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RESEARCH PAPER

Spinicaudata (“Conchostraca,” Crustacea) from the Middle Keuper (Upper Triassic) of the southern Germanic Basin, with a review of Carnian–Norian taxa and suggested biozones

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Abstract The Coburg Sandstone member of the Hassberge Formation, Middle Keuper, Carnian, Upper Triassic, in the Germanic Basin of Central Europe contains spinicaudatan branchiopods which considerably broaden the known spectrum and provide important data on the phylogenetic history and intercontinental correlation of this systematic group. The spinicaudatan fauna for this lithostratigraphic unit is described in detail and includes *Euestheria kozuri* sp. nov., *E.*? sp. nov. A, *Gregoriusella striatula* sp. nov., *Laxitextella freybergi* Kelber and Kozur in Kozur and Weems, 2007, *L. dorsorecta* (Reible, 1962), and *Laxitextella*? sp. A. Additional discussions deal with *Euestheria multicostata* (Geyer, 1987), *E. winterpockensis* (Bock, 1953a), *Laxitextella laxitexta* (Sandberger in Jones, 1890), *Laxitextella multireticulata* (Reible, 1962), and “*Laxitextella*? *hausmanni* (Schmidt, 1938),” as well as problems with (sub)global zonations that are based on spinicaudatans and suggested to be of Carnian and Norian age.

Keywords Branchiopoda · Spinicaudata · Triassic · Biostratigraphy · Germanic Basin

Kurzfassung Der karnische Coburger Sandstein, ein Schichtglied der Hassberge-Formation des Mittleren Keupers (Trias) im Germanischen Becken Mitteleuropas, beinhaltet spinicaudate Branchiopoden, die das bekannte Artenspektrum deutlich erweitern und wichtige Daten zur Phylogenie und zur interkontinentalen Korrelation dieser systematischen Gruppe liefern. Die Spinicaudata aus dieser lithostratigraphischen Einheit werden detailliert beschrieben. Sie beinhalten *Euestheria kozuri* sp. nov., *E.*? sp. nov. A, *Gregoriusella striatula* sp. nov., *Laxitextella freybergi* Kelber und Kozur in Kozur und Weems, 2007, *L. dorsorecta* (Reible, 1962), und *Laxitextella*? sp. A. Weitere Diskussionen betreffen *Euestheria multicostata* (Geyer, 1987), *E. winterpockensis* (Bock, 1953a), *E. buravasi* Kobayashi, 1975, *Laxitextella laxitexta* (Sandberger in Jones, 1890), *Laxitextella multireticulata* (Reible, 1962), und “*Laxitextella*? *hausmanni* (Schmidt, 1938)” sowie Probleme der (sub)globalen Zonen, welche auf Spinicaudata basieren und für Karnium und Norium vorgeschlagen wurden.

Schlüsselwörter Branchiopoda · Spinicaudata · Trias · Biostratigraphie · Germanisches Becken

Introduction

Spinicaudatan branchiopods constitute frequent faunal elements in the otherwise oligofossiliferous strata of the Keuper Group in the southern part of the Germanic Basin in Central Europe. Despite a long history of geological reconnaissance and research on these Ladinian–Rhaetian strata since the early nineteenth century (e.g., Berger 1854; Gümbel 1866; Nies 1868), systematic palaeontological studies have remained fairly rudimentary. Most groups of invertebrate fossils from the relevant strata have never undergone systematic or even monographic investigation.

“Conchostracans” (a paraphyletic group and thus to be abandoned; e.g., Olesen 2009) from the Keuper beds of

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southern Germany were recognized early on (e.g., Zieten 1833), but were widely neglected and commonly considered to belong to only three different species until Reible (1959, 1962) presented a reinvestigation of material from various Triassic horizons in the Germanic Basin, thereby distinguishing 14 species and subspecies for the entire Triassic, of which seven were new. Only six of these species or subspecies presented by Reible (1959, 1962) occur in the Keuper (partly annotated below). Warth (1969) added another species (now termed *Gregoriusella fimbriata*) and emphasized a certain biostratigraphic utility of spinicaudatans for the Keuper in the Germanic Basin. Additional data on spinicaudatans from the Keuper beds were published by Kozur (1982) and Geyer (1987), but fairly recent additions by Kozur and Mock (1993) and Kozur and Weems (2005, 2007, 2010) as well as several additional publications on the subject (e.g., Seegis 1999; Olempska 2004) have led to the view that this is a reasonably complete record of spinicaudatans and biostratigraphic zonation relevant to the intercontinental or even global correlation of nonmarine Late Triassic strata.

Kozur's strong commitment to "conchostracan" taxonomy and biostratigraphy resulted in great advances in these subjects, but his death in 2014 left several problems created by the preliminary notifications used in some of his publications, such as his notes on spinicaudatans from the Keuper beds of southern Germany and (particularly) northern Bavaria, with some species described in a provisional manner, partly with incomplete information on stratigraphy and localities. This publication complements and partly specifies information provided by Kozur and co-authors (particularly in Kozur and Weems 2007, 2010), and comments on poorly known and poorly defined relevant taxa.

Geological setting and lithostratigraphy of the Keuper in the southern part of the Central European Basin

The Permian–Jurassic history of the Central European Basin (termed "Germanic Basin" for the Triassic interval) reflects a dynamic evolution of an intracontinental sedimentary basin with variable deposition depending on Grand Cycle evolution (e.g., Stollhofen et al. 2008). Relatively short marine episodes with carbonate-dominated deposition in the Late Permian (Zechstein) and Mid-Triassic (Muschelkalk) were interrupted by extended periods of generally continental deposition during the Early (Buntsandstein) and Late Triassic (Keuper).

The Ladinian–Rhaetian Keuper beds of southern Germany are predominantly composed of rocks resulting from deposition in nonmarine environments (e.g., Geyer and Gwinner 1986; Beutler 1998; Geyer 2002). The Lower Keuper (Erfurt Formation) represents a transition period from marine to nonmarine deposition, composed of a remarkably thin (ca. 40–50 m) unit made up of shallow marine carbonates, brackish–deltaic variably developed siliciclastics, and fluvial sandstone (e.g., Beutler et al. 1999; Nitsch 2015).

The Middle Keuper strata are dominated by nonmarine deposits (mostly playa deposits) with episodic marginal marine intercalations. A traditional subdivision distinguishes a Lower Gipskeuper from an Upper Sandsteinkeuper unit. The Gipskeuper starts with the Grabfeld Formation, the lowermost part of which is characterized by sabkha deposits dominated by gypsum-bearing strata, which are overlain by typical cyclic evaporitic playa deposits with frequent thin dolostone beds (traditionally called "Steinmergel") resulting from playa lake sedimentation. Lateral stratigraphically equivalent fluvial sandstone deposits with shaly intercalations are termed the Benk Formation. Such frequently arkosic sandstones characterize the southern margin of the Germanic Basin as a clastic input of detritus from the Vindelician High in the south and southeast, whereas the playa deposits indicate the dominant depositional environment in the center of the Germanic Basin.

This pattern persists in a similar manner up to the Rhaetian except for short "wet intermezzos" (e.g., Kozur and Bachmann 2010; Franz et al. 2014; Ogg et al. 2014; Ogg 2015; Zhang et al. 2015). The most striking of these deviations in climate and resulting deposition, also termed the "Carnian Pluvial Event" (Simms and Ruffell 1989), coincides with the Stuttgart Formation ("Schilfsandstein" in traditional lithostratigraphic terminology), a widespread unit resting unconformably on the Grabfeld Formation and mainly consisting of fluvial deposits deposited in a multi-branched fluvial system that prograded southward from the Fennoscandian High in the north along the basinal axis of the Central European Basin. Although the Stuttgart Formation is dominated by fluvial deposits, thin units suggest short-lived marine incursions.

The Stuttgart Formation is overlain by the Steigerwald Formation (Lehrbergschichten in Bavaria, Rote Wand and Lehrbergschichten in Baden-Württemberg), made up of red and occasionally green shales with subordinate dolomite and gypsum/anhydrite intercalations deposited in a typical playa environment. This type of deposition persisted in the central part of the basin, where typically red shales characterize the Weser Formation that is overlain by typically gray deposits of the Arnstadt Formation. A relatively thick gypsum-dominated unit (Heldberg Gypsum Member) separates the formations and is traditionally considered to indicate a considerable hiatus correlated with the Early Cimmerian Unconformity ("Altkimmerische Hauptdiskordanz" of Beutler 1979) at the Carnian–Norian boundary.

However, there has been a considerable change of view regarding its extent: from a hiatus spanning the entire Early Norian ("Lacian") to a short-term or locally absent hiatus (e.g., Kozur and Bachmann 2003, 2008; Bachmann and Kozur 2004; Barnasch et al. 2005; Lucas et al. 2012) that is probably of only regional importance in parts of the Germanic Basin.

The marginal clastic belt to the south (traditionally termed the "Nürnberg facies" for the Keuper interval) is marked by fluvially dominated deposits termed the Hassberge Formation for the studied period (Figs. 1, 2, 3). This formation is traditionally subdivided into a Lower Blasensandstein and an Upper Coburger Sandstone unit in Bavaria (Kieselsandstein in Baden-Württemberg; e.g., Seegis 1997; Etzold and Schweizer 2005). Recent investigations, however, clearly indicate that the situation is more complicated: The marginal Nürnberg facies unit with its detritus from the Vindelician–Bohemian High varied considerably in lateral extent over time, and the Steigerwald Formation marks an episode with markedly reduced clastic input from the south, whereas the Coburg Sandstone unit indicates a wet intermezzo with forced erosion and transport from the granitoid rock source areas. The fluvial tongues, however, clearly did not form coherent sheets; they were broad bodies positioned in a subparallel or somewhat radial arrangement separated by playa. These "fingers" of Coburg Sandstone facies units are reflected in the major quarry districts in which the sandstone was exploited (Freyberg 1965a; Fig. 4). The typical Coburg sandstone is a fine- to medium-grained, feldspathic sandstone with high mica content deposited in high-energy fluvial channels indicated by large-scale cross-bedding, mud pebbles, and frequent erosional bases. Intercalated are reddish or brown shales and thin dolomite beds that represent overbank deposits (Fig. 3). In total, up to nine types of lithofacies and seven types of architectural elements with different sedimentological and petrophysical properties have been observed (e.g., Hornung and Aigner 2004).

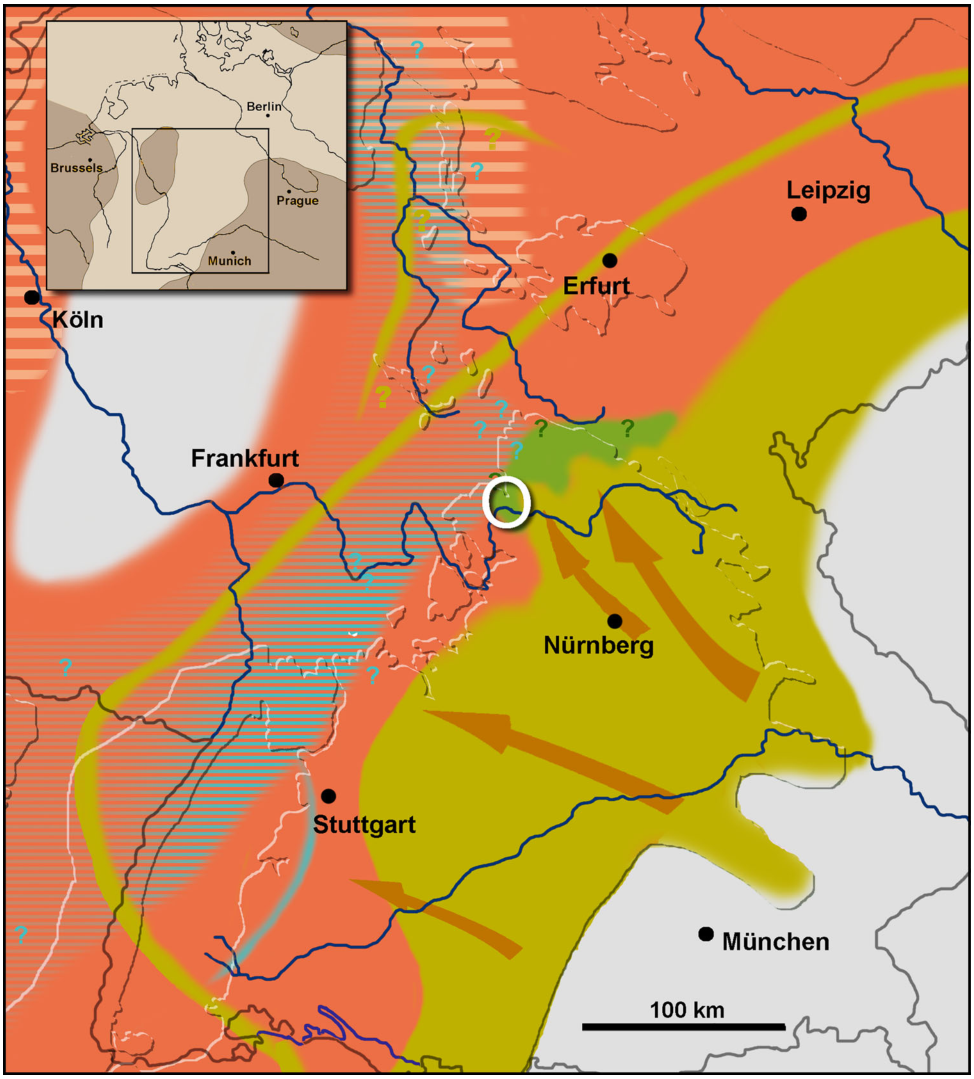


Fig. 1 Palaeogeographic situation in the southern Germanic Basin (transferred to the present-day geographic situation) during the Late Carnian and Early Norian. A siliciclastic marginal facies belt (*buff*) was derived from detritus of the Vindelician High in the southeast, with the Hassberge Formation characterized as the fluvially dominated mid- to distal part of this belt, creating the comparatively well-washed tongues of the Coburg Sandstone member in northern Franconia. Funkenloch strata shown in *green*, Weser Formation with its typical playa facies in *apricot*. Study area is indicated by a *white* circle (see Fig. 4 for details) Modified from Nitsch (2005)

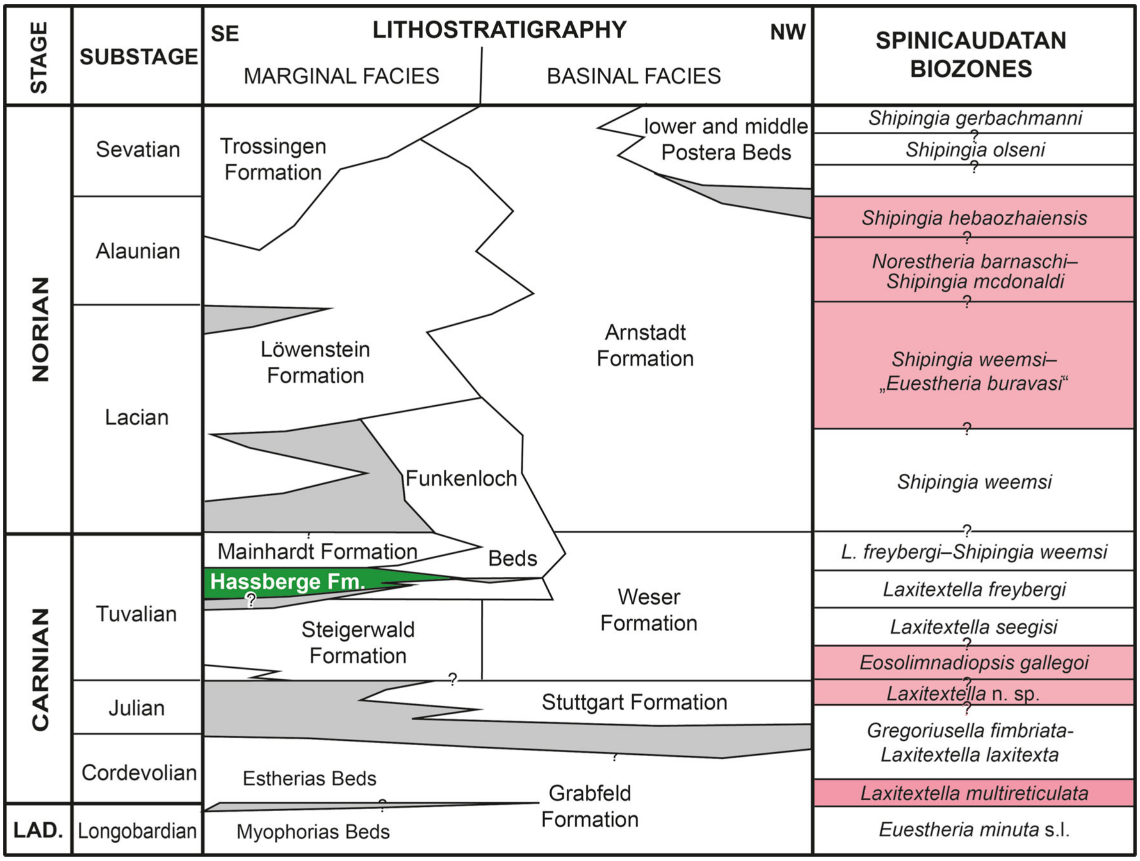


Fig. 2 Lithostratigraphy of the Middle Keuper succession (Cordevolian through Norian) in the southern part of the Germanic Basin, and spinicaundatan zones proposed by Kozur (1999), Kozur and Weems (2007, 2010), Kozur et al. (2013), and Hauschke (2014), with revisions suggested in this article. *LAD* Ladinian. Grey areas indicate gaps

The Hassberge Formation is overlain in the typical marginal belt by the Löwenstein Formation (Burgsandstein in Bavaria; Stubensandstein in Baden-Württemberg) that consists of generally medium- to coarse-grained arkosic sandstones and variably intercalated shales and pedogenic dolomite layers (“Steinmergel”). However, a transitional facies unit persists between the marginal “Nürnberg facies” and the basinal facies as a playa facies association from the Steigerwald Formation up to at least the middle part of the Löwenstein Formation. This stratigraphic unit, here informally termed the Funkenloch strata (G. Geyer, unpublished), persists with its relatively monotonous cyclic playa deposits dominated by reddish shales with thin gypsum horizons and only very few intercalated thin sandstones with great lateral persistence. They appear to suggest that a considerable unconformity does not exist (G. Geyer, unpubl. data).

The overlying Trossingen Formation (Feuerletten in Bavaria; Knollenmergel in Baden-Württemberg) is made up of reddish to purple playa-facies shales with dolomite nodules and beds as relics of pedogenic calcrete deposits.

The Rhaetian (Exter Formation) is separated from the Middle Keuper by an unconformity and attests to a multistep marine transgression, meaning that the lithological units show considerable variations. In the southern part of the Germanic Basin, the rocks are predominantly composed of varicoloured fluvial sandstones embedded in relics of the playa facies, overlain by black or purple shales.

The Hassberge Formation and its Coburg Sandstone member

The Coburg Sandstone (German: Coburger Sandstein) forms the upper part of the Hassberge Formation in the clastic marginal belt of the Keuper Basin and is thus more or less coeval with a similar development termed the Kieselsandstein in Baden-Württemberg. The succession is characterized by coarse- to fine-grained alluvial siliciclastics which are derived from the Vindelician and Bohemian High in the Southeast. They form tongues that interfinger basinward with playa deposits composed of clay- and siltstones with intercalated thin dolostone beds of the

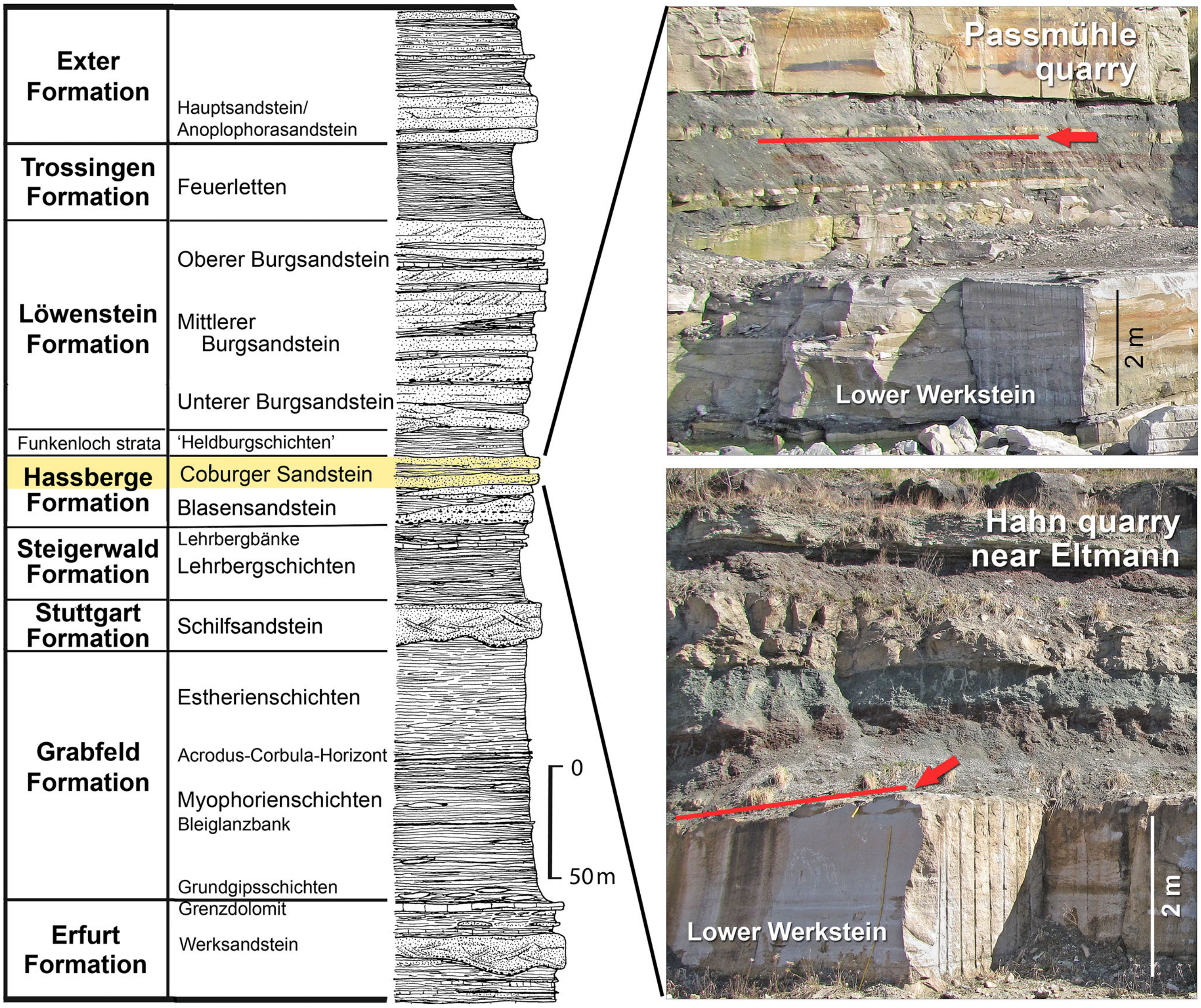


Fig. 3 Regional lithostratigraphy of the Keuper beds in northern Franconia/Bavaria, with position of the Coburg Sandstone member of the Hassberge Formation shown (*left*), and situation of the spinicaudatan-bearing horizons in the Ankenbrand/Passmühle Quarry (locality *A* in Fig. 4) and the Hahn Quarry (locality *B* in Fig. 4) also depicted. Note the position of spinicaudatan-bearing horizons in floodplain facies/overbank deposits above fluvial channel beds termed "Lower Werkstein." Photos K.-P. Kelber

central part of the Central European Basin (3D reconstruction in Feist-Burkhardt et al. 2008). The formation and extent of the terminal alluvial plain facies belts are influenced by sheet floods during dry periods, and its pro- and retrogradation depended on variations in megamonsoonal strength (e.g., Reinhardt and Ricken 2000).

Quarries in the Coburg Sandstone located in the Steigerwald and Hassberge regions have been operated to obtain important building stones (e.g., Grimm 1990; Fig. 4). These quarries expose successions of gray fluvial channel and sheet sandstone and intercalated varicoloured (light gray, greenish, yellow, and red) laminated lacustrine sedimentary rocks with small-scale cyclicity (Fig. 3). Of particular economic importance is an approximately 3–6 m thick basal layer of fine-grained sandstone termed the "Haupt-Werkstein" (Freyberg 1965a; Weinig 1986) or "Unterbank" (Freudenberger et al. 2000; Freudenberger 2005). Comprehensive studies of the Coburg Sandstone member have been provided by Freyberg (1965a), Stahl (1971), Mader (1990), Geyer (2002), and Hornung and Aigner (2004). For sedimentological and palaeoclimatological interpretations, see Kern and Aigner (1997), Reinhardt and Ricken (2000), Hornung and Aigner (2004), Beutler and Nitsch (2005), and Nitsch (2005).

Two different types of facies exist and provide different fossil assemblages in the Coburg Sandstone member, as shown in Fig. 3. Fluvial siliclastics occasionally yield rests of tetrapods (e.g., Kuhn 1936; Sulej 2002), tetrapod tracks (e.g., Freyberg 1965b; Karl and Haubold 1998, 2000; Werneburg 1998; Haubold and Klein 2000; Klein and

Haubold 2003), fishes (e.g., Dehm 1956; Doert and Rossner 1985; López-Arbarello 2008), and macroplant remains (e.g., Mägdefrau 1953, 1963; Kelber and Hansch 1995; Kelber 2007). Floodplain and lacustrine silt- and mudstones occasionally include fossils preserved as compressions. These include insects (e.g., Kelber and Nitsch 2005; Prokin et al. 2013; Fedorenko 2014) (e.g., Fig. 8B), Notostraca (Trusheim 1937; Kelber 1998a, 1998b; Kelber and Nitsch 2005) (see *Triops* in Figs. 11D, 12C), macroplants (rarely even with preserved cuticles; e.g., Mägdefrau 1953, 1956, 1963; Kelber and Hansch 1995; Kelber 2000, 2005) (see *Voltzia* in Fig. 8B), and charcoal (Kelber 1999, 2007), palynomorphs (e.g., Wille 2000), and various ichnofossils (e.g., von Freyberg 1965a, b; Schlirf et al. 2001).

The spinicaudatans from the Coburg Sandstone member described herein are exclusively preserved in shales of the intercalated lacustrine facies association, with fine lamination of the clay- and siltstones often destroyed by pedogenic processes or peloturbation (see Hornung and Aigner 2004 for the spatial relationship between lithofacies elements). Strong variation in the moistness prompted soils rich in clay with large capacities for expansion to shrink and create wide and deep cracks during dry seasons, which were subsequently filled with deposits from the overlying sediment sheets. These processes often happened repeatedly so that entire soil horizons may have rotated and turned. Red and purple colours indicate a pedogenic overprint of shales (Mader 1990). As a result, well-preserved fossils are not common in the Coburg Sandstone member, although the stratigraphic unit is renowned to occasionally host excellently preserved fossil remains.

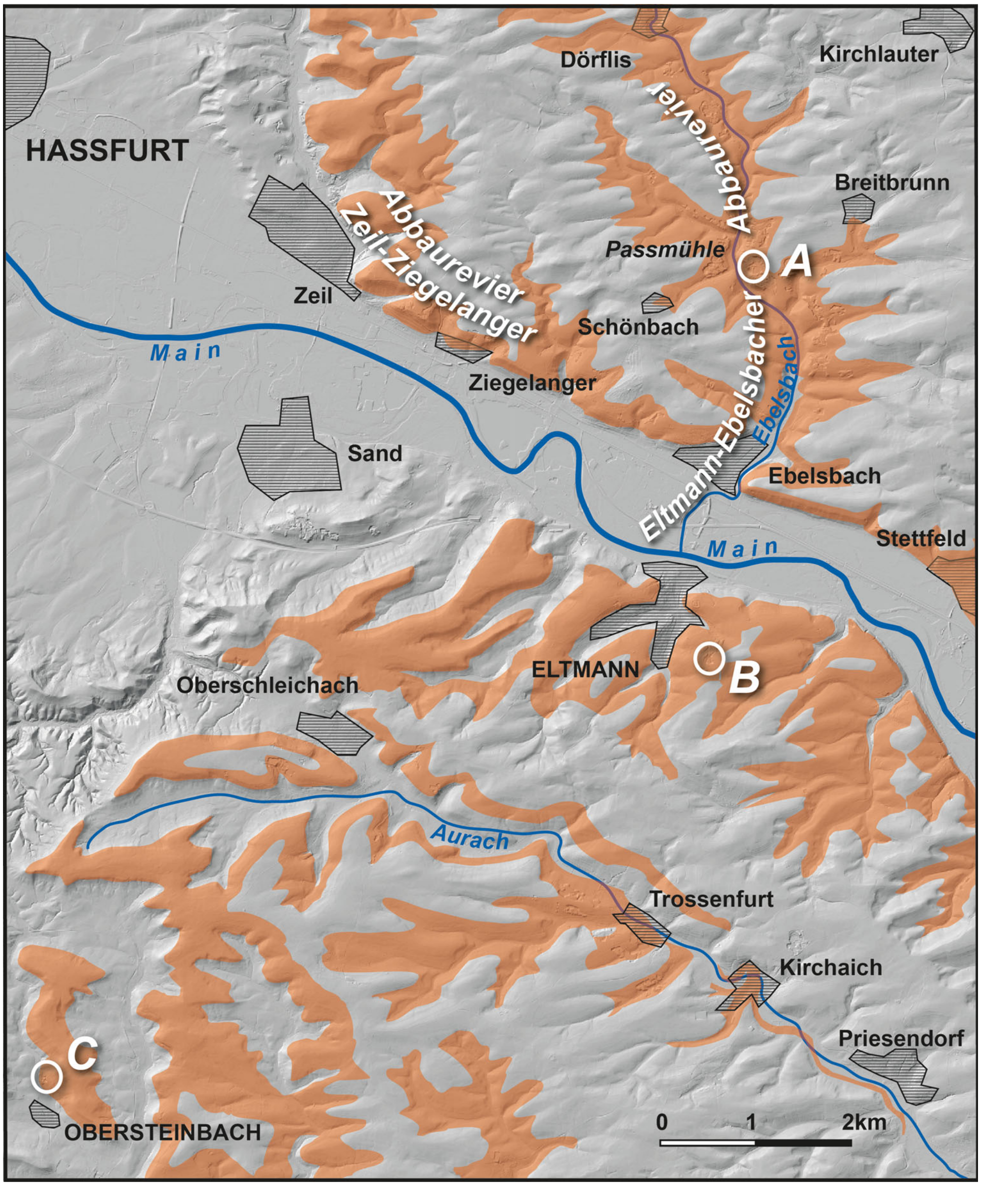


Fig. 4 Topographic map (based on digital terrain model/DGM) showing the northwestern Steigerwald and southwestern Hassberge ranges with outcrop of the Hassberge Formation (slightly idealized) and the major quarry areas of the Coburg Sandstone member of Zeil–Ziegelanger and Eltmann–Ebelsbach. Localities of the Spinicaudata described in this study: *A* Ankenbrand Quarry 800 m east of Passmühle; *B* Hahn Quarry southeast of Eltmann; *C* Steinberg Quarry near Obersteinbach. Detailed information in the text

Localities

The spinicaudatans from the Coburg Sandstone member described herein have been found in three quarries:

1. Ankenbrand Quarry (Fig. 3, upper right; Fig. 4).
   Quarry 800 m east of Passmühle in the Ebelsbach valley, expanded quarry of the Fränkische Schleifsteinwerke GmbH/Brünner, formerly known as Ankenbrand Quarry.
   Coordinates: 50° 00′ 56.19″ N, 10° 40′ 55.52″ E and R 44 05 670 H 55 44 210, respectively.
   Fossils: Spinicaudatans occur in densely rhythmically laminated yellow to greenish floodplain mudstone/siltstones from 3.9 m above the lower "Werkstein" bed (Figs. 3, 4), and were occasionally associated with notostracans (*Triops*; Fig. 12C), fish, macroplants, and charcoal chunks (Kelber 1998b, 2007).
2. Hahn Quarry near Eltmann (Fig. 3, lower right; Fig. 4).
   Quarry to the southeast of Eltmann, known as Hahn Quarry.
   Coordinates: 49° 57′ 37.74″ N, 10° 40′ 22.80″ E and R 44 04 890 H 55 36 850, respectively.
   Fossils: Spinicaudatans recovered from the basal 30 cm of blue gray claystone resting directly on the basal lower "Werkstein" level. Specimens occur with remains of macroplants (Fig. 8B), scattered insects (Fig. 8b), *Triops* (Fig. 11D), and charcoal particles. An additional photo of the outcrop is shown in Reimann and Schmidt-Kaler (2002, p. 86–87). For a detailed section of the quarry, see Blankmeister (1989).
3. Steinberg Quarry (Fig. 4).
   Quarry northwest of Obersteinbach.
   Coordinates: 49° 54′ 31.07″ N, 10° 31′ 15.52″ E and R 43 93 870 H 55 31 290, respectively.
   Fossils: Spinicaudatans recovered from shale blocks that fell from the outcrop wall, and most probably originates from the interval between the lower and the upper "Werkstein" levels. Photo of the outcrop shown in Reimann and Schmidt-Kaler (2002, p. 80).

Conchostracan biostratigraphy

The Keuper beds of the Germanic Basin are almost devoid of classical index fossils. For a long period, biostratigraphic subdivision of the Keuper relied on palynomorphs, and the only recognized correlation with the chronostratigraphically significant Alpine Triassic was based on animals from two horizons with supposed common occurrences of pelecypods [such as *Myophoria kefersteini okeni* in the Bleiglanzbank horizon of the lower part of the Grabfeld Formation (Urlichs and Tichy 2000) and *Myophoria raibliana* in the Raibl Formation]. The establishment of a surprisingly fine-scaled biostratigraphic framework based on "conchostracans" by Kozur and coauthors represented a promising and almost generally welcomed attempt at correlation with the Late Triassic in the Germanic Basin and other continental regions. Moreover, the continuous refinement of the zonation can be seen retrospectively as an amazing amendment, with gaps successively filled by new discoveries.

The first well-defined zones based on spinicaudatans were introduced by Kozur (1999), and the first continuous biostratigraphic zonation for the post-Ladinian Triassic in the Northern Hemisphere was presented by Kozur and Weems (2007), with the key to their correlation being the occurrences in the Germanic Basin Triassic. Kozur and Weems (2010) published a slightly revised Triassic biostratigraphy, with certain refinements for the Carnian through Rhaetian. They suggested that Triassic "conchostracan" zones often provide a stratigraphic resolution comparable to ammonoid and conodont zones of the marine Triassic.

A further revision of the Late Triassic spinicaudatan zones was published by Kozur et al. (2013), which led to a subdivision of Carnian and "conchostracan" zones similar to that illustrated in Fig. 2. Weems and Lucas (2015), however, suggested a revision of the biozones based on results from North America. A slightly modified version of this revision is presented in Lucas (2015). This revision affects the utility of *Laxitextella freybergi*, introduced in Kozur and Weems (2007) based on material from the Coburg Sandstone member. It should be noted that this revision somewhat undermines the scheme shown in Ogg et al. (2014, fig. 4) and Zhang et al. (2015, fig. A.2), which is used as an argument for a "short-Tuvalian" age model.

Weems and Lucas (2015) also emphasized that the suggested Norian (and Carnian) spinicaudatan zonation for North America includes zones based on the first appearance data (FADs) of species within a genus such as *Shipingia*, which is regarded as a descendent of *Laxitextella*. Other zones are acme zones based on species that suddenly appear in the stratigraphic record and then disappear after a short but prosperous phase. However, as correctly explained by Weems and Lucas (2015), there is a danger that, for such acme zones, the occurrences of the relevant species are governed by environment factors, so they do not depict true range zones and their utility for interregional correlation is limited.

The same problem exists for some of the zones in the Middle Keuper of the Germanic Basin, but the revision of *Palaeolimnadia schwanbergensis* and its stratigraphic range illustrates deficiencies associated with sampling and scientific scrutiny (see the documentation in Kozur et al. 2013). However, it is more problematic that zones were transferred to the Germanic Basin that are poorly supported by the fossil record or entirely lack the suggested index fossils. This is the case for all zones marked in pink in Fig. 2. Some of the identifications on which the intercontinental correlations are based are discussed in the systematic section below.

Most of the apparently well-established species from the Middle Keuper beds of Germanic Basin seemingly define zones introduced as interval zones, but are frequently derived from abundance zones, or their known ranges suffer from incomplete or biased sampling.

The Early Carnian (Cordevolian) *Laxitextella multireticulata* zone spans the lower part of the Estherienschichten (upper part of the Grabfeld Formation) and the *Laxitextella laxitexta* zone that encompasses the upper part of the Estherienschichten with its lower boundary lying within the Cordevolian. However, the upper boundary of the *Laxitextella laxitexta* zone has not been defined. A paucispecific association with *Euestheria* cf. *multicostata*, *Gregoriusella* aff. *fimbriata, Laxitextella laxitexta*, and an additional species from a stratigraphic horizon of an unnamed lithostratigraphic unit equivalent to the upper part of the Stuttgart Formation at Ansbach, Middle Franconia (G. Geyer, unpublished data), bridges the apparent gap between the *Laxitextella multireticulata* and the *Laxitextella laxitexta* zones and also indicates that a considerable hiatus below the Stuttgart Formation is unlikely, despite up to several meters of erosion (e.g., Aigner and Bachmann 1992).

Laxitextella seegisi is known from the Steigerwald Formation, but only from several horizons in the upper part. The taxon was recognized as a distinct species by Seegis (1997), but was dealt with as *Laxitextella* sp. therein. However, Seegis (1997) included a *Laxitextella* sp. (=*L. seegisi*) specimen from the Kieselsandstein (=Coburg Sandstone member) that had previously been identified as *Palaeestheria dorsorecta* (=*L. dorsorecta*) in Seegis (1983), so the exact biostratigraphic record remains problematic for the lower part of the Steigerwald Formation and the strata above the Lehrberg beds.

Laxitextella freybergi has been regarded as typical of the Hassberge Formation and the overlying Mainhardt Formation. However, the species is only known from the upper part of the Hassberge Formation and from rare records from the Mainhardt Formation, so the co-occurrence with *Shipingia weemsi* (earlier misinterpreted as *Palaeolimnadia schwanbergensis*; see Kozur et al. 2013) is poorly constrained.

The Norian formations in the southern part of the Germanic Basin are notoriously poor in spinicaudatans, whereas spinicaudatans of high biostratigraphical significance (e.g., *Shipingia gerbachmanni* and *Gregoriusella polonica*) are known from the Norian of Niedersachsen (Hauschke 2014). The as-yet poorly studied Funkenloch beds yield spinicaudatans of a similar morphology to *Euestheria buravasi*, but there are morphological problems with the identification of this species, as discussed below.

Systematic palaeontology

Most of the material used for this study is in a repository of the Kelber Collection, Würzburg, indicated by the acronym SKW. The acronym GIW refers to the collection of the former Institut für Geologie, Würzburg University, which is now housed in the Bayerische Staatssammlung für Paläontologie und Geologie, München. The acronym GZG refers to the collection of the Geowissenschaftliches Zentrum, Göttingen University.

The taxonomy adopted here mainly follows that of Chen and Shen (1985) and Martin and Davis (2001), but also refers to morphological terms employed by Reible (1962), who used “telliniform” (when the dorsal margin is joined without a notable kink with the posterior margin) and “cyciziform” or “cicladiform” (when there is an obtuse angle between the posterior and dorsal margins).

Subphylum **Crustacea** Brünnich, 1772
Class **Branchiopoda** Latreille, 1817
Order **Spinicaudata** Linder, 1945
[nom. transl. Tasch, 1969, ex “tribe Spinicaudata” Linder, 1945]

Superfamily **Eosestherioidea** Zhang and Chen in Zhang et al., 1976 (sensu Chen and Shen, 1985)
[=Lioestherioidea Raymond, 1946 sensu Zhang et al., 1976]

Discussion. The history of research has often had a strong impact on systematic–taxonomic and biostratigraphic concepts. Research on Triassic clam shrimps suffers from a Europaeo-centric nucleus and subsequently a focus on Eurasian aspects of the relevant groups. Kozur published a considerable number of articles (e.g., Kozur and Mock 1993; Kozur and Weems 2005, 2007, 2010; Kozur et al. 2013) in which Eurasian and particularly Central European genera and species were “globalized” and thus contributed to a remarkably unified distribution of mid- and Late Triassic spinicaudatans and a fairly robust framework of biozones for the upper part of the Triassic on a global scale. However, a large number of European specimens upon which taxa were based are imperfectly preserved in the region in which they were identified, and critical characters often have an ambiguous possible interpretation, so that the "internationalization" of species or even genera—and the use of such species in a consistent quasi-global biostratigraphic scheme (e.g., Kozur and Weems 2007; Lucas et al. 2012)—must be approached with caution. In particular, Late Triassic spinicaudatans from South America and Antarctica require critical reinvestigation with respect to their generic and sometimes suprageneric identities, as suggested by several authors (e.g., Gallego and Covacevich 1998; Gallego 2010; Vaz et al. 2015).

True apomorphic characters cannot be determined from the Triassic Spinicaudata, so generic concepts of the relevant taxa almost entirely lack true diagnostic features. Devoid of robust diagnoses, the genera of Triassic spinicaudatans are overwhelmingly developed into taxonomic waste baskets, meaning that generic characters are rarely discussed. It is a truism that generic concepts should depict phylogenetic affinities and kinship, but the Mesozoic spinicaudatan remains generally lack those features, so the relevant genera should be considered episystematic entities. Nevertheless, even these genera should provide the best possible basis to reflect close phylogenetic relatedness, so putative characters of substantial morphological significance need to be identical within genera, which is often not the case at present. As an example, collective entities dealt with as genera, such as *Euestheria* or *Laxitella*, should have identical shapes and umbo positions, which identify conditions relevant for systematics and phylogeny within the basic framework of valve morphology.

Family **Euestheriidae** Defretin-Lefranc, 1965

Remarks. The family Euestheriidae as revised by Zhang et al. (1976) and Chen and Shen (1985) is a paraphyletic taxon from which the Eosestheriidae Zhang and Chen, (1976) (in Zhang et al. 1976, p. 152) evolved. Given the poor state of phylogenetic analysis within this clade, we refer all relevant genera and species discussed below to the family Euestheriidae. For further critical appraisal of the families, see the annotations in Astrop and Hegna (2015).

Genus ***Euestheria*** Depéret and Mazeran, 1912

Type species. *Posidonia minuta* Zieten, 1833

Discussion. The genus *Euestheria* Depéret and Mazeran, 1912 is among the most frequent spinicaudatan genera found during the Mid- to Late Triassic in Europe, and Zhang et al. (1976) listed 53 species or tentatively assigned species and forms of *Euestheria* from the Triassic and Lower Jurassic of China. Nevertheless, *Euestheria* has been subject to considerable shifts in nomenclature over the years, so the correct status is briefly reviewed herein. The earliest representatives of the genus were attributed to *Estheria* Rüppell in Straus-Dürckheim, 1837, proposed for a Recent species from Abyssinia. However, *Estheria* was quickly identified as a junior homonym of *Estheria* Robineau-Desvoidy, 1830 (Diptera: Tachinidae). *Estheria* was replaced by *Cyzicus* Audouin, 1837, a genus introduced in the same year without a generic description, meaning that its validation awaited a formal proposal by Mattox (1958). *Cyzicus* was used as a collective taxonomic unit for Spinicaudata with an ordinary suboval outline of the carapace and distinct growth lines, and was split into several subgenera, such as *Euestheria* Depéret and Mazeran, 1912, and *Lioestheria* Depéret and Mazeran, 1912 (e.g., Tasch 1969, 1987). The near-simultaneous publication of the two generic names prompted Joly (1842) to introduce *Isaura* Joly, 1842 (non 1841), but this is clearly a junior synonym of *Cyzicus*. *Cyzicus*, in turn, has been subsequently restricted to Recent species with particular morphological features that are usually not preserved in fossil material, and the family Cyzicidae Stebbing, 1910 is based on the genus.

The Triassic representatives such as *dorsorecta*, *fimbriata*, *minuta*, and *multireticulata* have been placed under *Palaeestheria* Barnard, 1929, a genus based on a type species from the Early Cretaceous (*Estheria anomala* Jones, 1901), which can be separated from the Triassic species by a number of significant characters. The generic name *Palaeestheria* was proposed by Daday de Deés (1915), who introduced the taxon without providing a diagnosis, indicating a type species, or clearly indicating which species should be furnished under the genus, so that *Palaeestheria* Daday de Deés, 1915 must be regarded as a nomen nudum. The systematic position of *Palaeestheria* Barnard, 1929 (emend. Raymond 1946) is somewhat problematic because of incomplete knowledge of its Lower Cretaceous type species. However, a suitable genus for the relevant Triassic species is *Euestheria* Depéret and Mazeran, 1912, which is generally characterized by ornamentation consisting of a pattern of minute polygons between the growth lines.

In a publication on estheriids from the Keuper beds of the Germanic Basin, Warth (1990) claimed that *Euestheria* was an invalid taxon. Warth (1969, 1990) believed that the genus was founded on an incorrectly determined species. Indeed, Depéret and Mazeran (1912) declared "Estheria minuta d'Autun" to be the type species, which would have made the genotype a species from the latest Carboniferous or Early Permian of France, but this a species that does not belong to the genus *Euestheria* in the present concept. However, the name *Estheria minuta* suggested by Depéret and Mazeran (1912) did not in fact apply to the pre-Triassic clam shrimps from France. The authors suggested that, if their assignment of these forms to the Triassic *E. minuta* proved to be correct, then *E. minuta* first appeared in the Early Permian. This is not true, and the Permian "conchostracans" belong to the genus *Pseudestheria* Raymond, 1946. Indeed, Depéret and Mazeran (1912) emphasized that *Euestheria minuta* is typically found in Triassic rocks. Depéret and Mazeran (1912) also emphasized that the Late Triassic species *Estheria laxitexta* Sandberger in Jones, 1890 differs from *Euestheria minuta* and should thus be treated as a different taxon. Consequently, *Euestheria* is unequivocally based on Triassic material of *Estheria minuta* Alberti in Zieten, 1833. In any case, the species assigned to *Euestheria* cannot be furnished under *Palaeestheria* as done in Warth (1969, 1990) because *Palaeestheria* Barnard, 1929 would turn up as a junior synonym of *Euestheria* Depéret and Mazeran, 1912 if the two genera were to be merged.

An additional genus, *Howellisaura* Bock, 1953b, was introduced for a number of species that are currently distributed under several different genera. Its type species, *Howellites princetonensis* Bock, 1953a, was regarded as a particularly large species of *Euestheria* as suggested by Kobayashi (1951) and subsequent authors such as Tasch (1969) and Kozur and Weems (2007), which would make *Howellisaura* a junior synonym of *Euestheria*. Other authors, however, regarded *Howellisaura* as distinct from *Euestheria*. Kobayashi (1954) synonymized *Howellisaura* with *Estheriellites* Bock, 1953a as well, so *Howellisaura* can be regarded as a junior synonym of *Estheriellites* as discussed by Morris and Chen (1992) and as a taxon of the superfamily Estheriteoidea Zhang and Chen (in Zhang et al., 1976, p. 183) and the family Fushunograptidae Wang (in Hong et al., 1974), which is characterized by the presence of simple nonsinuous lirae. This concept is largely followed for the relevant species described from the Triassic of Argentina (e.g., Vaz et al. 2015), and is also applied here, so that *Howellites princetonensis* Bock, 1953a is regarded as a species of *Estheriellites*.

Howellites winterpockensis Bock, 1953a has been placed under *Euestheria* by Kozur and Weems (2007), with material described from the upper part of the Grabfeld Formation (Estherienschichten) of the Germanic Basin as *Cyzicus* (*Euestheria*) *minutus multicostatus* Geyer, 1987 synonymized with the species from Virginia. However, Bock's original material is not preserved in a way that permits the confident identification of all relevant characters (see below under *Euestheria multicostata*).

The eastern Asian genus *Estherites* Kobayashi and Huzita, 1943 has been suggested to be synonymous with *Euestheria*, but although Triassic representatives have been assigned to the genus (Kobayashi 1951), it is now generally regarded as a genus with an acme in the later Mesozoic, is even split into three subgenera (Li and Batten 2005), and is part of the family Estheriteidae.

Kobayashi (1954), Tasch (1969), and Morris (1980) made *Bairdestheria* Raymond, 1946 synonymous with *Euestheria*, but Kozur (1982) regarded *Howellisaura as* a junior synonym of *Bairdestheria*, and Tasch (1987) declared *Bairdestheria* as a junior synonym of *Lioestheria*. The type species of *Bairdestheria* is *Estheria mawsoni* Jones, 1897 from the Lower Cretaceous of Brasil and is distinctly distinguished from the typical species of *Euestheria* by its "lioestheriid" ornament of dense hachure markings.

A large number of genera published by N.I. Novozhilov have been regarded as junior synonyms of *Euestheria* at various times. These genera include *Indoestheria* Novozhilov, 1954; *Palaeoorthothemos* Novozhilov, 1954; *Paleoleptestheria* Novozhilov, 1954; *Pseudoasmussia* Novozhilov, 1954; *Rossoestheria* Novozhilov, 1954; *Trigonestheria* Novozhilov, 1954; *Trigononorassaia* Novozhilov, 1954; *Concherisma* Novozhilov, 1956; *Aquilonoglypta* Novojilov/Novozhilov, 1958; and *Sphaerorthothemos* Novozhilov, 1960. The majority of them originate from pre- or post-Triassic strata and are overwhelmingly imperfectly preserved as well as improperly illustrated. Each genus demands careful revision based on the type material, but probably none of them includes all of the criteria need to synonymize them with *Euestheria*.

More than 110 species have been attributed to *Euestheria* to date, with more than half of them reported from eastern Asia, but the status of the majority of them is equivocal. Their stratigraphic ranges stretch from the (Mid?) Permian to the Early Cretaceous, so the stratigraphic range of *Euestheria* exceeds that of all known spinicaudatan genera, which is undoubtedly a consequence of insufficient knowledge about important anatomical–morphological characters.

We believe that the genus *Euestheria* can be defined by the following characters: comparatively small in size, carapace subovate, shape cyziciform; umbo in in the anterior third or slightly posterior to one-third of the carapace length, barely rises above dorsal; larval carapaces small; growth bands regular to nearly regularly spaced, moderately narrow; ornamentation consists of irregular lirae or polygons.

Euestheria kozuri sp. nov.
Figures 5A–H, 6, 7, 11D

Derivation of name. Named after the late Heinz W. Kozur, in appreciation of his work on the taxonomy and biostratigraphy of Permian–Triassic clam shrimps.

Holotype. SKW PASS-227b (Fig. 5F), single valve.

Type locality. Extended Ankenbrand Quarry (Bayerische Schleifsteinwerke), east of Passmühle, Ebelsbach valley, Franconia, southern Germany.

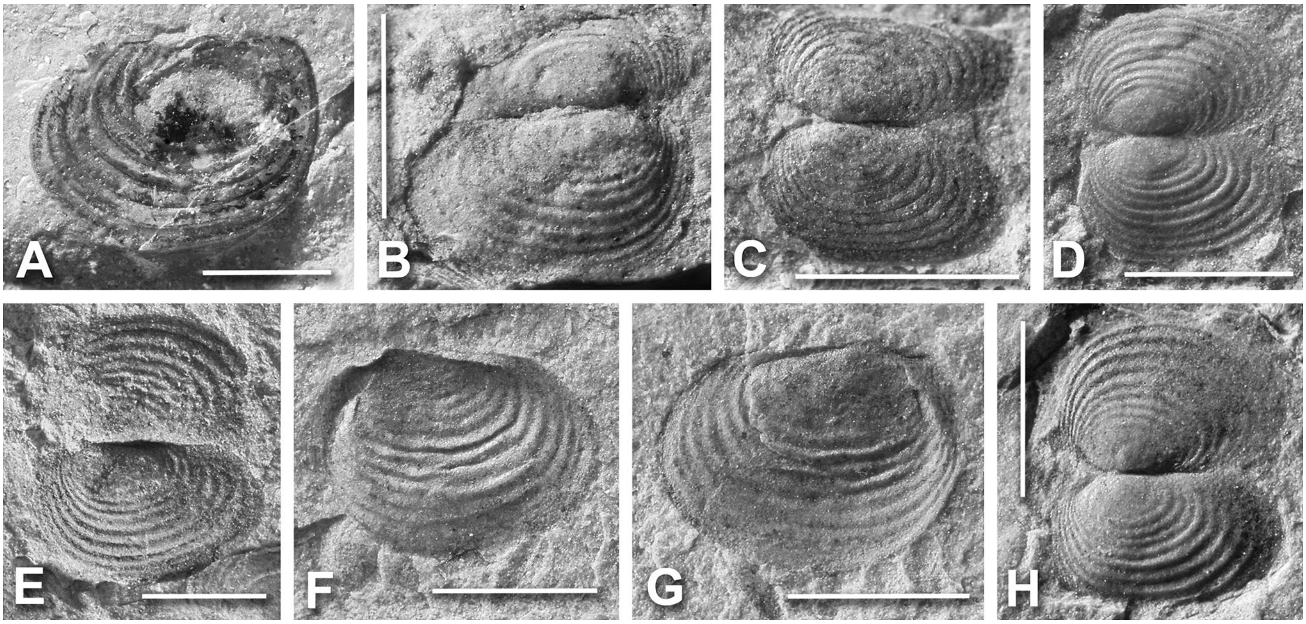


Fig. 5 *Euestheria kozuri* sp. nov., all specimens from Coburg Sandstone member, Hassberge Formation. **A** ELT-C-03, paratype, near-complete valve, with folds resulting from compaction, Hahn Quarry near Eltmann, Franconia. **B** OSTB-01b, paratype, carapace in butterfly configuration, Steinberg Quarry near Obersteinbach, Franconia. **C** OSTB-01a, paratype, carapace in butterfly configuration, Steinberg Quarry near Obersteinbach, Franconia. **D** PASS-229b, paratype, carapace in butterfly configuration, Ankenbrand Quarry above Ebelsbach valley, Franconia. **E** PASS-225a, paratype, carapace in butterfly configuration, Ankenbrand Quarry above Ebelsbach valley, Franconia. **F** PASS-227b, holotype, slightly flattened valve with blurry pattern of slightly irregular polygons, Ankenbrand Quarry above Ebelsbach valley, Franconia. **G** PASS-227a, paratype, valve with blurry pattern of slightly irregular polygons, Ankenbrand Quarry above Ebelsbach valley, Franconia. **H** PASS-229a, paratype, carapace in butterfly configuration, Ankenbrand Quarry above Ebelsbach valley, Franconia. *Scale bars* 2 mm

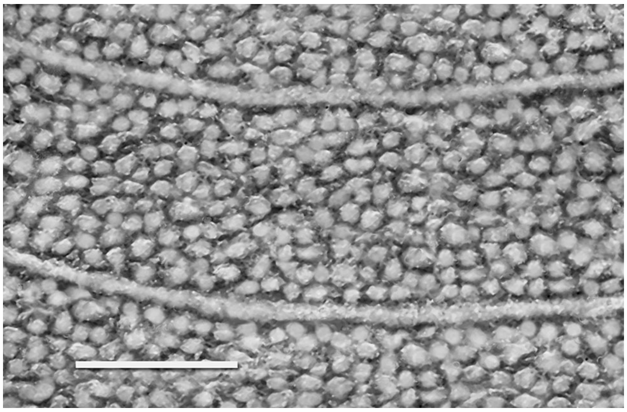


Fig. 6 *Euestheria kozuri* sp. nov., schematic graphic reconstruction illustrating details of the original ornamentation between growth lines. *Scale bar* 0.5 mm

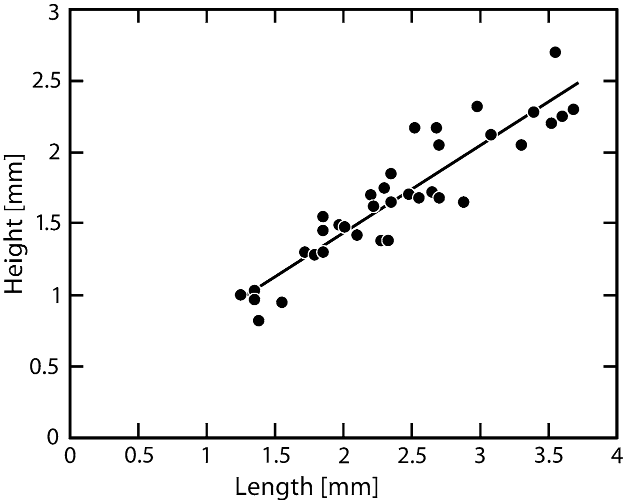


Fig. 7 *Euestheria kozuri* sp. nov., graphic illustrating the variations in the length and height of undeformed or barely deformed valves

Type stratum. Coburg Sandstein member, upper part of Hassberge Formation, about 3.9 m above the top of the lower "Werkstein" bed; *Laxitextella freybergi* Zone, late Tuvalian.

Paratypes. SKW ELT-C-03, valve, from Hahn Quarry near Eltmann; SKW OSTB-01a, OSTB-01b, two bivalved carapaces in butterfly configuration, OSTB-01c, OSTB-01d, OSTB-01e, OSTB-01g, OSTB-01h, five single valves, all from Steinberg Quarry near Obersteinbach; SKW PASS-225a, PASS-227c, PASS-227f, PASS-227m, PASS-227n, PASS-227r, PASS-227t, PASS-227x, PASS-227a′, PASS-227b′, PASS-229a, PASS-229b, PASS-229d, PASS-229i, 14 bivalved carapaces in butterfly configuration, SKW PASS-225c, PASS-229e, two bivalved specimens, SKW PASS-225b, PASS-225d, PASS-225e, PASS-227a, PASS-227d, PASS-227e, PASS-227g, PASS-227h, PASS-227i, PASS-227j, PASS-227k, PASS-227l, PASS-227s, PASS-227u, PASS-227v, PASS-227w, PASS-227z, PASS-227c′, PASS-227d′, PASS-229c, PASS-229f, PASS-229g, PASS-229h, PASS-229j, PASS-229k, PASS-229l, PASS-229o, PASS-227p, PASS-227q, 29 single disarticulated valves, from Ankenbrand Quarry, Ebelsbach valley; all from Coburg Sandstein member, upper part of Hassberge Formation.

Diagnosis. Species of *Euestheria* with generally moderately large carapace of elongate ovoidal to subrectangular outline, cyziciform to nearly telliniform; dorsal margin more or less straight, anterior dorsal corner subacute, posterior dorsal corner with narrow curvature. Anterior margin gently curved; anteroventral margin somewhat oblique; ventral margin moderately curved; posterior margin with considerably pronounced curvature. Umbo obtuse, in fairly anterior position, projects beyond dorsal margin by only a minor distance. Free umbonal area small. Growth bands 14–18, moderately broad, with fine to moderately coarse reticulation consisting of 4–6 polygons between growth lines. Polygons varying in outline between pentagonal or polygonal to subelliptical or irregularly oval.

Description. Carapace of small to mostly moderate size, varying in outline from elongate ovoidal to subrectangular, cyziciform to nearly telliniform in shape, up to ca. 4.5 mm long, adult valves usually between 1.5 and 3 mm in length, and up to ca. 3.7 mm high (usually between 1.3 and 2.3 mm). Height/length ratio varies in undeformed specimens between ca. 0.72 and 0.88 (Fig. 7). Lateral convexity reaches its maximum a short distance posterior and below umbo at about the anterior one-third of the valve length. Dorsal margin more or less straight, length of hinge line ca. 65% maximum length of carapace (Fig. 5G), anterior dorsal corner subangulate, angle on the order of 105°; posterior dorsal corner obtuse, with narrow curvature. Anterior margin gently curved, maximum curvature at about midheight of the valve; posterior margin forms a broad, nearly even curve with maximum curvature slightly below midheight in the ovoidal specimens; anteroventral margin somewhat oblique, faintly bent, ventral margin with moderate curvature.

Umbo subacute, in fairly anterior position at ca. 30% maximum length of carapace from anterior end of valve; projects beyond dorsal margin by only a minor distance. Free umbonal area small.

Growth bands moderately broad, number of visible growth bands 9–18 in the studied specimens, usually between 10 and 12 ($n = 51$), relatively evenly spaced in the ventral and midventral parts of the valves, growth bands in juvenile dorsal part of valve are clearly more closely spaced, but growth bands usually not preserved or are only poorly preserved toward the umbonal part of the valve; large specimens apparently with a few dense growth lines toward the ventral margin; surfaces of growth bands covered with moderately coarse reticulation that consists of 4–6 polygons between growth lines. Polygons varying in outline, pentagonal to subhexagonal, polygonal, subelliptical, or irregularly oval.

Dimensions. Length 1.3–4.5 mm ($n = 53$); height 1.00–3.7 mm ($n = 55$); length of hinge line 0.35–3.1 mm ($n = 18$).

Taphonomic aspects. A slight dimorphism appears to exist in the species, illustrated by slightly smaller valves of more elongate outlines (ratio height/length ca. 0.74–0.88) (Fig. 5A, F, G) and slightly larger valves with slightly higher height/length ratios (0.58–0.72) (Fig. 5C, D, E, H). In addition, the posterior margin has its maximum curvature at about midheight in valves with more elongate outlines whereas the maximum curvature lies slightly below midheight in valves with an ovoidal outline. These differences can be referred to taphonomic aspects. The more elongate valves are almost exclusively associated with preservation of the bivalve individuals in a butterfly-type preservation. It is obvious that in these cases the gaping valves were connected by soft-part tissues when they were embedded in the soft sediment. The valves were thus not oriented parallel to the bedding plane and presented an angle of distinctly less than 180°. During early diagenesis and compaction, they suffered a mild distortion which created the more strongly elongate outline and the apparently more ventral position of the maximum curvature of the posterior margin.

Discussion. *Euestheria kozuri* sp. nov. is among the relatively few species of the genus with a generally slightly elongate/cyziciform or slightly telliniform shape. It has a moderate number of growth lines, usually between 10 and 12, which is surprising given that the differences in size would suggest wider variation in the number of lines. *E. kozuri* is further characterized by its relatively beaked umbo, which is subacute rather than obtuse as in most of the co-occurring species, and which projects beyond the dorsal margin.

Euestheria? sp. nov. A, which co-occurs with *E. kozuri* in the Coburg Sandstone member, has a fairly distinct outline with its long and roughly subvertical anterior margin of the carapace, unlike the curved anterior margin in the valves of *E. kozuri*. In addition, *E.*? sp. nov. A is distinguished from *E. kozuri* by a higher number of growth lines and its prosopon of smaller, slightly irregular polygons.

The subacute umbo in *Euestheria kozuri* resembles that seen in *Euestheria multicostata* (Geyer, 1987), which is clearly distinguished by its more subovoid outline and the distinctly larger number of growth bands.

Euestheria minuta (Alberti in Zieten, 1833) from the Triassic, in most occurrences of such rocks in the Northern Hemisphere, has a long stratigraphic range from its common or even dominant occurrence throughout the Late Ladinian to the Early Cordevolian. Problems with *E. minuta* were recently indicated in a morphometric study by Morton et al. (2017). However, this species is clearly distinguished from *E. kozuri* by its lack of a clearly recognizable intercostal ornament, the more central position of its umbo, and by its slightly higher number of growth bands (10–20), particularly in individuals of the same size.

Euestheria albertii (Voltz, 1835) has two subspecies *E. albertii albertii* (Voltz, 1835) and *E. albertii mahlerselli* Kozur and Lepper in Kozur and Weems, 2010. These occur in the Early Anisian Röt Formation of the Upper Buntsandstein. They possess a similarly elongate outline of the carapace, but are characterized by a higher number of growth lines (ca. 15) which are more distinctly developed, by a less protruding umbo with relatively straight dorsal margins on both sides of it, and by other features.

Euestheria brodieana (Jones, 1862), from the Rhaetian to Hettangian of England, France, and northern Germany, has a subovoid carapace outline and usually more than 20 growth lines, but distinctly resembles *E. minuta*. It should be noted, however, that the material assigned to the species varies in respect to the number of growth bands, the expression of growth lines, and the shape and the position of the umbo to an extent that would be unusual for a species. A careful reinvestigation that clarifies some of the problems was recently performed by Morton et al. (2017).

Euestheria exsecta (Novozhilov, 1946) comes from the Olenekian of Russia and Poland. The species is similar to *E. kozuri* in size and number of growth lines, but has a subovoid valve outline with a strongly curved anterior margin, and a more subobtuse umbo.

Euestheria? *franconica* (Reible, 1962), from the Fassanian of the Germanic Basin, first described as *Cyclestherioides franconica* from the Ostrakodenton beds of the uppermost Muschelkalk, is based on relatively poorly preserved material characterized by valves with a distinctly ovoid outline and an obtuse umbo in a subcentral position with respect to the dorsal margin. The holotype (Reible 1962, pl. 9, fig. 6) has numerous (>25) growth lines despite Reible's description that characterizes the species as having 15–25 growth lines. The placement of the species under *Euestheria* reflects uncertainties in the characterization of the genus.

For *Euestheria buravasi* Kobayashi, 1975 and *E. winterpockensis* (Bock, 1953a), see discussions below under *E. buravasi* and *E. multicostata*.

Howellisaura? *ovata* (Lea, 1856), from the Tuvalian of eastern North America, had been assigned to *Euestheria*. The carapaces of *H.*? *ovata* are relatively large (6–8 mm in length), and can be distinguished from those of *E. kozuri* in numerous aspects such as the shape of the umbo, the strongly curved anterior margin and the more subovoid outline of the valves, and a distinctly larger number of growth lines, which are fairly sharply developed in well-preserved specimens.

Howellisaura princetonensis (Bock, 1953a), from the Tuvalian of eastern North America, placed under *Euestheria* by Kozur and Weems (2007) and revived as the type species of *Howellisaura* in Kozur and Weems (2010), is characterized by valves with a subovoid outline, an obtuse umbo, and numerous (>30) growth bands in adult individuals.

The slightly elongated valve outline easily distinguishes *Euestheria kozuri* from the co-occuring *Gregoriusella striatula* sp. nov. In addition, *G. striatula* shows the generic characteristics of an ornament consisting of slightly irregular or varying radial lirae.

Euestheria? sp. nov. A
Figure 8A, C

Material. SKW ELT-C-12a (Fig. 8A, C), carapace composed of two slightly rotated valves. Tentatively assigned to *Euestheria*? sp. nov. A: SKW ELT-C-12b, single, slightly distorted valve; from the same slab as SKW ELT-C-12a.

Locality and stratum. Hahn Quarry, SE of Eltmann, Franconia, southern Germany. Coburg Sandstein member, upper part of Hassberge Formation, 0.0–0.3 m above the top of the basal lower "Werkstein" bed; *Laxitextella freybergi* Zone, late Tuvalian.

Description. Carapace small- to medium-sized, outline of valves roughly subovoid and cyziciform, SKW ELT-C-12a ca. 3.9 mm long and ca. 3.0 mm high. Maximum lateral convexity located a short distance below umbo at about 40% of valve length from anterior margin.

Dorsal margin relatively short, more or less straight or faintly bent, length of hinge line ca. 45% maximum length of carapace; anterior dorsal corner obtuse to subangular, developed as a narrow curved extension that connects the dorsal with the anterior margin, situated ca. 12% of maximum valve length from the valve's anterior; posterior dorsal corner obtuse, developed as a small curve that connects dorsal to posterodorsal margin. Anterior margin gently and relatively evenly curved throughout so that it extends into the anteroventral section of the margin, which has a remarkably steep ventral direction; anterior and ventral margins merge at a subangular tip, which appears to become more pronounced with age, as indicated by the

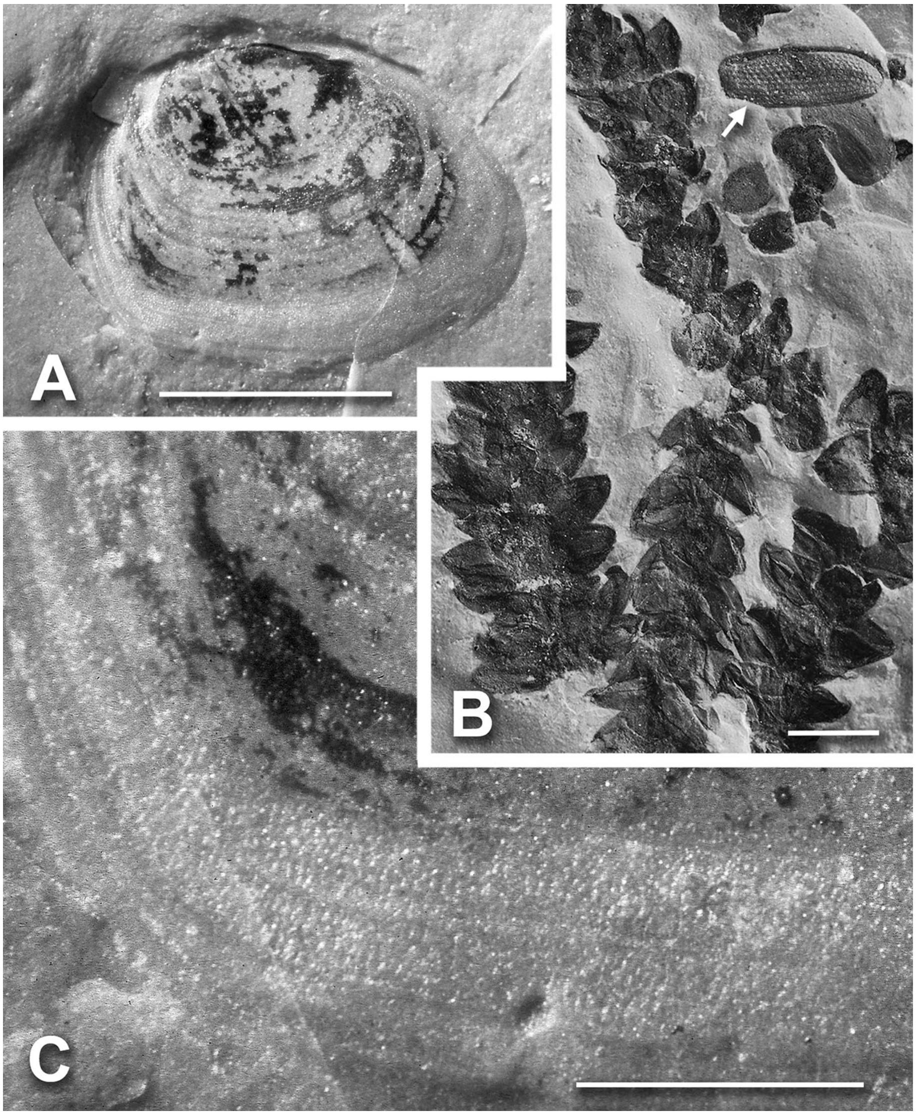


Fig. 8 **A**, **C** *Euestheria*? sp. nov. A, ELT-C-12a, valve with remnants of cuticle. **A** Entire specimen, *scale bar* 2 mm. **C** Detail of anteroventral portion showing prosopon of small elongated polygons with their length axes subperpendicular to growth lines, arranged in three or four series; *scale bar* 0.5 mm. **B** ELT-135, *Voltzia coburgensis*, shoots, associated with a dotted elytron of polyphagan coleopteran (*arrow*); *scale bar* 2 mm. All specimens from Coburg Sandstone member, Hassberge Formation, Hahn Quarry, SE of Eltmann, Franconia

course of the growth lines; ventral margin with gentle to moderate curvature; posterior margin sinuously curved in lateral view (similar to the tip of an egg) for the most part, but grades into a faintly curved and distinctly oblique posterodorsal section.

Umbo obtuse, in median position at slightly less than 40% of the valve length from anterior rim of the carapace, faintly projects beyond dorsal margin in lateral view (slightly compressed in SKW ELT-C-12a so that it seems to be at exactly the same level as the dorsal margin in lateral view). Free umbonal area small.

Valve with at least 24 growth bands in the holotype, which is an adult specimen; moderately broad in the median part of the valve, slightly narrower and more irregular towards the ventral margin; moderately broad and subevenly spaced growth bands in the median part of the valve with ca. 8–12 polygons between growth lines; more densely packed growth bands towards the ventral margin with apparently 5–10 polygons between growth lines; growth bands in juvenile dorsal part of valve similar in width to those in the median part, not sufficiently well preserved in the studied material to allow precise description.

Surface of growth bands covered with fine to minute polygons that vary in outline from subcircular to subelliptical, possibly pentagonal to subhexagonal; size of polygons varies considerably, even between adjacent meshes, from ca. 5 µm to nearly 20 µm in maximum diameter; polygons mostly arranged in stacked series, with their length axes subperpendicular to growth lines; the serial arrangement of polygons imitates weakly defined lines as a subdivision of the growth bands (Fig. 8C).

Discussion. The specimen(s) described herein as *Euestheria*? sp. nov. A certainly represents a new species. It is characterized by a fairly distinct outline with a long and roughly subvertical anterior margin of the carapace and a prosopon of small, slightly irregular polygons with their length axes subperpendicular to the growth lines and with a tendency to be arranged in series seen in the median part of the valve. It cannot be assigned with sufficient certainty to any of the existing eosestherioid genera; more material is necessary to evaluate the morphologic range of the species, which is therefore provisionally placed under the genus *Euestheria*.

Euestheria buravasi Kobayashi, 1975

Discussion. *Euestheria buravasi* Kobayashi, 1975 has been described from the Khorat Group of early Norian age in Thailand, and was subsequently reported from coeval strata of the Deep River and Sanford basins of eastern North America (e.g., Kozur and Weems 2007, 2010; Weems and Lucas 2015) and is now used as an important index fossil on a (sub)global scale. It should be emphasized, however, that Kobayashi's holotype of *E. buravasi* (Kobayashi 1975, pl. VII, fig. 9) is relatively strongly compressed and imperfectly preserved such that the exact length of the dorsal margin cannot be determined in the holotype or the paratype. The holotype has a relatively characteristic pattern of growth lines, with 18–20 wider, subequal growth bands in the juvenile/umbonal and median part of the valve and 13–16? narrow growth bands in the peripheral/ventral part of the valve. The growth bands show fine subradial lirae; their slightly oblique direction relative to the growth lines is attributed to slight tectonic distortion.

The specimens from North America identified as *E. buravasi* by Kozur and Weems (2007, pl. 5, fig. 2, 3) show the same pattern of wider adumbonal and narrower peripheral growth bands, but appear to have the umbo in a more central position, more peripheral growth lines, and finer striation, so more material is needed to ensure correct identification.

Euestheria multicostata (Geyer, 1987)

v 1987 *Cyzicus (Euestheria) minutus multicostatus* n. subsp.—Geyer: pp. 288, 289, text-fig. 7, figs. 1–15.

Discussion. *Euestheria multicostata* (Geyer, 1987) has been introduced as a subspecies of *E. minuta* simply to avoid an avalanche of species with roughly the same stratigraphical ranges distinguished by only minor differences in character sets. The species is characterized by small sizes of the cyziciform carapace and a multitude (ca. 20–40) of very narrow growth bands of somewhat irregular width throughout the valves. A distinct ornamentation is not unequivocally recognizable in the type material, but it seems to consist of minute polygons. It is especially noteworthy that the umbo clearly projects beyond the dorsal margin.

The species was found only in the so-called Modiola bed in the lower part of the Estherienschichten, upper part of Grabfeld Formation, and is thus of Cordevolian age. Its isolated occurrence is most likely a result of the depositional environments in this part of the Germanic Basin during this period: the region was a relatively central part of the basin, where there were rare episodes of brackish conditions which led to the occurrence of species of *Modiolus* in the Modiola bed as well, and conditions favorable for the existence and preservation of spinicaudatans were probably short-lived. Ignorance of these environmental conditions appears to have given rise to unresolved criticism by Warth (1990) of the descriptions.

A very similar species, *Howellites winterpockensis* Bock, 1953 (Bock, 1953a, p. 73, pl. 12, figs. 7, 8), was described from the basins of the eastern United States, and was later transferred to *Euestheria*. Like *E. multicoststa*, *Euestheria winterpockensis* is characterized by its numerous very narrow growth bands, which are typically 20–30 in number. Kozur and Weems (2007, p. 141) described that the number ranges from 19 to 46 and that "specimens with 19 or 20 growth lines overlap slightly with the forerunner species *E. minuta*, which has 10–20 growth bands," and that the type material from the early Cordevolian Tuckahoe Formation of the Richmond Basin in Virginia includes both *E. minuta* and *E. winterpockensis*.

As noted by Kozur and Weems (2007), Bock's (1953a) description distinguished an alpha form and a beta form, which were thought to represent male and female specimens. Specimens with 19 growth bands were assigned to the alpha form and specimens with 21 growth bands to the beta form, which was collected from strata above the interval in which the ranges of *E. minuta* and *E. winterpockensis* are believed to overlap. Consequently, the growing number of growth lines can be interpreted as an evolutionary development. It should also be emphasized that the increase in the number of growth lines in *E. winterpockensis* coincides with considerable growth in the size of the carapace from Early Cordevolian to Late

Cordevolian specimens, which at some point were distinguished as *Euestheria* sp. cf. *E. winterpockensis* in Kozur and Weems (2007).

This procedure for species identification is based on the fossil record, but it differs from concepts applied in other cases of spinicaudatan taxonomy. It becomes even more problematic if the species is used as an index fossil for intercontinental correlation, as done in this case. The utility of *E. winterpockensis* for this purpose is partly founded on the assumption that *E. multicostata* is a junior synonym of *E. winterpockensis*. This, however, is uncertain due to certain morphological differences between the species. The number of growth lines in *E. multicostata* vacillates between ca. 20 and 40, as described for the aggregate forms identified as *E. winterpockensis*, but 20–25 growth lines occur in *E. multicostata* in nonadult specimens only, whereas the large valves all show more than 25 growth lines. In addition, the umbo in *E. multicostata* is relatively acute and clearly projects beyond the dorsal margin, whereas the umbo in *E. winterpockensis* is much more stout and barely reaches beyond the dorsal margin. In any case, material of *E. winterpockensis* from the type strata (Kozur and Weems 2007, pl. 1, fig. 1) clearly has fewer and more widely spaced growth lines and is so poorly preserved that a precise comparison appears to be impossible. Additional material figures by Kozur and Weems (2007, pl. 1, fig. 4) again appear to suggest that it has fewer growth lines and can be distinguished from *E. multicostata* by a more subovoid outline of the valve. For the moment, the synonymy of *E. winterpockensis* and *E. multicostata* appears to be quite unsettled, and thus an *E. winterpockensis* zone can only be suggested for the North American regions and should be approached cautiously, even though this zone (established by Kozur and Weems 2007) has been merged with the *Laxitexta multireticulata* zone by Kozur and Weems (2010).

Occurrences. Lower part of Estherienschichten, upper part of Grabfeld Formation in Germany (late Cordevolian).

Genus **Gregoriusella** Kozur and Weems, 2010

Type species. *Gregoriusella polonica* Kozur, Niedźwiedzki and Sulej in Kozur and Weems, 2010 (by original designation).

Discussion. The genus *Gregoriusella* has been introduced by Kozur and Weems (2010) based on three species. The type species, *Gregoriusella polonica* Kozur, Niedźwiedzki and Sulej, 2010 (in Kozur and Weems 2010), has its type locality and type stratum in the uppermost/latest Norian to lowermost/earliest Rhaetian of Upper Silesia, Poland, but the species had already been identified at the time of its publication from the basal Exter Formation (earliest Rhaetian) in the Tarnow borehole, northern Germany, and from the earliest Rhaetian Duke Ranch Member of the Redonda Formation of New Mexico in the US. It was subsequently observed in the Bigoudine Formation of the Argana Basin, Morocco (Weems and Lucas 2015). The other species assigned to the genus are *Palaeestheria fimbriata* Warth, 1969, from the Gipskeuper (see remarks below) of Baden-Württemberg, and *Menucoestheria bocki* Olempska, 2004, from the Late Carnian of Krasiejów, Upper Silesia, southwestern Poland.

All three species present a small carapace with suboval outlines and an umbo located in the anterior third that projects beyond the short dorsal margin. The number of growth bands is moderate (12–25 according to Kozur and Weems 2010), and they are relatively narrow and fairly uniform in width. The concept of the genus clearly relies on the microsculpture: Kozur and Weems (2010, p. 392) indicate that the outer growth bands carry "often indistinct, short radial lirae; on the inner growth bands there are short radial lirae, fine reticulations or a pitted surface. If the outer layer of the shell is present, then between the radial lirae or within the reticulations a pitted surface can be recognized." In fact, *Gregoriusella fimbriata* has a microsculpture that does not unequivocally show the mentioned reticulation and is devoid of the pits, but strongly resembles the sculpture seen in *G. bocki*, indicating that at least these two species should be placed in the same genus. The large stratigraphic gap betweem *G. fimbriata* and *G. bocki* on the one hand and *G. polonica* on the other could explain the disparity in microsculpture and may be filled in future by as-yet unknown specimens that demonstrate an evolutionary gradient. One species that fits into this gap is described below as *Gregoriusella striatula* sp. nov. and comes from the Tuvalian Coburg Sandstein member of the Hassberge Formation. Its microscupture consists of radial lirae that are aligned slightly subvertical to the growth lines. These striae are often slightly irregular or vary in thickness, as in *G. fimbriata*. They may even develop thickened and almost node-like tips or they may be dumbbell-shaped, (rarely) bifurcated, or show faintly sinuous courses.

It should be noted that the stratigraphic occurrence of *Gregoriusella fimbriata* remains somewhat unsettled. In his original description, Warth (1969, p. 137) indicated that his material came from two localities from the upper part of the Gipskeuper, in dark green or dark gray marls. His holotype was collected at Spitzberg in the county of Tübingen, southern Germany, which points to the Late Cordevolian Estherienschichten of the Grabfeld Formation as the type stratum, and the other figured and correctly identified specimens appear to come from the same stratigraphic level. This is in accordance with the ranges indicated in Warth's text-fig. 2, whereas the upper part of the

Gipskeuper would usually refer to the Early Tuvalian Steigerwald Formation.

Gregoriusella striatula sp. nov.

Figure 9A–F

Derivation of name. Named after the gently striated ornament between the growth lines.

Holotype. SKW ELT-C-04c (Fig. 9A, B), carapace.

Type locality. Hahn Quarry, SE of Eltmann, Franconia, southern Germany.

Type stratum. Coburg Sandstein member, upper part of Hassberge Formation, 0.0–0.3 m above the top of the basal lower "Werkstein" bed; *Laxitextella freybergi* Zone, late Tuvalian.

Paratypes. SKW ELT-C-04d, ELT-C-04g, ELT-C-07b, ELT-C-07c, ELT-C-07d, five valves; SKW ELT-C-04f, slightly distorted bivalved specimen; all topo- and stratotypic.

Diagnosis. Species of *Gregoriusella* with medium-sized carapace, valves subovoid in outline, cyziciform. Dorsal margin short, straight to slightly convex, ventrally projected; anterior end of dorsal margin grades into anterior margin, posterior dorsal corner obtuse. Anterior margin gently curved; anteroventral margin somewhat oblique, gently curved; ventral margin moderately curved; posterior margin with considerably pronounced curvature. Umbo obtuse, in fairly median position, projects somewhat beyond dorsal margin. Free umbonal area small. With more than 30 growth bands in adult individuals: narrow to moderately broad in the median part of the valve; narrow towards the ventral margin; with fine to moderately coarse striae subvertical to growth lines.

Description. Carapace medium-sized, outline of valves subovoid, distinctly cyziciform, up to ca. 2.4–3.4 mm long and up to ca. 2.5 mm high, with a somewhat obliquely directed poorly curved posterodorsal margin. Lateral convexity reaches its maximum a short distance below umbo at about 35–40% of the valve length from anterior margin. Dorsal margin short, more or less straight or weakly curved, length of hinge line ca. 50–55% maximum length of carapace, anterior end of dorsal margin curved and thus without distinct angulation, grades into anterior margin; posterior dorsal corner obtuse with narrow curvature. Anterior margin gently curved or almost straight for a short section; anteroventral margin somewhat oblique, gently curved, ventral margin with relatively modest curvature; posterior margin forms a sinuous curve for most part, but grades posterodorsally into a more weakly curved section.

Umbo obtuse, in fairly median position at ca. 40–45% of the maximum length of the carapace from the anterior end of the valve; it projects slightly beyond dorsal margin. Free umbonal area is small.

Growth bands relatively narrow, more than 30 in adult individuals; relatively evenly spaced in the ventral and median parts of the valves, somewhat more densely packed close to the ventral margin, growth bands in juvenile dorsal parts of valves more closely spaced or invisible; surfaces of growth bands covered with fine to moderately coarse striae or radial lirae subvertical to growth lines, often slightly irregular or varying in thickness and then with almost nodular tips or dumbbell-shaped, rarely bifurcated, or with a faintly sinuous appearance, tightly packed, 50–85 lirae per mm (Fig. 9B).

Dimensions. $L = 3.4$ mm, $H = 2.5$ mm (holotype); L ca. 2.4–3.4 mm, H ca. 2.0–2.5 mm.

Discussion. *Gregoriusella striatula* sp. nov. is mainly characterized by its ornament, consisting of slightly irregular fine to moderately coarse striae or radial lirae subvertical to growth lines. *Gregoriusella fimbriata* (Warth, 1969) is distinguished in that it has more than 20 growth lines and a similar microornament of lirae, which however fray from its main strand and create a fringe-type pattern in the growth bands. Kozur and Weems (2010) emphasized that Warth's (1969, text-fig. 5c) reconstruction of the ornament is partly based on valve fragments that do not belong to the species and that the lirae in *G. fimbriata* are less distinct and less branched. The valves of *Gregoriusella bocki* (Olempska, 2004) have only 14–24 growth bands that are covered with a weak reticulate pattern in the juvenile part of the valve, whereas growth bands on the median and ventral parts of the valves are covered with densely spaced, minute, and somewhat anastomosing radial striae.

The co-occurring *Euestheria kozuri* sp. nov. from the Coburg Sandstone member is distinguished by its slightly elongate, often subrectangulate, or even nearly telliniform shape, a more subacute umbo, generally less than 20 growth bands, and by its ornamentation consisting of slightly irregular polygons. *Euestheria*? sp. nov. A has a fairly distinct outline with a long and roughly subvertical anterior margin of the carapace and a prosopon consisting of small, slightly irregular polygons.

Genus ***Laxitextella*** Kozur, 1982

Type species. *Estheria laxitexta* Sandberger in Jones, 1890 (by original designation).

Emended diagnosis. Carapace of moderately large to large size, shape cycladiform to telliniform; umbo in relatively anterior position, roughly one-third of the maximum valve length from the tip of the anterior margin, barely rises above the dorsal margin or is on the same level as the dorsal margin; larval carapaces small; growth bands regularly to slightly

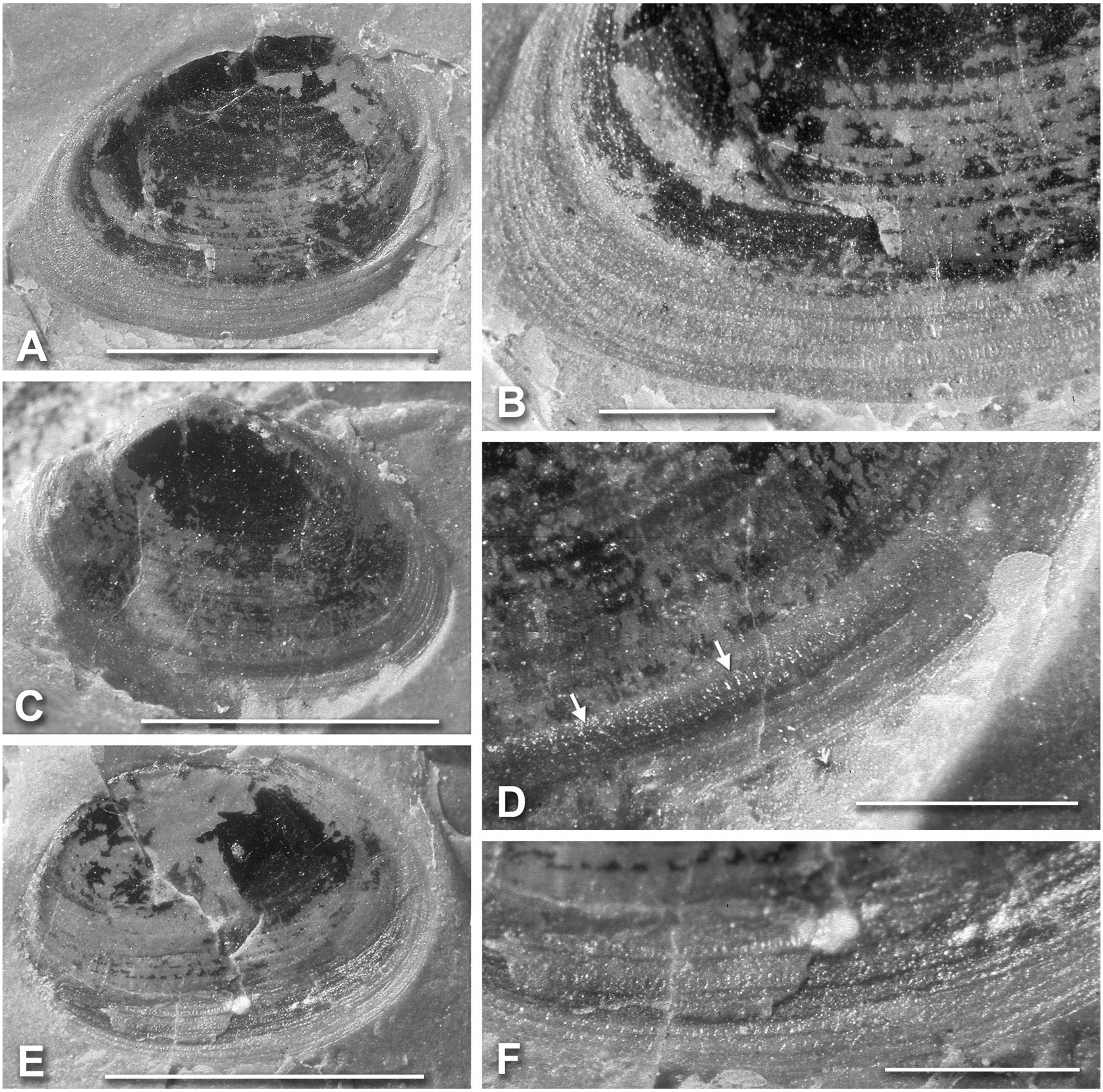


Fig. 9 *Gregoriusella striatula* sp. nov., all specimens from Coburg Sandstone member, Hassberge Formation, Hahn Quarry near Eltmann, Franconia. **A**, **B** ELT-C-04c, holotype, slightly flattened valve, entire specimen and detail of posteroventral portion showing prosopon of fine to moderately coarse radial lirae subvertical to growth lines. **C**, **D** ELT-C-07b, paratype, entire specimen and detail showing rare branched lirae (*arrows*). **E**, **F** ELT-C-04d, paratype, entire specimen and detail showing narrowly spaced growth lines and prosopon with transition of lirae to narrow polygons near ventral margin. *Scale bars* 2 mm in **A**, **C**, **E**; 0.5 mm in **B**, **D**, **F**

irregularly spaced, moderately narrow; ornamentation consists of more or less irregular reticulation.

Discussion. The generic assignment of the Triassic reticulate forms is a difficult problem, and most of the assignments that have been made are in need of revision. Kozur (1982) erected *Laxitextella* to include the Triassic European species *L. laxitexta* (Jones, 1890) (as the type species), *L. ovata* (Lea, 1856), *L. multireticulata* (Reible, 1962), and *L. dorsorecta* (Reible, 1962), as well as an American species, *L. forbesi* (Jones, 1862). According to Kozur (1982), *Laxitextella* is defined as a genus that presents a large or very large carapace with a straight or slightly curved dorsal margin that grades into the anterior and posterior margins; a terminal umbo that does not project above the dorsal margin; a small free umbonal area; and a coarsely reticulate sculpture on the growth bands.

Kozur (1982) obviously mainly had in mind the spinicaudatan genera from the Germanic Basin when discussing their differences from other genera and emphasizing their large size and reticulate ornament. Surprisingly, no attempt has been made since to base the genus on characters that are phylogenetically more robust. Regardless, it is evident that the genus is a useful construction rather than a true clade, and stratigraphic arguments certainly contributed to its present-day concept. In addition, Kozur and Weems (2005) transferred the genus to the newly erected family Shipingiidae Kozur and Weems, 2005, but did not discuss or even mention the systematic placement of the Shipingiidae within a superfamily. As briefly discussed in Cuvellier et al. (2015), the Shipingiidae in Kozur's recent publications furnish spinicaudatans with different fundamental morphologic features.

The closest relatives according to the known morphological characters of *Laxitextella* are genera such as *Gregoriusella*, *Anyuanestheria*, *Menucoestheria*, *Howellisaura*, *Krasiestheria*, *Wannerestheria*, *Shipingia*, and *Loxomegaglypta*.

Gregoriusella Kozur and Weems, 2010 has been introduced for species with a small carapace and an umbo in the anterior third of the valve that slightly projects beyond the short dorsal margin; and with a microsculpture consisting of short radial lirae in the adult parts of the valves, but with short radial lirae, fine reticulations, or a pitted surface on the juvenile parts. Kozur and Weems (2010) included *Gregoriusella polonica* Kozur, Niedźwiedzki, and Sulej in Kozur and Weems, 2010, *Menucoestheria bocki* Olempska, 2004, and *Palaeestheria fimbriata* Warth, 1969 in the genus. The latter is characterized, as emphasized by Warth (1969), by an ornament of lirae that fray from their main thread, thus creating a fringe-type pattern in the growth bands. However, Kozur and Weems (2010) pointed out that the sculpture shown on Warth's plate (1969, pl. 3, figs. 3, 4) in two SEM photographs does not in fact depict the holotype or other specimens of the species but instead shows shell fragments of transitional forms between *Laxitextella* and *Anyuanestheria* with a much more distinct microsculpture. This erroneous concept also led Warth (1969) to identify two specimens identified as *Isaura laxitexta laxitexta* in Reible (1962, pl. 8, figs. 5, 6) as *Palaeestheria fimbriata.* Over the years, the species has been placed in the genera *Palaeestheria*, *Howellisaura*, and *Anyuanestheria*, and is presently believed to be an index fossil for the Late Cordevolian (see Kozur and Weems, 2010).

Anyuanestheria Zhang and Chen, 1976 (in Zhang et al. 1976) (type species *A. subquadrata* Zhang and Chen in Zhang et al., 1976) is characterized by an umbo located in a relatively central position along the dorsal rim of the carapace, and by relatively faint and irregularly developed radial lirae on the outer growth bands and more pronounced reticulation on the inner growth bands. It should be emphasized, however, that distinct differences can be seen between the eight species described from China (see Zhang et al. 1976, pls. 29–31), so several species appear to be in need of revision. In addition, two species from North America have been attributed to *Anyuanestheria*.

Menucoestheria Gallego and Covacevich, 1998 and *Howellisaura* Bock, 1953b show the same developmental trend of a gradual change in ornamentation pattern during ontogeny, starting from a reticulate pattern which can be seen in the dorsal growth bands of the juvenile parts of the valves, and gradually developing a radial striation towards ventral growth bands, as previously emphasized by Olempska (2004). However, Bock (1953a) defined *Howellisaura* as a genus with species that have growth bands ornamented by straight radial striae, anastomosing radial striae, or a reticulate ornament. Thus, the concept was used to include species with quite different prosopons, and species assigned to *Howellisaura* were identified from North America (Bock 1953a), Central Europe, and China (Zhang et al. 1976). In turn, Kobayashi (1954) and Tasch (1969) suggested that *Howellisaura* and *Bairdestheria* Raymond, 1946, are both junior synonyms of *Euestheria* Depéret and Mazeran, 1912, whereas Kozur (1982) regarded *Howellisaura* as a junior synonym of *Bairdestheria* only. By contrast, *Menocoestheria* was regarded as a synonym of *Anyuanestheria* in Kozur and Weems (2007), but at that time the concept of *Anyuanestheria* sensu Kozur and Weems (2007) was actually that of the subsequently introduced genus *Gregoriusella.*

Krasiestheria Olempska, 2004 is a monotypic genus characterized by small valves with subcircular outlines and growth bands covered with a combined ornament of minute punctae in the adumbonal part and radial striae towards the ventralward side of each growth band. Olempska (2004) placed the genus tentatively among the Palaeolimnadiidae, but its systematic position requires additional data to be confirmed.

Furthermore, *Loxomegaglypta* Novojilov, 1958 has a superficial similarly with *Laxitextella*, which has its umbo located close to the anterior end of the dorsal margin (and not about one-third the valve length distant) and shows a distinctly reticulate pattern which is not present in *Loxomegaglypta*.

Wannerestheria Kozur and Weems, 2010 was introduced for a single species, transferred from *Estheria mangaliensis pennsylvanicus* Wanner, 1926, with a medium-sized, subovate to suboblong carapace and the unique character of densely spaced small nodes on the growth lines. A second species, *W. kozuri*, was introduced by

Weems and Lucas (2015) from the Mid-Norian (Alaunian) of Virginia. The genus is otherwise closely related to *Euestheria*, which has a shorter straight part of the dorsal margin.

Shipingia Shen in Zhang et al., 1976 is considered to be characterized by very large carapaces that are distinctly telliniform in shape, with the umbo close to the anterior end of the dorsal margin and often with a certain serial arrangement of the polygons on the growth bands (e.g., *Shipingia olseni*). The genus is regarded as typifying the family Shipingiidae Kozur and Weems, 2005. However, the earliest representative, *S. weemsi*, clearly has smaller carapaces, and is based on material from the Carnian–Norian boundary interval of the Germanic Basin that had been erroneously identified as *Palaeolimnadia schwanbergensis* by Reible (1962).

Laxitextella laxitexta (Sandberger in Jones, 1890)
Figure 11E

pars ? 1854 *Posidonomya minuta* Bronn—Berger: p. 414.
pars ? 1862 *Estheria minuta*, Alberti—Jones: p. 56–57.
1866 Estheria minuta—Gümbel: p. 58.
? 1867 Estheria minuta—Zelger: p. 116.
1868 Estheria—Nies: p. 44–46.
? 1870 Estheria minuta R. Jones—Roemer: p. 174–176, pl. 15, figs. 10, 11.
1871 *Estheria laxitexta*—Sandberger: p. 48 (nomen nudum).
1878 *Estheria laxitexta,* Sandb.—Jones: p. 102.
1888 *Estheria laxitexta* Sdbg.—Thürach: p. 113–114.
*1890 *Estheria laxitexta,* Sandberger—Jones: p. 387–389, pl. XII, fig. 8a, b.
? 1908 *Estheria laxitexta* Sandb.—Zeller: p. 114–115.
non 1910 *Estheria laxitexta* Sandberger—Picard: p. 619–620, pl. 23, fig. 3.
non 1928 *Estheria laxitexta* SANDBERGER—Schmidt: p. 314, fig. 861.
1946 *Euestheria laxitecta* (Jones)—Raymond: p. 242. (type mistake)
1954 Euestheria laxitecta (Sandberger)—Kobayashi: p. 54, 98.
v 1962 *Isaura laxitexta laxitexta* (Jones 1890)—Reible: p. 210–212, text-fig. 15, pl. 8, figs. 3, 4, 6 (pars).
non v 1962 *Isaura laxitexta laxitexta* (Jones 1890)—Reible: pl. 8, figs. 5, 6 (pars).
non 1963 *Estheria laxitexta* (Jones, 1878)—Defretin-Lefranc: pl. I, figs. 8, 9.
non 1963 *Estheria laxitexta* (Jones, 1878)—Defretin-Lefranc: pl. I, figs. 10, 11.
1969 *Palaeestheria laxitexta* (Jones 1890)—Warth: p. 137–138, pl. 3, fig. 5, text-fig. 7.
? 1974 *Palaeestheria laxitexta* (Jones)—Sieber: p. A126.
non 1974 *Euestheria*? *laxitexta* (Jones)—Chen in Nanjing Institute: p. 318–320, pl. 100, fig. 1.
non 1975 *Estheria laxitexta* (Jones, 1878)—Guérin-Franiatte et al.: p. 213, 214, 216.
1982 *Laxitextella laxitexta* (Sandberger, 1871)—Kozur: p. 378, 379.
2004 *Laxitextella laxitexta* (Jones, 1890)—Olempska: p. 435–436, figs. 5 A, 7 A–D, tab. 1.
2007 *Laxitextella laxitexta*—Kozur and Weems: text-fig. 10.
2010 *Laxitextella laxitexta*—Kozur and Weems: p. 333, 381, 382, 393, text-fig. 17.
2014 *Laxitextella laxitexta*—Ogg et al.: text-fig. 4.
2015 *Laxitextella laxitexta*—Ogg: text-fig. 3.
2015 *Laxitextella laxitexta*—Zhang et al.: text-fig. A.2.
2015 *Laxitextella laxitexta*—Hagdorn: p. 135.
pars 2015 *Laxitextella laxitexta* (Jones, 1878) emend. Kozur, 1982—Cuvellier et al.: p. 126, text-fig. 2.
2015 *Laxitextella laxitexta*—Lucas: text-fig. 3.

Material. 6 valves; in repository: GIW S 29. All specimens from Bodenmühle section near Bayreuth, Franconia, Obere Bunte Estherienschichten, upper part of Grabfeld Formation, late Cordevolian.

Discussion. *Laxitextella laxitexta* has been chosen as the type species of *Laxitexta*, making it one of the most important genera in the later Triassic, but this poses a number of problems with respect to taxonomy, morphology, phylogeny, and nomenclature.

Laxitextella laxitexta has a bizarre nomenclatural history. The name of the species was first mentioned by Sandberger (1871) in a manner that suggested that the species had already been described by Rupert Jones, which in fact was not the case. Jones did indeed discuss the species, but not before his monograph (Jones 1890), and he referred the species to Sandberger, although he mentioned that the species had not been described and figured before. In addition, Jones (1890, p. 388) referred to written correspondence of Sandberger, who explained why he considered the species to be new. However, Jones also emphasized that he regarded the material provided by Sandberger as representing the well-known *Estheria minuta*, and thus Sandberger's *E. laxitexta* to be a junior synonym of *E. minuta*. Therefore, Jones cannot be credited for introducing the species. Rather, the species must be cited as *Estheria laxitexta* Sandberger in Jones, 1890. The type material briefly described and figured in Jones (1890) came from the upper part of the Grabfeld Formation (Estherienschichten) of Bad Windsheim, Middle Franconia (erroneously cited as Lower Keuper and misspelled as "*laxitecta*" in Raymond 1946). However, two years earlier, Thürach (1888) had published his monographic report on the Keuper beds in northern Franconia and referred to

"*Estheria laxitexta* Sdbg." in a way that suggested that he had a firm knowledge of its morphology. On the other hand, he also referred to specimens from the Bodenmühle section near Bayreuth, clearly believing that these strata (uppermost part of the Estherienschichten) were the source of Sandberger's (1871) material. Nevertheless, Thürach also wrote that he (provisionally?) regarded all spinicaudatans from the Middle Keuper as belonging to *E. laxitexta*. Specimens from the Bodenmühle section had been collected by Gümbel (1866) and were subsequently regarded as a new species by Nies (1868).

An *Estheria laxitexta* specimen mentioned by Zeller (1908) refers to the Steigerwald Formation (Lehrbergschichten), Picard's (1910) material from the Middle Buntsandstein (Olenekian).

The species was revived by Reible (1962) who distinguished two subspecies of *Isaura laxitexta*, *I. l. laxitexta* and *I. l. multireticulata* Reible, 1962, which are now regarded as separate species. Reible (1962) selected a neotype for *I. l. laxitexta*, which comes from the middle part of the Estherienschichten (upper part of the Grabfeld Formation) from the western tip of the Schwanberg (Horn locality) near Iphofen, Middle Franconia. Reible's selection is very unfortunate because the neotype (Reible 1962, pl. 8 figure 3) is a fairly poorly preserved specimen that does not exhibit details of the umbo and the hinge line. Another specimen from the same outcrop and the same slab figured by Reible (1962, pl. 8 figure 5) shows a distinct prosopon of fine radial lirae and obviously represents a different species that is closely related to *Gregoriusella fimbriata* (Warth, 1969), as already suggested by Kozur and Weems (2007). The two other specimens figured by Reible come from the upper part of the Estherienschichten in the Bodenmühle section close to Bayreuth. Reible's specimen on pl. 8 figure 4 nicely illustrates the typical reticulate prosopon with large polygons, but is an incomplete valve. Reible's "specimen" on pl. 8 figure 6 is in fact two valves with one lying above the other, and exfoliated regions of the upper valve ornamented with lirae allow us to discern details of the underlying valve, which exhibits a typical reticulate ornament. This misled Reible (1962) to suggest a "double ornament" with both polygons and lirae. A feature that may argue in favor of a double ornament is seen in a few specimens of *Laxitextella freybergi* sp. nov. (e.g., Figs. 10C, 11F), where a prosopon of small polygons grades into delicate lirae. It should be emphasized, however, that the lirae are particularly developed towards the anterior and posterior ends, show a staggered arrangement of small crests, and are underlain by a persisting reticulate pattern, meaning that they are completely different from the fimbriate patterns shown by Reible (1962, pl. 8, figs. 5, 6). The two specimens were interpreted by Warth (1969) as representing his species *Palaeestheria fimbriata* (now *Gregoriusella f.*), but Warth misinterpreted valve fragments with a similar sculpture to his material as representing *G. fimbriata*.

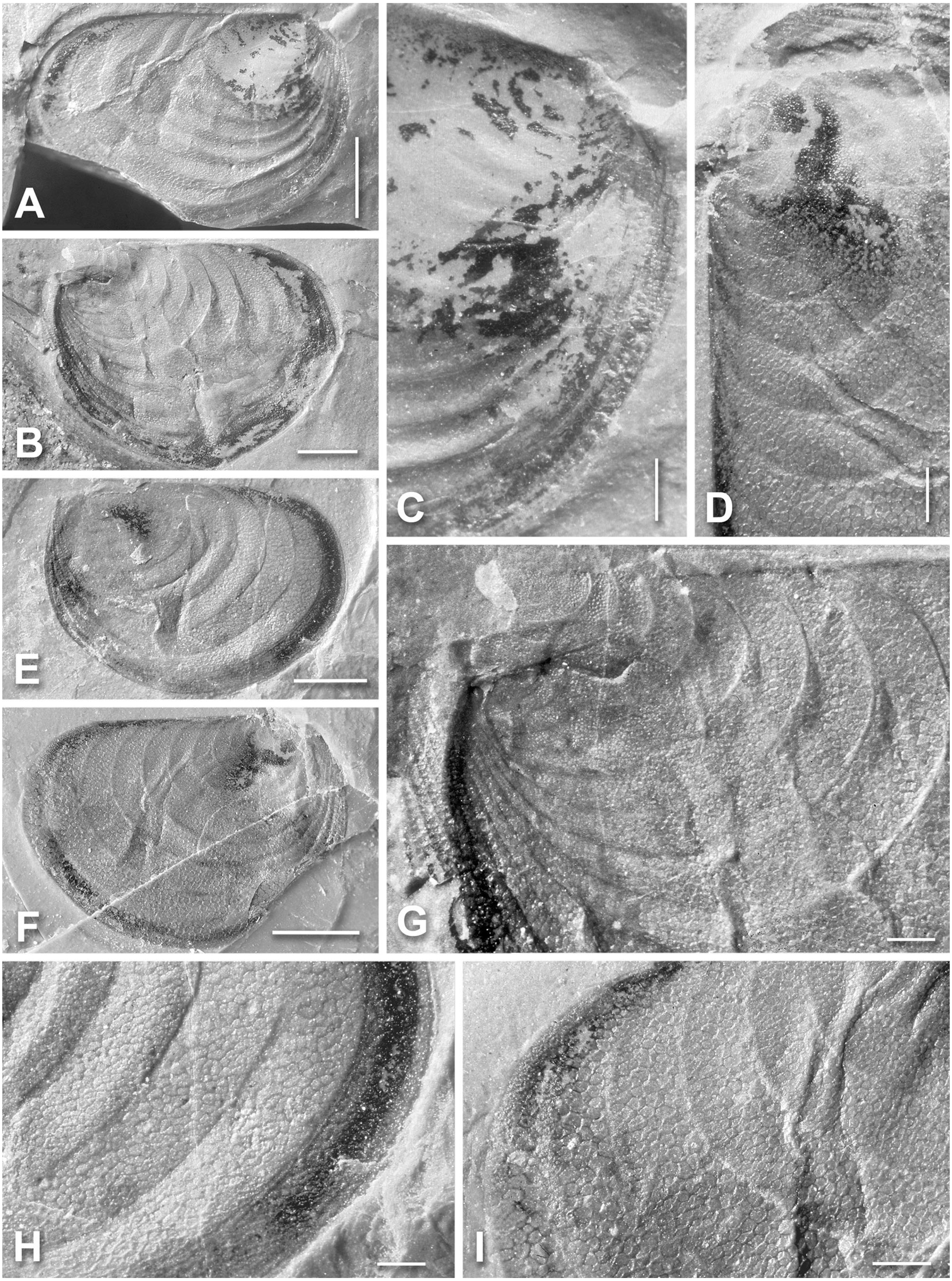
Reible's (1962) neotype appears to have polygons, so this type of ornamentation is regarded as typical of *Laxitextella laxitexta*. A nicely preserved valve from the Bodenmühle section with a superbly preserved prosopon is figured herein (Fig. 11E). It should be emphasized that this typical prosopon consists of large polygons which are largest around the central portion of the growth bands and diminish in diameter toward the growth lines—a feature that has not been noted to date.

In addition, Reible's (1962, text-fig. 15) reconstruction of the shape of the carapace is incorrect and shows a valve with a curved dorsal margin and a near-terminal position of the umbo. In fact, the valves of *Laxitextella laxitexta* typically have a subovoid, roughly cyziciform shape with a relatively long dorsal margin and the apex occurring ca. 30% of the maximum valve length posterior to the anterior margin. Thus, rather than having a very similar shape as suggested by Reible (1962), *Laxitextella laxitexta* is clearly differentiated from *Euestheria ovata* (Lea, 1856).

Occurrence. Reible (1962) mentioned that *Laxitextella laxitexta* ranges from the upper part of the Grabfeld Formation (Estherienschichten) up into the "Heldburger Stufe," which (at that time) he probably believed was directly below the Coburg Sandstone. This range would have been considerably wider than presently accepted. However, Reible (1962) did not provide any data for material studied by him from strata above the Estherienschichten so that this assumption may be based on data of other authors cited in his synonymy list.

The occurrence of *Laxitextella laxitexta* in Poland is based on the frequent occurrence in an unnamed lithostratigraphic unit of Carnian age at Krasiejów in Upper Silesia (Olempska 2004).

Assumptions that the material described and illustrated as *Estheria minuta* by Roemer (1870, pl. 15, fig. 10) in fact represents, or may represent, *Laxitextella laxitexta* are not supported by robust data. The material came from the Hellewalder Estherien-Schichten of Paulsdorf (now Pawłowice Gorzowskie) near Landsberg (now Gorzów Śląski) in Upper Silesia, which—despite uncertainty regarding their stratigraphic position—undoubtedly represent strata that are clearly younger than Carnian or earliest Norian. Neither the descriptions nor the figure provide valuable information suggesting that the specimens do indeed belong to *L. laxitexta*; indeed, the shapes visible in the figure actually indicate that the material does not belong to the species. The material has never been restudied to our knowledge, although Olempska (2004) suggested that the specimens represent a new species.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◀**Fig. 10** *Laxitextella freybergi* Kelber and Kozur in Kozur and Weems, 2007; all specimens from Coburg Sandstone member, Hassberge Formation, Hahn Quarry near Eltmann, Franconia. **A**, **c** ELT-C-04a, paratype, incomplete valve; **A** entire specimen; **C** detail showing prosopon of slightly irregular polygons on subcentral parts of the valve and a wrinkled appearance due to compactional distortion near anterior margin (*right*). **B**, **G** ELT-C-04b, paratype, incomplete valve; **B** entire specimen; **G** detail showing prosopon with polygons growing in size from anterior toward posterior within the same growth bands. **D**, **F**, **I** ELT-C-01, paratype, incomplete valve; **D** detail showing prosopon with larger adumbonal polygons grading into smaller but slightly more regular polygons at abumbonal parts of the growth bands; **F** entire specimen; **I** detail showing accretional pattern of growth lines at posterior corner of dorsal margin and changing size of polygons. **E**, **H** ELT-C-02, holotype, valve with slight folds resulting from compaction; **E** entire specimen; **H** detail showing irregular pattern and outlines of polygons. *Scale bars* 2 mm in **A**, **B**, **E**, **F**; 0.5 mm in **C**, **D**, **G–I**

Laxitextella freybergi Kelber and Kozur in Kozur and Weems, 2007
Figures 10A–I, 11A, B, F

v 2004 *Laxitextella* of the *L. laxitexta* group—Bachmann and Kozur: p. 49, 50.
v * 2007 *Laxitextella freybergi* Kelber and Kozur n. sp.—Kozur and Weems: p. 151, 155, 165, 172, text-fig. 10, pl. 10, fig. 1a, b.
2008 *Laxitextella freybergi* n. sp.—Franz: p. 114.
2010 *Laxitextella freybergi*—Kozur and Weems: p. 318, 338, 344, 355, 383, 384, 385, 386, text-fig. 17, table 1.
2010 *Laxitextella freybergi* Kozur—Kozur and Weems: p. 344.
2010 *Laxitextella freybergi* Kelber and Kozur—Kozur and Weems: p. 359, 383, 384, 385, 386.
2010 *Laxitextella freybergi* Kelber and Kozur—Kozur and Bachmann: p. 109.
2011 *Laxitextella freybergi* n. sp.—Olsen et al.: p. 216.
2012 *Laxitextella freybergi*—Ogg: fig. 25.7.
2012 *Laxitextella freybergi*—Lucas et al.: p. 7, 9.
2013 *Laxitextella freybergi*—Desojo et al.: p. 213.
2013 *Laxitextella freybergi*—Kozur et al.: p. 325, 326, 327, 329.
2014 *Laxitextella freybergi*—Ogg et al.: text-fig. 4.
2015 *Laxitextella freybergi*—Ogg: text-fig. 3.
2015 *Laxitextella freybergi*—Zhang et al.: text-fig. A.2.
2015 *Laxitextella freybergeri*—Lucas: text-fig. 3. (spelling mistake)

Holotype. SKW ELT-C-02 (Fig. 10E, H). The specimen has been figured in Kozur and Weems (2007, pl. 10, fig. 1a, b), but the authors omitted a collection number and the location of the repository.

Type locality. Hahn Quarry, SE of Eltmann, Franconia, southern Germany.

Type stratum. Coburg Sandstein member, upper part of Hassberge Formation, 0.0–0.3 m above the top of the basal lower "Werkstein" bed; *Laxitextella freybergi* Zone, late Tuvalian.

Material. Ca. 10 specimens, all from the Kelber Collection, Würzburg. Registered paratypes: SKW ELT-C-01, ELT-04a, ELT-04b, ELT-C-07a, all from Hahn Quarry, SE of Eltmann, Franconia.

Occurrence. All known material from Coburg Sandstein member, upper part of Hassberge Formation, southern Germany.

Emended diagnosis (modified from Kozur and Weems 2007). Species of *Laxitextella* with relatively large carapace, telliniform in shape; dorsal margin more or less straight, without dorsal corners. Anterior margin with relatively modest gentle curvature; anteroventral margin somewhat oblique; ventral margin with considerable curvature; posterior margin moderately curved. Umbo in anterodorsal position, barely projects beyond dorsal margin. Free umbonal area small. Growth bands sparse, up to ca. 14, broad, with coarse reticulation consisting of 6–10 polygons between growth lines. Polygons with irregular outline (pentagonal, hexagonal, polygonal, subelliptical, or elongated or irregularly oval).

Description. Carapace of moderate to large size, varying in outline from elongate ovoidal to ovoidal, of stout telliniform shape, up to ca. 8.5 mm long and up to nearly 6 mm high. Lateral convexity reaches its maximum a short distance posterior and below the umbo in the anterior third of the valve. Dorsal margin more or less straight, length of hinge line ca. 65% the maximum length of the carapace, without recognizable dorsal corners or angulations. Anterior margin with considerable curvature/broadly rounded; posterior margin moderately curved; ventral margin with moderate curvature.

Free umbonal area small. Umbo situated ca. 17–19% of maximum length of valve from anterior end of dorsal margin, directed anteriorly, projecting barely or only a minimum distance above the dorsal margin.

Growth bands relatively few in number, 9–14 in the studied specimens, broadly spaced, but ventral growth bands more closely spaced in large specimens; surfaces of growth bands covered with coarse reticulation. Large specimens have 6–8 meshes or polygons between the growth lines in the median part of the valve, 6–9 polygons in the midventral part of the carapace, and 7–12 polygons in the growth bands of the juvenile part of the carapace (Fig. 10D, H). Polygons irregular in outline and of pentagonal, hexagonal, polygonal, subelliptical, or elongated or irregularly oval outline, growing slightly in size from anterior toward posterior within the same growth band (Fig. 10G). In general, polygons at adumbonal parts of the growth bands are slightly larger and vary more in size than

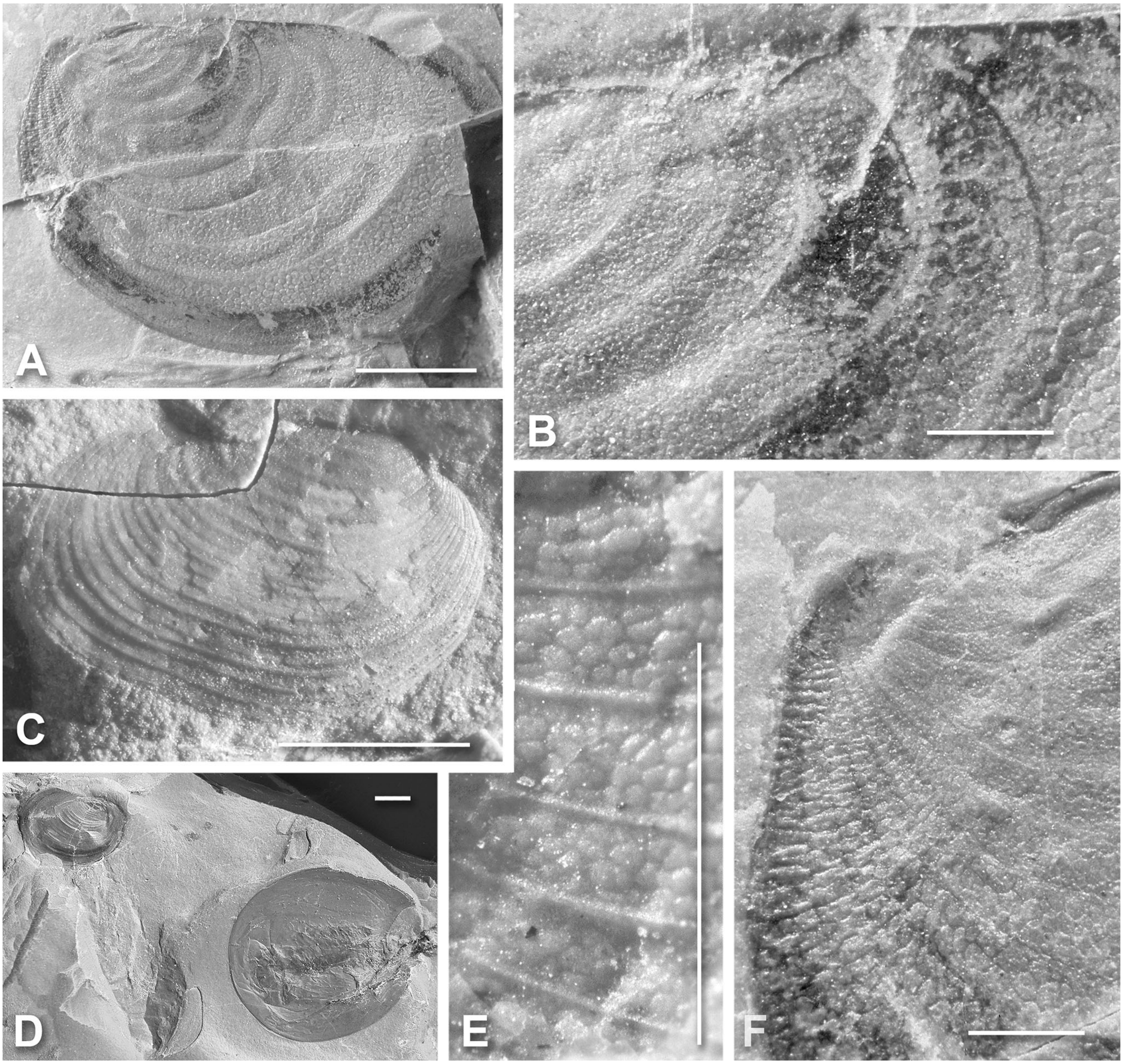

Fig. 11 **A**, **B**, **F** *Laxitextella freybergi* Kelber and Kozur in Kozur and Weems, 2007, ELT-C-07a, entire specimen (**A**), detail of posterior umbonal region (**B**), and magnification of anterior margin and subumbonal region showing considerable polygon shape transition (**F**); from Coburg Sandstone member, Hassberge Formation; Hahn Quarry near Eltmann, Franconia. **C** GIW R 1 I_4, *Laxitextella multireticulata* (Reible, 1962), carapace, internal mold; on the same slab as the holotype and paratype of Reible (1962, pl. 8, figs. 7, 8); from Acrodus bed, Grabfeld Formation, Schwanberg near Iphofen, Franconia. **D** *Triops* sp., ELT-C-08a, incomplete carapaces, together with *Euestheria kozuri* sp. nov.; from Hahn Quarry near Eltmann, Franconia. **E** GIW S 29, *Laxitextella laxitexta* (Sandberger in Jones, 1890), detail of valve fragment, external mold, showing typical ornamentation with large polygons tending to diminish in size toward the growth lines; probably topo- and stratotypic with type material used by Sandberger; from Estherienschichten, upper part of Grabfeld Formation, Bodenmühle section near Bayreuth, Franconia. *Scale bars* 2 mm in **A**, **C**, **D**; 0.5 mm in **B**, **E**, **F**

those in the abumbonal parts of the growth bands (Fig. 10D), but specimens with subequal polygons exist as well.

Dimensions. Length of holotype carapace 7.9 mm, height of holotype carapace 5.5 mm; length 6.7–8.6 mm; height = 4.7–5.9 mm.

Discussion. *Laxitextella freybergi* Kelber and Kozur in Kozur and Weems, 2007 is the youngest known species from what Kozur identified as the *Laxitexella laxitexta* group. However, as already mentioned in Kozur and Weems (2007), the species can also be interpreted as transitional in morphology between *Laxitextella* and *Shipingia*. It is obvious that *Shipingia* evolved from *Laxitextella*, as indicated by the modification of the ornamentation on the growth bands: early species of *Laxitextella* are characterized by a reticulated pattern consisting of small and often imperfectly developed polygons (characteristic of the species of the *Laxitextella dorsorecta* group), whereas the younger species of the *Laxitexella laxitexta* group have distinctly developed larger polygons. *Laxitextella freybergi* differs from the slightly older species of the *L. laxitexta* group, such as *L. laxitexta* (Sandberger in Jones, 1890) and *L. seegisi* Kozur in Kozur and Weems, 2007, in having more and therefore narrower growth bands and exhibiting slightly more plasticity in mesh shape. In addition, *L. freybergi* has a low umbo, similar to that in *L. seegisi*, but it clearly projects less than in *L. laxitexta*. In addition, *L. seegisi* has an ornamentation consisting of relatively conspicuous subelliptical to oval polygons with somewhat larger polygons that appear to be concentrated in the adumbonal half of the growth lines.

All carapaces show very similar outlines, so there is no obvious sexual dimorphism for *Laxitextella freybergi*.

Laxitextella freybergi presents most of the characters seen in *Shipingia* and may have been placed under the latter genus, as suggested for other species originally assigned to *Laxitextella*. Species of *Shipingia*, however, are characterized by large to very large carapaces that are distinctly telliniform in shape, with the umbo close to the anterior end of the dorsal margin, and we thus concur with Kozur and Weems' (2007) generic assignment.

Laxitextella multireticulata (Reible, 1962)
Figure 11C

? 1867 Estheria minuta Goldf. sp.—Zelger: p. 115.
? 1868 Estheria—Nies: p. 44.
v * 1962 *Isaura laxitexta multireticulata* n. subsp.—Reible: p. 212–213, text-fig. 17, pl. 9, fig. 3.
1969 *Palaeestheria multireticulata* (Reible)—Warth: p. 138, text-fig. 7.
? 1974 *Palaeestheria multireticulata* (Reible)—Sieber: p. A126.
1993 *Laxitextella multireticulata* (Reible)—Kozur and Mock: p. 265.
2004 *Laxitextella multireticulata* (Reible)—Bachmann and Kozur: p. 28, 50.
2006 *Laxitextella multireticulata* (Reible)—Gallois and Porter: p. 181.
2007 *Laxitextella multireticulata* (Reible, 1962)—Kozur and Weems: p. 138, 143, 147, 151, 152, 160, 164, text-fig. 10, pl. 1, figs. 3, 6, pl. 2, figs. 1–5, pl. 3, fig. 1.
2008 *Laxitextella multireticulata* (Reible)—Porter and Gallois: p. 395.
2010 *Laxitextella multireticulata* (Reible)—Kozur and Weems: p. 333, 341, 379, 380, 381, text-fig. 17, table 1.
2010 *Laxitextella multireticulata* (Reible)—Kozur and Bachmann: p. 108, text-fig. 1.
2014 *Laxitextella multireticulata*—Ogg et al.: text-fig. 4.
2015 *Laxitextella multireticulata*—Ogg: text-fig. 3.
2015 *Laxitextella multireticulata*—Zhang et al.: text-fig. A.2.
2015 *Laxitextella multireticulata*—Lucas: text-fig. 3.

Discussion. According to Reible's (1962) notes, his holotype came from the *Acrodus* bed in the middle part of the Grabfeld Formation from the foothills of the Schwanberg near Iphofen, Middle Franconia. The lithology of the sample instead points to the *Corbula* bed, slightly above the *Acrodus* bed, but both can be seen to represent the same age—earliest Cordevolian, at the turn from Ladinian to Carnian. The species is thus the oldest known species of *Laxitextella*.

Laxitextella multireticulata is characterized by a cyziciform to slightly telliniform, faintly subrectangular carapace with a prosopon consisting of very small polygons, which are sometimes arranged in a linear pattern (Kozur and Weems 2007, pl. 1, figs. 3, 4). Kozur and Weems (2007) illustrated "advanced forms" from the basins of the eastern United States with different outlines of the valves and different sizes of the polygons in different parts of the valves, reminiscent of the reticulation seen in the stratigraphically higher *L. laxitexta*. It is still somewhat unclear how those forms should be characterized taxonomically.

Occurrence. Known with certainty from the lower part of the Estherienschichten ("Untere Bunte Estherienschichten") of the upper Grabfeld Formation of the Germanic Basin (early Cordevolian) (Reible 1962) and the Dunscombe Mudstone of western England (Cordevolian) (Gallois and Porter 2006); also reported from the western part of the Southern Alps (early Cordevolian) (Kozur and Mock 1993); reports from the Briery Creek Basin (early Cordevolian), the Falling Creek Formation in the Taylorsville Basin (early Cordevolian), and an unnamed unit below the New Oxford Formation in the Gettysburg Basin (early Cordevolian) (see Kozur and Weems 2007, 2010) are in need of careful reinvestigation.

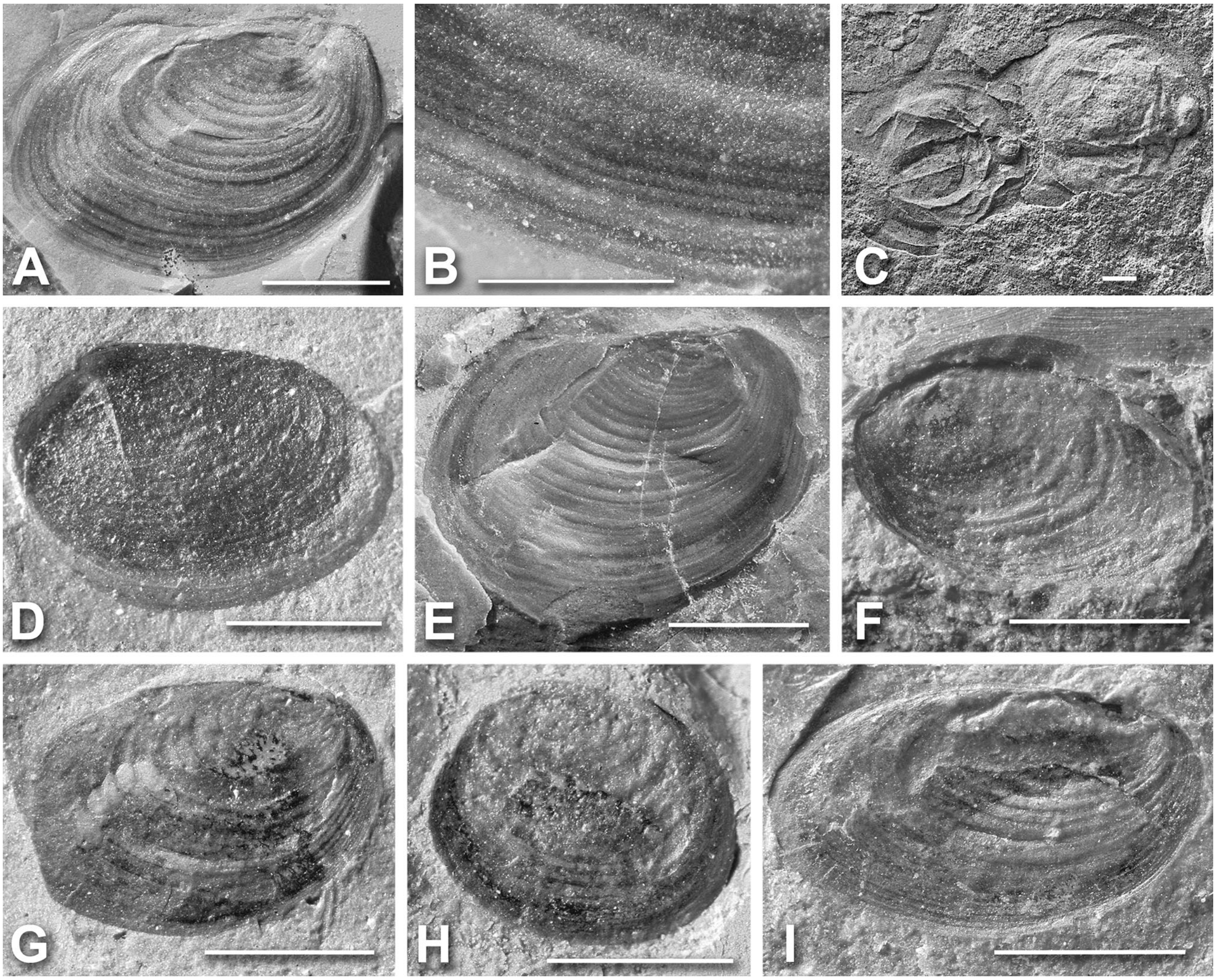

Fig. 12 **A**, **B** *Laxitextella dorsorecta* (Reible, 1962). **A**, **B** ELT-C-09, valve affected by compaction; **A** entire specimen; **B** detail showing densely spaced growth lines near anterior margin (*bottom*) and ornament of fine to minute polygons. **C** *Triops* sp., PASS-220; two head shields with typical wrinkles caused by dorsoventral compaction. **D–I** *Laxitextella*? sp. A, **D** ELT-C-05, carapace of two slightly dislocated valves leading to a seemingly short dorsal margin. **E** ELT-C-08a, single valve with cracks and folds resulting from compaction. **F** ELT-C-10a, bivalved carapace. **G** ELT-C-06a, lengthened and probably bivalved carapace. **H** ELT-C-06e, bivalved carapace. **I** ELT-C-06c, probably bivalved carapace, considerably lengthened during compaction/diagenesis. All specimens from Coburg Sandstone member, Hassberge Formation, Hahn Quarry, SE of Eltmann, Franconia. *Scale bars* 2 mm

Laxitextella dorsorecta (Reible, 1962)
Figure 12A, B

v *1962 *Isaura dorsorecta* n. sp.—Reible: p. 213–214, pl. 9, figs. 1, 2, text-fig. 16.

non 1983 *Palaeestheria dorsorecta* (Reible)—Seegis: p. 22, text-fig. 6.

1997 *Laxitextella dorsorecta* (Reible)—Seegis: p. 132.

2003 *Shipingia dorsorecta* (Reible)—Channell et al.: p. 95, 96.

2004 *Shipingia dorsorecta* (Reible, 1962)—Olempska: p. 435, 438, text-fig. 4.

2005 *Laxitextella dorsorecta*—Etzold and Franz: p. 17.

2007 *Laxitextella dorsorecta* (Reible, 1962) emend.—Kozur and Weems: p. 155, 172.

2010 *Laxitextella dorsorecta*—Kozur and Weems: p. 353, 383, 384.

2012 *Laxitextella dorsorecta* (Reible)—Lucas et al.: p. 7.

Holotype. Collection of the Geowissenschaftliches Zentrum, Göttingen University, GZG.INV 823-13A (old number 60; selected by Reible 1962).

Type locality. From Gänseheide locality near Stuttgart.

Type stratum. Mainhardt Formation ("Obere Bunte Mergel"), late Lacian (but see remarks below under *Discussion*).

Material. One unequivocally determinable valve, SKW ELT-C-09, three additional valves tentatively assigned to the species. All from Hahn Quarry, SE of Eltmann, Franconia, southern Germany; Coburg Sandstein member, upper part of Hassberge Formation, 0.0–0.3 m above the top of the basal lower "Werkstein" bed; *Laxitextella freybergi* Zone, late Tuvalian.

Emended diagnosis. Species of *Laxitextella* with medium-sized carapace, valves elongated cyziciform to stoutly telliniform in outline. Dorsal margin long, straight; anterior and posterior dorsal corner obtuse to subangular. Anterior margin gently curved; anteroventral margin gently to distinctly curved; ventral margin with moderate curvature; posterior margin with considerably pronounced curvature. Umbo obtuse, in relatively anterior position, situated at about the dorsal margin in lateral view. Free umbonal area small. With about 25–30 growth bands in adult individuals, moderately broad in the median part of the valve, narrower towards the ventral margin; ornament consists of fine, irregular polygons.

Description. Carapace medium-sized, outline of valves subovoid, elongated cyziciform to stoutly telliniform, up to ca. 6.5 mm long and up to ca. 5 mm high. Maximum lateral convexity located probably a short distance below and slightly posterior to umbo, at about 35–40% of valve length from anterior margin. Dorsal margin long, more or less straight, length of hinge line two-thirds maximum length of carapace, anterior dorsal corner recognizable as narrowly curved subangular point relatively close to anterior of valve, posterior dorsal corner obtuse, curved. Anterior margin gently curved; anteroventral margin somewhat oblique, gently to distinctly curved; ventral margin with moderate curvature; posterior margin sinuously curved in lateral view similar to the tip of an egg for the most part, but grades into a poorly curved posterodorsal section.

Umbo obtuse, in relatively anterior position about 25% of valve length from anterior tip of carapace, situated at about the dorsal margin or faintly projecting beyond it in lateral view. Free umbonal area small.

Growth bands relatively narrow to moderate in width, distinctly varying; about 25–30 growth bands present in typical adult specimens (Fig. 12B); moderately broad and subevenly spaced in the median part of the valve, with 6–11 polygons between growth lines; narrower and irregularly packed towards the ventral margin, with 4–7 polygons between growth lines; growth bands in juvenile dorsal part of valve relatively broad, similar in width to those in the median part, with 5–9 polygons, indications in some places of weak subdivision of growth bands by faint oblique lines (possibly a taphonomic effect). Surfacea of growth bands covered with small to minute polygons that vary in outline from pentagonal to subhexagonal, polygonal, subelliptical, or irregularly oval; size of polygons varies considerable even between adjacent meshes, from ca. 6 μm to nearly 30 μm in maximum diameter.

Discussion. *Laxitextella dorsorecta* (Reible, 1962) is best characterized by a long and nearly straight dorsal margin; a relatively strongly curved anterior margin; a moderately large number of growth lines; and a prosopon of small, densely spaced polygons.

It is surprising that Reible (1962) characterized the species by emphasizing the relatively low number of growth lines ("15–18 clear growth lines," Reible 1962, p. 213), whereas the holotype chosen by him has at least 22 growth lines plus those not preserved in the juvenile part of the valve. The topo- and stratotypic paratype chosen by Reible (GZG.INV 823-13C) has at least 25 growth lines which are difficult to count due to the poor preservation (see http://www.terra-triassica.de/museum-terra-triassica/sammlung-und-werkstatt/makrofossilien/arthropoda-siebold-stannius-1845/crustacea-pennant-1777/conchostrace-sars-1867/12406-2/). Seegis (1997) and H. Mahler and J. Sell (unpubl. data at the cited internet site) emphasize that the holotype is damaged along the dorsal and ventral margins so that the eponymous long dorsal margin is not visible. In addition, they also state that the paratype shows that the dorsal margin is short rather than long and gently curved. The provided illustrations, however, are unable to unequivocally clarify the problem. The paratype seems to be even more incompletely preserved, and the holotype rather incompletely prepared from the matrix. In any case, the courses and arrangement of the growth lines clearly suggest a nearly straight and fairly long dorsal margin similar to the specimen from the Coburg Sandstone member figured herein.

Occurrence and stratigraphic range. Kozur and Weems (2007, p. 155) regarded *Laxitextella dorsorecta* as a "transitional form between *Laxitextella* and *Shipingia*." However, they did not describe which morphological characters were seen as indicators of this transition. The notion appears to have been more strongly motivated by the relatively late occurrence of the species compared with all other species of the genus.

The Obere Bunte Mergel ("Upper Variegated Marls") from which the type material is described according to Reible (1962) is now known as the Mainhardt Formation and probably of uppermost/latest Carnian or uppermost/latest Carnian–lowermost/earliest Norian in age. Reible (1962) also mentioned determining the species from the (apparently lower part of the) Stubensandstein at Blindheim near Schwäbisch-Hall, Baden-Württemberg, but omitted any details or figures. This horizon probably dates to the Lower to Middle Norian. An additional report of *L. dorsorecta* from the Stubensandstein is mentioned by

Etzold and Franz (2005). Seegis (1997) emphasized that the rock fragments that bear the type material of Reible (1962) show lithologic criteria typical of the uppermost strata of the Kieselsandstein (Coburg Sandstone member) rather than of the "Obere Bunte Mergel."

The specimen figured herein is the first reported from the Coburg Sandstone member in a publication.

***Laxitextella*? sp. A**
Figure 12D–I

v ? 1962 *Isaura hausmanni* (Schmidt 1938). Reible, p. 214–215, fig. 17, pl. 9, fig. 3.

Material. Ca. 15 specimens; registered specimens: SKW ELT-C-06a (single valve), SKW ELT-C-06b (single valve), SKW ELT-C-06c (bivalved carapace), SKW ELT-C-06d (single valve), SKW ELT-C-06e (single valve), SKW ELT-C-06f (single valve tentatively assigned to *Laxitextella*? sp. A), SKW ELT-C-06g (partial valve), SKW ELT-C-06h (partial valve), SKW ELT-C-06i (partial valve), ELT-C-10 (bivalved carapace), ELT-C-11 (bivalved carapace tentatively assigned to *Laxitextella*? sp. A).

Occurrences. All specimens from Hahn Quarry, SE of Eltmann, Franconia, southern Germany; Coburg Sandstein member, upper part of Hassberge Formation, 0.0–0.3 m above the top of the basal lower "Werkstein" bed; *Laxitextella freybergi* Zone, late Tuvalian.

Description. Carapace of moderate to large size, varying in outline from cyziciform to stout telliniform shape, up to nearly 5.5 mm long and up to ca. 4.2 mm high. Lateral convexity reaches its maximum a short distance posterior and below the umbo. Dorsal margin apparently faintly curved, length of hinge line ca. 55% the maximum length of the carapace, without distinct dorsal corners. Anterior margin considerably and nearly evenly curved; ventral margin with gentle to moderate curvature; posterior margin moderately curved, with maximum curvature below half the valve height.

Umbo obtuse, in mid-anterior position about 35% of the valve length from anterior tip of carapace, situated at about the dorsal margin or faintly projecting beyond it in lateral view. Free umbonal area small.

Growth bands up to 23 in number (usually 18–21), moderately wide and subevenly spaced in the median and most of the juvenile parts of the valve, slightly more narrowly packed towards the ventral margin, change in the width appears to be gradual; growth bands in median parts sometimes with faint intraband growth lines. Surfaces of growth bands covered with fine to minute polygons that vary in outline and size, with more than 10 polygons between growth lines in the median part of the valve.

Dimensions. Length 3.6–5.4 mm; height = 3.5–4.2 mm.

Discussion. The described specimens most probably represent another species found in the Coburg Sandstone member, best characterized by a somewhat more ovoidal outline with the umbo roughly one-third of the valve length from the anterior margin; a moderate number of growth lines that indicate a tendency for distinctly narrower growth bands near the ventral margin; and a prosopon of minute polygons. The available material is limited and slightly distorted so that the preservation is regarded as insufficient to base a new species on it.

Laxitextella? sp. A is clearly not an intraspecific variety of *Laxitextella freybergi*, *L. dorsorecta*, or any other species described from the Coburg Sandstone member or stratigraphically adjacent beds, and it is definitely not a sexual dimorph of these species.

The species shows characters that would be regarded as typical for *Laxitextella*? *hausmanni* (Schmidt, 1938), but we regard this species as ill-defined (see discussion below). In turn, the neotype for *Isaura hausmanni* chosen by Reible (1962, pl. 9, fig. 3) from the Coburg Sandstone member of Weißenbrunn am Forst is regarded here as probably belonging to the species represented by *Laxitextella*? sp. A.

Laxitextella? sp. A is clearly distinguished from the co-occurring *Laxitextella freybergi* Kelber and Kozur, 2007 by the valve shape, the more closely spaced growth lines towards the ventral margin, and a prosopon of minute polygons. It is distinguished from *Laxitextella dorsorecta* (Reible, 1962) by the more centrally located umbo and the shorter dorsal margin as well as the pattern of growth lines. It is further distinguished from *Laxitextella laxitexta* (Reible, 1962) by the less regular growth bands and the narrower arrangement of growth lines towards the ventral margin as well as smaller polygons. The valves of *Laxitextella multireticulata* (Reible, 1962) are more subrectangular in outline with the umbo in a more central position, have more regular growth lines, and have a prosopon with slightly larger polygons.

Laxitextella seegisi Kozur in Kozur and Weems, 2007 from the upper part of the Tuvalian Steigerwald Formation has 20–30 growth bands with conspicuously different widths arranged in zones of subequal growth bands. Its ornamentation consists of subelliptical to oval polygons, apparently with somewhat larger polygons concentrated in the adumbonal half of the growth lines.

"*Laxitextella*? *hausmanni* (Schmidt, 1938)"

* 1854a *Posidonomya* Hausmanni m.—Bornemann: p. 63–64.
? 1860 Posidonomya Hausmanni Brnm.?—Credner: p. 300.
? 1860 Posidonomya Hausmanni Born.?—Credner: p. 307.
? 1871 Estheria minuta Goldf.—Brauns: p. 44.
? 1938 *Estheria hausmanni* BERGER—Schmidt: p. 46, fig. 861a.

non 1962 *Isaura hausmanni* (Schmidt 1938)—Reible: p. 214–215, fig. 17, pl. 9, fig. 3.

? 2007 *Euestheria hausmanni* (Schmidt, 1938) emend. Reible (1962)—Kozur and Weems: p. 139, 140, 151, 155, 161, 162, 165, 166, 175, pl. 4, figs. 2, 3.

? 2010 *Euestheria* n. sp.aff. *hausmanni* (Schmidt)—Kozur and Weems: p. 383, 386.

Discussion. In a short note, Schmidt (1938) described a "conchostracan" that he studied in the collection of the University of Göttingen under the name "*Estheria Hausmanni* BERGER." Schmidt (1938, p. 46) wrote that the species was represented by several specimens of "not mean size" that had 10–12 broadly spaced, sharp ribs in a conspicuously equidistant arrangement. The "hinge" was straight for only a short distance and was gradually curved beyond this straight section. A crude line drawing in the publication indicates that the portrayed valves were approximately 5.5 mm long, 4–4.5 mm high, and distinctly ovoid in outline.

Schmidt (1938) mentioned that the slab with the specimens originates from the collection of Bornemann, and that the label states "Keuper" for the origin. However, he suggested that the lithology could indicate that the specimens come from the Rhaetian.

Why Schmidt (1938) listed this material under the name provided is still rather puzzling, because Berger never described a species under this name. It is even more puzzling as to how the name made its way into the scientific "conchostracan" literature and is dealt with in several publications under the names *Euestheria hausmanni* (Bornemann, 1854a, b), *Isaura hausmanni* (Schmidt, 1938), and *Euestheria hausmanni* (Schmidt, 1938).

In fact, in his dissertation (Bornemann 1854a), J.G. Bornemann described a spinicaudatan that he interpreted to be a small clam named *Posidonomya Hausmanni*. The short description does not list any characteristics except the size, 5.8 mm in height, 7.9 mm in width, and a length to width ratio of 100:138, meaning that the species is unrecognizable. Remarkably, *Posidonia minuta*, thought to be similar, was mentioned by Bornemann (1854a) as being larger, and he considered *Posidonia bronni* (now the posidoniid pelecypod *Bositra buchi*) to be more similar. Unfortunately, Bornemann did not provide a figure. Remarkably, Bornemann described the available material (obviously numerous specimens) from Liassic shales near Elliehausen in the vicinity of Göttingen. The strata from near Elliehausen were later recognized as representing Keuper rather than Liassic rocks, but the precise stratigraphic level from which the specimens originated remains unclear.

Brauns (1871) regarded the species as a synonym of *Estheria minuta*, but still believed that Bornemann's original material came from the Liassic.

Reible (1962) revised the species and chose a neotype, which came from the Coburg Sandstone member of the Hassberge Formation, from an outcrop at Weißenbrunn am Forst near Coburg, northern Bavaria. This "neotype" is thus definitely from another lithostratigraphic unit, and his action must be regarded as illegal.

There is no hint as to why Schmidt (1938) used the name "Berger," so it could be just an error, as suggested by Mahler and Sell (http://www.terra-triassica.de/museum-terra-triassica/sammlung-und-werkstatt/makrofossilien/arthropoda-siebold-stannius-1845/crustacea-pennant-1777/conchostrace-sars-1867/euestheria-hausmanni-bornemann-1854/). Ironically, another publication of Bornemann (1854b) presents a short description of the bony fish species *Semionotus bergeri*, which was named after H.A.C. Berger, so Schmidt (1938) may have been referring to this publication. Bornemann's material described therein had not, however, been provided by Berger, and Berger never described a "conchostracan" named after Hausmann. Bornemann's slabs described in 1854 came from the Keuper of Haubinda near Römhild in southern Thuringia. Nevertheless, the horizon from which the material originated was first termed the Semionoten-Sandstein and subsequently became known as the Coburger Sandstein—the same stratigraphic unit in which most of the spinicaudatans in this study were found.

Apart from the uncertain characteristics of Bornemann's (1854a) original material, Reible's (1962, pl. 9, fig. 3) *Isaura hausmanni* from the Coburg Sandstone member of Weißenbrunn am Forst probably belongs to the same species dealt with above under *Laxitextella*? sp. A. It almost certainly cannot be assigned to *Laxitextella laxitexta* as suggested by Olempska (2004, p. 436).

More challenging still is the identification of the species as *Euestheria hausmanni* (Schmidt, 1938) from the Tuvalian in the Deep River Basin, Newark Basin, and the Gettysburg Basin, eastern U.S., by Kozur and Weems (2007). This is even more surprising because the authors describe the species as "very similar to *E. ovata* (Lea)" (Kozur and Weems, 2007, p. 139), but also state that "there is a possibility that *E. hausmanni* is the junior synonym of *E. pennsylvanica* (Wanner)." Apart from the problems involved in confidently identifying the species in the North American material from Reible's scarce material, Schmidt (1938) obviously did not intend to introduce a new species as "*Estheria Hausmanni* Berger," so the name *Euestheria hausmanni* (Schmidt, 1938) is a younger homonym.

In summary, the characteristics of the species suggested by Bornemann (1854a) are not currently known well enough to allow a confident determination. Reible's *Isaura hausmanni* and Kozur and Weems' (2007) *Euestheria hausmanni* are junior homonyms.

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