



Revision of Lower Devonian clam shrimp (Branchiopoda, Diplostraca) from the Rhenish Massif (Eifel, SW-Germany), and the early colonization of non-marine palaeoenvironments

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Abstract

Three collections of clam shrimp from the Lower Devonian (upper lower Emsian) Klerf Formation of Willwerath and Waxweiler in the western Eifel Mountains are herein studied. Four discernible morphotypes are present in the Willwerath assemblage. These morphotypes correspond to the previously described species from this locality: *Pseudestheria diensti* (Gross), *Pseudestheria subcircularis* Raymond, and *Palaeolimnadiopsis? eifelensis* Raymond. The fourth morphotype also closely corresponds to *Pseudestheria diensti*, but is slightly different in outline. *Asmussia willweratica* (Novozhilov) is an objective synonym of *Pseudestheria subcircularis*. In the Willwerath clam shrimp sample, it is difficult to disentangle taphonomic/preservational versus ontogenetic/sexual variation. If taphonomic/preservational causes could be confirmed, all the Willwerath specimens may represent just one taxon and *Pseudestheria subcircularis* and *Palaeolimnadiopsis? eifelensis* would be potential subjective synonyms of *Pseudestheria diensti*. However, we refrain from a formal taxonomic act, which requires a larger number of specimens to be analysed.

In addition, we investigated two samples from Waxweiler, which originate from distinct centimetre-thick layers and therefore represent associations. One of these associations comprises two discernible clam shrimp morphotypes. Because of limited preservation of morphological characters, one is here left in open nomenclature as *Spinicaudata incertae sedis*, whereas the other is recognised as a new species of the family Palaeolimnadiopseidae, *Palaeolimnadiopsis frankeorum* sp. nov. The second association from Waxweiler comprises at least four, possibly six different clam shrimp taxa. In addition to *Pseudestheria diensti*, *Palaeolimnadiopsis* sp., and poorly preserved *Asmussia*- and *Ulugkemia*-like specimens, two taxa can be described as new, namely the vertexiid *Cornia wasvilrensis* sp. nov. and the leaiine *Eicheleia wenndorfi* gen. nov. et sp. nov. Altogether, the Klerf Formation at Waxweiler yields a total of at least five (possibly eight) clam shrimp taxa. The palaeoenvironment of these early clam shrimp from the Klerf Formation is interpreted as a non-marine, relatively proximal deltaic setting with no or very minor marine influence, such as a deltaic freshwater pond or lake. The comparatively high diversity of these lower Devonian clam shrimp suggests a considerably earlier origin and cryptic evolution of the group.

Keywords Branchiopoda · Clam shrimp · Palaeoecology · Devonian · Emsian · Germany

Introduction

The paraphyletic group of branchiopod crustaceans commonly referred to as clam shrimp or conchostracans consists of three monophyletic entities: the Laevicaudata, Spinicaudata, and Cladoceromorpha (Negrea et al. 1999; Richter et al. 2007; Olesen 2009). Stem group diplostracans (‘conchostracans’ + cladocerans) have been suggested to have emerged in the Silurian (Walossek 1995) or Early Devonian (Tasch 1969; Fryer 1987). Hegna and Astrop (2020) briefly reviewed the supposed fossil record of

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pre-Devonian forms and found no compelling evidence for clam shrimp of this age (see also Hegna et al. 2020; Liao and Shen 2022). The hitherto recognised reliable fossil record of clam shrimp thus starts in the Early Devonian. Unfortunately, this record is still meagre and often restricted to few specimens from localities, which are, in part, poorly dated (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 exceptions were recently reported (Liao and Shen 2022). Quite a large number of clam shrimp species were described from the Middle to Upper Devonian (e.g. Pacht 1849; Lutkevich 1929, 1937; Glebovskaya 1947; Novozhilov and Varentsov 1956; Novozhilov 1961; Copeland 1962; Shen 1978, 1983; Brummer 1980; Xi 1981; Liu and Gao 1985; Liu 1990; Chen and Morris 1991; Gess and Hiller 1995; Martens 1996; He and Bu 2001; Gueriau et al. 2017; Hogancamp and Pocknall 2018; Shen and Wu 2022, and references therein) and specimens of this age were also recorded from the Rhenish Massif (e.g. Gosny 2010; Hartkopf-Fröder et al. 2010; Weber et al. 2014).

For an improved understanding of clade origins and historical biogeography, the Early Devonian clam shrimp occurrences need taxonomic revision and updated age constraints (Hegna and Astrop 2020). Here, we make an important step into this direction by providing descriptions, figures and taxonomic discussion of new clam shrimp material from the ‘classic’ localities of Willwerath and Waxweiler in the western Eifel Hills of the Rhenish Massif (Fig. 1). Furthermore, we provide evidence that these Early Devonian clam shrimp from marine–terrestrial transitional facies possibly populated freshwater habitats, that may have been, in part, ephemeral. Ecological stasis in clam shrimp from the Devonian to Recent times has been suggested but is an oversimplification based on modern examples (Hethke et al. 2019). The occupation of ephemeral freshwater habitats was likely an important ecological niche for clam shrimp throughout their hitherto known evolutionary history. Indeed, the ability to cope with ephemeral freshwater ponds likely occurred at the origin of the Branchiopoda (Fryer 1996), as nearly all of the constituent taxa have desiccation-resistant modes of reproduction (Anostraca, Notostraca, and Diplostraca).

Material and methods

About thirty hitherto unpublished clam shrimp specimens are described and figured herein (Tables 1–4). The Willwerath sample was collected by one of us (MJP) in the 1980s and 1990s from the Lower Devonian (lower Emsian) Klerf Formation (Fig. 1c) of the Willwerath Fossilagerstätte (Fig. 1a), a locality famous for the occurrence of chelicerate arthropods such as eurypterids (e.g. Størmer 1936; Poschmann

2021, and references therein). Clam shrimp are relatively rare at Willwerath. A reference excavation of a defined area of the main fossiliferous horizon, which is about 1.5 metres thick (Fig. 1e), yielded a mean clam shrimp abundance of 8 specimens per m². For comparison, we statistically recorded 760 bivalves, 56 leperditicopid ostracods, 6.7 eurypterids and 8.1 vertebrate remains (usually isolated plates) within the same rock volume (MJP, unpublished data). A second important site, the Köppen Quarry at Waxweiler is situated about 18 kilometres southwest of Willwerath (Fig. 1a). It is renowned for yielding a variety of fossil plants, arthropods, and vertebrates (e.g. Schweitzer 1983; Rebske et al. 1985; Franke 2006; Poschmann and Franke 2006; Poschmann et al. 2022; Steemans et al. 2022, and references therein). A considerable collection of fossils from this site has been gathered by the Rebske family and forms the base of an exhibition in the local museum ‘Devonium’ at Waxweiler (Wuttke 2006). A rock sample from Waxweiler provided by Dr. C. Franke (Wallendorf) was split into thin pieces and yielded a leperditicopid-clam shrimp mass occurrence (here informally termed ‘LCMO’, see below). In contrast to the Willwerath sample, which may comprise a substantial amount of transported elements, this Waxweiler sample is considered as essentially comprising autochthonous material and therefore probably represents a life association or palaeocommunity only lacking the original soft-bodied fauna. A second clam shrimp-bearing layer from Waxweiler was detected in October 2022 and yielded a more diverse clam shrimp association than the LCMO. These fossils come from a roughly 15 centimetre-thick, dark-grey siltstone deposited on the delta plain (here informally termed layer ‘102022’). Associated with four species of clam shrimp is plant debris, some larger (up to a few cm-long) plant axes (including *Drepanophycus* sp., undetermined lycopsids, *Rebskia musaeformis* Schweitzer, and *Taeniocrada dubia* Kräusel and Weyland), very few ostracodes (*Kloedenella poschmanni* Becker and Franke, and *Euprimites? koepfeni* Bless), leperditicopids, microconchids, bivalves, eurypterid cuticle fragments, and isolated bony plates of early vertebrates. On some layers, clam shrimp form a mass occurrence but are mostly poorly preserved. Judging from the high degree of fragmentation, at least the plant, eurypterid, and vertebrate remains were probably transported into a shallow, ephemeral body of water, such as a delta lake or pool, where they were finally buried.

Specimens were prepared using pneumatic chisels. Photographs were taken using a Canon 600D SLR-camera equipped with a Canon EF-S 60 mm or Canon MP-E 65 mm macro-lens, respectively, with specimens under alcohol immersion (if not stated otherwise) and with polarizing filters crossed to various degrees. SEM images were taken using a Zeiss Merlin Gemini 2 high-resolution field emitter scanning electron microscope (HR-FE SEM). Samples were not coated with gold or carbon but wrapped in aluminium

foil instead to provide conductivity during examination. The acceleration voltage of the electron beam ranged between 3 and 5 kV, the beam current density between 50 and 150 pA and the working distance between 5 and 20 mm. Sometimes a gas injection system was used to reduce charging effects.

The specimens are deposited in the State Collection of Natural History of Rhineland-Palatinate at the Natural History Museum at Mainz, Germany (NHMMZ). The original material of Gross (1934) is deposited in the Museum für Naturkunde Berlin (MB.A.0039–MB.A.0044).

In the application of morphological and descriptive terms, we follow Scholze and Schneider (2015).

History of research

The Willwerath Fossilagerstätte is situated to the west of the Prüm Valley, on a hill between the villages of Willwerath and Hermespannd (Fig. 1a). It is a small quarry in the Hermespannd district that was sporadically worked for solid sandstones suitable as decorative stone. The fossil deposit, known to experts as an important site for animal and plant fossils, was discovered in 1930 by the then Frankfurt geologist Dr. Hans Theodor Reuling (Kräusel and Weyland 1930; Størmer 1936). The fossil-rich layer is a 1.5 metres thick grey to grey-green, clayey siltstone (Fig. 1e), which today is barely accessible, but still visible.

Mauz (1933) referred to a fossil from Willwerath as the bivalve *Paracyclas rugosa* Goldfuß. Further specimens collected by P. Dienst and W. Gross prompted the latter to assign these fossils to the ‘conchostracans’ and to erect the new species *Estheria diensti* with the holotype being the specimen in his fig. 5 (now number MB.A.0043, details of ornament in his figs. 8–9). Gross’ specimens were, in part, assigned to the newly erected genus *Pseudestheria* by Raymond (1946, p. 244), who also erected a new species, *Pseudestheria subcircularis*, for a specimen figured by Gross (1934, fig. 6; now number MB.A.0044) based on a more rounded outline and a slightly higher number of ribs (20 or more opposed to 15–18 ‘narrow lirae’). Furthermore, Raymond (1946, p. 271–272) assigned a specimen figured by Gross (1934, fig. 2; now number MB.A.0040) to another new genus as *Palaeolimnadiopsis ? eifelensis*, although expressing doubt about the genus attribution by using a quotation mark.

Novozhilov (1961, p. 52) designated three specimens figured by Gross (1934, figs. 1, 3, 5) as *Pseudestheria (Pseudestheria) diensti* (Gross, 1934) and assigned Raymond’s (1946) *Palaeolimnadiopsis ? eifelensis* to the genus *Concherisma* Novozhilov and Varentsov, 1956 (Novozhilov 1961, p. 86). The same author erected a new species in the genus *Glyptoasmussia* Novozhilov and Varentsov, 1956 as *G. willweratica* Novozhilov, 1961 (Novozhilov 1961, p. 62–64). This was based on the specimen in Gross (1934, fig. 6),

despite the fact that this specimen was earlier designated the holotype for *Pseudestheria subcircularis* by Raymond (1946). Furthermore, Novozhilov’s drawing of the specimen was strongly idealised and has little congruence with the fossil figured by Gross. However, the nomenclatorial practice of Novozhilov was repeatedly criticised (e.g. Tasch 1958; Warth 1963; Goretzki 2003). *Concherisma* was subsequently regarded by Tasch (1969) as a junior synonym of *Cyzicus (Euestheria)* Depéret and Mazeran, 1912 (*Euestheria* has variously been regarded as both a proper genus (i.e. Zhang et al. 1976) and subgenus (i.e. Gallego and Breitreuz 1994) in the time since Tasch’s work) and *Glyptoasmussia* as a junior synonym of *Asmussia* Pacht, 1849. Chen and Shen (1985) subsequently regarded *Glyptoasmussia* as a valid genus within the family Euestheriidae.

Damaged clam shrimp carapaces from Willwerath were considered by Poschmann et al. (2016) as possible eurypterid prey items. Clam shrimp were also reported from the Klerf Formation of Waxweiler (Franke 2006; Poschmann and Franke 2006; Becker and Franke 2012).

With respect to Rhenish Lower Devonian clam shrimp, further occurrences must be considered. Maillieux (1939) described three valves from the Lower Devonian of Wépion/Namur in Belgium. These specimens, along with further three fossils described by Defretin (1950) from Vinclin (Pas-de-Calais, France) are thought to be of lower Emsian age (Em 1 II; Our Formation; *Rhinopteraspis dunensis*-biozone sensu Blicek and Janvier 1989; cf., Cuvelier et al. 2015; Dejonghe et al. 2017) and thus may be approximately contemporaneous with the Willwerath and Waxweiler specimens. Originally designated *Estheria (Euestheria) stockmansi*, Maillieux’s three specimens were later assigned to two different taxa by Novozhilov (1958, 1961), apparently without consulting the original material and with problematic declarations about the type material (for details see Webb 1978). Besides *Belgolimnadiopsis stockmansi*, Novozhilov (1958) also assigned a second species to *Belgolimnadiopsis*: *B. australensis* Novozhilov, 1958 from the Triassic of Australia (originally illustrated as *Estheria coghlani* Mitchell, 1927). Tasch and Jones (1979) removed the Australian species and placed it in *Cyzicus (Lioestheria)*. The drawings of *B. stockmansi* given in Novozhilov (1958: fig. 1) and Novozhilov (1961: fig. 74-I) do not show a recurved posterior margin or growth lines (contra Liao and Shen 2022), and Maillieux (1939) also described the postero-dorsal angle as weakly obtuse. This, together with the polygonal ornamentation, led Webb (1978) to assign this species to the genus *Euestheria* Depéret and Mazeran, 1912 and consequently to consider *Belgolimnadiopsis* Novozhilov, 1958 a junior subjective synonym of *Euestheria*. Later workers (e.g. Chen and Shen 1985; Cuvelier et al. 2015) did not accept Webb’s (1978) synonymy, and instead kept the species assigned to *Belgolimnadiopsis*. Webb’s (1978) conception of *Euestheria* is inconsistent with a recent review



		Middle Rhine, Lower Mosel, Lower Lahn		Eifel area		
Eifelian	lower	Wissenbach Fm		Nohn Fm		
				Lauch Fm		
	upper (Kondel)	Kondel Group	Kieselgallenschiefer	Heisdorf Fm		
			Flaserschiefer			
		Laubach Group	Laubach Fm	Wetteldorf Fm		
	lower (Lahnstein)	Lahnstein Group	Hohenrhein Fm	Wiltz Fm		
			Emsquarzit Fm	Berle Fm		
	upper (Vallendar)	Vallendar Group	Nellenköpfchen/Klerf Fm	Klerf Fm		
			Rittersturz/Gladbach Fm	Stadtfeld Fm		
	middle (Singhofen)	Singhofen Group	Bendorf Fm	Singhofen Group	Neichnerberg Fm	
				Gefell Fm		
lower (Ulmen)		Isenburg Fm	Ulmen Group	Reudelsterz Fm		
				Eckfeld Fm		
PRAGIAN	upper	Wied Group	Rüscheld Fm	Upper Siegen Group	Saxler Fm	
			Augustenthal Fm	Monschau Fm	Nitztal Fm	
	Leutesdorf Fm		Middle Siegen Group		Ramersbach Fm	
	middle			Mayen Fm	Lower Siegen Group	
			lower			

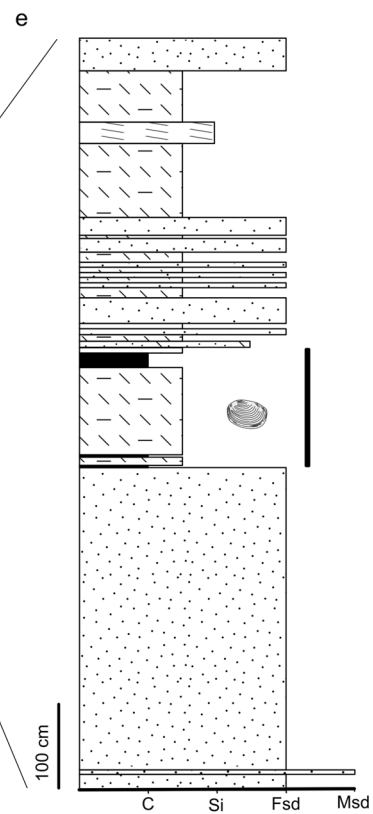


Figure 1. **a** Geographical position of the Willwerath and Waxweiler localities in Rhineland-Palatinate; **b** photography of clam shrimp-bearing deltaic succession in the Köppen Quarry at Waxweiler; note channel sandstones at base and fine-grained, red-grey alternating deltaic succession above; height of outcrop about 20 metres; photograph re-orientated to show succession as vertical pile; **c** dessication cracks from supposed floodplain/overbank deposits of Waxweiler; hammer for scale; **d** stratigraphic position of the clam shrimp-bearing sites in the Rhenish Early Devonian; modified from Jansen (2019). **e** lithological log of the Willwerath Quarry with the main fossiliferous layers indicated by black bar; abbreviations: *C* claystone; *Si* siltstone; *Fsd* fine sandstone; *Msd* medium sandstone

of the genus (Geyer and Kelber 2018), and would extend the range of *Euestheria* from the Triassic all the way back to the dawn of clam shrimp. *Belgolimnadiopsis stockmansii* remains in need of reillustration and revision. *Pseudestheria (Tuvinopsis) arduennae* Novozhilov, 1961 based on one of Maillieux's specimens is considered herein as a preservational variant of *B. stockmansii*. However, we refrain from a formal taxonomic act as this should be done after re-examination of the type material (partially listed in Cuvelier et al. 2015).

Systematic palaeontology

Class Branchiopoda Latreille, 1817

Order Diplostraca Gerstaecker, 1866

Suborder Spinicaudata? Linder, 1945

Diagnosis: See Hegna (2021, p. 2).

Discussion: Hegna and Astrop (2020) expressed some skepticism about being able to concretely determine whether or not early clam shrimp fossils belong in the Spinicaudata stem group or Spinicaudata crown group. The problem is that too few characters are known at present from early clam shrimp. Attempts to use carapace ornamentation patterns hold a lot of potential (e.g. Sun and Cheng 2022), but unfortunately, Palaeozoic clam shrimp often have very poorly preserved carapaces with little to no original shell material left. Plausibly, clam shrimp fossils with growth lines could sit in a stem group Onychocaudata position or even a stem group Cladocromorpha position, depending on the optimization/evolution of the incomplete molting character (see Hegna and Astrop 2020, fig. 1). Thus, the fossils discussed herein are assigned, with question, to the suborder Spinicaudata.

Expectations for the appearance of crown group fossil clam shrimp can be informed by molecular clock studies. The divergence of Diplostraca, resulting in the clades Laevicaudata and Onychocaudata (Spinicaudata + Cladocera), was dated by Sun et al. (2016) at about 430–457 Ma (Late Ordovician to early Silurian). This date was calculated using the split between Spinicaudata and Cladocera (i.e. the diversification of the Onychocaudata) as a calibration point, with a minimum constraint of 416

Ma and a maximum constraint of 515 Ma. Schwentner et al. (2020, suppl. figs. 10–11) predicted an age of divergence for the Spinicaudata clade at between the Silurian and Permian, under varying parameters. Van Damme et al. (2022) found predicted ages of the most recent common ancestor of Diplostraca to be in the Ordovician, and the most recent common ancestor of the Onychocaudata to be in the Devonian. Consequently, it is plausible to already have at least stem group spinicaudatans present in the Devonian.

The presence of the family Palaeolimnadiopseidae with *Palaeolimnadiopsis* in this Devonian fauna is interesting. Some authors (i.e. Astrop and Hegna 2015; Sun and Cheng 2022) have allied the family Palaeolimnadiopseidae with the extant genus *Limnadiopsis*. This would place Palaeolimnadiopseidae within the bounds of the extant family Limnadiidae (phylogenetically defined herein as the least inclusive clade including at least the following genera: *Limnadia*, *Imnadia*, *Limnadiopsis*, and *Eulimnadia*). Accordingly, the first occurrence of *Palaeolimnadiopsis* would represent an occurrence of crown group spinicaudatans. However, the key characteristic of the family—recurved growthlines—is problematic, as observed by Liao et al. (2019) and Liao and Shen (2022). Thus, the fossil evidence for crown group spinicaudatans should be regarded with skepticism.

Superfamily Vertexioidea Kobayashi, 1954 sensu Zhang et al. 1976 (=Lioestheriacea Raymond, 1946, emended Holub and Kozur 1981, sensu Chen and Shen 1985)

Diagnosis: See Astrop and Hegna (2015).

Discussion: Astrop and Hegna (2015) discussed the problems with superfamily-level classification of clam shrimp. Important here is the distinction between Vertexioidea and Lioestheriacea/Lioestherioidea; between the publication of Zhang et al. (1976) and Chen and Shen (1985), the content of Lioestheriacea/Lioestherioidea changed completely due to the reassignment of *Lioestheria* by Chen and Shen (1985). In order to avoid confusion, Astrop and Hegna (2015) advocated Vertexioidea over Lioestheriacea/Lioestherioidea. This recommendation was missed by Li et al. (2016), who followed Chen and Shen (1985). Li et al.'s (2016) taxonomy was subsequently followed by Scholze et al. (2021).

Sun and Cheng (2022), in contrast to Astrop and Hegna (2015), moved Lioestheriidae Raymond, 1946 from the Vertexioidea to the Eoestherioidea Zhang and Chen, in Zhang et al. 1976 without a clear explanation. However, *Pseudestheria* has a more limnadiiform carapace (typifying Vertexioidea) rather than cyziciform, cycladiform, and telliniform (typifying Eoestherioidea) (see Astrop and Hegna 2015). Until a better diagnosis for the superfamily level is created, we prefer to keep *Pseudestheria* (and therefore, Lioestheriidae) in the Vertexioidea.

A couple of broader taxonomic observations should be made. The conception of Eoestherioidea used by Astrop and Hegna

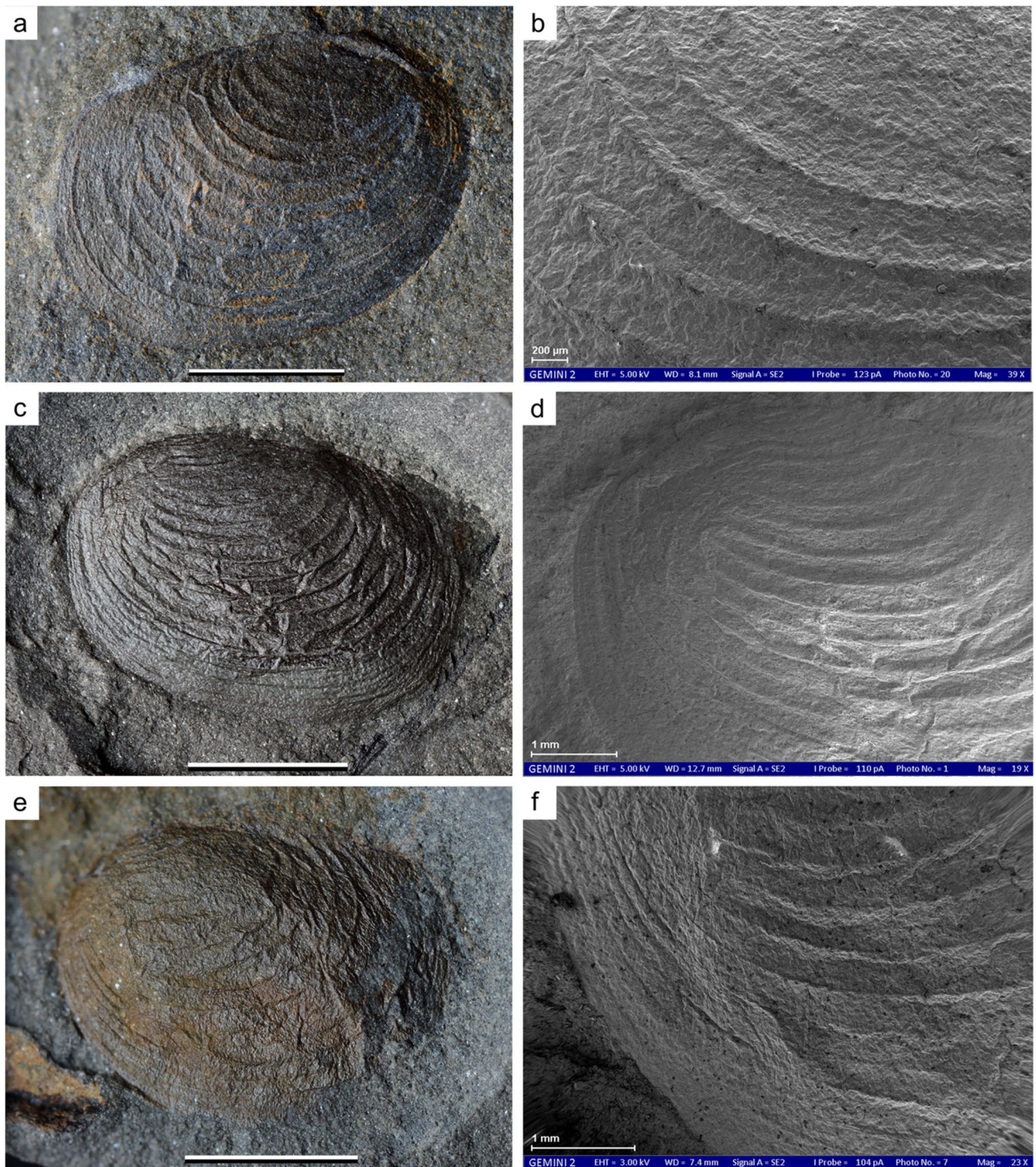


Figure 2. *Pseudestheria diensti* from the Klerf Formation at Willwerath; photographs and SEM images, respectively; **a–b** NHMMZ PWL 2021/6143-LS; **c–d** NHMMZ PWL 2021/6008-LS; **e–f** NHMMZ PWL 2021/6006-LS; scale bars in **a**, **c**, and **e** = 3 mm

(2015)—i.e. notably, including the extant genera of *Cyzicus*, *Eocyclus*, *Eoleptestheria*, *Leptestheria*, *Maghrebstheria*, and *Ozestheria*—is paraphyletic (see Schwentner et al. 2020; Sun and Cheng 2022). Until the affinities of the Eocycticidae and

Leptestheriidae are clarified, we recommend that Eosestherioidea is abandoned as paraphyletic, and in its place, Cyzicoidea Stebbing, 1910, is used. Cyzicoidea would essentially become the name for the total group Cyzicidae Stebbing, 1910. Likewise,

in current use, the Vertexioidea is essentially the name for the total group Limnadiidae Baird, 1849.

Family ?Lioestheriidae Raymond, 1946

Remarks: The genus *Pseudestheria* has had several different familial-level placements over the last few years. Liao and Shen (2022) placed it in the Euestheriidae Defretin-Lefranc, 1965 without comment. Scholze et al. (2019, 2021) placed it in the Lioestheriidae without comment (as did Lipatova and Lopato 2000). Martens (2020) placed it in the Pseudestheriidae Martens, 1983 (containing only *Pseudestheria* (inclusive junior subjective synonyms *Polygrapta* and *Pemphicyclus*) and *Palaeolimnadiopsis*). Cuvelier et al. (2015) speculated that *Pseudestheria* may belong in the Orthothemosiidae Defretin-Lefranc, 1965. Chen and Shen (1985) notably left *Pseudestheria* out of their conception of Lioestheriidae, preferring instead to consider it as incertae sedis. Going back further, Tasch (1969,

p. R151) regarded *Pseudestheria* as a synonym of *Cyzicus* (*Lioestheria*) within the Superfamily Cyzicoidea. All this shifting of *Pseudestheria* inhibits clarity with regards to its taxonomic and phylogenetic position. The type material needs to be revised. However, the type material likely does not preserve the ornamentation patterns, so it is unclear how much a revision would actually help to clarify the situation.

In general, the larval shell is not centrally-placed enough to warrant inclusion in the Orthothemosiidae (see Raymond 1946, for the genus *Orthothemos*). Martens' (1983) conception of Pseudestheriidae is an uncomfortable union of *Pseudestheria* and *Palaeolimnadiopsis*—putatively united by the synapomorphy of 'oblique fibers' on the dorsal margin (Tasch 1975; Martens 1983). It is not clear what this feature represents—indeed, no analogue is known from modern clam shrimp. The feature identified by Tasch (1975, pl. 2.3) has a different expression (and taphonomy) from Martens' (1983) specimen and may have a different genesis. Euestheriidae

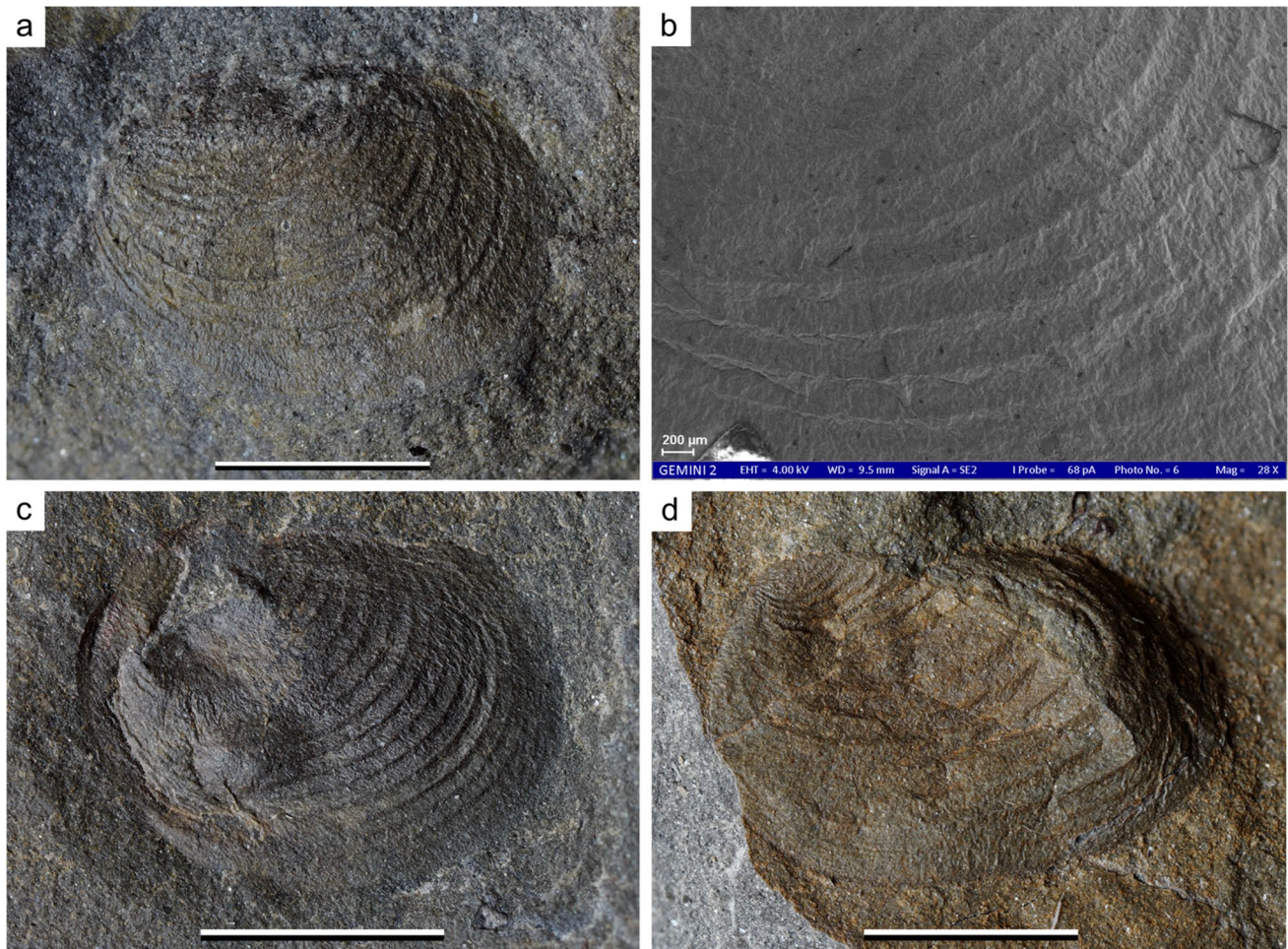


Figure 3. Clam shrimp from the Klerf Formation at Willwerath; photographs and SEM images, respectively; **a–b** *Pseudestheria* cf. *diensti*, NHMMZ PWL 2021/6009-LS; **c** *Pseudestheria* cf. *diensti*,

NHMMZ PWL 2021/6005-LS; **d** (?) *Palaeolimnadiopsis* ? *eifelensis*, NHMMZ PWL 2021/6142-LS; scale bars in **a**, **c**, and **d** = 3 mm

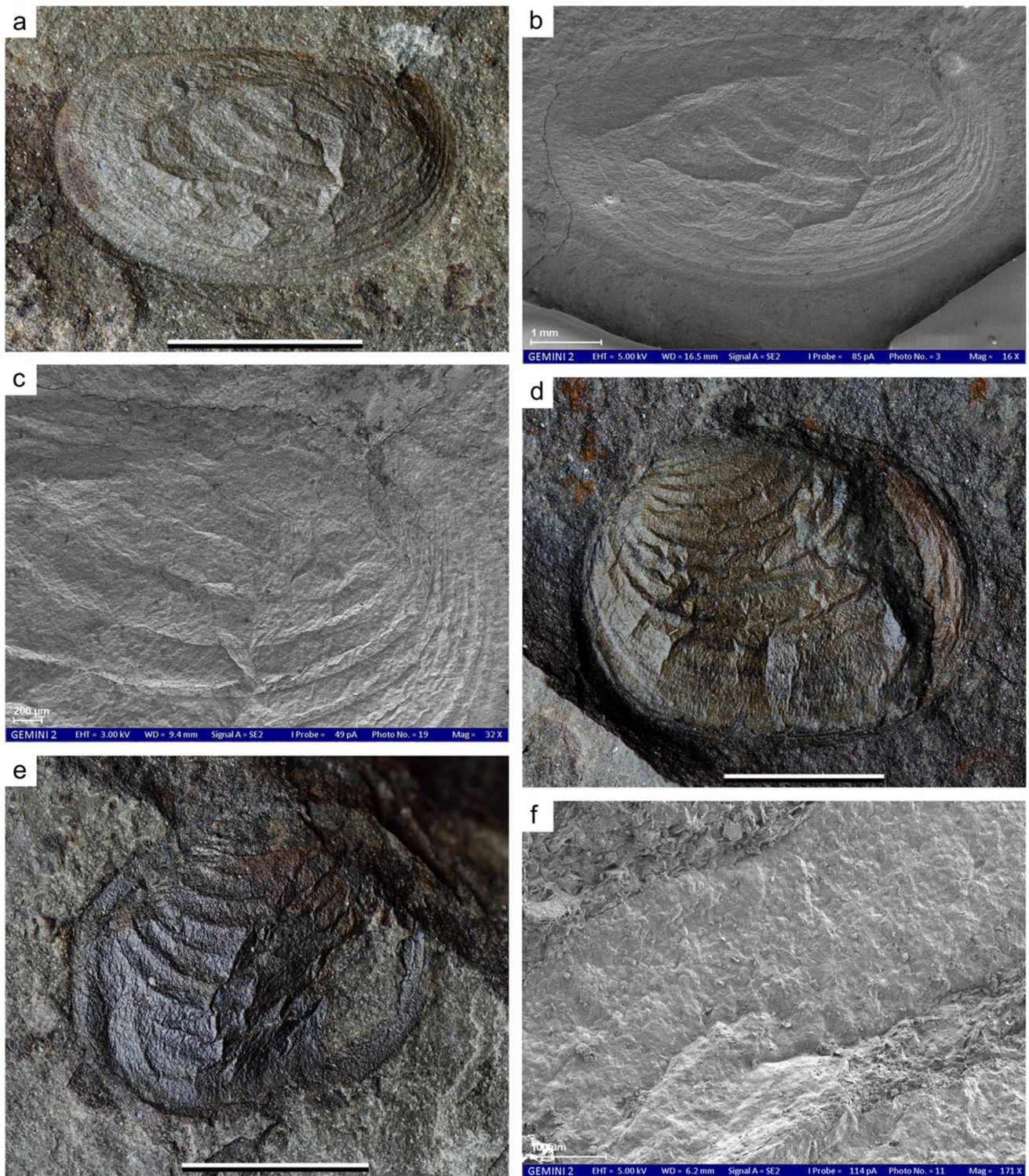


Figure 4. Clam shrimp from the Klerf Formation at Willwerath; photographs and SEM images, respectively; **a–c** *Palaeolimnadiopsis ? eifelensis*, NHMMZ PWL 2021/6139-LS; **d–f** *Pseudestheria*

subcircularis; **d** NHMMZ PWL 2021/6007-LS; **e–f** NHMMZ PWL 2021/6141-LS; scale bars in **a**, **d**, and **e** = 3 mm

typically contains members with a reticulate ornamentation pattern (Astrop and Hegna 2015). This is not present in the studied specimens (though, the ornamentation pattern may

have been obliterated by diagenesis). Lioestheriidae typically includes members with protuberances on the larval shell (Astrop and Hegna 2015). However, previous usage of the family

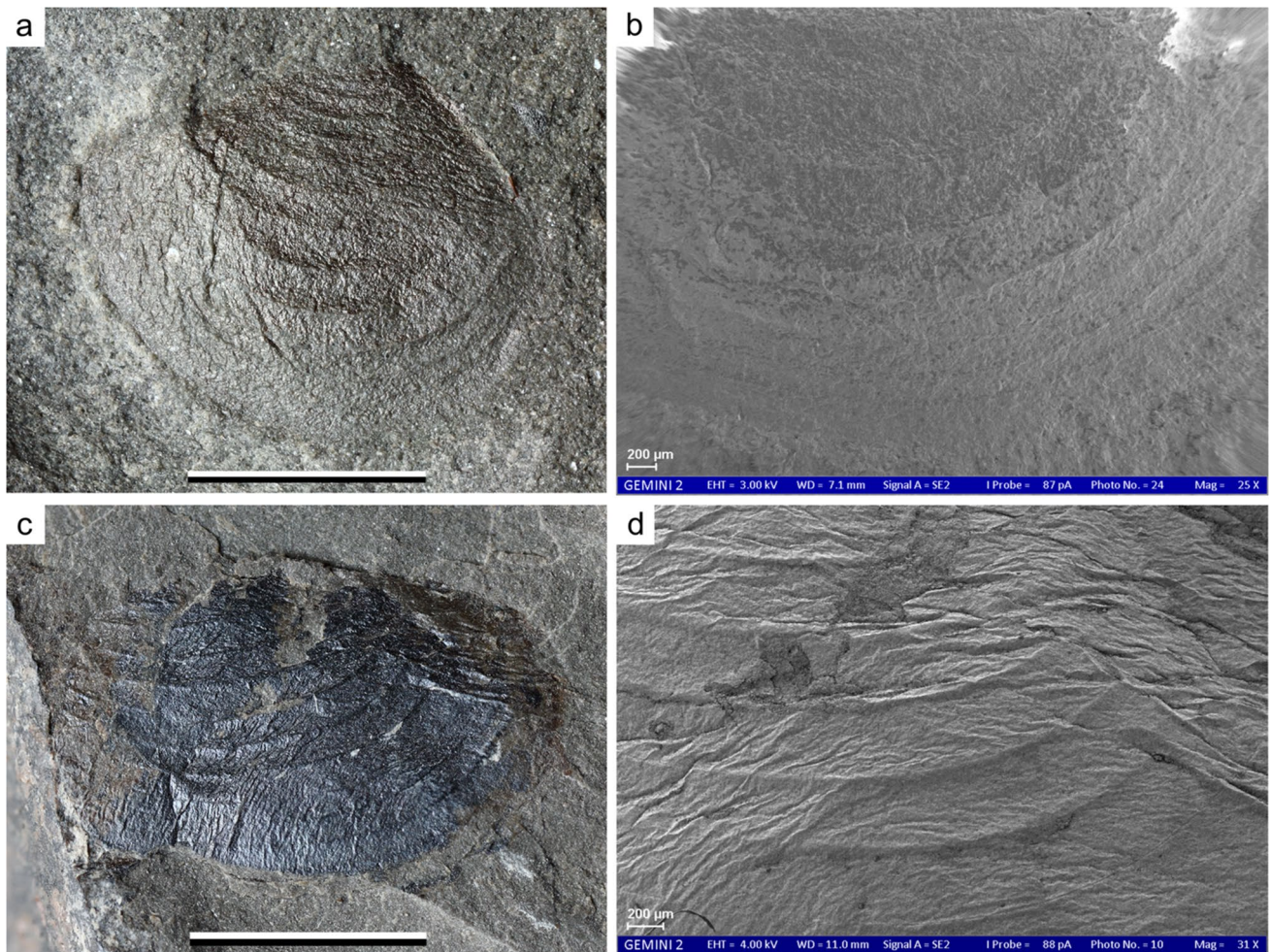


Figure 5. Poorly preserved and deformed clam shrimp, Spinicauda? incertae sedis, from the Klerf Formation at Willwerath; photographs and SEM images, respectively; **a–b** NHMMZ PWL 2021/6140-LS; **c–d** NHMMZ PWL 2021/6144-LS; scale bars in **a** and **c** = 3 mm

suggests that this characteristic is frequently not present. With this admittedly weak rationale, we opt to leave *Pseudestheria* in the Lioestheriidae until type material can be revised.

Scholze et al. (2019, 2021) put *Pseudestheria* into Lioestheriidae. However, there is a species-level problem with their assignment. Scholze et al. (2019) followed Martens' (1983) suggestion that *Polygrapta* is a junior subjective synonym of *Pseudestheria*. The specimens that Scholze et al. (2019) treat as *Pseudestheria chatangensis* (Novozhilov, 1946) have a fundamentally different type of ornamentation (punctae) when compared to the newly revised type material of *Polygrapta chatangensis* (reticulations, see Li 2020). Thus, the specimens assigned by Scholze et al. (2019) to *Pseudestheria chatangensis* do not belong to the species *chatangensis* Novozhilov, 1946, but nonetheless still represent the genus *Pseudestheria*.

Genus *Pseudestheria* Raymond, 1946

Type species: *Pseudestheria brevis* Raymond, 1946.

Diagnosis: Small to very large valves; oval to round shape; straight to slightly curved dorsal margin; umbo convexly curved, position of the umbo submedian 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).

Discussion: In the occurrence section presented by Scholze et al. (2021, p. 290), it is implied that occurrences of *Pseudestheria* outside of the late Carboniferous to late Permian are incorrect, due to a „...too broadly formulated definition of this genus.“ A restudy of the Permian type species, *Pseudestheria brevis* Raymond, 1946, is necessary to assess Scholze et al.'s (2021) claim.

Pseudestheria diensti (Gross, 1934)
(Figs. 2a–f, 6b–c, 7e–f, 9e–f)

*1934 *Estheria diensti*–Gross (in part)

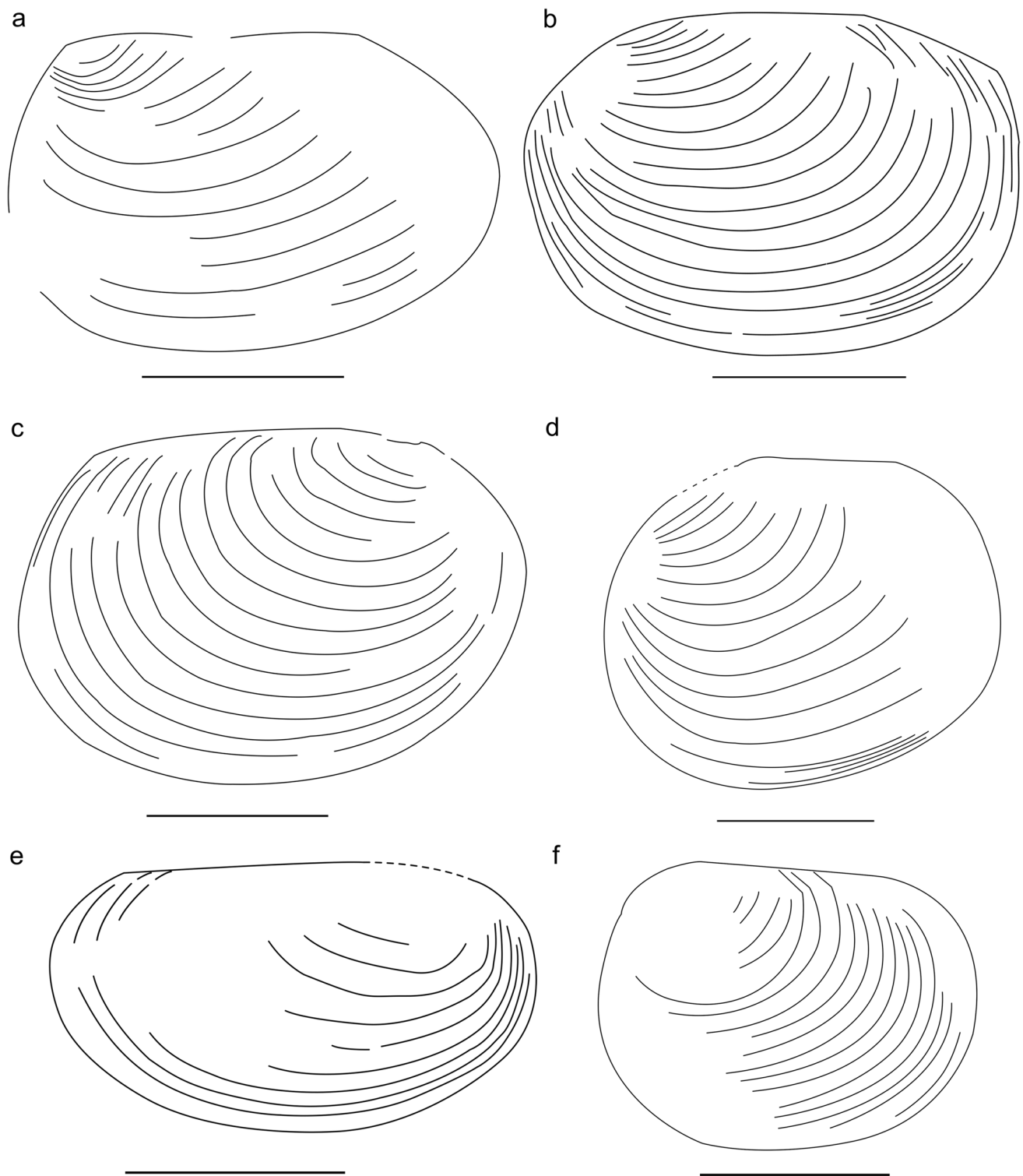


Figure 6. Clam shrimp from the Klerf Formation at Willwerath; sketch line drawings showing morphological variability; **a** (?) *Palaeolimnadiopsis* ? *eifelensis*, NHMMZ PWL 2021/6142-LS; **b** *Pseudestheria diensti*, NHMMZ PWL 2021/6008-LS; **c** *Pseudestheria*

diensti, NHMMZ PWL 2021/6143-LS; **d** *Pseudestheria subcircularis*, NHMMZ PWL 2021/6007-LS; **e** *Palaeolimnadiopsis* ? *eifelensis*, NHMMZ PWL 2021/6139-LS; **f** *Pseudestheria* cf. *diensti*, NHMMZ PWL 2021/6005-LS; all scale bars = 3 mm

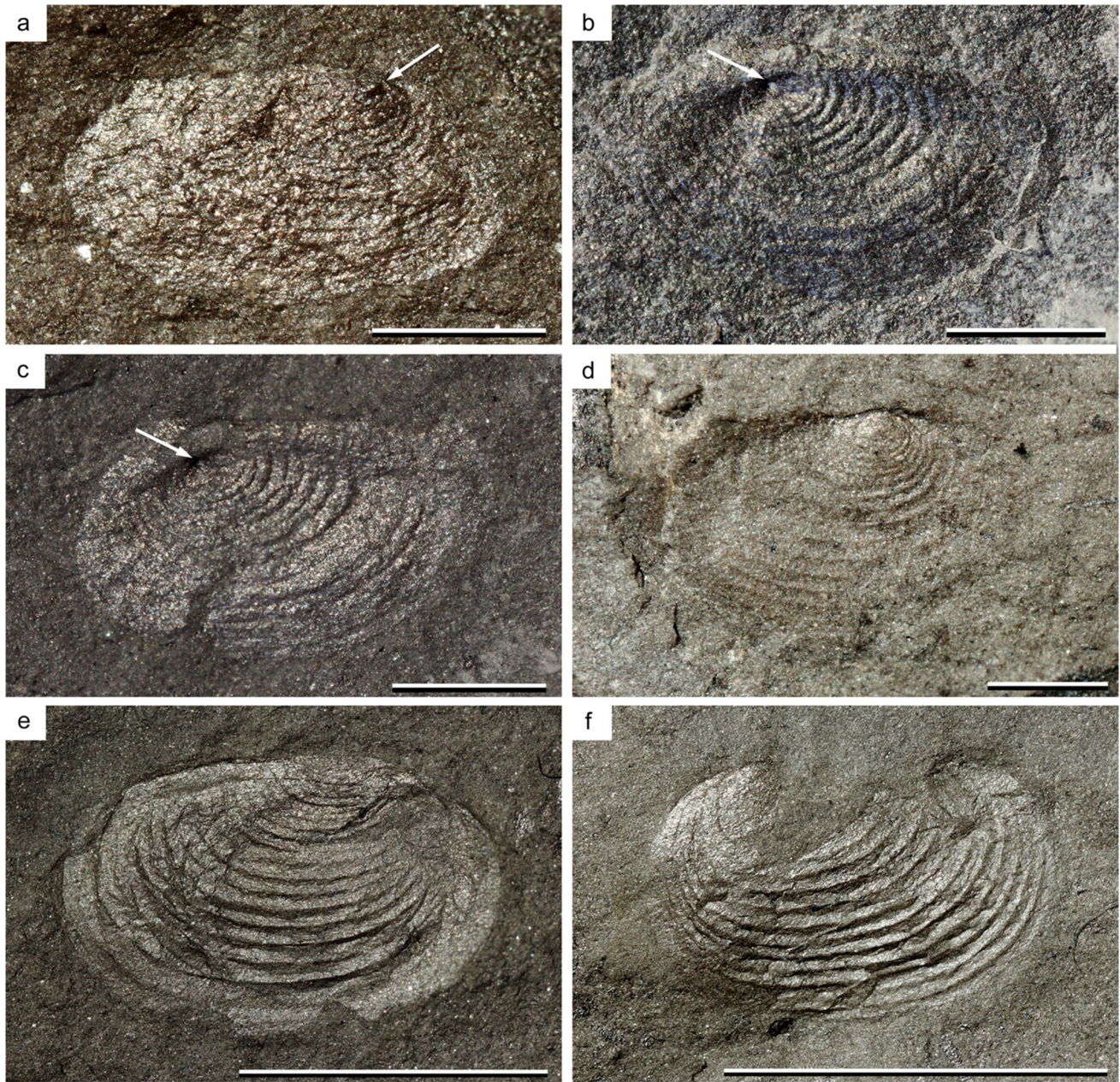


Figure 7. Clam shrimp from layer 102022 at Waxweiler; **a–c** *Cornia wasvilrensis* sp. nov.; white arrows indicate umbonal tubercle-like structure; **a** paratype NHMMZ PWL 2023/6009-LS a; **b** holotype NHMMZ PWL 2023/6004-LS a, photographed dry; **c** same specimen

photographed under alcohol immersion; **d** undetermined Spinicaudata, NHMMZ PWL 2023/6002-LS a (1); **e–f** *Pseudestheria diensti*; **e** NHMMZ PWL 2023/6105-LS a; **f** NHMMZ PWL 2023/6001-LS; scale bars in **a–d** = 1 mm, and in **e–f** = 5 mm

1946 *Pseudestheria diensti* (Gross, 1934)–Raymond: p. 244 (in part)

2006 *Estheria diensti* Gross, 1934–Franke: pl. 11, fig. 2

2012 *Estheria diensti*–Becker and Franke: pl. 2, figs. 7–8

2016 conchostracan–Poschmann et al.: fig. 4b

Material: NHMMZ PWL 2021/6143-LS, NHMMZ PWL 2021/6009-LS, NHMMZ PWL 2021/6005-LS, NHMMZ PWL 2021/6142-LS.

Description: Characterised by an oval outline, height 4.8–5.8 mm, length 7.3–8.4 mm, height/length ratio of 0.66–0.73, very small larval valve, a long and almost straight to very slightly curved dorsal margin, and the number of growth lines is 15–21. This morphotype most closely corresponds to *Pseudestheria diensti* (see also Table 1).

Pseudestheria cf. *diensti* (Gross, 1934)
(Figs. 3a–c, 6f)

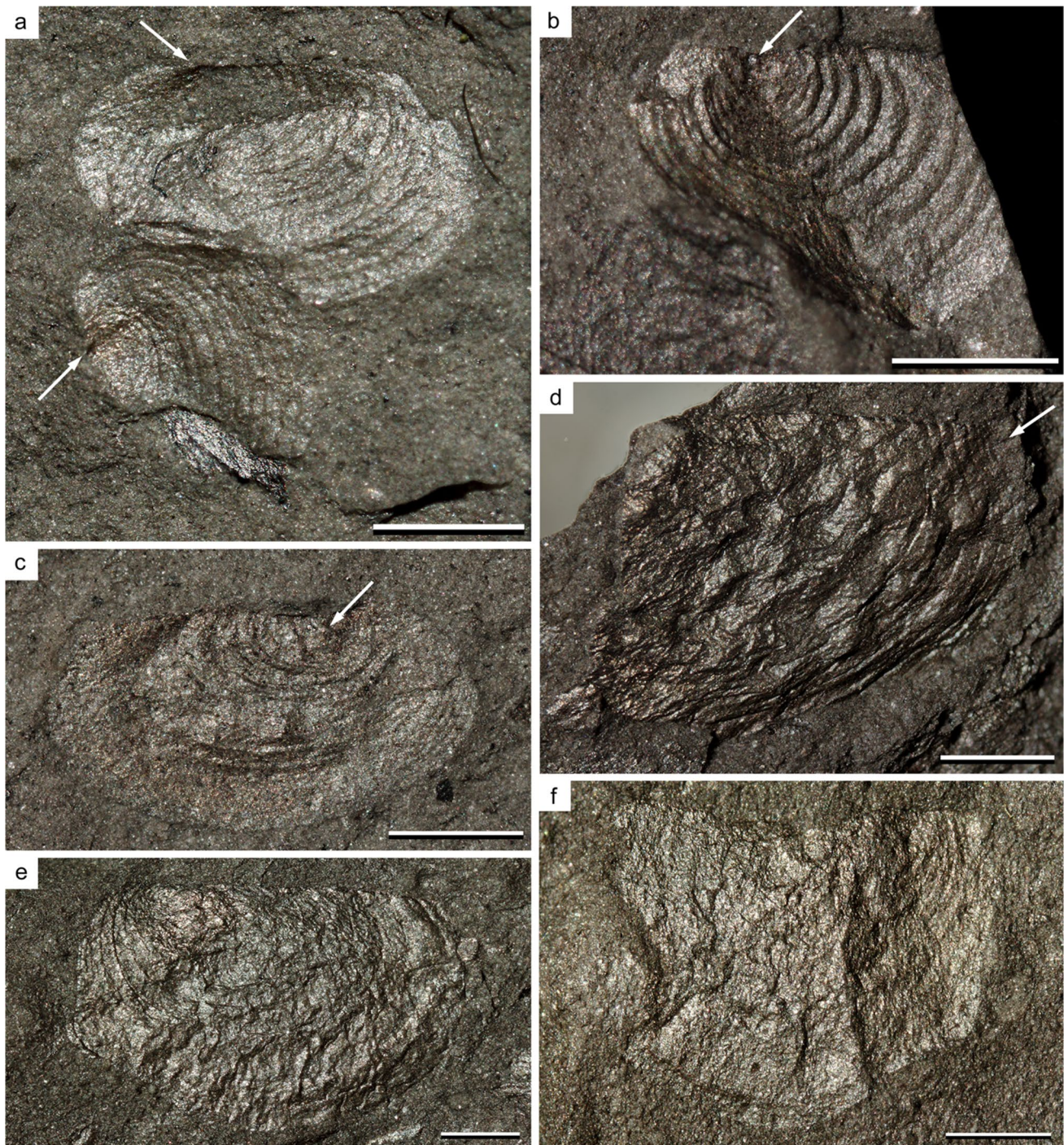


Figure 8. Clam shrimp from layer 102022 at Waxweiler; **a–c** *Cornia wasvilrensis* sp. nov.; white arrows indicate umbonal tubercle-like structure; **a** NHMMZ PWL 2023/6000-LS a, two left valves and one right valve (uppermost one) in close association; **b** NHMMZ PWL 2023/6108-LS; **c** NHMMZ PWL 2023/6107-LS a; **d** *Palaeolimnadi-*

opsis sp. cf. *P. frankeorum* sp. nov., NHMMZ PWL 2023/6252-LS a; white arrow indicates recurved growth lines and posterior margin; **e** *Spinicaudata?* incertae sedis, NHMMZ PWL 2023/6250-LS; **f** *Spinicaudata?* incertae sedis, NHMMZ PWL 2023/6254-LS; note blunt anterior margins in **e** and **f**; all scale bars = 1 mm

Material: NHMMZ PWL 2021/6009-LS, NHMMZ PWL 2021/6005-LS

Description: These specimens have a valve shape in between that of *Pseudestheria diensti* and *Pseudestheria*

subcircularis with a height/length ratio of 0.76 and 0.77, respectively. Otherwise, it is very close to *Pseudestheria diensti*. These specimens are assigned here to *Pseudestheria* in open nomenclature as *Ps.* cf. *diensti*.

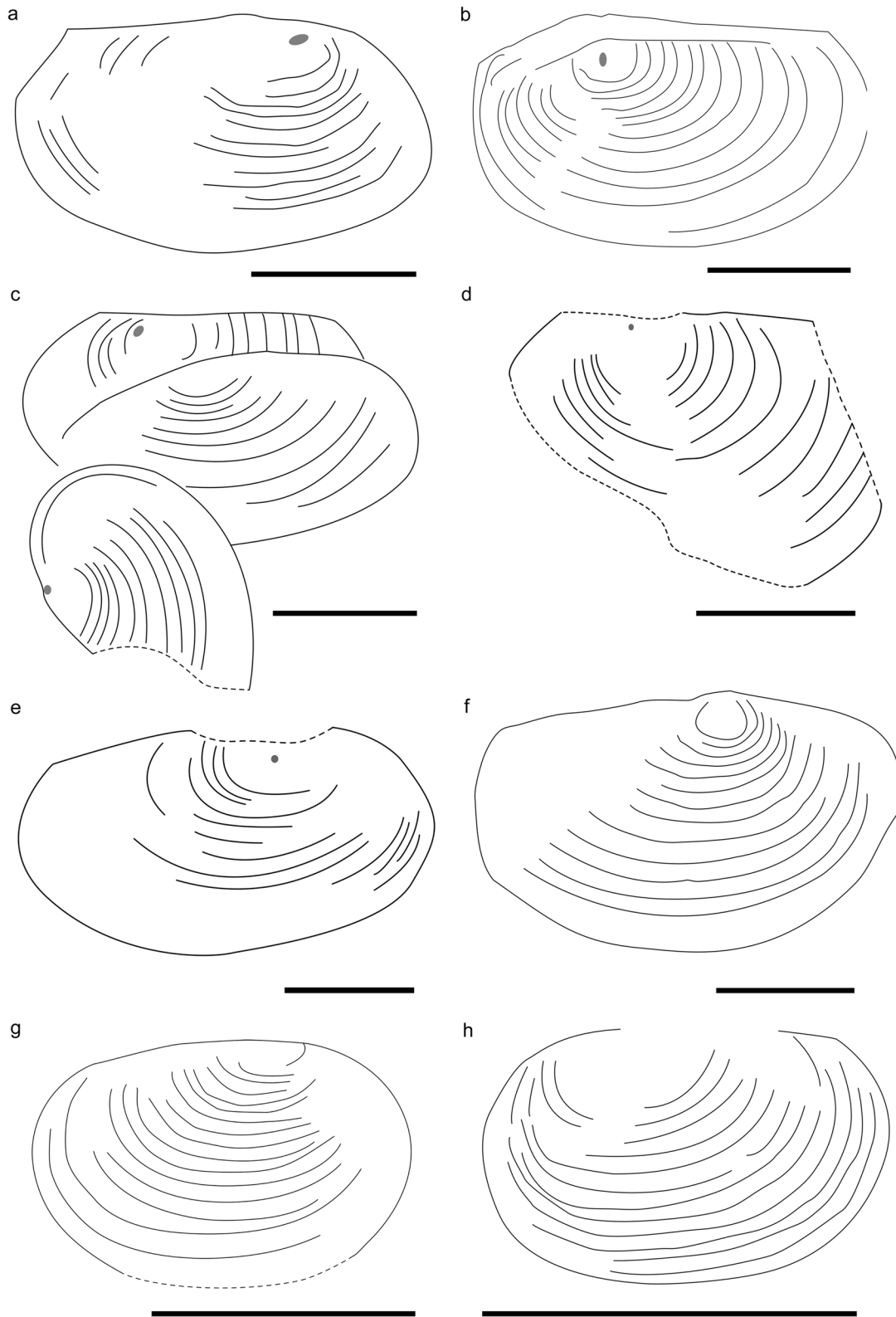


Figure 9. Clam shrimp from layer 102022 at Waxweiler; sketch line drawings showing morphological variability; **a–e** *Cornia wasvillensis* sp. nov.; **a** paratype NHMMZ PWL 2023/6009-LS a; **b** holotype NHMMZ PWL 2023/6004-LS a; **c** paratype NHMMZ PWL 2023/6000-LS a; **d** NHMMZ PWL 2023/6108-LS; **e** NHMMZ PWL

2023/6107-LS a; **f** undetermined Spinicaudata?, NHMMZ PWL 2023/6002-LS a (1); **g–h** *Pseudestheria diensti*; **g** NHMMZ PWL 2023/6105-LS a; **h** NHMMZ PWL 2023/6001-LS; scale bars in **a–f** = 1 mm, and in **g–h** = 5 mm

Table 1. Overview of morphometric data of clam shrimp from the Klerf Formation attributed to *Pseudestheria*. Abbreviations (see also Scholze and Schneider, 2015, fig. 1): dm, dorsal margin; e, extend of curvature of dorsal margin; *H* total height of valve; *L* total length of valve; *Ldm* length of dorsal margin; *Wax* Waxweiler; *Wi* Willwerath

Repository number	Height; Length; H/L ratio	Length dm; Ldm/L	e; e/Ldm	Approximate number of visible growth lines; comments	Fig.	Taxon (locality or layer)
MB.A.0039	3.5; 5.4; 0.61	4.1; 0.76	0.46; 0.11	16; dm slightly curved	Gross 1934, fig. 1	<i>Pseudestheria diensti</i> (Wi)
MB.A.0041	4.0; 6.0; 0.67	4.5; 0.75	0.34; 0.08	12; dm slightly curved	Gross 1934, fig. 3	(?) <i>Pseudestheria diensti</i> (Wi)
MB.A.0042	4.4; -	-	-	> 10; posterior end damaged; dm straight	Gross 1934, fig. 4	(?) <i>Pseudestheria diensti</i> (Wi)
MB.A.0043	4.9; 7.2; 0.68	6.2; 0.68	0.26; 0.04	16; dm slightly curved	Gross 1934, figs. 5, 8, 9	<i>Pseudestheria diensti</i> (Gross), holotype (Wi)
NHMMZ PWL 2021/6005-LS	4.6; 6.0; 0.77	4.1; 0.68	0.53; 0.13	17	3c, 6f	<i>Pseudestheria</i> cf. <i>diensti</i> (Wi)
NHMMZ PWL 2021/6006-LS	5.3; 7.3; 0.73	5.0; 0.68	-	16	2e–f	<i>Pseudestheria diensti</i> (Wi)
NHMMZ PWL 2021/6008-LS	5.3; 7.6; 0.70	4.8; 0.63	0.48; 0.10	21	2c–d, 6b	<i>Pseudestheria diensti</i> (Wi)
NHMMZ PWL 2021/6009-LS	5.0; 6.6; 0.76	4.1; 0.62	-	> 15	3a–b	<i>Pseudestheria</i> cf. <i>diensti</i> (Wi)
NHMMZ PWL 2021/6143-LS	5.8; 8.4; 0.69	6.0; 0.71	0.48; 0.08	16	2a–b, 6c	<i>Pseudestheria diensti</i> (Wi)
NHMMZ PWL 2023/6001-LS	3.4; 5.4; 0.63	3.7; 0.69	-	> 12	7f; 9f	<i>Pseudestheria diensti</i> (Wax 102022)
NHMMZ PWL 2023/6005-LS	4.7; 7.1; 0.66	5.0; 0.70	-	15	7e; 9e	<i>Pseudestheria diensti</i> (Wax 102022)
MB.A.0044	6.0; 6.6; 0.91	4.2; 0.64	0.62; 0.15	18; dm strongly curved	Gross 1934, fig. 6	<i>Pseudestheria subcircularis</i> Raymond, holotype (Wi)
NHMMZ PWL 2021/6141-LS	5.2; 5.8; 0.90	damaged	-	> 13	4e–f	<i>Pseudestheria subcircularis</i> (Wi)
NHMMZ PWL 2021/6007-LS	6.4; 7.6; 0.84	5.9 ?; 0.78	-	17	4d, 6d	<i>Pseudestheria subcircularis</i> (Wi)

Table 2. Overview of morphometric data of *Cornia wasvilrensis* sp. nov. from the Klerf Formation of Waxweiler, layer 102022. Abbreviations as in table 1

Repository number	Height; Length; H/L ratio	Length dm; Ldm/L	Approximate number of visible growth lines	Fig.	Remark
NHMMZ PWL 2023/6000-LS (1)	1.2; 2.4; 0.50	1.6; 0.64	> 8	8a; 9c	Paratype
NHMMZ PWL 2023/6000-LS (2)	1.3; 2.6; 0.51	-	10	8a; 9c	Paratype
NHMMZ PWL 2023/6004-LS	1.6; 2.8; 0.59	1.7; 0.61	12	7b–c, 9b	Paratype
NHMMZ PWL 2023/6009-LS	1.5; 2.6; 0.57	1.5; 0.59	12	7a, 9a	Holotype
NHMMZ PWL 2023/6107-LS	1.8; 3.2; 0.56	about 2.1; 0.66	13	8c, 9e	-
NHMMZ PWL 2023/6108-LS	1.8; -	-	11	8b, 9d	-

Table 3. Overview of morphometric data of clam shrimp from the Klerf Formation attributed to *Palaeolimnadiopsis*. Abbreviations as in table 1

Repository number	Height; Length; H/L ratio	Length dm; Ldm/L	e; e/Ldm	Approximate number of visible growth lines; comments	Fig.	Taxon (locality or layer)
MB.A.0040	4.6; -	-	-	11; anterior part damaged; dm straight	Gross 1934, fig. 2	<i>Palaeolimnadiopsis</i> ? <i>eifelensis</i> Raymond, holotype (Wi)
NHMMZ PWL 2021/6139-LS	3.7; 6.6; 0.56	5.1; 0.77	0.34; 0.07	10	4a–c, 6e	<i>Palaeolimnadiopsis</i> ? <i>eifelensis</i> (Wi)
NHMMZ PWL 2021/6142-LS	4.8; 7.3; 0.66	4.8; 0.66	0.37; 0.13	15	3d, 6a	possibly <i>Palaeolimnadiopsis</i> ? <i>eifelensis</i> (Wi)
NHMMZ PWL 2022/5003-LS a (3)	3.2; 3.8?; 0.84?	3.0; 0.79?	-	-; posterodorsal spine indicated	11e	<i>Palaeolimnadiopsis frankeorum</i> sp. nov. (Wax LCMO)
NHMMZ PWL 2022/5004-LS a (1)	3.4; 4.2; 0.81	3.5; 0.83	0.23; 0.07	12	11f, 12c	<i>Palaeolimnadiopsis frankeorum</i> sp. nov. (Wax LCMO)
NHMMZ PWL 2022/5004-LS c (1), left valve	2.8; 4.2; 0.67	3.1; 0.74	0.23; 0.07	-	11b, 12e	<i>Palaeolimnadiopsis frankeorum</i> sp. nov., paratype (Wax LCMO)
NHMMZ PWL 2022/5004-LS c (2), right valve	3.0; 4.5?; 0.67	3.4; 0.76	0.23; 0.07	> 14	11b, 12e	<i>Palaeolimnadiopsis frankeorum</i> sp. nov., paratype (Wax LCMO)
NHMMZ PWL 2022/5004-LS d	4.0; 4.7; 0.85	3.5; 0.74	0.38; 0.11	9; anterior slightly crushed	11d	<i>Palaeolimnadiopsis frankeorum</i> sp. nov. ? (Wax LCMO)
NHMMZ PWL 2022/5006-LS	3.0; 4.5; 0.67	3.3; 0.74	0.27; 0.08	16; dm spinose; uppermost posterior margin concave + small projection	10a–e, 12a	<i>Palaeolimnadiopsis frankeorum</i> sp. nov., holotype (Wax LCMO)
NHMMZ PWL 2023/6252-LS	2.9; -;			14	8d	<i>Palaeolimnadiopsis</i> sp. cf. <i>P. frankeorum</i> sp. nov. (Wax 102022)

Pseudestheria subcircularis Raymond, 1946 (Figs. 4d–f, 6d)

1934 *Estheria diensti*–Gross: fig. 6

*1946 *Pseudestheria subcircularis*–Raymond: p. 244

1961 *Glyptoasmussia willweratica*–Novozhilov p. 62, fig. 25, pl. 15, fig. 5

Material: NHMMZ PWL 2021/6007-LS, NHMMZ PWL 2021/6141-LS.

Description: These specimens are characterised by an almost round outline, height 5.2–6.4 mm, length 5.8–7.6 mm, height/length ratio of 0.84–0.90, very small larval valve, a short and almost straight dorsal margin, and 13–17 growth lines. They clearly correspond to the specimen described as *Pseudestheria subcircularis* by Raymond (1946).

Remarks: *Pseudestheria subcircularis* Raymond, 1946 should not be confused with *Estheria subcircularis*

Chernyshev, 1934, which has been transferred to *Asmussia* (Novozhilov 1956a; Zaspelova 1973).

Subfamily Vertexiinae Kobayashi, 1954

Genus *Cornia* Lutkevich, 1937

Remarks: Following the emended diagnosis of Kozur and Seidel (1983) the genus *Cornia* has a long, straight dorsal margin and a spine at the umbo (Scholze et al. 2015). A small tubercle or radial element, possibly representing the base of a hollow spine, and a straight dorsal margin are both present in our material. Therefore, we assign the Waxweiler specimens tentatively to this genus.

Type species: *Cornia papillaria* Lutkevich, 1937 from the upper Permian (Lopingian) at Kuznetsk Basin, Siberia, Russia, by original designation.

Cornia wasvilrensis sp. nov. (Figs. 7a–c, 8a–c, 9a–e)

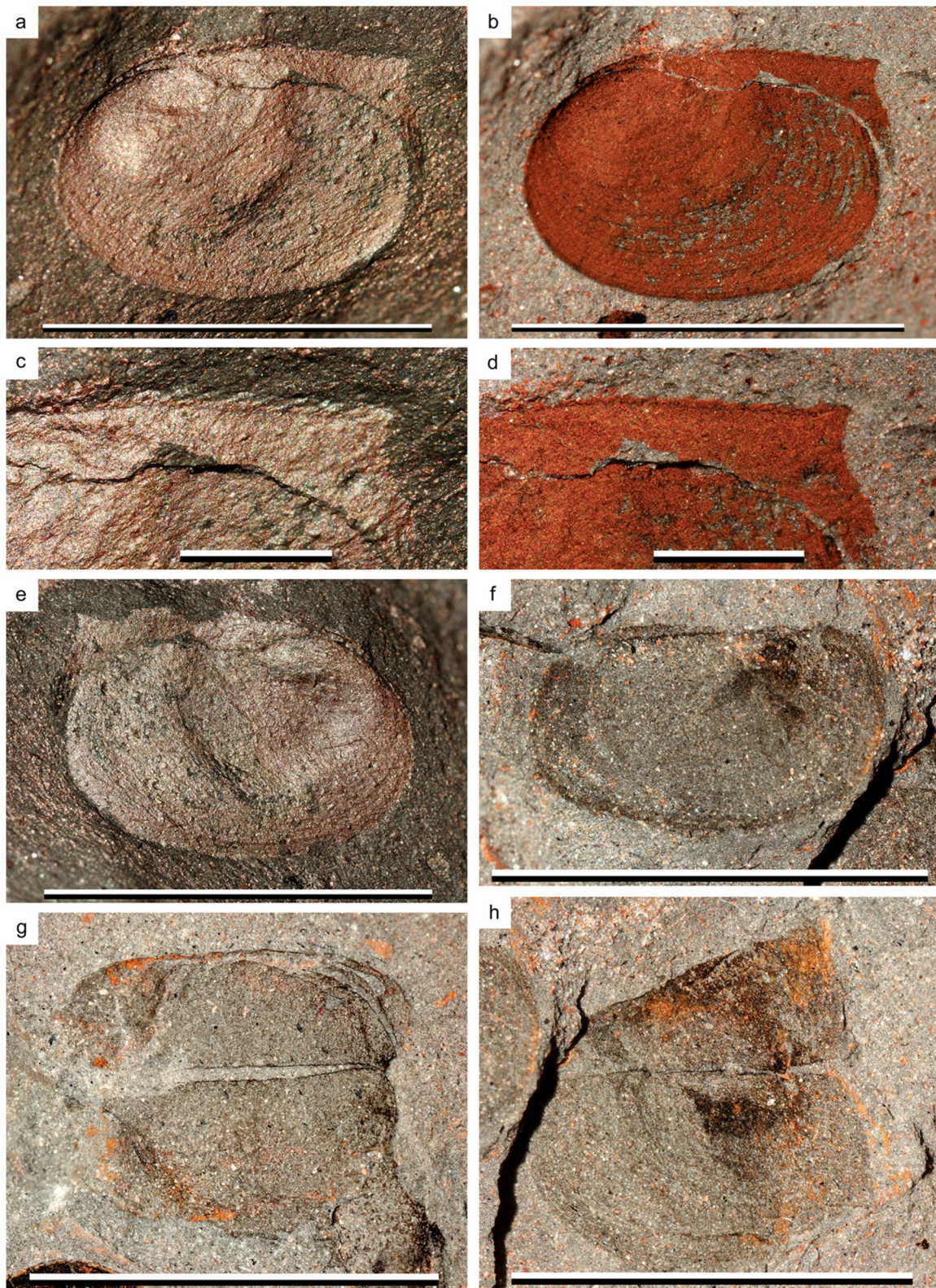


Figure 10. Clam shrimp from the LCMO at Waxweiler; **a–e** *Palaeolimnadiopsis frankeorum* sp. nov.; **a–d** holotype NHMMZ PWL 2022/5006-LS **a**; exceptionally well-preserved specimen showing spinose dorsal margin and concave posterodorsal margin; various degrees of crossing polarizing filters in **a**, **c** and **b**, **d**, respectively;

e counterpart of holotype NHMMZ PWL 2022/5006-LS **b**; **f–h** *Spinicaudata?* incertae sedis; **f** NHMMZ PWL 2022/5001-LS (1); **g** NHMMZ PWL 2022/5005-LS; specimen in butterfly position; **h** NHMMZ PWL 2022/5001-LS (2), specimen in butterfly position; all scale bars = 5 mm, except in **c–d** = 1 mm

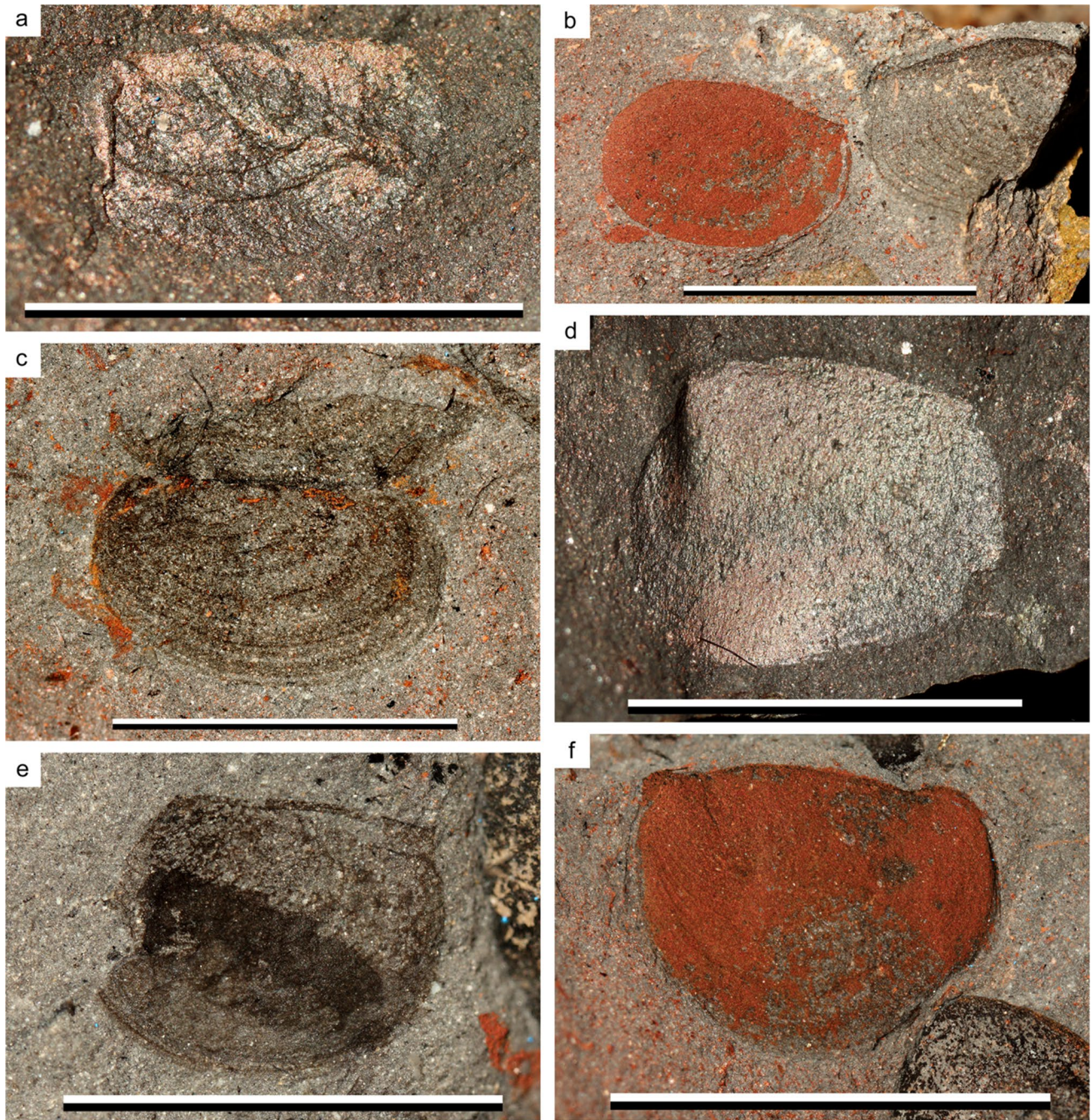


Figure 11. Clam shrimp from the LCMO at Waxweiler; **a** *Spinicaudata? incertae sedis*, small specimen NHMMZ PWL 2022/5003-LS a (2); **b** *Palaeolimnadiopsis frankeorum* sp. nov., paratype NHMMZ PWL 2022/5004-LS c; **c** *Spinicaudata? incertae sedis*, NHMMZ

PWL 2022/5003-LS b (1), specimen in butterfly position; **d–f** *Palaeolimnadiopsis frankeorum* sp. nov.; **d** NHMMZ PWL 2022/5004-LS d; **e** NHMMZ PWL 2022/5003-LS a (3); **f** NHMMZ PWL 2022/5004-LS a (1); all scale bars = 5 mm

Derivation of name: After ‚Wasvire‘, the medieval name of the village of Waxweiler.

Holotype: NHMMZ PWL 2023/6009-LS a, b, part and counterpart (Figs. 7a, 9a).

Paratypes: NHMMZ PWL 2023/6004-LS a, b, part and counterpart (Figs. 7b–c, 9b); NHMMZ PWL 2023/6000-LS a, b, part and counterpart (two right and one left valve associated on one slab) (Figs. 8a, 9c).

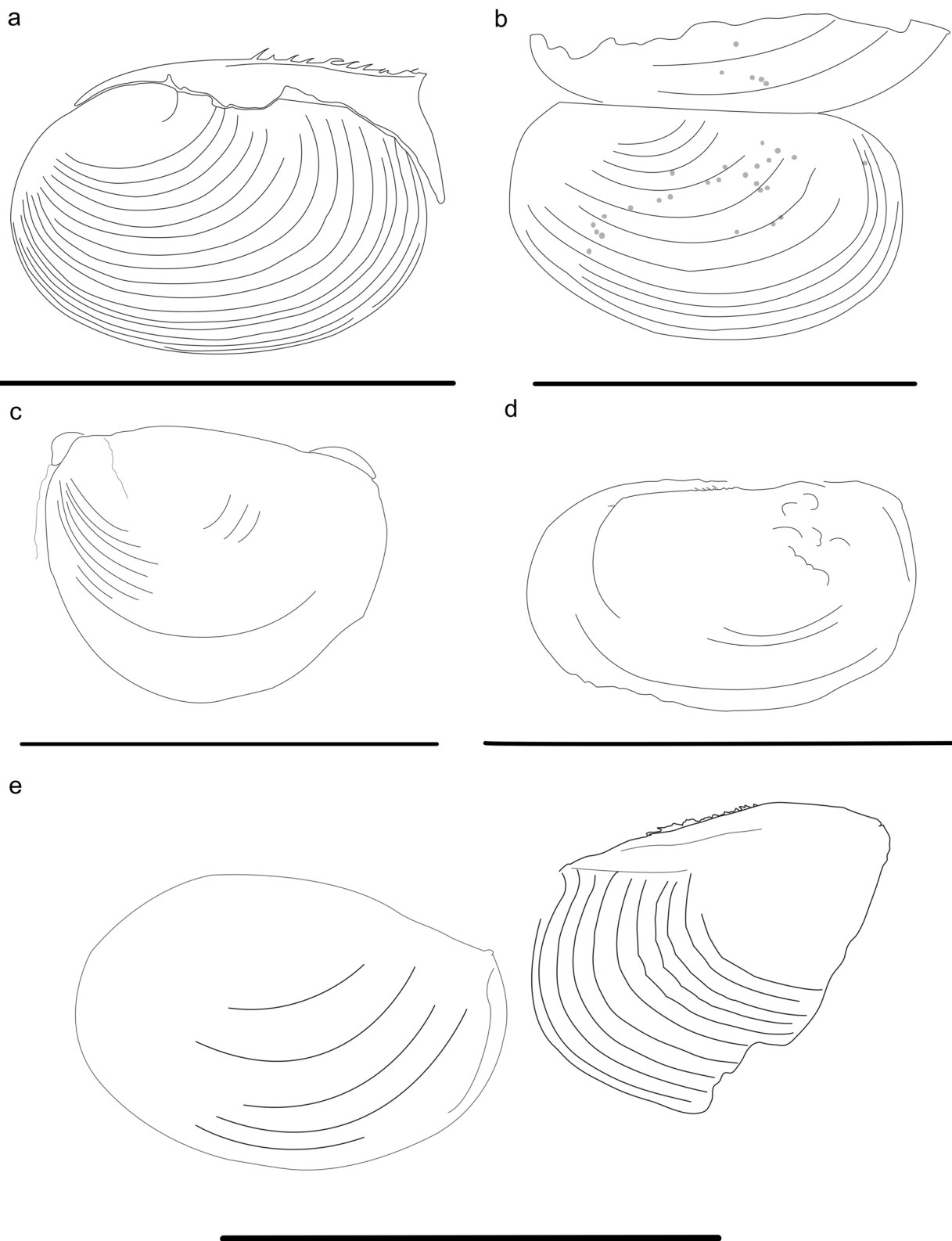


Figure 12. Clam shrimp from the LCMO at Waxweiler; **a** *Palaeolimnadiopsis frankeorum* sp. nov., holotype NHMMZ PWL 2022/5006-LS a; **b** *Spinicaudata?* incertae sedis, NHMMZ PWL 2022/5003-LS b (1); **c** *Palaeolimnadiopsis frankeorum* sp. nov., NHMMZ PWL

2022/5004-LS a (1); **d** *Spinicaudata?* incertae sedis, NHMMZ PWL 2022/5001-LS a (1); **e** *Palaeolimnadiopsis frankeorum* sp. nov., paratype NHMMZ PWL 2022/5004-LS c; all scale bars = 5 mm

Table 4. Overview of morphometric data of Spinicaudata? inc. sed. from the Klerf Formation. Abbreviations as in table 1

Repository number	Height; Length; H/L ratio	Length dm; Ldm/L;	Approximate number of visible growth lines; comments	Fig.	Taxon (locality or layer)
NHMMZ PWL 2021/6140-LS	-	-	13; anterior part missing	5a–b	Spinicaudata? inc. sed. (Wi)
NHMMZ PWL 2021/6144-LS	-	-	> 11; anterior part missing	5c–d	Spinicaudata? inc. sed. (Wi)
NHMMZ PWL 2022/5001-LS (1)	2.3; 4.1; 0.56	3.1; 0.76	-; possible remains of soft parts	10f, 12d	Spinicaudata? inc. sed. (Wax LCMO)
NHMMZ PWL 2022/5001-LS (2)	2.5; 4.3; 0.58	3.0; 0.70	-; „butterfly“ position	10h	Spinicaudata? inc. sed. (Wax LCMO)
NHMMZ PWL 2022/5003-LS a (2)	2.1; 3.5; 0.60	2.8; 0.80	about 7; anterior slightly crumbled	11a	Spinicaudata? inc. sed., juvenile? (Wax LCMO)
NHMMZ PWL 2022/5003-LS b (1)	3.0; 5.2; 0.58	3.2; 0.62	10; 2 valves associated	11c, 12b	Spinicaudata? inc. sed. (Wax LCMO)
NHMMZ PWL 2022/5005-LS	4.5?; -	2.8?; -	-; „butterfly“ position	10g	Spinicaudata? inc. sed. (Wax LCMO)
NHMMZ PWL 2023/6002-LS	1.9; 3.6; 0.53	1.7; 0.47	12	7d; 9f	Spinicaudata? inc. sed., Asmussiidae-like type (Wax 102022)
NHMMZ PWL 2023/6250-LS	3.1; 5.1; 0.61	4.2; 0.82	> 10	8e	Spinicaudata? inc. sed., <i>Ulugkemia</i> -like type 1 (Wax 102022)
NHMMZ PWL 2023/6254-LS	3.0; 4.4; 0.68	3.5; 0.80	about 12	8f	Spinicaudata? inc. sed., <i>Ulugkemia</i> -like type 2 (Wax 102022)

Additional material: NHMMZ PWL 2023/6102-LS a, b, part and counterpart (not figured); NHMMZ PWL 2023/6107-LS a, b, part and counterpart (Figs. 8c, 9e); NHMMZ PWL 2023/6108-LS (Figs. 8b, 9d).

Type locality: Köppen Quarry north of Waxweiler/Eifel.

Type stratum: Klerf Formation, uppermost lower Emsian in the regional stratigraphic frame; probably corresponding to the early to mid Emsian in terms of the international chronostratigraphic frame (see discussion in Steemans et al. 2022).

Diagnosis: Medium-sized, elongated oval valves with about 11–13 growth lines; dorsal margin short to long (sensu Scholze and Schneider 2015) and almost straight; umbo in submedial and marginal position; larval valve very small; ornament unknown.

Description: This new species attributed to *Cornia* is the dominant clam shrimp taxon in the association of layer 102022 from Waxweiler and is represented by some well-preserved specimens (Figs. 7a–c, 8a–c, 9a–e) characterised by elongated oval, medium-sized carapace valves with mostly short (sometimes long; see Table 2) dorsal margins and well-rounded ventral margins. The length is 2.6–3.2 mm, height 1.3–1.8 mm, height/length ratio 0.51–0.59, with very small larval valve and 10–13 visible growth lines. Well-preserved specimens show a small tubercle-like structure (diameter approx. 80–110 µm) on the larval valve. A micro-ornament is not observed.

Discussion: As pointed out by Scholze and Matamales-Andreu (2021), the genus *Hornestheria* Kozur and Lepper,

in Kozur and Weems (2010) has a low convexity of the carapace valves and an almost straight dorsal margin, an anterior margin with greatest curvature above the midline and with the lower part strongly oblique (in most species), a posterior margin strongly rounded with greatest curvature somewhat below the midline and with often oblique upper part. The larval carapace valve (=umbonal area of the valve free of growth lines) bears a rather distinct to unrecognisable radial element depending on the state of preservation. This radial element closely resembles that of *Lioestheria* Depéret and Mazeran, 1912, which has a similar structure on the larval carapace valves. On the other hand, the size of the larval carapace valve in adult individuals of *Lioestheria* is greater than 1/3 of the total carapace valve length (Holub and Kozur 1981), which is much larger than in *Hornestheria* and in the Waxweiler specimens. Similar sculptures are also found on the larval carapace valves of *Cornia* Lutkevich, 1937 (e.g. Kozur and Seidel 1983; Kozur and Mock 1993; Tassi et al. 2013; Scholze et al. 2016). However, the generally radial shape of the larval sculpture in *Hornestheria* makes it consistently different from the circular shape of the corresponding umbonal structure in *Cornia* (Scholze and Matamales-Andreu 2021). The rather small larval valve and round larval sculpture in the Waxweiler specimens prompt us to tentatively assign them to the genus *Cornia*, rather than to *Lioestheria* or *Hornestheria*. *Cornia* is a genus most widely distributed in the upper Permian and Triassic (e.g.

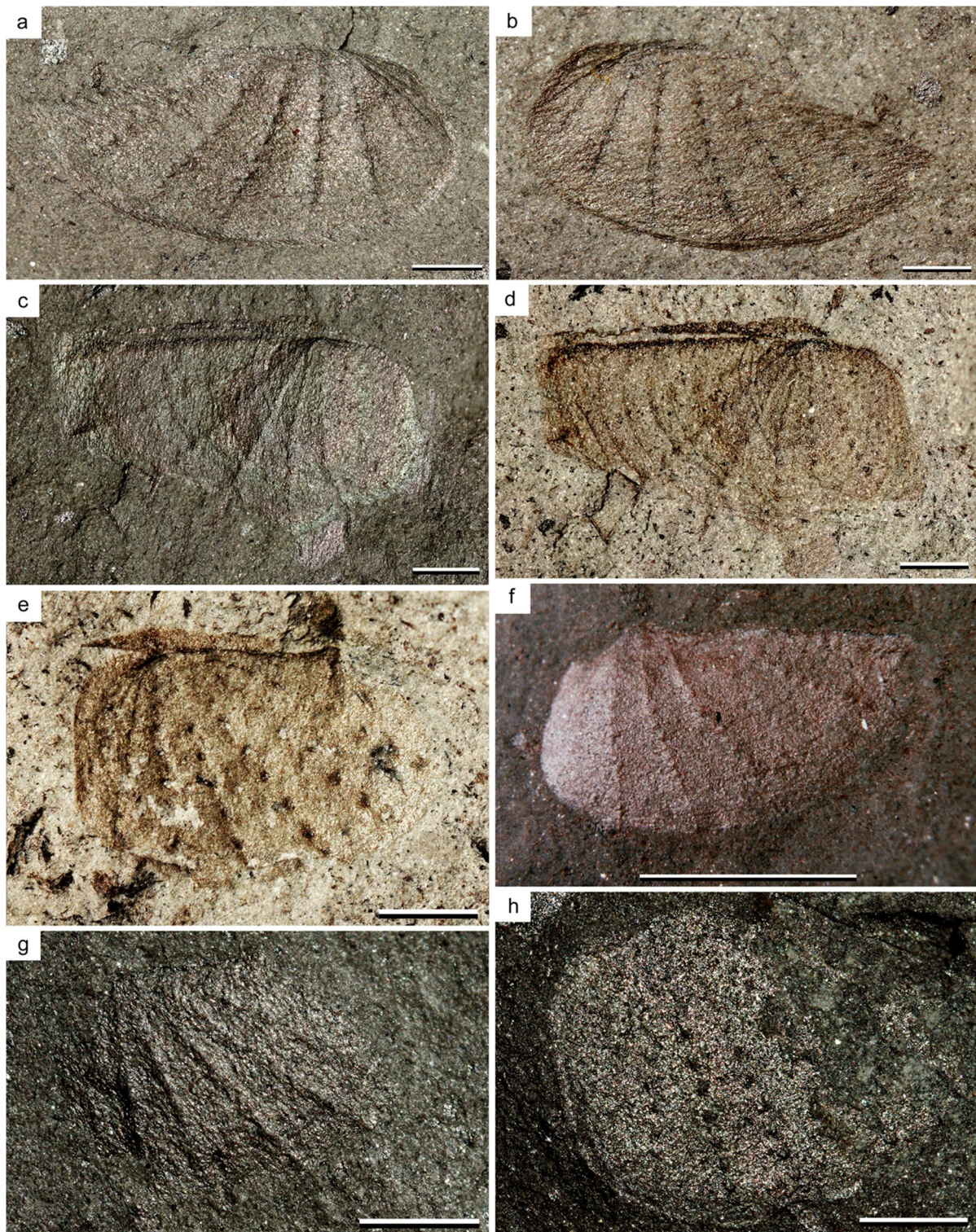


Figure 13. The leaiane clam shrimp *Eicheleia wenndorfi* gen. et sp. nov. from the Klerf Formation at Waxweiler; **a–b** holotype NHMMZ PWL 2023/6110-LS, from layer 102022; **a** part, polarizing filters uncrossed; **b** counterpart, polarizing filters crossed; **c–d** paratype NHMMZ PWL 2023/6111-LS, from layer 102022; counterpart, in **c** with polarizing filters uncrossed, in **d** with polarizing filters crossed; **e** NHMMZ 2023/6104-LS b, from layer 102022, polarizing filters

crossed; **f** specimen Wax 240a from the Rebske collection (see also Poschmann and Franke 2006); **g** NHMMZ PWL 2023/6005-LS, from layer 102022; **h** specimen NHMMZ PWL 2023/6003-LS a, from layer 102022; note preservational differences affecting the appearance of carinae and nodes; scale bars in **a–e** and **g–h** = 1 mm, and in **f** = 3 mm

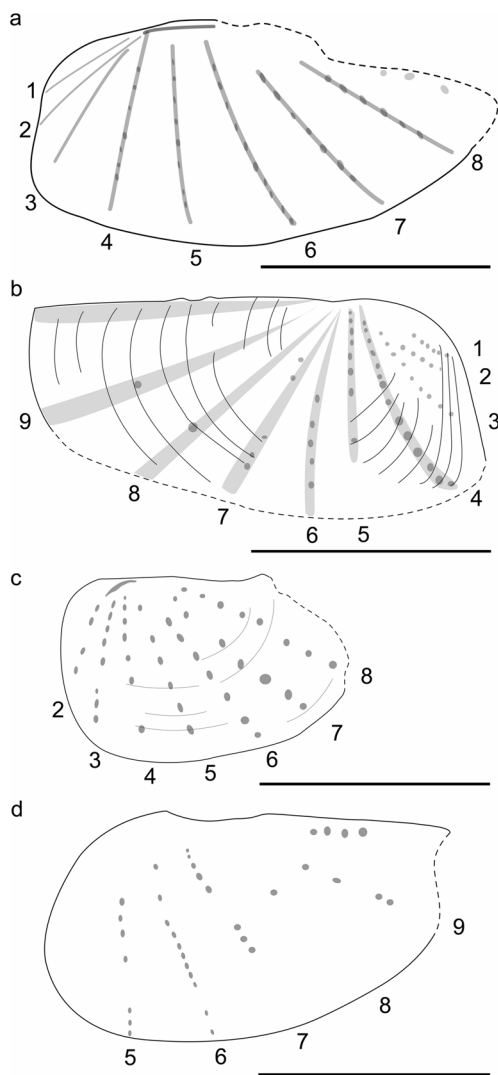


Figure 14. *Eicheleia wenndorfi* gen. et sp. nov. from the Klerf Formation at Waxweiler, sketch line drawings; **a** holotype NHMMZ PWL 2023/6110-LS, from layer 102022; **b** paratype NHMMZ PWL 2023/6111-LS b, from layer 102022; **c** NHMMZ 2023/6104-LS b, from layer 102022; **d** specimen Wax 240a from the Rebske collection (see also Poschmann and Franke 2006); lateral carinae numbered; all scale bars = 3 mm

Kozur and Seidel 1983; Kozur and Mock 1993; Tassi et al. 2013; Scholze et al. 2016; Scholze and Matamales-Andreu 2021). *Cornia wasvilrensis* sp. nov. differs (among other characters) from the type species *C. papillaria* Lutkevich, 1937 in a more anteriorly positioned umbo and much more elongate valves. It differs from other stratigraphically younger Carboniferous to Jurassic species such as *C. panchetella* Tasch, 1987, *C. angolata* Tasch, 1987, and *C. portenta* Novozhilov, 1970 in a less centrally positioned and much smaller larval valve and smaller tubercle, from *C. coghiani* (Etheridge, 1888), *C. salairica* Novozhilov, 1970, *C. jugensis* Novozhilov, 1966, and *C. sileenica* Molin, in

Molin and Novozhilov 1965 in a more elongate valve and smaller tubercle. *Cornia wasvilrensis* sp. nov. resembles *C. germari* (Beyrich, 1857) in the presence of an elongate valve with anteriorly positioned umbo and a comparable relative length of the straight, dorsal margin, but it differs in the smaller larval valve with uniformly smaller tubercle. It differs from the only other Early Devonian *Cornia* species, *C. cheni* Liao and Chen, 2022 from China in a considerably smaller size ($L < 3.0$ mm versus 3.2–4.1 mm), more elongate valve ($H/L < 0.60$ versus > 0.63) and less marginally positioned, smaller tubercle.

Family Palaeolimnadiopseidae Defretin-Lefranc, 1965

Diagnosis: Posterior margin recurved dorsally becoming carinate at apex. Apex can be oriented dorsally producing a ‘saw-toothed’ dorsal margin (translation from Zhang et al. 1976 after Astrop and Hegna 2015; see also Li 2017).

Remarks: Subfamily divisions used by Chen and Shen (1985) (see also Liu 1982; Shen 1985; Gallego 2005) may not be useful. The monogeneric (according to Chen and Shen 1985) Anomalonematinae Novozhilov, 1958 may just be a highly autapomorphic member of the Palaeolimnadiopseinae Defretin-Lefranc, 1965. This would make Palaeolimnadiopseinae paraphyletic. Webb (1978) further synonymised two additional genera into *Palaeolimnadiopsis* (*Macrolimnadiopsis* Beurlen, 1954, *Pteriograptia* Novozhilov, 1954) and one subgenus (*Falsica* Novozhilov, 1970). Webb (1978) was apparently unaware of the work being done by Chinese palaeontologists (Zhang et al. 1976), which had raised *Falsica* to genus level and placed it into the family Perilimnadiidae Zhang and Chen in Zhang et al., 1976 (a conclusion maintained by Chen and Shen 1985). Chen and Shen’s (1985) classification monograph on fossil clam shrimp returned *Macrolimnadiopsis* to the Palaeolimnadiopseidae and *Pteriograptia* was placed in the family Fushunograptidae Wang in Hong et al., 1974.

Genus *Palaeolimnadiopsis* Raymond, 1946

Diagnosis: Recurved postero-dorsal margin, dorsal margin varying from almost straight to markedly spinose, with spines at end of growth bands; lacking umbonal tubercule, anterior rib, and undulations in growth lines (from Webb 1978; after Tasch 1969).

Remarks: The relationship between the two Devonian palaeolimnadiopseids, *Palaeolimnadiopsis* and *Belgolimnadiopsis* Novozhilov, 1958, needs to be re-evaluated. Novozhilov (1958) created *Belgolimnadiopsis* based on the original illustrations of ‘*Estheria* (*Euestheria*) *stockmansii*’ Maillieux, 1939. However, Novozhilov’s reillustrations of it take significant liberties with the outline—in particular, Novozhilov’s fig. 1 shows a sharp anterior-dorsal corner not visible in Maillieux’s photo.

Type species: *Palaeolimnadiopsis carpenteri* Raymond, 1946.

Palaeolimnadiopsis ? *eifelensis* Raymond, 1946 (Figs. 3d ?, 4a–c, 6a ?, 6e)

1934 *Estheria diensii*–Gross: fig. 2

*1946 *Palaeolimnadiopsis* ? *eifelensis*–Raymond pp. 271–272

1953 *Euestheria eifelensis* (Raymond)–Novozhilov p. 948, fig. 2b

1961 *Concherisma eifelense* Raymond–Novozhilov p. 86 (in part)

Material: NHMMZ PWL 2021/6139-LS, ? NHMMZ PWL 2021/6142-LS.

Description: Specimen NHMMZ PWL 2021/6139-LS has an elongate shape, height 3.7 mm, length 6.6 mm, a small height/length ratio of 0.56, somewhat larger larval valve, a long and almost straight dorsal margin, and shows only 10 growth lines. Specimen NHMMZ PWL 2021/6142-LS is only tentatively attributed to this taxon (see Table 3).

Remarks: Although the long and straight dorsal margin corresponds to *Palaeolimnadiopsis*? *eifelensis*, our specimen shows no recurved dorso-posterior margin or growth lines. This may be an indication that the curved growth lines, that led Raymond (1946) to assign the specimen in question to *Palaeolimnadiopsis* is a misconception of a preservational feature. Indeed, there is considerable crumbling of this carapace apparent from Gross (1934, fig. 2).

Palaeolimnadiopsis frankeorum sp. nov. (Figs. 10a–e, 11b, 11d–f, 12a, 12c, 12e)

Holotype: NHMMZ PWL 2022/5006-LS a, b, part and counterpart (Figs. 10a–e, 12a).

Paratype: NHMMZ PWL 2022/5004-LS c (a left and a right valve associated on one slab) (Figs. 11b, 12e).

Additional material: NHMMZ PWL 2022/5003-LS a (3) (Fig. 11e), NHMMZ PWL 2022/5004-LS a (1) (Figs. 11f, 12c). Specimen NHMMZ PWL 2022/5004-LS d (Fig. 11d) is only tentatively assigned to this taxon.

Derivation of name: For Dr. Christian Franke and Mouna Franke (Wallendorf) in recognition of Christian's enthusiasm and achievements with respect to the local Devonian fauna and Mouna's understanding and support.

Diagnosis: Large, oval valves with about 12–16 growth lines; dorsal margin long and very slightly curved, serrated, with small postero-dorsal projection; anterior and ventral margins well-rounded; umbo in anterior and marginal position; larval valve small; posterior margin and youngest 3–4 growth lines dorsally recurved; ornament unknown.

Description: In the specimens from Waxweiler LCMO we recognise two morphotypes (see Table 6). The first is represented by an exceptionally well-preserved specimen (Figs. 10a–e, 12a) and three further specimens (one represented by two valves) (Figs. 11b, 11e–f, 12c, 12e) plus one more strongly deformed specimen, which is assigned with reservation to the same morphotype (Fig. 11d). For these specimens, we propose a new species characterised by an oval outline with a long and slightly curved dorsal margin and well-rounded anterior and ventral margins. The height is 2.8–3.4 (4.0?) mm, length 4.2–4.5 (4.7?) mm, height/length ratio 0.74–0.81 (0.84?), with a small larval valve and 12–16 visible growth lines (see also Table 3). The holotype specimen NHMMZ PWL 2022/5006-LS (Figs. 10a–e, 12a) clearly shows a recurved uppermost posterior margin with an acute postero-dorsal projection and a „toothed“ posterior dorsal margin. The toothed appearance is due to the presence of thorn-like, postero-dorsal pointing projections. These characters are also indicated in specimens NHMMZ PWL 2022/5004-LS c (Figs. 11b, 12e) and more faintly in NHMMZ PWL 2022/5003-LS a (3) (Fig. 11e).

Palaeolimnadiopsis sp. cf. *P. frankeorum* sp. nov. (Fig. 8d)

Material: PWL 2023/6253-LS a, b, part and counterpart.

Remarks: The single left valve from Waxweiler 102022 lacks the anterior part, but shows recurved growth lines and uppermost posterior margin, and a long, straight dorsal margin. This specimen clearly differs from *Palaeolimnadiopsis* ? *eifelensis* from Willwerath in the distinct recurved growth lines, which are also more numerous (at least 14 can be counted). This specimen is too poorly preserved to assess its species affinities and is therefore left in open nomenclature.

Spinicaudata? incertae sedis (from Willwerath) (Fig. 5a–d)

Material: NHMMZ PWL 2021/6140-LS, NHMMZ PWL 2021/6144-LS.

Remarks: These specimens from Willwerath are poorly preserved and do not allow a closer determination. For morphometrics of individual specimens see Table 4.

Spinicaudata? incertae sedis (morphotype 2 from Waxweiler LCMO) (Figs. 10f–h, 11a, 11c, 12b, 12d)

Material: NHMMZ PWL 2022/5001-LS (1), NHMMZ PWL 2022/5001-LS (2), NHMMZ PWL 2022/5003-LS (1), ? NHMMZ PWL 2022/5003-LS a (2), NHMMZ PWL 2022/5005-LS.

Table 5. Overview of morphometric data of clam shrimp attributed to *Euestheria stockmansii* (Maillieux, 1939) from the lower Devonian of Belgium and France

Specimen	Height; Length; H/L ratio	Length dm; Ldm/L	Approximate number of visible growth lines; comments	Source of data
Estinnes-au-Mont 1	3.0; 4.5; 0.67	3.5; 0.78	-	Maillieux 1939, fig. 1a
Estinnes-au-Mont 2	dito	dito	-	Maillieux 1939, fig. 1b
Estinnes-au-Mont 3	3.0; 4.5; 0.67	3.5; 0.78	-	Maillieux 1939, fig. 2
Vincly 1	2.5; 4.1; 0.61	3.5; 0.85	12–14	Defretin 1950, fig. 6
Vincly 2	2.0; 3.5; 0.57	3.5; 1.0	12–14; dorso-ventrally compressed	Defretin 1950, fig. 7

Remarks: The second morphotype from the Waxweiler LCMO is characterised by smaller, elongate-oval, approximately sub-rectangular specimens with a straight dorsal margin and more submedially positioned umbo (Figs. 10f–h, 11c, 12b, 12d; see also Table 4). In specimens NHMMZ PWL 2022/5001-LS (1) (Fig. 10f) and NHMMZ PWL 2022/5001-LS (2) (Figs. 10h, 12d) the preservation of indistinct „soft-parts“ is indicated. In specimen NHMMZ PWL 2022/5003-LS (1) small round structures scattered in the central area of the valve hint at the possible preservation of eggs (Figs. 11c, 12b). These structures show up under crossed polarizing filters, however, preservation is poor and does not allow a more detailed description or certain identification. Specimen NHMMZ PWL 2022/5003-LS a (2) (Fig. 11a) is only tentatively referred to this morphotype.

Spinicaudata? incertae sedis (three different morphotypes from Waxweiler layer 102022) (Figs. 7d, 8e–f, 9f)

Material: NHMMZ PWL 2023/6002-LS, NHMMZ PWL 2023/6250-LS, NHMMZ PWL 2023/6254-LS.

Description: Specimen NHMMZ PWL 2023/6002-LS is a large, elongated oval right valve with about a dozen growth lines; marginally positioned umbo in approximately medial position; larval valve very small (Figs. 7d, 9f; see also Table 4).

NHMMZ PWL 2023/6250-LS is a very large, left valve with about 10 growth lines visible (there were probably more); the straight dorsal margin is long to very long and the umbo in marginal or inframarginal position (Fig. 8e; see also Table 4). NHMMZ PWL 2023/6254-LS is a large valve with about 12 growth lines; the straight to slightly concave dorsal margin is long and the umbo is in medial and inframarginal position (Fig. 8f; see also Table 4). Both NHMMZ PWL 2023/6250-LS and NHMMZ PWL 2023/6254-LS show blunt anterior margins with an indentation in their ventral regions.

Remarks: NHMMZ PWL 2023/6002-LS bears some resemblance to *Asmussia* Pacht, 1849 or *Ubsanuria* Novozhilov and Varentsov, 1956. The indented anterior margins of NHMMZ PWL 2023/6250-LS and NHMMZ PWL 2023/6254-LS are reminiscent of *Ulugkemia* spp. (Novozhilov 1955; but see Zharinova et al. 2017 for comment on the doubtful validity of this character). However, we prefer to leave the taxonomic status of these three specimens open until there is further, better-preserved material available. It should be noted here that *Asmussia* has previously been reported from a palaeo-ecologically comparable association of the Middle Devonian Brandenburg Formation in the Rhenish Massif (Gosny 2010).

Suborder Leaiina Kobayashi, 1972

Family incertae sedis

Table 6. Distribution of clam shrimp taxa with respect to localities or layers considered herein

	Willwerath	Waxweiler LCMO	Waxweiler 102022
<i>Pseudestheria diensti</i>	X		X
<i>Pseudestheria subcircularis</i>	X		
<i>Cornia wasvilrensis</i> sp. nov.			X
<i>Palaeolimnadiopsis</i> ? <i>eifelensis</i>	X		
<i>Palaeolimnadiopsis frankeorum</i> sp. nov.		X	
<i>Palaeolimnadiopsis</i> sp. cf. <i>P. frankeorum</i> sp. nov.			X
<i>Eicheleia wenddorfi</i> gen. nov. et sp. nov.			X
unassigned morphotype 2		X	
unassigned <i>Asmussia</i> -like morphotype			X
unassigned <i>Ulugkemia</i> -like morphotypes			X

Remarks: Fossil radially-carinate clam shrimp are considered to belong to three clades: the Devonian to upper Permian leaiids, the Triassic estheriellids, and the Upper Triassic? to Cretaceous afrograptids (e.g. Novozhilov 1957; Gallego and Caldas 2001; Shen 2003; Kozur and Hauschke 2008). The Estherielloidea evolved from forms lacking lateral carinae and are therefore not regarded as close relatives or descendants of the Palaeozoic leaiids (Kozur and Hauschke 2008). The Waxweiler leaiids differ from morphologically similar estheriellids, i.e. *Estheriella nodosocostata* (Giebel, 1857), by possessing a longer, less rounded valve, a smaller number and more evenly distributed lateral carinae, nondescript growth lines, and indistinct larval valve (cf., e.g. Kozur 1983).

Superficially close to *Praeleaia* Lutkevich, 1929 (see Lutkevich 1929, pl. 36, figs. 17–21), the Waxweiler specimens do not readily fit any diagnosis of previously established family or genus of Leaiina (see Jones and Chen 2000) as they show a higher number of radiating carinae. The specimens may be attributed, with emended diagnosis, either to Praeleiidae Novozhilov, 1956b (due to the high number of carinae) or to Rostroleiidae Novozhilov, 1956b (due to the sharp posterior angle). Due to the small number of available specimens, it is still not clear if there is a dorsal carina and/or a recurved posterodorsal margin or not. For this reason, we leave the family attribution open until there is more material.

Genus *Eicheleia* gen. nov.

Type species: *Eicheleia wenddorfi* sp. nov.

Derivation of name: A combination honouring Dr. Otto Eichele (Koblenz), co-founder of the Palaeontological Working Group Koblenz, in recognition of his achievements in the exploration of Rhenish Lower Devonian fossils, and the genus *Leaia*.

Diagnosis: Very large, elongated oval valves (H/L ratio about 0.5) with blunt anterior, evenly rounded ventral, and long, almost straight dorsal margin; valves with up to nine lateral carinae; seven lateral carinae clearly visible and strongly nodose; umbo in anterior and marginal position; larval valve indistinct and ornament unknown.

Remarks: Two of the most remarkable characteristics possessed by *Eicheleia* are the large number of carinae and the strongly nodose nature of the carinae. Two to five carinae (Novozhilov 1956b) are exhibited by praeleaiids—*Eicheleia* almost doubles the number of lateral carinae possessed by other praeleaiids with up to nine. Carinae with nodose-like swellings are known in leaiids like those in the species *Hemicycloleaia ingens* (Novozhilov, 1956b; pl. 8.2). Nodose carinae-like structures are known in estheriellids, like *Acadiestheria* Kozur and Weems, 2010. No known genus combines these characteristics, and thus these specimens are placed into the new genus *Eicheleia*.

Eicheleia wenddorfi sp. nov.

(Figs. 13a–h, 14a–d)

2006 ?Leaioid conchostracan—Poschmann and Franke: pl. 1, fig. 3.

Derivation of name: The species epithet honours Dr. Klaus-Werner Wenddorf (Braubach), co-founder of the Palaeontological Working Group Koblenz, in recognition of his achievements in the exploration of Rhenish Lower Devonian trilobites and brachiopods.

Holotype: NHMMZ PWL 2023/6110-LS a–b, part and counterpart (Figs. 13a–b, 14a).

Paratype: NHMMZ PWL 2023/6111-LS a–b, part and counterpart (Figs. 13c–d, 14b).

Additional material: NHMMZ PWL 2023/6104-LS a–b, part and counterpart (Figs. 13e, 14c); NHMMZ PWL 2023/6003-LS (Fig. 13h); NHMMZ PWL 2023/6005-LS a–b, part and counterpart (Fig. 13g); specimen from the Rebske collection number Wa 240, figured in Poschmann and Franke (2006). The current whereabouts of the latter fossil is unknown, therefore, it is expressively not part of the type series, but it is refigured here as it contributes important morphological information (Figs. 13f, 14d).

Type locality: Köppen Quarry north of Waxweiler/Eifel.

Type stratum: Klerf Formation, uppermost lower Emsian in the regional stratigraphic frame; probably corresponding to the early to mid Emsian in terms of the international chronostratigraphic frame (see discussion in Steemans et al. 2022).

Diagnosis: As for genus, because of monotypy.

Description: Five fossils from layer 102022 from Waxweiler and specimen Wa 240 from the Rebske collection and from the same quarry can be attributed to this taxon. Despite considerable variation due to preservation, their matching characters with respect to the umbonal area, anterior margin, and lateral carinae suggest that all belong to one and the same taxon, which furthermore differs from previously described taxa.

The holotype NHMMZ PWL 2023/6110-LS is a well-preserved, very large right valve lacking the postero-dorsal region (Figs. 13a–b, 14a). Preserved length is about 6.1 mm, height 3.1 mm, with the umbo in anterior and marginal position. Anterior margin blunt, ventral margin evenly rounded. Eight lateral carinae can be observed; carinae 1–3 terminating in the anterior valve margin, carinae 4–8 terminating in the ventral to posterior valve margin, each carina ornamented with up to about 10 subcircular tubercles.

The paratype NHMMZ PWL 2023/6111-LS is an almost complete left valve with a stripe of cuticle belonging to the right valve preserved above the dorsal margin (Figs. 13c–d, 14b). The ventral margin of the left valve is partly damaged

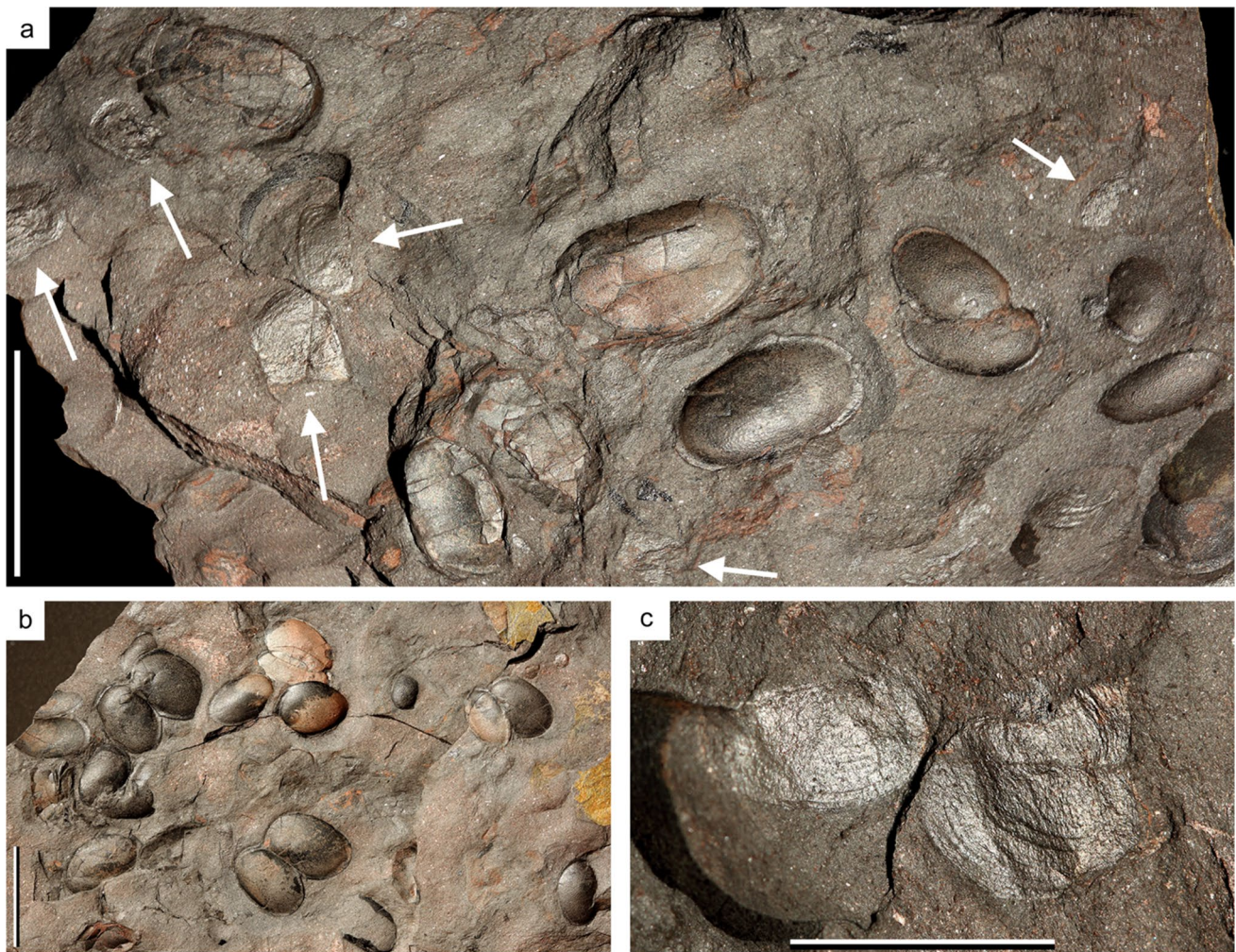


Figure 15. Leperditicoid-clam shrimp mass occurrence (LCMO) from the Klerf Formation at Waxweiler; a slab NHMMZ PWL 2022/5001-LS **a**; white arrows indicate clam shrimp; **b** NHMMZ PWL 2022/5002-LS **a**; slab with multiple leperditicopids in butterfly

position; **c** detail from slab in **(a)** showing clam shrimp (*Spinicaudata?* *incertae sedis*) in lateral view and in butterfly position (same specimens as in Fig. 10f, 10h); scale bars in **a–b** = 10 mm, in **c** = 5 mm

and poorly preserved. Estimated height is 2.8 mm, length 5.8 mm (H/L 0.48). The umbo is in anterior and marginal position. The dorsal margin is straight and about 4.4 mm long, the anterior margin blunt. Nine lateral carinae can be counted, a possible one along the dorsal margin not included. Up to 14 tubercles can be counted on the fourth carina. Up to about 10 growth lines are faintly preserved.

NHMMZ PWL 2023/6104-LS is also lacking the postero-dorsal region, but is otherwise well-preserved (Figs. 13e, 14c). A small stripe of cuticle belonging to the right valve is preserved near the umbo. The preserved length of the (incomplete) left valve is about 3.7 mm, height 2.4 mm. The umbo is in anterior and marginal position. The dorsal margin is almost straight and shows a small humpback before it is broken. The latter is reminiscent of the brood-chamber of modern Limnadiidae, but if this structure is a taphonomic feature or not remains open to question. The antero-dorsal

corner is rounded and merges into a blunt, almost straight anterior margin. A rounded antero-ventral corner merges into an oblique ventral and incompletely preserved posterior margin. Clearly preserved are seven carinae (numbers 2–8), that originate in the umbonal area and cross the valve with posteriorly slightly increasing distances. The most anterior carinae are more crowded and the presence of an additional small, indistinct, anteriormost carina is indicated. Carinae 2–8 are strongly nodose, i.e. they are marked by a row of about eight subcircular tubercles. Generally, the tubercles appear as darker spots under crossed polarizing filters (Fig. 13b, 13e) suggesting the presence of thickened cuticle.

Specimen Wax 240a from the Rebske collection (Figs. 13f, 14d) is a left valve with a maximum preserved length of 5.2 mm and height of 3.0 mm. The antero-dorsal corner is slightly damaged, but the remaining valve is rather completely preserved with a blunt anterior margin, oblique

postero-ventral margin, and an almost straight dorsal margin. The latter shows a shallow depression posterior to the umbo and a hint on several tubercles along its posterior part. There is a possible indentation at the postero-dorsal margin. Five nodose lateral carinae (numbers 5–9) can be matched, not counting for a very faint indication of a more anterior one and a possible one along the dorsal margin.

NHMMZ PWL 2023/6003-LS (Fig. 13h) is fragmentarily preserved and shows the anterior portion of a left valve with umbo and typically blunt anterior margin. Four lateral carinae, clearly marked by rows of up to nine tubercles can be seen, and there is a very faint indication of an additional, anteriormost lateral carina.

Specimen NHMMZ PWL 2023/6005-LS (Fig. 13g) is the fragment of an anterior part of left valve, with five lateral carinae clearly preserved as ridge-like structures and with tubercles only faintly indicated.

Remarks: Conceivably, the specimens currently allotted to *Eicheleia wenndorfi* gen. nov. et sp. nov. could represent multiple taxa. Partial specimens NHMMZ 2023/6104-LS b (Fig. 13e) and NHMMZ PWL 2023/6003-LS (Fig. 13h) seem to display stronger nodes set more apart than in other specimens. However, sexual dimorphism and taphonomy cannot be ruled out as potential causes for the differential appearance.

Discussion

The effects of distortion by compaction of non-mineralized arthropod cuticle at the Willwerath site are impressively illustrated by remains of eurypterids such as *Adelophthalmus*. The length/width ratios of dorsal shields in *A. sievertsi* were found to range from 0.47–0.80 when also heavily distorted specimens were considered (Poschmann 2006). This approximately matches the variation of height/length ratios in our clam shrimp carapace sample from Willwerath (Table 1). Often, the clam shrimp integument appears somewhat crumbled and a microsculpture cannot clearly be discerned. This is interpreted as taphonomic and partly due to sediment grains overprinting the original ornament as a clearly smooth valve is also not present. Given the morphological/preservational variation in particular clam shrimp taxa, which is evident from multiple modern approaches (e.g. Kozur 1983; Martens 1983, 2020; Kozur and Weems 2005, 2010; Gosny 2010; Gallego et al. 2013; Geyer and Kelber 2018; Scholze et al. 2015, 2017, 2019; Hethke and Weeks 2020), we cannot exclude the possibility that much of the variation present in our sample from Willwerath and also in the Gross (1934) specimens is attributable to individual/ecophenotypic variation and, for the most part, to preservation. Height/length ratios of valves are particularly unreliable in terms of taxonomic evaluation ranging from stocky semicircular to slender elongate oval in

one fossil population (or species) (e.g. Gosny 2010: pl. 1). Even a long dorsal margin can be deformed to show a roof-like kink (e.g. Kozur 1983: fig. 1 G). Furthermore, with respect to Rhenish Lower Devonian specimens, we note that Novozhilov (1961: pl. 7, caption 1) implied that the microornament in *Pseudestheria diensti*, *Pseudestheria subcircularis* (= *Glyptoasmussia willweratica*), and in „*Belgolimnadiopsis*“ *stockmansii* is the same by using the same image to illustrate all three species. Gross (1934) explicitly stated, that the microornament can only be recognised in one of his specimens (the type of his *Estheria diensti*). In our sample, the same microornament present in Gross's *Estheria diensti* is also present in *Pseudestheria subcircularis* (compare Gross 1934, p. 311, Abb. 9 to our Fig. 4f).

It must be stressed that all specimens from Willwerath (Figs. 2–6) share very large carapaces with an elongate-oval to round shape and a weakly expressed umbo in an anterior-medial to median-anterior and marginal position. The larval valve is hardly recognisable and apparently very small. The microsculpture consists of a dense, fine network of reticulate cells (approx. 10 µm; Fig. 4f), but it is rarely clearly recognisable. Furthermore, Liao and Shen (2022) remarked that among their specimens assigned to *Pseudestheria* cf. *P. diensti* the shape varies from oval and sub-oval to round and these authors regarded these different shapes as possibly due to compression deformation or sexual heteromorphism. A comparably strong preservational variation within the limits exhibited by the Willwerath spinicaudatan sample is also found in the associated bivalves. Effects of distortion had prompted Mauz (1933) to erect 4 subspecies of bivalve from Willwerath, which were regarded as belonging to just one taxon by Hilden (1978) based on morphometric analyses. The specimens figured by Mauz (1933) range in the H/L ratio from about 0.52 to 0.70. The same phenomenon has been recognised in other thin-shelled bivalves from broadly similar facies, for example in *Naiadites* from the Late Devonian of South Africa (Scholze and Gess 2021). If deformation is found to be the cause of the Willwerath specimen shape variation, it would raise serious questions about the taxonomy of Devonian clam shrimp.

The description of our sample does not exclude the possibility, that all of the Willwerath specimens may represent just one taxon and that the observed morphotypes (or named Willwerath taxa) may be preservational variants and possibly ontogenetic and/or sexual heteromorphs of just one taxon (see Table 1–5 for morphometric data). If confirmed by further sampling, the Willwerath clam shrimp may be placed in the genus *Pseudestheria* as diagnosed by Scholze et al. (2019). Martens (1983) emended *Pseudestheria* to show, among other characters, a bending of growth lines along the dorsal margin at the contact of the left and right valve. However, this character state can only be recognised in appropriately, more or less 3D-preserved specimens not present in our Willwerath sample. According to Scholze

et al. (2019), *Pseudestheria* can be differentiated from the morphologically similar *Euestheria* Depéret and Mazeran, 1912 by a less convex valve and umbo. The carapaces in our sample appear rather flat and a notably high convexity is absent. However, given the limited preservation of our material the generic attribution must remain tentative.

With respect to the Waxweiler LCMO-sample, one morphotype is, in gross morphology and in size, close to *Belgolimnadiopsis stockmansi* (Maillieux, 1939) (cf. Table 3 and Table 5), which has been described from the Lower Devonian of Belgium and France (Maillieux 1939; Defretin 1950). It differs in the morphology of the serrate dorsal margin and its recurved uppermost posterior margin from the Belgian and French specimens. The latter characters undoubtedly show that this morphotype is to be assigned to the family Palaeolimnadiopseidae Defretin-Lefranc, 1965. We therefore propose a new species for these Waxweiler specimens, which we assign to the genus *Palaeolimnadiopsis* Raymond, 1946. Within the Devonian, this genus has also been recognised from the Lower Devonian of Hunan Province, China (Liao and Shen 2022). Chen and Shen (1985) regarded the range of *Palaeolimnadiopsis* as extending from the Carboniferous to the Permian. However, other more recent authors have expanded the concept of *Palaeolimnadiopsis* (based on South American material) to include specimens as young as the Cretaceous (e.g. Carbonaro et al. 2013; Carvalho and Srivastava 1996; Rohn and Cavalheiro 1996).

The association of Waxweiler 102022 is the most diverse with respect to the clam shrimp fauna. Six different morphotypes corresponding to at least five different taxa are present, two of which can be described as new taxa. It has only one taxon (*Pseudestheria diensti*) in common with the Willwerath association and only possibly one (the palaeolimnadiopseid) with the Waxweiler LCMO association (Table 6).

Geologic age and palaeoenvironment

Palaeogeographically the Early Devonian Rhenish Shelf was situated south of the Old Red Continent at the southern margin of Laurussia and separated from Gondwana by the Rheic Ocean. In Siegenian and Emsian times, the coastline was relatively stable and the water was generally shallow as indicated by the so-called Rhenish or rhenotypic siliciclastic facies (Jansen 2016) as opposed to the more argillaceous and calcareous Hercynian facies reflecting deeper and calmer depositional environments. Sediments delivered by rivers and deltas accumulated to kilometre-thick siliciclastic successions on the subsiding shelf (e.g. Meyer and Stets 1980; Walliser and Michels 1983; Stets and Schäfer 2002, 2011)

and various subfacies indicated by different faunas can be discerned (Jansen 2016).

The uppermost lower Emsian Klerf Formation in the Eifel region is approximately contemporaneous to and intergrades with the Nellenköpfchen Formation of the lower Moselle region (Solle 1956, 1976; Poschmann and Gossmann 2013). Localities such as Alken, Konderbachtal, and Treis (Nellenköpfchen Formation; e.g. Solle 1970; Wehrmann et al. 2005, 2010; Poschmann 2016, 2017) or Willwerath and Waxweiler (Klerf Formation; e.g. Mentzel 1966; Huwe et al. 2003; Franke 2006) reflect a strong regional regression and can be attributed to the pararenotypic or terrestrial subfacies sensu Jansen (2016). Here, invertebrate fossils suitable for stratigraphic purposes are generally lacking. However, both the Willwerath and Waxweiler sites yielded miospores indicating an Emsian age (Huwe et al. 2003; Steemans et al. 2022). Furthermore, localities elsewhere in the Klerf Formation as well as in the underlying Stadtfeld Formation and the overlying Berlé Formation all yield brachiopods that indicate an upper lower Emsian age (upper Vallendar Group) in terms of the Rhenish stratigraphy for the Klerf Formation at Willwerath and Waxweiler (e.g. Solle 1976; Fuchs 1982; Mittmeyer 1982, 2008; Franke 2016; Jansen 2016, 2019). In terms of the international chronostratigraphic scale, the Klerf Formation of Willwerath and Waxweiler probably has a lower to mid Emsian age (see e.g. discussion in Steemans et al. 2022).

In the past, Willwerath was interpreted as reflecting a marine to terrestrial transitional facies and a brackish to freshwater habitat (e.g. Anderson et al. 1998). However, palaeontological evidence for a marine influence, as it is often encountered in successions of the Nellenköpfchen Formation (e.g. Wunderlich 1970; Wehrmann et al. 2005, 2010; Tetlie and Poschmann 2008), is much less clear at Willwerath, with only some scolecodonts perhaps hinting at a restricted marine (brackish) component (Huwe et al. 2003). Layers with tentaculitids, impoverished brachiopod communities or scattered trilobite remains as well as chitinozoans or acritarchs are completely lacking at Willwerath (Mentzel 1966; Anderson et al. 1998; Huwe et al. 2003). Notably, there are striking differences in faunal composition in the respective eurypterid-bearing strata within the Nellenköpfchen Formation compared to those of the Klerf Formation, which also yielded the clam shrimp at Willwerath and Waxweiler. For example, in the former the adelophthalmid *Parahughmilleria* dominates the eurypterid associations, whereas *Adelophthalmus* and the stylonurid *Rhenopterus* are far more common than *Parahughmilleria* at Willwerath and Waxweiler. This has been interpreted as being related to the palaeoecological setting, namely a more proximal deltaic setting for the eurypterid localities in the Klerf Formation (Poschmann and Tetlie 2006; see also Stets and Schäfer 2002). It also ties in

with often monotypic modiolopsid bivalve assemblages (see Hilden 1978) and the occurrence of leperditicopid ostracods in association with the clam shrimp. Furthermore, the ostracod assemblages of Willwerath and Waxweiler (see also Rebske et al. 1985) were interpreted as reflecting a non-marine limnic-brackish environment (Becker and Franke 2012). Swimming traces of early vertebrates (*Undichna*) associated with trackways of supposed myriapod-like arthropods (*Diplichnites*) indicate very shallow water (Poschmann and Franke 2006) and *in situ* root-like traces of early tracheophytes as well as desiccation cracks are not uncommon at Waxweiler (Schweitzer 1983; Poschmann and Gossmann 2014; Fig. 1c). The sedimentary succession at Waxweiler can be interpreted as channel sandstones overlain by floodplain/overbank deposits, the latter yielding clam shrimp (Fig. 1b). In contrast, closely comparable associations have hitherto not been recorded from the Nellenköpfchen Formation, where instead layers indicating a marine influence and in part attributable to storm events are encountered more regularly (e.g. Wunderlich 1970; Wehrmann et al. 2005, 2010; Poschmann 2016, 2017).

Usually, at Willwerath and Waxweiler clam shrimp and leperditicopids occur more or less isolated in the host sediment with multiple fossils on one slab being an exception. Recently, we identified a dark-grey clayey siltstone up to three centimetres thick from Waxweiler, which yielded a mass occurrence of leperditicopid crustaceans in association with clam shrimp (the so-called „LCMO“; Fig. 15). The valves of the leperditicopids strongly vary in size suggesting the presence of multiple growth stages and the occurrence of mass mortality rather than e.g. death after reproductive senescence. In contrast, the valves of the clam shrimp may correspond to individuals of essentially the same age. This may be interpreted as hinting at different modes of reproduction in clam shrimp versus leperditicopids. The valves of both, leperditicopids and clam shrimp, here often occur in butterfly position with their two valves still connected at the hinge line or lying next to each other. In bivalved arthropods, the butterfly position requires decay or severing of the carapace adductor muscle. While the leperditicopid valves retained their original convexity or are slightly crushed, the clam shrimp valves are invariably strongly flattened and the carapace integument is often crumbled and poorly preserved. These bivalved crustaceans are the almost exclusive faunal remains recorded in this association, with only occasional land plants being present. Such a very low diversity coupled with extraordinary high numerical abundance is characteristic of opportunistic populations in stressed habitats (see Vannier et al. (2001) with respect to leperditicopids), although the possible presence of different growth stages in the leperditicopids stands in contrast to this interpretation. Additionally, millimetre-thin calcitic crusts are recorded within the sediment. This finding strongly suggests that

dense populations of both leperditicopids and clam shrimp thrived in a very shallow ephemeral body of water, such as a floodplain lake.

It is currently impossible to unequivocally prove an entirely freshwater habitat for the Willwerath and Waxweiler clam shrimp, but the available evidence strongly speaks for a proximal deltaic setting with only a weak brackish influence, if at all. Such parameters are met in e.g. floodplain lakes or ponds. This also has implications for the biogeography of Early Devonian clam shrimp and suggests that wind-blown dispersal of their eggs from periodically dried-out water-bodies (cf. Webb 1979; Tasch 1987; Gallego et al. 2020) may have originated or have even been firmly established at that time and contributed to the success of the group. Today, dispersal mediated by wind or animal predators is the chief way that branchiopod eggs get moved to new ponds (Graham and Wirth 2008, and references within). The fact that the ability to withstand passage through a predator's digestive tract is present throughout Branchiopoda indicates an origin for the trait with the origin of crown group branchiopods. Among taxa recorded from Willwerath and Waxweiler, the eurypterids and particularly *Adelophthalmus sievertsi* have been considered possible predators of clam shrimp (Poschmann et al. 2016). *Adelophthalmus* was primarily aquatic (Braddy et al. 2021) but has been confirmed as a facultative amphibious animal in a study by Lamsdell et al. (2020). Thus, in addition to wind dispersal, *Adelophthalmus* (and possibly other eurypterids) may indeed have migrated from one pond to another spreading clam shrimp eggs, either through their digestive tract or by transport of cyst-bearing substrate adhering to their bodies (cf., Pérez-Bote et al. 2005).

Conclusions

Morphological analysis of new clam shrimp specimens from the Early Devonian (lower to middle Emsian) of Willwerath suggests that these may have been taxonomically oversplit by previous workers. Some of the previously recognised morphological differences (or morphotypes) are possibly due to intraspecific variability and preservational variants. The individual Early Devonian clam shrimp associations, i.e. supposed populations, from the Klerf Formation of both Willwerath and the approximately contemporaneous Köppen Quarry at Waxweiler show remarkable differences with respect to clam shrimp abundance and diversity. Altogether, a total of at least five clam shrimp taxa can firmly be established, with up to four, possibly five taxa present in one association. This comparatively high taxonomic diversity in these Early Devonian clam shrimp associations suggests a considerably earlier origin and cryptic evolution of the group.

The Waxweiler LCMO, as well as the association of layer 102022, indicate that ephemeral pools or lakes on the proximal delta floodplain may have been occupied by up to four or five clam shrimp taxa. A similar diversity has been recorded by Liao and Shen (2022) in an Early Devonian clam shrimp association from China. Co-occurrence of up to four spinicaudatan species has also been reported from modern ponds (Gottwald and Eder 1999). However, it is worth pointing out that the co-occurrence of multiple spinicaudatan species in one water body occurs very rarely today (Wiese 1964; Webb 1979); how the Rhenish Devonian species partitioned their ecological niches to avoid competitive exclusion remains unresolved. On the other hand, limited transport and/or time averaging of clam shrimp taxa cannot be completely ruled out for the associations discussed here.

The palaeoenvironment of the earliest conchostracan palaeo-communities, as represented by the Willwerath and Waxweiler samples, can be interpreted as a deltaic brackish to freshwater pond or lake; this makes them palaeoecologically similar to the Late Devonian branchiopod community of the Strud locality in Belgium (Gueriau et al. 2016, 2017). Clam shrimp thus have occupied non-marine biotopes since the Early Devonian and throughout their subsequent diversification, albeit not exclusively (summarised by Hegna 2022; cf., Kozur and Mock 1993; Hethke et al. 2019; Jones and Chen 2000).

Although it has been shown that assuming ecological stasis in clam shrimp from the Devonian to Recent times is an oversimplified view (Hethke et al. 2019), the occupation of ephemeral freshwater habitats probably was an important ecological niche for clam shrimp throughout their entire, hitherto known evolutionary history.

Future research

Although clam shrimp from the Klerf Formation of Willwerath may have been taxonomically oversplit by previous workers, the Early Devonian deltaic, marine-terrestrial transitional facies of the Rhenish Massif provides a unique view into the early evolution of Diplostraca with respect to both the origin of particular clades and the palaeoenvironment in which these flourished. Active quarries in the West-Eifel, Belgium, and Luxembourg, such as the Köppen Quarry at Waxweiler, should be monitored for potentially productive fossil-bearing beds yielding diplostracans. Recovering and subsequent fine-splitting of such material in the laboratory holds great potential to yield more fossils and provide further insights into the morphology and variability of hitherto poorly known taxa (e.g. Spinicaudata? incertae sedis of the present contribution), to test the validity of previously described taxa (in particular those from Willwerath), and to decipher the palaeoecological settings at the root of the possible crown group of these fascinating animals.

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Data availability The specimens are deposited in the State Collection of Natural History of Rhineland-Palatinate at the Natural History Museum at Mainz, Germany (NHMMZ). The original material of Gross (1934) is deposited in the Museum für Naturkunde Berlin (MB.A.0039–MB.A.0044).

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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