (Lower), Moqui (Middle) and Holbrook (Upper) members of the Moenkopi Formation, and we employ that nomenclature here. Also note that the Moenkopi lithosome is relatively thin across much of northern Arizona (and in New Mexico), so we treat the unit as a formation divided into members in Arizona (south of the Little Colorado River) and New Mexico (Fig. 77-78).

The most extensively studied Moenkopi tracksites in Arizona are in the Wupatki Member at Meteor Crater and in Moqui Wash, and the Holbrook Member near Cameron and Penzance (Peabody, 1948; Klein and Lucas, 2010b; Figs. 75, 77). Other, less extensive sites are known from the Wupatki and/or Holbrook members near Winslow, Agathla and Snowflake. Tracksites in the Wupatki Member are Spathian (Nonesian) in age (see above), whereas those in the Holbrook Member are early Anisian (Perovkan) in age (Lucas and Schoch, 2002) (Figs. 77-78).

Kirby (1987) reported swim traces from Wupatki National Monument. In the Holbrook Member at Holbrook, Hunt et al. (1993) named the new ichnogenus *Therapsipus*.

Klein and Lucas (2010b) revised the ichnotaxonomy of the Arizona Moenkopi tracks published by Peabody (1948, 1956). The tracks from the Lower Moenkopi Formation (Wupatki Member) were assigned to *Synaptichnium diabloense*, *Chirotherium sickleri*, *C. rex* ("*C. moquinense*"), *Isochirotherium coltoni*, *Rotodactylus cursorius*, *Rhynchosauroides* isp. and *Procolophonichnium* isp. (Figs. 79-86). Known vertebrate body fossils from this unit are fishes, amphibians (*Wellesaurus*, *Cosgriffius*), archosauromorphs, archosauriforms and other diapsids (Heckert et al., 2005).

Klein and Lucas (2010b) assigned the tracks from

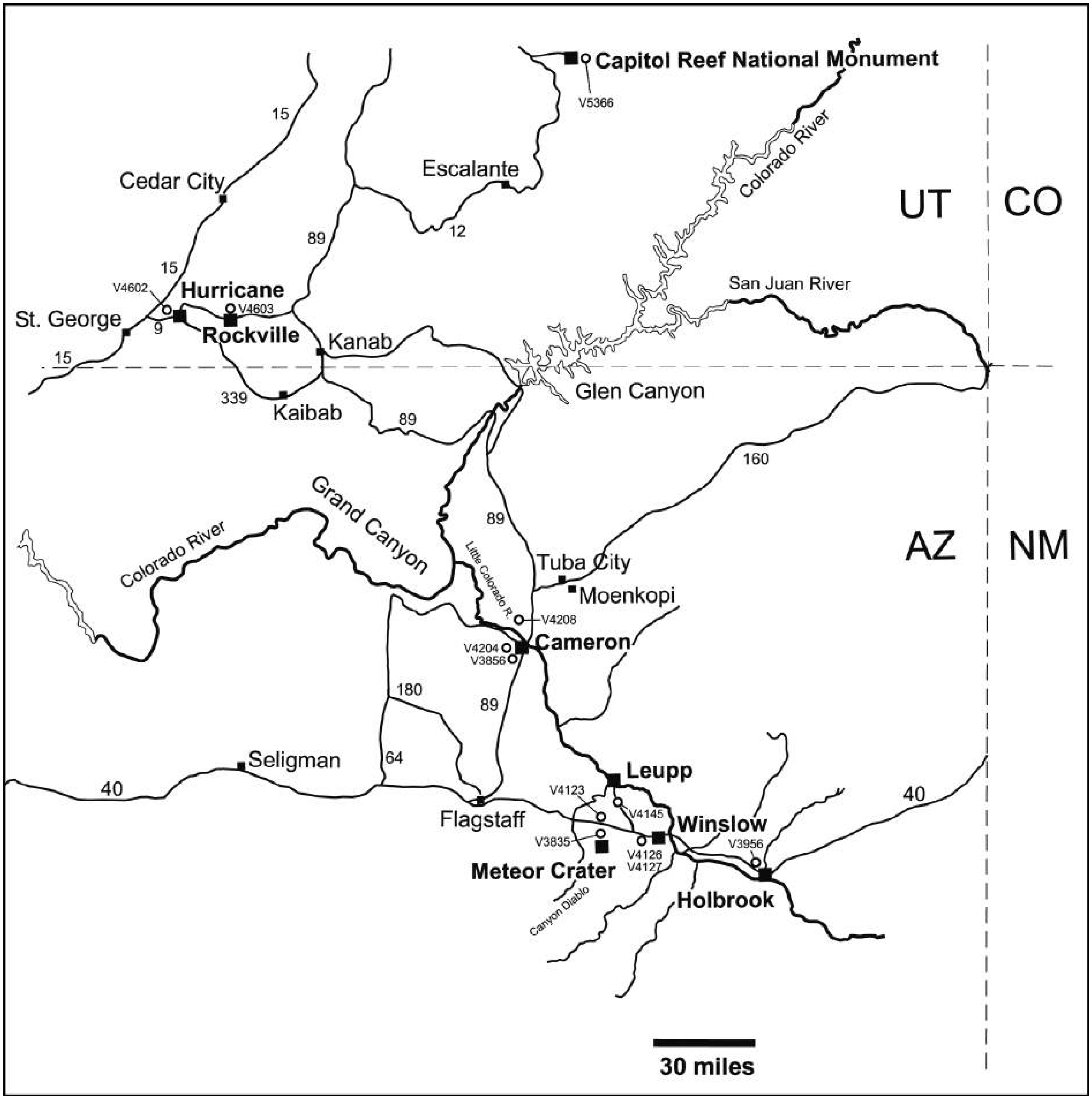

FIGURE 75. Map showing distribution of Moenkopi Group track localities in Arizona and Utah. From Klein and Lucas (2010b).

the upper Moenkopi Formation (Holbrook Member) to *Chirotherium barthii*, *C. sickleri*, *C. rex*, *Isochirotherium marshalli*, *Synaptichnium cameronense*, *Rotodactylus cursorius* ("*Rotodactylus mckeei*"), *R. bradyi*, *Rhynchosauroides schochardti* ("*Rhynchosauroides moenkopiensis*"), *Therapsipus cumminsi*, and tetrapod footprints indet. (?capitosaurid) (Fig. 87-91).

New Mexico

Only one tetrapod tracksite has been discovered in strata of the Moenkopi Formation in New Mexico, in the Anton Chico Member at Bluewater Creek in Cibola County (Lucas and Hayden, 1989; Hunt and Lucas, 1993; Lucas et al., 2003). Tracks at this site are not numerous and are poorly preserved. They have been assigned to *Chirotherium*, *Therapsipus* and *Characichnos* (Fig. 92).

Chinle Group/ Glen Canyon Group

Upper Triassic nonmarine strata of western North America mostly pertain to the Chinle Group and have yielded an important record of tetrapod tracks over the last 100 years (e.g., Riggs, 1904; Lockley and Hunt, 1995). There is an extensive literature on these ichnofaunas, and Hunt and Lucas (2007) provided the most recent synthesis.

Lucas (1993) named the Chinle Group to encompass a genetically-related suite of nonmarine redbeds in western North

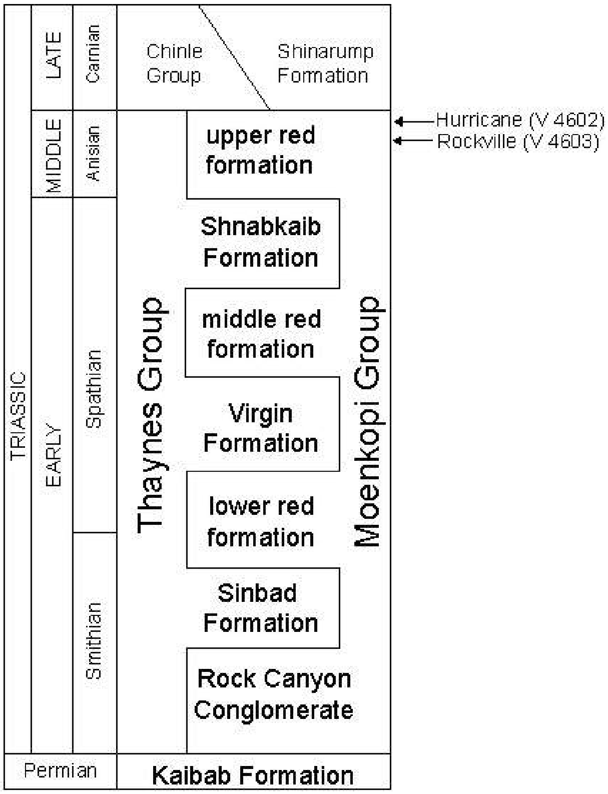

FIGURE 76. Moenkopi Group subdivisions and position of tracksites in southwestern Utah. From Klein and Lucas (2010b).

America that extends from Idaho in the north to Texas in the south (Fig. 93A). The Chinle Group is composed of a number of formations that, in general, include a basal conglomeratic interval (e.g., Shinarump, Gartra, Camp Springs formations), a lower fine-grained interval (e.g., Blue Mesa Member of Petrified Forest Formation; Bluewater Creek, Tecovas, Garita Creek and Monitor Butte formations), a medial, sandstone-dominated interval (e.g., Sonsela Member of Petrified Forest Formation; Moss Back, Poleo and Trujillo formations), an upper fine-grained interval (e.g., Painted Desert Member of Petrified Forest Formation; Bull Canyon and Owl Rock formations) and an upper silty/fine sandstone interval (Rock Point, Redonda, Sloan Canyon formations) (Fig. 93B).

Overlying, Upper Triassic strata at the base of the Glen Canyon Group include parts of the Wingate and Moenave formations. The Wingate Sandstone is a prominent, cliff-forming unit in the Four Corners region that thins and is erosionally truncated to the east and south, and interfingers laterally to the west, with the Dinosaur Canyon Member of the Moenave Formation (e.g., Harshbarger et al., 1957; Clemmensen et al., 1989). Over much of its outcrop belt, the Wingate Sandstone appears to conformably overlie the sheet sandstones and siltstones that comprise the Rock Point Formation of the Chinle Group (*sensu* Lucas, 1993; Lucas et al., 1997b, 2006c; Lucas and Tanner, 2007). The Dinosaur Canyon Member, as described at the type area east of Cameron, Arizona, comprises siltstones and sandstones, in varying proportions, deposited in streams, lakes and eolian dunes at the margin of the Wingate erg (Harshbarger et al., 1957; Clemmensen et al., 1989; Lucas et al., 2006b, c; Tanner and Lucas, 2007).

Locally, portions of the upper Chinle Group in New Mexico may be age equivalent to the lower Wingate Sandstone and Dinosaur Canyon Member. These units are the Sheep Pen Sandstone of northeastern New Mexico and the Wallace Ranch Member of the Redonda Formation in east-central New Mexico, which at times has been termed Wingate.

The Chinle Group has an extensive record of vertebrate body-fossils including temnospondyls, therapsids, mammals, phytosaurs and other non-archosaurian archosauriforms, aetosaurs, poposauroids, "rauisuchids," crocodylomorphs, pterosaurs, nondinosaurian dinosauromorphs and theropods. Here, we review the Chinle Group tetrapod ichnoassemblages in temporal order, from oldest to youngest (Figs. 94-96).

Otischalkian

St. George, Utah–The only possible Otischalkian tetrapod track localities in western North America are from the Shinarump Formation of southwestern Utah (Lockley and Milner, 2006). Two localities yield specimens of swimming traces and the tracks of a small ?theropod.

Adamanian

Petrified Forest National Park, Arizona– Tetrapod tracks have been reported at four localities in Petrified Forest National Park (Santucci and Hunt, 1993; Santucci et al., 1995, 1998, 2006: Martin and Hasiotis, 1998; Hunt et al., 2005b; Hunt and Lucas, 2006a), but only one, in sandstone in the Teepees area, is Adamanian in age. This locality is in the Newspaper Rock Bed of the upper Carnian Blue Mesa Member (Adamanian lvf; St. Johnsian sub-lvf), not the Monitor Butte Member as reported by Martin and Hasiotis (1998). Specimens from this locality have been described or mentioned by several authors (Caster, 1944; Santucci and Hunt, 1993; Santucci et al., 1995; Martin and Hasiotis, 1998; Hunt et al., 2005b; Santucci et al., 2006). This unit has produced the majority of walking traces from the park, included numerous specimens of the limulid trace *Kouphichnium* (Caster, 1944; Hunt et al., 1993b). The tetrapod tracks from this locality are: *Rhynchosauroides* isp., cf. *Grallator* isp., *Eubrontes* isp., and indeterminate large tracks and swimming traces. This is the oldest occurrence of *Eubrontes* in the western USA (Hunt et al., 2006a).

Gateway, Colorado– Tracks have been known for more than 30 years from the Alabaster Box Mine in the Gateway area (Parrish and Lockley, 1984; Lockley and Jennings, 1987; Lockley and Hunt, 1995; Gaston et al., 2003). These tracks are from stratigraphically low in the Chinle Group, just above the Shinarump Formation, probably from the Monitor Butte Formation (Adamanian). Specimens from this locality pertain to cf. *Grallator* isp. and cf. *Brachychirotherium* isp.

Fort Wingate, New Mexico– There is a small number of specimens from the Bluewater Creek Formation (Adamanian) near Fort Wingate in west-central New Mexico (Hasiotis et al., 1994; Heckert et al., 2000; Lucas and Heckert, 2002). These specimens represent *Grallator* isp. and aff. *Brachychirotherium* isp. (Lucas and Heckert, 2002; Hunt and Lucas, 2006a).

Conchas Dam, New Mexico– Hunt and Lucas (2001) described a tetrapod track from the Garita Creek Formation (Adamanian; Lamyan) near Conchas Dam in east-central New Mexico. This poorly preserved specimen likely represents *Brachychirotherium* isp.

Revueltian

Petrified Forest National Park, Arizona– There are two Revueltian track localities in Petrified Forest National Park (Hunt et al., 2006a). Both are in the Agate Bridge Bed of the Sonsela Member of the Petrified Forest Formation: (1) near the Rainbow Forest (*Rhynchosauroides* isp. and cf. *Barrancapus* isp.); and (2) Flattops area (*Rhynchosauroides* isp.).

Barranca Creek, New Mexico– The Barranca Creek badlands in east-central New Mexico yield a large body fossil fauna and a small tetrapod ichnofauna (Hunt et al., 1993a; Hunt, 2001). This ichnofauna from the Bull Canyon Formation (Revueltian; Barrancan) includes the holotype of *Barrancapus cresapi* and swimming traces (Hunt et al., 1993a; Hunt et al.,

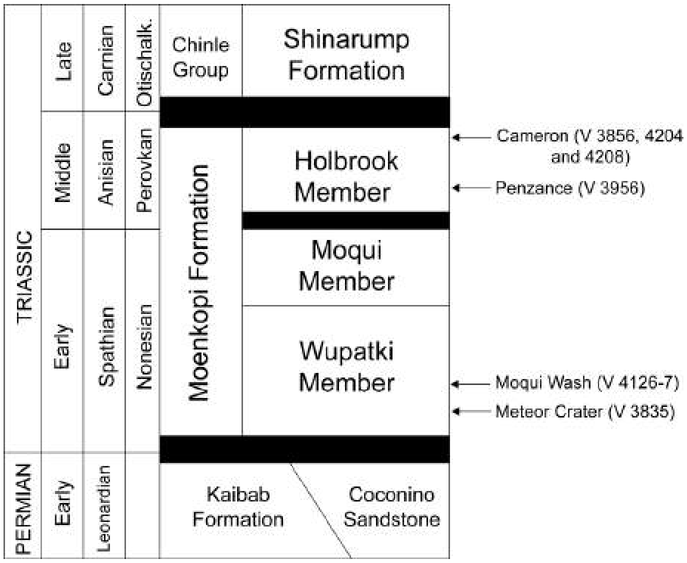

FIGURE 77. Moenkopi Formation subdivisions and position of tracksites in northern Arizona. From Klein and Lucas (2010b).

2001).

Grand Staircase-Escalante National Monument, Utah– The only Revueltian tracksites in the Chinle Group in Utah are at Grand Staircase-Escalante National Monument in Utah. The Brinkerhof locality is in the upper portion of the Owl Rock Formation in the northeastern Circle Cliffs (Foster et al., 2000). The most unusual specimen from this locality is a trackway of *Apatopus lineatus*, a taxon very rare in the Chinle Group. Other specimens represent *Rhynchosauroides* isp. and ?*Gwyneddichnium* isp. A second locality at Long Canyon Pass yields tracks of *Grallator* isp. and *Evazoum* isp. (Hamblin and Foster, 2000; Foster et al., 2003).

Apachean

Hunt and Lucas (1992) first noted that the majority of tracks from the Chinle Group are from the upper part of the lithosome, the Apachean interval. Recently, Lucas and coworkers (e.g., Lucas et al., 2006b-c) have demonstrated that the lower track-bearing portions of the Wingate Sandstone and Dinosaur Canyon Member of the Moenave Formation are also of latest Triassic (Apachean) age (Lucas and Tanner, 2007; Lucas et al., 2011; Lucas and Tanner, 2015).

Wind River basin, Wyoming– Branson and Mehl (1932) described *Agialopous wyomingensis* from the Bell Springs Formation of the Wind River basin (Lucas, 1994). This ichnotaxon is a subjective junior synonym of *Grallator cursorius*.

Glen Canyon National Recreation Area and vicinity, Utah– The spectacular canyons of the Glen Canyon area expose extensive outcrops of the Chinle Group and Wingate Sandstone. The only track record from the Rock Point Formation (Chinle Group) within Glen Canyon National Recreation Area is *Atreipus milfordensis*, the only western occurrence of this ichnogenus (Lockley et al., 1992d, 1998; Lockley and Hunt, 1995). The cliff-forming Wingate Sandstone in this area yields many more tracks, but all are assignable to *Grallator cursorius* (Riggs, 1904; Lockley et al., 1992d, 1998; Lockley and Hunt, 1995). North of the recreation area, the Rock Point Formation yields numerous specimens of *Grallator cursorius* in the Dirty Devil River valley (Lockley and Eisenberg, 2006).

Shay Canyon, Utah– Shay Canyon, east of Canyonlands National Park, preserves a large tracksite in the Rock Point Formation. This tracksite includes multiple specimens and long trackways (Lockley and Hunt, 1995, figs. 3.8-3.10). The ichnofauna includes *Brachychirotherium*, *Anchisauripus* and *Pentasauropus* (Lockley, 1986; Lockley and Hunt, 1995).

Dinosaur National Monument Area, Utah– Strata of the Rock Point Formation in and around Dinosaur National Monument in northeastern Utah have yielded a diverse ichnofauna, including: *Gwyneddichnium majore*, *Brachychirotherium parvum*, *Grallator cursorius*, *Evazoum sirigui*, *Eosauropus* isp. and a synapsid track (Lockley et al., 1991, 1992a-c; Lockley, 2006).

In northeastern Utah, the basal unit of the Glen Canyon Group, the "Glen Canyon Sandstone," is equivalent to the Wingate Sandstone (Poole and Stewart, 1964). About 7 m above its base are tracks of *Brachychirotherium* reported by Lockley et al. (1992a-c), who also mentioned probable *Grallator* and *Eosauropus* tracks from the Wingate Sandstone equivalent in this area (Lucas et al., 2006b-c).

Moab, Utah– There are several tracksites in the Rock Point Formation in the Moab area that include assemblages with *Grallator* isp., *Atreipus* isp. and *Eoanomoepus latus* (Lockley and Gierliński, 2009; Lockley et al., 2018; Foster and Lockley, 2019). Tracks are more common in the overlying Wingate Sandstone. There are two *in situ* tracksites in the lower part of the Wingate in Kane Springs Canyon, south of Moab, about 15 m above the base of the Wingate (Lucas et al., 2006b). These sites yield numerous *Grallator cursorius* and *Brachychirotherium* isp. and less common *Eosauropus* isp. Two sites north of Moab, near Corral Canyon, are about 2 m above the Wingate base and yield numerous *Grallator cursorius* and *Brachychirotherium* isp. (Lucas et al., 2006b). The total thickness of the Wingate Sandstone in the Moab area is about 100 m, so these tracksites are stratigraphically very low in the Wingate (Lucas et al., 2006b).

Indian Creek, Bears Ears National Monument, Utah– The Rock Point Formation from this area yielded small chirotheriid pes and manus imprints that were identified as the first "*Chirotherium*" *lulli* tracks from western North America (Milner et al., 2021).

Northwestern Colorado– The Rock Point Formation in northwestern Colorado yields a significant ichnofauna that includes *Grallator cursorius*, *Rhynchosauroides* isp. and *Gwyneddichnium majore* (Lockley and Gillette, 1989; Lockley and Hunt, 1995; Lockley, 2006).

Colorado National Monument, Colorado– In Colorado National Monument near Grand Junction, there are six tracksites in the Wingate Sandstone. These sites yield tracks assignable to *Grallator cursorius*, *Eosauropus* isp., ?*Brachychirotherium* isp. and ?*Brasilichnium* isp. The tetrapod tracks in the Wingate Sandstone at Colorado National Monument are in the lower one-fourth of the unit (Lucas et al., 2006b).

Gateway, Colorado– The deep canyons associated with the Dolores River Valley south of Gateway yield abundant tracks in the uppermost Rock Point Formation. This ichnofauna includes *Rhynchosauroides* isp., *Brachychirotherium* isp., *Grallator cursorius*, *Evazoum gatewayensis*, *Eosauropus cimarronensis* and *Pentasauropus* isp. (Lockley et al., 1996, 2004; Gaston et al., 2003; Lockley and Lucas, 2013).

Lockley et al. (2004) reviewed the numerous tracksites in the Wingate Sandstone in this area (also see Lockley, 1991; Lockley and Hunt, 1995; Schultz-Pittman et al., 1996; and Lockley and Peterson, 2002). Most of the Wingate tracks in this area are on fallen blocks (though a few sites *are* in situ) that can be confidently assigned to the lower third of the Wingate Sandstone cliff (Lucas et al., 2006b). The tracks are mostly *Grallator cursorius* and *Brasilichnium elusivum*, but also include records of *Brachychirotherium* isp. and *Eosauropus* isp. (Lockley, 1991; Lockley and Hunt, 1995; Schultz-Pittman et al., 1996; Lockley and Peterson, 2002; Lockley et al., 2004; Lucas

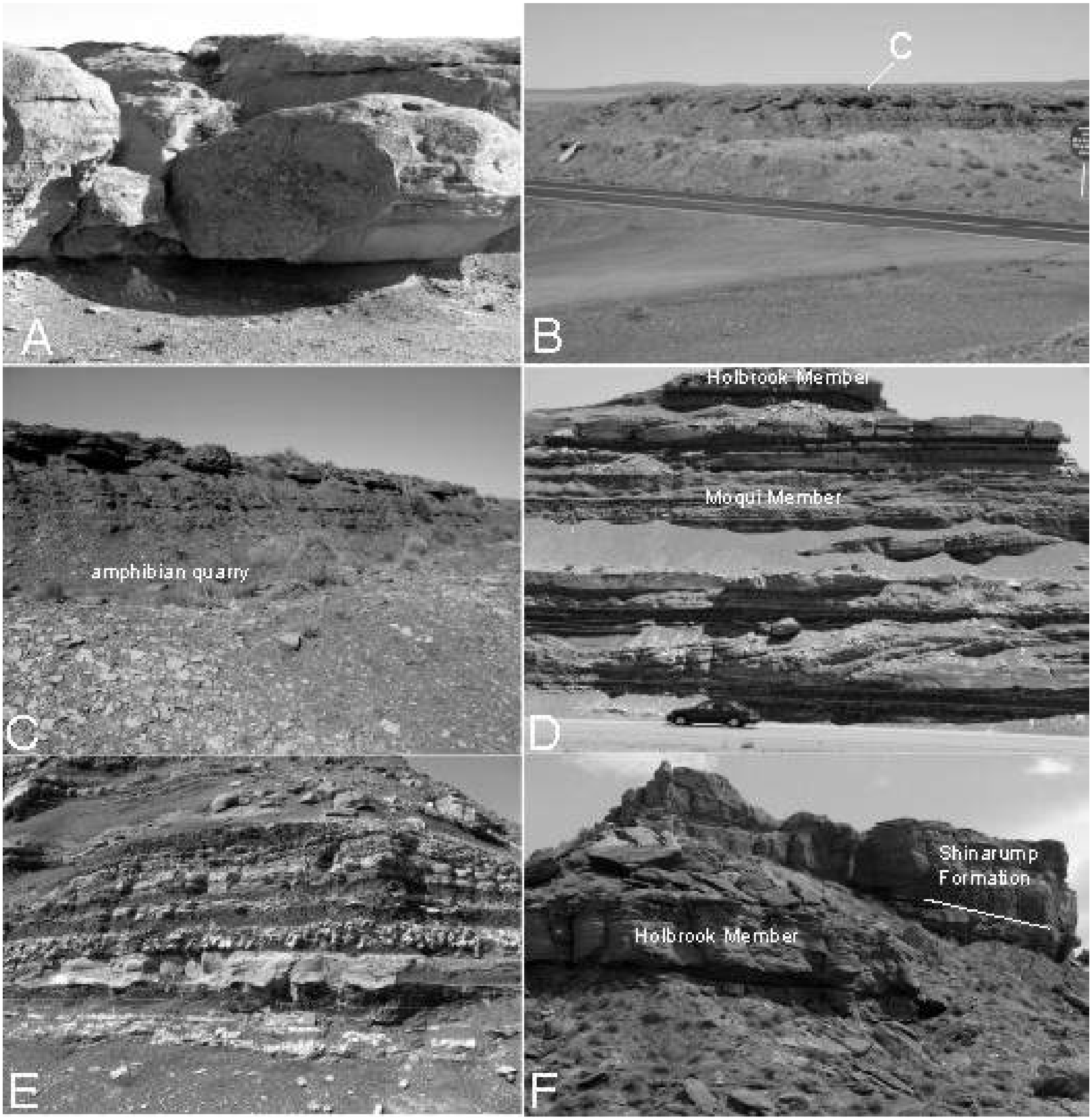

FIGURE 78. Moenkopi Fm. outcrops in northern Arizona. **A,** Lower massive sandstone of Wupatki Member (Olenekian) near Winslow. **B,** Amphibian quarry in Wupatki Member near Metor Crater, Winslow, where numerous vertebrate skeletons and footprints have been discovered by S.P. Welles, F.E. Peabody and others; C demarcating track-bearing sandstone. **C,** Amphibian Quarry, detail. **D-E,** Gypsiferous Moqui Member outcrops near Holbrook. **F,** Holbrook Member (Anisian) overlain by Shinarump Fm. (Chinle Group, Carnian) near Holbrook. From Klein and Lucas (2010b).

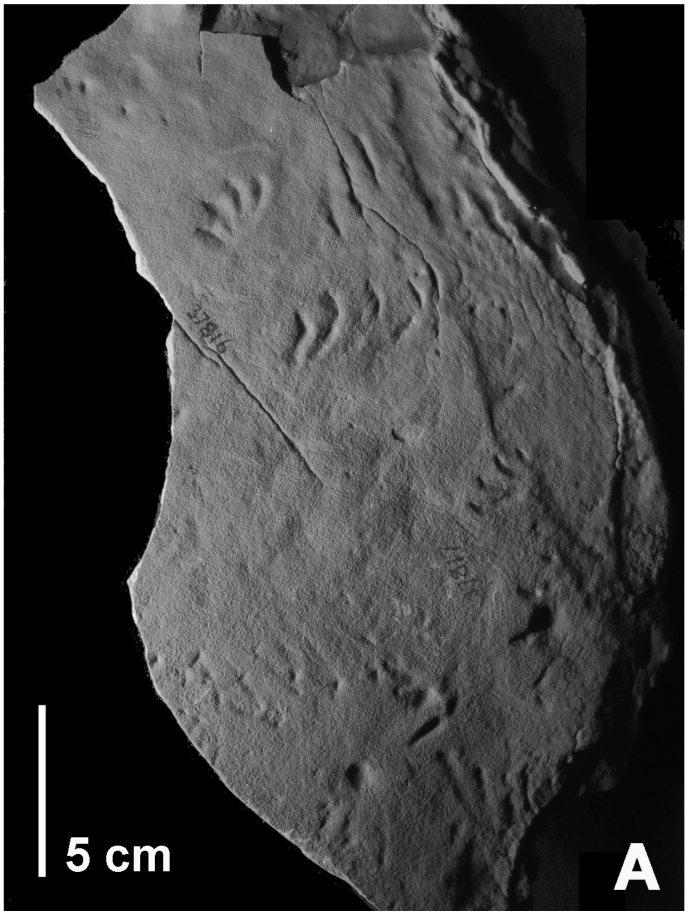

FIGURE 79. *Rhynchosauroides* isp. pes and manus imprints from Wupatki Member of Moenkopi Fm. near Meteor Crater.

et al., 2006b; Lucas and Tanner, 2007).

Southeastern Colorado– In southeasternmost Colorado, there are limited exposures of track-bearing Upper Triassic strata. The largest tracksite is in Furnish Canyon, where multiple trackways of *Eosauropus cimarronensis* are preserved in the Sloan Canyon Formation (Lockley et al., 2001). Closer to the Three Corners area, the Sheep Pen Sandstone yields a small ichnofauna that includes *Grallator cursorius* and ?*Brachychirotherium* (Conrad et al., 1987). From the Alejandro Canyon area of the Pugatoire Valley, McClure et al. (2021) described an *Eosauropus* trackway with 17 consecutive pes and a few manus tracks.

Ward Terrace, Arizona– On Ward Terrace, in the Navajo Nation of northeastern Arizona, the Moenave Formation is about 100 m thick and is mostly fine-grained sandstone, siltstone and minor shale (Lucas et al., 2006b). In the lower part of the Moenave Formation, eolian sandstones represent an interfingering tongue of the Wingate Sandstone that is well exposed from Tohachi Wash to Dinosaur Canyon (Lucas et al., 2005, 2006b; Lucas and Tanner, 2007). In this Wingate tongue, there is a tracksite that covers an area of approximately 930 m^2. Morales (1986) first reported this tracksite, at which the majority of tracks pertain to *Grallator cursorius*, but there are also small (up to 6 cm long), poorly preserved tracks that may be synapsid, and large tracks of *Eosauropus* isp. (Lucas et al., 2006b).

Dry Cimarron Valley, New Mexico– The deep canyon of the Dry Cimarron Valley parallels the New Mexico/Colorado border and exposes a Triassic-Cretaceous sequence of strata. The largest tracksite in this area is preserved in the Sloan Canyon Formation at Peacock Canyon (Conrad et al., 1987). Extensive exposures of several bedding planes expose multiple trackways (Conrad et al., 1987, fig. 3). The ichnofauna includes *Rhynchosauroides* isp., *Apatopus lineatus*, *Brachychirotherium eyermani*, *Grallator cursorius*, *Eosauropus cimarronensis* and a possible therapsid.

Farther east down the valley are track-bearing exposures in the Sloan Canyon area. Here, a tracksite in the Sloan Canyon Formation yields *Brachychirotherium* isp., ?*Eosauropus* isp. and *Anchisauropus sillimani* (Lockley and Hunt, 1993). In the same drainages, an exposure of the overlying Sheep Pen Sandstone contains a tracksite with *Grallator cursorius* and *Evazoum sirigui* (Lockley et al., 1993).

East-central New Mexico– The mesalands of Quay County contain extensive exposures of the upper Chinle Group. The Redonda Formation (San Jon Creek Member: Lucas et al., 2006a) yields ichnofaunas in two areas (Lucas et al., 2010). At Mesa Redonda, an extensive ichnofauna has been collected for three-quarters of a century and includes *Brasilichnium elusivum*, *Rhynchosauroides* isp., *Gwyneddichnium majore*, *Brachychirotherium parvum*, *Grallator cursorius* and *Evazoum sirigui* (Hunt and Lucas, 1989; Hunt et al., 1989; Lockley et al., 2000; Lucas et al., 2001; Klein et al., 2006; Lucas et al., 2010; Figs. 94-96). 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* spp., *Grallator cursorius* and *Evazoum sirigui* (Hunt and Lucas, 1989; Hunt et al., 2000; Lucas et al., 2001, 2010).

Oklahoma Panhandle– Cimarron County, in the easternmost Panhandle of Oklahoma, has limited outcrops of Upper Triassic strata. The Sheep Pen Sandstone in this area contains well-preserved specimens of *Grallator cursorius* and ?*Brachychirotherium* isp. (Conrad et al., 1987).

Newark Supergroup

The Newark Supergroup (Froelich and Olsen 1984) encompasses the thick succession of nonmarine sedimentary and intercalated igneous rocks of Triassic-Jurassic age that fill a series of half-graben extensional basins developed along the eastern seaboard of North America (Fig. 97). At least 13 large basins and a number of small basins expose these strata at the surface, and an extensive series of related structures are buried by the thick, post-rift strata on the continental shelf. The Newark

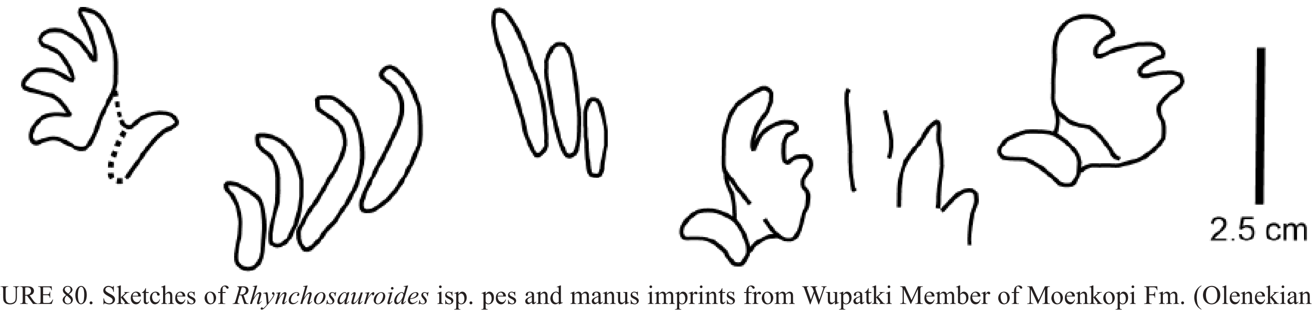

FIGURE 80. Sketches of *Rhynchosauroides* isp. pes and manus imprints from Wupatki Member of Moenkopi Fm. (Olenekian) of Arizona. From Klein and Lucas (2010b).

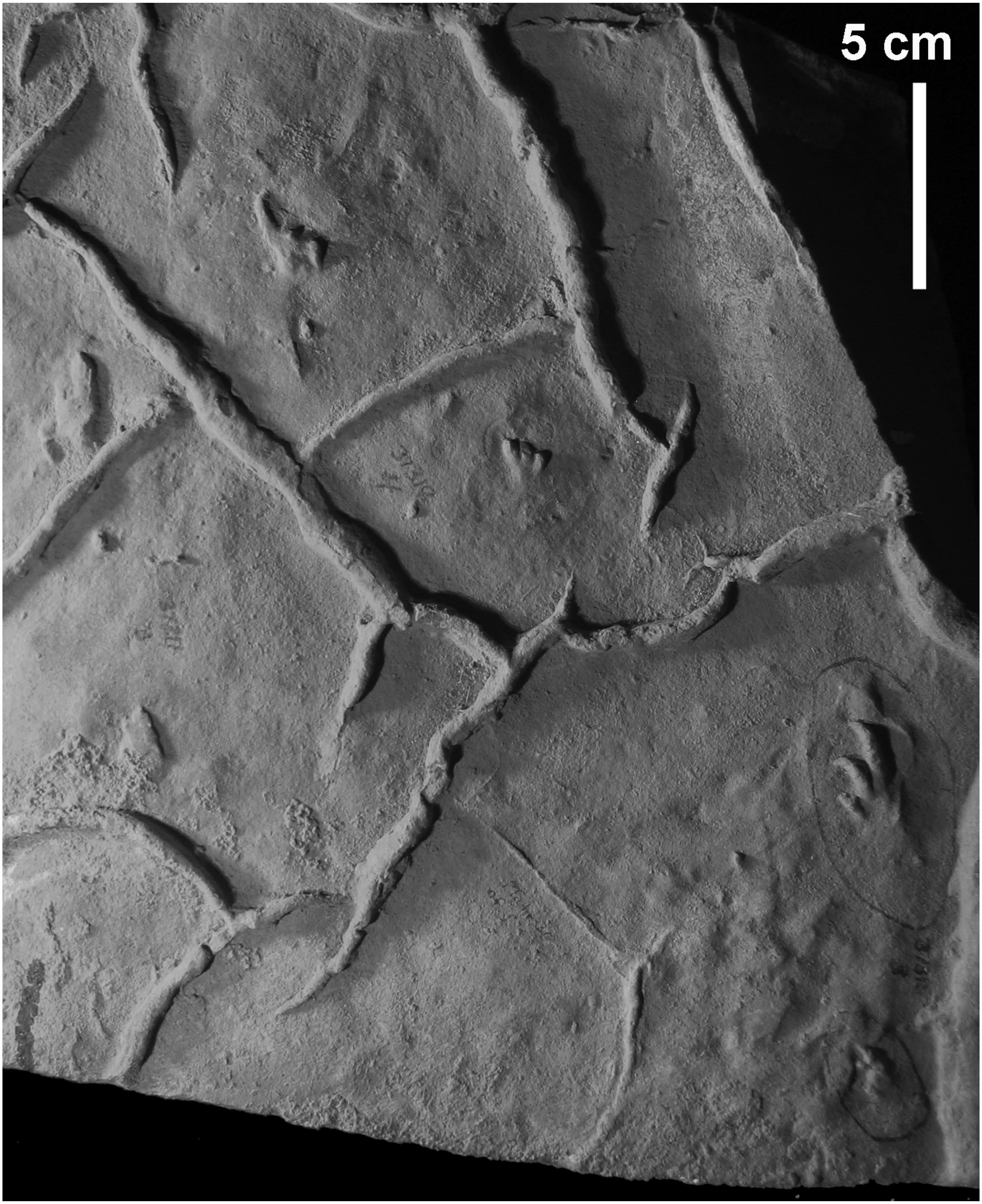

FIGURE 81. Slab with *Rotodactylus cursorius* trackways from Wupatki Member of Moenkopi Fm. (Olenekian) near Meteor Crater, Arizona.

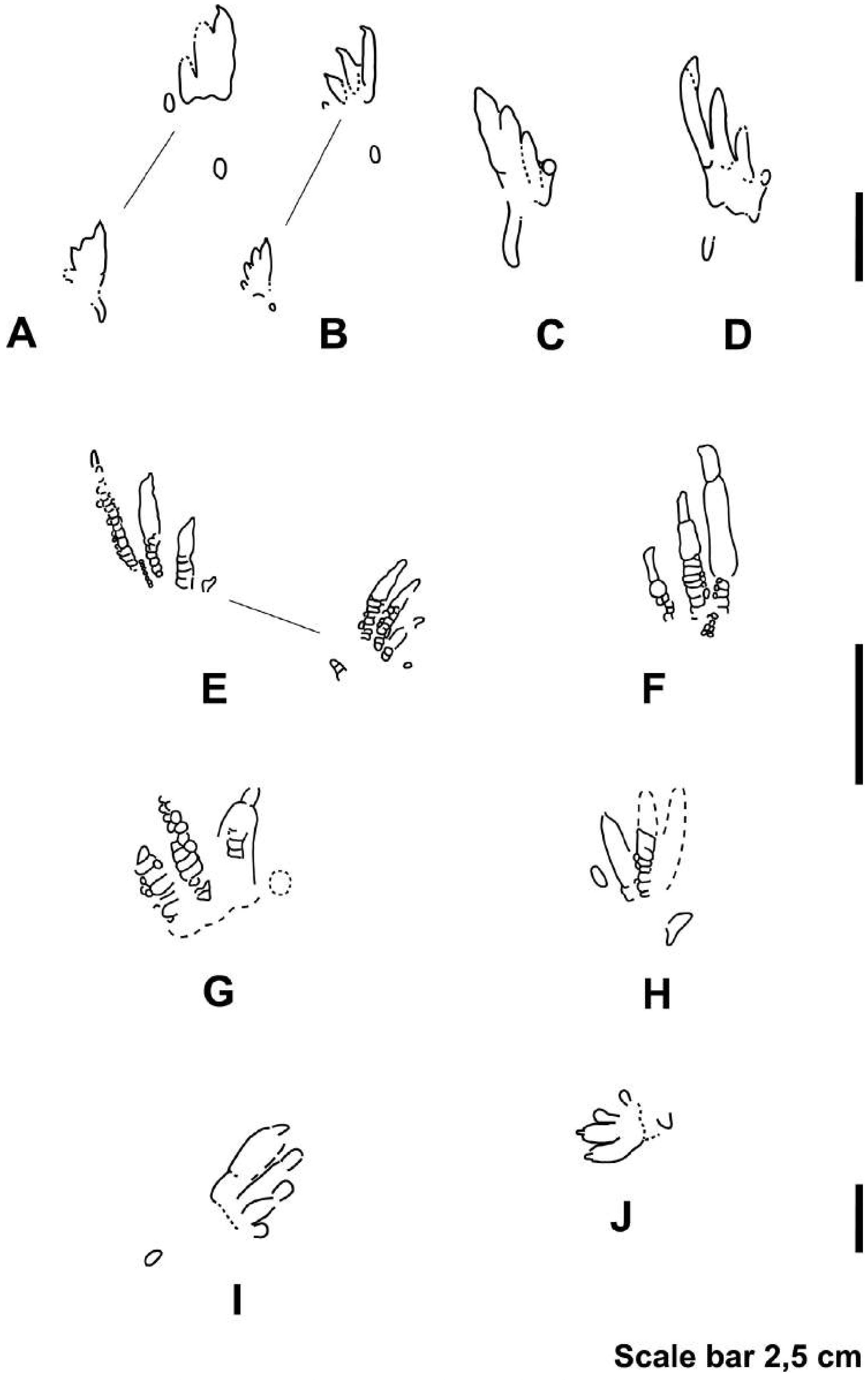

FIGURE 82. *Rotodactylus* footprints from Moenkopi Fm. of Arizona and Utah as sketches. **A-H,** *Rotodactylus cursorius* from Wupatki Member (Olenekian). **I-J,** *R. bradyi* from Holbrook Member (Anisian). From Klein and Lucas (2010b).

FIGURE 83. *Synaptichnium diabloense* trackway from Wupatki Member of Moenkopi Fm. (Olenekian) of Amphibian Quarry near Meteor Crater, Arizona.

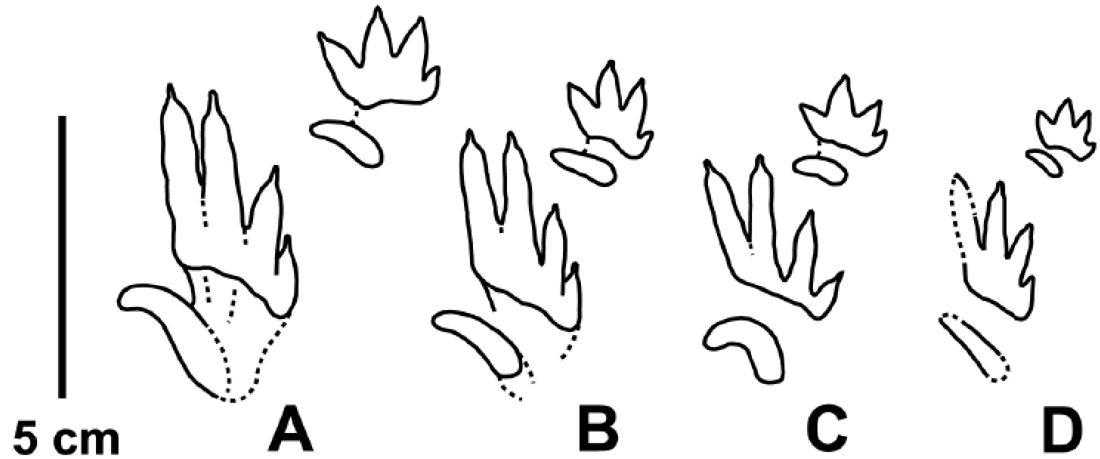

FIGURE 84. *Synaptichnium diabloense* pes and manus imprints from Wupatki Member of Moenkopi Fm. (Olenekian) as sketches. From Klein and Lucas (2010b).

synrift basins parallel the Appalachian orogeny, and their origin is attributed to early Mesozoic crustal extension concurrent with the initial breakup of Pangea (e.g., Manspeizer et al., 1978; Manspeizer, 1982, 1988; Olsen, 1997).

A diverse vertebrate fauna is known from skeletal remains belonging to fishes, amphibians, procolophonids, archosauromorphs and archosaurs. In particular, the well preserved skeleton of *Postosuchus alisonae* is a very spectacular fossil that has been found in the Deep River Basin of North Carolina.

The Newark has an extensive and well-known tetrapod footprint record of Early Jurassic age, the focus of the classic early studies of ichnology by Hitchcock (e. g., 1858, 1865). Nevertheless, it does include some extensive Late Triassic footprint assemblages (Fig. 98-102). Here, we review that record by depositional basin.

Fundy basin, Nova Scotia– Olsen (1997) reported poorly preserved footprints from the Honeycomb Point Formation of the Fundy basin in New Brunswick, but these have not been described. Sues and Olsen (2015) considered the Honeycomb Point Formation to be of Permian age. Indeed, Olsen and Et-Touhami (2008, fig. 22) and Sues and Olsen (2015, fig. 7), who illustrated some of the tracks, note that they are too poorly preserved to be identified but that they do not resemble typical Triassic ichnotaxa. Also note that the "Triassic" tracks from Lepreau Falls in New Brunswick reported by Sarjeant and Stringer (1978) and assigned to a new ichnospecies, *Isocampe lepreauense*, are actually from Mississippian strata and have been reassigned to *Matthewichnus* (Stimson et al., 2016).

After stratigraphic revision, tracks formerly said to be from the Wolfville Formation (now considered a member of the Passaic Formation: Weems et al., 2016) in the Fundy basin (Olsen and Baird, 1986; Olsen et al., 1989) are from the Red Head Member of the Blomidon Formation (Sues and Olsen, 2015). These tracks have been assigned to *Atreipus, Brachychirotherium, Evazoum* and *Rhynchosauroides* (Sues and Olsen, 2015). The overlying "White Water Member" of the Blomidon Formation also yields footprints assigned to *Rhynchosauroides*, cf. *Brachychirotherium*, aff. *Atreipus* and *Anchisauripus* (Sues and Olsen, 2015).

Newark basin, New Jersey-Pennsylvania– The most extensive Late Triassic footprint record in the Newark Supergroup is from the upper Stockton and the Lockatong and Passaic formations in the Newark basin. The combined ichnoassemblage includes archosaur footprints identified as *Brachychirotherium parvum*, *Chirotherium lulli*, *Apatopus lineatus*, *Atreipus milfordensis* and *Batrachopus* isp.; the other footprints belong to the ichnogenera *Dicynodontipus*, *Rhynchosauroides*, *Gwyneddichnium* and *Procolophonichnium* (Baird, 1954, 1957, 1986; Bock, 1952; Olsen, 1980, 1983, 1988; Olsen and Galton, 1984; Olsen and Baird, 1986; Olsen and Padian, 1986; Olsen and Flynn, 1989; Silvestri and Olsen, 1989; Olsen et al., 1989, 1998, 2002, 2003; Szajna and Silvestri, 1993; Santucci and Hunt, 1995; Olsen and Rainforth, 2001; Rainforth, 2003, 2005, 2007; Szajna and Hartline, 2003; Lucas and Sullivan, 2006; Osborne and Rainforth, 2006; Szajna et al., 2012).

Fillmore et al. (2017) recently documented an extensive invertebrate ichnoassemblage from the Lockatong Formation at a locality near Souderton in eastern Pennsylvania. Associated vertebrate footprints were assigned to *Atreipus, Gwyneddichnium* (also see Lucas et al., 2014), *Rhynchosauroides* and indeterminate tracks.

Culpeper basin, Virginia– Weems (1987) described an ichnoassemblage from the Blass Bluff Sandstone at the Culpeper Crushed Stone Quarry, assigning the footprints to two new ichnogenera, *Agrestipus* and *Gregaripus*, and to *Anchisauripus, Eubrontes* and *Grallator*. Olsen et al. (1989) regarded all of these footprints as indeterminate, but some are clearly assignable to *Grallator* and *Eubrontes*. Weems (1993; also see Weems 2006a, b) later assigned some of the tracks to *Kayentapus*.

Weems (2018) provides a useful summary of the Triassic tetrapod footprints from the Culpeper basin, all of which are in the Passaic Formation. In stratigraphic order (oldest to youngest) these are: (1) lower part of Manassas Sandstone Member of the Passaic Formation—*Brachychirotherium, Chirotherium* and "*Plesiornis*" (Weems and Kimmel, 1993); (2) upper part of Manassas Sandstone Member—*Brachychirotherium, Chirotherium* and *Grallator*; (3) Groveton Member at the Culpeper Crushed Stone Quarry (see above) and nearby localities—*Brachychirotherium, Gwyneddichnium, Grallator*, *Kayentapus* and *Rhynchosauroides*; and (4) Catharpin Creek Member—*Grallator*.

Richmond basin, Virginia--From the Richmond basin of Virginia, Shaler and Woodworth (1899) published an outline drawing of footprints from the "Productive coal measures," which is the Vinita Member of the Doswell Formation. These are tracks of chirotheres, a theropod and ?*Rhynchosauroides*.

Dan River-Danville basin, North Carolina-Virginia– The Cow Branch Formation in the Solite Quarry, Virginia, has yielded footprints identified as *Apatopus, Atreipus, Grallator* and *Gwyneddichnium* (Olsen, 1988; Olsen et al., 1978, 1989).

FIGURE 85. (facing page) *Chirotherium sickleri* pes-manus set from Wupatki Member of Moenkopi Fm. (Olenekian) at locality near Meteor Crater, Arizona.


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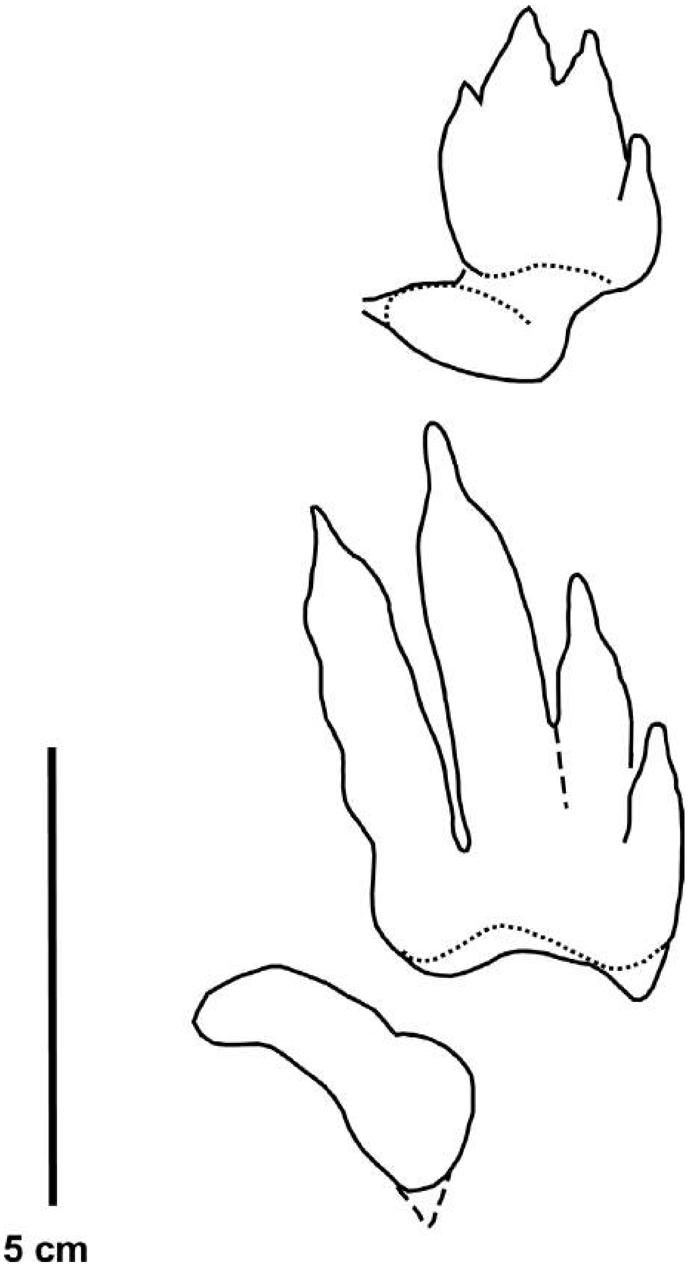


FIGURE 86. Sketch of *Chirotherium sickleri* pes-manus set from Wupatki Member of Moenkopi Fm. (Olenekian) at locality near Meteor Crater, Arizona. From Klein and Lucas (2010b).

In Pittsylvania County, Virginia, the Dry Fork Member of the Stockton Formation contains footprints named *Banisterobates* by Fraser and Olsen (1996).

Deep River basin, North Carolina– The Boren and Pomona quarries (clay pits) yield footprints from the Stockton Formation (formerly the "Middle Pekin Formation"). Only tridactyl tracks are known from the Boren pit, but footprints from the Pomona pit have been identified as *Apatopus*, *Brachychirotherium* and *Coelurosaurichnus* (Olsen, 1988; Olsen et al., 1989). This tracksite has been identified as of "middle" Carnian age and therefore the oldest footprint site in the Newark Supergroup (Olsen et al., 1989). The ichnoassemblage was described in detail by Olsen and Huber (1998), who assigned the tracks to *Brachychirotherium*, *Apatopus*, a new ichnogenus (according to them, likely made by a rauisuchian) and tridactyl tracks that are "probably" dinosaurian. As Huber et al. (1993) argued, this track assemblage is of Sanfordian (= Otischalkian) age, so it is likely Julian in age.

Greenland

Greenland has rich tetrapod footprint assemblages from the Upper Triassic Fleming Fjord Group, in particular from the Malmros Klint and Ørsted Dal formations (Norian-Rhaetian) of the eastern part of the country (Fig. 103). It is important to note that Clemmensen et al. (2020) recently revised the Triassic lithostratigraphy of East Greenland, giving the rank of a group and formation to some units formerly defined as formation and member, respectively. Jenkins et al. (1994) and Clemmensen et al. (1998) described trackways of sauropodomorphs and tridactyl theropod tracks that were assigned to the ichnogenus *Tetrasauropus* and to grallatorids by Lockley and Meyer (2000). Gatesy et al. (1999) analyzed the formation of the tridactyls with computer models. The different preservation was also the focus of Milàn et al. (2004, 2006). Ichnotaxonomically, they can be referred to the *Grallator-Anchisauripus-Eubrontes* plexus (Fig. 104). Based on new finds, the sauropodomorph tracks were re-evaluated and assigned to the ichnogenera *Eosauropus* and *Evazoum* by Lallensack (2017), mostly known from North America and Italy (Fig. 105; Lallensack et al., 2017; see also Niedźwiedzki et al., 2014 and Sulej et al., 2014). During a 2014 expedition of paleontologists and ichnologists from Denmark, Germany and Portugal, footprints of basal archosaurs were discovered that have been referred to cf. *Brachychirotherium* by Klein et al. (2015c) (Figs. 106-107). There are dozens of pes and manus tracks from small individuals (up to 4.5 cm pes length and width). Interestingly, they lack the impression of a fifth pedal digit, possibly due to their early ontogenetic stage (Klein et al., 2015c).

The Fleming Fjord Group also yielded a rich vertebrate body fossil fauna with fish (sharks, *Saurichthys*, coelacanths, lungfish), temnospondyls (*Gerrothorax*, *Cyclotosaurus*), sphenodontians, ?lepidosaurs, turtles, ?phytosaurs, ?rauisuchids, aetosaurs (*Aetosaurus*, *Paratypothorax*), pterosaurs, prosauropods (*Plateosaurus*), theropods and mammals (Mateus et al., 2014). The depositional environment can be characterized as ephemeral lacustrine.

South America

Triassic tetrapod footprints from South America are from Brazil, Bolivia and Argentina (e.g., Leonardi, 1994).

Argentina

Most of the Triassic tetrapod footprint record of South America comes from Argentina and was reviewed by Melchor and De Valais (2006) (Fig. 108A-D). Huene (1931) first reported Triassic footprints from Argentina. Extensive studies by Rusconi (1951) and Casamiquela (1964, 1975, 1984) followed, with much greater activity during the last 25 years, as reviewed by Melchor and De Valais (2006). This record is from Triassic strata in three sedimentary basins in western Argentina: (1) Ischigualasto-Villa Unión basin in San Juan and La Rioja provinces; (2) Cuyo basin in Mendoza and San Juan provinces; and (3) the Los Menucos depocenter in Río Negro Province, Patagonia. These are extensional basins that developed along the western margin of southwestern Gondwana.

The Triassic footprint record is most extensive in the Ischigualasto-Villa Unión basin, where most of the lithostratigraphic units in a very thick (2500 m +) section contain tracks:

1. The Talampaya Formation has yielded footprints assigned to *Rhynchosauroides* (cf. Melchor and De Valais, 2006, text-fig. 6C).
2. At Quebrada de Ischichuca, the Tarjados Formation yields footprints assigned to *Rhynchosauroides* and *Brachychirotherium* (Zavattieri and Melchor, 1999; Melchor et al., 2001; Melchor and De Valais, 2006) (Fig. 108D). However,

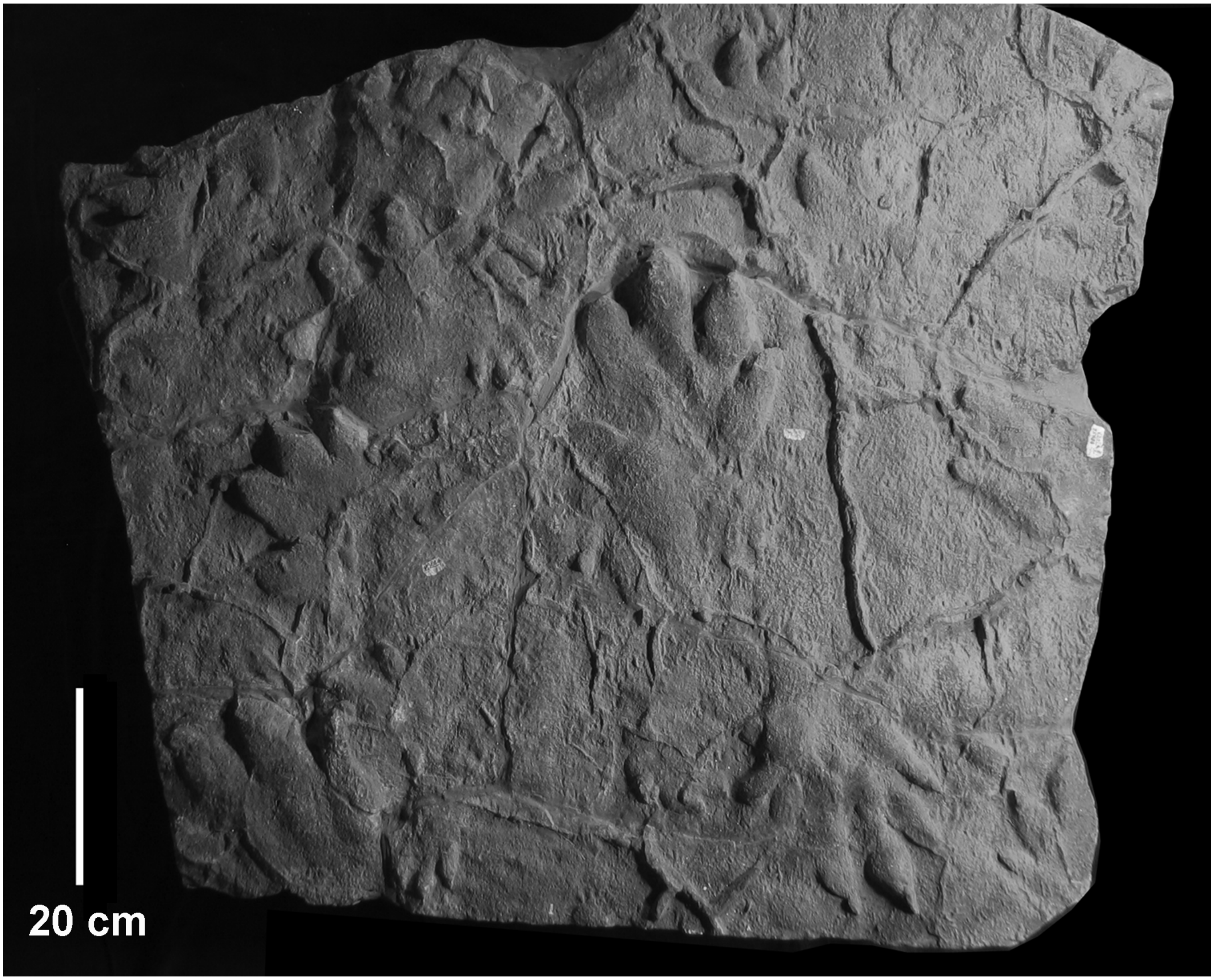


FIGURE 87. Slab with *Chirotherium barthii* (center and bottom right) and *C. rex* (holotype, left) from Holbrook Member of Moenkopi Fm. (Anisian) at Cameron, Arizona. Specimen in the University of California Museum for Paleontology, Berkeley, California.

the supposed record of *Brachychirotherium* is here considered an indeterminate chirotheriid (see systematics section above).

3. The Chañares Formation yields undetermined tridactyl footprints as well as some assigned to *Grallator* by Melchor et al. (2001) and Melchor and De Valais (2006).

4. Chirothere tracks, "*Rigalites,*" and tridactyl footprints comparable to *Anchisauripus* are known from the Ischichuca Formation (Melchor et al., 2001; Melchor and De Valais, 2006).

5. The Los Rastros Formation yielded the type material of *Rigalites ischigualastianus* Huene, 1931. That material is lost, so Melchor and De Valais (2006, p. 368) designated a plaster cast of the type trackway as a neotype. However, a type specimen must be a natural object—fossil or natural mold/cast (see ICZN, article 72.5)—not a manmade replica, so this neotype designation is invalid (Lucas and Harris, 2019). Other footprints from the Los Rastros Formation are of *Rhynchosauroides* or indeterminate tridactyl forms (Bonaparte, 1966; Rusconi, 1967; Leonardi and De Oliviera, 1990; Melchor et al., 2001, 2003; Melchor and De Valais, 2006; Marsicano, 2006, 2010).

The Middle Triassic age of the Chañares and Los Rastros formations was recently questioned by Marsicano et al. (2016), based on zircon spectrometric age dating, and the units were re-assigned by these authors to the Upper Triassic (Carnian). However, this is in contrast to all biostratigraphic data (see Lucas, 2010).

6. Only indeterminate tridactyl footprints are known from the Ischigualasto Formation (Adamanian) (Melchor and De Valais, 2006).

7. From the Los Colorados Formation (Revueltian), small pes and manus imprints of *Brachychirotherium* were described (Leonardi, 1994; Leonardi and De Oliveira, 1990; Arcucci et al., 2004; Melchor and De Valais, 2006) (Fig. 108A). Indeterminate tridactyl footprints have also been reported (Melchor and De Valais, 2006).

The Santo Domingo basin is an isolated half-graben tectonically related to the Ischigualasto-Villa Unión basin. Melchor et al. (2002) reported bird-like footprints supposedly from the upper part of the Santo Domingo Formation that were later assigned to *Gruipeda*, cf. *Alaripeda* and an inderminate ichnogenus (De Valais and Melchor, 2008). The Late Triassic age of these tracks was supposedly determined by associated fossil wood and an isotopic age of about 212 Ma. However, further research revealed that the bird-like footprints were actually from a thrust sheet of the late Eocene Laguna Brava Formation, which contains a tuff that was ^{206}Pb/^{238}U dated at about 37 Ma (Melchor et al., 2013a, b). Thus, the Late Triassic record of the bird-like tracks from the Santo Domingo Formation was in error and has been retracted. Associated footprints assigned to

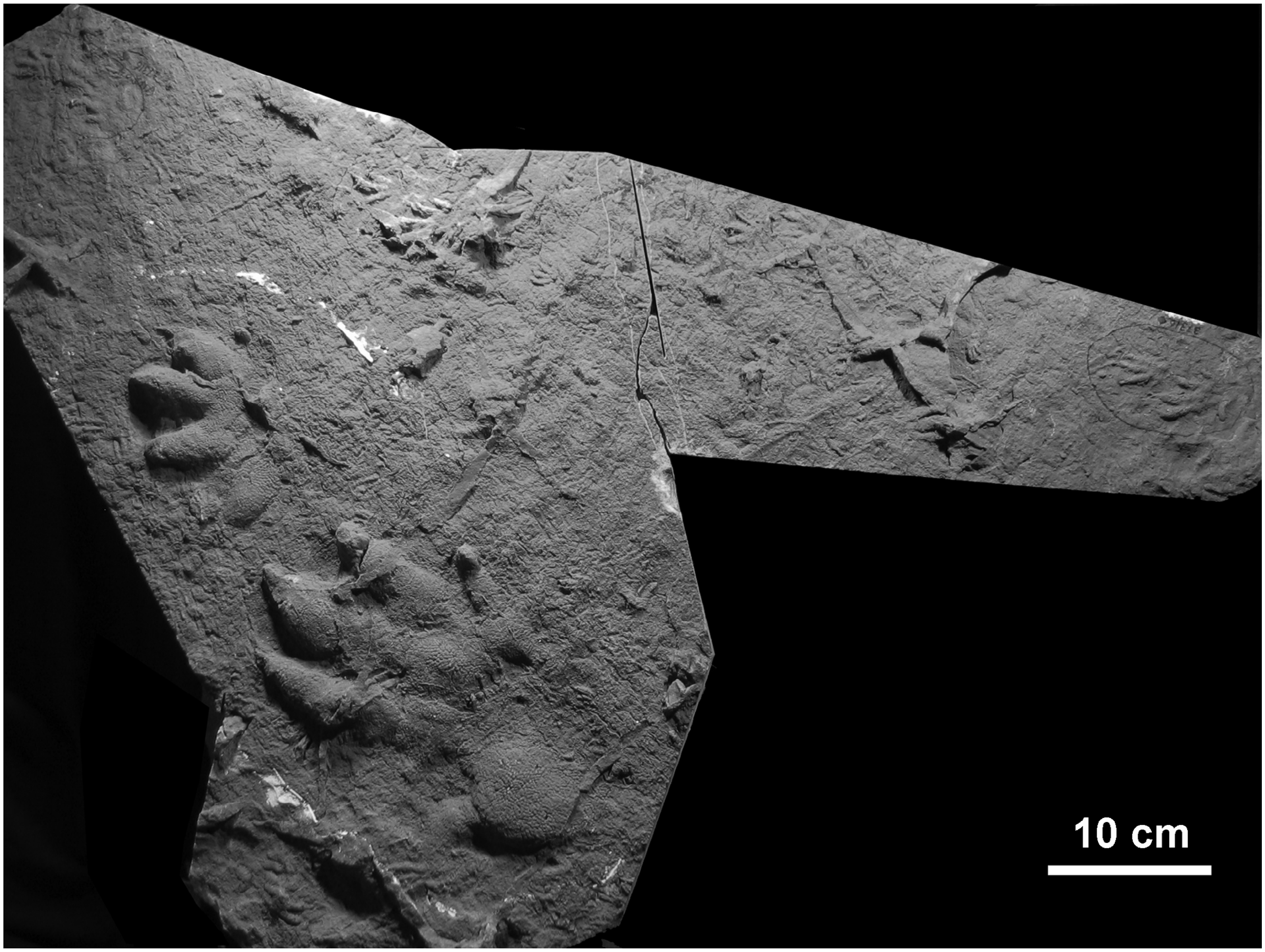


FIGURE 88. Slab with *Chirotherium barthii* pes-manus set (bottom) and *Synaptichnium cameronense* trackway (holotype, top) from Holbrook Member of Moenkopi Fm., Arizona. Specimen in the University of California Museum for Paleontology, Berkeley, California.

Dicynodontipus and *Tetrasauropus* by Melchor and De Valais (2006) are presumably mammal, but have not been reassigned.

In the Cuyo basin, the Cerro de las Cabras Formation yields a diverse footprint assemblage assigned to *Brachychirotherium*, *Chirotherium*, *Dicynodontipus*, "*Rigalites*," *Tetrasauropus* and tridactyl tracks (Melchor and De Valais, 2006). *Chirotherium* is obviously represented by the type ichnospecies *C. barthii* (Peabody, 1955). Rusconi (1951) also reported possible amphibian tracks from the Cerro de las Cabras Formation. Some therapsid tracks from this unit have recently been re-assigned to a new ichnospecies, *Pentasauropus argentinae* (Lagnaoui et al., 2019; Fig. 108C).

In the northern part of the Cuyo basin, the Rincon Blanco depocenter contains undescribed tracks from the Middle Triassic Cerro Amarillo Formation. The overlying ?Upper Triassic Portezuelo Formation yields an ichnoassemblage of likely chirothere, theropod, sauropodomorph, cynodont and dicynodont tracks described (but not assigned to ichnotaxa) by Marsicano and Barredo (2004). The illustrated chirothere tracks strongly resemble *Chirotherium barthii* and indicate a likely Middle Triassic rather than Upper Triassic age of the track-bearing strata.

A unique assemblage dominated by the footprints of therapsids comes from a volcanic-sedimentary sequence, the Vera Formation (?Early Triassic) of the Los Menucos depocenter. For many years the age of the Vera Formation had been considered Late Triassic (Carnian). Recently new discoveries of similar footprints in the Los Menucos Complex, in a position between two levels that could be more accurately dated from zircons by U-Pb radiometric methods, suggest a stratigraphic age constrained between the latest Permian (Changhsingian) and the Early Triassic (Olenekian) (Citton et al., in press). The Los Menucos assemblage includes trackways that were assigned to various new ichnotaxa by Casamiquela (1964, 1975, 1984) but referred to *Dicynodontipus* by Melchor and De Valais (2006) (but see Domnanovich and Marsicano, 2006 and Domnanovich et al., 2008 for a different ichnotaxonomy) (Fig. 108B). It also contains chirothere and sauropodomorph tracks according to Melchor and De Valais (2006). Recently Citton et al. (2018) identified large dicynodont tracks from the Vera Formation, which they assign to the ichnogenus *Pentasauropus*.

Melchor and De Valais (2006, text-fig. 10) organized the Argentine Triassic footprint record into eight ichnofaunas. Their correlations suggest that *Grallator* and tridactyl tracks are present throughout the Middle and Late Triassic and that "*Rigalites*" is restricted to the late Middle Triassic.

Brazil

Brazil has a few Triassic footprint sites, all from the southern part of the country in sediments that were deposited

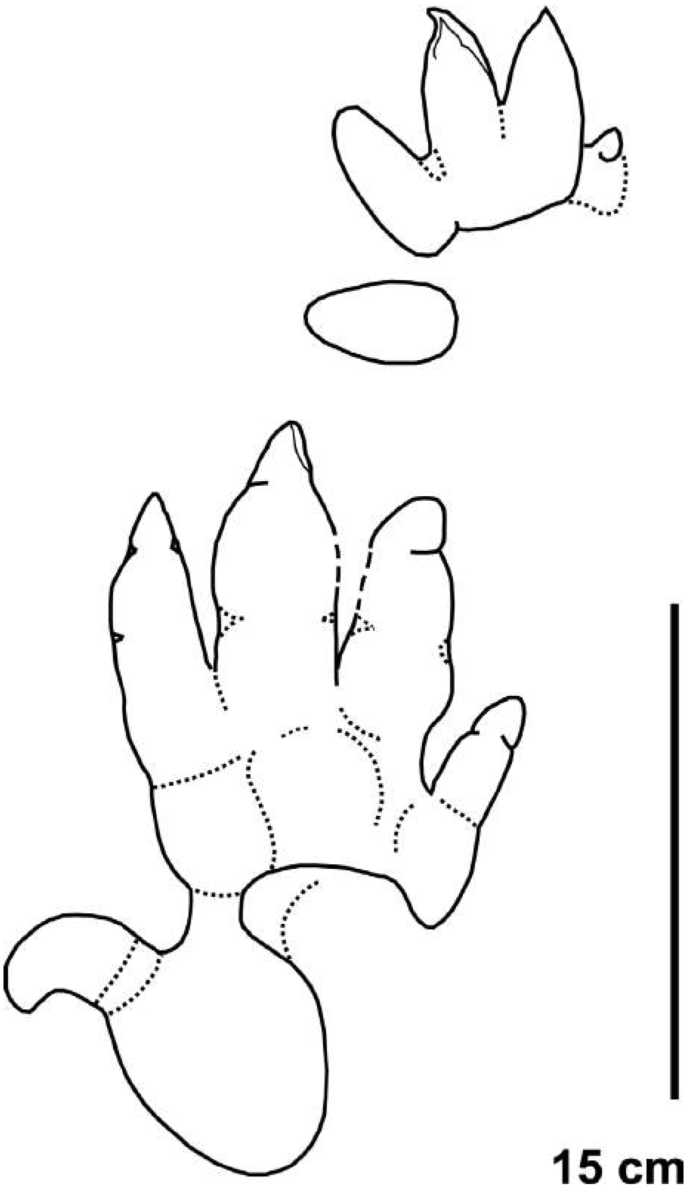


FIGURE 89. Sketch of *Chirotherium barthii* pes-manus set from Holbrook Member of Moenkopi Fm., Arizona. From Klein and Lucas (2010b).

in the intracratonic Paraná basin. Leonardi (1994) reported (but did not illustrate) a poorly preserved footprint, possibly of an amphibian or therapsid, from the Sanga do Cabral Formation, which is of Lootsbergian age (Lucas, 2010). We know of no further published information on this record. The Pirambóia Formation, eolian facies deposits of late Permian (Lopingian) and possible Early Triassic (Induan) age contains footprints that have been described by Francischini et al. (2018) and assigned to *Dicynodontipus* isp., *Chelichnus bucklandi* and indeterminate tracks.

The Upper Triassic tetrapod footprint record from Brazil is very limited. Silva et al. (2008a) described lacertoid *Rhynchosauroides* footprints from the Santa Maria Formation of southern Brazil, introducing a new ichnospecies. From the same unit, Silva et al. (2008b) documented imprints of theromorphoid or *Procolophonichnium*-like shape, which they

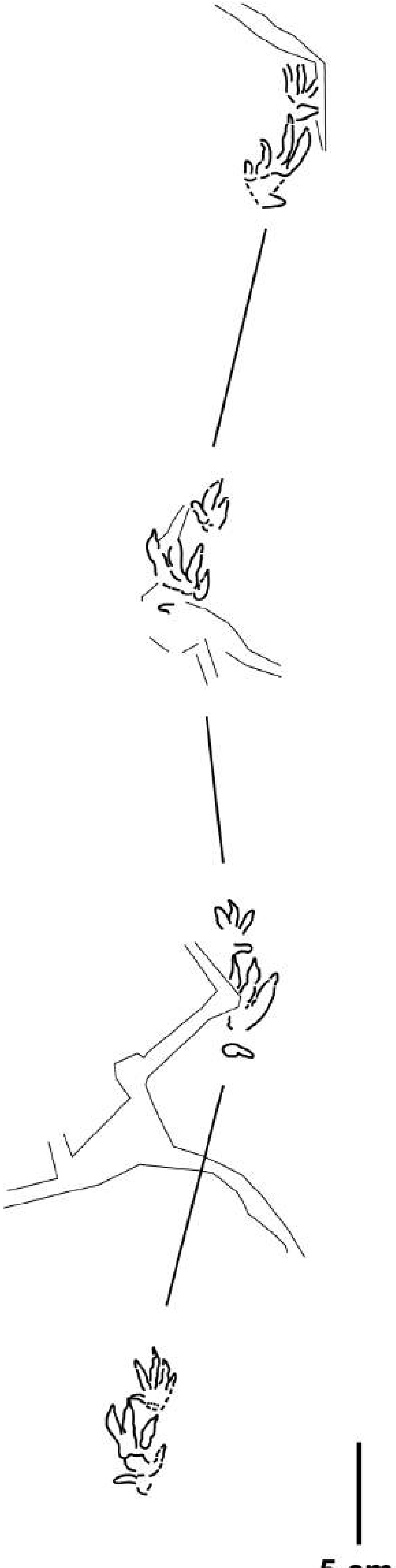


FIGURE 90. (to right) Sketch of *Synaptichnium cameronense* trackway from Holbrook Member of Moenkopi Fm. (Anisian) of Arizona. From Klein and Lucas (2010b).

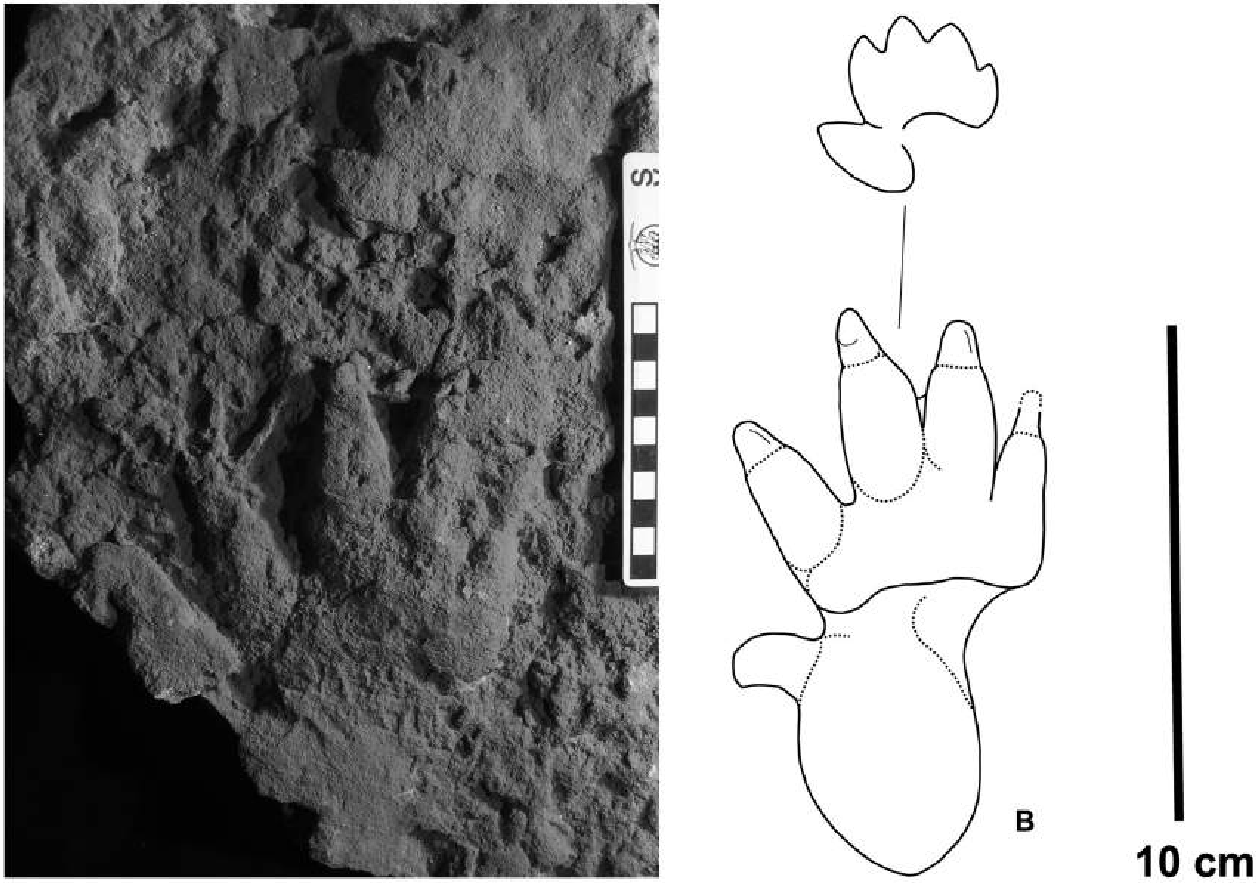


FIGURE 91. *Isochirotherium marshalli* holotype from Holbrook Member of Moenkopi Fm. **A,** Photograph. **B,** Sketch. From Klein and Lucas (2010b).

assigned to *Dicynodontipus* and another new ichnospecies. Extramorphological variation and influence of the substrate, not the anatomy of the trackmaker, is obviously responsible for many features observed in these footprints. The Santa Maria Formation is famous for its tetrapod skeletons, in particular cynodonts, rhynchosaurs, aetosaurs, "rauisuchians," sauropodomorphs and other basal saurischians (Langer et al., 1999, 2010, 2013).

Eubrontes isp. with large footprints (up to 43 cm length) come from the Caturrita Formation of Rio Grande do Sul (Silva et al., 2012). The Late Triassic (Adamanian) age of the Caturrita Formation is well established by its tetrapod body fossils with sphenodontians, procolophonids, lepidosauriforms, cynodonts, ?pterosaurs and dinosaurs (?*Guaibasaurus*) (Lucas 2010, 2018), so this is yet another Late Triassic record of *Eubrontes* (cf. Lucas et al. 2006).

Bolivia

From the Ipaguazú Formation (?Lower-?Middle Triassic) of Bolivia, Sempere et al. (2003, 2004) illustrated a chirotheriid pes-manus set and compared it with *Chirotherium barthii*. According to Fichter and Kunz (2015), it shows similarities to the ichnogenus *Protochirotherium*. We agree with this latter evaluation. If this is truly *Protochirotherium*, this would support an Early Triassic (Olenekian) age of the track-bearing strata. From the same unit, Apesteguia et al. (2020) describe two other localities with abundant trackways of medium-sized-large chirotheriids, which these authors assign to cf. *Brachychirotherium* and indeterminate chirotheriids. Some of them have formerly been described as thyreophoran tracks, and the track-bearing strata considered as Jurassic-Cretaceous (Apesteguia and Gallina, 2011). After new dating of the strata from overlying basalt rock and the re-evaluation of the tracks, Apesteguia et al. (2020) attribute the footprints to a higher level in the Ipaguazú Formation, Middle-Upper Triassic in age. The tracks described as cf. *Brachychirotherium* (Apesteguia et al., 2020) show strong similarities with "*Brachychirotherium*" described from Middle Triassic strata in France and Germany and here considered as a potential new ichnogenus (see above).

Europe

Europe has continental Triassic strata with tetrapod footprints in the Central European Basin/Germanic Basin and along the western Tethys coast in Great Britain, France, The Netherlands, Germany, Switzerland, Austria, Sweden, Poland, Slovakia, northern Italy and Spain. A complete sequence with multiple tetrapod footprint levels extending from the early Olenekian through the Norian is documented from southern Germany. Also, the northern part of Italy has abundant tetrapod footprints, in particular from the Middle Triassic (Anisian) to the Late Triassic (Carnian-Norian). The best Early Triassic footprint documentation from a global view comes from the Holy Cross Mountains region in Poland.

Depositional environments of the European deposits with tetrapod footprints were mostly fluvio-lacustrine and alluvial-floodplain. Marginal marine, partly tidally influenced regions with abundant footprints are also known from the Muschelkalk (Anisian-Ladinian) of the Netherlands and Germany, and from France and Spain.

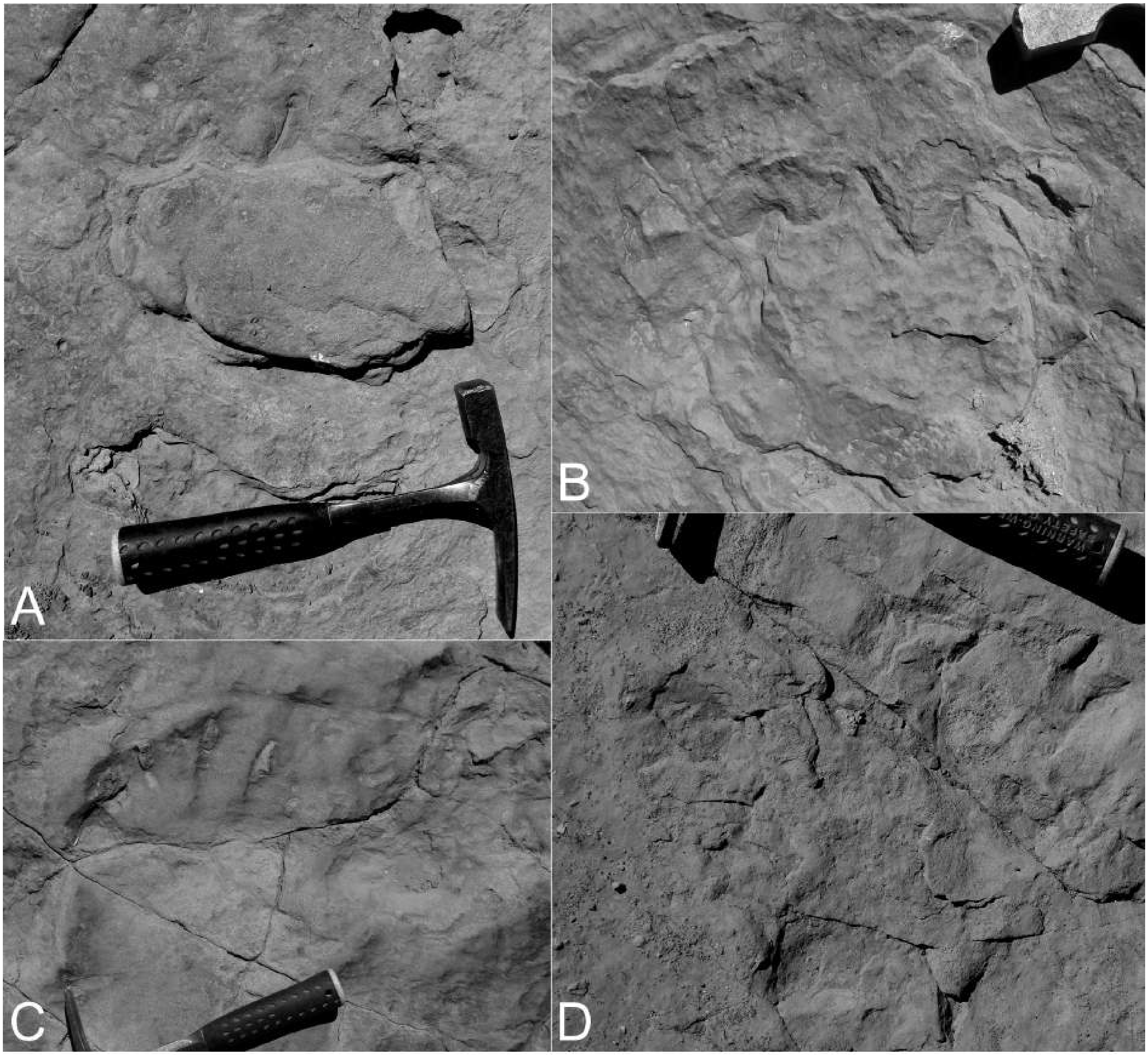


FIGURE 92. *Therapsipus cumminsi* footprints from new locality in the Holbrook Member of the Moenkopi Fm. south of Holbrook, Arizona.

Austria

In southern Austria, in the Drau Range region, the Upper Alpine Sandstone (Lower Olenekian) yielded a tetrapod ichnofauna consisting of chirotheriids–aff. *Protochirotherium* isp. and cf. *Synaptichnium* isp.–and small lacertoid imprints, *Rhynchosauroides* isp. (Krainer et al., 2012). The depositional environment was a fluvial distal braidplain. The assemblage is one of the oldest records of chirotheriids and confirms the wide distribution of *Protochirotherium*, an ichnogenus that is characteristic of the Olenekian and the *Protochirotherium* biochron.

France

Equivalents of the Buntsandstein (Olenekian-Anisian) in the Grès à Voltzia (Couches Intermediaire) of the Vosges mountain region and in the Lodéve Basin of southern France contain *Chirotherium barthii*, *Brachychirotherium gallicum*, *Rotodactylus bessieri*, and *Rhynchosauroides lutevensis* (Daubret, 1857; Christol, 1945; Demathieu, 1984; Gall and Grauvogel-Stamm, 2005). The most abundant ichnoassemblages come from coastal deposits and equivalents of the Muschelkalk (Anisian-Ladinian) of the Germanic Basin along the Massif Central. Sandstones and carbonates of the Grés de Lyonnais yielded a diverse assemblage with the following tetrapod ichnotaxa: *Longipes planus*, *Minutipes gracilis*, *Procolophonichnium* (*Circapalmichnus*) *nectouxi*, *Rhynchosauroides petri*, *R. majus*, *R. maximus*, *R. sphaerodactylus*, *R. triangulus*, *Chirotherium barthii*, *Brachychirotherium circaparvum*, *B. gallicum*, *B. lorteti*, *B. pachydactylum*, "*B. tintanti*" (a manus imprint), *Isochirotherium coureli* (*I. circademathieui*, *I. combelei*, *I. demathieui*), *I. felenci*, *I. delicatum*, *Sphingopus ferox*, *Synaptichnium priscum*, *S. argantobrivense*, *Rotodactylus lucasi*, *R. rati*, *R. velox*, and *Atreipus-Grallator* ("*Coelurosaurichnus*" *largentierensis*, "*C.*" *palissyi*, "*C.*" *perriauxi*, "*C.*" *sabinensis*,

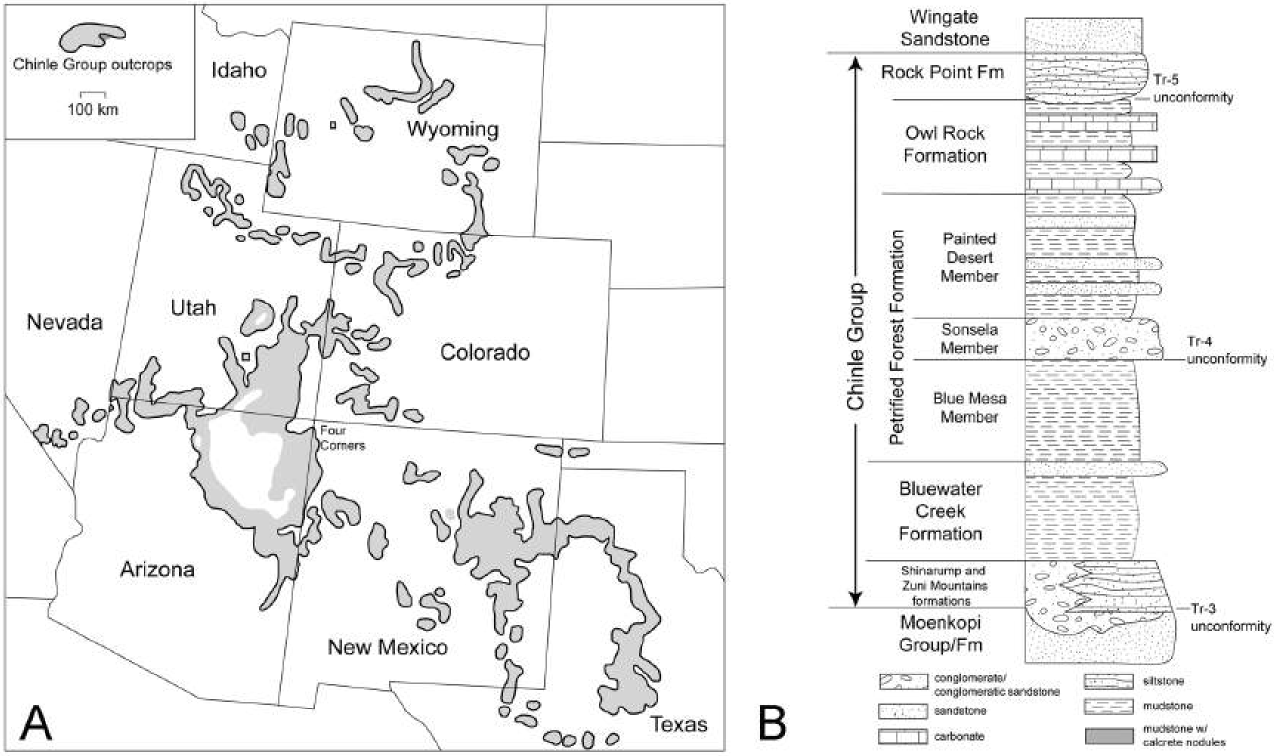


FIGURE 93. Chinle Group in the North American Southwest. **A,** Map showing geographic distribution. **B,** Stratigraphic overview section. After Lucas and Tanner (2018).

“*Anchisauripus*” *bibractensis*) (Demathieu, 1966, 1970, 1971, 1973, 1976, 1977, 1984, 1985, 1989, 1995, 1998; Montenat, 1968; Courel and Demathieu and Gand, 1972, 1973, 1986; ; Gand, 1974 a, b, 1975a, b, 1976 a, b, 1977, 1978, 1979 a, b; Gand and Pellier, 1976 a, b; Demathieu and Demathieu, 2004; Gand and Demathieu, 2005; Gand et al., 2010) (Fig. 109).

Upper Triassic deposits with tetrapod footprints are scarce in France. Carnian sandstones of the Ardéche region yielded small tridactyl footprints (“*Coelurosaurichnus*” *grancieri*, *Grallator* isp.) that can be assigned to *Atreipus-Grallator* (Courel and Demathieu, 2000; Gand et al., 2000, 2005). The Grés Supérieur (Keuper, Carnian-Rhaetian) in the southwestern part of France, in the Grand Combe area, provided footprints that have been attributed to prosauropod trackmakers (“*Otozoum*” *grandcombensis*). Small to large tridactyl pes imprints of the *Grallator-Eubrontes* plexus are associated (Gand et al., 2000).

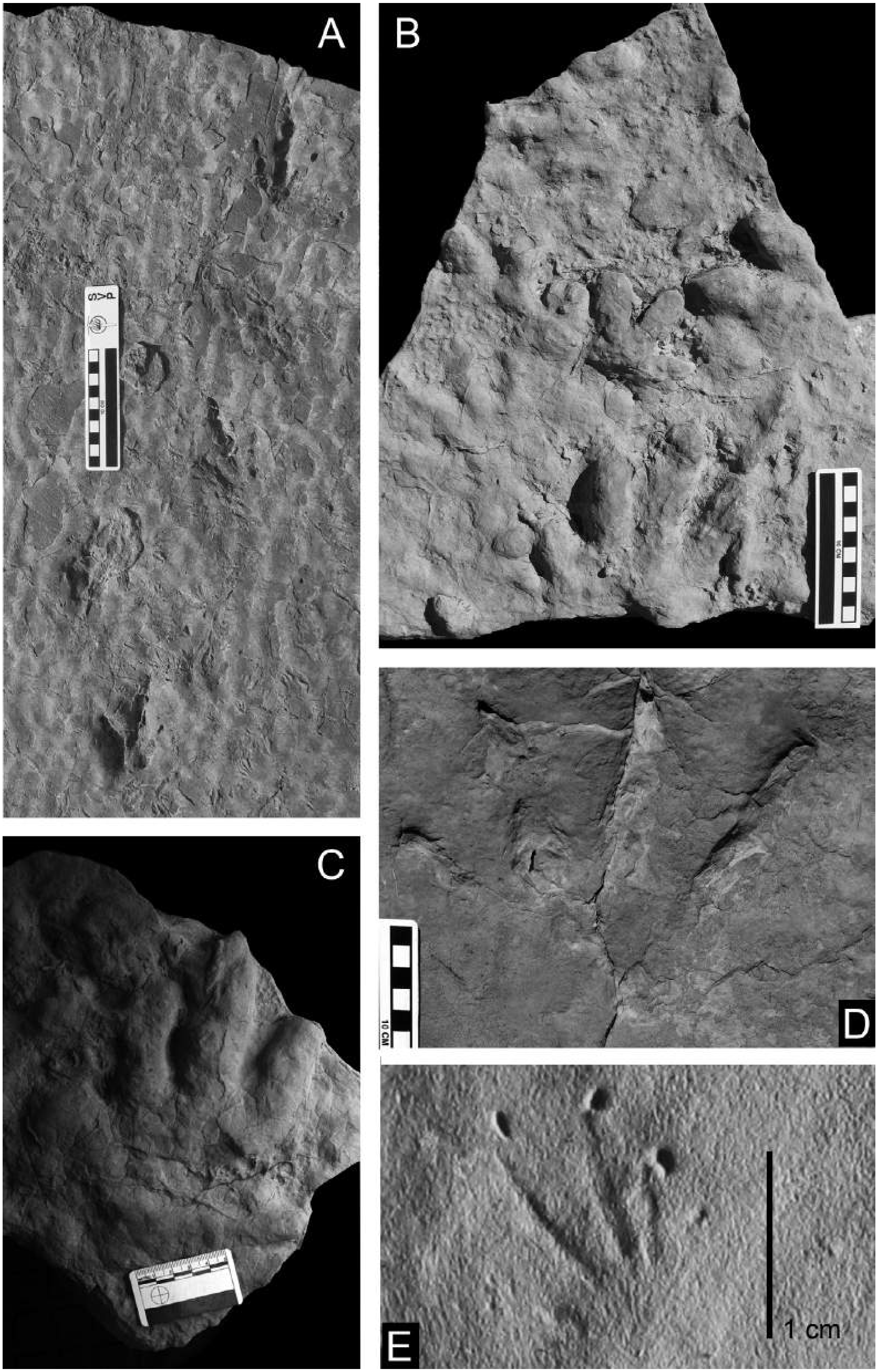
In the surroundings of the city of Anduze, surfaces in fluvial deposits yield footprints belonging to *Pseudotetrasauropus* and large pes imprints that can be assigned to *Grallator/Eubrontes* (Ellenberger, 1965; Ellenberger and Ellenberger, 1970).

Germany

Germany has an extensive Triassic footprint record from the Germanic Basin (Fig. 110). The oldest footprints come from the Volpriehausen Formation (Early Olenekian, Middle Buntsandstein) of Thuringia (Figs. 111A, 112, 113A). These are *Protochirotherium* isp., partly preserved with skin texture, and indeterminate small lacertoid imprints and scratches, possibly *Rhynchosauroides* (Gümbel, 2009; Klein et al., 2013). The Detfurth Formation (Late Olenekian, Middle Buntsandstein) near Wolfhagen, northern Hesse, yielded an ichnofauna containing the type material of *Protochirotherium wolfhagense* (Fichter and Kunz, 2004) (Figs. 111A, 113B). According to Fichter and Kunz (2007, 2009, 2011, 2013, 2015), additional ichnotaxa are present at this locality: “*Palaeochirotherium macrodactylum,*” *Synaptichnium* cf. *pseudosuchoides*, *Synaptichnium priscum*, *Prorotodactylus* isp., *Rotodactylus* isp., *Rhynchosauroides* isp., *Procolophonichnium* isp., ?*Dicynodontipus* isp., and *Capitosauroides* isp. The overlying Hardegsen and Solling formations (Figs. 111A, 112) in Hesse have chirothere-dominated ichnofaunas with *Protochirotherium* (“*Isochirotherium sanctacrucense*,” “*Isochirotherium archaeum*”), *Synaptichnium primum*, *S.* cf. *pseudosuchoides*, *S.* isp., “*Brachychirotherium*” *kuhni*, “*B*.” *praeparvum* and *Rhynchosauroides schochardti* (Demathieu and Haubold, 1982; Fichter, 1995; Fichter and Lepper, 1997; Fichter and Kunz, 2004, 2011, 2013, 2015; Fichter et al., 1999; Gümbel, 2009; Klein et al., 2013). The Solling Formation, named after the type locality in lower Saxony, Germany, encompasses the Lower-Middle Triassic (Olenekian-Anisian) boundary.

From uppermost layers of the “Thüringischer Chirotheriensandstein” of the Solling Formation (Anisian) of southern Thuringia, the type material of *Chirotherium barthii* and *C. sickleri* is extensively documented. It comes from the famous Winzer quarry near Hildburghausen, which has also yielded other chirotheriid and non-chirotheriid footprints such as *Isochirotherium soergeli*, *I. herculis*, *I. hessbergense*, *I. jenense*, “*Brachychirotherium*” *praeparvum*, “*B*.” *harrasense*, *Synaptichnium hildburghausense*, *Rotodactylus matthesi*, *Rhynchosauroides schochardti*, *R. bornemanni*, *R. pusillus*, *Dicynodontipus geinitzi*, *Procolophonichnium haarmuehlensis*, *Capitosauroides bernburgensis*, *Chelonipus torquatus* and indeterminate footprints (Sickler, 1834, 1836; Voigt, 1835; Kaup, 1835a, b; Walther, 1917; Willruth, 1917, Soergel, 1925;

FIGURE 94. (facing page) Footprints from Redonda Fm. (Chinle Group, Norian-Rhaetian) of east-central New Mexico. **A,** *Grallator cursorius* trackway. **B-C,** *Brachychirotherium parvum* pes and manus imprints. **D,** *Evazoum sirigui* pes imprint. **E,** *Rhynchosauroides* isp. pes imprint.


A
S V P
10 CM
B
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D
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FIGURE 95. *Evazoum sirigui* trackway and *Grallator cursorius* tracks, in situ on lower bed surface as interpretive outline drawing. From Lucas et al. (2010).

FIGURE 96. *Grallator cursorius* trackway and isolated pes imprints from Redonda Fm. (Chinle Group, Norian-Rhaetian) of east-central New Mexico, in situ on lower bed surface as interpretive outline drawing. From Lucas et al. (2010).

Rühle v. Lilienstern, 1939, 1944; Haubold, 1966, 1967, 1969, 1971a, b, 1984, 1999, 2006). An ichnoassemblage with very small chirotheriid footprints, probably belonging to juvenile individuals, comes from nearby deposits in the Solling Formation near Harras, Eisfeld, Thuringia, with *Chirotherium sickleri*, *Isochirotherium soergeli*, "*Brachychirotherium*" *praeparvum* and "*B.*" *harrasense* (Bornemann, 1886, 1889; Haubold, 1966, 1967). Associated are *Rotodactylus matthesi*, *Rhynchosauroides bornemanni*, *R. pusillus* and *Dicynodontipus geinitzi* (Fig. 113C).

The Solling and Roet formations (Middle-Upper Buntsandstein) also yielded footprints at numerous other localities in Thuringia (Koch and Schmid, 1841; Kolesch, 1922; Soergel, 1925; Puff and Klein, 2011), Saxony, Lower Saxony (see Haubold, 1971a and references therein; Mattner and Müller, 1988), Hesse (Hornstein, 1876; Demathieu and Haubold, 1982; Demathieu and Fichter, 1989; Krause and Haubold, 2008) and Bavaria (Sandberger, 1867; Soergel, 1925; Kirchner, 1927, 1934, 1941; Schuster, 1936; Demathieu and Leitz, 1982), and also from different Buntsandstein units in Baden-Wuerttemberg (Haderer et al., 1995), Rhineland-Palatinate (Haderer and Sachs, 2012), Saarland (Rücklin, 1936; Kuhn, 1958) and North Rhine-Westphalia (Jux and Pflug, 1958). In Hesse, equivalents of the "Thüringischer Chirotheriensandstein" provided an extensive surface with an assemblage similar to that from Hildburghausen. From the Eiterfeld locality, Krause and Haubold (2008) document 2700 imprints belonging to 70 trackways assigned to *Chirotherium barthii*, *C. sickleri*, *Isochirotherium* cf. *herculis*, cf. *Brachychirotherium* isp. and *Dicynodontipus geinitzi*.

Marginal marine deposits of the Muschelkalk in North Rhine-Westphalia, Hesse, Saxony-Anhalt and Thuringia (Fig. 111C), locally have abundant lacertoid footprints of the ichnogenera *Rhynchosauroides* and *Procolophonichnium*. The tetrapod ichnofauna is similar to that found at the famous Winterswijk locality of The Netherlands. Less common are archosaur footprints such as chirotheriids and tridactyl forms. Chirotheriids are more common at the Bernburg locality in Saxony-Anhalt, close to the City of Magdeburg. Here, a large surface in the Karlstadt Formation (Middle Muschelkalk, Anisian) shows several long trackways of the ichnotaxa *Isochirotherium herculis*, *Chirotherium barthii* and *Synaptichnium* isp. (Diedrich, 2009, 2012, 2015, Marchetti et al., 2020b). Nevertheless, most abundant at the Bernburg locality are small *Rhynchosauroides* and Procolophonichnium footprints, while chirotheriids, despite the presence of these trackways, remain minor components. This is different from siliciclastic deposits of the marginal Muschelkalk, where chirotheriids are dominant. Obviously, the composition of these tetrapod footprint assemblages is strongly ecologically controlled (see also De Jaime-Soguero et al., 2021).

Siliciclastic fluvial deposits of the marginal Muschelkalk (Anisian-Ladinian) yielded chirothere-dominated ichnofaunas along the Bohemian Massif in the Germanic Basin of northeastern Bavaria (Fig. 111C). According to Klein and Lucas (2018), the following ichnotaxa are present: *Procolophonichnium* isp. *Dicynodontipus* isp., *Rhynchosauroides* isp., *Rotodactylus* isp., *Gwyneddichnium majore*, *Atreipus-Grallator*, *Synaptichnium pseudosuchoides*, *Synaptichnium* cf. *S. diabloense*, *Isochirotherium coureli*, *"Sphingopus" ferox*, *Chirotherium* isp. and chirotheriid footprints indet. (see also Haubold and Klein, 2002) (Fig. 114A, B). The ichnofauna is similar to that from the Massif Central in France (see below).

The Lettenkeuper unit of the Erfurt Formation (Ladian) of Baden-Wuerttemberg in southern Germany yielded small tetrapod footprints that were recently described and attributed to temnospondyl amphibians by Mujal and Schoch (2020). They have some similarity with turtle tracks.

A late Ladinian-early Carnian assemblage is known from the Bohemian Massif in northeastern Bavaria, near the city of Bayreuth. Fluvial deposits of the Benk Formation (Fig. 111B) contain *Chirotherium ("Parachirotherium") postchirotherioides, "Brachychirotherium" isp., Atreipus-Grallator* isp., and *Rhynchosauroides* isp. (Fig. 114C). In particular, the presence of *Chirotherium* ("*Parachirotherium*") is identical to coeval ichnofaunas in the Timezgadiouine Formation (T5, early Carnian) of the Argana Basin, Morocco, and the Pekin Formation (Carnian) of North Carolina, USA.

Carnian (Tuvalian) footprint assemblages of Germany come from the Stuttgart Formation (Schilfsandstein) and the Steigerwald Formation (Ansbacher Sandstein) of the Stuttgart region and northern Bavaria. Ichnofaunas comprise the turtle track *Chelonipus torquatus*, as well as *Apatopus lineatus*, *Chirotherium wondrai* and *Atreipus-Grallator* (*Atreipus metzneri*) (Plieninger, 1838; Meyer and Plieninger, 1844; Heller, 1952; Haubold, 1971a; Olsen and Baird, 1986; Haubold and Klein, 2002, 2004; Klein and Lucas, 2013; Lichtig et al., 2017).

In northern Bavaria and Baden-Wuerttemberg

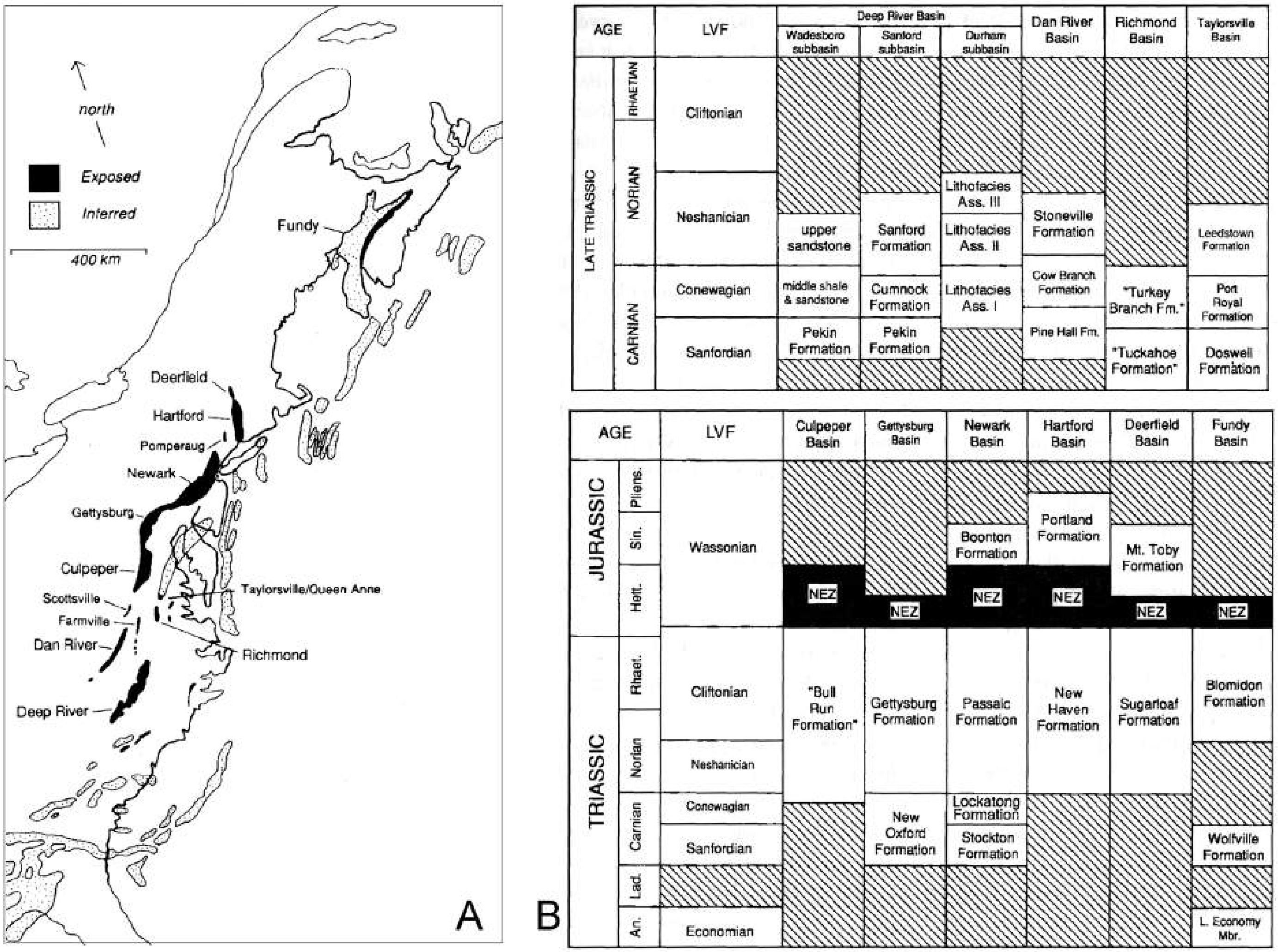


FIGURE 97. Geographic distribution of rift basins (**A**) and stratigraphic units (**B**) of Newark Supergroup in Eastern North America. From Lucas and Huber (2003). Note that Weems et al. (2016) have revised some of the lithostratigraphic names in B.

(Stuttgart area), the Hassberge Formation (Blasensandstein, Kieselsandstein, Coburger Sandstein) provided a rich ichnofauna with the type material of *Brachychirotherium hassfurtense* and *B. thuringiacum* (Figs. 111B, 115).

Accompanying ichnotaxa are *Apatopus lineatus*, *Atreipus-Grallator* isp., *Grallator cursorius*, *Atreipus* isp., *Evazoum* isp., *Brachychirotherium* isp., *Rhynchosauroides* isp. and *Procolophonichnium lockleyi* (Obermeyer, 1912; Kuhn, 1937, 1958b; Rühle v. Lilienstern, 1938; Beurlen, 1950; Heller, 1952, 1958; Freyberg, 1965a, b; Haderer, 2012, 2015; Karl and Haubold, 1998, 2000; Werneburg, 1998; Haubold and Klein, 2000, 2002; Klein and Lucas, 2013; Klein et al., 2015b), Similar assemblages with *Atreipus-Grallator* isp., *Brachychirotherium* isp. and *Rhynchosauroides* isp. come from the Norian Löwenstein Formation (Stubensandstein, Burgsandstein) in Baden Wuerttemberg (Stuttgart region) and northern Bavaria (Huene, 1931, 1935, 1943; Kuhn, 1937, 1958b; Heller, 1952, 1958; Aumann, 1960; Haderer, 1990, 1991, 1996, 2012, 2015).

Great Britain

England, and also some regions of Scotland and Wales along the coast, have provided tetrapod footprint assemblages that are mostly chirothere dominated. Indeterminate chirotherian footprints come from the Hollington Formation of Staffordshire, England (King, 1996; King et al., 2005).

From the Auchenhew beds of the Isle of Arran, Scotland, Clark et al. (2002) described *Chirotherium barthii*; some of the material was later re-assigned to *Isochirotherium herculis* by Clark and Corrance (2009).

The classical British Triassic footprint record comes from the Lower-Middle Triassic Hellsby Sandstone and Tarporley Siltstone formations. Known ichnotaxa are *Chirotherium barthii* (*C. storetonense*, *C. vorbachi*), *C. sickleri*, *Isochirotherium herculis*, *I. lomasi*, *Synaptichnium pseudosuchoides, Rotodactylus matthesi*, *R. tumidus*, *Rhynchosauroides rectipes*, *R. articeps*, *R. beasleyi*, *R. minutipes* and *Dicynodontipus geinitzi* (Egerton, 1838; Beasley, 1896, 1904, 1905, 1907, 1908, 1910; Woodward, 1902, 1905; Maidwell, 1911, 1914; Sarjeant, 1967, 1974; Tresise, 1969, 1989, 1991a, b, 1993a, b, 1994, 1996; Old et al., 1991; Tresise and Sarjeant, 1997; Clark et al., 2002; King et al., 2005; Clark and Corrance, 2009; Coram and Radley, 2015; Pollard, 2016; Thompson et al., 2016; Warrington et al., 2016).

From the Mercia Mudstone Group (Upper Triassic, Norian) of Wales, *Grallator-Eubrontes*, *Brachychirotherium*, *Evazoum* and *Eosauropus* ("*Pseudotetrasauropus,*" "*Tetrasauropus*") have been reported (Sollas, 1879; Thomas, 1879; Bassett and Owens, 1974; Tucker and Burchette, 1977; Lockley et al., 1996; Lockley and Meyer, 2000). The assemblage documents a mixture of pseudosuchians and theropod and sauropodomorph dinosaurs.

Stratigraphically youngest Triassic footprints from Great

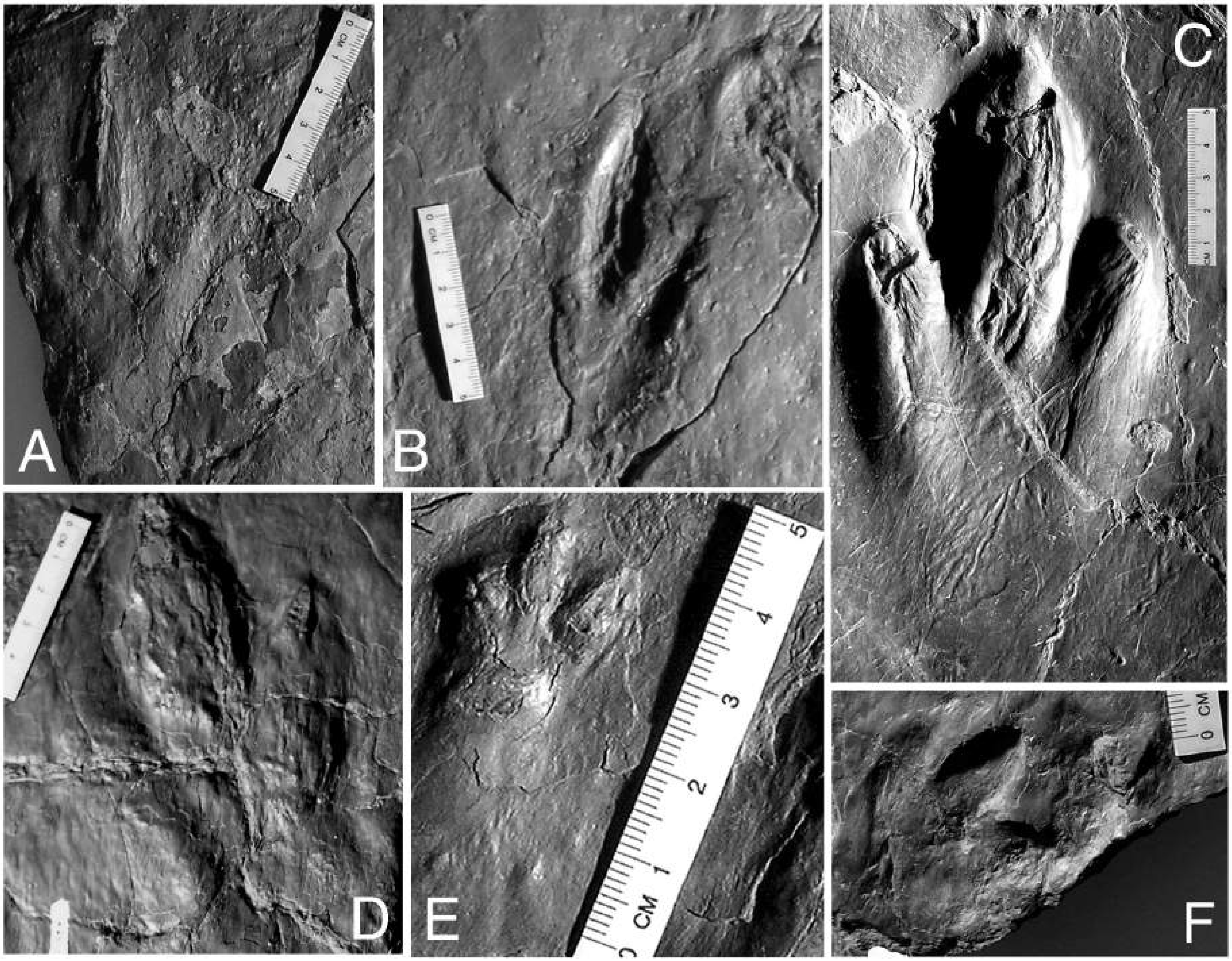


FIGURE 98. *Atreipus milfordensis* footprints from the Passaic Fm. (Norian) of Graterford, Pennsylvania. **A, C, D,** Pes imprints. **B,** Pes-manus set. **E-F,** Manus imprints. From Lucas and Sullivan (2006).

Britain come from a Rhaetian nearcoast limestone from the Westbury Formation (Penarth Group) at Aust Cliff near Bristol, Wales, which also yielded bivalve body fossils (Larkin et al., 2020). These are isolated small tridactyl-tetradactyl imprints with tapering digits and a large round to oval sole impression. Larkin et al. (2020), assigned these to the ichnogenus Procolophonichnium.

Italy

Italy has abundant Triassic footprints, in particular from the Middle Triassic (Anisian-Ladinian) of the southern Alps, but also from stratigraphically older and younger strata (Fig. 116). A review of Triassic tetrapod ichnofossils was recently presented by Mietto et al. (2020). This comprises localities in the Southern Alps, Western Alps, Northern Apennines, Maritime Alps and Sardinia. The authors recognize two chronostratigraphic sections: 1) Olenekian–late Anisian with dominance of *Rhynchosauroides* and other small lacertoid tracks and gradual increase of archosauriform tracks such as chirotheriids; 2) Middle Carnian–Rhaetian, first with chirotheriids, but with increase of dinosaur tracks and their dominance beginning with the Carnian Pluvial Episode. However, tridactyl footprints of true dinosaurs from the early Late Triassic, can hardly be distinguished from tridactyl dinosauriform tracks, the latter being abundant from the Middle Triassic (Ladinian) (Haubold and Klein, 2002, Klein and Lucas, 2018). Therefore, based on the footprint record, a "dinosaurian explosion" triggered by the suggested global climatic event cannot be supported (see also Klein et al., 2018).

From the Werfen Formation, small lacertoid archosauromorph/lepidosauromorph tracks of *Rhynchosauroides schochardti* and the possible temnospondyl track *Capitosauroides bernburgensis* are known (Avanzini and Mietto, 2008). Recently Petty et al. (2020) described chirotheriid tracks and trackways from an Early Triassic (?Olenekian) assemblage of the Western Alps and assigned these to a new ichnospecies *Isochirotherium gardettensis* and to *Chirotherium* isp.

Middle Triassic fluvial-marginal marine deposits have provided a huge number of tetrapod tracks. Here, along the margin of the western Tethys, sandstones, siltstones and limestones preserved chirotheriid and other footprints such as *Procolophonichnium* isp., *Rhynchosauroides tirolicus*, *R. peabodyi*, *Synaptichnium pseudosuchoides*, *S. cameronense*, *S. diabloense*, *Parasynaptichnium gracilis*, *Chirotherium barthii*, *C.* cf. *rex*, "*Sphingopus*" *ladinicus*, "*Brachychirotherium*" *paeneparvum*, "*B.*" *circaparvum*, *Isochirotherium infernense*, *I. delicatum*, *Rotodactylus* isp., *R.* cf. *cursorius* and *R. lucasi* (Abel, 1926; Brandner, 1973; Mietto, 1987; Avanzini and Neri, 1998; Avanzini, 1999, 2000, 2002, 2003; Avanzini et al., 2001a, b, 2011; Avanzini and Leonardi, 2002; Avanzini and Lockley, 2002; Avanzini and Renesto, 2002; Avanzini and Mietto, 2008;

FIGURE 99. *Brachychirotherium parvum* pes imprint from Passaic Fm. of New Jersey. Original in Lafayette College collection.

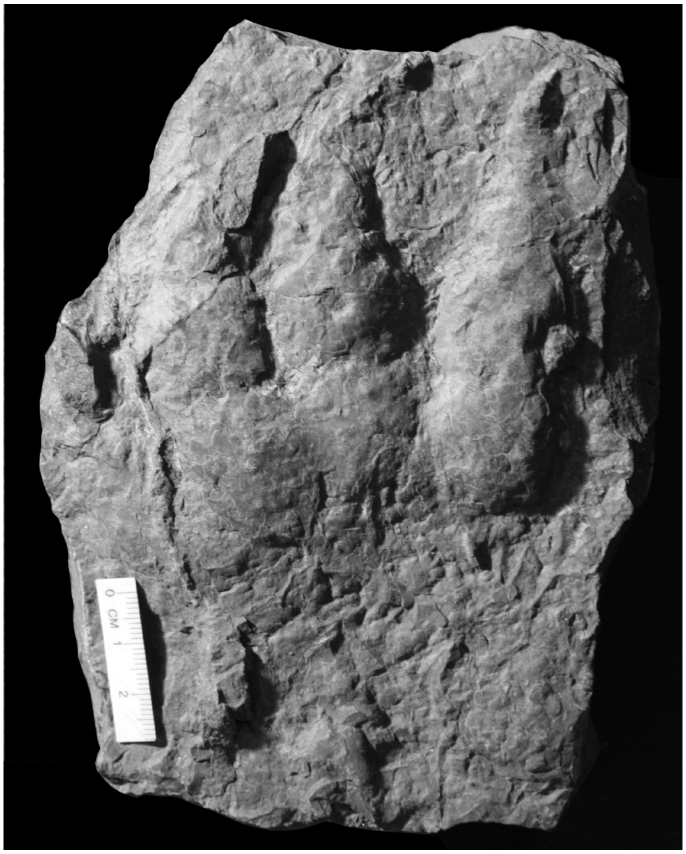


FIGURE 100. *Apatopus lineatus* pes imprint from Passaic Fm. of New Jersey. Original in Lafayette College collection.

Valdiserri and Avanzini, 2007; Todesco et al., 2008a, b; Gand et al., 2010; Avanzini and Wachtler, 2012; Petti et al., 2013; Wachtler, 2018) (Fig. 117). The track-bearing strata belong to the Voltago conglomerate (?Bithynian-earliest Pelsonian), the Recoaro limestone (Pelsonian), the Richthofen conglomerate (Illyrian) and the Morbiac limestone (Illyrian).

From Middle Triassic (Ladinian) deposits of the Tuscany region a diverse tetrapod ichnofauna was described by Huene (1941). The Quarziti di Monte Serra Formation provided different chirotheriid, lacertoid and other footprints, including the type of *Coelurosaurichnus toscanus,* which is here considered a *nomen dubium*. While some of the material can be assigned to *Chirotherium barthii*, many specimens described by Huene (1941) are poorly preserved and do not allow a distinct determination. These are considered here as tetrapod footprints indet. Huene (1941) described numerous ichnotaxa, including several new ones such as "*Chirotherium angustum*" (*C. barthii*), "*Thecodontichnus fucinii*," "*T. verrucae*," "*Rhynchocephalichnus etruscus*," "*R. pisanus*," "*Procolophonipus italicus*" and "*Cryptobranchichnus infericolor*." Most of them probably should be attributed to chirotheriids and to the ichnogenus *Rhynchosauroides.* Unfortunately, Huene (1941) documented most of the material as interpretive outline tracings and by very few low-quality photographs. Recently Marchetti et al. (in press) revised this ichnofauna, partly re-locating some original type material. These authors list the following ichnotaxa: *Atreipus* isp., *Chirotherium barthii*, *C. gallicum*, *Rotodactylus* isp., *Rhynchosauroides palmatus*, *Circapalmichnus* isp. and *Procolophonichnium haarmuehlensis*.

Middle Triassic (Anisian) footprints have been described from NW Sardinia by Citton et al. (2020). They come from Buntsandstein facies deposits called Arenarie di Cala Viola and have been assigned to the ichnogenera *Rhynchosauroides* and *Rotodactylus*.

Footprints in Upper Triassic deposits of Italy are less abundant when compared to the Middle Triassic. The Montemarcello and Travenanzes formations and the Dolomia Principale, (Carnian-Norian-Rhaetian) contain some surfaces that have been documented in detail. The Montemarcello Formation near the city of La Spezia yielded the possible sauropodomorph footprint *Evazoum* (type material) and *Brachychirotherium*. The Travenanzes Formation yielded *Evazoum* and *Atreipus* isp. Other footprints from the Dolomia Principale are *Grallator-Eubrontes* (Dalla Vecchia, 1996; Dalla Vecchia and Mietto, 1998; Nicosia and Loi, 2003; Avanzini et al., 2007, 2010; D'Orazi-Porchetti et al., 2008; Petti et al., 2009; Bernardi et al., 2010, 2013; Meyer et al., 2013).

Poland

In Poland, fluvial successions of the Wiòry and Samsonów formations (Olenekian, Spathian) exposed in the Holy Cross Mountains region have abundant tetrapod footprints (Figs. 118-119). These are one of the best documented Lower Triassic footprint assemblages in the world. The ichnotaxonomy of the Wiòry Formation has been revised by Klein and Niedźwiedzki (2012): *Protochirotherium hauboldi* ("*Brachychirotherium*" *hauboldi*, "*B. wiorense,*" "*Isochirotherium sanctacrucense,*" "*I. gierlinskii,*" "*Synaptichnium chirotherioides*"), *Synaptichnium*

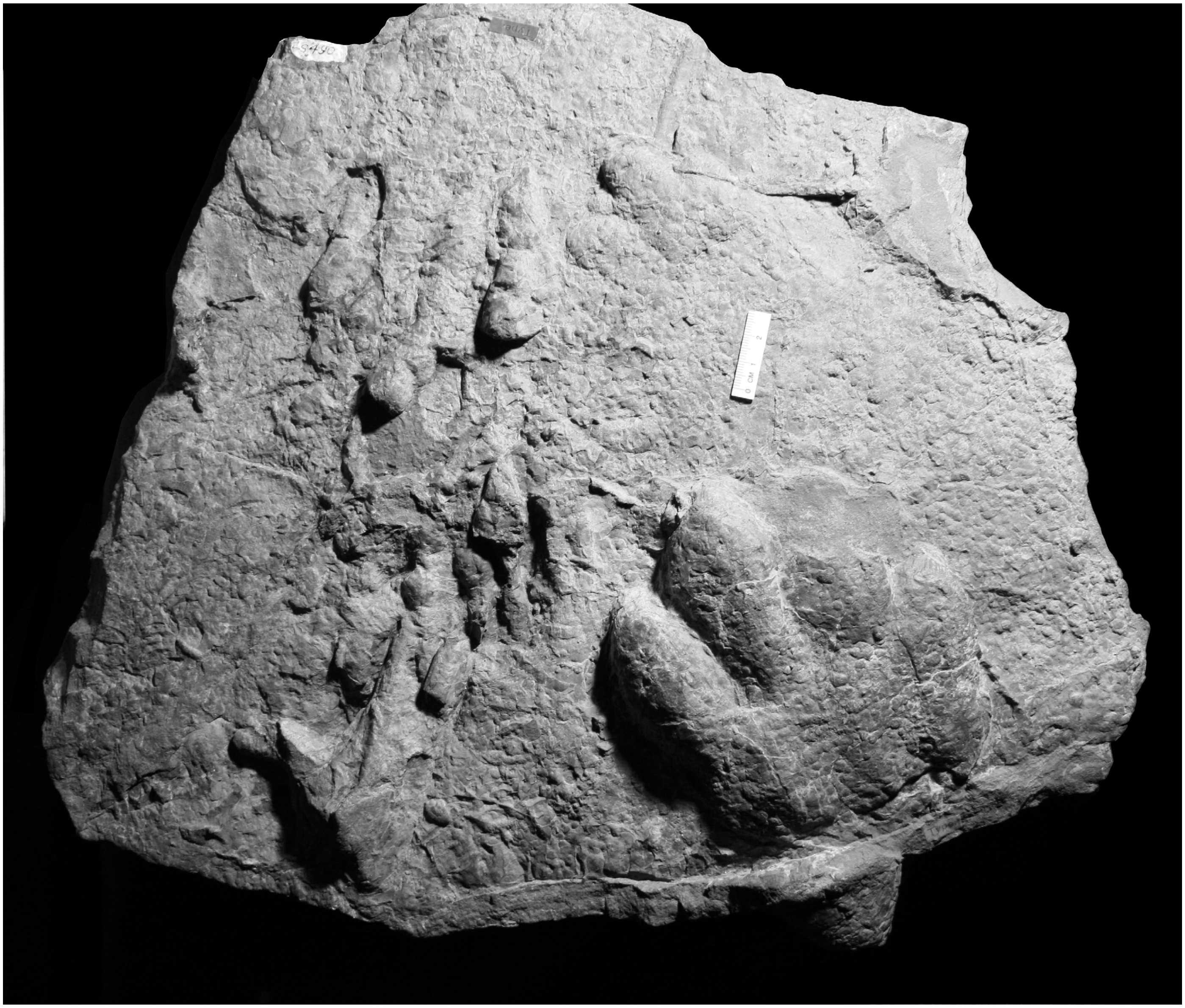


FIGURE 101. Slab with *Brachychirotherium parvum* holotype (right) and part of *Apatopus lineatus* holotype trackway (left) from Passaic Fm. of New Jersey. Original in Lafayette College collection.

kotanskii, large chirotheriids indet. ("*Brachychirotherium kalkowensis,*" "*Synaptichnium senkowiczowae*"), *Prorotodactylus mirus*, cf. *Rotodactylus*, *Rhynchosauroides rdzaneki*, *R. brevidigitatus*, *R.* isp., *Procolophonichnium polonicum*, "*Capitosauroides*" *fuglewiczi*, cf. *Therapsipus*, and therapsid footprints indet. (Fuglewicz et al., 1990; Ptaszyński, 2000; Niedźwiedzki and Ptaszyński, 2007; Niedźwiedzki et al., 2013; Brusatte et al., 2011; Klein and Niedźwiedzki, 2012; Klein et al., 2013) (Figs. 120-121). Skeletal remains of temnospondyls have been found in the same strata (Klein and Niedźwiedzki, 2012).

From the fluvial Baranów Formation (Anisian) of the Holy Cross Mountain region, Kuleta et al. (2005, 2006) and Brusatte et al. (2010) reported the ichnotaxa ?*Chirotherium barthii*, ?*Synaptichnium* isp., ?*Isochirotherium*, *Sphingopus* isp., "*Brachychirotherium,*" *Rhynchosauroides* isp. and "*Capitosauroides.*"

From Upper Triassic (Carnian) deposits of Woźniki, southern Poland, Sulej et al. (2010) mentioned an assemblage with cf. *Grallator*, cf. *Atreipus*, cf. *Brachychirotherium* isp., cf. *Apatopus* isp., Chirotheriidae indet., Rhynchosauroidae indet. and tetrapod footprints indet. The same unit provided vertebrate skeletal remains of sharks, temnospondyls, dicynodonts, phytosaurs and dinosauriforms (Sulej et al., 2010).

Slovakia

In the Slovakian Tatra mountains, the Tomanová Formation (Upper Triassic, ?Late Norian- Rhaetian) is a limnic sandstone-claystone succession that contains a dinosaur ichnofauna with tridactyl grallatorid pes imprints that have been assigned to cf. *Grallator*-cf. *Eubrontes*, and cf. *Kayentapus* (Michalik et al., 1976; Michalik and Kundrat, 1998; Gierlinski and Sabath, 2005; Niedźwiedzki, 2011). Remarkable is the occurrence of large *Eubrontes* tracks confirming the cosmopolitan distribution of large theropods before the Triassic-Jurassic boundary (cf. Lucas et al., 2006). The assignment of some tridactyl footprints with wide digit divarication to the "ornithischian" (originally Jurassic) ichnogenus *Anomoepus* (Niedźwiedzki, 2011) is doubtful. These may be extramorphologically (substrate-related) deformed *Eubrontes* tracks. Isolated possible sauropodomorph tracks were also described (Niedźwiedzki, 2011) but are too

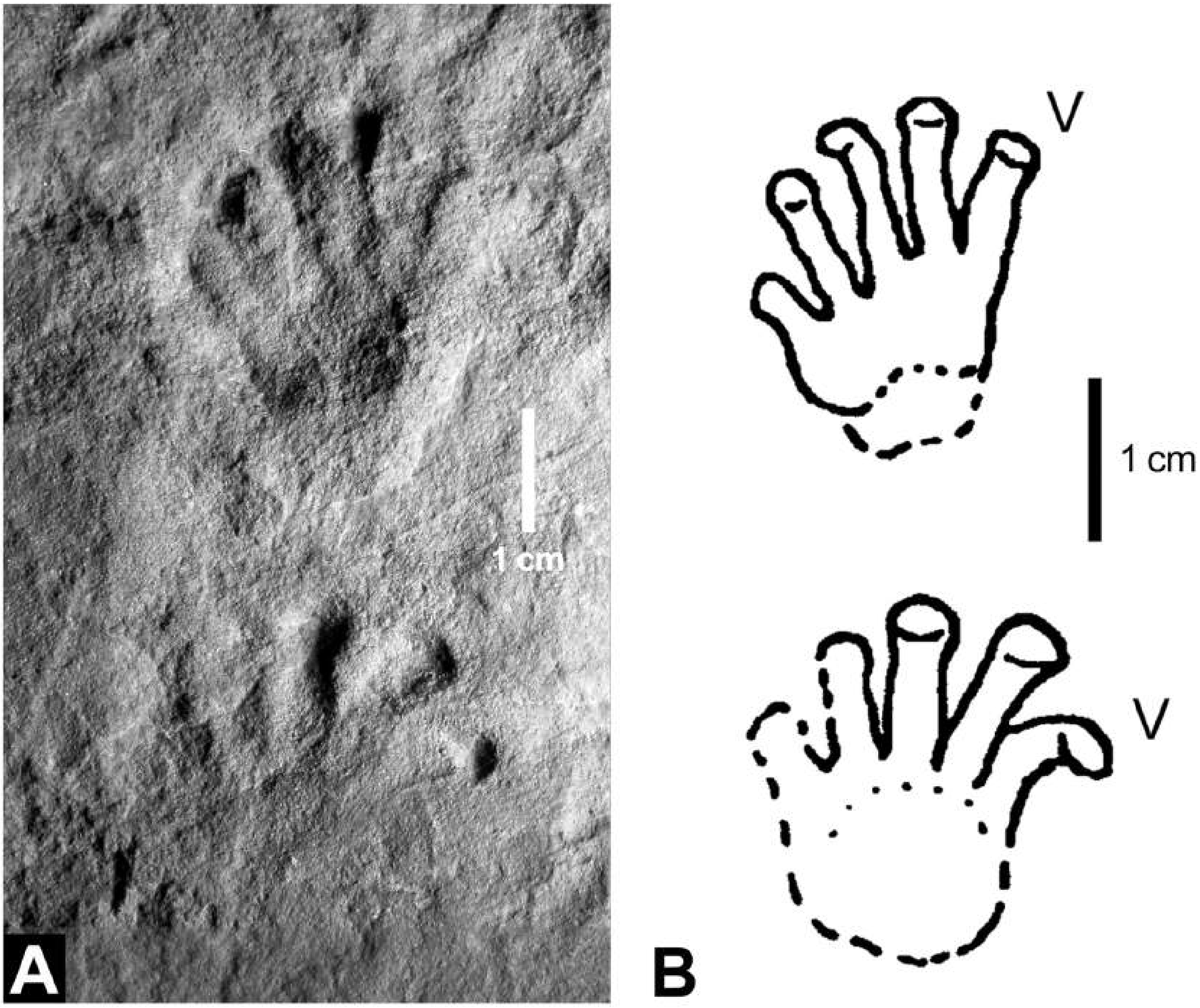


FIGURE 102. *Procolophonichnium* ispp. pes-manus set from Passaic Formation of New Jersey. **A,** Photograph by S. Dalman. **B,** Sketch from Baird (1986).

poorly preserved to distinguish them from chirotheriid tracks.

Spain

Footprint-bearing Lower-Middle Triassic deposits are present in the Catalan Basin, the Iberian Ranges, the Aragon region and on the island of Mallorca. These are equivalents of the Buntsandstein and Muschelkalk (Anisian-Ladinian) in the Germanic Basin. Tetrapod ichnotaxa reported from different localities are *Rhynchosauroides* cf. *beasleyi*, *R*. isp., *Chirotherium barthii*, "*Chirotherium*" sp., *Synaptichnium* isp., *Isochirotherium soergeli*, cf. *Isochirotherium* isp., *Chirotherium* isp., *Rhynchosauroides* isp., "*Chirotherium*" sp., cf. "*Brachychirotherium,*" cf. "*Brachychirotherium*" *gallicum, Dicynodontipus*, *Rotodactylus* and ?*Procolophonichnium*. Skeletal vertebrate fossils are also present with remains of capitosaurs, archosauriforms and procolophonids (Calderon, 1897; Navas, 1906; Leonardi, 1959; Casanovas-Cladellas et al., 1979; Calafat et al., 1986; Calzada, 1987; Pérez-López, 1993; Garcia-Bartual et al., 1996; Pascual-Arribas and Latorre-Macarrón, 2000; Valdiserri et al., 2009; Fortuny et al., 2011; Díaz-Martínez and Pérez-García, 2012; Díaz-Martínez and PérezGarcía, 2012; Díaz-Martínez et al., 2015; Gand et al., 2010; Mujal et al., 2015 ; De Jaime-Soguero et al., 2021).

?Middle -?Upper Triassic (Carnian) fluvial deposits with footprint-bearing layers are preserved in a "Keuper facies" near Jaén (Soria). A chirotheriid trackway with six successive pes and manus imprints has been assigned to "*Brachychirotherium*" *gallicum* (Pérez-López, 1993), but is considered here as tetrapod footprints indet.

Sweden

In southern Sweden (Scania province), the fluvial-deltaic Höganäs Formation (Latest Triassic-Early Jurassic, Rhaetian-Hettangian) yielded tridactyl footprints that have been assigned to the *Grallator-Eubrontes* plexus, cf. *Kayentapus*, and probable thyreophoran tracks (Bölau, 1952; Gierlinski and Ahlberg, 1994; Milàn and Gierliński, 2004; Gierlinski and Sabath. 2005). These tracks frequently occur as natural casts in the roof layer of coal mines.

Switzerland

A series of sandstones and siltstones of the Vieux Emosson Formation in the region of Lake Emosson, near Martigny, western Swiss Alps and the so-called Röti Dolomite of the Röti Formation, Tödi Mountain (Glarus) region of the eastern Swiss Alps (Middle Triassic, Anisian), contain large assemblages with chirothere footprints (Wizevich et al., 2019; Fig. 122). The following ichnotaxa are present: *Chirotherium barthii*, ? *C.*

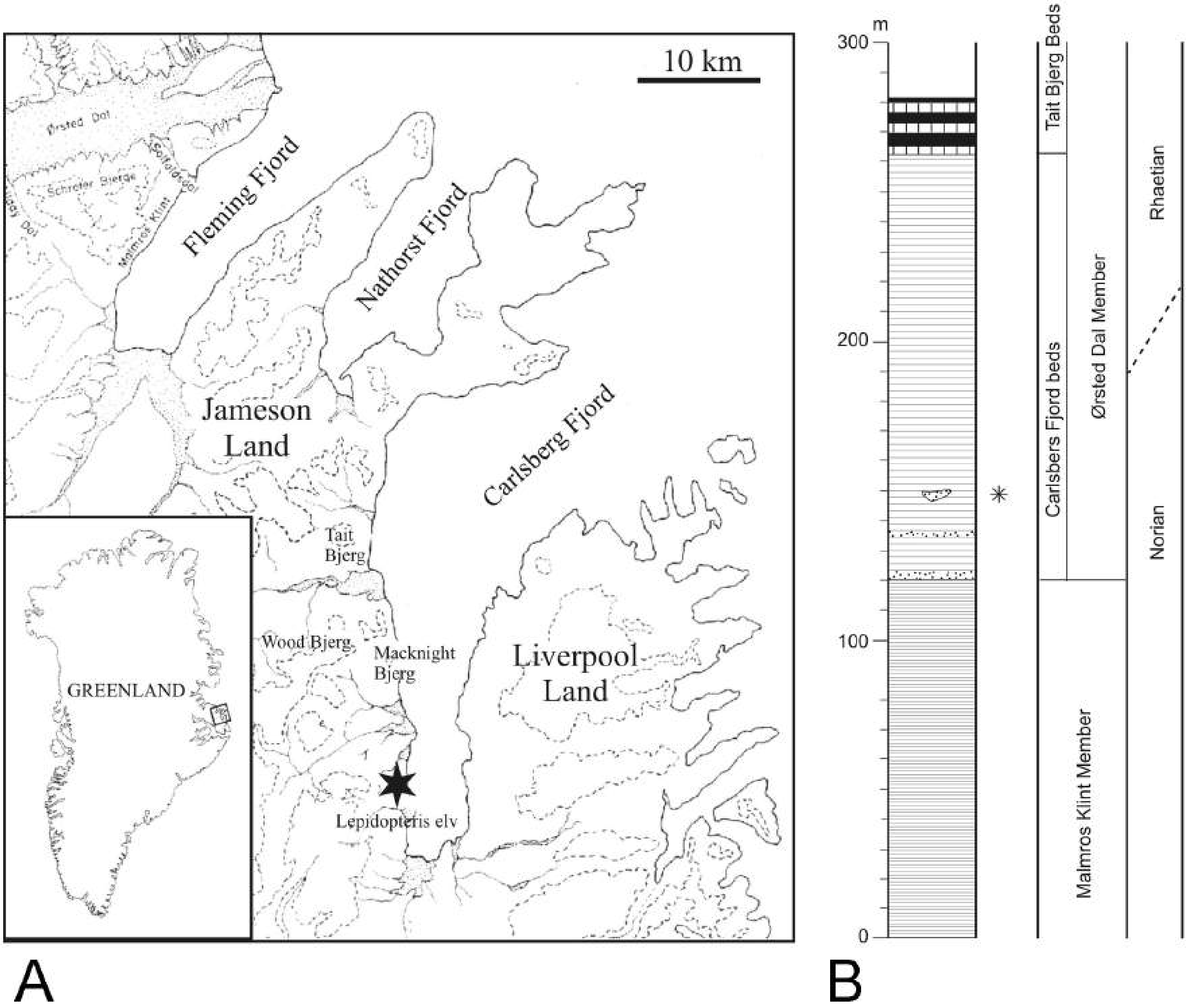


FIGURE 103. Geographic and stratigraphic position of cf. *Brachychirotherium* and other footprint localities in eastern Greenland. **A,** Map of Carlsberg Fjord area with tracksites. **B,** Stratigraphic section. From Klein et al. (2015). Note that units demarcated in B as "Formation" and "Member" are now considered as "Group" and "Formation," respectively (see Clemmensen et al., 2020).

sickleri, *Isochirotherium herculis*; *I.* isp., and chirotheriids indet. (Klein et al., 2015a; 2016; Wizevich et al., 2019; Cavin and Piuz, 2020) (Fig. 123A-H). Poorly preserved tri- to pentadactyl imprints from the Vieux Emosson Formation were originally assigned to the ichnogenera "*Paratrisauropus,*" "*Deuterosauropodopus,*" "*Prototrisauropus,*" "*Pachysaurichnium,*" "*Bifidichnium,*" *Isochirotherium* and "*Brachychirotherium*" by Demathieu and Weidmann (1982), partly based on the ichnotaxonomy of Ellenberger (1972).

According to Cavin et al. (2012), all of the footprints identified by Demathieu and Weidmann (1982) from the Vieux Emosson Formation are poorly preserved chirothere tracks. This was supported by Meyer et al. (2014) and Klein et al. (2016) (see also Meyer and Thüring, 2003). Cavin et al. (2012) illustrated an incomplete trackway with well-preserved pes and manus imprints that they tentatively assigned to *Chirotherium* cf. *C. barthii*, but that was referred to *C. barthii* by Klein et al. (2016). Another trackway illustrated and described in Avanzini and Cavin (2009) and assigned to *Isochirotherium* isp. is probably a slightly deformed *C. barthii* in which the fourth pedal digit appears rather short (Klein et al. 2016). A short pedal digit IV is generally diagnostic of the ichnogenus *Isochirotherium*. However, this trackway shows a narrow pattern with the pes imprints oriented (along digit III) parallel to the midline. This is unusual for *Isochirotherium*, which generally shows pes imprints that are strongly turned outward. The recent discovery of new surfaces in the Vieux Emosson region was followed by a re-examination of old and new surfaces in 2013 by one of the authors (HK) as part of an international team under the lead of Christian Meyer, Basel. It revealed that all imprints on the Vieux Emosson surfaces belong to chirotheriids. These are *Chirotherium barthii*, *C. sickleri*, *Isochirotherium* cf. *I. herculis* and *I.* isp.

The tracks from the Röti Formation in the Tödi (Glarus) region were originally described by Feldmann and Furrer (2009) and assigned to the ichnogenus *Isochirotherium*, but referred to *Chirotherium barthii* by Klein et al. (2016) (Fig. 123I-J). Both assemblages represent typical Middle Triassic (Anisian) ichnofaunas and can be considered as equivalent to the ichnofauna from the uppermost Middle Buntsandstein (Solling Formation, Thüringischer Chirotheriensandstein) of the Germanic Basin. Paleogeographically, the occurrence in Switzerland is at the southern margin of the Germanic Basin.

The Hauptdolomit (Dolomia Principale in Italy) and

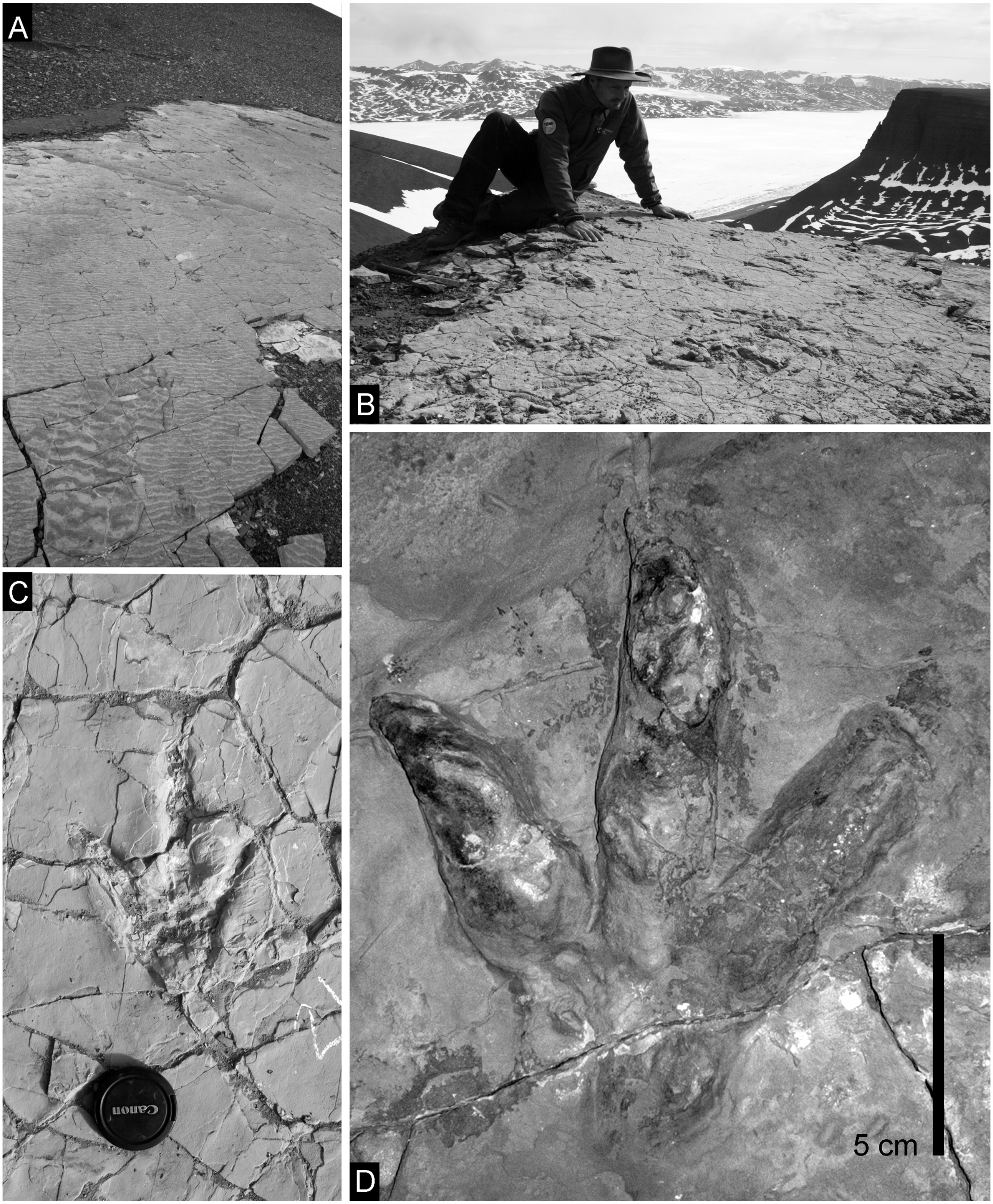


FIGURE 104. Tridactyl pes imprints of the *Grallator-Anchisauripus-Eubrontes* plexus from the Ørsted Dal Formation of the Fleming Fjord Group (Upper Triassic, Norian-Rhaetian) of East Greenland. **A,** Surface with grallatorid trackways, ripple marks and mudcracks. **B,** Jesper Milàn (Geomuseum Faxe, Denmark) sitting on footprint surface at Carlsberg Fjord during expedition in 2012. **C-D,** Details of grallatorid footprints. Photographs courtesy Jesper Milàn.

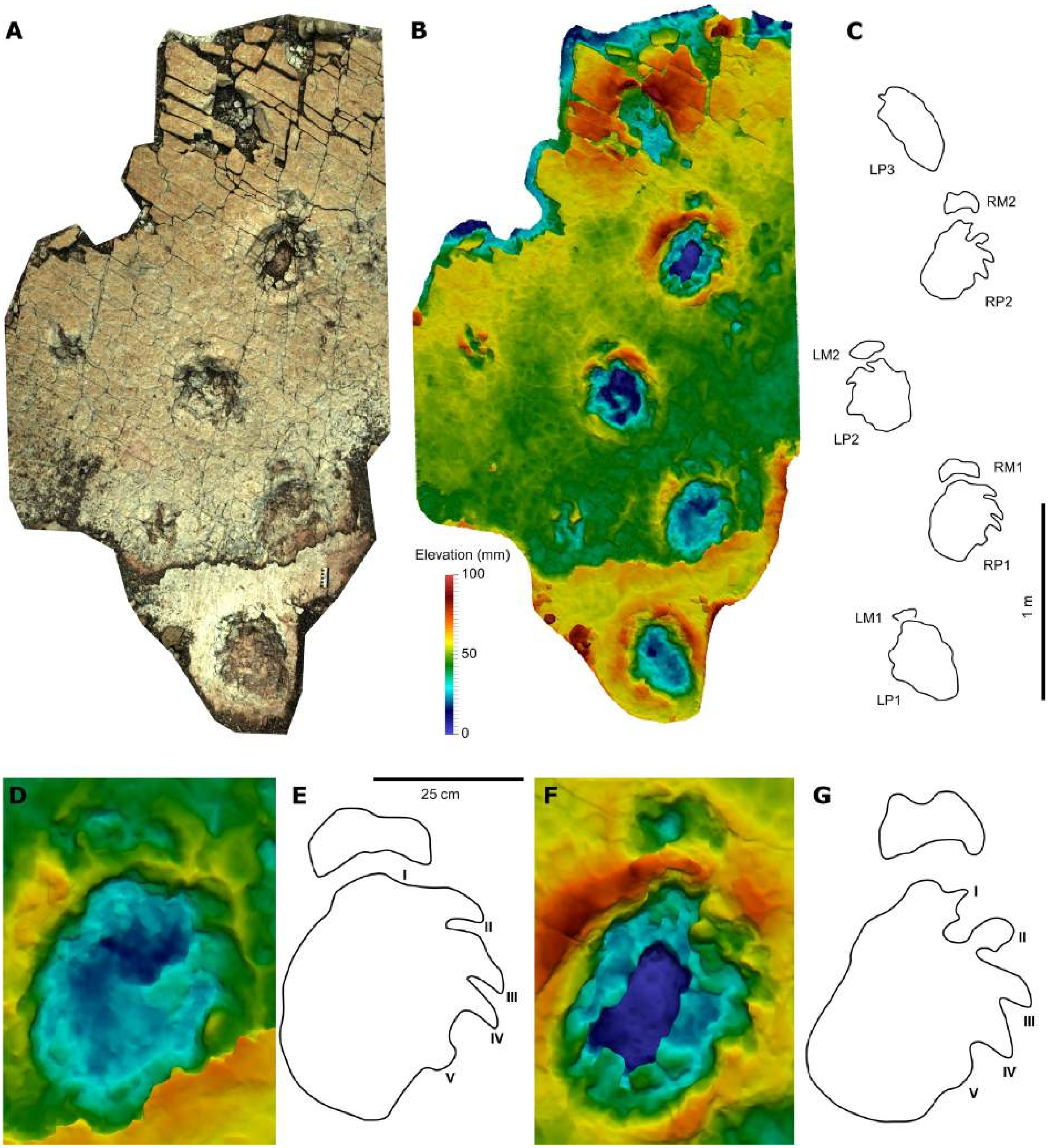


FIGURE 105. Sauropodomorph trackway *Eosauropus* isp. from the Ørsted Dal Formation of the Fleming Fjord Group (Norian-Rhaetian) of eastern Greenland. **A,** Photogrammetric orthophoto. **B, D, F,** Depth color images as overview and details. **C, E, G,** Outline. From Lallensack et al. (2017).

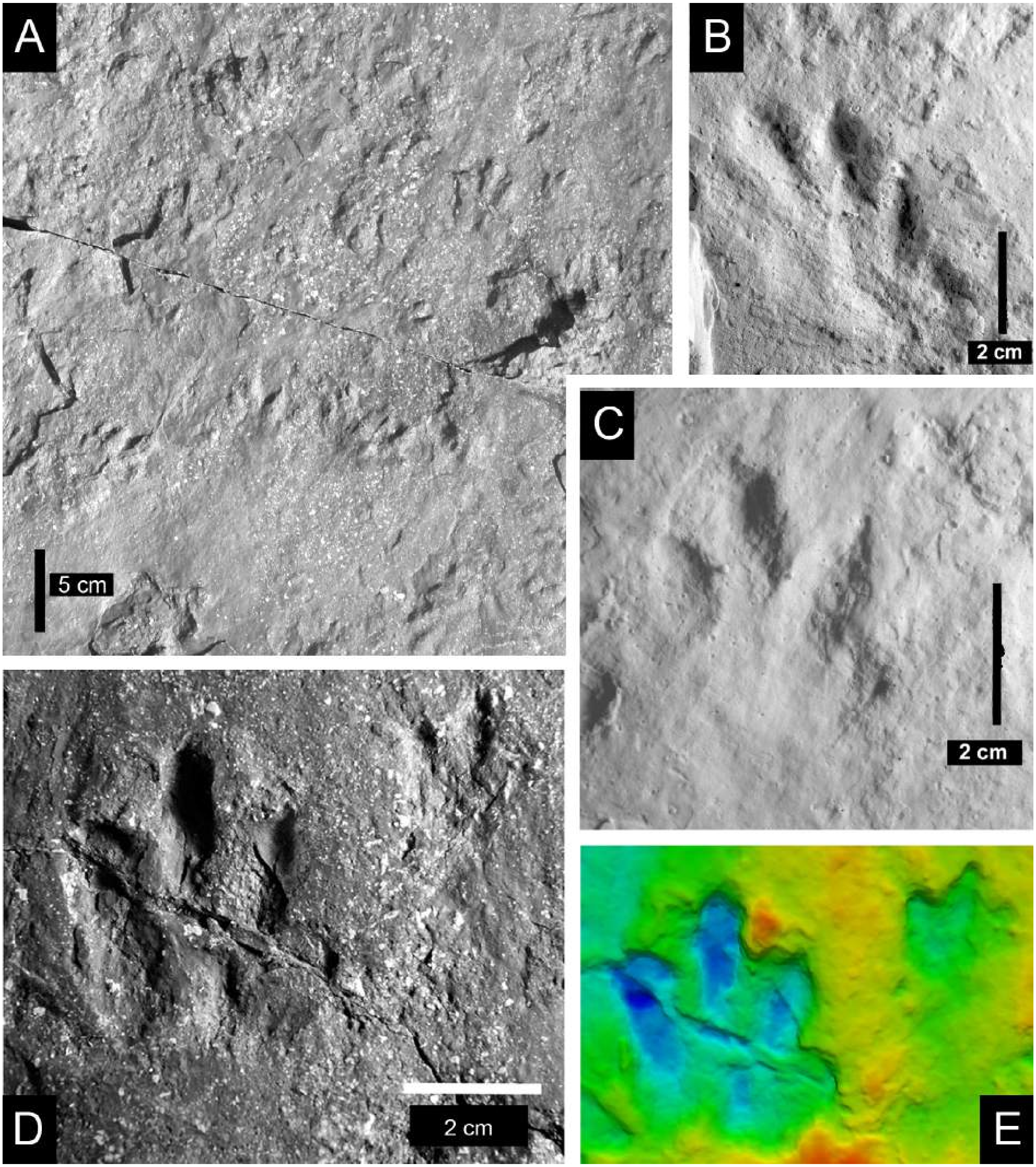


FIGURE 106. Cf. *Brachychirotherium* from the Ørsted Dal Formation of the Fleming Fjord Group. (Norian-Rhaetian) of eastern Greenland. **A,** Section from large slab with numerous pes and manus imprints. **B-D,** Details. **E,** Depth color image of pes-manus set in D. From Klein et al. (2015).

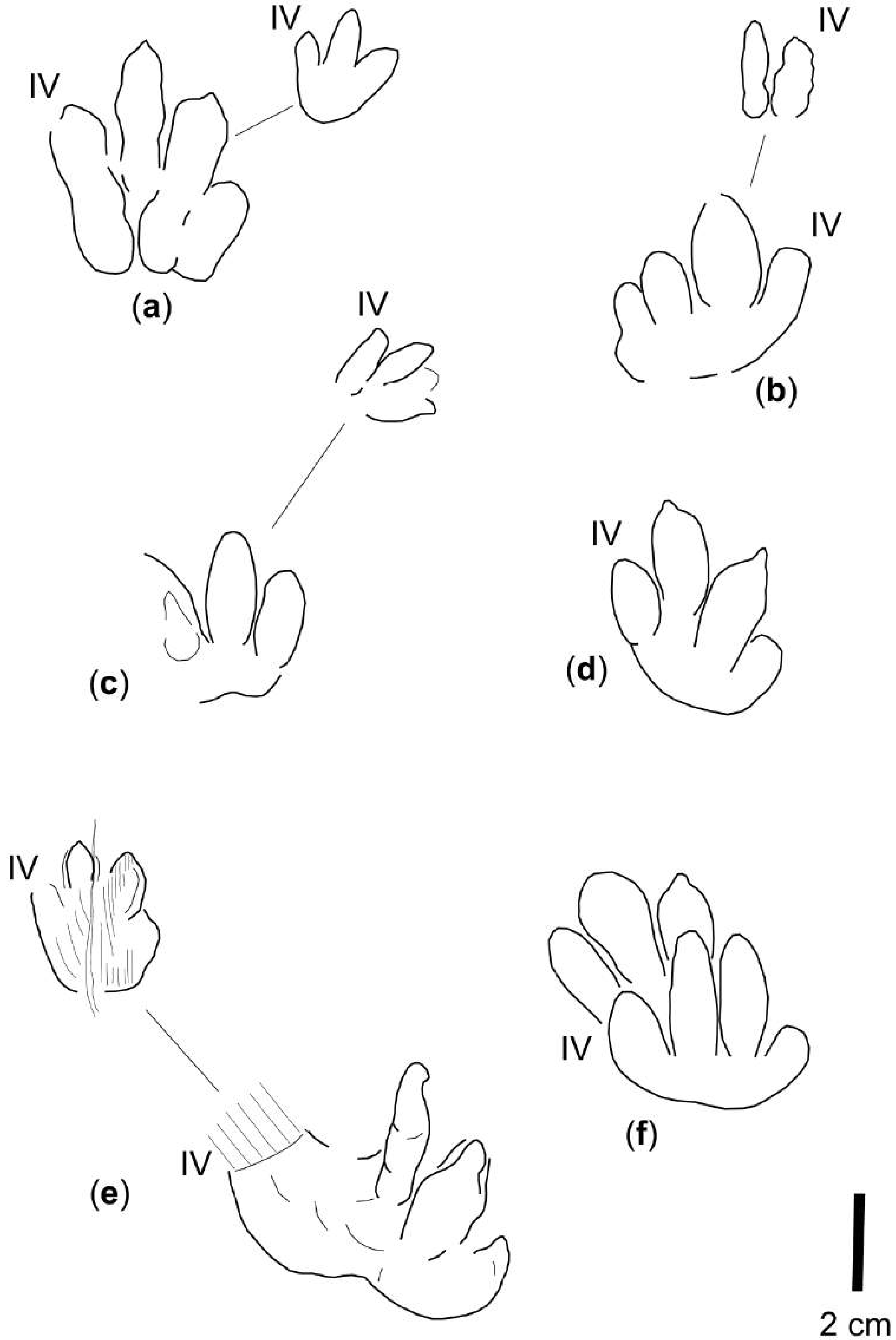


FIGURE 107. Sketches of cf. *Brachychirotherium* pes and manus imprints on different slabs from the Ørsted Dal Formation of the Fleming Fjord Group (Norian-Rhaetian) of eastern Greenland. From Klein et al. (2015).

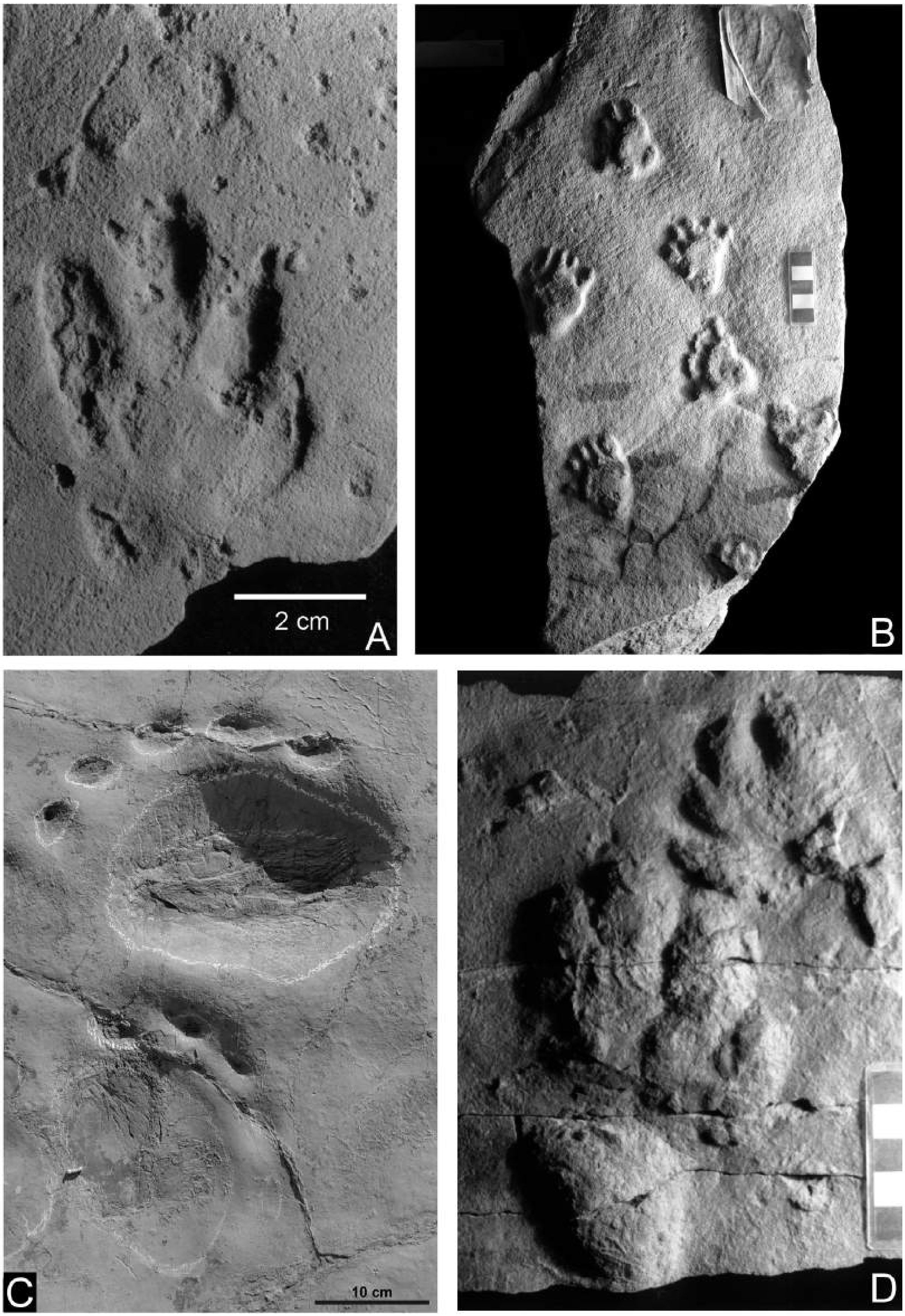


FIGURE 108. Triassic tetrapod footprints from Argentina. **A,** *Brachychirotherium parvum* from Los Colorados Fm. (Norian). **B,** *Dicynodontipus* isp. from Vera Fm. (?Early Triassic). **C,** *Pentasauropus argentinae* from Cerro de las Cabras Fm. (Anisian-Ladinian). **D,** Indeterminate chirotheriid “*Brachychirotherium*” from Tarjados Fm. (?Olenekian-Anisian). C. From Lagnaoui et al. (2019).

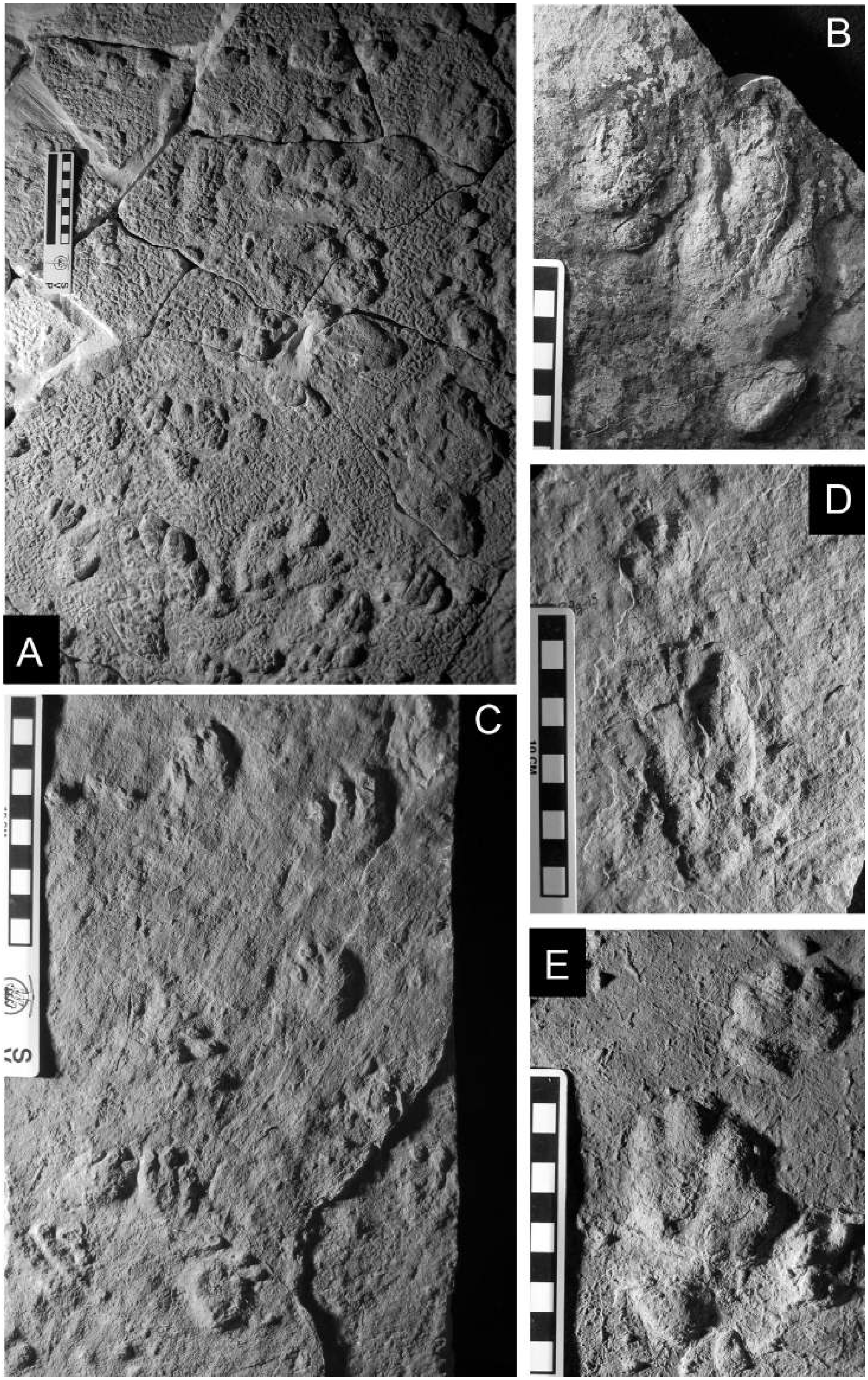


FIGURE 109. Tetrapod footprints from the Middle Triassic of the Massif Central in France. **A,** Section of large slab from La Pissoire (surface BF2) in the Museum of Natural History, Autun with "*Brachychirotherium*" *pachydactylum* (holotype). **B,** *Chirotherium* ("*Sphingopus*") *ferox* comb. nov. **C,** *Rotodactylus rati*. **D,** *Atreipus*-*Grallator* ("*Coelurosaurichnus*"). **E,** "*Brachychirotherium*" *circaparvum*.

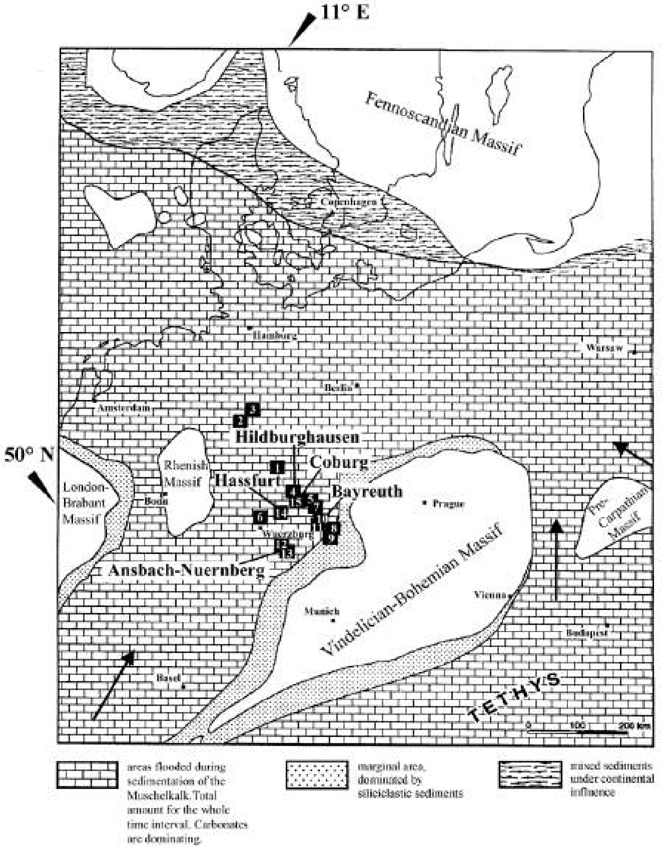


FIGURE 110. Paleogeographic map showing distribution of landmasses and marine ingressions in the Germanic Basin during the Middle Triassic. Numbers give position of tetrapod footprint localities of the whole Triassic. Base map after Ziegler (1982) and Geyer (2000). Numbers correspond to those in Figure 112.

Kössen formations (NorianRhaetian) in the Graubünden area have large surfaces with dinosaur footprints. In particular, the regions of Park Ela and Swiss National Park yielded trackways with tridactyl *Eubrontes*-like theropod tracks and large tetradactyl imprints that show some resemblance with typical sauropodomorph tracks such as *Pseudotetrasauropus* or *Tetrasauropus.* The sauropodomorph tracks document both bipedal and quadrupedal producers, probably prosauropods and basal sauropods (Furrer, 1993; Furrer and Lozza, 2008; Meyer et al., 2013).

The Netherlands

Marginal marine limestones of the Vossenfeld Formation (Lower Muschelkalk, Anisian) deposited along the western margin of the Rhenish Massif, and exposed in a local quarry near the town of Winterswijk, are rich in tetrapod footprints. The locality is famous for its skeletons of marine reptiles and other vertebrates such as fishes, temnospondyl amphibians, nothosaurs, placodonts and tanystropheids, but also for the terrestrially influenced ichno-assemblage, which is dominated by small lacertoid forms (Faber, 1958; Demathieu and Oosterink, 1983, 1988; Oosterink, 1988; Diedrich and Oosterink, 2000; Marchetti et al., 2019d). Demathieu and Oosterink (1983, 1988) listed the following tetrapod ichnotaxa: *Capitosauroides* isp., *Phenacopus faberi*, *P. agilis*, *Sustenodactylus hollandicus*, *Procolophonichnium winterswijkense*, *Rhynchosauroides peabodyi*, "*Brachychirotherium*" *paraparvum*, and "*Coelurosaurichnus*" *ratumensis*. Most rare are the footprints of archosaurs.

Only a few imprints have been described, and they have been assigned to "*Brachychirotherium*" *paraparvum*, and "*Coelurosaurichnus*" *ratumensis*. The former probably belongs to a single chirotheriid trackway, the latter is obviously a misinterpretation of a chirotheriid manus associated with a fragmentary pes impression. The footprints occur on larger surfaces characterized by microbial mats and syneresis cracks. The environment was interpreted as a tidal flat (Diedrich, 2001). Obviously archosaurs avoided the unsafe grounds while crossing the area searching for food that might partly have consisted of small vertebrates, such as the producers of the *Rhynchosauroides* tracks, as well as marine invertebrates that have also been found in these sediments, such as ammonites, brachiopods, bivalves, gastropods and crustaceans.

North Africa

Algeria

The Middle Triassic dolomitic-siliciclastic Haizer-Akouker unit of Algeria yielded small pes and manus imprints (Kotanski et al., 2004) that can be assigned to *Rotodactylus* isp. and *Rhynchosauroides* isp.

Morocco

In Morocco, the stratigraphically oldest Triassic deposits with tetrapod footprints are probably Olenekian in age. These are coarse to fine-grained sandstones of the Tanamert Member (T3) of the Timezgadiouine Formation in the Argana Basin that were deposited in a braided river fluvial environment. Identified ichnotaxa are *Protochirotherium* – *Synaptichnium* isp. and cf. *Rhynchosauroides* (Klein et al., 2009, 2010; Tourani et al., 2010; El Hachimi et al., 2011) (Fig. 124). The Aglegal Member (T4, Anisian-Ladinian) of the Timezgadiouine Formation has extensive surfaces with tetrapod footprints. During systematic excavations in 2010, a rich assemblage was documented with *Chirotherium barthii*, *Isochirotherium coureli*, *Synaptichnium* isp., *Atreipus-Grallator* isp., *Rotodactylus* isp., *Rhynchosauroides* isp. and *Procolophonichnium* isp. (Klein et al., 2011; Fig. 125).

Furthermore, numerous complex tetrapod burrows, possibly made by therapsids, were found (Voigt et al., 2011). Body fossils from the Aglegal Member are charophytes, ostracodes and capitosaur temnospondyls (Medina et al., 2001; Jalil, 2009). The mudstone-sandstone depositional environment is characteristic of playa and sheetflood-ephemeral stream sedimentation.

The Irohalene Member (T5) of the Timezgadiouine Formation and the Tadart Ouadou Member (T6) of the Bigoudine Formation in the Argana Basin (Western High Atlas) yielded rich tetrapod footprint assemblages. Early descriptions by Biron and Dutuit (1981) illustrated different tridactyl-pentadactyl morphotypes that were assigned by these authors to several new ichnotaxa such as "*Tridactylus machouensis,*" "*Anomoepus moghrebensis,*" "*Quadridigitus dubius,*" "*Pentichnus largus,*" "*Palaeosauropus triasicus*" and "*Molapopentapodiscus* isp." In recent years, extensive research in this unit and abundant new finds with complete trackways allowed a re-evaluation of this material. According to Lagnaoui et al. (2012, 2016) and Zouheir et al. (2018) the following ichnotaxa can be identified from the Irohalene Member: *Apatopus lineatus*, *Atreipus-Grallator* isp., *Eubrontes* isp., *Brachychirotherium parvum*, *Brachychirotherium* isp. *Parachirotherium* cf. *Parachirotherium postchirotherioides*, *Parachirotherium* isp., *Synaptichnium* isp., *Rhynchosauroides* isp. as well as dinosauromorph footprint indet. and tetrapod footprints indet. (Fig. 126). *Parachirotherium* is here considered a junior synonym of *Chirotherium* (see above).

Important is the co-occurrence of tridactyl grallatorid footprints with pentadactyl chirotheres. This is similar to other assemblages recognized in Germany and North America across the Middle Triassic-Upper Triassic (Ladinian-Carnian) boundary

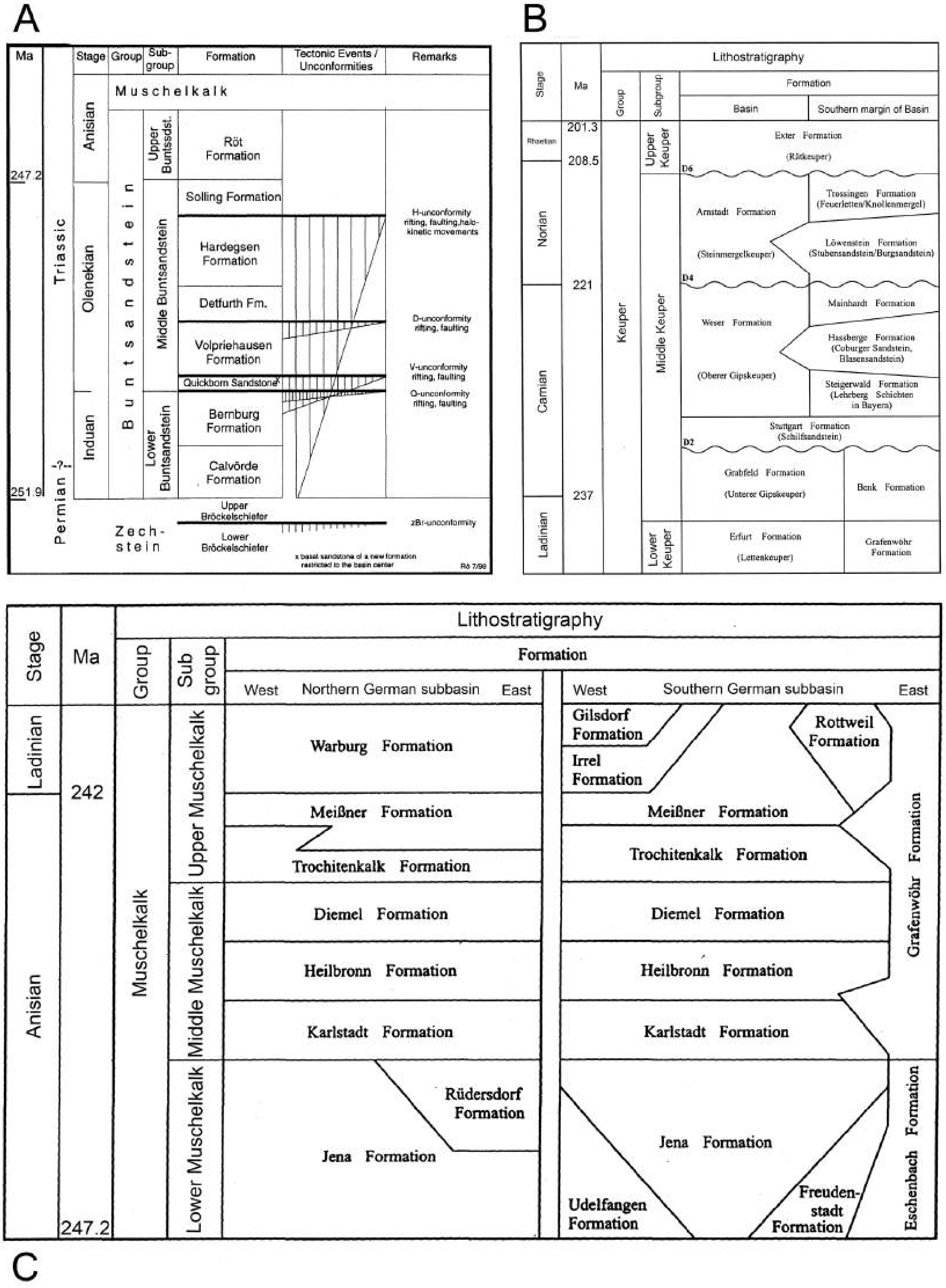


FIGURE 111. Triassic stratigraphic units in the Germanic Basin of Germany. **A,** Lower-Middle Triassic. **B,** Middle-Upper Triassic. **C,** Middle Triassic. From Lepper and Röhling (1998), Hagdorn et al. (1998) and Beutler (1998). Numerical ages updated based on Cohen et al. (2013).

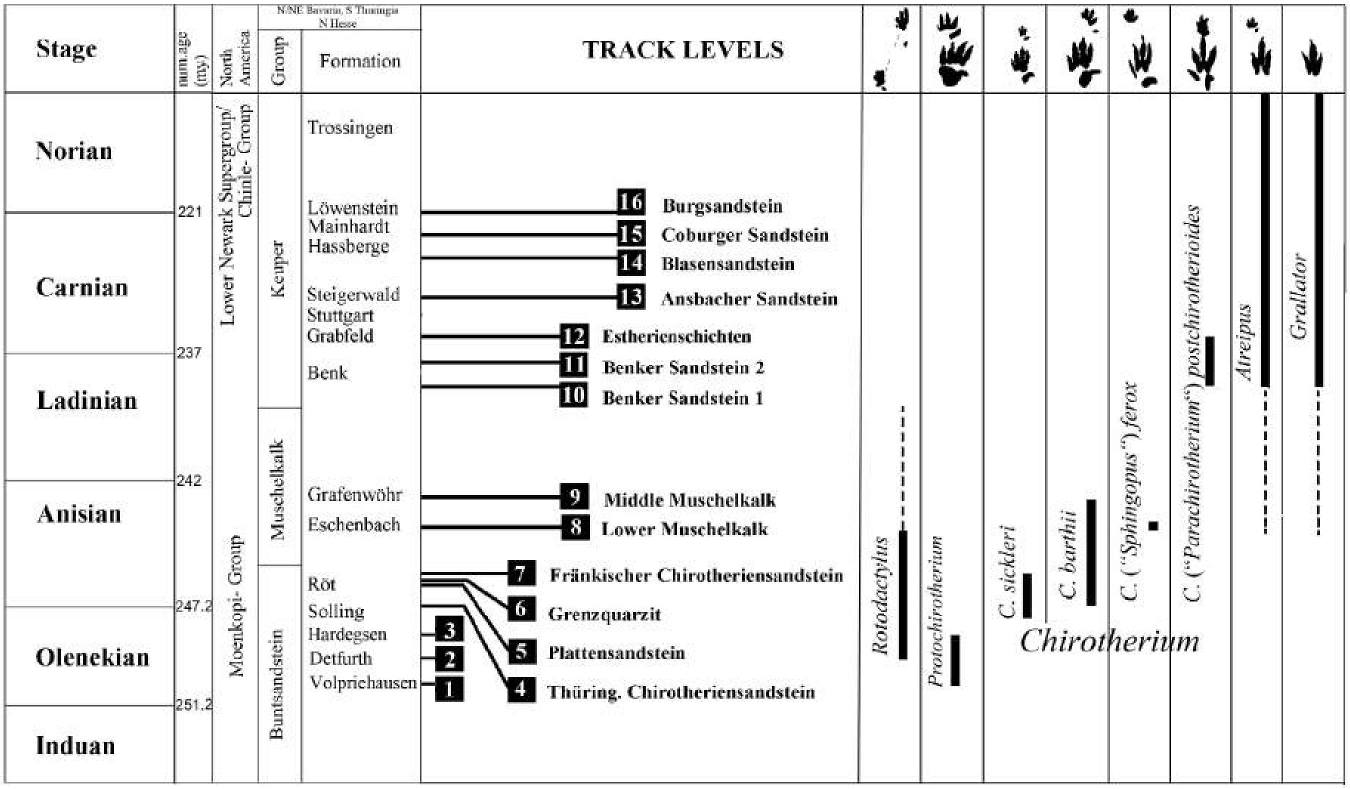


FIGURE 112. Tetrapod footprint horizons and range chart of archosaur footprints from the Lower-Upper Triassic of the Germanic Basin in southern Germany. Numbers correspond to those in Figure 110.

(Olsen and Huber, 1998; Haubold and Klein, 2000, 2002; Klein et al., 2018) and documents the early rise of dinosauromorphs. *Chirotherium* ("*Parachirotherium*") with strongly reduced pedal digits I and V was documented by a trackway with 10 successive pes prints (Zouheir et al., 2018). The lack of a manus impression, if not a preservational artifact, indicates possible bipedal movement of the trackmaker. This observation corresponds to the interpretations of Haubold and Klein (2000, 2002), who considered trackways of the "*Parachirotherium*"-*Atreipus-Grallator* plexus from the latest Ladinian of Germany to belong to facultatively bipedal dinosauromorphs. The sandstone-mudstone successions of the Irohalene Member indicate an alluvial plain depositional environment.

Probable Carnian deposits of the Ourika Basin contain the phytosaur track *Apatopus lineatus* and an indeterminate chirotheriid assigned by Biron and Dutuit (1981) to a new ichnotaxon named "*Chirotherium atlensis*." Furthermore, several indeterminate small tracks were also described by these authors as different new ichnotaxa such as "*Rectilinetopus ourikensis,*" "*Pseudochirotherium oukaimedensis,*" "*Prochirotherium triasicum,*" "*Chirotherium atlensis,*" "*Enigmatopus atlensis*" and *Hyloidichnus triasicus*.

In the Moroccan coastal Meseta, the fluvio-lacustrine Machr'a Abbess Member of the Oued Oum Er Rbiaa Formation (Carnian-Norian) of the Sidi Saïd M'aachou area yielded the chirotheriids *Brachychirotherium parvum* and *B. thuringiacum* (Hminna et al., 2009, 2013, 2019) with a complete trackway and several isolated pes and manus imprints. The associated ichnofauna consists of *Rhynchosauroides* isp. and invertebrate traces. No body fossils have been found in the Oued Oum Er Rbiaa Formation thus far. However, the Irohalene Member (T5) of the Timezgadiouine Formation in the Argana Basin has an important vertebrate fauna with fishes, amphibians (metoposaurs and others), dicynodonts and archosaurs (phytosaurs, "rauisuchians," aetosaurs, archosauromorphs) (Jalil, 1999).

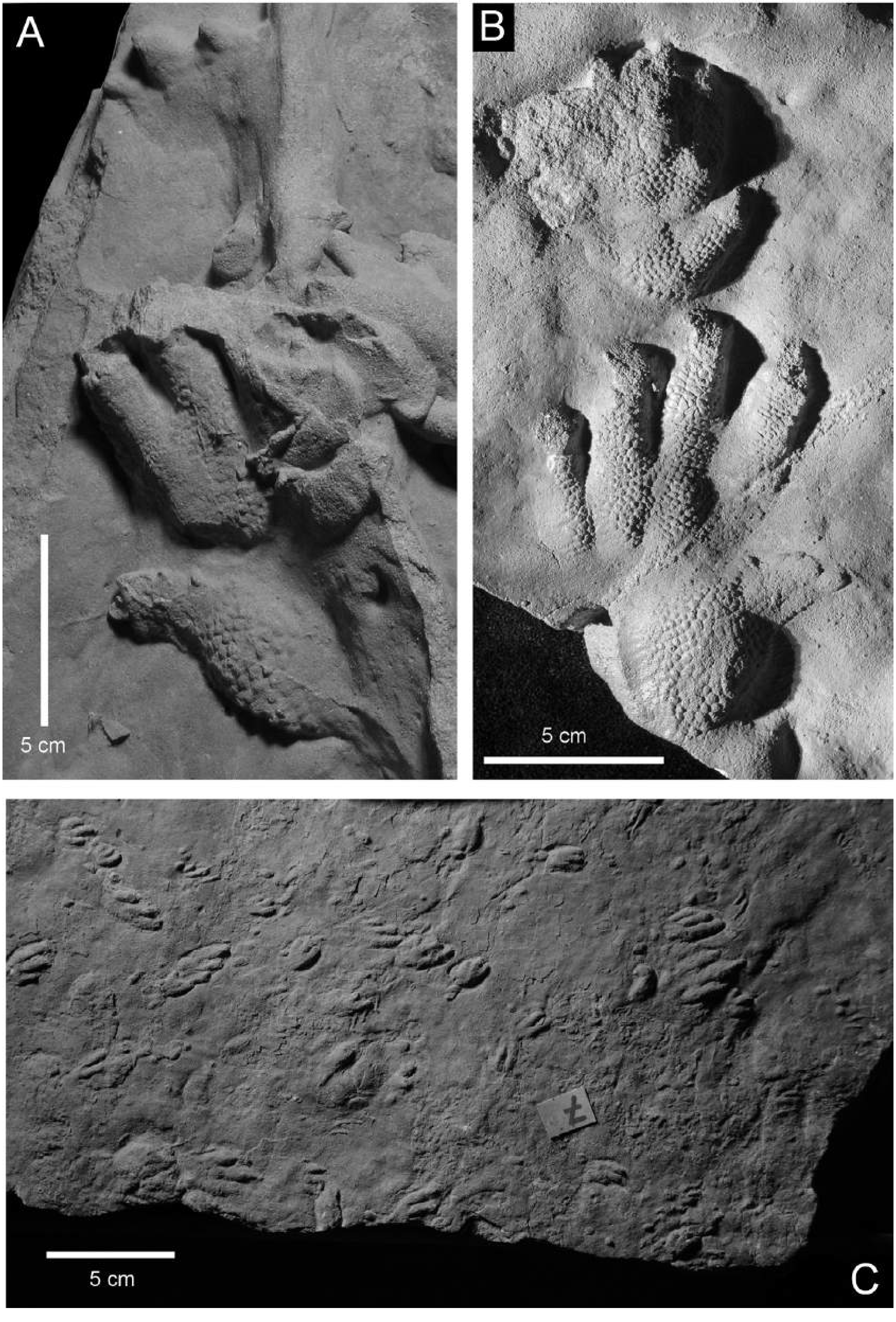
Niger

From the Teloua Formation (Lower Triassic) of the Agadez region of central Niger, Ginsburg et al. (1968) described chirotheriid and small lacertoid footprints that they assigned to *Chirotherium* and the trackway of a small amphibian. The published illustrations are only interpretive drawings and no photographs, so we are not able to provide an ichnotaxonomic assessment based on the original publication. However, Taquet (1976) published a photograph of a surface with chirothere tracks from this unit South of Agadez that show some similarity to the ichnogenus *Protochirotherium.* The trackway could be a typical *Rhynchosauroides* with the manus being laterally overstepped by the pes and with an associated tail trace. The material needs to be restudied.

Tunisia

Niedźwiedzki et al. (2017) described tridactyl-pentadactyl tracks, which they attribute to Dinosauromorpha and Therapsida, respectively, from the Middle-Upper Triassic Ouled Chebbi, Kirchaou and Azizia formations (Anisian, Ladinian–Carnian) of southeastern Tunisia. They are moderately-poorly preserved, and probably can be assigned to the *Atreipus-Grallator-*

FIGURE 113. (facing page) Tetrapod footprints from the Lower-Middle Triassic of the Germanic Basin in Germany. **A,** *Protochirotherium* isp. from Volpriehausen Fm. (Olenekian). **B,** *Protochirotherium wolfhagense* from Detfurth Fm. (Olenekian). **C,** Slab with small *Chirotherium sickleri* trackway and abundant *Rotodactylus matthesi* pes and manus imprints from Solling Formation (Anisian).


A
5 cm
B
5 cm
5 cm
C

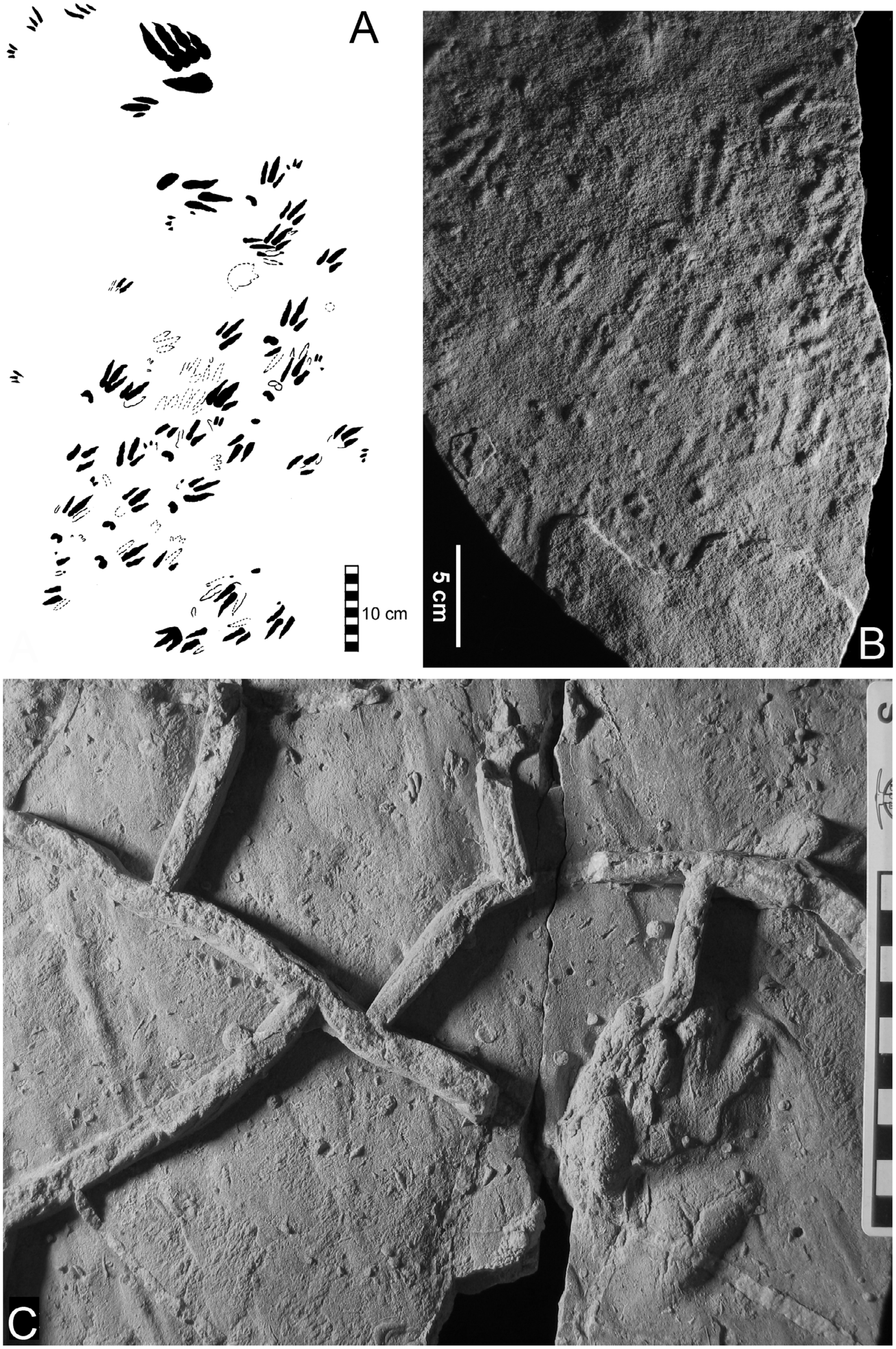


FIGURE 114. Tetrapod footprints from the Middle Triassic of the Germanic Basin in Germany. **A,** Sketch showing distribution of numerous juvenile *Chirotherium ferox* pes and manus imprints co-occurring with larger *Synaptichnium pseudosuchoides* and *Rhynchosauroides* isp. pes and manus imprints (top left) on large slab from Eschenbach Fm. (Anisian). **B,** Photograph with section of large slab in A. **C,** Photograph showing "*Brachychirotherium*" isp. pes and manus on slab with isolated *Rhynchosauroides* isp., Skolithos isp. and mudcracks from Benk Fm. (Ladinian). A. From Haubold and Klein (2002).

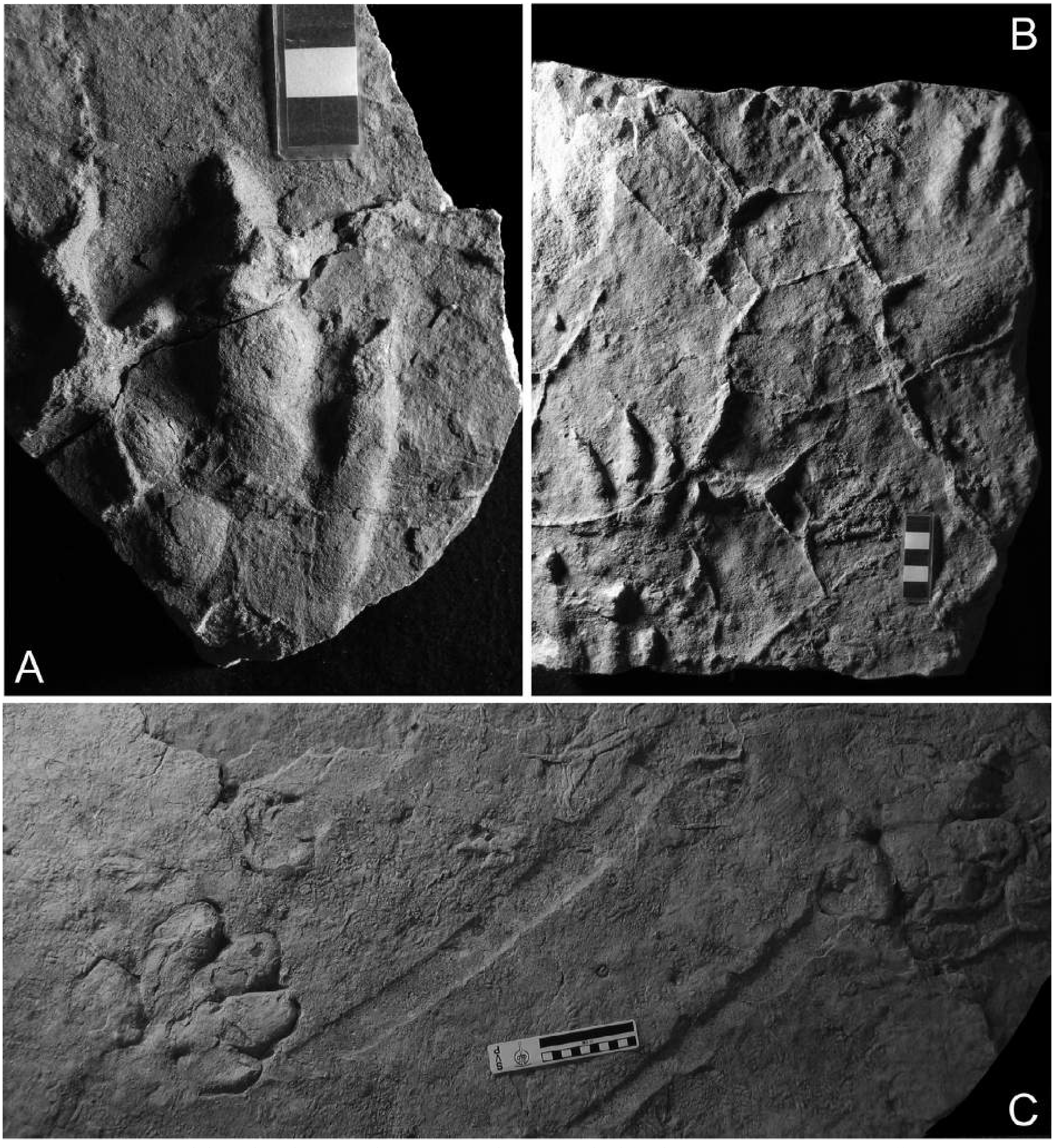


FIGURE 115. Tetrapod footprints from Hassberge Fm. (Coburger Sandstein) of Germany. **A,** *Atreipus-Grallator*. **B,** *Apatopus lineatus*. **C,** *Brachychirotherium thuringiacum* co-occurring with *Atreipus-Grallator*.

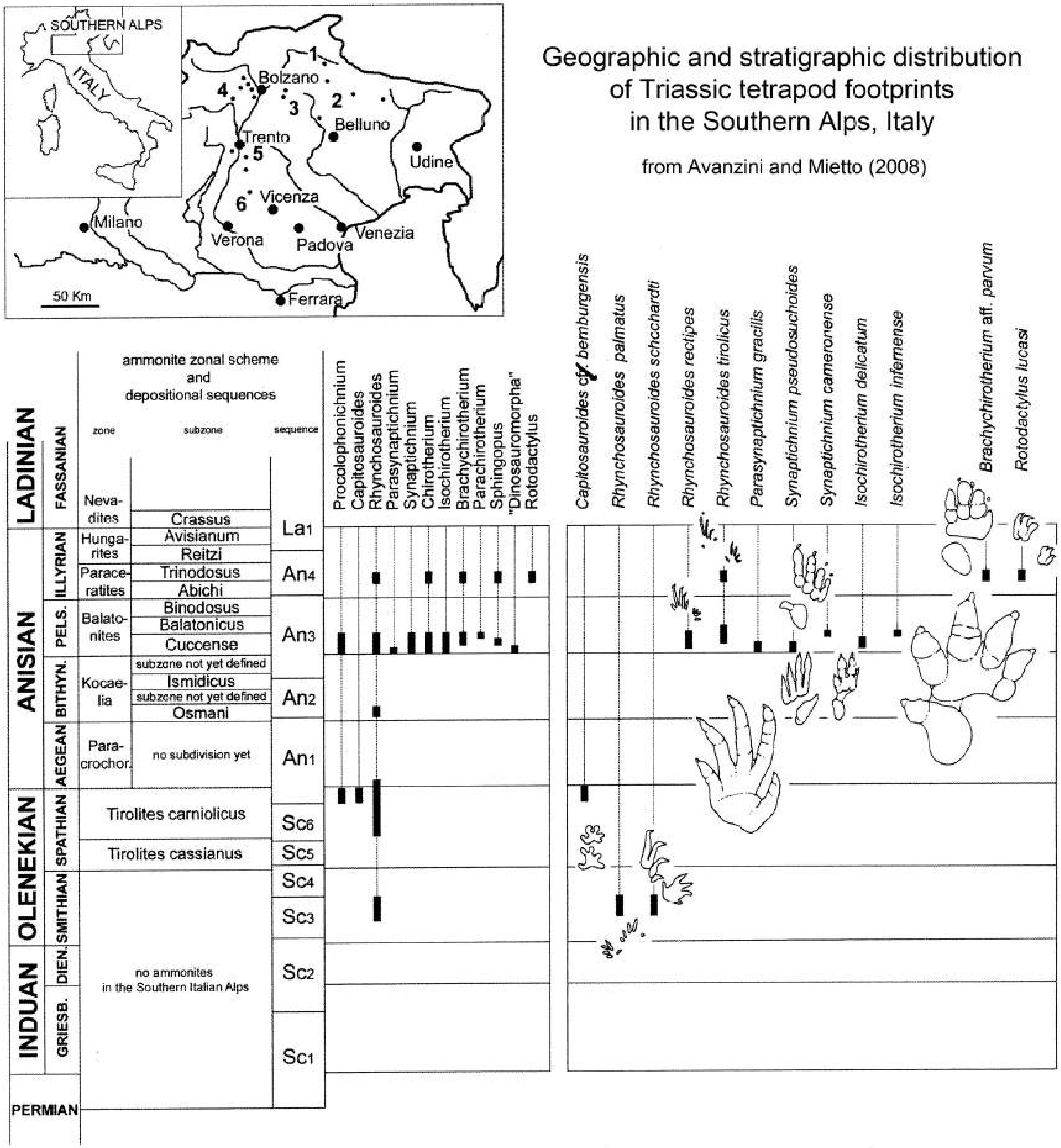
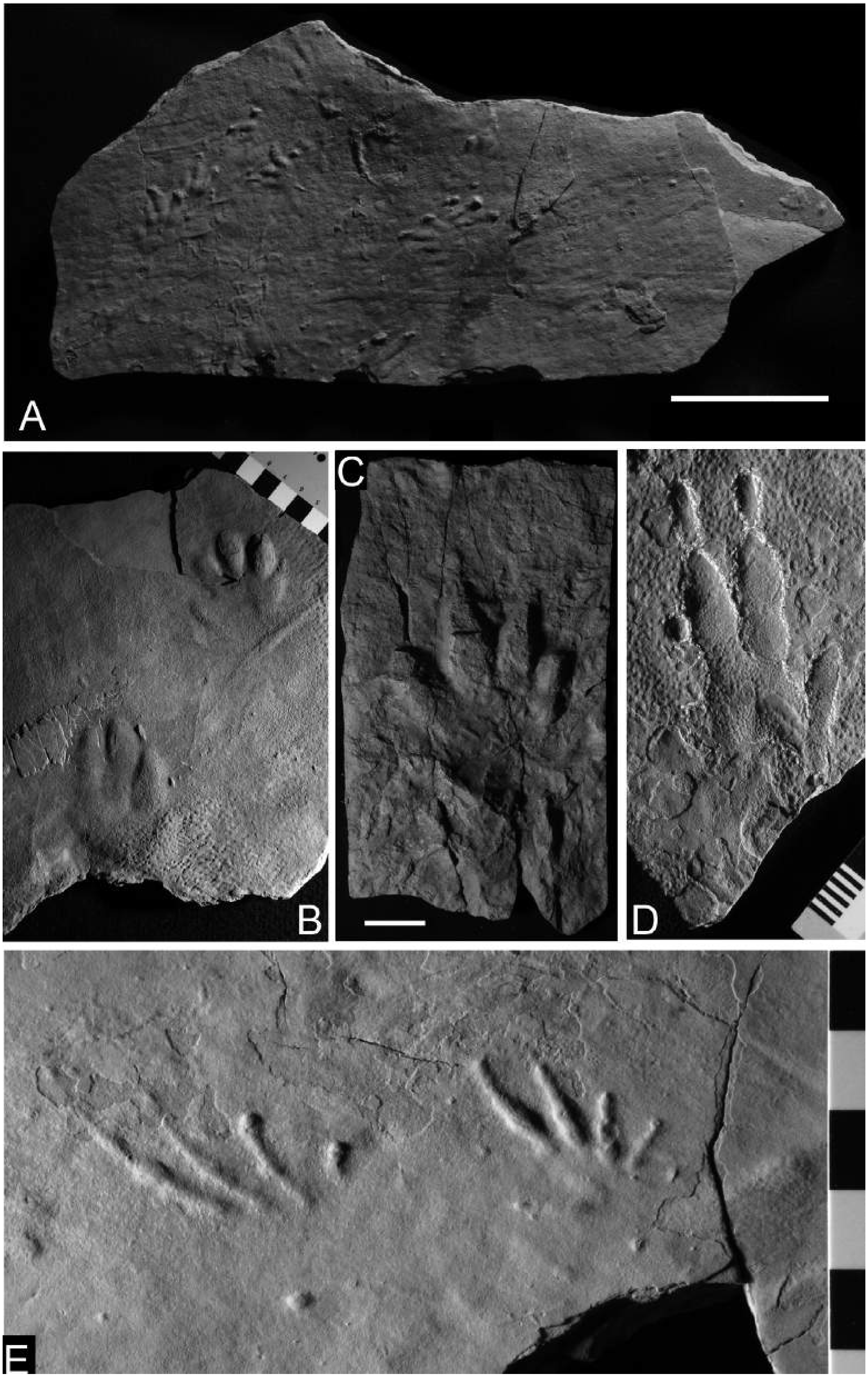


FIGURE 116. Geographic and stratigraphic distribution of Triassic tetrapod footprints in the Southern Alps, Northern Italy. From Avanzini and Mietto (2008b).

FIGURE 117. (facing page) Tetrapod footprints from the Middle Triassic of Southern Alps, Northern Italy. **A,** *Procolophonichnium haarmuehlensis*. **B,** “*Brachychirotherium*” aff. *parvum*. **C,** *Isochirotherium inferni*. **D,** *I. delicatum*. **E,** *Rhynchosauroides tirolicus*.


A
B
C
D
E

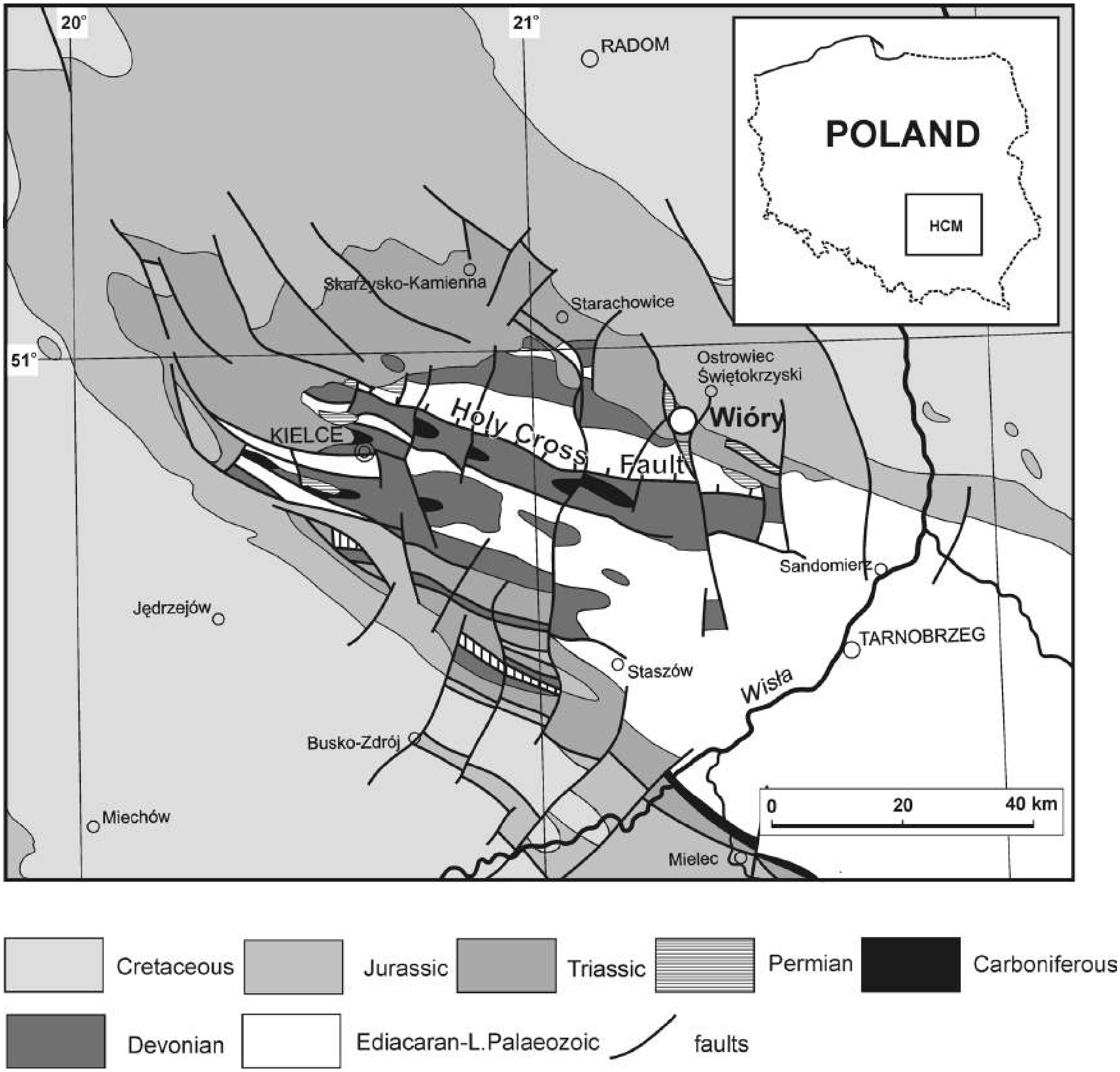


FIGURE 118. Position and geological map of the Holy Cross Mountains in Poland with the Wióry footprint locality. From Klein and Niedźwiedzki (2012).

Eubrontes plexus, incomplete chirotheriid, and indeterminate therapsid tracks.

Southern Africa

Besides the abundant record from Upper Triassic localities, southern Africa has only a few Lower-Middle Triassic tetrapod footprint occurrences. This might be due to a taphonomic phenomenon and (thus far) lack of surfaces with high footprint preservation potential.

South Africa

Occurrences are in the Palingkloof Member of the Balfour Formation (*Lystrosaurus* assemblage zone, Induan) of the Karoo Basin in South Africa. Assemblages comprise the cynodont tracks cf. *Dicynodontipus* and *Dolomitipes accordii*, the latter originally known from the upper Permian of the Val Gardena Formation in northern Italy. Further components are *Procolophonichnium nopcsai* (procolophonid) and *Rhynchosauroides* isp. (neodiapsid) (see Marchetti et al., 2019b; Fig. 127). The lower Elliot Formation (Norian) of the Karoo Basin yielded swim traces of tetrapods and fishes (*Undichna*) (Sciscio et al., 2020 in press).

Lesotho

Rich vertebrate ichnofaunas from the Molteno and Lower Elliot formations of Lesotho (?Carnian-Norian-Rhaetian) are well known from the extensive documentation of Ellenberger (1970, 1972, 1974) (Figs. 128-131). Subsequently, different authors re-evaluated and discussed these assemblages in numerous papers (Olsen and Galton, 1982; Raath et al., 1990; Knoll, 2004; D'Orazi-Porchetti and Nicosia, 2007; Bordy et al., 2017). While Ellenberger (1970, 1972, 1974) introduced a large number of new ichnotaxa with only limited comparison to other forms outside of southern Africa, it was soon clear that most of them are *nomina dubia* or represent junior synonyms of ichnotaxa described formerly from North America and Europe (see discussion above). In particular, tridactyl theropod tracks of the *Grallator-Eubrontes* plexus were hidden behind ichnotaxa introduced by Ellenberger as "*Anatri-*", "*Qemetri-*", "*Prototri-*", "*Seakatri-*", "*Bosiutri-*", "*Deuterotri-*" and "*Mafatrisauropus*"

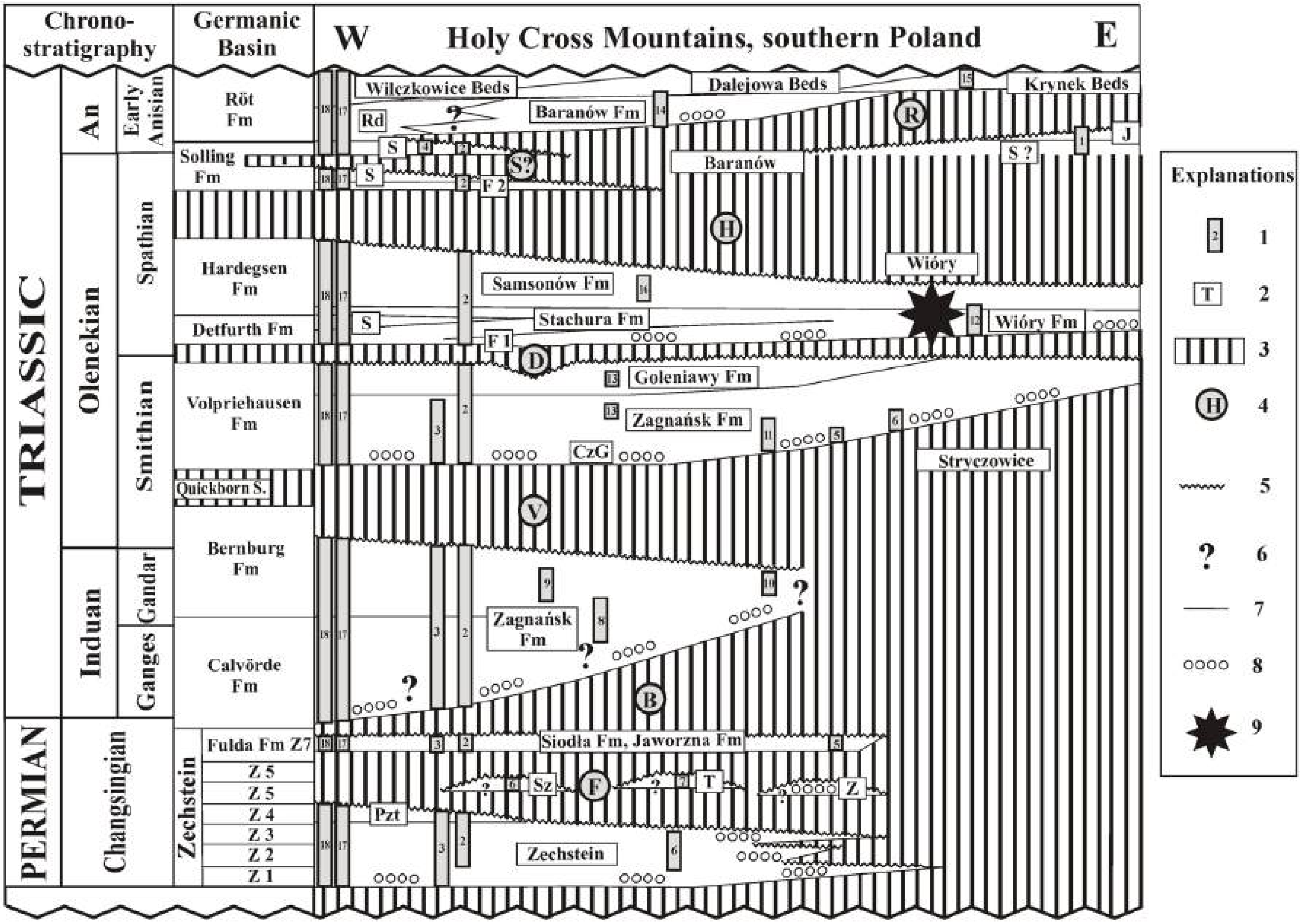


FIGURE 119. Chronostratigraphic scheme of the Buntsandstein in the Holy Cross Mountains with lithostratigraphic correlation to units in the Germanic Basin. Explanations: 1, borehole profiles and outcrops; 2, lithostratigraphic units; 3, stratigraphic gaps; 4, unconformities; 5, erosional boundaries; 6, presence of the formation not certain; 7, boundaries (without erosion); 8, conglomerates; 9, lithostratigraphic position of Wióry tracksites. From Klein and Niedźwiedzki (2012).

(D'Orazi-Porchetti and Nicosia, 2007). *Tetrasauropus* and *Pseudotetrasauropus* are valid ichnogenera (see above) and probably represent the footprints of sauropodomorphs, while *Deuterosauropodopus* is obviously synonymous with the archosaur ichnogenus *Brachychirotherium* (D'Orazi-Porchetti and Nicosia, 2007). *Pentasauropus* indicates the presence of dicynodont therapsids co-occurring with the dinosaurs (D'Orazi-Porchetti and Nicosia, 2007; Bordy et al., 2017). Numerous small footprints still have to be re-evaluated. The footprints occur in fluvio-lacustrine deposits of sandstones, siltstones and claystones. A rich vertebrate body fossil fauna is known from the Lower Elliot Formation. These are stereospondyls, "?rauisuchians," theropods, prosauropods, sauropods and cynodonts (Lucas and Hancox, 2001).

China

Guizhou Province

The Guanling Formation (Middle Triassic, Anisian) of Guizhou Province yielded numerous tetrapod footprints from three localities, in particular from the lower part of the formation (Songzikan Member, Member I; Wang and Ji, 1989). These occur on two different levels in a sequence of argillaceous dolomite (Fig. 132). The assemblage from the upper level at the Longchang and Niuchang localities in the southwestern region of the province comprises several long trackways of terrestrial archosaurs (*Chirotherium barthii*) that are preserved in concave epirelief (Wang, 1996; Zhen et al., 1996; Lü et al., 2004; Lockley and Matsukawa, 2009; Klein and Lucas, 2010a; Lockley et al., 2013; Xing et al., 2013a). The lower horizon at the recently discovered Qingyuan site in west-central Guizhou has abundant trackways of marine reptiles, probably placodonts and/or saurosphargids, possibly also nothosaurs, that have been assigned to *Dikoposichnus luopingensis* and a new ichnotaxon *Anshunpes aquacursor* (Klein et al., 2019; Xing et al., 2020; see above). These were obviously left by swimming and bottom-walking individuals along the coast of the eastern Tethys. Indeed, Guizhou Province is well-known for its marine Triassic faunas with abundant skeletons of marine reptiles such as nothosaurs, placodonts, saurosphargids, turtles, protorosaurs and archosaurs adapted to marine environments, but also crinoids, ammonites and bivalves. Most of these occur in the Upper Triassic Xiaowa Formation (Carnian), but also the Middle Triassic Guanling Formation yielded faunas with marine reptiles, bivalves etc. (Benton et al., 2013).

The depositional environment of the track-bearing strata can be characterized as shallow marine, with intertidal and lagoonal areas under a hot and dry climate. At some levels, the facies resembles that of the Muschelkalk (Anisian-Ladinian) from Central Europe. However, while the Guanling Formation yielded both trackways of terrestrial and marine tetrapods, the European Muschelkalk, despite abundant marine reptile skeletons, has only the footprints of terrestrial forms (Demathieu

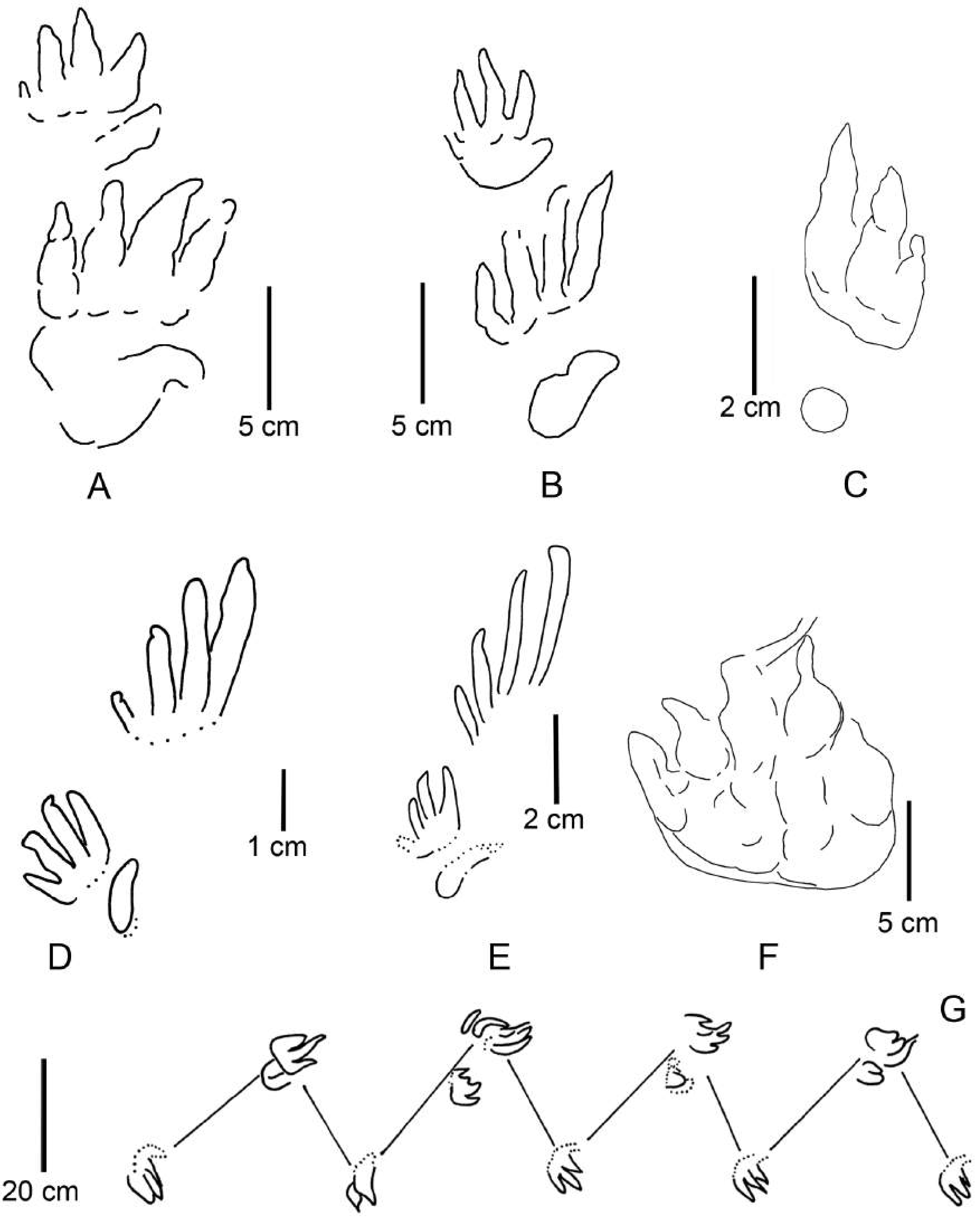


FIGURE 120. Footprints and trackways from Wióry Fm. (Olenekian) of the Holy Cross Mountains, Poland as sketches. **A,** *Protochirotherium hauboldi*. **B,** *Synaptichnium kotanskii*. **C,** cf. *Rotodactylus* isp. **D,** *Prorotodactylus mirus*. **E,** *Rhynchosauroides rdzaneki*. **F,** cf. *Therapsipus* isp. **G,** "*Capitosauroides*" *fuglewiczi*. From Klein and Niedźwiedzki (2012).

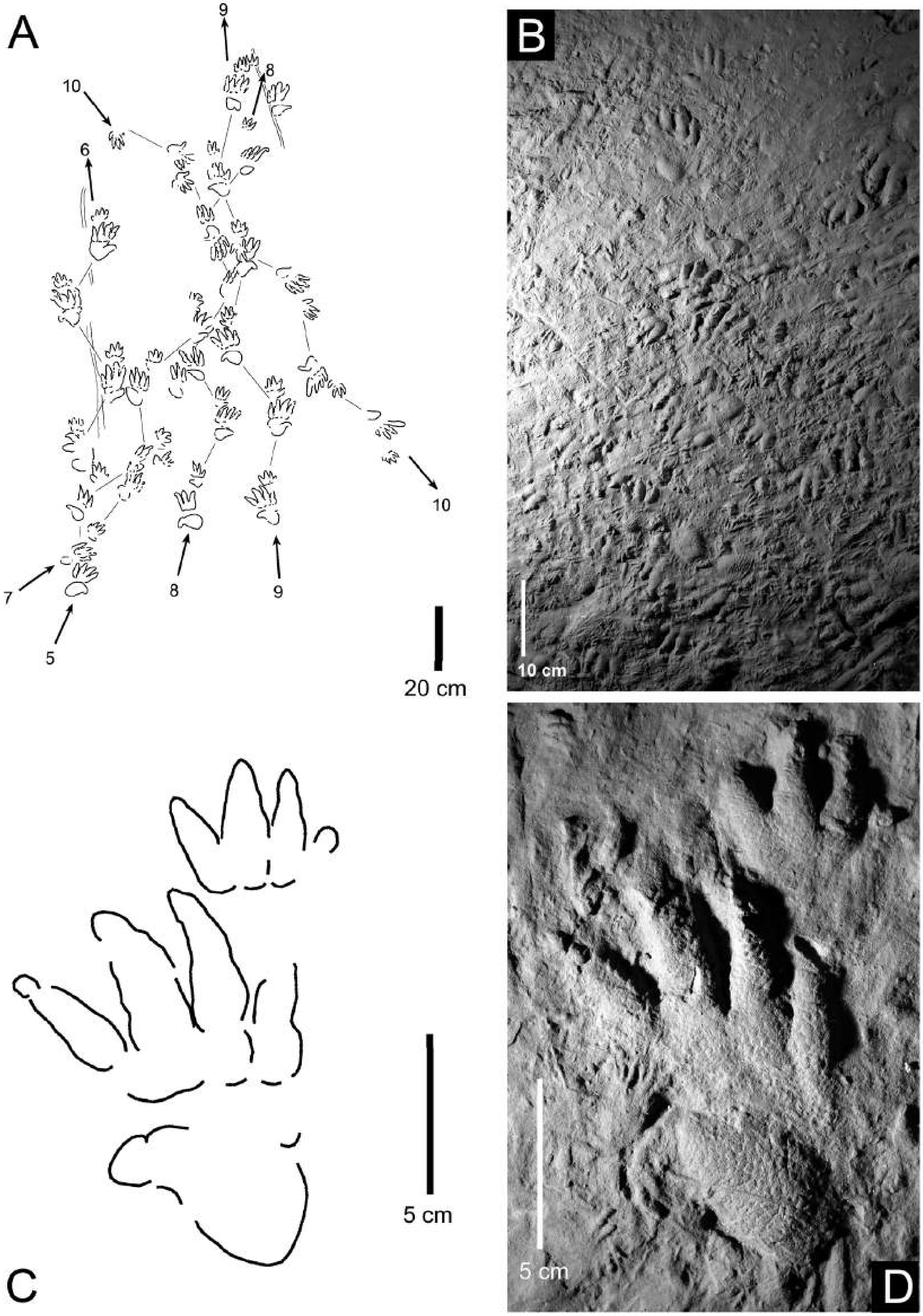


FIGURE 121. Chirotheriid footprints, *Protochirotherium hauboldi* from Wióry Fm. (Olenekian) of Holy Cross Mountains, Poland. **A,** Large slab with numerous trackways as interpretive outline drawing. **B,** Photograph showing section of large slab. **C-D,** Details as sketch and photograph showing skin impressions. From Klein and Niedźwiedzki (2012).

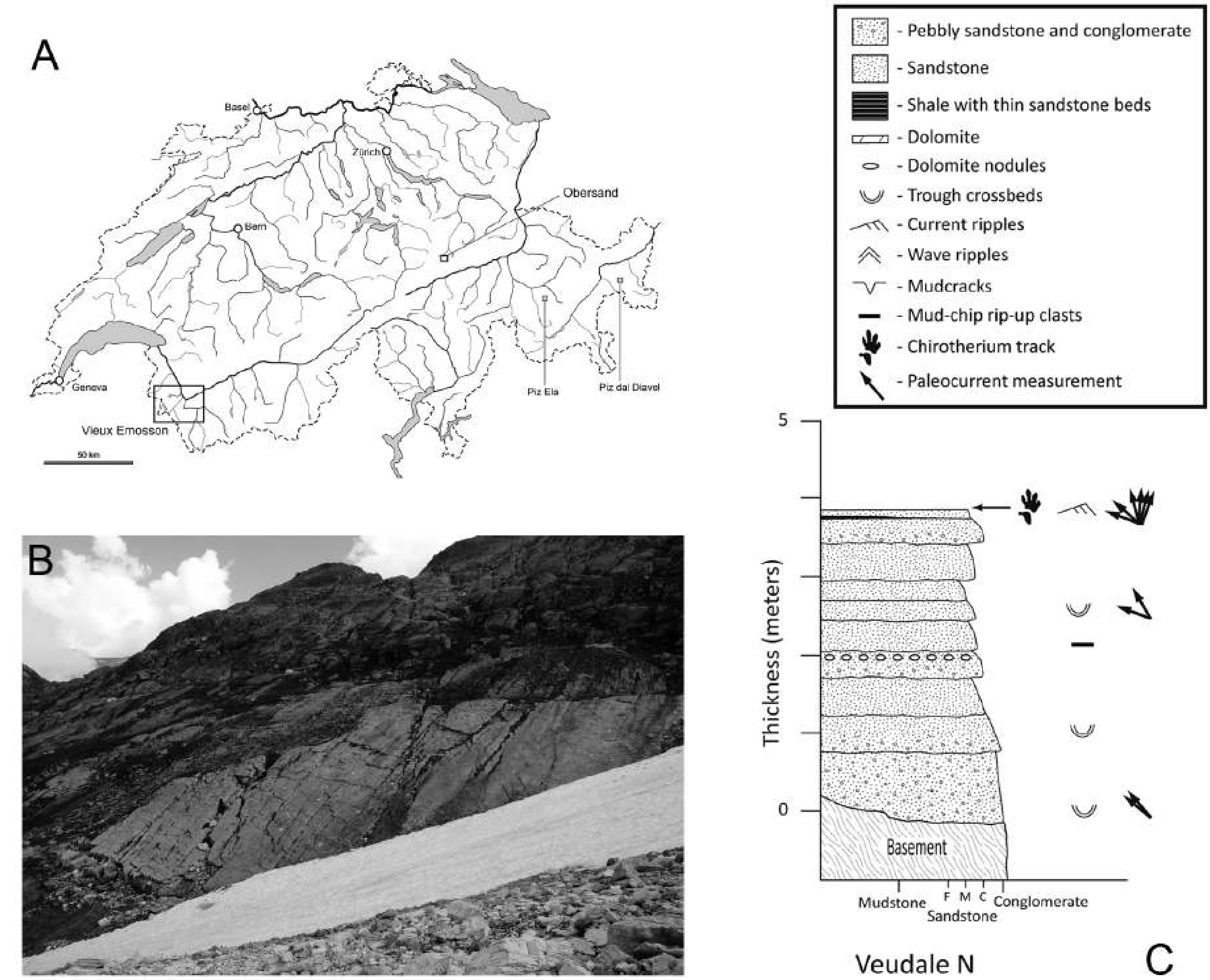


FIGURE 122. Triassic tetrapod footprint localities in Switzerland. **A,** Map showing position of tracksites. **B,** Overview of Veudale N locality in the Emosson region (steep surface) with extremely abundant chirotheriid footprints from Vieux Emosson Fm. (Olenekian-Anisian). **C,** Section at Veudale N with position of footprints. From Klein et al. (2016).

and Oosterink, 1983, 1988; Klein and Lucas, 2018).

Sichuan Province

The Xujiahe Formation (Rhaetian) of the western Sichuan Basin and the Baoding Formation (?Norian-Rhaetian) of southernmost Sichuan Province both yield footprints. These are assigned to *Pengxianpus cifengensis* and cf. *Pengxianpus*, and are trackways of bipeds with large (over 25 cm length) and small (11 cm length) pes imprints with relatively wide digit divarication, that can be attributed to theropods (Yang and Yang, 1987; Wang et al., 2005; Xing et al., 2013c). Small, mammal-like footprints are known from the Xujiahe Formation (Xing et al., 2013c). A poorly preserved trackway of a possibly bipedal archosaur from the same unit resembles *Eosauropus* from the Chinle Group of North America, which has been attributed to facultatively bipedal sauropodomorphs. However, the Chinese trackway shows an inward rotation of the footprints, whereas in *Eosauropus* these are outward directed. Therefore, the former was considered as an indeterminate archosaur trackway (Xing et al., 2013b).

The Baoding Formation of Sichuan provided several trackways with very large (up to 41 cm length) pes tracks. They have been assigned to *Chirotherium* indet. based on the principal chirotheriid shape similar to *C. barthii* known from the Middle Triassic with a pronounced functionally tridactyl digit group II–IV and a posterolaterally positioned digit V. However, the lack of digit I and manus impressions led Xing et al. (2014) to consider a more tentative attribution. It cannot be excluded that these footprints represent a new ichnospecies.

Yunnan Province

In the Lower Guanling Formation (Songzikan Member, Anisian) tetrapod footprints occur on a mudcracked layer in a succession with argillaceous dolostones (Fig. 133). A first description was given by Zhang et al. (2018). Recently, Xing and Klein (2019) provided detailed documentation and interpretation. Based on the latter authors, four trackways assigned to *Chirotherium barthii* are present: 1) four consecutive pes-manus sets, 2) five consecutive pes-manus sets and two pes prints, 3) a single pes-manus set and six pes prints lacking a manus print and 4) nine sets and two pes prints. Furthermore, several isolated prints are documented. Another trackway with five pes-manus sets and several isolated prints and partial trackways belongs to *Rhynchosauroides* isp., and is the first evidence of the ichnogenus from the Asian continent. All are preserved as concave epi-reliefs.

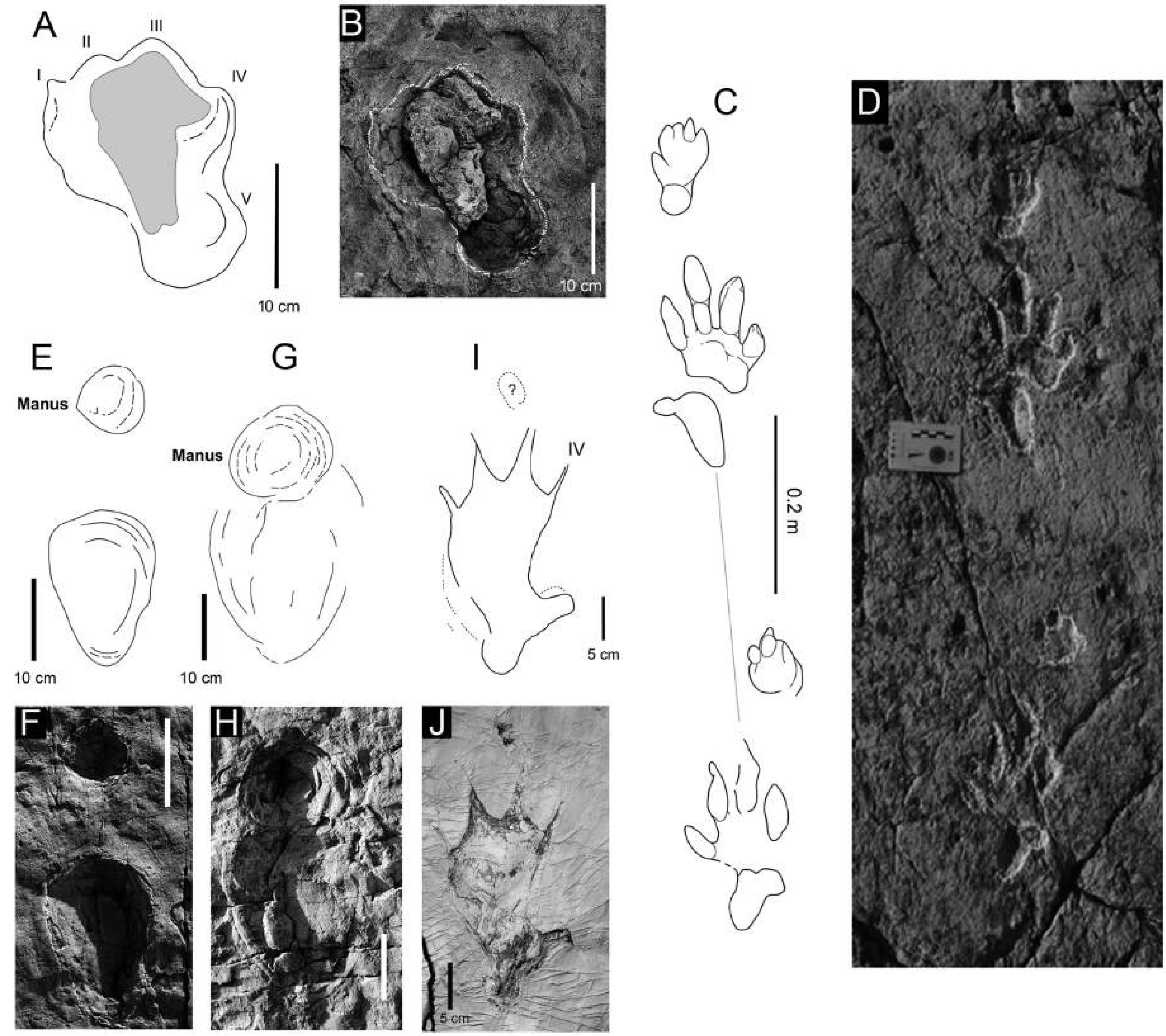


FIGURE 123. Chirotheriid footprints from Vieux Emosson Fm. (Olenekian-Anisian) of the Western Swiss Alps and from Middle Triassic Röti Dolomite unit of the Eastern Swiss Alps. **A-B,** *Isochirotherium herculis* pes imprint as photograph and interpretive outline drawing. From Klein et al. (2016). **C-D,** *Chirotherium barthii* as interpretive outline drawing and photograph. **E-H,** Indeterminate chirotheriids, some with hour-glass shape morphology, the characteristic preservation at Vieux Emosson and La Veudale N localities, representing pes and associated manus impressions. **I-J,** *Chirotherium barthii* pes-manus set from Röti Dolomite in the Eastern Swiss Alps. From Klein et al. (2016).

The Upper Guanling Formation (Shizishan Member, Anisian) of Yunnan Province provided an ichnofauna with the footprints of marine reptiles that have been assigned to foraging nothosaurs and the new ichnotaxon *Dikoposichnus luopingensis* (Zhang et al., 2014). They occur in a unit that contains a fauna with abundant marine reptile skeletons, the so-called Luoping Biota.

Body fossils of the Guanling Formation consist of bivalves, crinoids, ammonites (Zhang et al., 2009) and marine reptiles (Benton et al., 2013; Zhang et al., 2009). The depositional environment was a marginal marine setting along the coast of the eastern Tethys.

Thailand

Three longer tetrapod trackways occur in the Huai Hin Lat Formation (Upper Triassic, Norian) of northeastern Thailand. These were assigned to archosaur trackways by Le Loeuff et al. (2009) and more precisely referred to the phytosaur ichnospecies *Apatopus lineatus* by Klein and Lucas (2013). They are preserved as concave epireliefs on the upper surface of a large sandstone slab. Body fossils from the Huai Hin Lat Formation are known with fishes, amphibians, turtles and phytosaurs, resembling the vertebrate fauna of the Norian Stubensandstein in the Germanic Basin (Le Loeuff et al. (2009). The depositional environment and sediments of the Huai Hin Lat Formation can be characterized as fluviolacustrine siliciclastics with limestones and volcaniclastic input (Chonglakmani, 2011).

Australia-Antarctica

Relatively few Triassic footprints are known from Australia

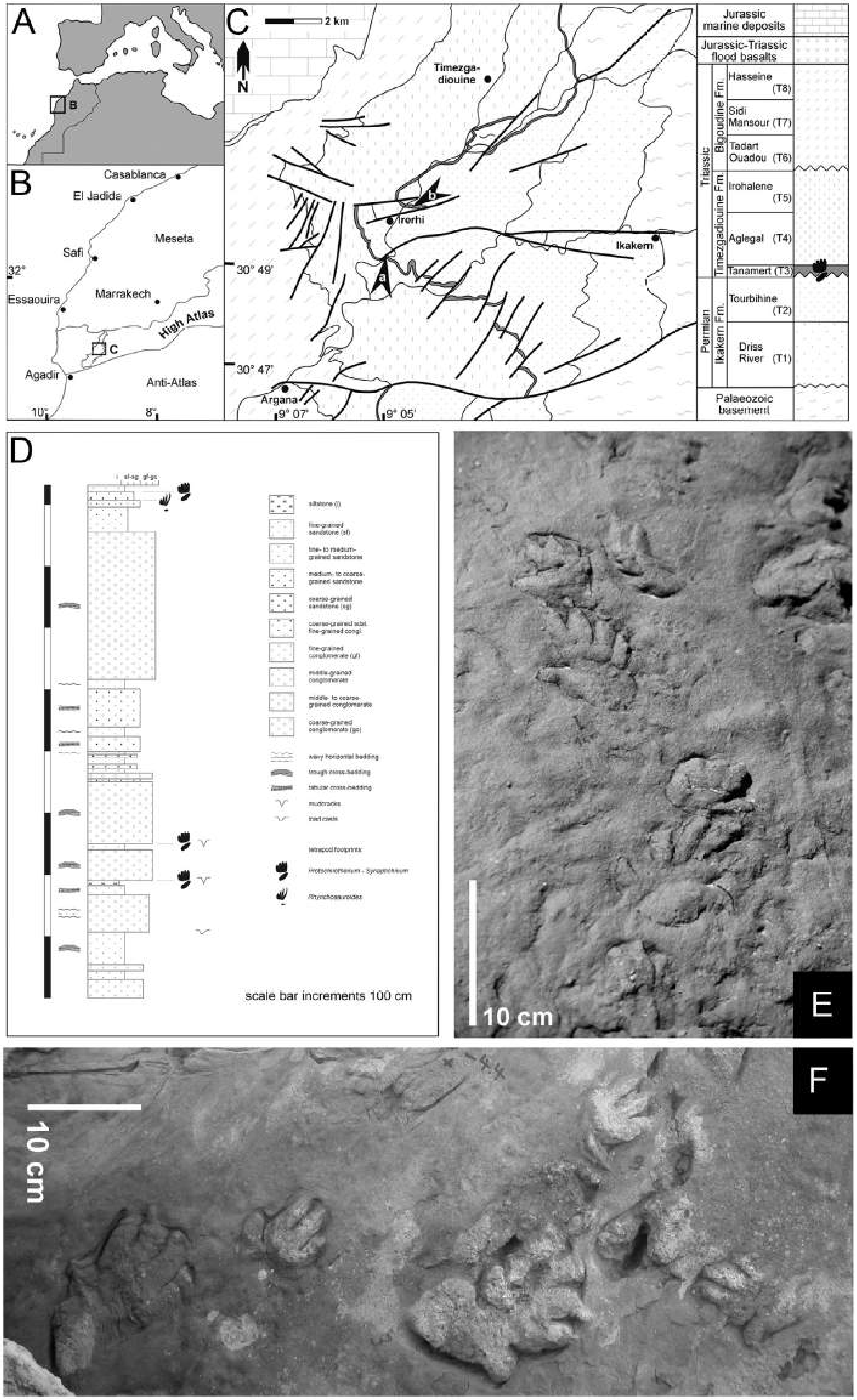


FIGURE 124. Tetrapod footprint assemblages from the Timezgadiouine Fm. (T3, Olenekian) of the Argana Basin, Morocco. **A-C,** Map showing geographic and stratigraphic position of footprint localities. **D,** Stratigraphic section with details. **E-F,** *Protochirotherium-Synaptichnium* plexus footprints. **E,** On lower surface of loose block. **F,** *In situ* trackways on lower surface of a streambed channel. From Klein et al. (2010).

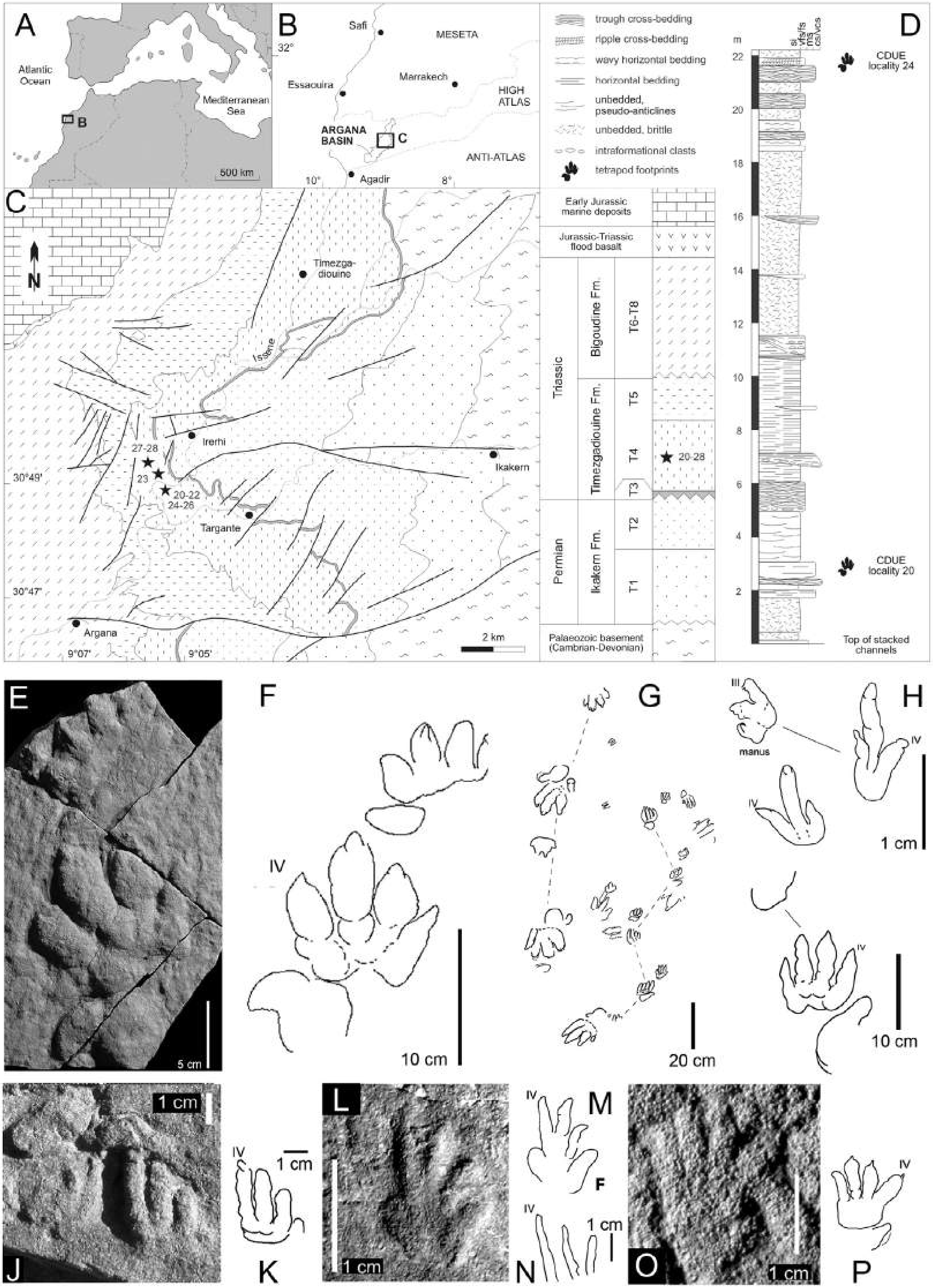


FIGURE 125. Tetrapod footprint assemblages from the Timezgadiouine Fm. (T4, AnisianLadinian) of the Argana Basin, Morocco. **A-C,** Maps showing geographic and stratigraphic position of footprint localities. **D,** Stratigraphic section with details. E-P. Footprints as photographs and interpretive outline drawings. **E-F,** *Chirotherium barthii* pes-manus set. **G,** Surface with *C. barthii* (left) and *Synaptichnium* isp. trackways (right), and isolated imprints. **H,** *Atreipus-Grallator* pes-manus set and isolated pes (top). **I,** *Isochirotherium coureli* pes-manus set (bottom). **J-K,** *Rotodactylus* isp. **L-N,** *Rhynchosauroides* isp. manus and pes imprints (bottom). **O-P,** *Procolophonichnium* isp. From Klein et al. (2011).

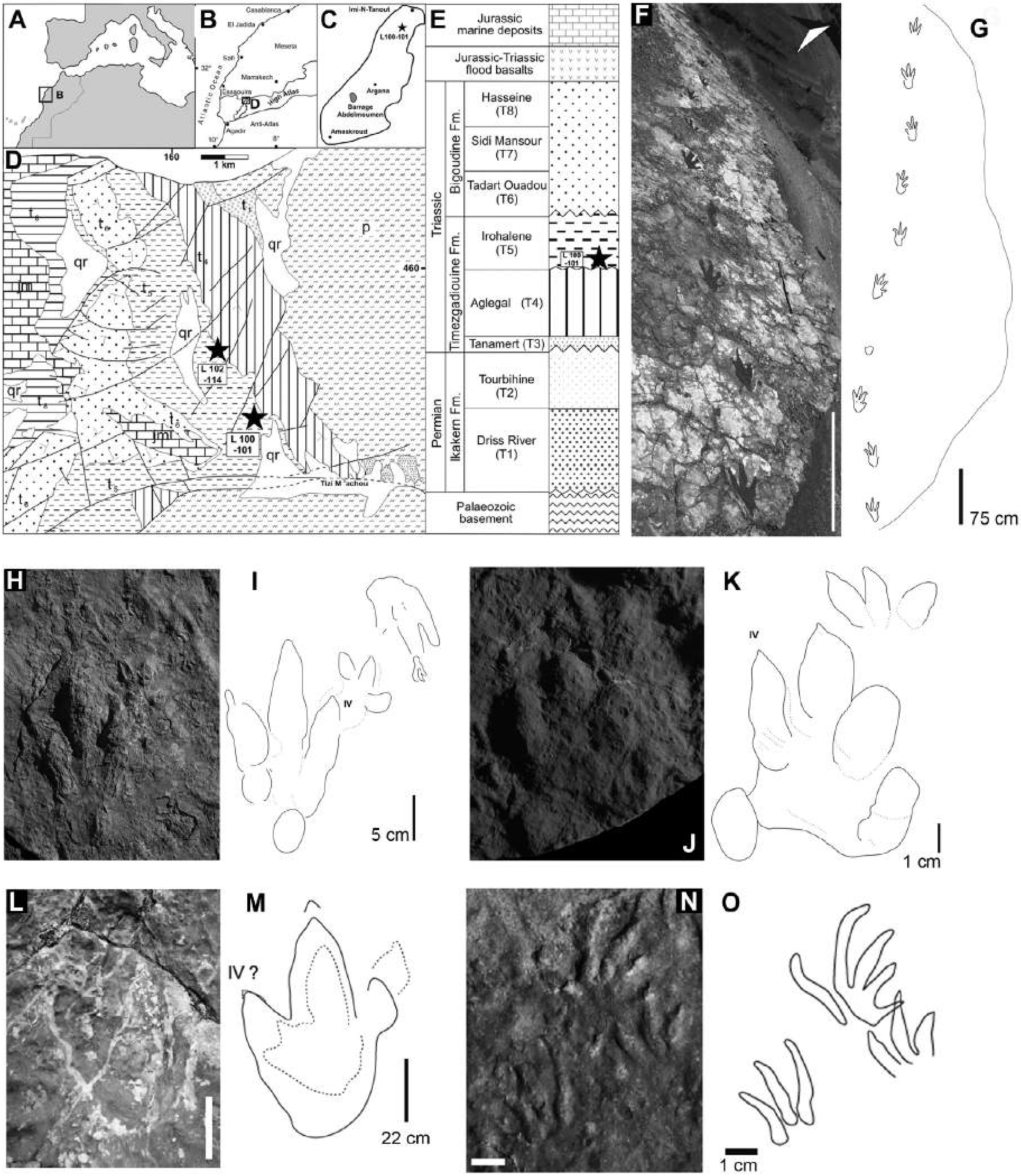


FIGURE 126. Tetrapod footprint assemblages from the Timezgadiouine Fm. (T5, Carnian) of the Argana Basin, Morocco. **A-E,** Maps showing geographic and stratigraphic position of footprint localities. F-O. Footprints as photographs and interpretive outline drawings. **F-G,** Trackway of *Chirotherium* ("*Parachirotherium*") isp. **H-I,** cf. *Atreipus*. **J-K,** *Brachychirotherium* isp. **L-M,** *Eubrontes* isp. **N-O,** *Rhynchosauroides* isp. From Lagnaoui et al. (2016) and Zouheir et al. (2018).

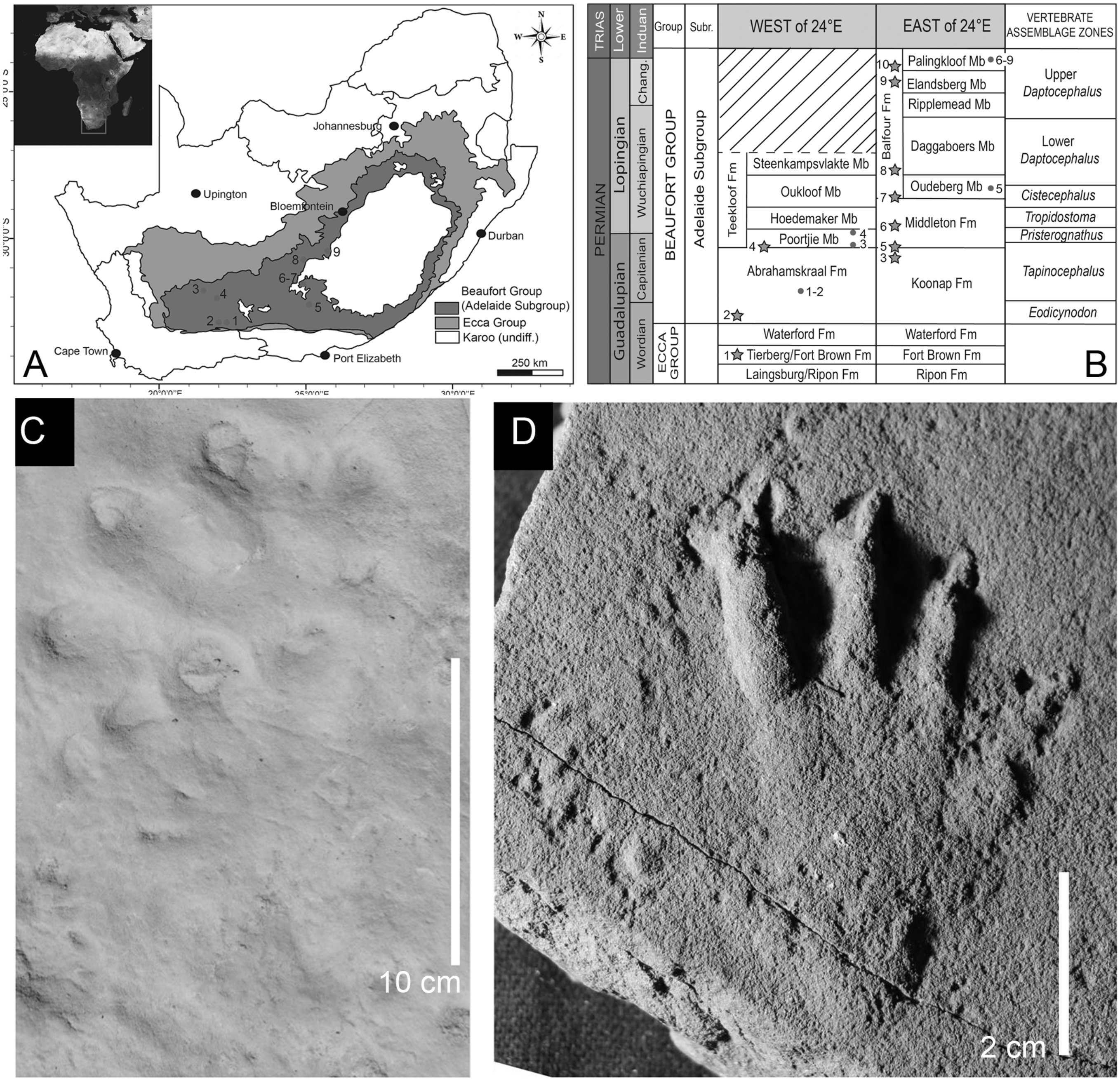


FIGURE 127. Early Triassic tetrapod footprints from South Africa. **A,** Map of Southern Africa with Permian-Early Triassic tetrapod footprint localities; Early Triassic sites are demarcated with 9 and 8. **B,** Permian-Triassic stratigraphic succession and units in Southern Africa; stars demarcate units with known radioisotopic ages (252.5 ± 0.7 Ma for the Palingkloof Member of Balfour Fm; Coney et al., 2007). **C,** *Dolomitipes accordii* pes-manus set from Palingkloof Member of Balfour Fm. (Induan) of Bethel locality (9), South Africa. **D,** *Rhynchosauroides* isp. from Palingkloof Member of Balfour Fm. (Induan) of Arundel locality (8). From Marchetti et al. (2019b).

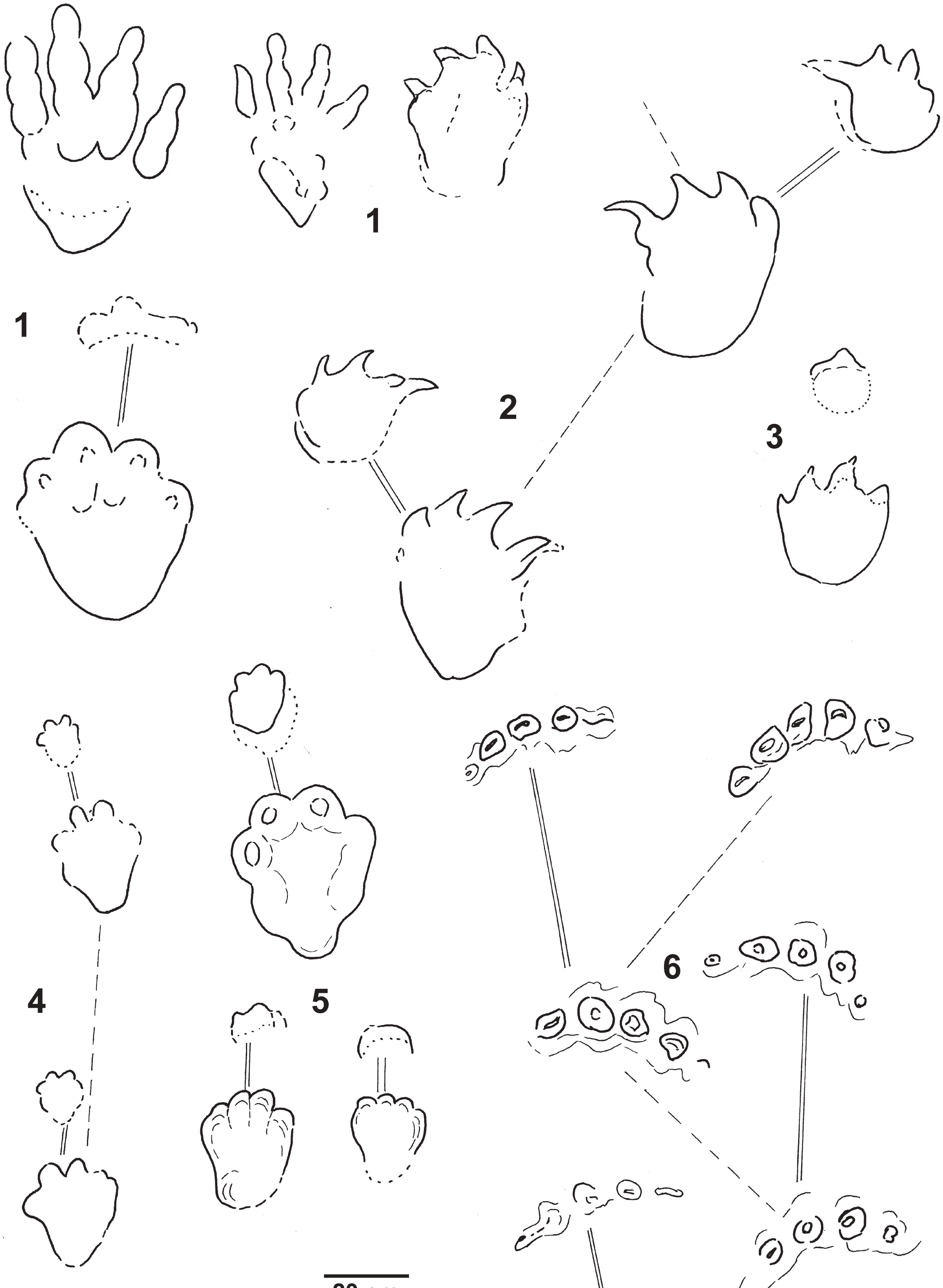


FIGURE 128. Tetradactyl-pentadactyl tetrapod footprints from Lower Elliot Fm. of Southern Africa from Ellenberger (1972) and published by this author under different names (mostly *nomina dubia*). Only *Pseudotetrasauropus* (1), *Tetrasauropus* (2) and *Pentasauropus* (6) are here considered as valid.

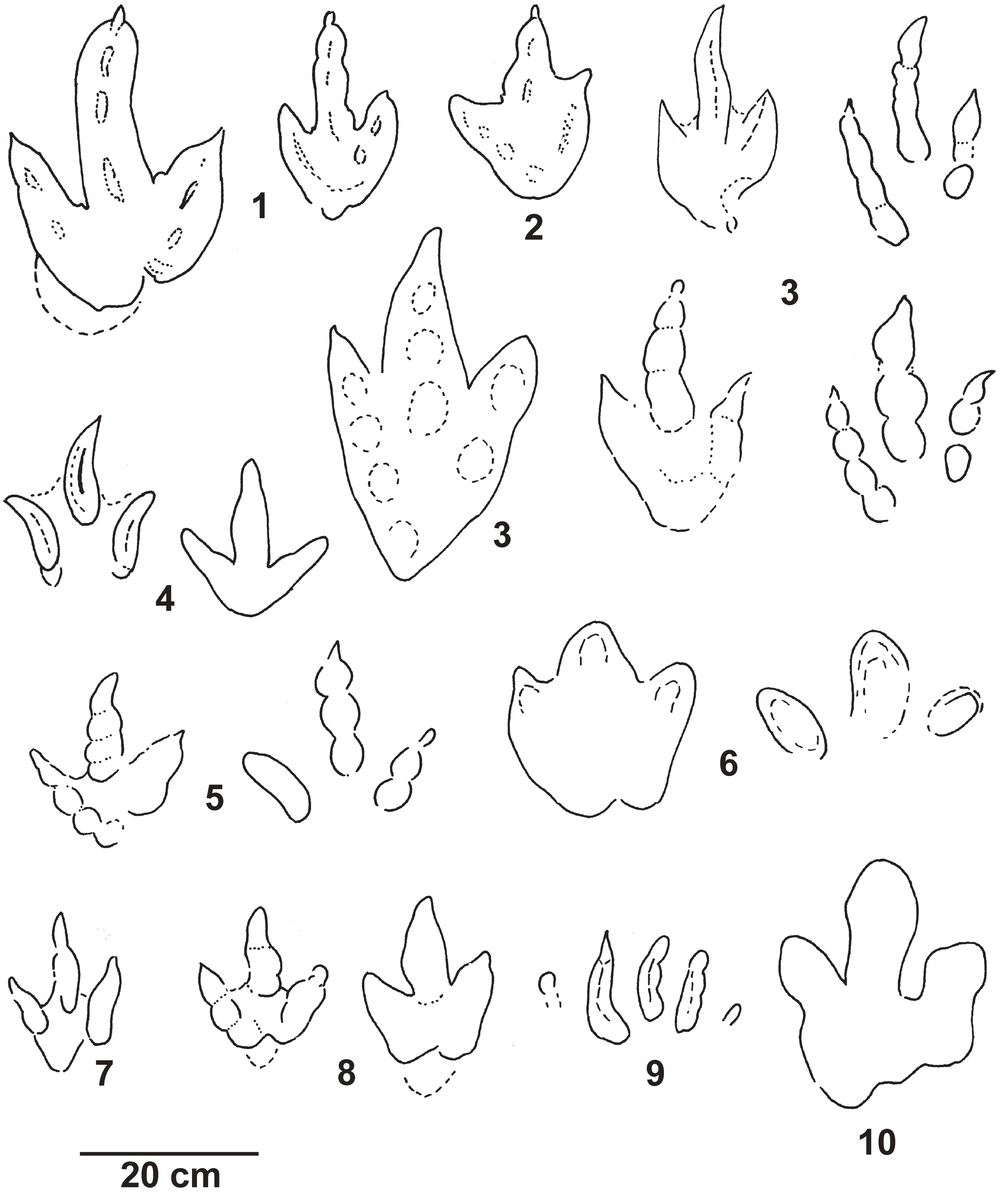


FIGURE 129. Tridactyl tetrapod footprints from Lower Elliot Fm. of Southern Africa from Ellenberger (1972) and published by this author under different names (*nomina dubia*). Most of them can be assigned to *Grallator-Eubrontes*.

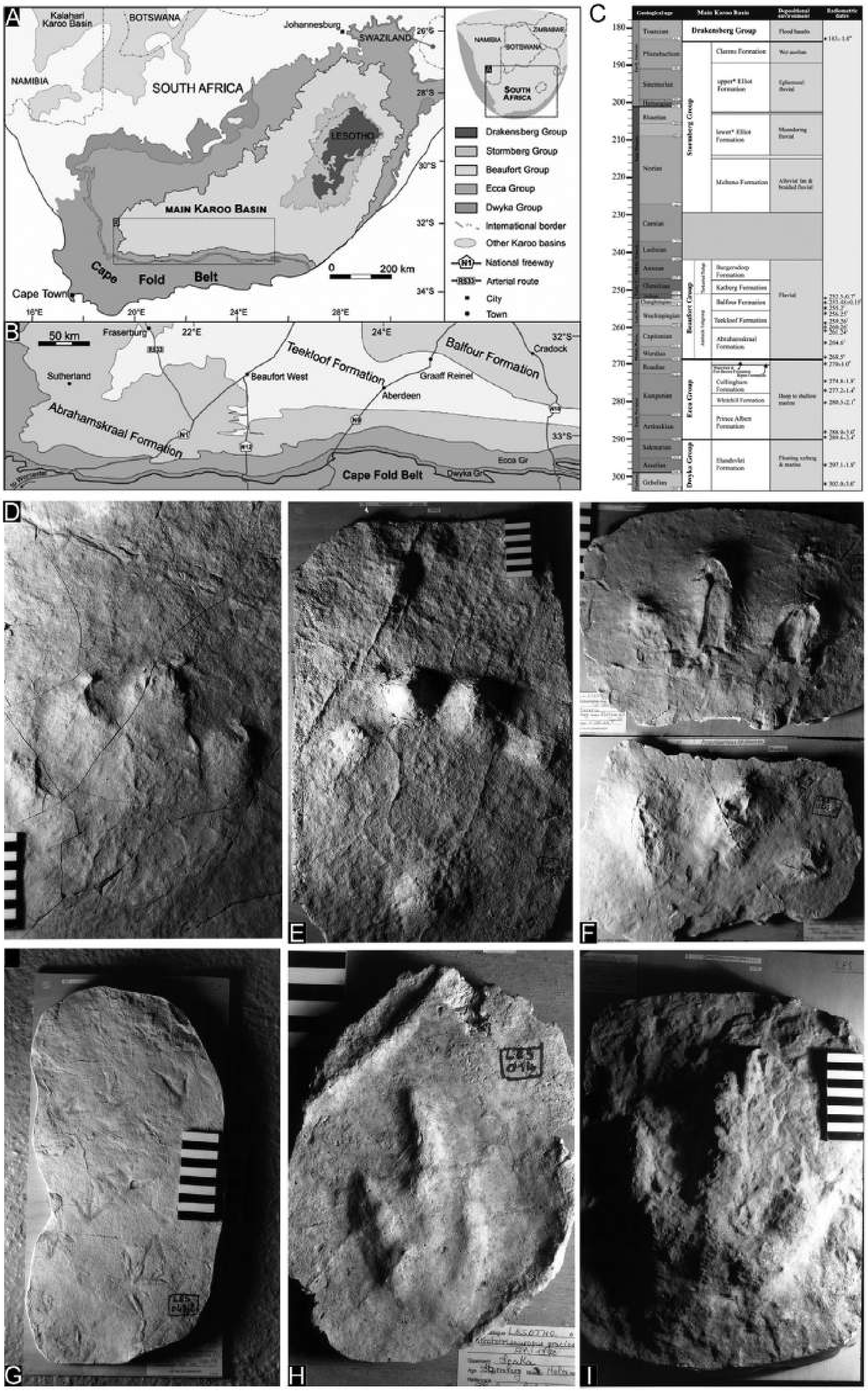


FIGURE 130. **A-B,** Geological maps with distribution of stratigraphical units in the main Karoo Basin, Southern Africa. A. Overview. B. Detail. **C,** Chronostratigraphic succession of Carboniferous-Jurassic units in the Karoo Basin. D-I. Plaster casts of tetrapod footprints from the Lower Elliot Fm. (Stormberg Group) of Southern Africa in the collection of Paul Ellenberger, University of Montpellier, France [*nomina dubia* of Ellenberger (1970, 1972) in quotation marks]. **D,** "*Paratetrasauropus seakensis*." **E,** "*Pseudotetrasauropus elegans*." **F,** "*Paratrisauropus lifofanensis*." **G,** *Trisauropodiscus aviforma*. **H-I,** *Grallator-Eubrontes* ("*Prototrisauropus graciosus*," "*Qemetrisauropus princeps*"). A-C. From Bordy and Sciscio (2017).

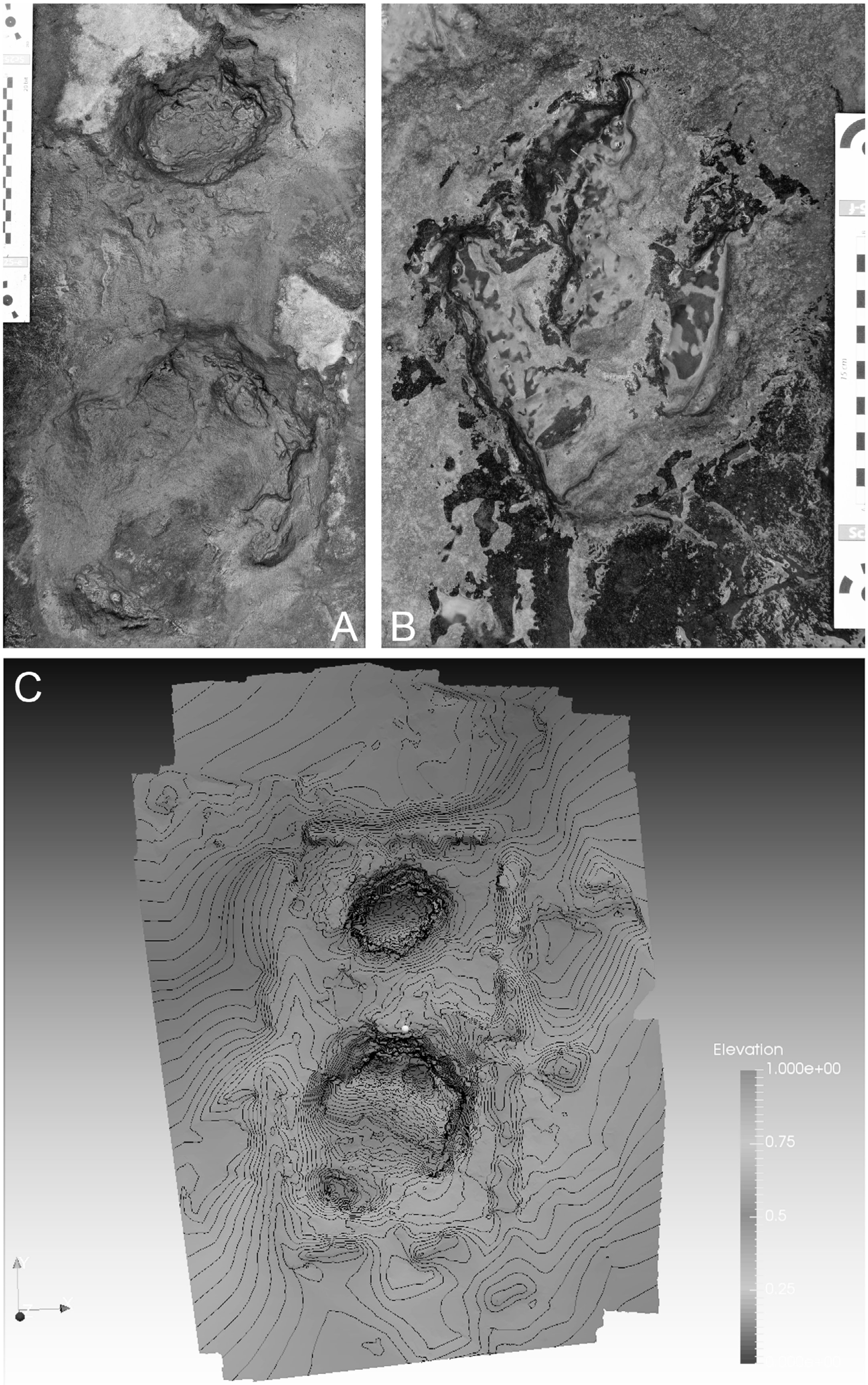


FIGURE 131. Tetrapod footprints from Lower Elliot Fm. of Lesotho, Southern Africa (originals from Ellenberger 1970, 1972) as recently documented in situ by one of us (HK). **A-B,** *Brachychirotherium* isp. ("*Deuterosauropodopus minor*") and *Eubrontes* isp. ("*Deuterotrisauropus socialis*"). **C,** Photogrammetric contour map of A by Christian Meyer, Basel.

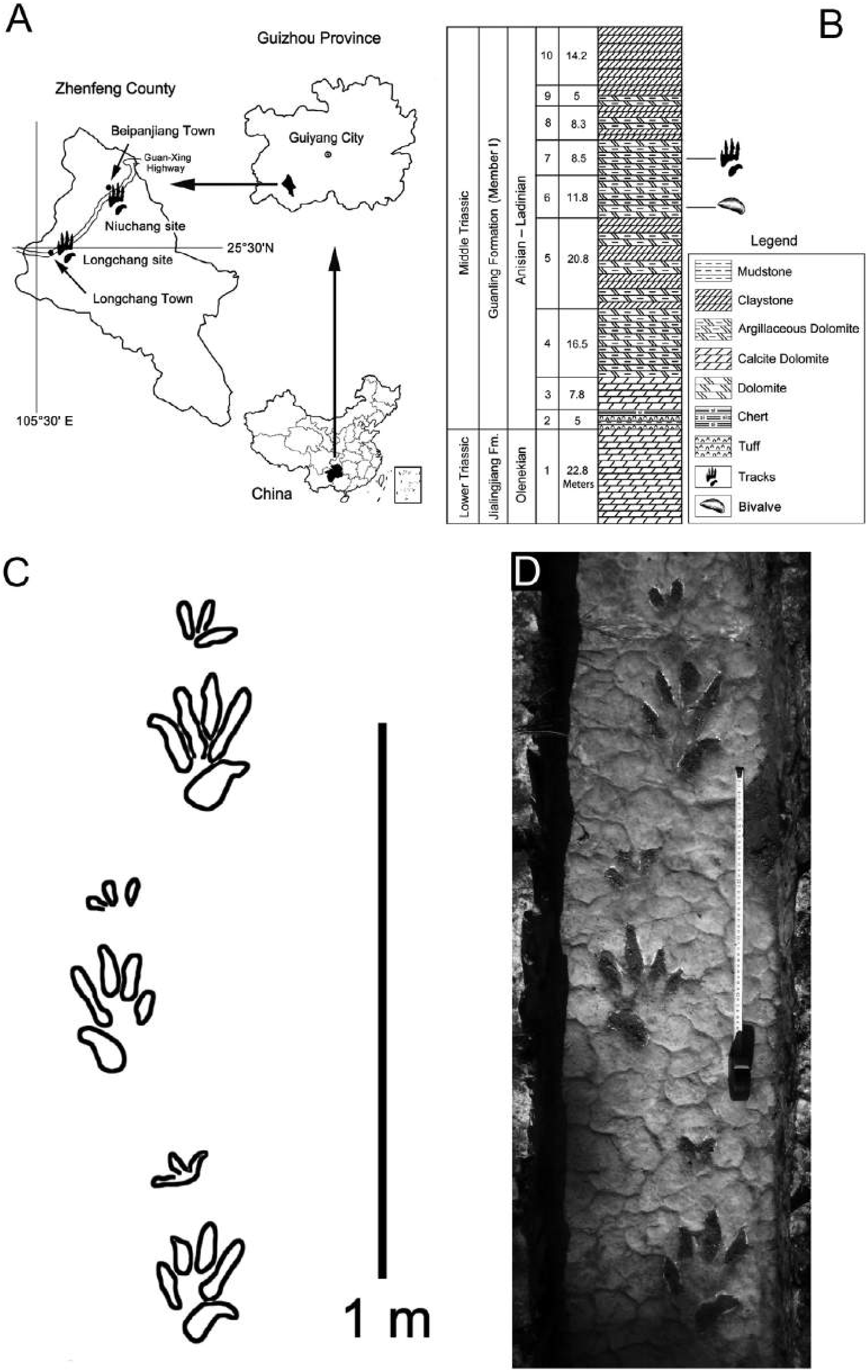

A
Guizhou Province
Zhenfeng County
Beipanjiang Town
Guan-Xing Highway
Guiyang City
Niuchang site
25°30'N
Longchang site
Longchang Town
105°30' E
China
B
Middle Triassic
Guanling Formation (Member I)
Anisian – Ladinian
Lower Triassic
Jialingjiang Fm.
Olenekian
10 14.2
9 5
8 8.3
7 8.5
6 11.8
5 20.8
4 16.5
3 7.8
2 5
1 22.8 Meters
Legend
Mudstone
Claystone
Argillaceous Dolomite
Calcite Dolomite
Dolomite
Chert
Tuff
Tracks
Bivalve
C
1 m
D

FIGURE 132. (facing page) Chirotheriid assemblages from the Guanling Fm. (Middle Triassic, Anisian) of Guizhou Province, China. **A,** Geographic position of footprint localities. **B,** Stratigraphic section with position of footprints. **C-D,** *Chirotherium barthii* trackway as interpretive outline drawing and photograph. From Xing et al. (2013). Photo in D courtesy Martin Lockley.

and Antarctica.

Australia

Most of the Triassic tetrapod footprints known from Australia are from the Sydney basin in the southeastern part of the country. The oldest record is of tracks assigned to *Dicynodontipus* from Lower Triassic strata at Bellambi Colliery (Retallack, 1996). These have been claimed to be the tracks of *Lystrosaurus* (Retallack, 1996), but that relationship is not certain (see above).

Staines and Woods (1964) reported a trackway found in roof shales of the Striped Bacon Coal Seam at Rhonda Colliery in the Sydney basin. The best-preserved track is 43 cm long (31 cm long for the digitigrade portion) and 38 cm wide, and the stride of the trackway is 2 m (Hill et al., 1965; Bartholomai, 1966; Molnar, 1991; Thulborn, 1998; Lucas and Tanner, 2004; Lucas et al., 2006). The tracks closely resemble tracks of *Eubrontes giganteus* from the Newark Supergroup as redescribed by Olsen et al. (1998). The Australian tracks are from the Blackstone Formation of the Ipswich Coal Measures near Dinmore in southeastern Queensland, a unit of well-established Triassic age (probably late Carnian: Balme and Foster, 1996). Several trackways from the Hawkesbury Sandstone (Middle Triassic, Anisian) in the Sydney Basin of New South Wales have recently been identified as tetrapod swim tracks (Farman and Bell, 2020). These are monodactyl-tridactyl imprints or arrangements of scratches that are thin, elongate, straight or curved, with acuminate distal endings.

Thulborn (2003) argued that the Australian Triassic record of *Eubrontes* refutes the notion that its LO is at the base of the Jurassic. Olsen et al. (2003), nevertheless, claimed that the Australian *Eubrontes* tracks are actually tridactyl underprints of a pentadactyl chirothere track. However, the footprint of *Eubrontes* is mesaxonic (symmetrical around its long axis), as are the Australian *Eubrontes* tracks. Tridactyl underprints of chirotheres are paraxonic (asymmetrical around their long axis). Therefore, the *Eubrontes* tracks from the Upper Triassic of Australia are correctly identified. Indeed, they are part of a diverse record of Triassic *Eubrontes* tracks (Lucas et al., 2006; and see above).

Tracks found in Triassic strata at Bergin Hill quarry at Goodna near Brisbane in Queensland have been mentioned in print but not described or illustrated (Molnar, 1982, 1991; Kear and Hamilton-Bruce, 2011). Molnar (1982, 1991) states that these are tracks of a quadruped similar to Hitchcock's ichnogenus "*Plectroperna*." Molnar (1982, 1991) also notes the tracks reported by Fletcher (1948) from Triassic strata on Berowra Creek in New South Wales and states that they are not dinosaurian.

Antarctica

The first Antarctic Triassic tetrapod footprints came from the Fremouw Formation (Middle Triassic) in the Queen Alexandra Range (e. g., MacDonald et al., 1991). These are poorly preserved, and some of them have been attributed to a dicynodont maker, likely *Lystrosaurus* (MacDonald et al., 1991). More data and better footprints are needed to further evaluate this record.

More recently, Mörs et al. (2019) published an isolated imprint from the Beacon Supergroup (?Middle, ?Late Triassic) of northern Victoria Land which they refer to the ichnogenus *Procolophonichnium*. The assignment is doubtful, and the specimen could represent two overlapping imprints, which is suggested by the unusual morphology and attachment of digit V.

BIOSTRATIGRAPHY

Lucas (2007) reviewed the Phanerozoic record of tetrapod tracks (Devonian-Neogene) and noted that three principal factors limit their use in biostratigraphy and biochronology: (1) invalid ichnotaxa based on extramorphological variants; (2) slow apparent evolutionary turnover rates; and (3) facies restrictions. As noted at the outset of this monograph, 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 or taphotaxa that confound biostratigraphic correlation and biochronological subdivision.

Tracks rarely allow identification of a trackmaker 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.). For example, the tridactyl theropod foot and corresponding track pattern is rather conservative, and evolutionary developments at a genus and species level may have involved changes in body parts other than the foot. 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, individual footprint morphotypes cannot provide as refined a subdivision of geological time as do body fossils, although ichnological assemblages are more useful.

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).

Nevertheless, the composition and distribution of Triassic tetrapod footprint assemblages reflect ecological/taphonomical phenomena as well as different stages in the evolutionary development of the locomotor apparatus of some tetrapod groups. In particular, some archosaur footprints show a limited vertical (stratigraphic) range. Their occurrences are restricted to distinct time intervals, thus demarcating distinct biochronological units (Lucas 2003, 2007; Hunt and Lucas 2007b; Klein and Haubold 2007; Klein and Lucas, 2010a).

There is a diverse literature on Triassic tetrapod footprint biostratigraphy, especially based on the European and North American records. The most comprehensive earlier publications of Demathieu (e.g., 1977, 1982, 1984, 1994; Demathieu and Haubold 1972, 1974) 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 recognized.

Between the late Olenekian/Anisian and the Norian the development of the tridactyl mesaxonic foot and bipedal gait of dinosaurs is reflected by the footprint record and can be followed in a functional evolutionary succession: *Chirotherium–Sphingopus–Parachirotherium–Atreipus–Grallator* (Haubold and Klein 2000, 2002). This has been used for biostratigraphy and biochronology by Klein and Haubold (2007). Thus, *Chirotherium* spans the Olenekian–Anisian, *Sphingopus* the Anisian–Ladinian, *Parachirotherium* the Ladinian, *Atreipus* the Carnian–Norian and *Grallator* the Norian–Rhaetian interval.

Klein and Haubold (2007) discriminated six biochrons (I–VI)

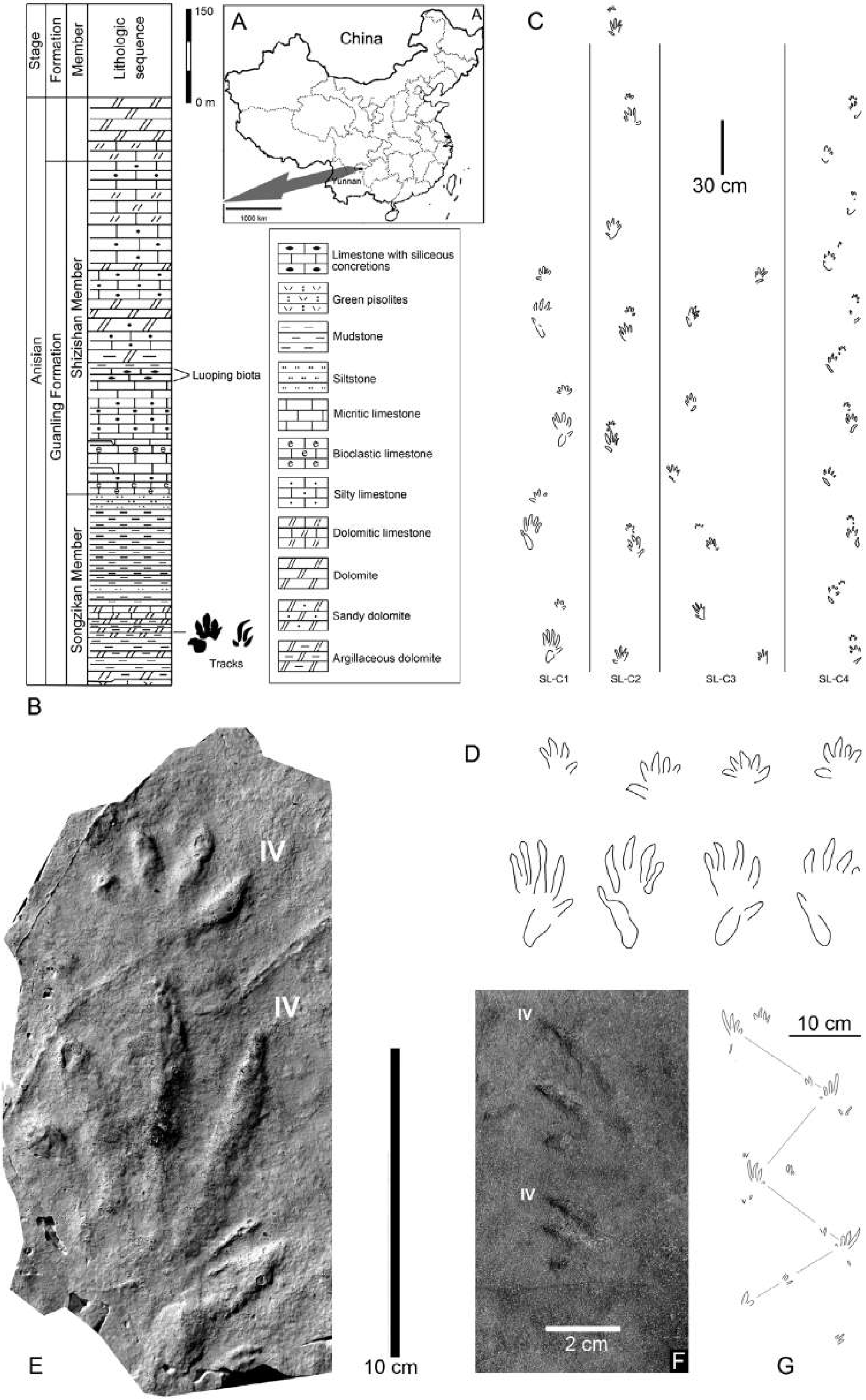

Stage
Formation
Member
Lithologic sequence
150
0 m
Anisian
Guanling Formation
Shizishan Member
Songzikan Member
Luoping biota
Tracks
B
A
China
A
Yunnan
1000 km
Limestone with siliceous concretions
Green pisolites
Mudstone
Siltstone
Micritic limestone
Bioclastic limestone
Silty limestone
Dolomitic limestone
Dolomite
Sandy dolomite
Argillaceous dolomite
C
30 cm
SL-C1
SL-C2
SL-C3
SL-C4
D
IV
IV
E
10 cm
IV
IV
2 cm
F
10 cm
G

FIGURE 133. (facing page) Chirotheriid assemblages from the Guanling Fm. (Middle Triassic, Anisian) of Yunnan Province, China. **A,** Geographic position of footprint locality. **B,** Stratigraphic section with position of footprints. **C,** *Chirotherium barthii* trackways from the tracksite as interpretive outline drawings. **D,** Details. **E,** Replica of well preserved *C. barthii* pes-manus set. **F-G,** *Rhynchosauroides* isp., photograph with detail and interpretive outline drawing of trackway. From Xing and Klein (2019).

by the range of archosaur footprint assemblages. The beginning of each is marked by the first appearance datum (FAD) of a characteristic index ichnotaxon (in bold): **I. *Protochirotherium***, 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 and **VI. *Grallator***–*Eubrontes*, *Brachychirotherium*, Norian–Rhaetian. Lucas (2003, 2007) recognized five Triassic footprint assemblages: **1**. Dicynodont tracks, earliest Triassic; **2.** Chirothere, Olenekian–Anisian; **3.** *Procolophonichnium– Rhynchosauroides*, Anisian–Ladinian; **4.** Dinosauromorph, Ladinian–Carnian; and **5.** Dinosaur, Carnian–Rhaetian. In this scheme, **2** corresponds to **II** and **III**, **3** to **III**, **4** to **IV**, and **5** to **V** and **VI** of Klein and Haubold (2007). Hunt and Lucas (2007*b*) proposed five assemblages: **1.** Dicynodont tracks, earliest Triassic; **2.** Chirothere, Olenekian–early Anisian; **3.** Dinosauromorph, late Anisian–Ladinian; **4.** Tridactyl dinosaur, Carnian–early Norian; and **5.** Sauropodomorph, late Norian–Rhaetian.

In addition to Lucas (2003, 2007), Hunt and Lucas (2007b) recognize a sauropodomorph track assemblage in the Late Norian–Rhaetian based on the ichnotaxa *Evazoum* and *Eosauropus* (see above), purportedly first appearing in the late Norian. This is contrary to Klein et al. (2006) and Klein and Haubold (2007), who considered the footprints of *Evazoum* to be extramorphological variants of *Brachychirotherium*, a crurotarsan track characteristic of the entire Late Triassic. Furthermore, *Evazoum* was first described from the Carnian of Italy by Nicosia and Loi (2003), thus indicating an earlier appearance.

Independent of further subdivisions proposed by various authors, we follow Klein and Lucas (2010a) and recognize five tetrapod footprint biochrons of Triassic age that can be identified across the Pangaean footprint record (Fig. 134):

1. Earliest Triassic dicynodont footprints. These tracks are from strata of the *Lystrosaurus* assemblage zone and thus are of Lootsbergian (= latest Changshingian-Induan) age (Lucas 1998). However, there are only a few records of this assemblage and they are restricted to Gondwana, so it needs further documentation before its Pangaea-wide significance can be established.
2. *Protochirotherium* is characteristic of strata of Nonesian age (=Olenekian). Morphologically, and based on its temporal distribution, it can be considered as the hypothetical "root" of later locomotory developments in archosaurs. Associated forms are *Rhynchosauroides*, *Procolophonichnium* and footprints of temnospondyls.
3. The appearance of *Chirotherium barthii* and *C. sickleri*, *Rotodactylus*, *Isochirotherium* and *Synaptichnium* ("*Brachychirotherium*") roughly demarcates the Nonesian-Perovkan (late Olenekian-Anisian) transition. *Chirotherium barthii* and *C. sickleri* disappear during the Anisian. The range of the other ichnotaxa spans most of the Middle Triassic (Perovkan-Berdyankian = Anisian-Ladinian) together with *Rhynchosauroides*, *Procolophonichnium*, dicynodont and temnospondyl footprints that continue from the Nonesian. *Rotodactylus* and *Isochirotherium* disappear before the end of the Berdyankian (Ladinian).
4. The appearance of tridactyl footprints and quadrupedal to bipedal trackways of the *Atreipus-Grallator* type ("*Coelurosaurichnus*") demarcates the late Perovkan-Berdyankian (= late Anisian-Ladinian) as do pentadactyl footprints of *Sphingopus* and *Parachirotherium*. Other ichnotaxa continue from the Nonesian (see above).
5. *Brachychirotherium* (*sensu stricto*) appears at the beginning of the Otischalkian (=early Carnian). It is a characteristic ichnotaxon of the Late Triassic, together with *Atreipus Grallator* (quadrupedal to bipedal trackways), *Grallator* and *Eubrontes* (bipedal trackways). The stratigraphical upper limit of *Brachychirotherium* is the Triassic-Jurassic boundary (end of the Apachean); there is no evidence of *Brachychirotherium* in post-Triassic strata (Lucas and Tanner 2007a, b). The same is true for other chirotheres, and for *Apatopus*, *Procolophonichnium* and *Gwyneddichnium*. The range of *Rhynchosauroides* continues into the Jurassic (Avanzini et al. 2010a), and the same is true of *Batrachopus* and the mammal-like forms, as might be expected.

Rhynchosauroides and *Procolophonichnium*, as well as some dicynodont and temnospondyl footprints, have a long stratigraphic range. They span the complete Triassic Period, with early roots in the late Permian, therefore, they are of less utility for biostratigraphy as long as their taxonomy is unclear, as is the case presently. Their dominance in some assemblages (see above) is extremely facies-controlled and biased by ecological and taphonomical effects. *Rhynchosauroides* and *Procolophonichnium* trackmakers obviously frequented some Anisian–Ladinian carbonate tidal flats (assemblage 3 of Lucas, 2003, 2007; Demathieu and Oosterink, 1983, 1988; Diedrich, 2008), an environment that archosaurs (chirothere trackmakers) mostly avoided. However, a few chirotheres are present as well (Demathieu and Oosterink, 1983, 1988; Diedrich, 2012, 2015) and, on the other hand, *Rhynchosauroides* is common at least on some fluvial-lacustrine surfaces of the Early through Late Triassic (Demathieu 1966; Haubold 1971a, b).

Evolutionary, rather than facies-controlled, signals from footprints are suitable to demarcate distinct time intervals in the Triassic and to outline a coarse biostratigraphy and biochronology of the Triassic. This footprint biochronology identifies five intervals of Triassic time, which is less resolution than the eight land-vertebrate faunachrons of Triassic age based on tetrapod body fossils (Klein and Lucas, 2010a).

ICHNOFACIES AND ICHNOCOENOSES

Introduction

Hunt and Lucas (2007d, 2016a) provided a discussion of terminology relevant to the study of tetrapod footprint 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, 2007d). 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 (2007d) defined five archetypal tetrapod footprint ichnofacies for nonmarine environments: *Chelichnus*, *Grallator*, *Brontopodus*, *Batrachichnus* and *Characichnos* ichnofacies and diverse ichnocoenoses (Table 1). The following review is principally based on Hunt and Lucas (2006b, 2007d-e, 2016a) and Hunt et al. (2018).

Batrachichnus Ichnofacies

Hunt and Lucas (2007d) proposed the *Batrachichnus* ichnofacies for ichnofaunas in which the majority of tracks are

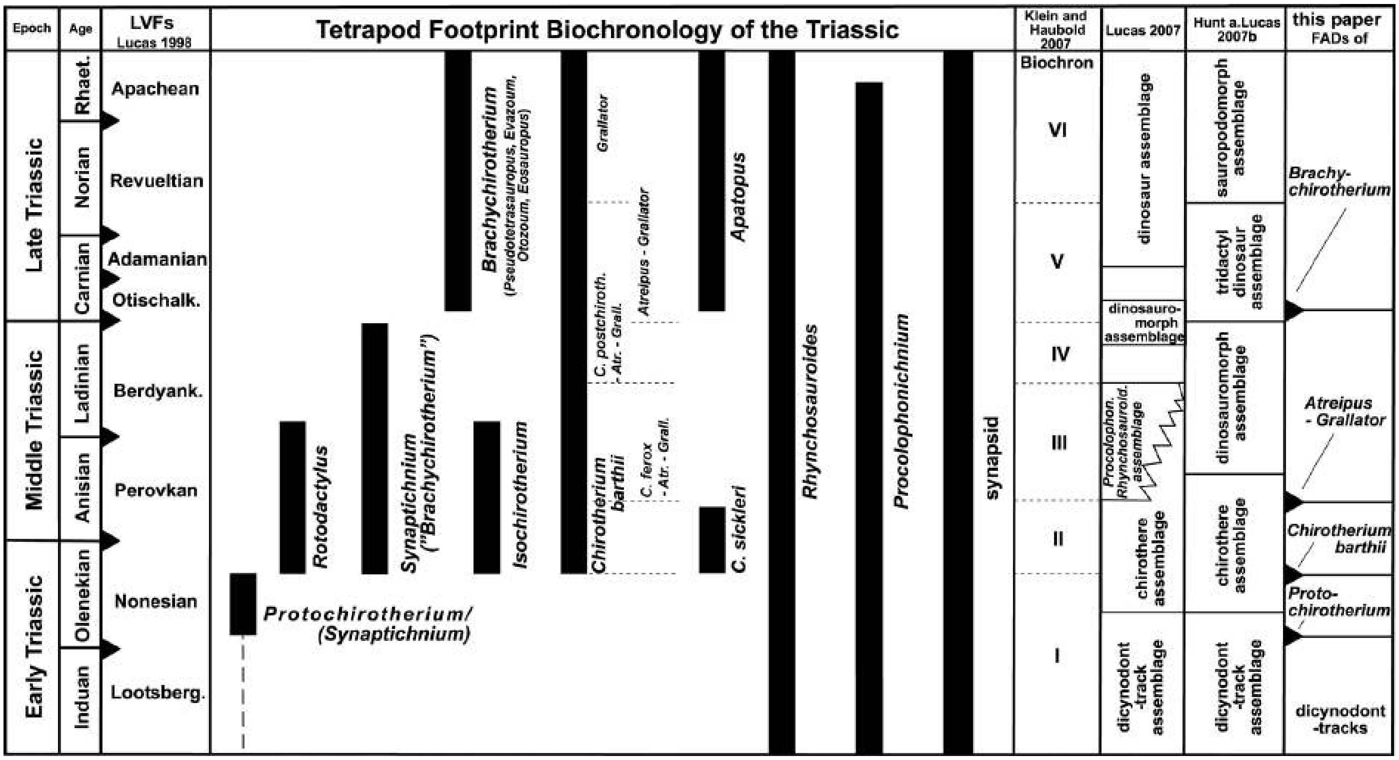


FIGURE 134. Stratigraphic distribution of tetrapod footprint taxa in the Triassic with biochrons and characteristic assemblages. After Klein and Haubold (2007) and Klein and Lucas (2010a), updated.

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, 2007d) recognized two ichnocoenoses of this ichnofacies in the Triassic (Table 1).

Hunt and Lucas (2007d) 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; Klein and Lucas, 2010a). 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 (2007d) 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, 2007d,e) recognized five ichnocoenoses within this ichnofacies in the Triassic (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.

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). Hunt et al. (2018) identified 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).

Grallator Ichnofacies

Hunt and Lucas (2007d) 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. Known from the Late Triassic to the Recent, this ichnofacies often characterizes lacustrine margin environments. We recognize four ichnocoenoses of the *Grallator* ichnofacies during the Triassic (Table 1).

As noted above, Hunt and Lucas (2007d) 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 in the uppermost strata of the Chinle Group or in the overlying

Wingate Sandstone in Colorado (e. g., 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 subichnocoenoses. Thus, for example, on the Colorado Plateau in the western USA, the upper and lower Wingate Sandstone have different sub-ichnocoenoses: a lower *Eosauropus* subichnocoenosis includes *Brasilichnium*, *Brachychirotherium*, and *Eosauropus*, and an upper *Otozoum* sub-ichnocoenosis includes *Eubrontes*, *Batrachopus* and *Otozoum* (Lucas et al. 2006a, c; Lockley et al., 2018).

Chelichnus Ichnofacies

Hunt and Lucas (2007d) 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 (2007d) redefined the *Brasilichnium* ichnofacies of Lockley et al. (1994) as an ichnocoenosis of this ichnofacies (Table 1). *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; Lockley et al., 2004; Hunt and Lucas, 2006b).

Characichnos Ichnofacies

Hunt and Lucas (2007d) 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 Group (Lower-Middle Triassic) 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; Lovelace and Lovelace, 2012; Thomson and Lovelace, 2014) and the Chinle Group (Upper Triassic) in Arizona and New Mexico (e.g., Hunt et al. 1993a; Hunt and Lucas 2006b; Lucas et al., 2010). There is no named Triassic ichnocoenosis of this ichnofacies.

ICHNOLOGICAL PERSPECTIVE ON TRIASSIC TETRAPOD EVOLUTION

Introduction

Most of what has been written about Triassic tetrapod evolution is based on their body-fossil record of teeth, bones and skeletons. Here, we focus on what we know about Triassic tetrapod evolution based on the footprint record. In particular, we address these topics: (1) extinctions across the Permo-Triassic boundary; (2) rise to dominance of archosaurs; (3) evolution of the upright gait; (4) Triassic synapsid evolution; (5) origin of turtles; (6) origin of dinosaurs; and (7) tetrapod extinctions across the Triassic-Jurassic boundary.

Extinctions Across the Permo-Triassic Boundary

Late Permian tetrapod footprint assemblages contain definite pareiasaur and therapsid tracks, as well as captorhinomorph, eureptilian and early saurian tracks. These are tracks of the *Paradoxichnium* biochron of Voigt and Lucas (2017). Triassic tetrapod footprint assemblages are archosaur dominated, at least from Olenekian time forward (Fig. 135).

Marchetti et al. (2019) recently documented what is now the best tetrapod footprint record across the Permo-Triassic boundary (PTB), which is in the Karoo basin of South Africa (which also contains the best PTB boundary tetrapod body-fossil record). Here, many of the latest Permian footprint ichnogenera

TABLE 1. Archetypal tetrapod ichnofacies, ichnocoenoses and inferred environments. From Hunt and Lucas (2007c).

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

also known from the earliest Triassic within the *Lystrosaurus*-bearing interval of the Balfour Formation: *Dolomitipes*, cf. *Dicynodontipus*, *Procolophonichnium* and *Rhynchosauroides* (Fig. 127). Some workers consider these strata to be latest Permian rather than Early Triassic (Gastaldo et al., 2015, 2017, 2018, 2020), although the most conspicuous faunal change possibly related to the PTB is at the base of *Lystrosaurus* Assemblage Zone, and this is a Permian age stratigraphic level (Marchetti et al., 2019e; Gastaldo et al., 2020). Thus, the best records (though all of the South African footprints may be Permian) show the continuity of most late Permian tetrapod footprint ichnogenera from the late Permian into the Early Triassic, and thus do not support the concept of a tetrapod mass extinction at the PTB. Petti et al. (2020) re-evaluate the recovery of terrestrial low-latitude tetrapod faunas during the Early-Middle Triassic, after a purported mass extinction. Their study is partly based on chirotheriid tracks from ?Olenekian deposits of the Western Alps. These authors conclude that the trackmakers, which they consider to have been erythrosuchids, were able to withstand the extremely high temperatures in these regions. Given that climate models are correct, interpretations of faunal diversity and distribution based on tetrapod tracks have to be considered cautiously against the background of incomplete sampling in Induan-early Olenekian deposits.

It should be noted that Early Triassic footprint assemblages before the Olenekian are rare and usually limited to a few therapsid or neodiapsid footprints (Klein and Lucas, 2010a; Marchetti et al., 2019). No pareiasaur footprints are known from the Early Triassic, and the range of several other footprint ichnogenera also ends during the *Paradoxichnium* biochron (Fig. 132). This is consistent with what is known of evolutionary turnover/tetrapod extinctions across the PTB based on their body-fossil record (see also Romano et al., 2020). Nevertheless, although the footprint record lacks stratigraphic density across the PTB, it provides no support for a supposed end-Permian tetrapod mass extinction.

Rise to Dominance of Archosaurs

The Triassic was the time period when archosaurs rose to dominate terrestrial tetrapod communities in terms of abundance and diversity. Nevertheless, the footprint record documents that the archosaur rise to dominance began during the late Permian and was not really completed until well after the beginning of the Triassic. Thus, tetrapod footprints from the upper Permian of the Southern Alps of northern Italy are of surprisingly advanced archosauriforms (chirotheres) not previously known before the Olenekian (Bernardi et al., 2015). They indicate that archosauriforms had already diversified substantially by the late Permian, more than previously envisioned. Bernardi et al. (2015, p. 18) correctly observed, “the integrative study of body and track records allows a better understanding of the origin of archosauriforms.” These newly discovered Permian archosauriform tracks further undermine the old idea that the change from therapsid-dominated to archosaur-dominated tetrapod assemblages coincided with the Permo-Triassic boundary.

Evolution of the Upright Gait and Bipedality

The shift from the sprawling gait to the upright gait has long been considered to have taken place during the Triassic (e. g., Kubo and Benton, 2007). However, it is now clear that late Permian archosauriform footprints indicate that the shift from sprawling to upright gaits had taken place well in advance of the end of the Permian (Bernardi et al., 2015). The same is true for newly-described Permian cynodont and gorgonopsid therapsid footprints (Marchetti et al., 2019a, b). There are also older, narrow gauge trackways, so the capability of at least short term use of semi-upright gaits by tetrapods may go back to the Carboniferous (Lucas, 2019).

During the Triassic several tetrapod groups evolved an advanced locomotory style. In particular, this concerns the narrow limb posture and parasagittal movement in some archosauriform groups, but also in synapsid therapsids (Kubo and Benton, 2007, 2009). Dinosauriform avemetatarsalians developed bipedality or facultative bipedality, for example in silesaurids.

Some crocodilian-stem archosaurs such as the poposauroid *Poposaurus gracilis* independently evolved bipedal progression. The latter also developed a tridactyl mesaxonic pes similar to the typical morphology of theropod dinosaurs (Farlow et al., 2015).

Bipedal or facultative bipedal movement also evolved in ornithosuchids, some rauisuchids (*Postosuchus*) and in crocodylomorphs. The latter bipeds were very small, however, from the Early Cretaceous of Korea, Kim et al. (2020) described trackways of large bipedal forms, and it can be speculated that there may be some unknown forms like these from the Triassic.

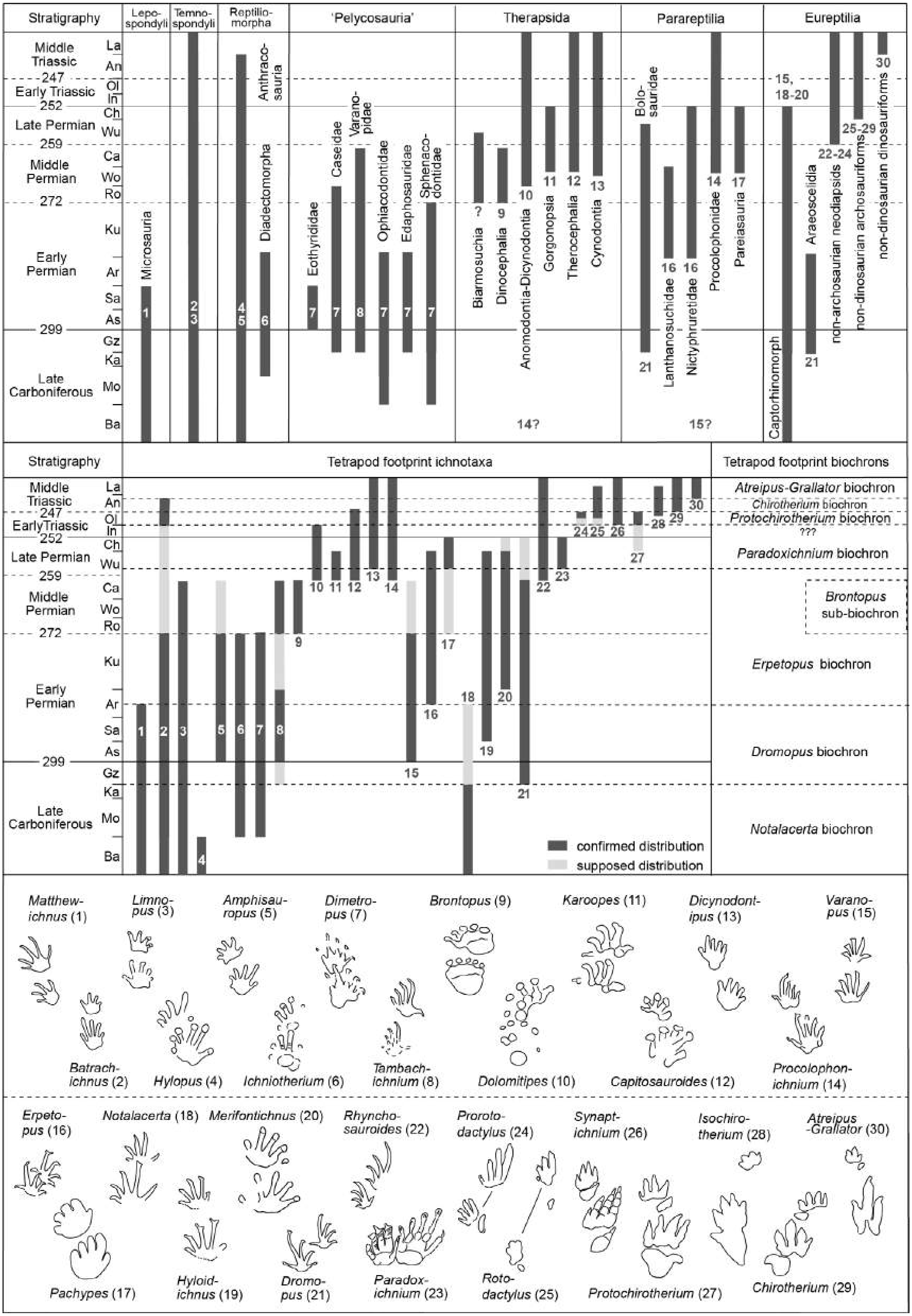
Bipedal progression was performed even earlier in the early Permian by some parareptilian bolosaurids, whose skeletal remains have been found at the famous Bromacker locality in Germany (*Eudibamus*; Berman et al., 2000), but has not been documented for Triassic parareptiles. In contrast, no synapsid groups evolved bipedality before the late Mesozoic, when hopping mammals left their trackways, for example in the Jurassic-Cretaceous Botucatu Formation of Brazil (Leonardi and De Oliveira, 1990; Leonardi, 1994; Rainforth and Lockley, 1996). Some lepidosauromorph lizards, including modern representatives (*Basiliscus*), have the ability to run bipedally over a short distance, while escaping from predators. The earliest bipedal progression of lepidosauromorphs is demonstrated by trackways no older than Early Cretaceous (Lee et al., 2018).

Triassic Synapsid Evolution

The dinocephalian extinction event near the end of the middle Permian opened up the tetrapod herbivore niches to dicynodonts (Lucas 2017a; Schneider et al., 2020). During the late Permian and Early Triassic, successive tetrapod assemblages were dominated by a single dicynodont genus, most famously *Lystrosaurus* of the earliest Triassic. However, other than in South America, by Berdyankian time dicynodont domination of the tetrapod herbivore niches had diminished. Dicynodont diversity was low in the Late Triassic, with only one-two genera per LVF, and dicynodonts are only abundant in some South American assemblages. Late Triassic dicynodonts are also known from mass death assemblages in Arizona, Morocco and Poland (Racki and Lucas, 2018).

The first cynodonts appear at about the end of the middle Permian and gradually increased in generic diversity through the Permo-Triassic boundary, the prelude to a much greater diversification during the Middle-Late Triassic (e. g., Abdala and Ribeiro, 2010; Smith et al., 2012; Ruta et al., 2013; Abdala and Gaetano, 2018). Late Triassic cynodont familes are primarily the Traversodontidae, Trithelodontidae and Tritylodontidae. Traversodontids were most diverse (~ 17 genera), mostly of Adamanian age and mostly known from Gondwana (Liu and

FIGURE 135. (facing page) Stratigraphic distribution of tetrapod taxa and attributed ichnotaxa across the Permian-Triassic boundary (from Schneider et al., 2020).


Stratigraphy
Lepo-spondyli
Temno-spondyli
Reptilio-morpha
'Pelycosauria'
Therapsida
Parareptilia
Eureptilia
Middle Triassic
La
An
247
Early Triassic
Ol
In
252
Late Permian
Ch
Wu
259
Middle Permian
Ca
Wo
Ro
272
Early Permian
Ku
Ar
Sa
As
299
Late Carboniferous
Gz
Ka
Mo
Ba
Microsauria
Anthraco-sauria
Diadectomorpha
Eothyrididae
Caseidae
Varano-pidae
Ophiacodontidae
Edaphosauridae
Sphenaco-dontidae
Biarmosuchia
Dinocephalia
Anomodontia-Dicynodontia
Gorgonopsia
Therocephalia
Cynodontia
Bolo-sauridae
Lanthanosuchidae
Nictyphruretidae
Procolophonidae
Pareiasauria
Captorhinomorph
Araeoscelidia
non-archosaurian neodiapsids
non-dinosaurian archosauriforms
non-dinosaurian dinosauriforms
14?
15?
15, 18-20
22-24
25-29
Tetrapod footprint ichnotaxa
Tetrapod footprint biochrons
Atreipus-Grallator biochron
Chirotherium biochron
Protochirotherium biochron
???
Paradoxichnium biochron
Brontopus sub-biochron
Erpetopus biochron
Dromopus biochron
Notalacerta biochron
confirmed distribution
supposed distribution
Matthew-ichnus (1)
Batrach-ichnus (2)
Limno-pus (3)
Hylopus (4)
Amphisau-ropus (5)
Ichniotherium (6)
Dimetro-pus (7)
Tambach-ichnium (8)
Brontopus (9)
Dolomitipes (10)
Karoopes (11)
Capitosauroides (12)
Dicynodont-ipus (13)
Procolophon-ichnium (14)
Varano-pus (15)
Erpeto-pus (16)
Pachypes (17)
Notalacerta (18)
Hyloid-ichnus (19)
Merifontichnus (20)
Dromo-pus (21)
Rhyncho-sauroides (22)
Paradox-ichnium (23)
Proroto-dactylus (24)
Roto-dactylus (25)
Synapt-ichnium (26)
Protochirotherium (27)
Isochiro-therium (28)
Chirotherium (29)
Atreipus -Grallator (30)

Abdala, 2014). The only well-documented, post-Adamanian traversodontid is *Scalenodontoides* from the Revueltian Lower Elliott Formation of South Africa

Tritylodontids were very mammal-like, especially in their postcranial anatomy. Their first appearance is during the Revueltian. However, most of their diversity is Early Jurassic.

Trithelodontids (including the "dromatheres") were also not very diverse during the Late Triassic, but they most likely include the ancestors of mammals.

The Triassic footprint record tells us relatively few details about synapsid evolution because the footprints of synapsids are rare in Triassic strata. However, what is known is consistent with a pattern of dicynodont diminishment and extinction during the Late Triassic, and cynodont diversification throughout the Triassic. Thus, dicynodont tracks are relatively few and mostly limited to Early-Middle Triassic strata. Cynodont tracks are more common through the entire Triassic, and apparently common during the Late Triassic, especially if many of the small tetrapod tracks from southern Africa were made by cynodonts.

Origin of Turtles

The origin of turtles (Testudines, including *Odontochelys*) has been debated for more than a century. Recently, a wealth of new body fossil material of early turtles, including Late Triassic *Odontochelys* from China (Li et al., 2008) and *Chinlechelys* from the USA (Joyce et al., 2009) has further informed this debate. This has led to the revival of interest in the hypothesis of Permian *Eunotosaurus* as the ancestral turtle (Lyson et al., 2010, 2013, 2016). More recently, *Pappochelys,* from the Middle Triassic of Germany, was proposed as an ancestral turtle (Schoch and Sues, 2015). Nevertheless, recent literature on turtle origins has focused entirely on the body fossil record to the exclusion of the track record.

Turtle tracks, *Chelonipus torquatus*, reported from the early Middle Triassic (Anisian) of Germany, and *Chelonipus* isp. from the late Early Triassic (Spathian) of Wyoming and Utah, are the oldest fossil evidence of turtles, but have been omitted in recent discussions of turtle origins. These tracks provide significant clues as to how early the turtle Bauplan originated. Turtle trackways are quite distinctive: the manus and pes form tracks nearly parallel to the midline and indicate an unusually wide gait in which the trackway width is nearly equal to the stride length. These tracks do not fit what would be expected to be made by Triassic *Pappochelys* or *Odontochelys*, a supposed prototurtle and an early turtle, respectively (Lichtig et al., 2018). In contrast, these tracks are consistent with what would be expected from the Triassic turtles *Proganochelys* and *Palaeochersis*. The features inferred to be present in Triassic turtle tracks support the notion that *Odontochelys* is a derived aquatic branch of the turtle stem lineage rather than the ancestral state of all turtles. *Chelonipus* also resembles the Permian track *Pachypes dolomiticus*, generally assigned to a pareiasaur trackmaker (Lichtig et al., 2018). These revelations highlight the need to consider all available evidence regarding turtle origins, rather than just the body fossils.

Chelonipus trackways from the Buntsandstein of Germany do not correspond to the body fossil taxa *Pappochelys* and *Odontochelys*. These taxa lack a connection between the limbs and the vertebral column, which would have made walking with the abdomen raised off of the ground difficult (Storrs, 1991; Li et al., 2009). Furthermore, *Chelonipus* indicates a trackmaker with proportions different from those of placodonts. *Henodus* and other armored placodonts have the pectoral girdle located outside the rib cage (Storrs, 1993), so they had a larger range of motion of the forelimb than would a turtle. Indeed, the recently described *Anshunpes*, a likely placodont track from the Triassic of China (see above), bears little resemblance to bona fide turtle tracks (Xing et al., 2020 in press).

Possible nothosaur tracks have been reported from the marine Guanling Formation in China (Zhang et al., 2014), which is of similar age (Anisian) to the part of the terrestrial Buntsandstein of Germany that yielded the type material of *Chelonipus*. Named *Dikoposichnus* (Zhang et al., 2014), these tracks were made by an animal with distinctly paddle-shaped limbs contacting the substrate in a symmetrical or synchronous rowing motion, as is commonly associated with sea turtles. This is quite different from the alternating left-right progression of the opposing limbs seen in *Chelonipus* and extant non-marine turtle locomotion. Furthermore, given the long tails and lack of an ossified connection between the pelvis and the spine in sauropterygians, *Pappochelys*, and *Odontochelys*, we question the likelihood of these animals leaving tracks without tail or belly drag marks. For example, modern marine turtles leave a distinctive drag mark as they lack the ability to stand upright on land (Hunt and Lucas, 2007). *Odontochelys* would appear unlikely to have been able to stay upright for the full length of the *C. torquatus* holotype trackway, given its lack of an ossified connection between the pelvis and spine. Thus, resting or drag traces would be expected, and these are not seen in *Chelonipus*.

In addition, the holotype trackway of *Chelonipus* has a trackway width-to-stride-length ratio close to one, which indicates a broader animal than a placodont such as *Pappochelys*. As noted earlier, this wide trackway is forced in turtles by the placement of the limb girdles inside the shell. The presence of this wide gait in *Chelonipus* suggests a turtle trackmaker that already had some of the defining features of a turtle, including ventral armor.

The footprints of Early and Middle Triassic turtles support the hypothesis of Reisz and Head (2008) that *Odontochelys* is a derived aquatic morphotype rather than the ancestral state of all turtles. This fits with the pattern of reduction of the number of ribs, as was pointed out by Szczgielski and Sulej (2016). As noted above, the oldest body fossils of turtles are of *Odontochelys*, which is ~233-237 million years old, and the oldest turtle tracks are 247-249 million years old (see above). These tracks indicate that as much as 10 or more million years of turtle history as shelled animals are still missing from our body-fossil collections. This parallels a distinct gap in microvertebrate sampling in the fossil record. Little effort has been expended in this gap on such sampling, such as that which recovered *Chinlechelys* in the Upper Triassic of North America (Lucas et al., 2000). The thin-shelled nature of *Chinlechelys* may also explain the apparent difficulty in finding some early turtle body fossils. The North American Chinle Group was explored for over a century before the first fragments of *Chinlechelys* were found in newly started screen washing efforts.

It is worth noting that by the Late Triassic turtles had diversified into at least four family level groups present on four continents (Joyce, 2017). This suggests extensive ghost lineages going back to an original turtle far older than those that we have now. In short, there is a great deal left to be discovered about the earliest turtles.

Origin of Dinosaurs

Understanding dinosaur origins has been beset by three problems: (1) semantic, namely what is and what is not a dinosaur; (2) cladistic—disagreements over the phylogeny of dinosaur origins, confounded by an inability to sort out convergence; and (3) biochronologic—disagreements over the actual age of the "oldest dinosaur." Despite these problems, all agree that the oldest dinosaur body fossils are Carnian (e.g. Langer et al. 2009; Lucas 2010; Benton 2012; Nesbitt and Ezcurra 2015). More precisely, they are Otischalkian, from the Chinle Group in the western USA (*Lepidus*) and the Maleri Formation of India (*Alwalkeria*). Otischalkian or Adamanian records of "dinosaurs" (*Azendohsaurus*) from Morocco and Madagascar have been discounted as not being based on dinosaurs (see Langer 2014 for discussion). Records from South America are Adamanian, so they are not the oldest records of dinosaur body fossils (contra Langer et al. 2009; Langer 2014).

The footprint record of the earliest dinosaurs also does not demonstrate dinosaurs older than Carnian. This, despite diverse claims (one of the most recent being by Marsicano et al. 2007) that tridactyl, apparently mesaxonic footprints from Middle Triassic strata are dinosaurian. Most of these are tridactyl remnants of chirothere tracks (see review by Klein and Lucas 2010a). Also, some could be the tracks of dinosauromorphs (Fig. 9) or of ornithodirans close to dinosaur origins, as discussed by Marsicano et al. (2007).

Particularly misleading, however, was the claim of dinosauromorph tracks in the Lower Triassic of Poland (Brusatte et al. 2011). This claim was based on the ichnogenus *Protorodactylus*, which is barely, if at all distinguishable from *Rhynchosauroides* (Klein and Niedźwiedzki 2012). The so-called "dinosauromorph" tracks of Brusatte et al. (2011) are likely the tracks of lepidosauromorphs though an archosauromorph attribution cannot be totally excluded.

To conclude, the oldest dinosaur fossils are Carnian, more specifically of Otischalkian age. Importantly, they are not from South America, as many have erroneously claimed, though, clearly, much more remains to be discovered of dinosaur origins.

Tetrapod Extinctions Across the Triassic-Jurassic Boundary

Colbert (1958) long ago drew attention to the striking differences between Late Triassic and Early Jurassic tetrapod faunas. Late Triassic tetrapod faunas are populated by many "thecodonts," notably phytosaurs, aetosaurs and rauisuchians. Dinosaurs were not major components of most Late Triassic tetrapod faunas, and metoposaurs dominated the amphibians. In strong contrast, Early Jurassic tetrapod faunas are dinosaur dominated, with various crocodylomorphs, and totally lack "thecodonts" and metoposaurs, taxa that suffered extinction across the Triassic-Jurassic boundary (TJB). The question has been when and how did these extinctions take place.

Lucas and Tanner (2015, 2018) recently analyzed the Late Triassic tetrapod extinctions to conclude that they were not a single extinction at the Triassic-Jurassic boundary. Using the best temporal resolution, the Late Triassic looks like a prolonged interval of stepwise tetrapod extinctions and low origination rates (Rigo et al., 2020). However, none of these is a mass extinction, and no reliable data support continued claims of a tetrapod extinction just before or at the end of the Triassic. With new and more detailed stratigraphic data, the perceived Triassic-Jurassic boundary tetrapod extinction is mostly an artifact of coarse temporal resolution, the compiled correlation effect. The amphibian, archosaur and synapsid extinctions of the Late Triassic were not concentrated at the Triassic-Jurassic boundary, but instead occured stepwise, beginning in the Norian and extending into the Hettangian.

The Newark Supergroup in eastern North America has a body fossil record of tetrapods that is sparse across the TJB and inadequate to evaluate a possible tetrapod extinction. Thus, the tetrapod footprint record in the Newark Supergroup has been used as a proxy (e.g., Olsen and Sues, 1986; Szajna and Silvestri, 1996; Olsen et al., 2002a,b). However, detailed stratigraphic study of the Newark footprint record indicates nothing more than moderate turnover in the footprint assemblage at a within-Rhaetian stratigraphic level below the lowest CAMP basalt sheet, which is of latest Triassic age. Similar changes in tetrapod footprint assemblages are also known from the Chinle Group-Glen Canyon Group section of the American Southwest and from the Germanic Basin (e. g., Lucas et al., 2006; Lucas, 2007).

The footprint turnover in the Newark section is supposedly the disappearance of four ichnogenera in the uppermost Passaic Formation, and the appearance of three ichnogenera at that datum (Olsen et al., 2002a, b). The ichnogenera that disappear represent phytosaurs (*Apatopus*: Klein and Lucas, 2013), aetosaurs (*Brachychirotherium*: Lucas and Heckert 2011) and tanystropheids (*Gwynnedichnium*: Lucas et al., 2014). There are single Newark records of *Procolophonichnium* (procolophonid: Baird, 1986; Klein et al., 2015) just below the turnover level and a single record of *Ameghinichnus* (mammaliaform: Valais, 2009) above that level. According to Olsen et al. (2002a, b), the ornithischian dinosaur footprint ichnogenus *Anomoepus* first appears at this level, but a later detailed review of the ichnogenus by Olsen and Rainforth (2003) indicated that the lowest stratigraphic record of *Anomoepus* is stratigraphically higher, in the Newark extrusive zone. The crocodylomorph footprint ichnogenus *Batrachopus* appears at this level, but there are older Triassic body fossil records of crocodylomorphs (Klein and Lucas, 2010c). Olsen et al. (2002a, b) showed the prosauropod-dinosaur-footprint ichnogenus *Otozoum* appearing in the upper Passaic Formation, but a later revision of the ichnogenus by Rainforth (2003) established its stratigraphically lowest record as Jurassic, in the Newark extrusive zone. The lacertoid footprint ichnogenus *Rhynchosauroides* has its last Newark record in the upper Passaic Formation, but this ichnogenus has Jurassic records elsewhere (e. g., Avanzini et al., 2010).

Thus, what the Newark tetrapod footprint and body-fossil record shows is the local extinction of phytosaurs (they have a younger record elsewhere: Lucas, 2018), aetosaurs, tanystropheids and procolophonids (this may be the level of their global extinction). That is the extent of the turnover in tetrapod taxa it documents, and the turnover level in the Newark is at a Rhaetian horizon, not at the TJB.

Part of the footprint turnover in the Newark section is the local lowest occurrence of the theropod footprint ichnogenus *Eubrontes*. For decades, much was made of this record of *Eubrontes*. Thus, Olsen and Galton (1984) concluded that the lowest occurrence of *Eubrontes* is the base of the Jurassic, and Olsen et al. (2002a, b) later argued that the sudden appearance of *Eubrontes* in the "earliest Jurassic" strata of the Newark Supergroup indicates a dramatic size increase in theropod dinosaurs at the TJB. They interpreted this as the result of a rapid (thousands of years) evolutionary response by the theropod survivors of a mass extinction and referred to it as "ecological release" (Olsen et al. 2002a, p. 1307). They admitted that this can be invalidated by the description of *Dilophosaurus*-sized theropods or diagnostic *Eubrontes* tracks in verifiably Triassic-age strata.

Indeed, tracks of large theropod dinosaurs assigned to *Eubrontes* (or its possible synonym *Kayentapus*) are known from the Triassic of Australia, Africa (Lesotho), Europe (Great Britain, France, Italy, Germany, Poland-Slovakia, Scania) and eastern Greenland, invalidating the "ecological release" hypothesis (Lucas et al. 2006; Niedźwiedzki, 2011; Bernardi et al. 2013). A detailed review of these records (see above) indicates Carnian, Norian and Rhaetian occurrences of tracks that meet the definition of *Eubrontes* established by Olsen et al. (1998). Also, theropods large enough to have made at least some *Eubrontes*-size tracks have long been known from the Late Triassic body-fossil record (e.g., Langer et al. 2009). Thus, the sudden abundance of these tracks in the Newark Supergroup cannot be explained simply by the rapid evolution of small theropods to large size following a mass extinction. The concept of a sudden appearance of *Eubrontes* tracks due to "ecological release" at the TJB proposed by Olsen et al. (2002a, b) thus can be abandoned, though some workers (e.g., Barras and Twitchett 2016) continue to endorse it.

CONCLUSIONS

Triassic tetrapod footprint assemblages reflect the increase in dominance of archosauromorphs with abundant chirotheriid and other tracks attributed to this group during the period. The early evolution of dinosaur- and crocodylian-stem archosaurs is largely related to developments in their locomotor apparatus and gait, expressed in preserved footprints and trackways. Digit proportions of chirotheriid footprints indicate different toe reduction in various archosaur lines. The early formation of a functionally tridactyl, mesaxonic pes (digits II, III, IV) can be followed in some chirotheriids that formerly have been assigned to distinct ichnogenera, but are here referred to the ichnogenus *Chirotherium*. The functionally tridactyl pes distinguishes *Chirotherium* from all other chirotheriid ichnogenera such as *Synaptichnium*, *Protochirotherium*, *Isochirotherium* and *Brachychirotherium*, which are functionally tetra-pentadactyl. *Chirotherium* comprises the ichnospecies *C. barthii*, *C. sickleri*, *C. ferox* comb. nov., *C. ladinicum* comb. nov. and *C. postchirotherioides* comb. nov. The ichnogeneric assignment of *C. rex* is tentative, but kept here until more complete material is known.

More advanced archosaurs and dinosauriforms–dinosaurs are indicated by *Rotodactylus* and tridactyl *Atreipus-Grallator-Anchisauripus-Eubrontes* plexus footprints.

Locally abundant are *Evazoum* and *Eosauropus* (sauropodomorphs and earliest sauropods). *Rhynchosauroides* (lepidosauromorphs/archosauromorphs) is common and dominates ichnoassemblages from some tidal flat environments in the Germanic Basin. Less common are *Apatopus* (phytosaur), *Dicynodontipus, Capitosauroides*, *Procolophonichnium* and *Dolomitipes* (therapsids). Additionally present are rare *Chelonipus* (turtle), *Dikoposichnus* (nothosaur), *Anshunpes* (placodont) and numerous uncertain ichnotaxa and indeterminate forms that are revised here in detail.

Triassic ichnoassemblages suggest diverse tetrapod communities, many of them with counterparts in known skeletal fossils. Biostratigraphically important are chirotheriids and other footprints that allow the subdivision of the Triassic into five biochrons based on the first appearance datum (FAD) of characteristic ichnotaxa and ichnofaunas: 1) Dicynodont (Lootsbergian, latest Changshingian-Induan); 2) *Protochirotherium* (Nonesian, Olenekian); 3) *Chirotherium barthii* (Nonesian-Perovkan, late Olenekian-Anisian); 4) *Atreipus-Grallator* (Perovkan-Berdyankian, late Anisian-Ladinian); and 5) *Brachychirotherium* (Otischalkian, early Carnian). Furthermore, five archetypal ichnofacies can be distinguished: 1) *Chelichnus*, 2) *Batrachichnus*, 3) *Brontopodus*, 4) *Grallator* and 5) *Characichnos.*

The tetrapod footprint record supports studies from body fossils that find no mass extinction in terrestrial forms at the P-T and Tr-J boundaries. Instead, a prolonged interval with stepwise extinction and low origination rates can be observed across the Tr-J boundary. Late Permian-Early Triassic successions with tetrapod footprints in South Africa and Northern Italy show that ichnogenera such as *Dolomitipes*, *Dicynodontipus*, *Procolophonichnium* and *Rhynchosauroides* continue into the Triassic. The same is true for chirothere-like archosaur footprints. Triassic-Jurassic boundary sections in the Newark Supergroup of eastern North America document the Late Triassic disappearance of footprints such as *Apatopus, Brachychirotherium*, *Gwyneddichnium* and *Procolophonichnium*, whereas *Batrachopus*, *Grallator* and *Eubrontes* continue, becoming more abundant in the Early Jurassic.

The Triassic footprint record documents the rise and diversification of tetrapods such as mammaliamorphs, turtles, pseudosuchians and dinosaurs. Despite their presence in the body fossil record, no Triassic pterosaur tracks are known. However, this may be a taphonomic effect and due to different habitats of early pterosaurs. Innovations in locomotory style recorded by the Triassic tetrapod footprint record include upright stance, parasagittal movement and bipedality, which evolved independently in several tetrapod groups.

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