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SEM morphological study of the Late Permian clam shrimp *Polygrapta chatangensis* (Spinicaudata, Crustacea)

GANG LI

State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology and Center for Excellence in Life and Palaeoenvironment, Chinese Academy of Sciences, East Beijing Road 39, Nanjing 210008, PR China

✉ gangli@nigpas.ac.cn; <https://orcid.org/0000-0002-6390-3042>

Abstract

A re-examination of the metatype of the type species *Polygrapta chatangensis* has revealed new characters that were overlooked in the original description and it is determined here that *Polygrapta* should be maintained as a genus separate from *Pseudestheria*.

Keywords: Clam shrimp, Upper Permian, *Polygrapta*, taxonomy

Introduction

Clam shrimp are large branchiopod crustaceans with bivalved chitinous or complex chitin-mineral carapace (Astrop & Hegna, 2015; Li, 2017a). Their fossil records extend back to the Devonian Period (Tasch, 1969), and they play an important role in the subdivision and correlation of nonmarine strata (Li *et al.*, 2006, 2007, 2017; Chen *et al.*, 2007; Kozur & Weems, 2010; Li & Matsuoka, 2012, 2015; Boukhalfa *et al.*, 2015; Scholze *et al.*, 2015, 2019; Schneider & Scholze, 2016; Teng & Li, 2017, 2018, 2019, 2020; Hasegawa *et al.*, 2018; Liao *et al.*, 2019; Gallego *et al.*, 2020a).

Polygrapta Novojilov, 1946 was first described from the Russian Upper Permian Tatarian (upper Guadalupian–Lopingian, Okuyucu *et al.*, 2017). Subsequently, it was recovered from the Upper Permian of Liaoning Province (Shen & Li, 1986) and Xinjiang Uygur Autonomous Region of China (Liu, 1985, 1987, 1993), from the Lower and Middle Triassic of the Ordos basin in northwestern China (Wang & Liu, 1980; Shen *et al.*, 1982), and from the Upper Triassic of Chile (Gallego *et al.*, 2005). The original description was made only with the help of light microscopy (Novojilov, 1946). This means that the detailed delicate ornamentation on the growth bands could not be observed clearly. A new examination of the metatype specimens of *Polygrapta chatangensis* Novojilov, 1946

has revealed new features that were overlooked in the original description.

Material and methods

The figured specimens are a metatype (a specimen subsequently designated by Novojilov (1958)), a right valve, broken in the posterior dorsal margin, PIN No. 401/118 (Collection of Palaeontological Institute of Russian Academy of Sciences), and a right valve, broken in the ventral margin, PIN No. 401/120. Both specimens are preserved in one rock slab. They were collected from the Tatarian (Upper Permian) deposits of the borehole P-2 (at the depth of 1274–1280 m) on the southern shore of the Khatanga Bay, northeastern Russia.

The previous research on the metatype (PIN No. 401/118) was based on the light microscopy imaging (Novojilov, 1958: pl. 1, figs 1c, 4). In this study, a Tescan Vega II SEM (scanning electron microscope) of the Palaeontological Institute of Russian Academy of Sciences was used for the detailed observation and imaging of the delicate ornamentation of clam shrimp carapaces (without coating). Nowadays SEMs are widely available, and necessary for the taxonomy of fossil clam shrimp in the clear observation of the precise carapace ornamentation features of potential taxonomic values (Li & Batten, 2004a, 2004b, 2005; Li *et al.*, 2009, 2010, 2016; Li, 2017b).

Systematic palaeontology

Traditionally, the carapace size of the fossil clam shrimp was described as small (carapace length <5 mm), medium (carapace length between 5 mm and 15 mm) or large (carapace length >15 mm) (Chen & Shen, 1985). Recently, Scholze & Schneider (2015, table 1) proposed another,

more subdivided, terminology to describe the size of clam shrimp. The author finds that the tripartite category of Chen & Shen (1985) is easy to follow for describing the carapace size.

Order Diplostraca Gerstaecker, 1866
Suborder Spinicaudata Linder, 1945
Superfamily Eosestherioidea Zhang & Chen in Zhang et al., 1976

Diagnosis. The carapace size is small to large; carapace outline is rounded, elliptical, ovate, oblong or rhombic. The umbo is small, located in the anterior part of the dorsal margin. Growth bands numerous; those near the umbo are ornamented with polygonal reticulation, which can transition to radial lirae on growth bands near the ventral margin.

Remarks. Chen & Shen (1985) named the superfamily Eosestherioidea and credited the authorship to Zhang & Chen (in Zhang et al., 1976). But there was no diagnosis published yet. The above mentioned diagnosis of the superfamily Eosestherioidea is a summary of the included forms.

Family Polygraptidae Novojilov, 1954 [nom. transl. Wang & Liu, 1980 (ex Polygraptinae Novojilov, 1954)]

Type genus. *Polygrapta* Novojilov, 1946; SD Wang & Liu, 1980.

Revised diagnosis. Carapace small or medium in size, ovate, elliptical or rounded in outline. The dorsal part of the carapace ornamented with polygonal fine reticulation, the ventral part of the carapace ornamented with radial lirae, between which crossbars are developed.

Remarks. Novojilov (1946) erected the subgenus *Polygrapta* under the invalid genus *Estheria*, which has the priority in the taxonomy of insects (Raymond, 1946). Later, he elevated *Polygrapta* to a genus rank, and erected the subfamily Polygraptinae to include the forms bearing simple or branching, dotted or dashed radial lirae sculpture on the growth bands (Novojilov, 1954). Novojilov originally allocated Polygraptinae under his new family Bairdestheriidae Novojilov, 1954. But in consideration of the fact, that its genotype *Bairdestheria* Raymond, 1946 is a junior synonym of *Cyzicus* Audouin, 1837 (Rogers, 2020), Bairdestheriidae is no longer a valid family. Wang and Liu (1980) elevated the subfamily Polygraptinae to a family rank and revised the diagnosis as having fine reticulation on growth bands in the dorsal part of the carapace, and radial lirae on growth bands in the ventral part of the carapace. Kozur & Seidel (1983) also revised Polygraptinae to a family rank, but they did not mention the reticulation ornamentation on the dorsal

part of the carapace. Subsequently, Polygraptidae was widely accepted by many scientists (Shen et al., 1982; Liu, 1985; Gallego et al., 2005, 2020b).

Novojilov (1954) erected Polygraptinae and included the following additional taxa except for the type genus: *Cyclograpta* Novojilov, 1954, *Opsipolygrapta* Novojilov, 1954, *Pemphicyclus* Ramond, 1946, *Pteriograptia* Novojilov, 1954 and *Rhombograptia* Novojilov, 1954. *Cyclograpta* has fine radial lirae on growth bands and was considered as a synonym of *Eremograptia* Novojilov, 1960 (Chen & Shen, 1985: p. 128), or treated as a junior synonym of *Asmussia* Pacht, 1849 (Tasch, 1969). *Opsipolygrapta* was interpreted as a junior synonym of *Cyzicus* Audouin, 1837 (Rogers, 2020). *Pemphicyclus* was later moved to the subfamily Vertexiinae Kobayashi, 1954 because of the presence of an umbonal node (Chen & Shen, 1985). *Pteriograptia* and *Rhombograptia* have simple radial lirae on growth bands and were moved to Fushunograptidae Wang in Hong et al., 1974 (Chen & Chen, 1985).

Tianzhuestheria Shen et al., 2002 was originally assigned to the family Polygraptidae, but in consideration of the presence of puncta on growth bands, it was moved to Triglyptidae Wang, 2014. In contrast to Triglyptidae, Polygraptidae lacks puncta, but has clear reticulation on growth bands near the umbo. They can be easily differentiated from each other.

Polygraptidae is similar to Aquilonoglyptidae Novojilov, 1958 (Li, 2020) by having fine polygonal reticulation on growth bands near the umbo. But Polygraptidae lacks puncta on growth bands in the middle and ventral parts of the carapace, it is easy to differentiate it from the punctate aquilonoglyptids.

Genus *Polygrapta* Novojilov, 1946

Type species. *Estheria (Polygrapta) chatangensis* Novojilov, 1946, OD, from the Tatarian, Upper Permian on the southern coast of the Khatanga Bay, northeastern Russia.

Revised diagnosis. Carapace of small to medium size; oval or elliptical in outline. Dorsal margin straight, with the narrow umbo located in its anterior part. Growth bands variable from a few to 60 in number or more; those near the umbo ornamented with fine polygonal reticulation, which transition to radial lirae with intercalated crossbars on growth bands in the ventral part of the carapace. Crossbars connected to form a distinct ridge along the upper margin of each growth line (or lower margin of each growth band).

Locality and horizon. Upper Permian to Upper Triassic; Chile, China, Russia.

Remarks. Novojilov (1946) first erected the subgenus *Polygrapta* and allocated it under the invalid clam shrimp genus *Estheria* Rüppell in Straus-Dürckheim, 1837

(Spinicaudata) (non *Estheria* Robineau-Desvoidy, 1830 (Diptera: Tachinidae)). Later, Novojilov (1954) elevated it to a genus rank. The growth band ornamentation has been described as simple or branched, dotted or dashed radial lirae (Novojilov, 1954: p. 99, fig. 71a). Subsequently, this genus was cited by many scientists (Kapel'ka & Novojilov, 1962; Defretin-Lefranc, 1965; Molin, 1966, 1978; Novojilov & Kapel'ka, 1967; Duan, 1978; Chen & Shen, 1985; Shen & Li, 1986; Lipatova & Lopato, 2000; Gallego *et al.*, 2005). Wang & Liu (1980) revised the diagnosis of *Polygrapta*, and described fine reticulation on the dorsal part of the carapace. Later, Liu (1985) described the "striated-reticulate" ornamentation on growth bands in *Polygrapta*. Recently Scholze *et al.* (2019) interpreted *Polygrapta* as a junior subjective synonym of *Pseudestheria* Raymond, 1946. But in contrast to *Pseudestheria*, *Polygrapta* has clear ornamentation of reticulation and radial lirae. *Pseudestheria* has only punctate ornamentation (Raymond, 1946). In light of these differences, it is better to maintain them as different genera.

Defretin-Lefranc (1967: p. 68) described *Polygrapta biaroensis* from the Upper Jurassic (Kimmeridgian) Stanleyville serie in Congo. Although it has radial lirae ornamentation, but the lirae are rather loose, about 25 per mm. But in *Polygrapta chatangensis* Novojilov, 1946 (Figure 1D–1F), the radial lirae are rather dense, ca 60–80 per mm. Thus, *Polygrapta biaroensis* needs further morphological study for confirming its taxonomic position.

***Polygrapta chatangensis* Novojilov, 1946**

1946 *Estheria* (*Polygrapta*) *chatangensis* subgen. et sp. nov.: Novojilov, p. 174, pl. 1, figs 1–3.

1958 *Polygrapta chatangensis* Novojilov, 1946: Novojilov, p. 20, fig. 4, 5; pl. 1, figs 1a–c, 1–4.

1965 *Polygrapta chatangensis* Novojilov: Defretin-Lefranc, p. 30, pl. II, figs 1, 2, 5; text-fig. 10.

Emended diagnosis. Carapace medium in size, oval in outline. Dorsal margin straight and long, forming a sharp angle with the posterior margin. Umbo small, ornamented with polygonal fine reticulation, located at the anterior end of the dorsal margin. Growth bands in the dorsal part ornamented with polygonal fine reticulation (mesh diameter about 15–30 μm); those in the ventral part of the carapace ornamented by dense radial lirae with intercalated crossbars. Growth lines ornamented by dense ridges or fine reticulation (mesh diameter about 6–10 μm), the upper edge of each growth line (or the lower edge of each growth band) is a distinct ridge formed by the connection of crossbars.

Locality and horizon. Upper Permian (Tatarian), southern coast of the Khatanga Bay of Russia.

Dimensions. In order: specimen no., number of growth bands, length (mm), height (mm), height/length ratio: PIN No. 401/118, 26, 5.3, 3.5, 0.66; PIN 401/120, 24, 5, 3.5, 0.70.

Description. Carapace medium in size (5.3–7.5 mm long; 3.5–5.0 mm high, Novojilov, 1958: p. 20); oval in outline. Small umbo (ornamented with polygonal fine reticulation, Fig. 2B) located at the anterior part of the long and straight dorsal margin, which forms a sharp obtuse angle with the posterior margin. The anterior margin narrowly rounded, posterior margin widely rounded, ventral margin widely arched. The great length is at the middle height of the carapace; the great height is at the posterior one-third of the carapace length. Growth bands flat, wide in the middle part of the carapace, but narrow near the ventral margin. Growth bands near the umbo ornamented with fine, polygonal reticulation with mesh diameter between 15 and 30 μm (Fig. 1B). In the middle part of the carapace, polygonal reticulation transitions to elongated reticulation or radial lirae (with intercalated crossbars) in the lower part of each growth band (Figs 1D, F, 2D, F). In the posterior and ventral parts of the carapace, growth bands are ornamented by radial lirae with dense crossbars (Figs 1E, 2E, G), sometimes forming radially aligned reticulation (Fig. 1G). Growth lines in the middle and ventral parts of the carapace ornamented with densely spaced fine ridges or fine reticulation (Fig. 1D, G), mesh diameter about 6–10 μm . The upper margin of each growth line (or lower margin of each growth band) is a distinct ridge formed by connected crossbars (Figs 1D, G, 2C, E–H).

Remarks. The holotype was originally assigned to PIN No. 401/7 (or No. P-2 1278–7, mentioned in the plate explanation) in Novojilov (1946). Later, Novojilov (1958) re-assigned PIN No. 401/50 as the holotype. PIN No. 401/2 was assigned as the paratype. At the same time, he assigned PIN No. 401/9 and PIN No. 401/118 as two metatypes, and figured their carapace ornamentation patterns by light microscopy imaging (Novojilov, 1958: pl. 1, fig. 1a–c). In this study, the author has the chance to study the metatype specimen PIN No. 401/118 and its associate PIN No. 401/120. The other type specimens are not available.

In the original description, Novojilov (1946) only mentioned the radial lirae sculpture, which are simple or branching, continuous or formed by one row of separate rods or granules. But, the new imaging under an SEM has clearly shown that the radial lirae are continuous, crossbars are located between them. And Novojilov overlooked the polygonal fine reticulation on the dorsal part of the carapace.

In the original description, growth lines were described as narrow gutter-like grooves (Novojilov,

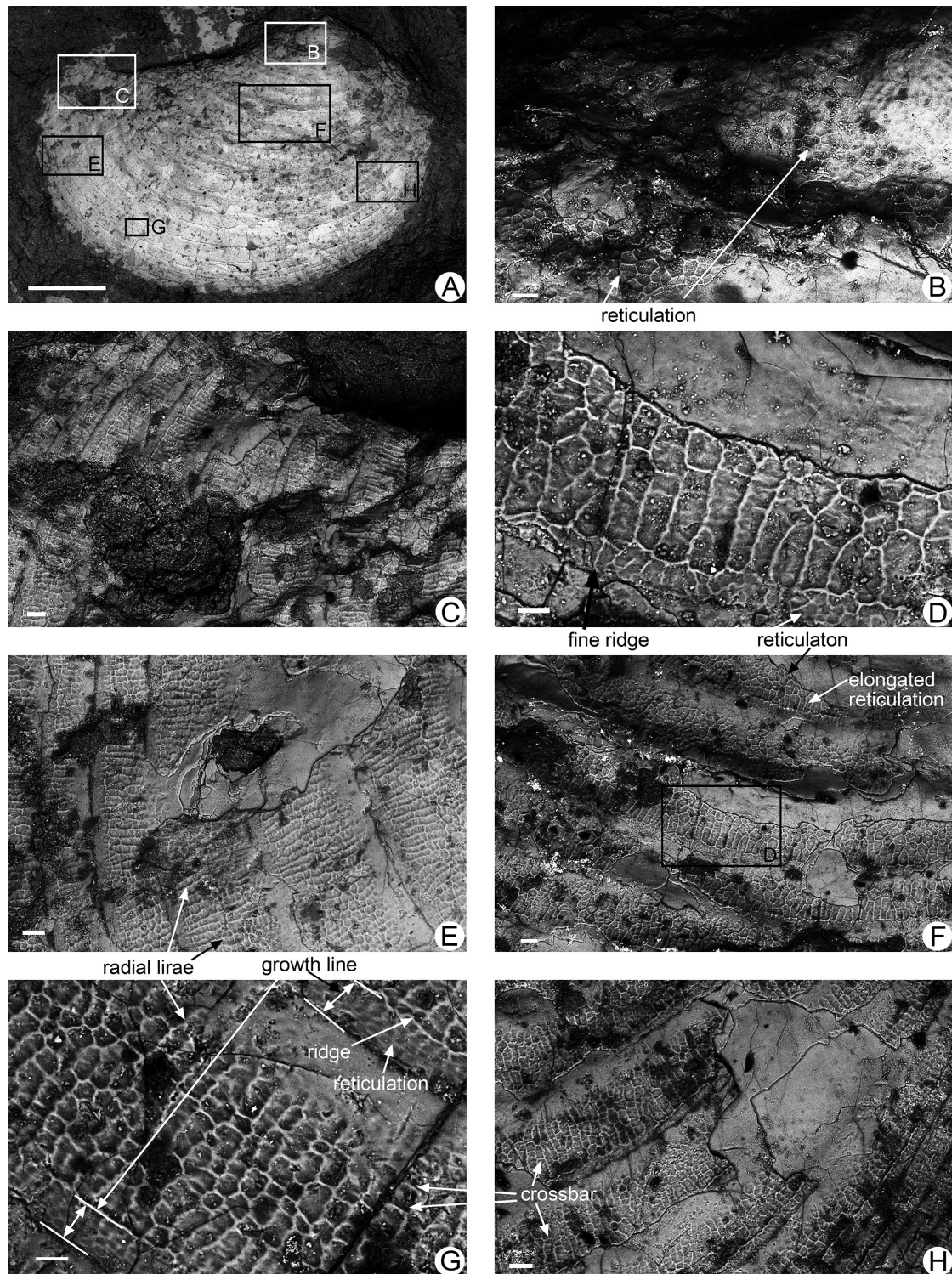


FIGURE 1. *Polygrapta chatangensis* Novojilov, 1946. SEM images of the metatype specimen PIN No. 401/118 from drill core P-2 (1274–1280 m deep) on Cape Ilia on the southern shore of the Khatanga bay, Upper Permian (Tatarian). **A**, A right valve. **B**, Polygonal reticulation ornamentation on growth bands near the umbo. **C**, Radial lirae with intercalated crossbar ornamentation on growth bands in the postero-dorsal part of the carapace. **D**, Reticulation and radial lirae ornamentation on growth band in the upper middle part of the carapace; growth line ornamented with fine ridge and fine reticulation. **E**, Ornamentation on growth bands near the posterior margin of the carapace, showing radial lirae with intercalated crossbars. **F**, Ornamentation on growth bands in the dorsal middle part of the carapace, showing transition from reticulation to elongated reticulation and radial lirae. **G**, Radial lirae with crossbars forming longitudinally aligned reticulation on a growth band in the postero-ventral part of the carapace, showing fine reticulation on growth lines. **H**, Ornamentation on growth bands in the antero-ventral part of the carapace, showing radial lirae with crossbars, forming longitudinally aligned reticulation. Scale bars = 1 mm in **A**, 20 μ m in **D** and **G**, 40 μ m in **B**, **C**, **E**, **F**, and **H**.

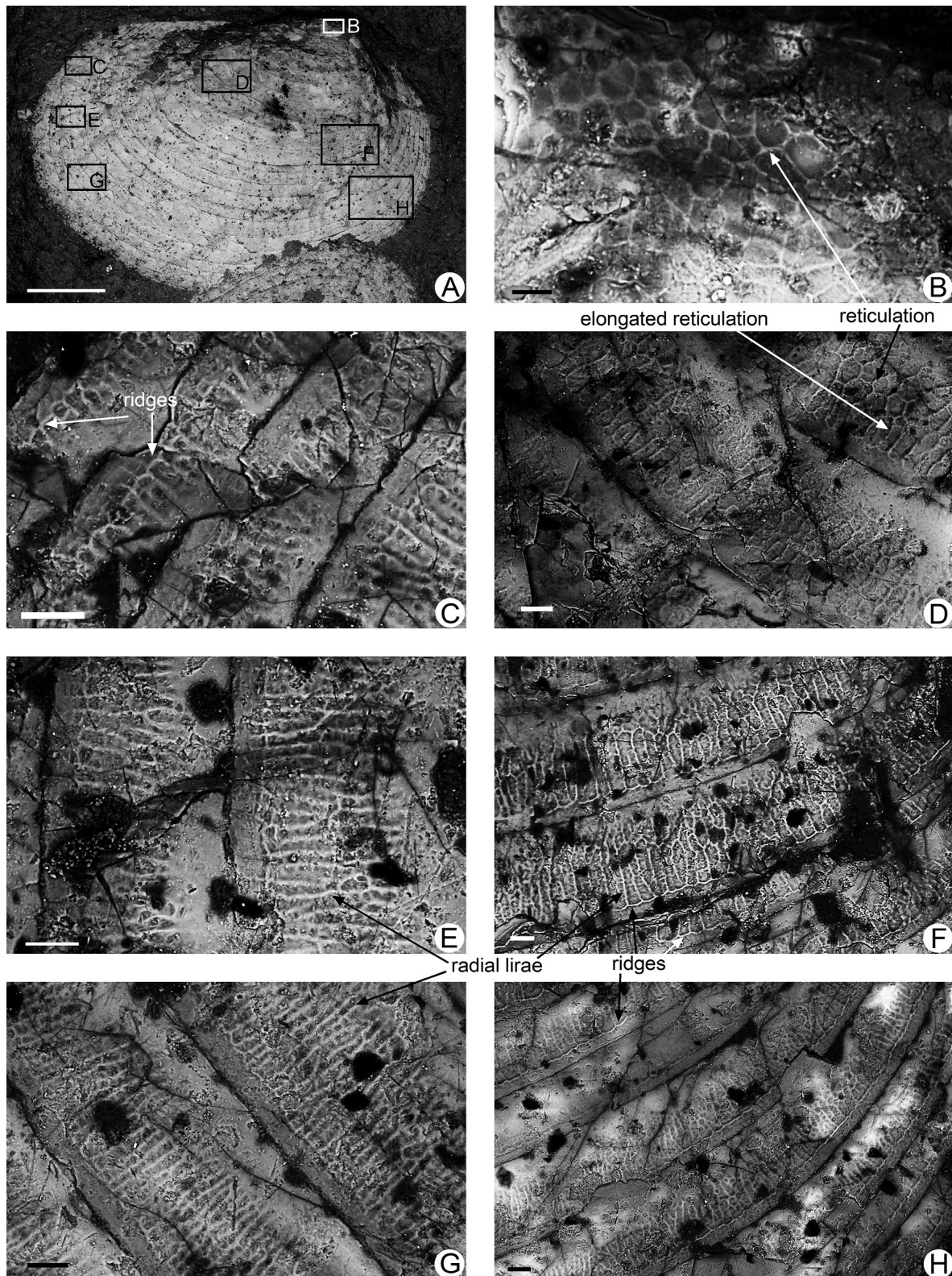


FIGURE 2. *Polygrapta chatangensis* Novojilov, 1946. SEM images of the specimen PIN No. 401/120 from the drill core P-2 (1274–1280 m deep) on Cape Ilia on the southern shore of the Khatanga bay, Upper Permian (Tatarian). **A**, A right valve. **B**, Reticulation ornament on the umbo. **C**, Radial lirae ornamentation on growth bands in the postero-dorsal part of the carapace. **D**, Ornamentation on growth bands near the umbo, showing transition from reticulation to radial lirae. **E**, Radial lirae ornamentation on growth bands near the posterior margin of the carapace. **F**, Ornamentation on growth bands in the antero-middle part of the carapace, showing radial lirae intercalated with crossbars. **G**, Radial lirae ornamentation on growth bands in the postero-ventral part of the carapace. **H**, Ornamentation on growth bands in the antero-ventral part of the carapace, showing radial lirae with cross bars, forming radially aligned reticulation. Scale bars = 1 mm in **A**, 20 µm in **B**, 40 µm in **C–H**.

1946), but the SEM images clearly demonstrate that the growth lines in *Polygrapta chatangensis* are narrow and flat, ornamented with fine ridges or fine reticulation. The upper edge of each growth line (or the lower edge of each growth band) is a distinct ridge, which is formed by the connection of crossbars.

Scholze *et al.* (2019) assigned *Polygrapta chatangensis* to *Pseudestheria*. But, in consideration of the radically different ornamentation in *Pseudestheria*, the species should be maintained in *Polygrapta*.

Discussion

In the description of *Polygrapta*, Novojilov (1946, 1954, 1958) described that the carapace sculpture consists of irregular radial lirae, which are simple or branched, continuous or formed by separate granules tightly adjacent to one another (Novojilov, 1954: p. 99, fig. 71a). But the re-examination of specimens of the metatype PIN No. 118 and its associate PIN No. 401/120 under an SEM has demonstrated that the densely spaced radial lirae are continuous with intercalated crossbars (Figs 1D, E, 2E–G). In addition, growth bands in the dorsal part near the umbo are ornamented by polygonal fine reticulation (mesh diameter 15–30 µm). In the ventral part of the carapace crossbars connected with radial lirae and forming radially aligned reticulation (Fig. 1G, H). This research result is consistent with the revised diagnosis of *Polygrapta* in Wang & Liu (1980). Although Kozur & Seidel (1983) revised the diagnosis of *Polygrapta*, their research was based on light microscopy imaging, no precise observation could be obtained.

In addition to the type species *Polygrapta chatangensis*, Novojilov (1946) named nine further Late Permian (Tatarian) species: *Polygrapta arangastachia*, *P. ignota*, *P. intaminata*, *P. laptewi*, *P. laxa*, *P. limbata*, *P. multinstita*, *P. necta* and *P. strictocostata*. Later, Novojilov (1958) described two new Late Permian (Tatarian) species: *Polygrapta evenkorum*, *P. sibirica*, and assigned *Polygrapta arangastachia* to *Pemphicyclus* Raymond, 1946 (Novojilov, 1958: p. 23); *P. ignota* to the invalid genus *Bairdestheria* (Novojilov, 1958: p. 24); *P. limbata* doubtfully to *Brachigrapta* (Novojilov, 1958: p. 27); and *P. strictocostata* to *Liograpta* (Novojilov, 1958: p. 25). At the same time, he assigned *Polygrapta laxa* as a synonym of the type species *P. chatangensis*; *P. intaminata* as a synonym of *P. necta*, respectively. These Late Permian species need further study by the help of SEM microscopy imaging in the future to clarify their taxonomic position. Kobayashi (1954: p. 131) interpreted *Polygrapta* as a junior synonym of *Euestheria* Deperet &

Mazeran, 1912, but *Polygrapta* has clear ornamentation of reticulation and radial lirae, it should be separate from reticulate *Euestheria*.

Wang *in* Wang & Liu (1980) described *Polygrapta wupuensis* from the Middle Triassic Ermaying Formation, and another two species *Polygrapta subelliptica* and *P. xuefengchuanensis* from the Lower Triassic Heshangou Formation of the Ordos basin. *Polygrapta wupuensis* differs from *P. chatangensis* by its trapezium outline, small size and few growth bands. *Polygrapta subelliptica* is similar to *P. chatangensis* in outline, but differs from the latter by the limited area of the radial lirae ornamentation occurring in the marginal part of the carapace (Wang *in* Wang & Liu, 1980: p. 108). *P. xuefengchuanensis* differs from *P. chatangensis* by the carapace outline, its anterior margin widely rounded, its posterior margin sharply rounded.

Liu (1985) described two species: *Polygrapta minuta* and *P. xinjiangensis* from the Upper Permian Wutonggou Formation in Xinjiang Uygur Autonomous Region of China. These two species differ from the type species by small carapace size and well developed lirae-reticulation ornamentation (Liu, 1985: pl. 1).

Polygrapta hongluoxianensis Shen & Li, 1986 was described from the Upper Permian Hongla Formation in Liaoning of China. It differs from the type species in carapace size and outline. *P. hongluoxianensis* is of a smaller size, and rounded or ovate outline, but with a higher anterior height. In contrast, the type species has smaller anterior height. *Polygrapta troncosoi* (Gallego *in* Gallego & Covacevich, 1998) was described from the Upper Triassic in Atacama region of Chile. It differs from the type species by having rounded carapace outline.

Conclusion

Fossil clam shrimp are a valuable group in the subdivision and correlation of non-marine strata. In order to make precise correlation of fossil clam shrimp bearing strata, detailed and precise descriptions of fossil taxa are needed. In the present paper, the author emended the diagnosis of the type species *Polygrapta chatangensis* Novojilov, 1946. Through the SEM microscopy imaging new features of the carapace ornamentation are recovered, such as the polygonal fine reticulation in the dorsal part of the carapace, which were overlooked in the original description. These new features demonstrate that *Polygrapta* differs from *Pseudestheria*, because the latter has only punctate ornamentation, and they should be maintained as separate genera.

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