Journal of Paleontology

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Mass mortality of clam shrimp (Crustacea, Branchiopoda) from the Lower Devonian (Emsian) Fossil-Lagerstätte of Consthum, Luxembourg—paleoecologic and taxonomic implications

Invited Article

Cite this article: Poschmann M.J., Hegna T.A., Numberger-Thuy L., and Thuy B. 2025. Mass mortality of clam shrimp (Crustacea, Branchiopoda) from the Lower Devonian (Emsian) Fossil-Lagerstätte of Consthum, Luxembourg—paleoecologic and taxonomic implications. *Journal of Paleontology*, 1–13
https://doi.org/10.1017/jpa.2024.82

Received: 09 August 2024
Revised: 18 October 2024
Accepted: 22 October 2024

Guest Editor:
Carrie Schweitzer

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Abstract

The hitherto oldest known mass mortality of clam shrimp is described from the Early Devonian (Emsian) of Luxembourg. This (almost) monospecific clam shrimp association allows for a much more comprehensive assessment and understanding of preservational and ontogenetic variation in a single taxon, *Pseudestheria diensti* (Gross, 1934). This suggests that other taxa originally described from the "classical" Willwerath locality, the type locality of *P. diensti*, are variants of the latter, and thus *Pseudestheria subcircularis* Raymond, 1946 and *Palaeolimnadiopsis* ? *eifelensis* Raymond, 1946 are synonymized here with *P. diensti.* A further clam shrimp taxon, for which we propose a new species, *Palaeolimnadia stevenbeckeri* n. sp., is found in the same stratum, but not in the mass mortality layer itself. The clam shrimp mass mortality is interpreted to reflect sudden destruction of the original habitat on a delta plain and subsequent transport and burial in a marginal marine low-energy setting.

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Non-technical Summary

Clam shrimp are branchiopod crustaceans with a fossil record starting in the Early Devonian and consisting mainly of their bivalved carapaces. A new Fossil-Lagerstätte from Luxembourg yielded the oldest known mass mortality of clam shrimp, providing new insights into the extent of morphological/preservational variation within a single species. This allows us to show that some previously described "species" fall within this variation and must therefore be considered synonyms. Other finds are described as a new species. We assume that these clam shrimp populated a freshwater-dominated delta platform and were rapidly buried in a marginally marine environment following the destruction of their original habitat, possibly by a storm.

Introduction

The informal group of the clam shrimp encompasses the three monophyletic clades Laevicaudata Linder, 1945, Spinicaudata Linder, 1945, and Cyclestherida Sars, 1899 (Negrea et al., 1999; Richter et al., 2007; Olesen, 2009). The oldest unequivocal fossil clam shrimp known are from the Early Devonian (Hegna and Astrop, 2020; Hegna et al., 2020; Liao and Shen, 2022; Poschmann et al., 2024).

Until recently, the earliest record of clam shrimp was rather meager. Although Devonian clam shrimp are known from multiple sites on several continents, the individual faunas are often restricted to few specimens from insufficiently dated occurrences (e.g., Gross, 1934; Péneau, 1936; Maillieux, 1939; Defretin, 1950; Tasch, 1987; Boucot et al., 1989; Franke, 2006; Poschmann and Franke, 2006; Becker and Franke, 2012), although the situation started to improve with accounts on newly discovered finds (Liao and Shen, 2022; Poschmann et al., 2024).

Here we report on a new discovery of Early Devonian clam shrimp, which stands apart from previously reported finds as it represents an almost monospecific mass mortality averaging many thousands of specimens per square meter. Furthermore, this mass occurrence provides a way to assess preservational and intraspecific variation hitherto impossible for Early Devonian clam shrimp. This may have far-reaching implications for the taxonomy of early clam shrimp.

Materials and methods

Materials. The clam shrimp fossils described herein originate from the Rinnen Quarry west of Consthum in northern Luxembourg (Fig. 1). This locality has been known for some time to yield Early Devonian fossils, such as early land plants, bivalves, tentaculitids, arthropods, vertebrates, and trace fossils (Delsate et al., 2003). In 2022, two distinct fossiliferous layers of gray siltstone, each several decimeters thick, were detected and informally termed Consthum I and Consthum II. Note that "Consthum" without any suffix denotes the Rinnen Quarry near the village of Consthum, whereas particular fossil-bearing horizons have a suffix (I or II) following. Consthum I yielded mainly early land plants in association

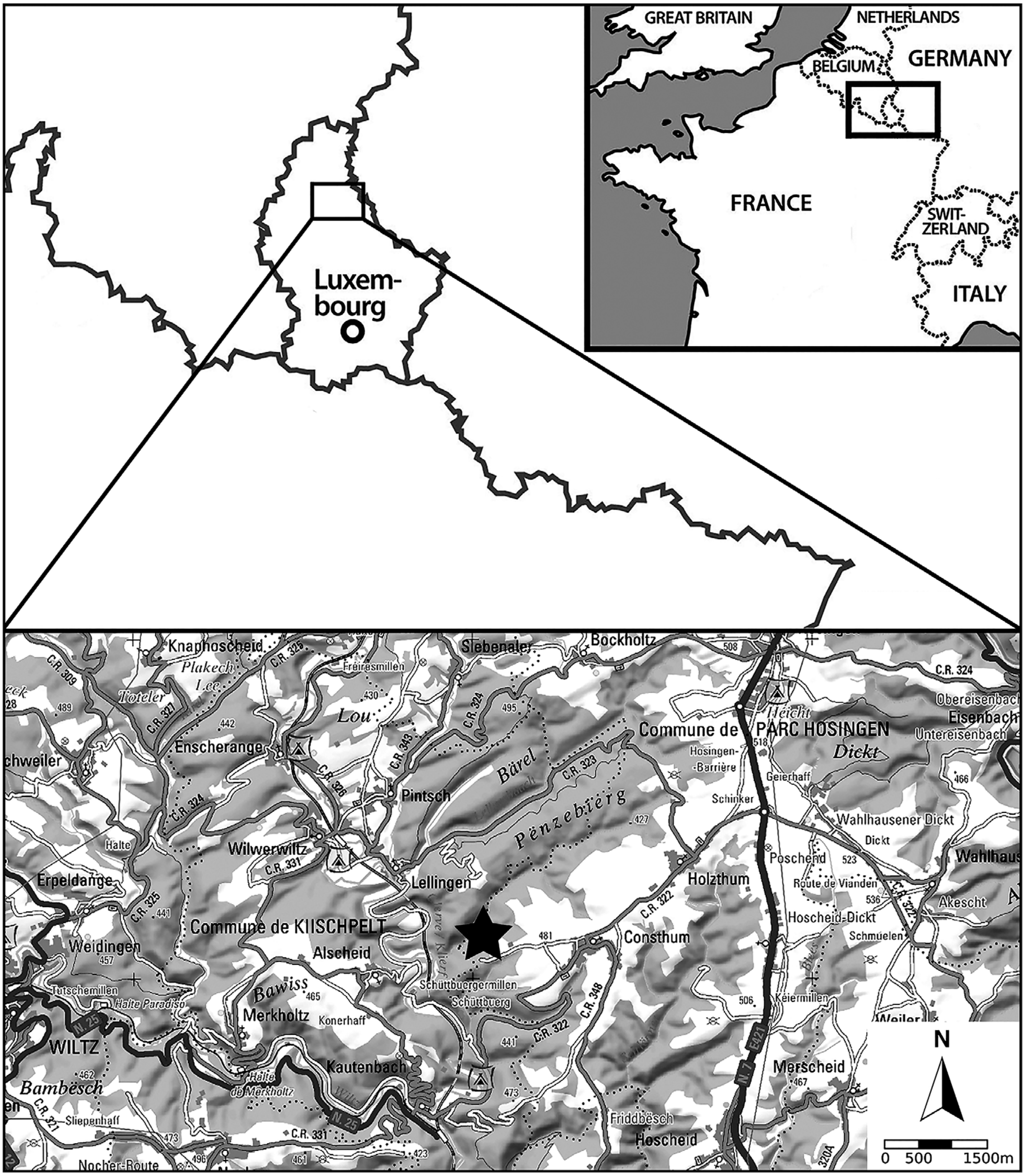

Figure 1. Geographical position of the Rinnen Quarry at Consthum, Luxembourg.

with some bivalves, placoderm plates, eurypterid remains, and leperditicopid ostracodes (Capel et al., 2024).

The clam shrimp mass mortality bed was excavated from Consthum II at the northeastern part of the Rinnen Quarry (coordinates 49.9779564966292, 6.035034995082548) in the years 2023 and 2024. This layer, a medium-gray mudstone, has a thickness of about 20 cm and yielded abundant fossils, in particular from its lower part. The strata at the Rinnen Quarry have an Early Devonian (lower Emsian) age (Lucius, 1950; Maquil et al., 1984; Poschmann and Franke, 2006; Dejonghe et al., 2017). Other fossils from Consthum II include a few fragments of early land plants, bivalves, lingulid brachiopods, isolated clam shrimp, rare ostracods, chelicerate arthropods such as the eurypterids and scorpions, and few vertebrate bony plates. In addition to the clam shrimp mass mortality, isolated clam shrimp specimens are scattered in the sediment. The new taxon described in the following is represented by only few isolated specimens from Consthum II.

Methods. Specimens were prepared using pneumatic chisels. Photographs were taken by M.J.P. with the specimens immersed in isopropanol using a Canon 600D SLR camera equipped with a Canon EF-S 60 mm or Canon MP-E 65 mm macro-lens. Line drawings were prepared by M.J.P. using Inkscape. Figure 1 was made by L.N.-T. using Photoshop. In the application of morphological and descriptive terms, we follow Scholze and Schneider (2015).

Repository and institutional abbreviation. All specimens are deposited in the National Museum of Natural History Luxembourg (MnhnL).

Systematic paleontology

Class **Branchiopoda** Latreille, 1817
Order **Diplostraca** Gerstaecker, 1866
Suborder **?Spinicaudata** Linder, 1945
Superfamily **Vertexioidea** Kobayashi, 1954 sensu Zhang et al., 1976 (= **Lioestheriacea** Raymond, 1946, emended Holub and Kozur, 1981, sensu Chen and Shen, 1985)
Family **?Lioestheriidae** Raymond, 1946

Diagnosis. See Scholze et al. (2019).

Remarks. As briefly outlined by Poschmann et al. (2024), the familial-level taxonomy of *Pseudestheria* and related genera is confusing, and repairing it is beyond the scope of the present work.

Genus ***Pseudestheria*** Raymond, 1946

Type species. Pseudestheria brevis Raymond, 1946; by original designation.

Diagnosis. Small to very large valves; oval to round shape; straight to slightly curved dorsal margin; umbo convexly curved, position of the umbo submedial to anterior and inframarginal to supramarginal; larval valve very small to small; variable number of growth lines; pitted (punctate) ornamentation (from Scholze et al., 2019; see also Scholze, 2021; Poschmann et al., 2024 for remarks).

Pseudestheria diensti (Gross, 1934)

Figures 2, 3.3–3.8, 4, 5.1–5.4, 6.1–6.6

1933 *Paracyclas rugosa* Goldfuß; Mauz, p. 275.
*1934 *Estheria diensti* Gross, p. 309, figs. 1–6, 8, 9.
1946 *Pseudestheria diensti*; Raymond, p. 244.
1946 *Palaeolimnadiopsis ? eifelensis* Raymond, p. 271.
1946 *Pseudestheria subcircularis* Raymond, p. 244.
1953a *Euestheria eifelensis*; Novozhilov, p. 948, fig. 2b.
1961 *Concherisma eifelense;* Novozhilov, p. 86 (in part).
1961 *Glyptoasmussia willweratica* Novozhilov, p. 62, fig. 25, pl. 15, fig. 5.
2006 *Estheria diensti*; Franke, pl. 11, fig. 2.
2012 *Estheria diensti*; Becker and Franke, pl. 2, figs. 7, 8.
2016 conchostracan; Poschmann et al., fig. 4b.
2024 *Pseudestheria diensti*; Poschmann et al., p. 543, figs. 2a–f, 6b, c, 7e, f, 9g, h.
2024 *Pseudestheria* cf. *P. diensti*; Poschmann et al., p. 545, figs. 3a–c, 6f.
2024 (?) *Palaeolimnadiopsis ? eifelensis*; Poschmann et al., figs. 3d, 6a.
2024 *Palaeolimnadiopsis ? eifelensis*; Poschmann et al., p. 556, figs. 4a–c, 6e.
2024 *Pseudestheria subcircularis*; Poschmann et al., p. 549, figs. 4d–f, 6d.

Holotype. The specimen figured by Gross (1934, fig. 5), now in the Museum für Naturkunde Berlin, Germany, number MB.A.0043 (Poschmann et al., 2024).

Description. Clam shrimp individuals attributed to *Pseudestheria diensti* were found scattered within the most fossiliferous layer. On one (?bedding) plane, the clam shrimp carapaces form laterally discontinuous pavements with a density of up to 30 specimens per 10 cm^2, which can be extrapolated to around 30.000 specimens per m^2.

In 33 measured, reasonably well-preserved specimens, the height ranges from (?1.6) 2.3 to 6.2 mm (average 4.1 mm), the length from (?2.4) 3.2 to 9.2 mm (average 5.9 mm), the length/width ratio from 0.55 to 0.89 (average 0.70), and the number of growth lines ranges from about 9 to 21 (Table 1). The specimens share the following morphological traits. Carapace shape elongate-oval to round with a weakly expressed umbo in anterior-median to median-anterior and marginal position, dorsal margin long and almost straight to very slightly curved, larval valve very small and hardly recognizable; microsculpture indistinct (as in the Willwerath specimens; see Poschmann et al., 2024), probably consisting of a dense, fine network of reticulate cells; some specimens among both, those with very high as well as those with very low height/length (H/L) ratios, show a longitudinal, fan-like striation in the region between umbo and posterior end of the dorsal margin. The striations originate from a common point near the umbo and are roughly perpendicular to the distal growth lines.

Remarks. The morphological traits and their variation observed in the Consthum clam shrimp mass layer correspond largely to the morphology and variation documented in the approximately contemporaneous Willwerath association (Poschmann et al., 2024), with the exception of size variation, which is much greater among the Consthum specimens, suggesting the presence of various growth stages. Clam shrimp from Willwerath were attributed to *Pseudestheria diensti* (Gross, 1934), *Pseudestheria subcircularis* Raymond, 1946, and *Palaeolimnadiopsis ? eifelensis* Raymond, 1946 (see Poschmann et al., 2024 for history of research). Poschmann et al. (2024) recorded a fourth morphotype closely corresponding to *Pseudestheria diensti* but with a slightly different carapace outline. These authors furthermore

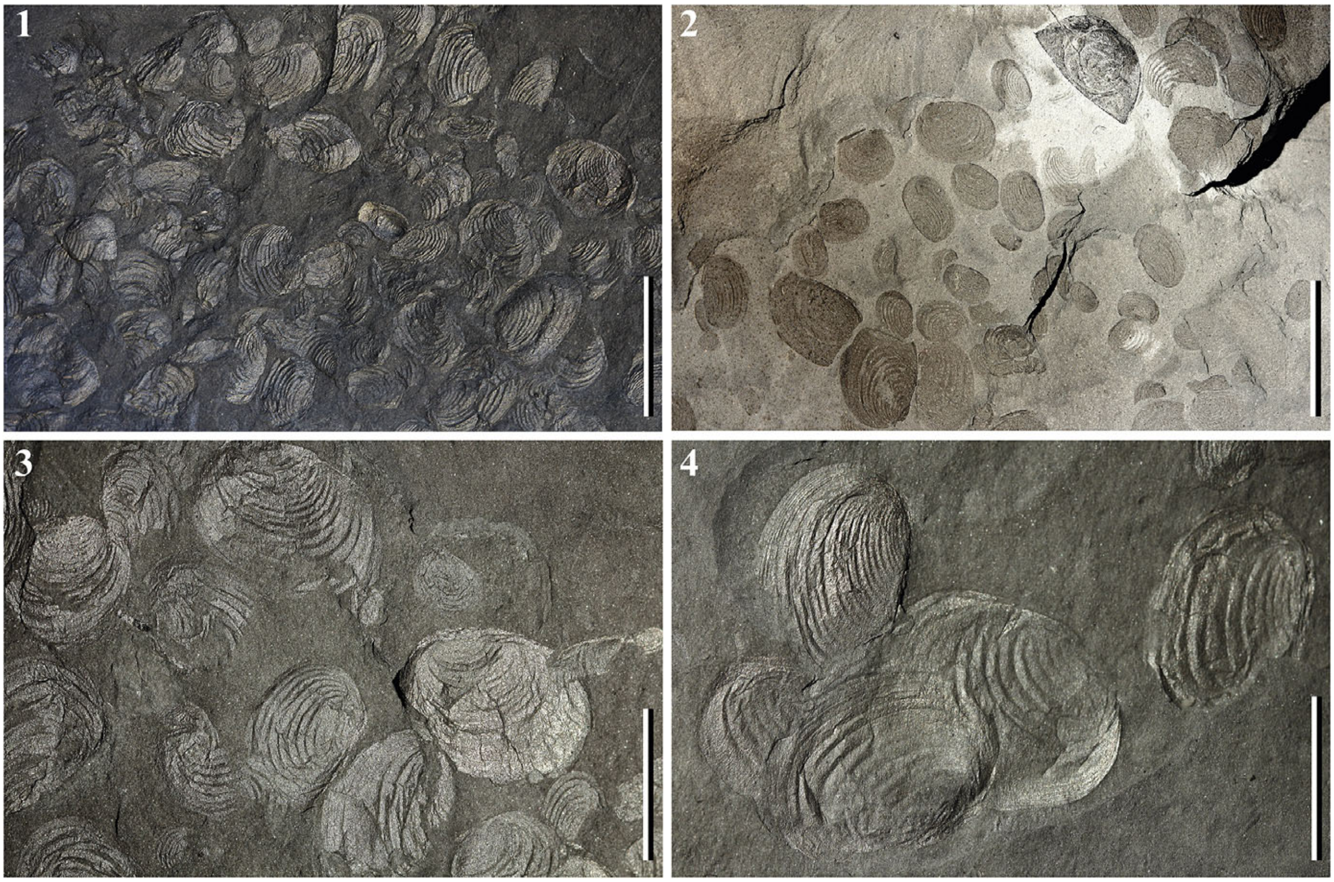

Figure 2. Examples from the Consthum clam shrimp mass layer. (**1**) Detail from slab EiB552b; note associated lingulid brachiopod near center. (**2**) Detail from slab EiB549a; note associated head shield of the eurypterid *Adelophthalmus sievertsi* (Størmer, 1969) (upper right), crossed polarizing filters. (**3**) Detail from slab EiB552a; note differences in size and form of dorsal margin. (**4**) Detail from slab EiB551a; note differences in the spacing of growth lines. (**1, 2**) Scale bars = 10 mm; (**3, 4**) scale bars = 5 mm.

stated that the observed differences in these taxa may be attributed to taphonomic/preservational and/or ontogenetic/sexual variation and suspected that all taxa previously described from Willwerath may represent just one species. *Pseudestheria subcircularis* and *Palaeolimnadiopsis* ? *eifelensis* should then be synonymized with *Pseudestheria diensti* as diagnosed by Scholze et al. (2019). Due to a very limited sample size from Willwerath (about a dozen specimens), Poschmann et al. (2024) refrained from a formal taxonomic act pending a larger base to substantiate their view. In his emendation of *Pseudestheria*, Martens (1983) showed, among other characters, a bending of growth lines along the dorsal margin at the contact of the left and right valves. This character state can be recognized only in appropriately three-dimensionally preserved specimens and could not be seen in the specimens from Willwerath (Poschmann et al., 2024). By contrast, some exceptionally preserved specimens from Consthum do show a fine, fan-like, subparallel striation at the dorsal margin (Figs. 4, 5.1, 5.3, 5.4, 6.1–6.4, 6.6), which corresponds to the structure elaborated by Martens (1983, 2020). This striation is interpreted to reflect a bending of the growth lines at the dorsalmost edge of each valve and their course along the “inner” dorsal rim (Martens, 1983, fig. 7). Thus, the actual hinge of the valves runs along a median depression. The presence of this feature, which in Martens’ (1983, 2020) view defines the family Pseudestheriidae Martens, 1983, furthermore backs an attribution to *Pseudestheria*, the most common Early Devonian genus (Liao and Shen, 2022). This feature may also explain some variation in our *Pseudestheria* samples, which seems unusual at first. We suspect that the particular morphology of the dorsal region in *Pseudestheria* in concert with various degrees of sediment cover of some parts and with a possible sexual dimorphism may have promoted different outlines of the valve as a result of compression as well as seemingly various degrees of protrusion of the umbo. The result is fossils with low (Figs. 3.8, 4.5, 5.4, 6.4) to high (Figs. 5.1–5.3, 6.5, 6.6) H/L ratios and straight (Figs. 3.6, 5.4, 6.4) to more rounded (Figs. 3.3, 3.4, 5.1–5.3, 6.5, 6.6) outlines of the dorsal margin—in other words, with an elongate “eifelensis preservation” to rounded “subcircular preservation.” In addition, Liao and Shen (2022) mentioned that among their specimens assigned to *Pseudestheria* cf. *P. diensti*, the carapace shape varies from oval and sub-oval to round and considered these different shapes as possibly due to compression deformation or sexual dimorphism. This fan-like feature on the dorsal margin may be distinctive, but it cannot yet be treated as a phylogenetic panacea. Although it may be widespread, we cannot as yet determine exactly how widespread it is among clam shrimp due to the rarity of its preservation. Martens’ (1983, 2020) interpretation of the feature implies that we should often see the outer growth lines overprinted on the fan-like lines in compressed fossils with rigid carapaces. While we see this in the specimens illustrated by Tasch (1975a, note: Tasch’s specimens have the fan-like lines at a significantly higher angle than in the Consthum II specimens), we do not see overprinting in the Consthum specimens. In a re-examination of the type specimen of *Palaeolimnadiopsis* (T.A.H.), we did not see the fan-like dorsal lines mentioned by Martens (1983). (Note: Raymond, 1946, spelled *Palaeolimnadiopsis* two different ways,

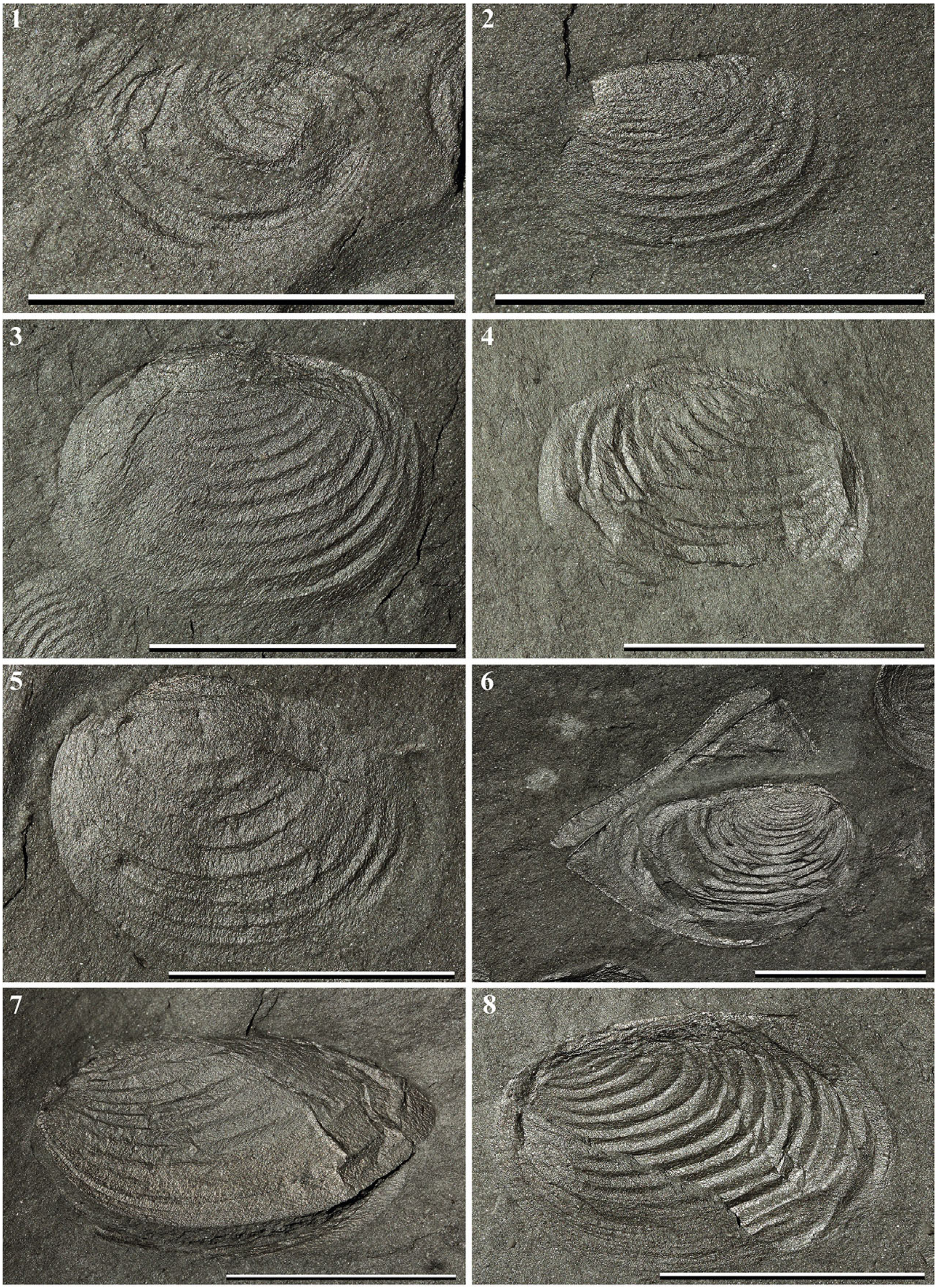

Figure 3. Individual clam shrimp specimens from the Consthum mass layer. (**1**) Undetermined, relatively small specimen EiB551b_3. (**2**) Undetermined, relatively small specimen EiB551b_4. (**3**) *Pseudestheria diensti*, mid-sized specimen, EiB551b_7. (**4**) *Pseudestheria diensti*, mid-sized specimen, EiB551b_5. (**5**) *Pseudestheria diensti*, EiB551b_2. (**6**) *Pseudestheria diensti* overlying *Adelophthalmus sievertsi* head shield, EiB551a_5. (**7**) *Pseudestheria diensti*, large specimen, EiB551b_10; note protruding right valve at lower margin. (**8**) *Pseudestheria diensti*, large specimen; note bivalved preservation. Scale bars = 5 mm.

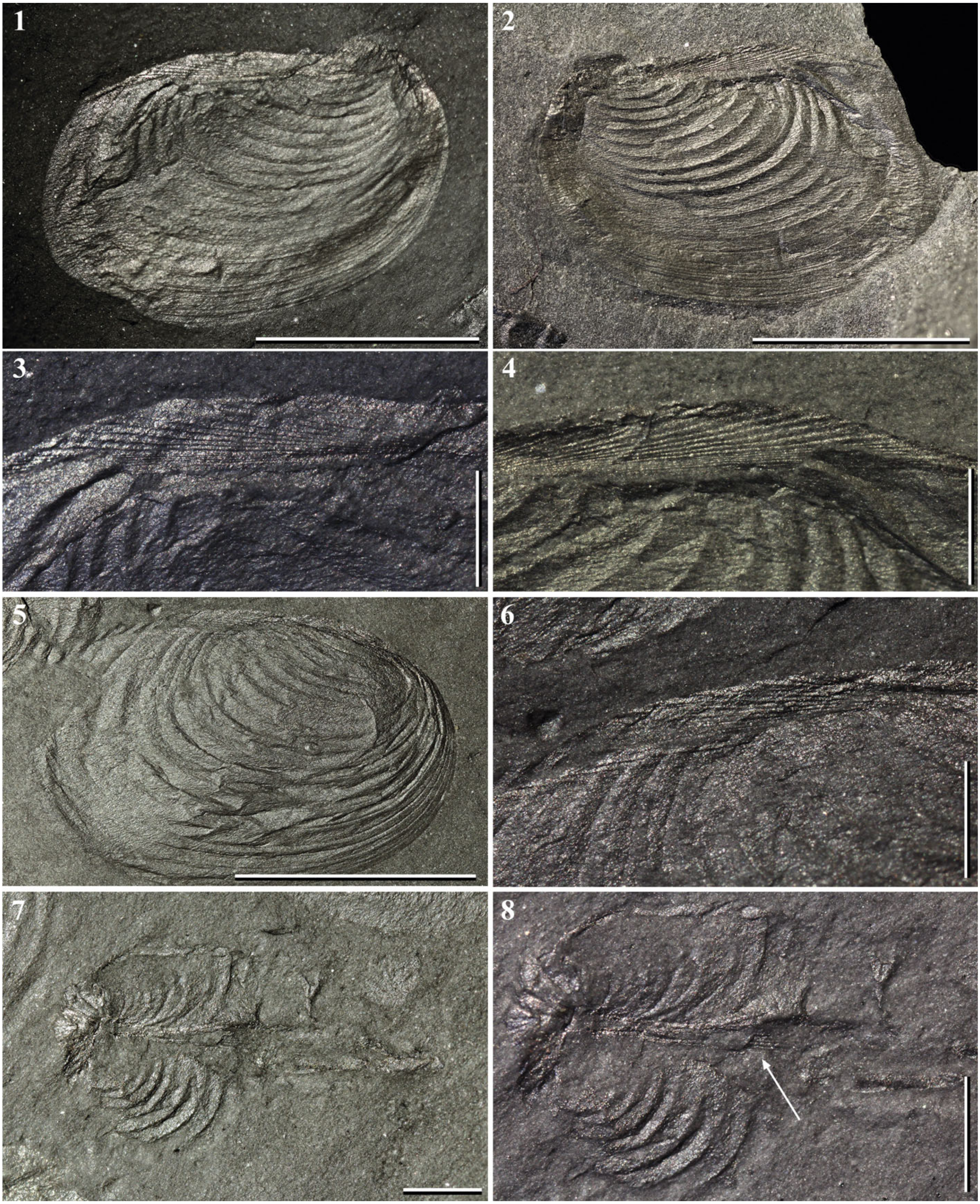

Figure 4. *Pseudestheria diensti* from Consthum showing striated dorsal regions. (**1, 2**) Specimen EiB535a and b, part and counterpart, respectively. (**3, 4**) Details from the dorsal regions in (**1**) and (**2**), respectively. (**5, 6**) Specimen EiB551b_1 and detail from the dorsal region, respectively. (**7, 8**) Specimen EiB551b_13 in dorsal view and detail, respectively; arrow indicates striation. (**1, 2, 5**) Scale bars = 5 mm; (**3, 4, 6–8**) scale bars = 1 mm.

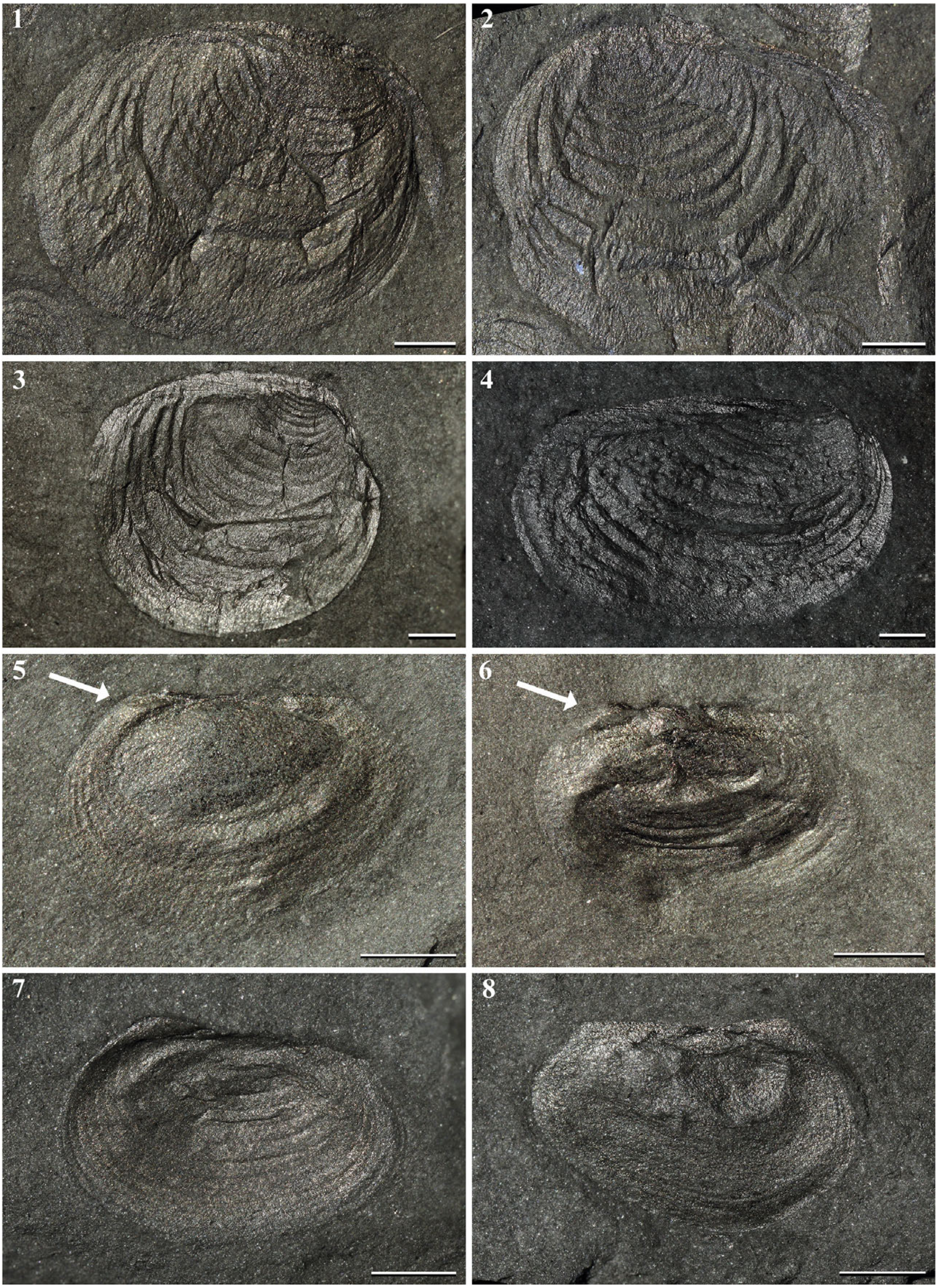

Figure 5. (**1–3**) *Pseudestheria diensti* from Consthum, specimens with high H/L ratios. (**1**) Specimen EiB552b_2. (**2**) Specimen EiB552b_3. (**3**) Specimen EiB560a. (**4**) *Pseudestheria diensti* from Consthum, specimen with low H/L ratio, EiB559a. (**5–8**) *Palaeolimnadia stevenbeckeri* n. sp. from Consthum. (**5**) Holotype EiB555. (**6**) Slightly deformed paratype EiB558. (**7**) Paratype EiB702. (**8**) Paratype EiB722. White arrows indicate anterodorsal swelling. Scale bars = 1 mm.

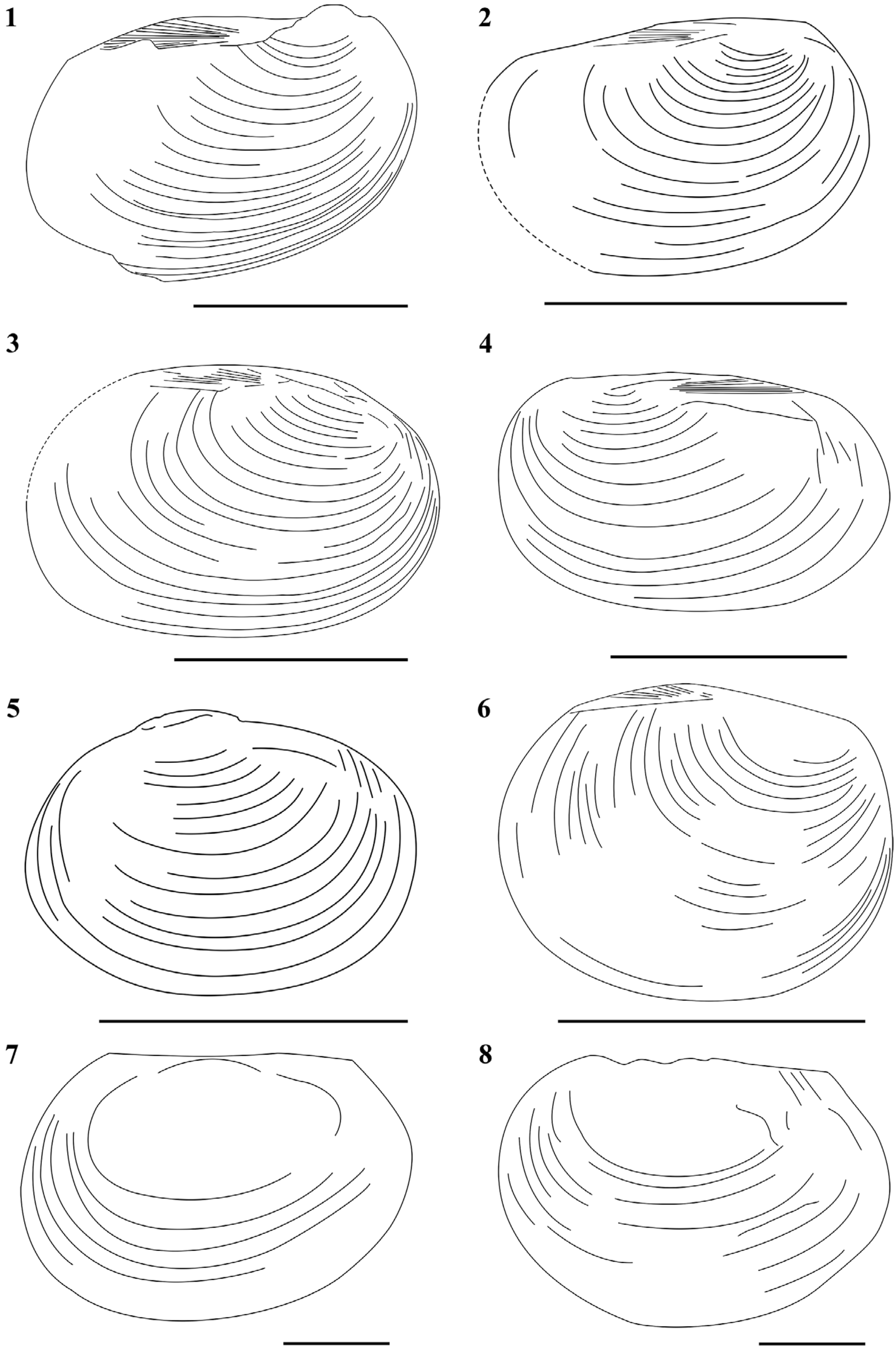

Figure 6. Line drawings of clam shrimp from Consthum. (**1–6**) Variation in *Pseudestheria diensti.* (**1**) Specimen EiB535a. (**2**) Specimen EiB551a_5. (**3**) Specimen EiB551b_1. (**4**) Specimen EiB559b. (**5**) Specimen EiB551b_7. (**6**) Specimen EiB552b_2. (**7, 8**) *Palaeolimnadia stevenbeckeri* n. sp. (**7**) Holotype EiB555. (**8**) Paratype EiB558. (**1–6**) Scale bars = 5 mm; (**7, 8**) scale bars = 1 mm.

Table 1. Morphometric data of *Pseudestheria diensti* from Consthum.

Specimen	Height	Length	H/L	Approximate number of visible growth lines
EiB535	6.2	9.2	0.67	21
EiB549a_01	3.2	5.1	0.63	13
EiB549a_02	2.5	4.2	0.60	12
EiB549a_03	4.0	5.0	0.80	—
EiB549a_04	2.5	4.1	0.61	11
EiB549a_05	4.5	6.0	0.75	15
EiB549a_06	3.6	4.1	0.88	11
EiB549a_07	3.2	4.0	0.80	11
EiB549a_08	2.6	3.9	0.67	—
EiB549a_09	3.1	5.6	0.55	12
EiB549a_10	3.0	4.3	0.70	11
EiB549a_11	3.0	4.5	0.67	12
EiB549a_12	2.5	3.6	0.69	11
EiB549a_13	4.0	5.5	0.73	12
EiB549a_14	4.3	7.0	0.61	13
EiB549a_15	3.0	4.3	0.70	12
EiB549a_16	2.3	3.2	0.72	11
EiB549a_17	1.6	2.4	0.67	9
EiB551a_st5_18	4.1	6.3	0.65	17
EiB552a_st2_19	4.6	6.3	0.73	13
EiB551a_st3_20	5.1	8.9	0.57	15
EiB551a_st7_21	4.4	7.2	0.61	—
EiB551a_st7_22	4.8	7.4	0.65	16
EiB551a_st9_23	4.8	6.6	0.73	14
EiB551a_st9_24	6.0	7.9	0.76	17
EiB551a_st9_25	5.8	7.2	0.81	17
EiB551b_st1	5.6	8.9	0.63	19
EiB551b_st2	5.1	6.3	0.81	10
EiB551b_st7	4.2	5.9	0.71	14
EiB552b_st2	5.3	6.4	0.82	17
EiB552b_st3	4.5	5.9	0.76	16
EiB559	4.9	7.8	0.63	14
EiB560	5.6	6.3	0.89	18
∑	1,353	1,931	2,321	
average (N = 33)	4.1	5.9	0.70	

Paleolimnadiopsis [p. 270] and *Palaeolimnadiopsis* [p. 271, at the introduction of *P. carpenteri*]. As the first usage (*Paleolimnadiopsis*) is the only instance of that spelling outside of the table of contents, we regard it as an error; Raymond likely intended *Palaeolimnadiopsis* as the proper spelling.) Thus, we feel that use of this feature to unite *Pseudestheria* and *Palaeolimnadiopsis* is invalid. *Palaeolimnadiopsis* itself does not seem to be a synonym of *Pseudestheria*. *Palaeolimnadiopsis* is represented by a number of distinctive species later in the Paleozoic. We suspect that some of the Devonian species assigned to *Palaeolimnadiopsis* may need re-evaluation.

It is a fortunate circumstance that shortly after the revision of Rhenish Lower Devonian clam shrimp by Poschmann et al. (2024), the Consthum clam shrimp mass layer was discovered in the summer of 2023. With the additional evidence at hand, we can now substantiate that both the Willwerath association and the Consthum mass layer association comprise (mainly) clam shrimp that share important morphological characters and differ mainly in size, the (corresponding) number of recognizable growth lines, and H/L ratios (elongate oval to round). The observed variation can be attributed to intraspecific variability (ontogeny and possibly sexual dimorphism/ecophenotypic variability) and preservation (tectonic and compressional deformation), and perhaps sediment still covering deeply buried parts (for examples of preservational/intraspecific variation in clam shrimp, see e.g., Kozur, 1983; Martens, 1983, 2020; Kozur and Weems, 2005, 2010; Gosny, 2010; Astrop et al., 2012; Gallego et al., 2013; Scholze et al., 2015, 2017, 2019; Geyer and Kelber, 2018; Hethke et al., 2018, 2021; Sell, 2018; Hethke and Weeks, 2020). We found only simple correlations of length to height of the valves or number of growth lines and valve length, while the number of growth lines remains generally the same in (similarly sized) elongate and rounded specimens. Furthermore, the feature of a striated dorsal margin has been documented in both elongate and rounded specimens (Figs. 5, 6). It is thus impossible to draw a clear demarcation between these forms.

In our view, it is warranted to formally synonymize *Pseudestheria subcircularis* with *Pseudestheria diensti* as already suspected by Poschmann et al. (2024). Present evidence suggests that *Palaeolimnadiopsis* ? *eifelensis* is a preservational variant of *Pseudestheria diensti* (Poschmann et al., 2024) as well (although, as outlined in the preceding, this does not seem to apply more broadly to other species assigned to *Palaeolimnadiopsis*). Approximately contemporaneous clam shrimp from the Lower Devonian of Belgium and France (Maillieux, 1939; Defretin, 1950) and originally designated *Estheria (Euestheria) stockmansi* Maillieux, 1939 need re-examination and revision and will not be considered herein (see discussion in Poschmann et al., 2024).

Family **Paleolimnadiidae** Tasch, 1956 sensu Zhang et al., 1976

Diagnosis. Carapace with a large larval shell and few growth lines, smooth to faintly reticulate ornamentation. Limnadiform and cycladiform carapace shapes (translation from Zhang et al., 1976; see Astrop and Hegna, 2015).

Remarks. Astrop and Hegna (2015) observed that past conceptions of the family (i.e., Zhang et al., 1976) implied that it was paraphyletic, and Sun and Cheng (2022) hypothesized that the family might be polyphyletic due to the variance in ornamentation patterns. Usage of Paleolimnadiidae herein is not meant to imply monophyly. Indeed, the general diagnosis seems to suggest that paleolimnadiids are perhaps plesiomorphic vertexioids with large larval shells. The large larval shell is likely due to the initiation of carapace molt retention happening later in ontogeny.

Genus ***Palaeolimnadia*** Raymond, 1946

Type species. *Estheria wianamattensis* Mitchell, 1927; by original designation.

Palaeolimnadia stevenbeckeri new species

Figures 5.5–5.8, 6.7, 6.8

Holotype. Figures 5.5, 6.7; specimen Eib555 (left valve, part only).

Diagnosis. A species of *Palaeolimnadia* with large (up to 3.6 mm long), oval carapace with straight to slightly concave and short dorsal margin, and with a slight bump in anterodorsal position; up to 13 (usually 6–10) growth lines; umbo in submedial and marginal position; larval valve moderately large.

Occurrence. Rinnen Quarry west of Consthum, fossil-bearing layer "Consthum II," at the northeastern part of quarry (coordinates 49.97799, 6.03504). Lower Devonian, lower Emsian Klerf Formation (Schuttbourg Member of the Our Formation sensu Dejonghe et al., 2017).

Description. Carapace large (L = 3.5–3.6 mm; H = 2.4–2.5 mm), shape oval (H/L = 0.69), with a slight swelling or bump in anterodorsal position (white arrow in Fig. 5.5, 5.6); dorsal margin straight to slightly concave and short (length of the dorsal margin (l) = 2.1–2.3 mm, l/L = 0.60–0.64); umbo in submedial and marginal position; larval valve small to large (height of the larval valve (h)/H = 0.44–0.5, about 0.25 in EiB702); up to 10 growth lines (about 13 in EiB702); ornamentation indistinct, possibly faintly reticulate.

Etymology. For Steven Becker (formerly Carrière Rinnen, Consthum), without whose generous help the Consthum excavations would not have been possible.

Additional material. Paratypes Eib558 (slightly deformed left valve, part only), EiB702 (right valve, part and counterpart), and EiB722 (right valve, part and counterpart).

Remarks. The second species present at Consthum is rare and found scattered in the sediment; it has not been recorded from the *Pseudestheria* mass occurrence. It has a relatively small carapace with a comparatively large, unornamented larval valve and straight dorsal margin and is therefore assigned to *Palaeolimnadia.* It shows a conspicuous small swelling or bump in anterodorsal position of the valve, which is probably not preservational but a genuine character of this species. In contrast to Bulbilimnadiidae Kozur and Weems, 2005, this swelling is situated anterior to, and not on, the larval valve. One specimen (EiB702; Fig. 5.7) has a higher number of growth lines and a smaller larval valve than other specimens assigned to this species. As it perfectly agrees in all other features with comparable specimens, it is assigned here to the same species. Whether this variation is due to preservation or may have some taxonomic significance can be reliably assessed only when more material is available. The new species is easily distinguishable from other Ardenno–Rhenish Early Devonian taxa, including the Belgian and French fossils (cf. Maillieux, 1939; Defretin, 1950; Poschmann et al., 2024). It is comparable (slightly larger) in size to the type species *P. wianamattensis* (Mitchell, 1927) but shows a straighter or even slightly concave dorsal margin. Considering that the occurrence of fossil spinicaudatan clam shrimp species is assumed to have at least some stratigraphical significance, we refrain from a comparison of our Early Devonian species with the Permian to Mesozoic *Palaeolimnadia*-like species, especially given the vast number of species, which includes many potential synonyms (e.g., Tasch, 1975b, 1987; Zhang et al., 1976; Kozur and Weems, 2010; Gallego et al., 2020, and literature therein). *Palaeolimnadia* is distributed mainly from the Late Permian to Jurassic, but Devonian records are rare. *Palaeolimnadia subquadrata* Novozhilov, 1953b from the Devonian of Kazakhstan is a much larger (6.4 mm long) and more rounded (H/L ratio 0.83) species. ?*Palaeolimnadia* sp. from the Emsian of Hunnan Province, China, is a larger species with a somewhat smaller (estimated) H/L ratio (0.60 versus 0.69) (Liao and Shen, 2022). *Palaeolimnadia atava* Liu in Liu and Gao, 1985 is comparable in size (up to 3.7 mm long, 2.3 mm high), whereas *P. changyangensis* Liu in Liu and Gao, 1985 and *P. luoyanshanensis* Liu in Liu and Gao, 1985 are smaller species. These three species from the Late Devonian of Hubei Province, China, all differ in lacking an anterodorsal carapace swelling and the associated tendency for a slightly concave dorsal margin.

Taphonomy/paleoecology

In Early Devonian times, the Rhenish Shelf was situated south of the Old Red Continent at the southern margin of Laurussia. The so-called Rhenish or rhenotypic siliciclastic facies (Jansen, 2016) of the Siegenian and Emsian was characterized by generally shallow water and huge amounts of clastic sediments delivered by rivers from the north accumulated to kilometer-thick siliciclastic successions on the subsiding shelf (e.g., Meyer and Stets, 1980; Walliser and Michels, 1983; Stets and Schäfer, 2002, 2011). This resulted in the formation of a deltaic system that extended several hundred kilometers along the coastline with a scale that may have resembled the present-day Mississippi Delta (Grigowski and McCann, 2021). The angle of the delta front slope is assumed to have been gentle with facies changes being gradual and extending over larger distances making the interpretation of the position of particular outcrops within the larger deltaic system difficult (Stets and Schäfer, 2002; Elkholy and Gad, 2006; Grigowski and McCann, 2021). However, for the clam shrimp associations of Willwerath and Waxweiler, a more proximal nonmarine, limnic–brackish paleoecological setting on the delta platform has been assumed (e.g., Poschmann and Tetlie, 2006; Becker and Franke, 2012; Poschmann et al., 2024). The Consthum depositional setting may have been positioned at the subaquatic delta platform in a brackish environment, possibly a lagoonal setting receiving freshwater-dominated input from more proximally situated areas. This would be in accordance with a large amount of parautochthonous elements probably introduced from nearby intertidal to terrestrial settings (land plants, clam shrimp, scorpions) in association with probably autochthonous to parautochthonous bivalves (*Limoptera* (*Klinoptera*) cf. *L.* (*K.*) *diensti* Dahmer, 1942 and *Archanodon* sp. among others) and lingulids with a preference for brackish environments. Most of the associated arthropod fossils probably represent exuviae, whereas the bivalves are, at least partly, preserved with their valves in articulation and in life position. In contrast to the clam shrimp association of Waxweiler "LCMO" (leperditicopid-clam shrimp mass occurrence, Table 2; see Poschmann et al., 2024 for details), many clam shrimp at Consthum are preserved with their valves articulated (e.g., Fig. 3.7, 3.8) but not in butterfly position (we recorded only one exception; Fig. 4.7, 4.8). Preservation in butterfly position has been interpreted as indicating decay or severing of the carapace adductor muscle (Poschmann et al., 2024). This noticeable difference in preservation suggests rapid burial of the Consthum clam shrimp coinciding with or shortly following death with the adductor muscle still intact. Reible (1962), in a statistical evaluation of Triassic clam shrimp from Germany, stated that brackish

Table 2. Overview of clam shrimp taxa recorded from associations of the Ardenno–Rhenish Early Devonian (updated from Poschmann et al., 2024; for details on the associations see there).

	Willwerath	Waxweiler LCMO	Waxweiler 102022	Consthum II
Pseudestheria diensti (Gross, 1934)	X		X	X
Cornia wasvilrensis Poschmann et al., 2024			X	
Palaeolimnadiopsis frankeorum Poschmann et al., 2024		X		
Palaeolimnadiopsis sp. cf. *P. frankeorum*			X	
Palaeolimnadia stevenbeckeri n. sp.				X
Eicheleaia wenndorfi Poschmann et al., 2024			X	
Unassigned morphotype 2		X		
Unassigned *Asmussia*-like morphotype			X	
Unassigned *Ulugkemia*-like (? preservational) morphotypes			X	

environments tend to yield species-poor associations rich in individuals, while it is the other way around in freshwater. If this applies to Early Devonian clam shrimp, a stronger brackish influence may be indicated at Consthum than at Waxweiler (Table 1). Until now, the only fossils indicating a marine influence in the Rinnen Quarry succession are few tentaculitids from the base of the Consthum II layer. These may have been introduced by storms as has been observed in comparable facies from the Nellenköpfchen Formation (e.g., Poschmann, 2017). Remains of echinoderms or trilobites have not been observed by us. A homalonotid trilobite record from Consthum (Van Viersen and Prescher, 2009) relies on a historical find and may not necessarily originate from the actual quarry but from the wider area (A. Van Viersen, written communication, 2024). Very shallow water is indicated by the presence of trackways of myriapod-like arthropods (*Diplichnites* isp.) and supposed microbially induced sedimentary structures somewhat higher in the sequence. In other parts of the quarry, we recorded the presence of channel lag deposits and plant root-like/rhizome structures, again indicating very shallow water or even terrestrial conditions. In the formation of the clam shrimp mass mortality, a flooding event during heavy rain or the destruction of a floodplain pond, the original habitat of the clam shrimp, by streaming water (?channel) may have been involved. In either case, an entire clam shrimp population comprising various ontogenetic stages of *Pseudestheria diensti* has been killed and washed into a more distally positioned low-energy depositional environment.

Conclusion

The Consthum clam shrimp mass mortality provides an interesting view on the paleoecology of clam shrimp early in the evolutionary history of the group. The association of the Consthum II Lagerstätte is interpreted as representing an association of organisms populating the freshwater-dominated delta platform and having been introduced into a subaquatic depositional environment probably positioned in a more distal position on the delta platform. There the clam shrimp were rapidly buried together with other organisms, mainly bivalves and lingulids, adapted to marginally marine, possibly brackish waters.

In terms of taxonomy, the Consthum clam shrimp provide an example of preservational/intraspecific variation in a clam shrimp population that emphasizes that the erection of taxa based on limited information available from published figures alone bears a great risk of creating synonyms. This practice likely accounts for a vast number of unjustified names (Goretzki, 2003) and should be abandoned.

Acknowledgments. We thank all the people involved in the fieldwork at Consthum, namely, K. Bernacki, R. Felten, N. Frenkel, L. Garbay, A. Hellemond and his students, F. Lerouge, S. Olive, H. Rapin, C. Rollinger, A. Sluiter, C. Sumrall, A. Thill, S. Voigt, and A. Van Viersen, S. Becker (Burden) and his staff for technical help, the management of the Rinnen Quarry at Consthum for access to the site, S. Voigt (Kusel) and A. Hellemond (Brussels) for discussions on depositional environments, A. Van Viersen (Maastricht) for useful hints, and the reviewers S. Charbonnier (Paris) and O.F. Gallego (Corrientes), whose comments improved an earlier version of the present article.

Competing interests. The authors declare no competing interests.

References

Astrop, T.I., and Hegna, T.A., 2015, Phylogenetic relationships between living and fossil spinicaudatan taxa (Branchiopoda Spinicaudata): reconsidering the evidence: *Journal of Crustacean Biology*, **v. 35**, p. 339–354, https://doi.org/10.1163/1937240X-00002317.

Astrop, T.I., Park, L.E., Brown, B., and Weeks, S.C., 2012, Sexual discrimination at work: spinicaudatan 'clam shrimp' (Crustacea: Branchiopoda) as a model organism for the study of sexual system evolution: *Palaeontologia Electronica*, **v. 15**, n. 20A, 15 p., https://doi.org/10.26879/307.

Becker, G., and Franke, C., 2012, Über Ostracoden in Luxemburg und West-Eifel – das Ardenno-rheinische Unter-Devon im Spannungsfeld zwischen Oldred-Kontinent und Gondwana – ein Beitrag zur Biogeographie des Variszikum, *in* Franke, C., ed., *Beiträge zur Paläontologie des Unterdevons Luxemburgs (3)*: Ferrantia, **v. 68**, p. 65–116.

Boucot, A.J., McClure, H.A., Alvarez, F., Ross, J.R.P., Taylor, D.W., Struve, W., Savage, N.N., and Turner, S., 1989, New Devonian fossils from Saudi Arabia and their biogeographical affinities: *Senckenbergiana Lethaea*, **v. 69**, p. 535–597.

Capel, E., Cascales-Miñana, B., Prestianni, C., Servais, T., Steemans, P., Poschmann, M., and Thuy, B., 2024, A new Early Devonian flora from Consthum Quarry (Luxembourg): *Review of Palynology and Palaeobotany*, **v. 331**, n. 105199, https://doi.org/10.1016/j.revpalbo.2024.105199.

Chen, P.-J. (陈丕基), and Shen, Y.-B. (沈炎彬), 1985, *[An Introduction of Fossil Conchostracans]*: Beijing, Science Press, 242 p., 26 pls. [in Chinese]

Dahmer, G., 1942, Die Aviculide *Klinoptera* Dienst: *Senckenbergiana*, **v. 25**, p. 103–111.

Defretin, S., 1950, Crustacés fossiles du Dévonien de l'Artois et du Boulonnais: *Annales de la Société Géologique du Nord*, **v. 70**, p. 55–66.

Dejonghe, L., Colbach, R., and Goemaere, E., 2017, The lithostratigraphy of the lower Devonian formations of the Eisleck region (northern Luxembourg). Comparison with their Belgian lateral equivalents: *Geologica Belgica*, **v. 20**, p. 33–42.

Delsate, D., Steur, H., Schneider, M., and Thuy, B., 2003, Preliminary report of lower to middle Emsian (Lower Devonian) flora and fauna from Consthum and Merkholtz (Grand Duchy of Luxembourg) with porolepid (Sarcopterygii) and heterostracan fish remains: *Travaux scientifiques du Musée national d'histoire naturelle Luxembourg*, **v. 36**, p. 9–27.

Elkholy, H., and Gad, J., 2006, Die Wied-Gruppe (vormals Hunsrückschiefer): Eine neue lithostratigraphische Einheit am Nordrand der Moselmulde – Untersuchungen zu ihrer faziellen und stratigraphischen Einordnung: *Mainzer geowissenschaftliche Mitteilungen*, **v. 34**, p. 49–72.

Franke, C., 2006, Die Klerf-Schichten (Unter-Devon) im Großherzogtum Luxemburg, in der Westeifel (Deutschland) und im Gebiet von Burg Reuland (Belgien): fazielle und biostratigraphische Deutungen, *in* Franke, C., ed., *Beiträge zur Paläontologie des Unterdevons Luxemburgs (1)*: Ferrantia, **v. 46**, p. 42–96.

Gallego, O.F., Monferran, M.D., Astrop, T.I., and Zacarías, I.A., 2013, Reassignment of *Lioestheria codoensis* Cardoso (Spinicaudata, Anthronestheriidae) from the Lower Cretaceous of Brazil: systematics and paleoecology: *Revista Brasileira de Paleontologia*, **v. 16**, p. 47–60.

Gallego, O.F., Monferran, M.D., Stigall, A.L., Zacarias, I.A., Hegna, T.A., Jiménez, V.C., Bittencourt, J.S., Li, G., and Barrios Calathaki, H.G., 2020, The Devonian–Cretaceous fossil record of "conchostracans" of Africa and their paleobiogeographic relationships with other Gondwanan faunas: *Journal of African Earth Sciences*, **v. 161**, n. 103648, https://doi.org/10.1016/j.jafrearsci.2019.103648.

Gerstaecker, K.E.A., 1866, Gliederfüssler (Arthropoda), *in* Bronn, H.G., ed., *Die Klassen und Ordnungen des Tierreichs 5*: Leipzig, Akademische Verlagsgesellschaft, 1029 p.

Geyer, G., and Kelber, K.-P., 2018, Spinicaudata ("Conchostraca", Crustacea) from the middle Keuper (Upper Triassic) of the southern Germanic Basin, with a review of Carnian–Norian taxa and suggested biozones: *Paläontologische Zeitschrift*, **v. 92**, 34 p., https://doi.org/10.1007/s12542-017-0363-7.

Goretzki, J., 2003, Biostratigraphy of conchostracans: a key for the interregional correlations of the continental Palaeozoic and Mesozoic—computer-aided pattern analysis and shape statistics to classify groups being poor in characteristics [Ph.D. dissertation]: Freiberg, Institut für Geologie, TU Bergakademie Freiberg, 243 p.

Gosny, O., 2010, Conchostraken und leperditicopide Ostracoden aus der mitteldevonischen Brandenberg-Formation des Bergischen Landes: *Decheniana (Bonn)*, **v. 163**, p. 159–167.

Grigowski, E., and McCann, T., 2021, Palaeogeography of the Rhenish Slate Mountain region during the Early Devonian: *Zeitschrift der Deutschen Gesellschaft für Geowissenschaften*, **v. 172**, p. 47–62, https://doi.org/10.1127/zdgg/2021/0252.

Gross, W., 1934, Eine *Estheria* aus dem rheinischen Unterdevon: *Senckenbergiana*, **v. 16**, p. 309–313.

Hegna, T.A., and Astrop, T.I., 2020, The fossil record of the clam shrimp (Crustacea; Branchiopoda): *Zoological Studies*, **v. 59**, n. e43, https://doi.org/10.6620/zs.2020.59-43.

Hegna, T.A., Luque, J., and Wolfe, J.M., 2020, The fossil record of the Pancrustacea, *in* Poore, G.C.A., and Thiel, M., eds., *The Natural History of the Crustacea*, Volume **8**, Evolution and Biogeography: Oxford, Oxford University Press, p. 21–52.

Hethke, M., and Weeks, S.C., 2020, Population density effects on carapace growth in clam shrimp: implications for palaeontological studies: *Zoological Studies*, **v. 59**, n. e33, https://doi.org/10.6620/ZS.2020.59-33.

Hethke, M., Fürsich, F.T., Morton, J.D., and Jiang, B., 2018, Analysis of morphological variability in the clam shrimp *Eosestheria middendorfii* (Crustacea, Spinicaudata) from the Lower Cretaceous of China, and its implications for spinicaudatan taxonomy: *Papers in Palaeontology*, **v. 4**, p. 21–53, https://doi.org/10.1002/spp2.1096.

Hethke, M., Weeks, S.C., Schöttle, V., and Rogers, D.C., 2021, Preliminary study of temperature effects on size and shape in the modern spinicaudatan *Eulimnadia texana* (Crustacea: Branchiopoda): *Zoological Studies*, **v. 60**, n. e2, https://doi.org/10.6620/ZS.2021.60-02.

Holub, V., and Kozur, H., 1981, Revision einiger Conchostracen-Faunen des Rotliegenden und biostratigraphische Auswertung der Conchostracen des Rotliegenden: *Geologisch-Palaeontologische Mitteilungen*, **v. 11**, p. 39–94.

Jansen, U., 2016, Brachiopod faunas, facies and biostratigraphy of the Pridolian to lower Eifelian succession in the Rhenish Massif (Rheinisches Schiefergebirge, Germany), *in* Becker, R.T., Königshof, P., and Brett, C.E., eds., *Devonian climate, sea level and evolutionary events*: Geological Society of London Special Publications, **v. 423**, p. 45–122, https://doi.org/10.1144/SP423.11.

Kobayashi, T., 1954, Fossil estherians and allied fossils: *Journal of the Faculty of Science*, University of Tokyo section 2, **v. 9**, 192 p.

Kozur, H., 1983, Intraspezifische und erhaltungsbedingte Variabilität der Conchostraca-Arten *Cornia germari* (Beyrich) und *Estheriella nodosocostata* (Giebel) aus dem Unteren Buntsandstein (Bernburg-Formation, Oberes Brahmanian, höheres Unterskyth): *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, **v. 166**, p. 404–430.

Kozur, H.W., and Weems, R.E., 2005, Conchostracan evidence for a late Rhaetian to early Hettangian age for the CAMP volcanic event in the Newark Supergroup, and a Sevatian (late Norian) age for the immediately underlying beds: *Hallesches Jahrbuch für Geowissenschaften B*, **v. 27**, p. 21–51.

Kozur, H.W., and Weems, R.E., 2010, The biostratigraphic importance of conchostracans in the continental Triassic of the Northern Hemisphere, *in* Lucas, S., ed., *The Triassic Timescale*: Geological Society of London Special Publications, **v. 334**, p. 315–417, https://doi.org/10.1144/sp334.13.

Latreille, M., 1817, Le règne animal distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée, par M. le Cher, Cuvier, avec figures, dessinées d'après nature, Tome III, contenant les crustacés, les arachnides et les insects: Paris, Deterville, 653 p.

Liao, H. (廖焕宇)**, and Shen, Y.** (沈炎彬), 2022, An Early Devonian clam shrimp community from Hunnan Province, China: *Journal of Paleontology*, **v. 96**, p. 164–173, https://doi.org/10.1017/jpa.2021.78.

Linder, F., 1945, Affinities within the Branchiopoda, with notes on some dubious fossils: *Arkiv för Zoologi*, **v. 37**, p. 1–28.

Liu, S.-W. (刘淑文)**, and Gao, L.** (高联达), 1985, Conchostracans and spores of Upper Devonian Huangjiadeng Formation in Hubei Province: *Bulletin of the Chinese Academy of Geological Sciences*. **v. 11**, p. 113–124.

Lucius, M., 1950, Geologie Luxemburgs. Das Oesling: *Erläuterungen zu der geologischen Spezialkarte Luxemburgs*, **v. 6**, 174 p.

Maillieux, E., 1939, Un Conchostracé nouveau de l'assise des grès et schistes de Wépion (Emsien Inférieur): *Bulletin du Musée Royal d'Histoire Naturelle de Belgique*, **v. 15**, p. 4–6.

Maquil, R., Mosar, J., and Thein, J., 1984, Unterdevon-Stratigraphie und variskischer Gebirgsbau im Eisleck/Nord-Luxembourg (Exkursion D am 26. und 27. April 1984): *Jahresberichte und Mitteilungen des Oberrheinischen Geologischen Vereines, neue Folge*, **v. 66**, p. 57–75.

Martens, T., 1983, Zur Taxonomie und Biostratigraphie der Conchostraca (Phyllopoda, Crustacea) des Jungpaläozoikums der DDR, Teil I: *Freiberger Forschungshefte*, **v. C382**, p. 7–105.

Martens, T., 2020, Taxonomie und Biostratigraphie der Conchostraken (Phyllopoda, Crustacea) aus dem terrestrischen Oberen Pennsylvanian und Cisuralian (unteres Perm) von Nord-Zentral Texas (USA): Göttingen, Cuvillier: 106 p.

Mauz, J., 1933, Zur Fauna der Unterkoblenz-Stufe: *Senckenbergiana*, **v. 15**, p. 274–295.

Meyer, W., and Stets, J., 1980, Zur Paläogeographie von Unter- und Mitteldevon im westlichen und zentralen Rheinischen Schiefergebirge: *Zeitschrift der deutschen geologischen Gesellschaft*, **v. 131**, p. 725–751.

Mitchell, J., 1927, The fossil Estheriae of Australia, part 1: *Proceedings of the Linnean Society of New South Wales*, **v. 52**, p. 105–112.

Negrea, S., Botnariuc, N., and Dumont, H.J., 1999, Phylogeny, evolution and classification of the Branchiopoda (Crustacea): *Hydrobiologia*, **v. 412**, p. 191–212, https://doi.org/10.1023/A:1003894207100.

Novozhilov, N.I. (**Новожилов, Н.И.**), 1953a, Dvustvorchatye listonogie rakoobraznye devona kurskoj oblasti [Bivalved phyllopod crustaceans from the Devonian of the Kursk area]: *Trudy Akademii Nauk SSSR*, **v. 91**, p. 947–948. [In Russian]

Novozhilov, N.I. (**Новожилов, Н.И.**), 1953b, Novyj kompleks dvustvorčatyh listonogih rakoobraznyh iz Devona Karatau (čimkentskaâ obl., Kazahskaâ SSR) [A new complex of bivalve phyllopod crustaceans from the Devonian Karatau (Chimkent region, Kazakh SSR)]: *Doklady Akademii Nauk SSSR*, **v. 91**, p. 1207–1209. [In Russian]

Novozhilov, N.I. (**Новожилов, Н.И.**), 1961, Dvustvorcatye Listonogie Devona [Devonian Conchostraca]: *Trudy Akademii Nauk SSSR*, **v. 81**, p. 1–133. [In Russian]

Olesen, J., 2009, Phylogeny of Branchiopoda (Crustacea)—character evolution and contribution of uniquely preserved fossils: *Arthropod Systematics and Phylogeny*, **v. 67**, p. 3–39, https://doi.org/10.3897/asp.67.e31686.

Péneau, J., 1936, Présence d'*Estheria* dans le Gothlandien du Synclinal de Laval: *Bulletin de la Société des Sciences Naturelles de l'Ouest de la France*, **v. 5**, p. 219–225.

Poschmann, M., 2017, Fossilien marin-terrestrischer Übergangsfazies der Nellenköpfchen-Formation (Unterdevon, höchstes Unter-Emsium) aus dem Dünnbachtal bei Treis-Karden (Untermosel, Rheinland-Pfalz, SW-Deutschland): *Mainzer naturwissenschaftliches Archiv*, **v. 54**, p. 47–63.

Poschmann, M., and Franke, C., 2006, Arthropods and trace fossils from the Lower Devonian (Emsian) of the West Eifel region/Germany and the Grand Duchy of Luxembourg, *in* Franke, C., ed., *Beiträge zur Paläontologie des Unterdevons Luxemburgs (1): Ferrantia*, **v. 46**, p. 97–115.

Poschmann, M., and Tetlie, O.E., 2006, On the Emsian (Lower Devonian) arthropods of the Rhenish Slate Mountains: 5. Rare and poorly known eurypterids from Willwerath, Germany: *Paläontologische Zeitschrift*, **v. 80**, p. 325–343, https://doi.org/10.1007/BF02990208.

Poschmann, M., **Schoenemann, B., and McCoy, V.E.**, 2016, Telltale eyes: the lateral visual systems of Rhenish Lower Devonian eurypterids (Arthropoda, Chelicerata) and their palaeobiological implications: *Palaeontology*, **v. 59**, p. 295–304, https://doi.org/10.1111/pala.12228.

Poschmann, M.J., **Hegna, T.A.**, **Astrop, T.I., and Hoffmann, R.**, 2024, Revision of Lower Devonian clam shrimp (Branchiopoda, Diplostraca) from the Rhenish Massif (Eifel, SW-Germany), and the early colonization of non-marine palaeoenvironments: *Palaeobiodiversity and Palaeoenvironments*, **v. 104**, p. 535–569, https://doi.org/10.1007/s12549-023-00597-9.

Raymond, P.E., 1946, The genera of fossil Conchostraca—an order of bivalved Crustacea: *Bulletin of the Museum of Comparative Zoölogy at Harvard College*, **v. 96**, p. 215–307.

Reible, P., 1962, Die Conchostraken (Branchiopoda, Crustacea) der Germanischen Trias: *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, **v. 114**, p. 169–244.

Richter, S., **Olesen, J., and Wheeler, W.C.**, 2007, Phylogeny of Branchiopoda (Crustacea) based on a combined analysis of morphological data and six molecular loci: *Cladistics*, **v. 23**, p. 301–336, https://doi.org/10.1111/j.1096-0031.2007.00148.x.

Sars, G.O., 1899, On some Indian Phyllopoda: *Archiv for Mathematik og Naturvidenskab*, **v. 22**, no. 9, p. 3–27, pls. 1–4.

Scholze, F., 2021, Spätpermische Conchostraken (Crustacea: Diplostraca) aus der Zechstein-Gruppe in Deutschland: *Abhandlungen und Berichte für Naturkunde*, **v. 36**, p. 203–224.

Scholze, F., and Schneider, J.W., 2015, Improved methodology of 'conchostracan' (Crustacea: Branchiopoda) classification for biostratigraphy: *Newsletters on Stratigraphy*, **v. 48**, p. 287–298, https://doi.org/10.1127/nos/2015/0065.

Scholze, F., **Golubev, V.K.**, **Niedźwiedzki, G.**, **Sennikov, A.G.**, **Schneider, J. W., and Silantiev, V.V.**, 2015, Early Triassic conchostracans (Crustacea: Branchiopoda) from the terrestrial Permian–Triassic boundary sections in the Moscow syncline: *Palaeogeography, Palaeoclimatology, Palaeoecology*, **v. 429**, p. 22–40, https://doi.org/10.1016/j.palaeo.2015.04.002.

Scholze, F., **Hamad, A.A.**, **Schneider, J.W.**, **Golubev, V.K.**, **Sennikov, A.G.**, **Voigt, S., and Uhl, D.**, 2017, An enigmatic 'conchostracan' fauna in the eastern Dead Sea region of Jordan: first records of *Rossolimnadiopsis* Novozhilov from the Early Triassic Ma'in Formation: *Palaeogeography, Palaeoclimatology, Palaeoecology*, **v. 466**, p. 314–325, https://doi.org/10.1016/j.palaeo.2016.11.047.

Scholze, F., **Golubev, V.K.**, **Niedźwiedzki, G.**, **Schneider, J.W., and Sennikov, A.G.**, 2019, Late Permian conchostracans (Crustacea, Branchiopoda) from continental deposits in the Moscow Syneclise, Russia: *Journal of Paleontology*, **v. 93**, p. 72–97, https://doi.org/10.1017/jpa.2018.58.

Sell, J., 2018, Die Euestheriidae (Conchostraca) des Oberen Muschelkalks und Unteren Keupers von Unterfranken: *Semana*, **v. 33**, p. 55–90.

Stets, J., and Schäfer, A., 2002, Depositional environments in the Lower Devonian siliciclastics of the Rhenohercynian Basin (Rheinisches Schiefergebirge, W-Germany)—case studies and a model: *Contributions to Sedimentary Geology*, **v. 22**, p. 1–78.

Stets, J., and Schäfer, A., 2011, The Lower Devonian Rhenohercynian Rift—20 Ma of sedimentation and tectonics (Rhenish Massif, W-Germany): *Zeitschrift der deutschen Gesellschaft für Geowissenschaften*, **v. 162**, no. 2, p. 93–-115, https://doi.org/10.1127/1860-1804/2011/0162-0093.

Størmer, L., 1969, Eurypterids from the Lower Devonian of Willwerath, Eifel: *Senckenbergiana Lethaea*, **v. 50**, p. 21–35.

Sun, X., and Cheng, J., 2022, Sexually dimorphic ornamentation in modern spinicaudatans and the taxonomic implications for fossil clam shrimps: *Acta Palaeontologica Polonica*, **v. 67**, p. 475–492, https://doi.org/10.4202/app.00892.2021.

Tasch, P., 1956, Three general principles for a system of classification of fossil conchostracans: *Journal of Paleontology*, **v. 30**, p. 1248–1257, http://www.jstor.org/stable/1300622.

Tasch, P., 1975a, Dunkard estheriids as environmental and age indicators, *in* Barlow, J.A., and Burkhammer, S., eds., *Proceedings of the First I. C. White Memorial Symposium "The Age of the Dunkard,"* p. 281–294.

Tasch, P., 1975b, Non-marine Arthropoda of the Tasmanian Triassic: *Papers and Proceedings of the Royal Society of Tasmania*, **v. 109**, p. 97–106.

Tasch, P., 1987, Fossil Conchostraca of the Southern Hemisphere and Continental Drift. Paleontology, Biostratigraphy and Dispersal: *Geological Society of America Memoir*, **v. 165**, 290 p.

Van Viersen, A.P., and Prescher, H., 2009, Trilobites from the Longlier Formation (Lower Devonian; Neufchateau Synclinorium, southeast Belgium): first record of Pragian associated "Rhenish" and "Bohemian" assemblages from the Ardennes: *Bulletin de l'Institut Royal des Sciences naturelles de Belgique, Sciences de la Terre*: **v. 79**, p. 5–26.

Walliser, O.H., and Michels, D., 1983, Der Ursprung des Rheinischen Schelfes im Devon: *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, **v. 166**, p. 3–18.

Zhang, W.-T. (张文堂), **Chen, P.-J.** (陈丕基)**, and Shen, Y.-B.** (沈炎彬), 1976, *[Fossil Conchostraca of China]*: Beijing, Science Press, 325 p., 138 pls. [in Chinese]