

# Late Triassic spinicaudatan crustaceans from southwestern Poland

EWA OLEMPSKA



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An assemblage of well-preserved spinicaudatan crustaceans (“conchostracans”) is described from lacustrine late Carnian claystone at Krasiejów in southwestern Poland. Their shell microstructure is similar to that in extant spinicaudatans. Five species identified there are assigned to the genera *Laxitextella*, *Menucoestheria* (first record in the European Triassic), and *Menucoestheria bocki* sp. nov. and *Krasiestheria parvula* gen. et sp. nov. are erected. Specimens of *Laxitextella laxitexta* are the most abundant, comprising nearly half of the assemblage, those of *Menucoestheria bocki* one quarter, *Laxitextella* sp. A, *Menucoestheria?* sp., and *Krasiestheria parvula* form a minor component. Their ecological setting was probably similar to Recent relatives: temporary ponds of fresh water. The Late Triassic fauna in the German part of the same basin is closely similar to that in Poland. In Europe, the stratigraphic range of *Laxitextella laxitexta* is limited to the Middle Keuper (middle–late Carnian).

Key words: Crustacea, Spinicaudata, taxonomy, palaeoecology, shell structure, Triassic, Poland.

Ewa Olempska [olempska@twarda.pan.pl], Instytut Paleobiologii PAN, ul. Twarda 51/55, PL-00-818 Warszawa, Poland.

## Introduction

The Krasiejów locality, in the Opole Silesia, southwestern Poland (Fig. 1) is the most prolific vertebrate fossil collecting site in Poland. The lacustrine and deltaic sediments exposed there yield abundant cranial and postcranial material of metoposaur and capitosauroid labyrinthodonts, phytosaurs, aetosaurs, rauisuchians, and early dinosaurs (Dzik et al. 2000; Dzik 2001, 2003b; Sulej 2002).

The fossil-bearing level (Fig. 2) is probably a lateral equivalent of the late Carnian (Tuvalian) Lehrberg Beds in the western part of the Germanic Basin (Dzik 2001; Sulej 2002).

Besides the preliminarily identified ostracods (Olempska 2001) and characean gyrogonites (Gryglas 1999; Piechota and Zatoń 2002), Krasiejów fossils include unionid bivalves, spinicaudatan crustaceans (“conchostracans”), cyclid crustaceans, beetles, and a variety of fish (Dzik 2003a).

Spinicaudatans (clam shrimps) are small branchiopod crustaceans enclosed in a chitinous bivalved carapace. They occur in non-marine facies from the Devonian to the present day (Tasch 1969; Thiéry 1996). The origin of the group is clearly problematic and their initial radiation in the earliest Devonian is still poorly understood, but the Carboniferous was a period of diversification and evolutionary innovation for the spinicaudatans (Tasch 1969, 1987; Schram 1986; Gray 1988; Orr and Briggs 1999; Vannier et al. 2003). Pre-Devonian records are few and questionable (see discussion in Gray 1988).

The strong anatomical similarities between the exceptionally preserved spinicaudatans from the Upper Carboniferous of Ireland and extant spinicaudatans confirm that their

external morphology has remained essentially the same since at least the Late Carboniferous (Orr and Briggs 1999).

Spinicaudatans form a common element of the European Late Triassic continental faunas. The purpose of this paper is to present data on a new fauna of spinicaudatan branchiopods from the Krasiejów section and place their occurrence in the local stratigraphical framework.

All the studied material is deposited in the Institute of Paleobiology of the Polish Academy of Sciences in Warsaw, Poland (abbreviated ZPAL).

## Previous work

Few data are available on Triassic “conchostracans” from Poland. The earliest reference is by Roemer (1870), who reported *Euestheria minuta* (von Zieten, 1833) [?= *Laxitextella laxitexta* or a new species] from the Upper Keuper of the Upper Silesia. Later, Volz (1896) erected *Estheria kubaczeki* [?probably a juvenile bivalve] from the Lower Muschelkalk of the Upper Silesia. These two species also were mentioned by Assmann (1937) from the Triassic of Silesia.

For almost 70 years little further attention was paid to spinicaudatans from Poland, possibly due to the rarity and often poor preservation nature of the material. No systematic descriptions or illustrations have appeared since, although spinicaudatans have been recorded from the Early Triassic deposits of northeastern Poland (Szyperko-Śliwczyńska 1979), and the Buntsandstein of the Fore-Sudetic Monocline (Alexandrowicz and Słupczyński 1971).

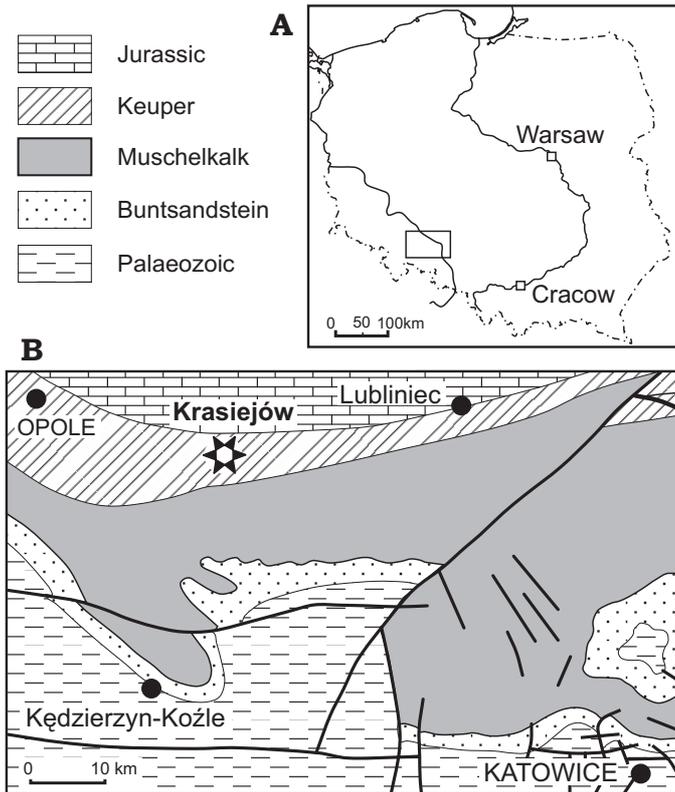


Fig. 1. Outline map of Poland (A), and simplified geological map of the Opolé area (B), showing position of the Krasiejów locality (indicated by an asterisk).

## Geological setting and materials

The Late Triassic deposits of the Krasiejów section are represented by a red and variegated, locally laminated, mudstone. The bone-bearing interval consists of red and grey, non-stratified claystone (Fig. 2). The sediment was deposited in a large lake-deltaic complex.

Spinicaudatan specimens occur in a thin horizon of grey claystone (about 30 cm thick), extending over an area of several square meters. This horizon is overlain by a fossiliferous claystone unit, 1 m thick, with *Metoposaurus*–*Paleorhinus* fauna (Fig. 2). Based on the occurrence of *Paleorhinus*, the probable age of this unit is restricted to late Carnian. Based on similarity in bathymetric evolution of the Germanic Basin in the Polish and German parts, the Krasiejów lacustrine bed is correlated with the Lehrberg Beds (Dzik et al. 2000; Dzik 2001).

Spinicaudatans occurring in the Krasiejów outcrop are preserved as closed carapaces filled with sediment and also disarticulated weakly calcified (“chitinous”) valves of light amber, honey, brown to brownish-black colour. The dorsal parts of valves are usually darker than the ventral margin. The valves, three-dimensionally preserved, always show clear growth lines and growth bands (Fig. 3). The shells are scattered throughout the sediment, not concentrated on any surface, and have no preferred orientation. Specimens appear

to represent both juveniles and adults. Spinicaudatans are common, but not abundant. More than 70 specimens were collected. The originally soft and flexible shells of spinicaudatans are usually flattened, extended or compressed parallel to their long axis or deformed obliquely into an asymmetric shape.

## Triassic spinicaudatan stratigraphy

The Buntsandstein spinicaudatan zonation in the Germanic Basin, established by Kozur and Seidel (1983a, b), was supplemented for the late Scythian and early Anisian by Kozur et al. (1993), and for the Middle Triassic part of the Keuper by Kozur (1993, 1999).

The Carnian spinicaudatan faunas of the Germanic Basin are characterized by the coarsely reticulated genus *Laxi-*

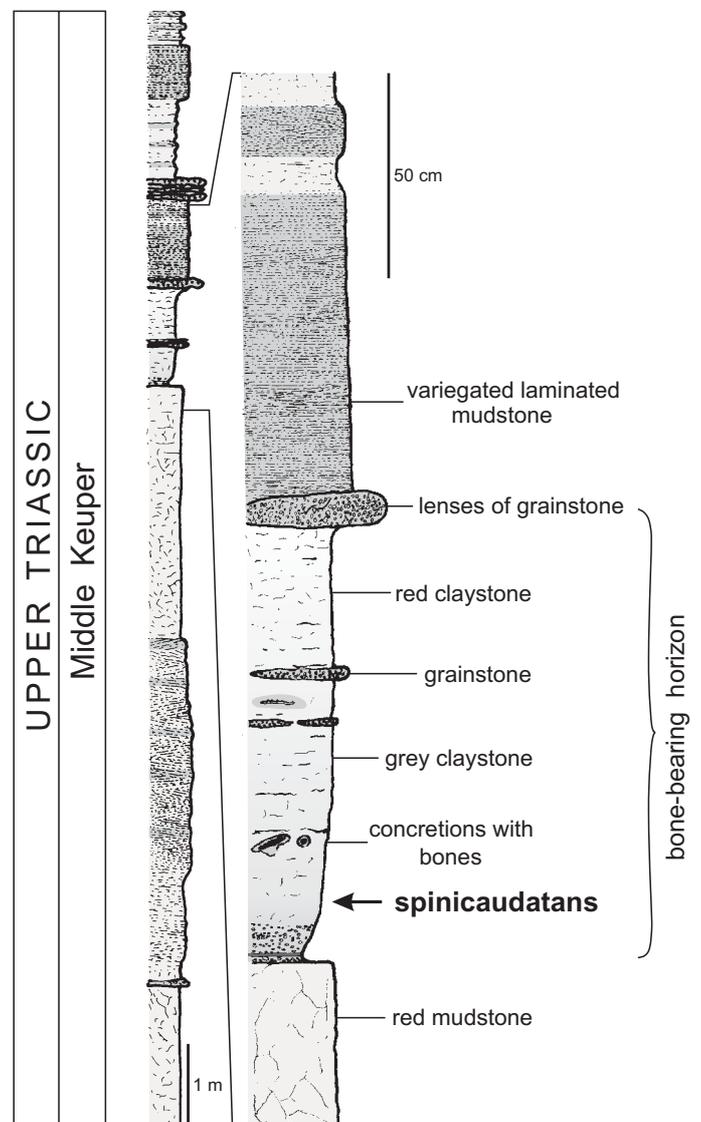


Fig. 2. Stratigraphical column of the locality studied showing position of the spinicaudatan samples.

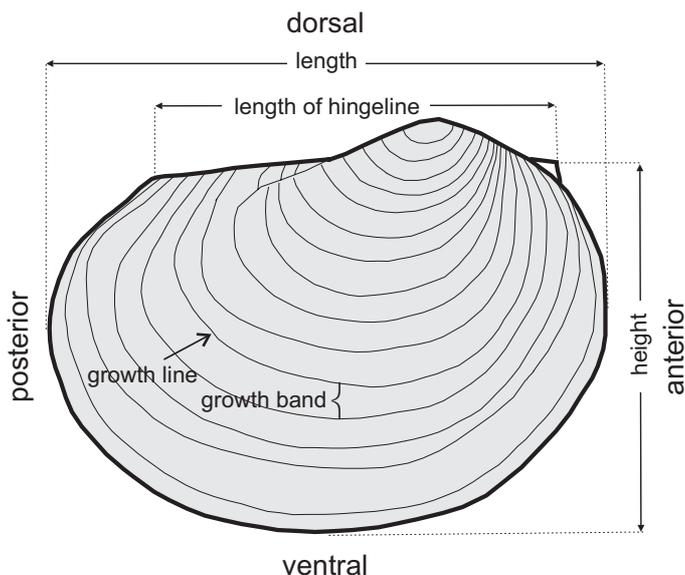


Fig. 3. Reconstruction of the right valve of *Laxitextella* showing positions of measurements.

*textella* Kozur, 1982 (Reible 1962; Warth 1969; Kozur et al. 1993; Kozur 1999; Seegis 1997). In the Germanic Basin *Laxitextella* represented by *L. multireticulata* (Reible, 1962) makes its first appearance in the upper part of the Lower Gipsium Keuper (Kozur and Mock 1993). The stratigraphic position or range of the Middle Keuper spinicaudatan fauna in the Germanic Basin correlated with marker beds (according to Aigner et al. 1999) is shown in Fig. 4. *Laxitextella* sp. is also present in the earliest Carnian of the Southern Calcareous Alps, northern Italy (Tintori 1990; Tintori and Brambilla 1991) and the Late Triassic of China (Qiqing 1993: 388).

The early Carnian (Cordevolian) *Laxitextella multireticulata* Zone, as equivalent of the Lower Gipskeuper (Lower “Estheria Beds”), and *Laxitextella laxitexta* Zone as equivalent of the Upper Gipskeuper (Upper “Estheria Beds”) with its lower boundary at the base of the Julian, have been proposed by Kozur (1999: fig. 5), however, the upper boundary of the latter zone has not been established.

The spinicaudatans of the Lehrberg Beds of southern Germany are represented by *Laxitextella* sp. belonging prob-

Stratigraphy			Important regional units + marker beds	Spinicaudatan fauna		
TRIASSIC	Norian	Middle Keuper	Knollenmergel	Knollenmergel	<i>Laxitextella multireticulata</i> ————— <i>Howellisaura fimbriata</i> ————— <i>Laxitextella laxitexta</i> ~~~~~ <i>Shipingia dorsorecta</i> ..... ■ <i>Laxitextella</i> sp. sensu Seegis (1997) ■ <i>Menucoestheria bocki</i> ■ <i>Menucoestheria?</i> sp. ■ <i>Krasiestheria parvula</i> ■ <i>Laxitextella</i> sp. A	
			Stubensandstein Formation	4. Stubensandstein		
				3. Hangendletten		
				3. Stubensandstein		
				2. Hangendletten		
				2. Stubensandstein		
	1. Hangendletten					
	Carnian	Middle Keuper	Bunte Mergel	Obere Bunte Mergel		
				Kieselsandstein		
				Lehrbergsschichten		
				Unt. Bunte Mergel		
			Schilfsandstein-Formation			
Gipskeuper						

Fig. 4. Stratigraphical distribution of the Middle Keuper spinicaudatan species in the Germanic Basin (after Reible 1962; Warth 1969; Kozur 1999; Seegis 1997) and Krasiejów. The Middle Keuper lithostratigraphy in the South Germanic Basin with important marker beds after Aigner et al. (1999), modified.

ably to a new species (Seegis 1997). *Laxitextella* specimens from the Middle Keuper of the Germanic Basin are generally variable and usually poorly preserved. The status of most of them is questionable (see discussion in Seegis 1997).

Bock (1953a, b) described faunas including *Laxitextella* and *Howellisaura* species from North America (*L. ovata*, *H. winterpockensis*, *H. princetonensis*, *H. berryi*), comparing and correlating the faunas with those from Germany the Middle Keuper Schilfsandstein up to Bunte Mergel.

The Carnian spinicaudatan fauna from Krasiejów consist of *Laxitextella laxitexta* (Jones, 1890), *Laxitextella* sp. A, *Menucoestheria bocki* sp. nov., *Menucoestheria?* sp., and *Krasiestheria parvula* gen. et sp. nov. The fauna includes taxa both of the central European Germanic Basin (species of the *Laxitextella* lineage) and North America (species of the *Menucoestheria* lineage).

*L. laxitexta* occurs in Krasiejów in high relative frequency (up to 51%), *M. bocki* is also an important component of the assemblage (up to 26%), *L. sp. A* makes up 17.6% of the sample and *M.?* sp. and *K. parvula* formed a minor component.

Based on the evidence from *L. laxitexta* and *L. sp. A* it can be concluded that the age of Krasiejów spinicaudatan assemblage probably lies within the middle–late Carnian time span.

## Life habit and palaeoenvironmental reconstruction

Most modern spinicaudatans are limited to small, shallow (less than 1 m deep) ephemeral freshwater pools and ponds but also occur in permanent flowing or standing streams and in deeper and larger lakes. They appear incapable of persisting with a resident fish fauna, however it may not be totally exclusive when pools were temporarily connected with lakes or rivers inhabited by fishes. Occasionally, they also occur in more saline environments such as large playa lakes and coastal salt flats, they usually die when water salinity reaches about 5‰ (see Tasch 1969, 1987; Webb 1979; McKenzie 1979; Frank 1988; De Decker 1988; Thiéry 1996).

The life span of spinicaudatans is limited to a single season. Their growth rate as well as their final size, though genetically determined, are dependent on temperature and food supply. Low temperature retards carapace growth and is reflected in a smaller number of growth lines (see Kobayashi 1954; Doumani and Tasch 1965; Tasch 1969; Webb 1979; Frank 1988).

It appears that the adaptive zone of the Palaeozoic and Mesozoic spinicaudatans was much broader than it is now. Fossil spinicaudatans are common in brackish environments (Reible 1962; Webb 1979; Kozur and Mock 1993; Shen and Zhu 1990; Shen et al. 2002). They also have been found with fish deposits of Late Triassic–Middle Jurassic perennial lakes (Schaeffer 1972; Tasch 1987; Olsen 1988).

The restricted areal distribution of spinicaudatan-bearing interval and its thinness over the Krasiejów deposits, suggests that spinicaudatans lived in a small pool. There is no indication of current activity or rapid burial. The absence of size sorting of shells suggests rather local burial. Abundant and well-preserved floral debris, and well-preserved spinicaudatan valves, suggest deposition in shallow, still water. Specimens in Krasiejów spinicaudatan concentrations vary in length and in number of growth bands, their valves occur on different bedding planes, suggesting that they do not represent a single population. Probably they lived in different seasons in an environment that persisted for a relatively short period of time.

The density of populations in the Krasiejów water body was rather low, in contrast to Recent and some fossil populations which are usually of high density with thousands of individuals inhabiting a pool at a particular time (Raymond 1946; Webb 1979; Tasch 1969). This suggests that the Krasiejów spinicaudatans lived in the unfavorable environmental conditions of a filling and stagnating pond.

Spinicaudatans co-occur in Krasiejów with the common ostracod *Darwinula*, rare *Suchonella* specimens, the freshwater bivalves and abundant characean gyrogonites. Abundant plant material also occurs in the spinicaudatan-bearing horizon. *Darwinula* is a nonswimming, infaunal ostracod which inhabits muddy substrates in fresh to slightly brackish waters (Sohn and Chatterjee 1979; Carbonel et al. 1988).

In the Upper Carnian Lehrberg Beds of southern Germany, which were deposited in shallow lake and playa environments, spinicaudatans are present and abundant in a carbonate complex, representing deposits of extensive, meromictic lakes, i.e., lakes showing a chemical water stratification (Seegis 1997). The spinicaudatan fauna is restricted, according to Seegis (1997), to shore zones of the lake, which had lower salt content due to continue fluvial inflows.

The modern spinicaudatan populations are of low diversity, and usually contain only one or two genera at a time, and no more than one species of the same genus lives in every pool (Kobayashi 1954; Tasch 1969, 1987; Webb 1979; Kozur 1983; Frank 1988). The occurrence of closely related fossil species in the same pool are known from fossil assemblages (see Webb 1979; Chen and Hudson 1991). Tasch (1969) and Kozur and Seidel (1983a, b), suggested that this may be a result of taxonomic splitting and insufficiently detailed study of the morphological variation within assemblages. However, the co-occurrence of related species in the same stratigraphic horizon does not necessarily imply co-occurrence in the same environment (Webb 1979).

In Krasiejów there are five species occurring together. Differences in the shape of the valves, and in the ornamentation pattern in *Laxitextella* and *Menucoestheria* species from Krasiejów, appear to be too great to be related to sexual dimorphism or to varying ontogenetic stages (see discussion in Kobayashi 1954; Tasch 1969; Babcock et al. 2002; Tintori and Brambilla 1991).

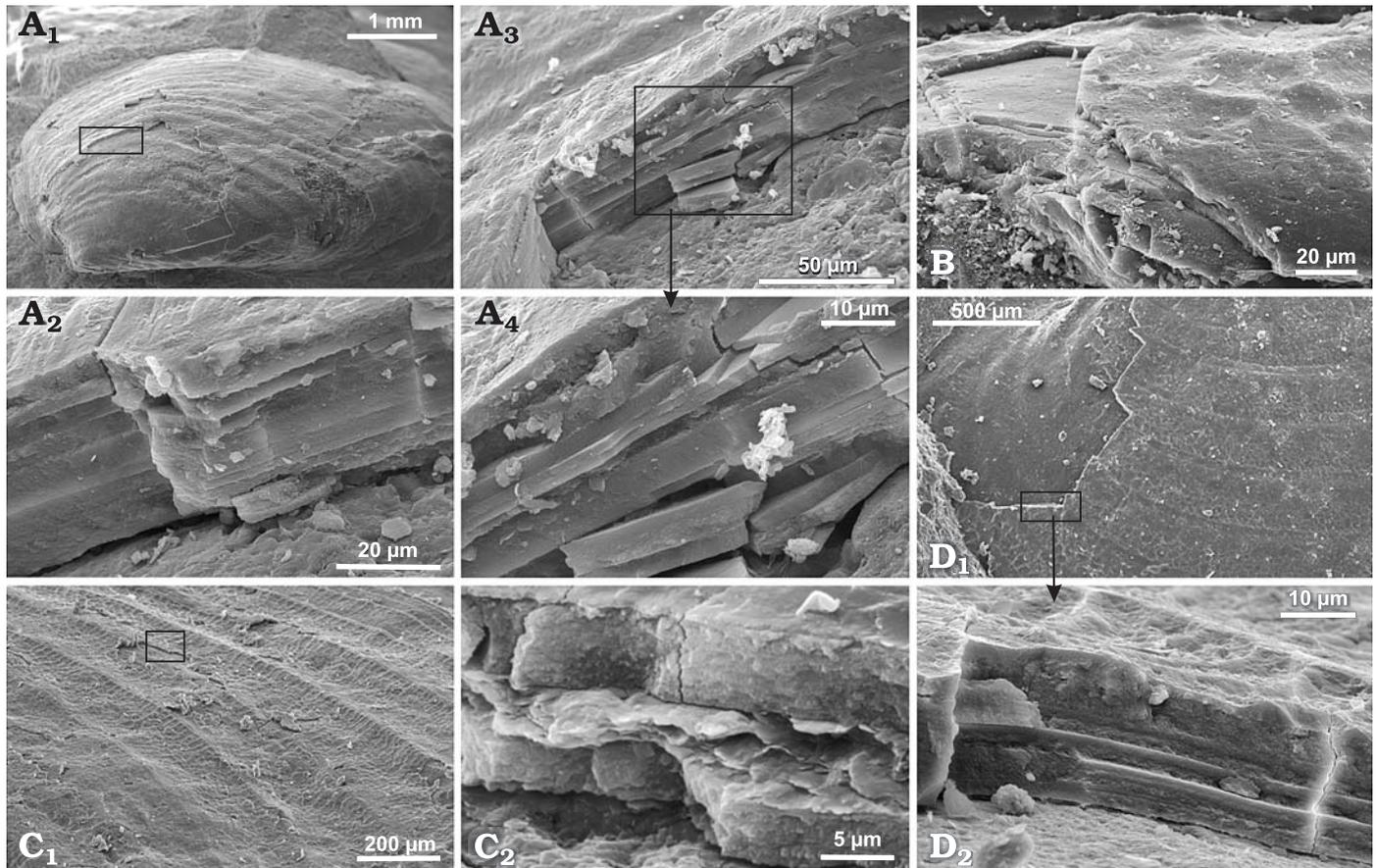


Fig. 5. **A.** *Laxitextella laxitexta* (Jones, 1890). Left valve ZPAL Cr. 6/2 in oblique dorsal view ( $A_1$ ), and details of shell structure showing layers of cuticle ( $A_2$ – $A_4$ ). **B.** *Menucoestheria?* sp. Right valve ZPAL Cr. 6/3 with details showing layers of cuticle in mid-dorsal area. **C, D.** *Menucoestheria bocki* sp. nov. **C.** Specimen ZPAL Cr. 6/28, showing growth bands ornamentation ( $C_1$ ), and details of shell structure showing layers of cuticle in median area ( $C_2$ ). **D.** Specimen ZPAL Cr. 6/15, showing growth band reticulate ornamentation in mid-dorsal part ( $D_1$ ), and details of cuticle layers in mid-dorsal area ( $D_2$ ).

## Shell structure

Shells of spinicaudatans are multilamellar, with lamellae expressing successive growth stages, due to retention of old carapaces upon moulting (Kobayashi 1954; Tasch 1969; Kozur 1982; Fryer 1987; Martin 1992; Thiéry 1996; Vannier et al. 2003). Living “conchostracans” undergo ecdysis approximately every three days and moult throughout life (Tasch 1969).

In living spinicaudatans, the cuticle consists of two layers: a thin outermost epicuticle and an internal, much thicker procuticle, composed of an outer preecdysial procuticle (exocuticle) and beneath it a postecdysial procuticle (endocuticle). The procuticle is composed of layers of fibrous lamellae parallel to the surface; often the exocuticle and endocuticle are divided into sublayers (see Rieder et al. 1984; Martin 1992; Thiéry 1996; Vannier et al. 2003).

Much less is known about the shell structure of fossil spinicaudatan branchiopods. Kozur (1982) published SEM picture showing well-defined lamellar structure of the shell of *Euestheria* from Triassic of Libya. Chen and Hudson (1991) published SEM photographs detailing construction of

the growth bands in some Jurassic spinicaudatan genera from Scotland.

The shell structure of spinicaudatans from the Krasiejów locality was examined both in broken valves under the SEM and in thin sections in transmitted light. For study in transmitted light, specimens partly covered by rock matrix were embedded in plastic resin and sectioned.

All the examined Polish spinicaudatans have the same general type of multilamellar shell structure (Figs. 5, 6). In sections cut perpendicularly to the surface of the shell of *Laxitextella* sp. (in the anterior part of the valve), single lamella (= cuticle) as seen in transmitted light (Fig. 6) shows the following parts: thin chitin layers dorsally and centrally, and much thicker distal parts including growth bands (Fig. 6). The lower margin of the distal part forms the free edge of the shell during successive growth stages.

The distal part as seen in thin section is composed of a much thicker outer layer, and the lower layer is divided into sublayers.

The outer layer has an amorphous transparent appearance in thin sections and appear as a single unit. The thickness of the outer layer is much thicker in the distal part of the lamella,

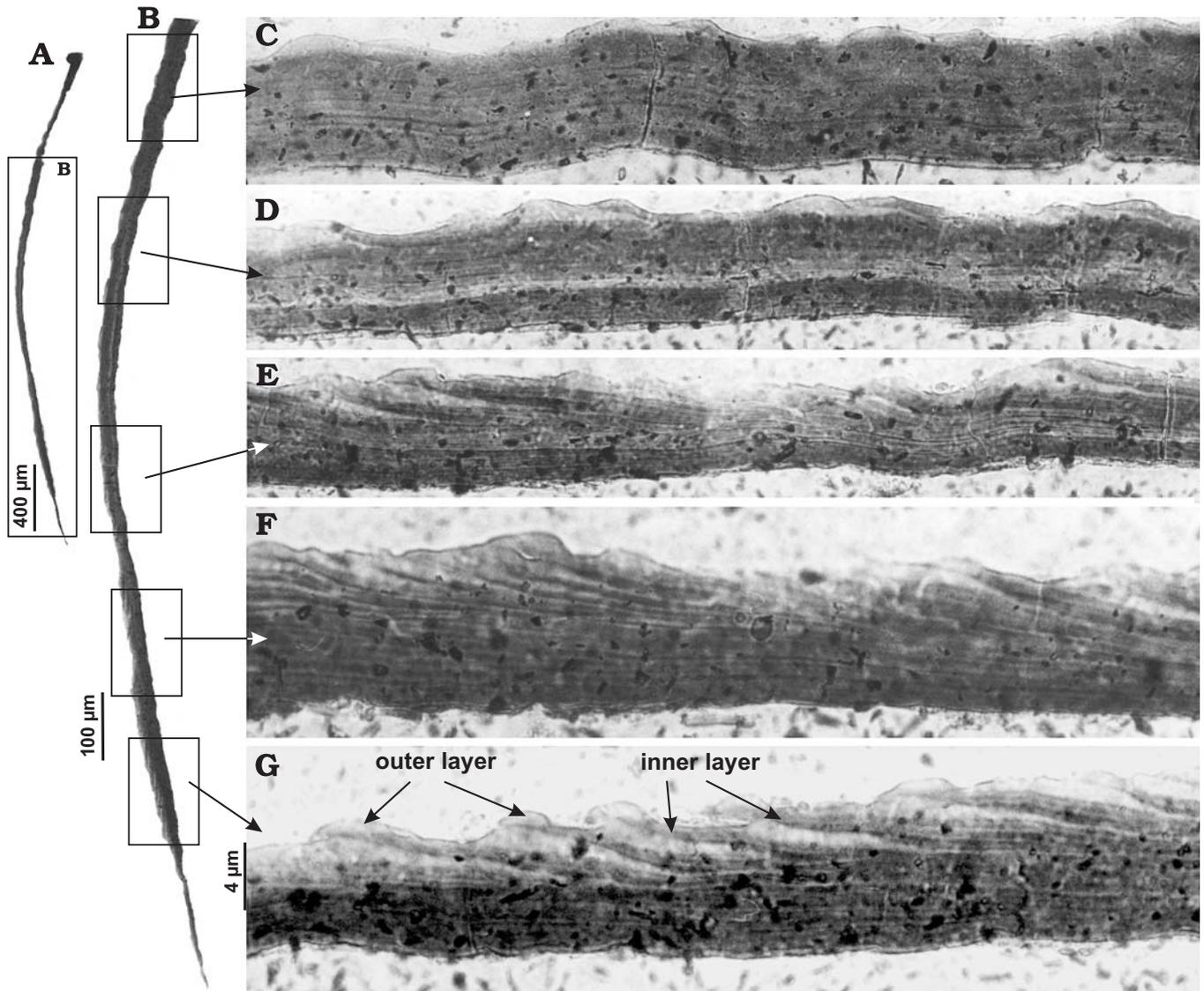


Fig. 6. *Laxitextella* sp. Transverse section of the valve ZPAL Cr. 6/53 (A, B), details of shell structure showing accumulated layers of cuticle in mid-dorsal part (C), middle part (D), mid-ventral part (E), and ventral part (F, G).

reaching up to 1  $\mu\text{m}$ , and thinner, reaching up to 0.5  $\mu\text{m}$ , in the middle and dorsal part of the lamellae.

Undulations of the outer layer in the distal part of the lamellae form the external shell ornamentation on the growth bands, largely in the form of reticulations, lateral striae or punctations.

Interior to the ornament-bearing outer layer there is a thinner inner layer. The inner layer is consisting of chitin and has a honey-brown appearance in thin section. These two layers appear to represent procuticle layer (exocuticle and endocuticle). The epicuticle is not preserved.

Pore canals extending through the carapace are not seen in Krasiejów spinicaudatans.

The shell of *Laxitextella* sp. A, as seen in broken valves under the SEM, are about 10  $\mu\text{m}$  thick in the mid-ventral part of the valve. Their valves are composed of up to 26 lamellae (Fig. 8). The thickness of the shell of *Laxitextella laxitexta* is

about 33  $\mu\text{m}$  in the dorsomedian part of the valve. Its lamellae are of different thickness, ranging from 1.4 to 6  $\mu\text{m}$  (Fig. 5A<sub>2</sub>–A<sub>4</sub>). The shell of *Menucoestheria*? sp., composed of more than 20 lamellae, is 25  $\mu\text{m}$  thick in the dorsal part of the valve (Figs. 5B, 10E). The shell of *Krasiestheria parvula* is about 20  $\mu\text{m}$  thick in the dorsal part of the valve (Fig. 11C). *Menucoestheria bocki* is 10  $\mu\text{m}$  thick in the ventral part of the valve (Fig. 5C<sub>2</sub>), and 20–25  $\mu\text{m}$  in the median part of the valve (Fig. 5D<sub>2</sub>).

## Systematic palaeontology

There is ongoing debate concerning the taxonomy of “conchostracans” (Spinicaudata + Laevicaudata; see Novojilov 1954, 1960; Raymond 1946; Tasch 1969, 1987; Zhang et al. 1976;

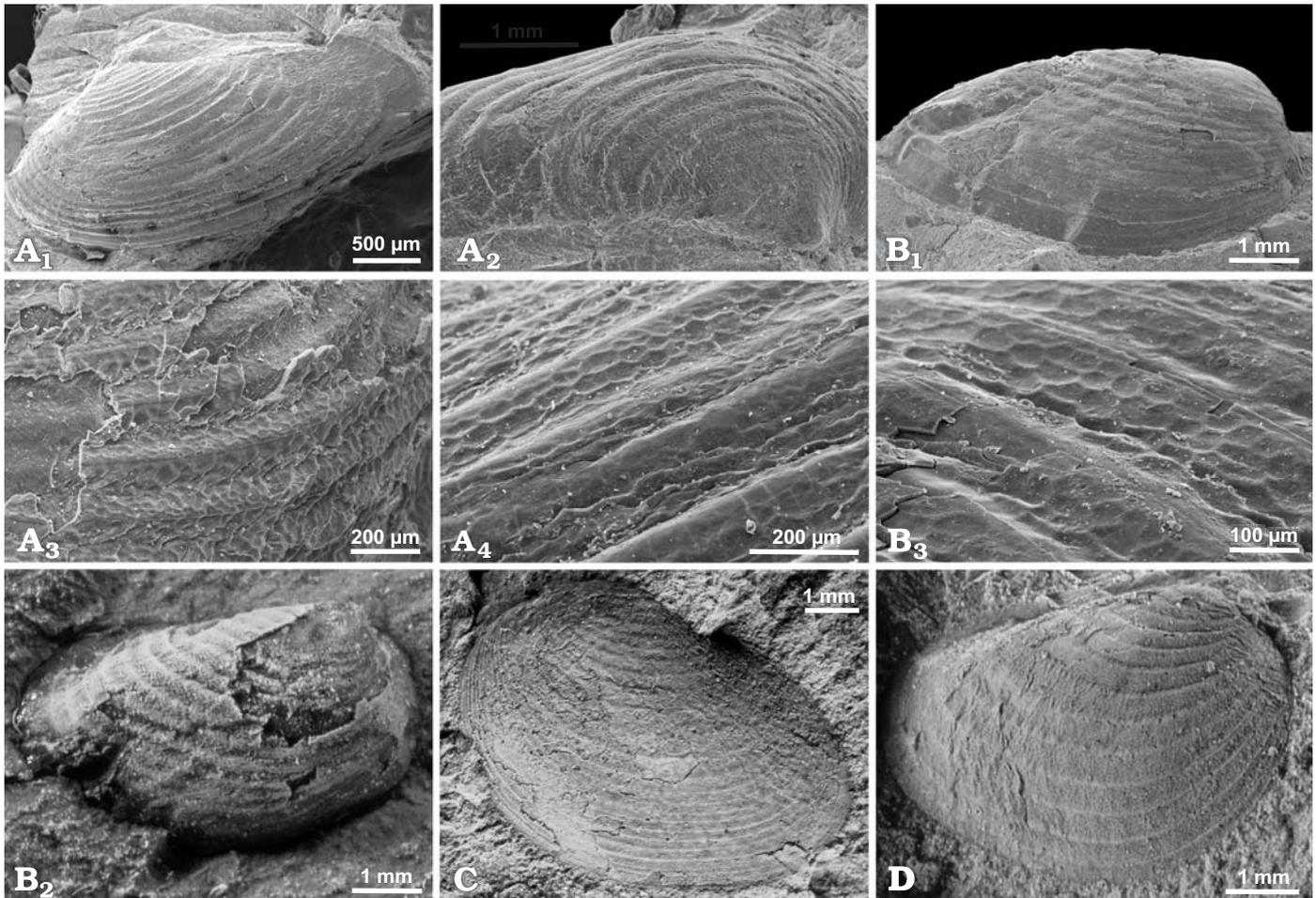


Fig. 7. *Laxitextella laxitexta* (Jones, 1890). **A.** Left valve ZPAL Cr. 6/2 in oblique lateral view ( $A_1$ ), in dorsal view ( $A_2$ ), the same with details of reticulate growth band ornamentation ( $A_3$ ,  $A_4$ ). **B.** Right valve ZPAL Cr. 6/4 in oblique ventral view ( $B_1$ ), in lateral view ( $B_2$ ), and the same with details of growth bands reticulate ornamentation ( $B_3$ ). **C.** Left valve ZPAL Cr. 6/52 in lateral view. **D.** Right valve ZPAL Cr. 6/50 in lateral view.

Chen and Shen 1982, 1985; Thiéry 1996; Negrea et al. 1999; Olesen et al. 1997; Olesen 1998, 1999, 2000; Fryer 1987, 2001; Martin and Davis 2001; Shen et al. 2002; Vannier et al. 2003).

Fossil spinicaudatans are difficult to classify objectively due to the morphological similarity of their carapaces, and the difficulty of establishing a hierarchical diagnostic characters. Tasch (1969, 1987) rejected the use of external ornamentation for classification of fossil “conchostracans” higher than at generic rank, but Novojilov (1954), Zhang et al. (1976), Chen and Shen (1985), Chen and Hudson (1991) valued the growth bands.

Due to the state of preservation, it was not possible to establish the sex of Krasiejów spinicaudatan specimens. Both males and females are probably present in the assemblage.

Subphylum Crustacea Brünnich, 1772  
Class Branchiopoda Latreille, 1817  
Order Spinicaudata Linder, 1945  
Superfamily Cyzicoidea Stebbing, 1910

## Family Euestheridae Defretin, 1965

### Genus *Laxitextella* Kozur, 1982

Type species: *Estheria laxitexta* Jones, 1890.

*Discussion.*—The generic assignment of the Triassic reticulate forms constitutes a difficult problem and most of them 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. multi-reticulata* (Reible, 1962), *L. dorsorecta* (Reible, 1962), and an American species *L. forbesi* (Jones, 1862). According to Kozur (1982) *Laxitextella* is distinguished by having coarse reticulation sculpture in the growth bands. *Laxitextella* differs from *Loxomegaglypta* Novojilov, 1958 in having umbo placed close to the anterior end of the dorsal margin and in ornamentation pattern.

### *Laxitextella laxitexta* (Jones, 1890)

Figs. 5A, 7.

*Estheria minuta*, Alberti; Jones 1862: 57, pl. 2: 1–7.

*Estheria laxitexta* Sandberger; Sandberger 1871: 48 (*nomen nudum*).

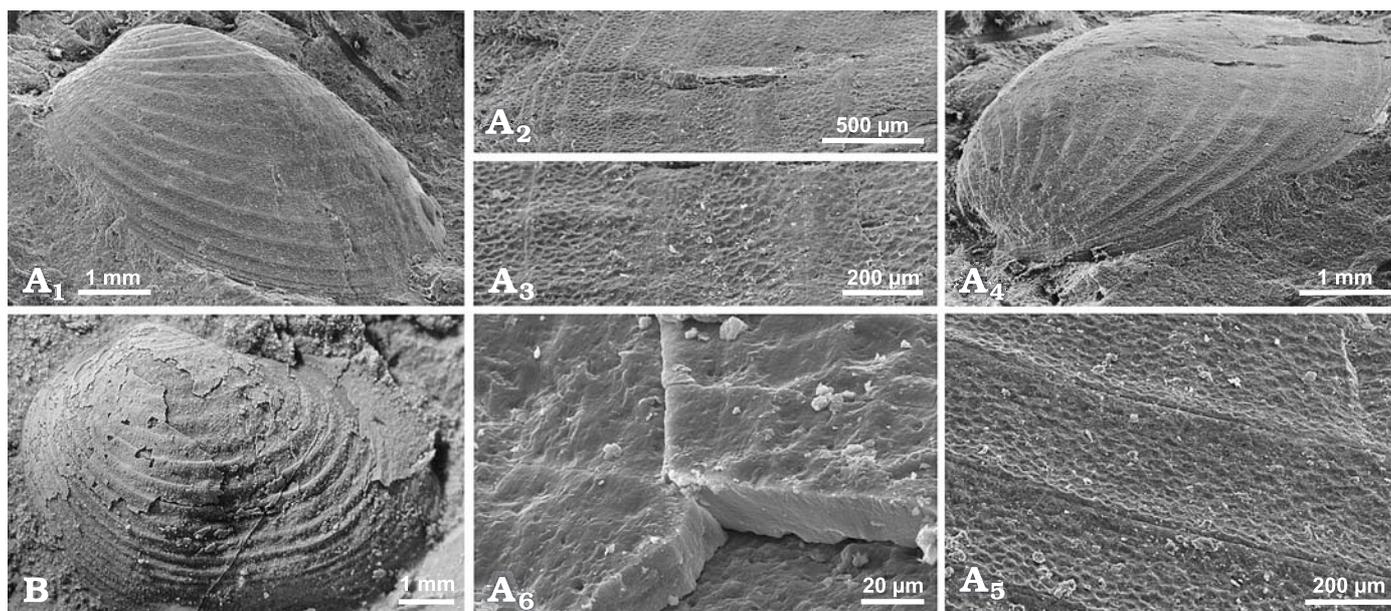


Fig. 8. *Laxitextella* sp. A. A. Left valve ZPAL Cr. 6/1 in oblique lateral-ventral view (A<sub>1</sub>), and details of growth bands reticulate ornamentation in mid-ventral area (A<sub>2</sub>, A<sub>3</sub>); the same in anterior view (A<sub>4</sub>); the same showing details of growth bands ornamentation in mid-anterior area (A<sub>5</sub>); details of shell structure in mid-anterior area (A<sub>6</sub>). B. Left valve ZPAL Cr. 6/13 in lateral view.

*Estheria minuta* Alberti (*E. laxitexta* Sandberger); Jones 1890: 387–388, pl. 12: 8.

*Euestheria laxitecta* (Jones); Raymond 1946: 242.

*Euestheria laxitecta* (Sandberger); Kobayashi 1954: 54, 98.

*Isaura laxitexta laxitexta* (Jones, 1890); Reible 1962: 210–212, fig. 15, pl. 8: 3, 4.

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

*Palaeostheria laxitexta* (Jones, 1890); Warth 1969: 137, fig. 7, pl. 3: 5.

*Laxitextella laxitexta* (Sandberger, 1871); Kozur 1982: 378–379.

**Material.**—18 complete or slightly damaged valves and 20 damaged specimens.

Table 1. Measurements of *Laxitextella laxitexta*

Specimens ZPAL	Length (mm)	Height (mm)	Length of hingeline (mm)	No. of growth bands
Cr. 6/2	6.8	?	3.7	24
Cr. 6/4	6.4	3.6	?	28?
Cr. 6/16	3.5	2.8	2.3	22
Cr. 6/37	5.2	4.0	?	23–24?
Cr. 6/40	8.0	5.2	3.2	18–20?
Cr. 6/41	7.2	4.6	3.3	20–22?
Cr. 6/42	5.7	4.0	?	18–19?
Cr. 6/44	9.0	5.5	6.4	?
Cr. 6/50	5.3	3.3	2.0	15
Cr. 6/51	6.6	4.2	3.9	14–15?
Cr. 6/52	8.1	5.3	3.5	28

**Description.**—Carapace of moderate size, varying in outline from elongate ovoidal to subquadrate, up to 9.0 mm long and up to 5.5 mm high; lateral convexity greatest just behind and

below the umbo in anterior third of valve; dorsal margin almost straight, varies in relative length; anterior margin broadly rounded, posterior ventrally truncated, ventral margin more or less convex; umbo small, situated close to anterior end of dorsal margin, protruding above dorsal margin; growth bands approximately 28 in largest specimens, ventral growth bands closely spaced in adult specimens, median widely spaced; surface of growth bands ornamented by polygonal reticulation, in largest specimens usually 2–3 meshes (0.026–0.039 mm in diameter) are present in growth bands in ventral part, 4 in mid-ventral part and 5–6 (0.065–0.091 mm in diameter) in median part of the carapace.

**Remarks.**—*Laxitextella laxitexta* is similar in ornamentation pattern to *Laxitextella* sp. *sensu* Seegis (1997) from the Lehrberg Beds of southern Germany.

The described species is also similar in surface ornament pattern to *Loxomegaglypta wetlugiana* Novojilov, 1958 from the Early Triassic of the Volga region (see Novojilov 1960: fig. 504) but differs from the latter in having the umbo situated close to the anterior end of the dorsal margin. *Laxitextella laxitexta laxitexta* illustrated by Reible (1962: pl. 8: 5, 6) probably represents *Howellisaura fimbriata* (Warth, 1969). *Estheria minuta* illustrated by Roemer (1870: pl. 15: 10) from the Late Triassic of the Upper Silesia (Hellewalder Estherien-Schichten), probably belongs to a new species, closely related to the *Laxitextella laxitexta*.

**Occurrence.**—Gipskeuper of South Germany; ?Late Triassic of England; late Carnian, Krasiejów, Poland.

### *Laxitextella* sp. A

Fig. 8.

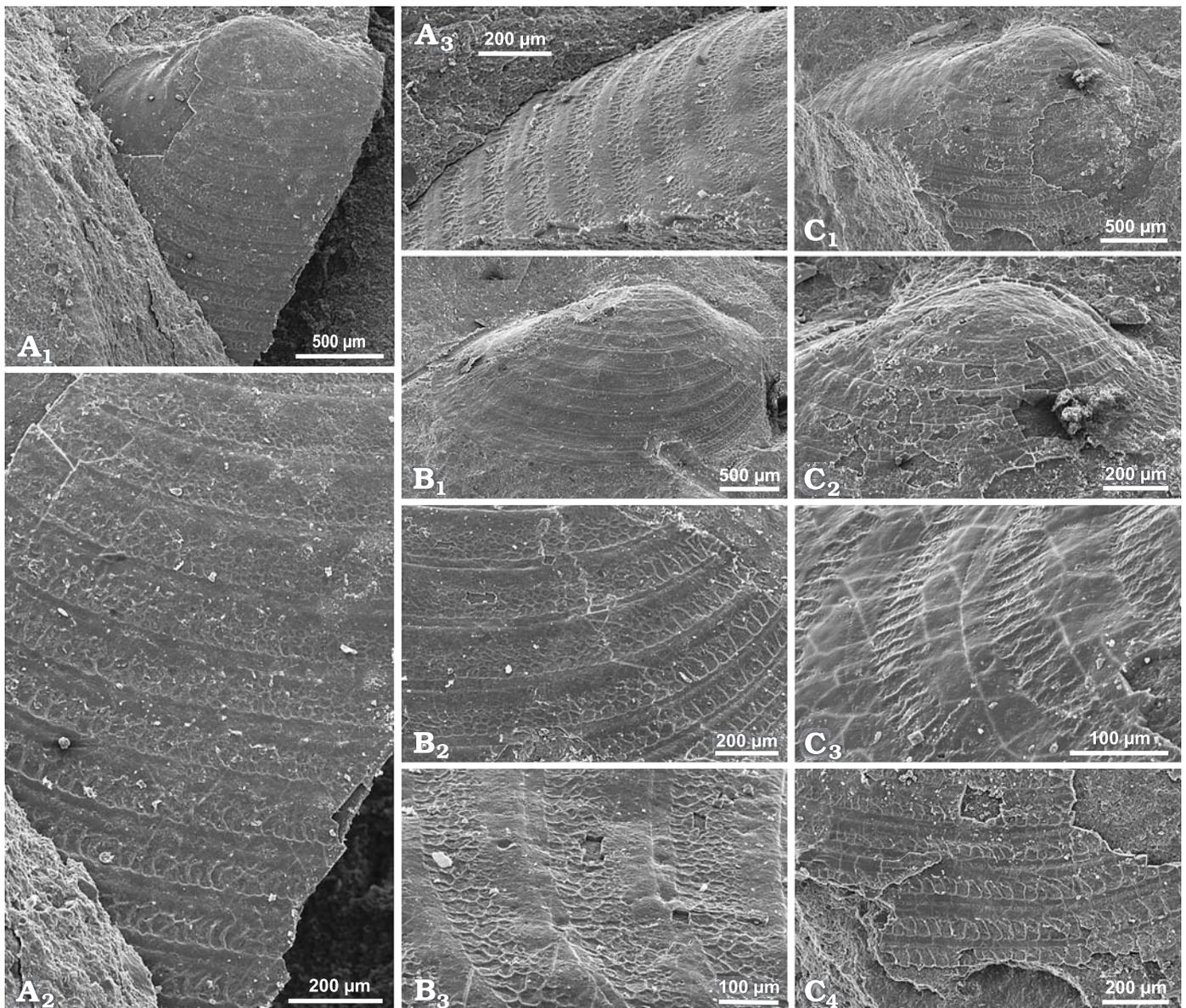


Fig. 9. *Menucoestheria bocki* sp. nov. A. Right valve ZPAL Cr. 6/15 in lateral view (A<sub>1</sub>), and details showing growth bands ornamentation, reticulate in dorsal and median areas, passing into radial striae in ventral part (A<sub>2</sub>), the same in oblique view (A<sub>3</sub>). B. Right valve ZPAL Cr. 6/29 in lateral view (B<sub>1</sub>), and details of growth bands ornamentation (B<sub>2</sub>, B<sub>3</sub>); holotype. C. Right valve ZPAL Cr. 6/20 in lateral view (C<sub>1</sub>), dorsal area (C<sub>2</sub>), and details of growth bands ornamentation (C<sub>3</sub>, C<sub>4</sub>).

**Material.**—Thirteen carapaces and valves (carapaces with only one valve visible).

**Description.**—Carapace of moderate size, varying from ovato-oblong to subrhomboidal in lateral outline, up to 7.4 mm long and up to 6.0 mm high; dorsal margin almost straight to slightly convex; umbo small, close to anterior end of dorsal margin; growth bands approximately 26 in largest specimens; growth bands widely spaced in median part and closely spaced in ventral part of valve; growth bands flattened with fine reticulate ornament; 3–4 meshes (0.020 mm in diameter) in narrow growth band in ventral part of carapace, 10–12 meshes (0.033 mm in diameter) in median part of carapace.

Table 2. Measurements of *Laxitextella* sp. A.

Specimen ZPAL	Length (mm)	Height (mm)	Length of hingeline (mm)	No. of growth bands
Cr. 6/1	5.6	4.5	?	19
Cr. 6/9	7.4	5.1	4.2	21
Cr. 6/12	7.0	4.5	3.8	26
Cr. 6/13	7.0	4.5	4.1	23?
Cr. 6/22	7.3	6.0	3.5	21
Cr. 6/39	7.0	4.2	?	22
Cr. 6/47	6.8	5.0	2.8	18–19?

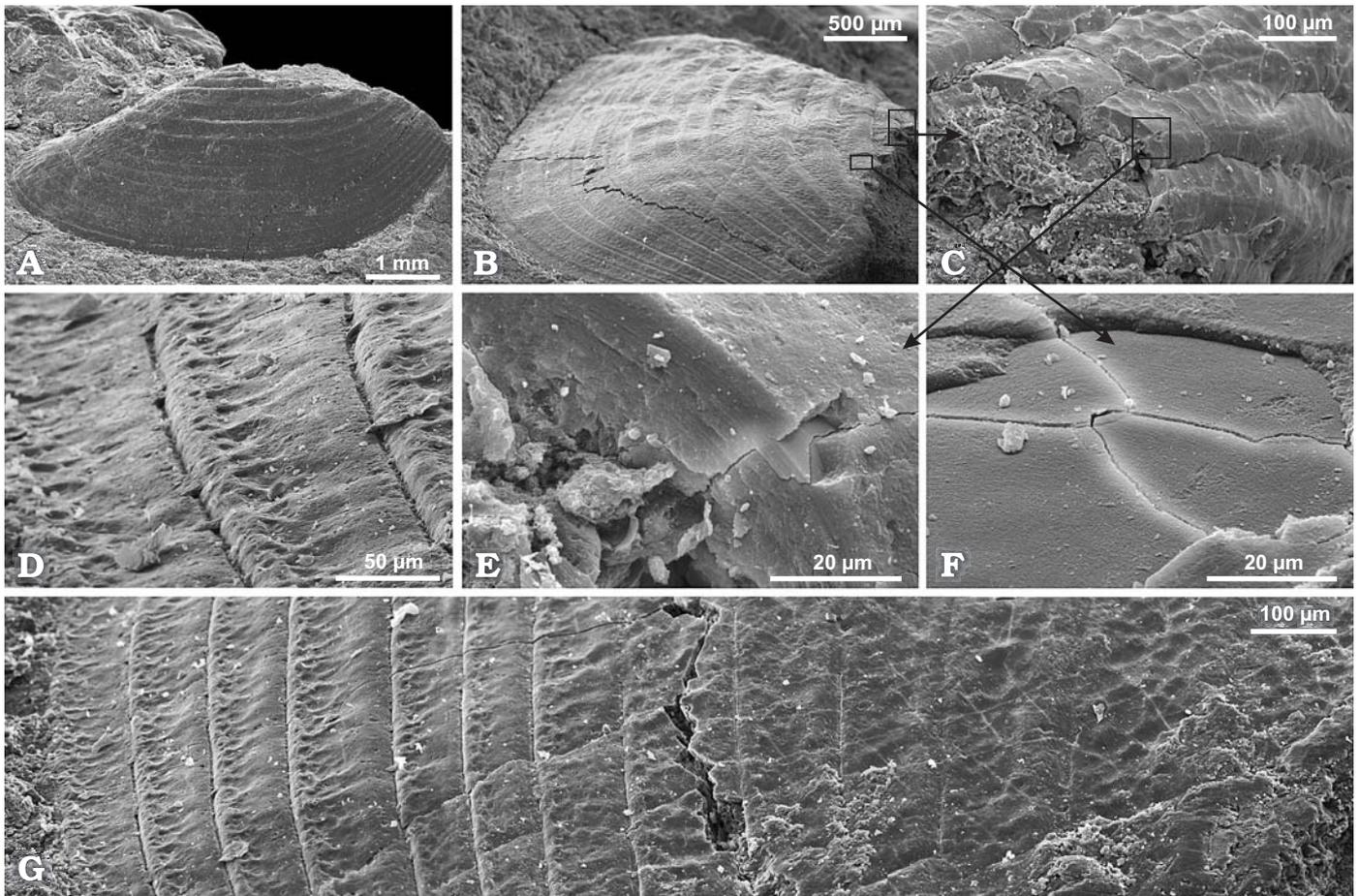


Fig. 10. *Menucoestheria?* sp. Right valve ZPAL Cr. 6/3 in lateral-ventral view (A), and oblique anterior view (B); the same showing details of growth bands ornamentation in dorsal area (C); the same with details of growth bands ornamentation in mid-ventral area (D); details of shell structure showing layers of cuticle in dorsal area (E, F); details showing gradually changed growth bands ornamentation during the successive growth stages (G).

**Remarks.**—The specimens from Krasiejów are similar in valve shape and ornamental pattern to those of *Shipingia dorsorecta* (Reible, 1962) from “obere Bunte Mergel” of Germany, but differ from the latter in larger size of valves, more growth bands, and the small umbo. However, the material of Reible (1962: pl. 9: 1, 2, fig. 16) is very poorly preserved and details of morphology are difficult to study (see also discussion in Seegis 1997 and Channell et al. 2003).

The specimens of *Laxitextella* sp. A from Krasiejów differ from those of *L. laxitexta* in their fine reticulate ornament (up to 10 meshes in median part), the presence of several closely spaced growth bands in ventral part of the carapace, and relatively more widely spaced growth bands in the median part of the carapace.

*Laxitextella* sp. A differs from *Laxitextella* sp. sensu Seegis 1997 in more delicate ornamentation on growth bands. It is similar in lateral outline and size of the valves to *Laxitextella forbesi* (Jones, 1862) from the Upper Triassic of Argentina, but the latter has granulate ornament on the growth bands. *L.* sp. A is also similar in ornamentation pattern to *Laxitextella* sp. sensu Tintori 1990.

**Occurrence.**—Late Carnian, Krasiejów, Poland.

#### Family Eosestheriidae Zhang and Chen, 1976 Genus *Menucoestheria* Gallego and Covacevich, 1998

*Type species:* *Menucoestheria terneraensis* Gallego, 1998.

**Discussion.**—*Menucoestheria* shows important similarities to *Howellsaura* Bock, 1953. They seem to belong to the same developmental trend of gradual change in ornamentation pattern during ontogeny, from reticulate in the dorsal growth bands to radial striae in the ventral growth bands. The *Howellsaura*–*Menucoestheria*–like forms probably represent the ancestral stock which gave rise to *Bairdestheria*, or *Eosestheria* Chen, 1976 (see Raymond 1946; Zhang et al. 1976; Chen and Shen 1985; Chen 1999).

As defined originally (Bock 1953a: 71), *Howellsaura* included species with growth bands ornamented by radial striae; radial anastomosing striae, or reticulate ornament. The Late Triassic (Keuper) species belonging to *Howellsaura* are also known from North America (Bock 1953a) and China (Zhang et al. 1976). Kobayashi (1954) and Tasch (1969) regarded *Howellsaura* and *Bairdestheria* Raymond, 1946, as junior subjective synonyms of *Euestheria* Depéret

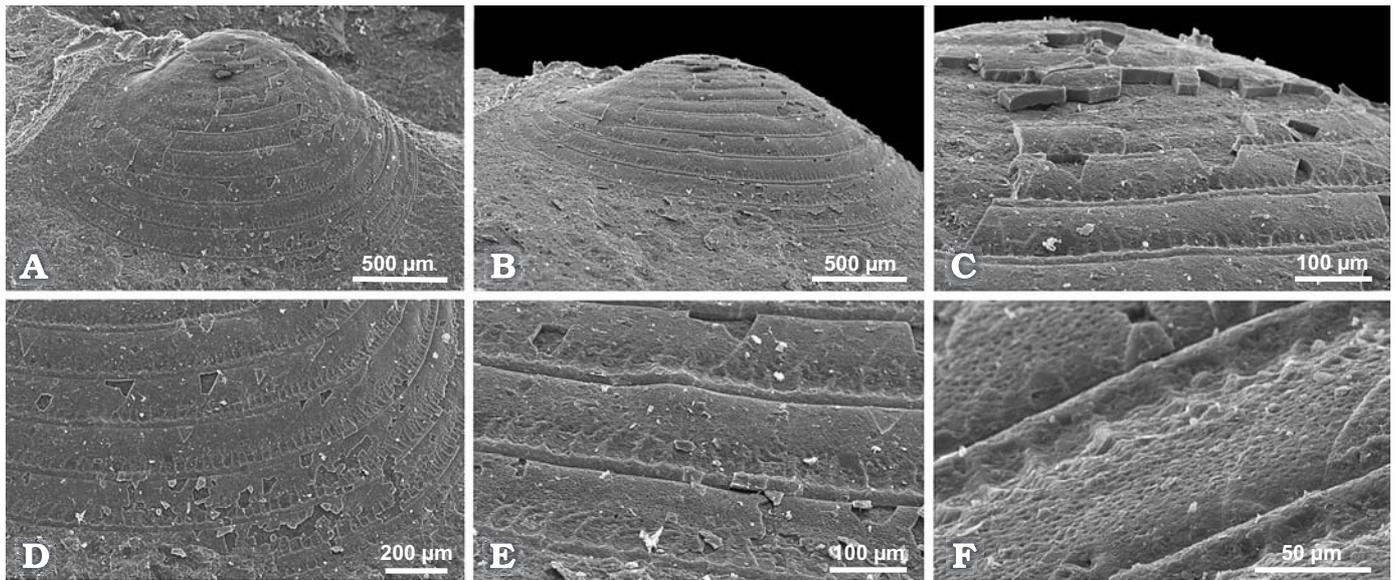


Fig. 11. *Krasiestheria parvula* gen. et sp. nov. Right valve ZPAL Cr. 6/5, holotype, in lateral view (A); in ventral view (B); the same with details of dorsal area (C); and details showing growth bands ornamentation, minute punctae pattern in upper part of each growth band and radial striae in lower part of each growth band (D–F).

and Mazeran, 1912. According to Kozur (1982), *Howellisaura* is a junior synonym of *Bairdestheria*.

#### *Menucoestheria bocki* sp. nov.

Figs. 5C, D, 9.

*Holotype*: ZPAL Cr. 6/29 (Fig. 9B).

*Type horizon and locality*: Late Triassic, late Carnian, Krasiejów, south-western Poland.

*Derivation of name*: In honour of Wilhelm Bock, a researcher of Triassic spinicaudatans.

*Diagnosis*.—Carapace oval in outline; moderate in size; growth bands ornamented with reticulation in dorsal and median areas of valve, passing into radial striae in ventral growth bands.

*Material*.—19 more or less fragmentary specimens.

Table 3. Measurements of *Menucoestheria bocki*.

Specimen ZPAL	Length (mm)	Height (mm)	Length of hingeline (mm)	No. of growth bands
Cr. 6/14	4.2	3.1	?	16?
Cr. 6/15	?	1.7	1.1	15
Cr. 6/19	4.4	2.6	?	?
Cr. 6/20	2.8	1.9	?	17
Cr. 6/21	3.5	2.1	?	17
Cr. 6/23	3.5	2.2	1.7	14?
Cr. 6/26	3.0	1.8	?	15
Cr. 6/27	4.8	3.1	3.0	19
Cr. 6/28	4.2	3.2	2.5	18?
Cr. 6/29	2.6	1.7	?	15

*Description*.—Carapace of moderate size, elliptical in outline, up to 4.8 mm long and 3.2 mm high; dorsal margin straight and long, umbo inset subcentral to subterminal, slightly raised above dorsal margin; anterior margin rounded, posterior more narrowly rounded; ventral margin slightly convex; growth lines 14–24 in number; dorsal and median growth bands representing younger moult stages ornamented by reticulate pattern, median-ventral growth bands ornamented by densely spaced, minute, slightly anastomosing radial striae, density of these structures averages about 10 per 0.20 mm.

*Remarks*.—*Menucoestheria bocki* sp. nov. exhibits a wide range of variation in its type of surface ornamental pattern (Fig. 9). The Polish material is similar to that of *Bairdestheria colombiana* (Bock, 1953) from the Rhaetic of Colombia (Bock 1953a: pl. 13: 5–7, 12) in having radial striae ornament in terminal growth bands and changing from anastomosing striae to reticulate ornament. *M. bocki* resembles representatives of *Menucoestheria* from the Late Triassic of Chile (Gallego and Covacevich 1998) in its carapace outline and appearance of the ornamentation pattern.

*Occurrence*.—Late Carnian, Krasiejów, Poland.

#### *Menucoestheria?* sp.

Figs. 5B, 10.

*Material*.—Two valves poorly preserved.

*Description*.—Carapace of moderate size, elliptical in outline, up to 5.8 mm long and up to 2.0 mm high; anterior and posterior margin rounded; umbo situated close to anterior end of dorsal margin; ventral margin slightly convex; more than 20 growth bands, ornamented by reticulate pattern in dorsal region and gradually changed into radial striae in lower part of each growth bands near ventral part of carapace.

*Remarks.*—*Menucoestheria*? sp. is morphologically similar to *Menucoestheria bocki*, but differs mainly in the presence of radial striae ornamentation occurring only in the lower part of the each growth band in ventral part.

*Occurrence.*—Late Carnian, Krasiejów, Poland.

### ?Family Palaeolimnadiidae Tasch, 1956

#### Genus *Krasiestheria* nov.

*Type species:* *Krasiestheria parvula* gen. et sp. nov.

*Derivation of name:* The name is derived from Krasiejów—type locality, and the genus name *Estheria*.

*Type horizon and locality:* Late Triassic, late Carnian, Krasiejów, south-western Poland.

*Diagnosis.*—A small spinicaudatan genus with subcircular outline; relatively large umbonal area; growth bands with ornamentation of minute punctae pattern in upper part of each growth band and radial striae in lower part of each growth band.

*Remarks.*—*Krasiestheria* shows certain resemblances to *Palaeolimnadia* Raymond, 1946, and to *Bilimnadia* Novojilov, 1960, in comparatively large umbonal region, but differs from them in its surface ornament pattern.

#### *Krasiestheria parvula* gen. et sp. nov.

Fig. 11.

*Holotype:* ZPAL Cr. 6/5, right valve (Fig. 11).

*Derivation of name:* From the Latin *parvulus*, very small.

*Type horizon and locality:* Late Triassic, late Carnian, Krasiejów, south-western Poland.

*Diagnosis.*—As for the genus.

*Material.*—Two valves.

*Description.*—Carapace of small size, up to 2.5 mm long and up to 1.6 mm high; subcircular in outline; anterior and posterior high nearly equal; dorsal margin straight; umbo of moderate size, 0.54 mm long, situated between its central and anterior end; anterior and posterior margins rounded, ventral margin curved; growth bands flattened, 14 in number, ornamented by radial striae occupying lower part of each growth band, upper parts of growth bands are finely punctated; width of interspace between growth lines gradually increasing from larval toward mature stage.

*Remarks.*—*Krasiestheria parvula* is characterized by its subcircular carapace, radial lines and punctate ornamentation of its growth bands, it is clearly distinct from any other described spinicaudatan species.

*Occurrence.*—Late Carnian, Krasiejów, Poland.

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