New Spinicaudatan Species of Late Jurassic Linglongta Phase of Yanliao Biota from Western Liaoning, China

Gang Li

State Key Laboratory of Palaeobiology and Stratigraphy, Center for Excellence in Life and Palaeoenvironment, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, East Beijing Road 39, Nanjing 210008, PR China. E-mail: gangli@nigpas.ac.cn

Received 1 August 2019 / Accepted 7 November 2019 / Published 5 August 2020

Special issue (articles 32-46) communicated by Thomas A. Hegna and D. Christopher Rogers

Abundant and diverse spinicaudatans are important components of the well-known Linglongta phase of the Yanliao Biota from the lower Upper Jurassic Tiaojishan Formation at the village Daxishan of Linglongta, Jianchang County, western Liaoning, north-eastern China. Herein a new spinicaudatan species Linglongtaestheria daxishanensis gen. and sp. nov. is described. It shows distinct carapace ornamentation patterns: (1) growth bands near the umbo ornamented with polygonal small-diameter reticulation; (2) growth bands in the middle part of the carapace ornamented with evenly distributed puncta; (3) growth bands in the ventral part of the carapace ornamented with punctate reticulation and radial lirae.

Key words: Early Late Jurassic, Clam shrimp, Taxonomy, Linglongta phase, Yanliao Biota.

BACKGROUND

During recent years many well-preserved vertebrate fossils of evolutionary importance have been recovered from the non-marine lower Upper Jurassic Tiaojishan Formation in the Linglongta area of Jianchang County, western Liaoning, north-eastern China (Fig. 1), including articulated skeletons of Archaeopteryx-like feathered theropod dinosaurs (Hu et al. 2009) (Anchiornis huxleyi Xu et al., 2009, Xiaotingia zhengi Xu et al., 2011), transitional, long-tailed pterosaurs with a pterodactyloid skull (Darwinopterus modularis Lü et al., 2009, D. robustodens Lü et al., 2011), a multituberculate mammal (Rugosodon eurasiacicus Yuan et al., 2013), and the earliest placental eutherian mammal (Juramaia sinensis Luo et al., 2011). These important fossil discoveries have not only shed additional light on the evolutionary biology of birds or on the mosaic (or modular) evolution of pterosaurs, but also have precisely calibrated the mammalian divergence age of eutherians from metatherians.

Extensive stratigraphic investigations on the Tiaojishan Formation exposed at Linglongta have revealed abundant spinicaudatans (clam shrimp, “conchostracans”) (Duan et al. 2009; Wang et al. 2013; Wang 2014; Liao et al. 2017). Spinicaudatans are small, bivalved branchiopod crustaceans with a chitin-mineral complex carapace (Tasch 1969) or chitin-mineral complex carapace (Astrop and Hegna 2015), which are abundant and widely distributed in sediments that accumulated in quiet, freshwater environments (Li 2004 2017a; Li and Matsuoka 2012 2013; Zhang et al. 2017). As a result, they are very useful index fossils for biostratigraphic subdivision and correlation of fossiliferous non-marine successions (Chen et al. 2007; Stigall and Hartman 2008; Li et al. 2009a 2010 2015 2017; Gallego et al. 2013; Boukhalfa et al. 2015; Tassi et al. 2015; Schneider and Scholze 2016; Teng and Li 2017 2018 2019; Hasegawa et al. 2018). On the other hand, their distinct mode of ecdysis and ecological behavior help us to understand the probable rate of growth of the animal (Li et al. 2009b), to decipher their phyletic evolution, and further to reconstruct the palaeoenvironmental conditions (Li et al. 2014 2016). Presented herein is
a systematic description of a new clam shrimp taxon from the Tiaojishan Formation near Daxishan village of Linglongta (Fig. 1).

**MATERIALS AND METHODS**

The spinicaudatan specimens were collected from the Tiaojishan Formation during a field survey supported by a National 973 Project in 2014 at the Daxishan village of Linglongta, Jianchang County. The described well-preserved clam shrimp specimens were collected from two horizons (L1 and L2) of the lacustrine shale and claystone beds in the lower and upper parts of the studied section, respectively (Fig. 2).

A LEO 1530 VP scanning electron microscope (SEM) of the State Key Laboratory of Palaeobiology and Stratigraphy was used for detailed observation of the carapace surface microstructure (Li and Batten 2004a b 2005; Li 2017b c) and a Zeiss V20 light microscope was used to document general morphology of the studied specimens.

The figured specimens are deposited in the

---

**Fig. 1.** Sampling locality at Daxishan village, Linglongta, Jianchang County, western Liaoning Province, China.

**Fig. 2.** Stratigraphic column of the Tiaojishan Formation exposed near Daxishan village, Linglongta, Jianchang County, showing the fossil clam shrimp sampling horizons (after Duan et al. 2009).
collections of the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGPCAS).

RESULTS

Traditionally, the carapace size of 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 and Shen 1985). Recently, Scholze and Schneider (2015, table 1) proposed another terminology to describe the size of clam shrimp. The author finds that the tripartite category of Chen and Shen (1985) is easy to follow for describing the carapace size.

Order Diplostraca Gerstaecker, 1866
Suborder Spinicaudata Linder, 1945
Superfamily Eosestherioidea Zhang and Chen in Zhang et al., 1976
Family Aquilonoglyptidae Novojilov, 1958

Discussion: Novojilov (1958, fig. 53a) proposed the family Aquilonoglyptidae including only one species with fish scale pit ornamentation on growth bands. Wang and Liu (1980) described three additional species from Triassic of China and demonstrated aquilonoglyptids having punctate ornamentation. Recently, the author checked the type specimen of Aquilonoglypta and found small-diameter reticulation on the dorsal part of the carapace. In this paper the author includes the new genus in the family Aquilonoglyptidae concerning the occurrence of fine reticulation on growth bands near the umbo and the punctate ornamentation on growth bands. It is clear that the herein described new genus could not be allocated in the family Triglyptidae Wang, 2014 because of the lacking of fine reticulation ornament in the dorsal part of the carapace in triglyptids.

Genus Linglongtaestheria gen. nov.
urn:lsid:zoobank.org:act:861FB496-4F6E-407E-8D69-CE183E7C38A0

Etymology: From Linglongta, a small town in the north-east of Jianchang County, western Liaoning Province.

Type species: Linglongtaestheria daxishanensis gen. and sp. nov., from the lower Upper Jurassic Tiaojishan Formation, Daxishan village, Linglongta, Jianchang County.

Diagnosis: Carapace small or moderate to the lower end in size; oval or elliptical in outline; growth bands near the umbo ornamented with small-diameter (8–15 µm) polygonal reticulation; growth bands in the middle part of the carapace ornamented with evenly distributed puncta (2–5 µm in diameter); the ornamentation gradually transforms to small-diameter (16–27 µm) reticulation or radial lirae in the lower part of the carapace, puncta occurring within reticulation or radially aligning between radial lirae.

Discussion: The new genus is similar to Triglypta Wang, 1984 and Tianzhuestheria Shen et al., 2002 in growth band ornamentation in the ventral part of the carapace, such as the occurrence of evenly distributed puncta, small-diameter punctate reticulation and radial lirae with intercalated radially aligned puncta. But, it differs from the latter two taxa in having small-diameter polygonal reticulation on growth bands near the umbo.

The new genus differs from Liaoxiestheria Liao et al., 2017 in that the latter lacks the reticulation and radial lirae ornament on growth bands in the ventral part of the carapace.

Linglongtaestheria daxishanensis gen. and sp. nov.
(Figs. 3, 4)
urn:lsid:zoobank.org:act:03DAF083-4D79-4FB6-BAE8-1B8A17268873

Material examined and dimensions: Holotype, displaced carapaces, NIGPCAS 163667 (L1–1); a right valve, NIGPCAS 163668 (L2–1); a broken right valve, NIGPCAS 163669 (L2–2); displaced carapaces, NIGPCAS 163670 (L2–3). Carapace measurements: number of growth lines, > 16, 24, 23, 17; length (mm), 4.6, 5.2, 3.6, 3.7; height (mm), 2.9, 3.3, 2.3, 2.5.

Etymology: From Daxishan, a village located in the south-west of Linglongta.

Diagnosis: Carapace of small or small moderate size; ovate or elliptical in outline; growth lines smooth, about 20 in total; growth bands near the umbo ornamented with fine, polygonal reticulation (diameter < 20 µm); growth bands in the middle part of the carapace ornamented with evenly distributed puncta (diameter < 5 µm); in the ventral part of the carapace each growth band is ornamented with puncta in the upper part, which transfer into punctate reticulation in the anterior part and radial lirae in the posterior part of each band.

Description: Carapace small or moderate in size, ovate or elliptical in outline; umbo small, located at the anterior half of the slightly arched dorsal margin; growth lines wide and smooth, about 20 in total; growth bands near the umbo ornamented with polygonal small-diameter reticulation, reticulum diameter is about 8–15 µm (Figs. 3.2 and 3.4; Figs. 4.4 and 4.7); growth bands in the middle part of the carapace ornamented
Fig. 3. 1–8, Linglongtaestheria daxishanensis gen. and sp. nov. 1, displaced carapaces, holotype, NIGPCAS 163667 (L1–1) (light microscopy). 2, small-sized polygonal reticulation on growth bands near the umbo (SEM). 3, evenly distributed small puncta on growth bands in the middle part of the carapace (SEM). 4, small-sized polygonal reticulation on growth bands in the antero-dorsal part of the carapace (SEM). 5, 7, two kinds of ornamentation pattern on growth bands in the postero-ventral part of the carapace, i.e., punctate ornamentation in the upper, radial lirae with two rows of intercalated radially aligned puncta in the lower part of each growth band (SEM). 6, small-sized, polygonal reticulation transitions to radial lirae with intercalated radially aligned puncta on growth bands in the antero-dorsal part of the carapace (SEM). 8, two kinds of ornamentation pattern on single growth bands in the antero-ventral part of the carapace, i.e., puncta in the upper, punctate small-sized reticulation in the lower part of each growth band (SEM). Scale bars: (1) = 1 mm; (2, 5) = 20 μm; (4) = 50 μm; (3, 6–8) = 100 μm.
Fig. 4. 1–8. Linglongaestheria daxishanensis gen. and sp. nov. 1, a right valve, NIGPCAS 163668 (L2–1) (light microscopy). 2, a broken right valve, NIGPCAS 163669 (L2–2) (light microscope). 3, displaced carapaces, NIGPCAS 163670 (L2–3) (light microscope). 4, small-sized polygonal reticulation on growth bands near the umbo of the specimen in figure 4.1 (SEM). 5, evenly distributed puncta on growth bands in the middle part of the carapace of the specimen in figure 4.1 (SEM). 6, two kinds of ornamentation pattern on growth bands in the postero-ventral part of the carapace of the specimen in figure 4.1, *i.e.*, puncta in the upper and radial lirae with intercalated radially aligned puncta in the lower part of each growth band (SEM). 7, small-sized polygonal reticulation on growth bands in the antero-dorsal part of the carapace of the specimen in figure 4.3 (SEM). 8, two kinds of ornamentation pattern on growth bands in the ventral part of the carapace of the specimen in figure 4.3, *i.e.*, puncta in the upper part and radial lirae with intercalated radially aligned puncta in the lower part of each growth band (SEM). Scale bars: (1–3) = 1 mm; (4) = 10 μm; (5) = 20 μm; (6–8) = 100 μm.
with evenly distributed puncta, punctum diameter is about 2–5 µm (Figs. 3.3, 4.5); growth bands in the lower part of the carapace ornamented with puncta in upper part (Figs. 3.5 and 3.8), and punctate reticulation in lower part of each growth band in the anteroventral part of the carapace (Fig. 3.8), and radial lirae intercalated with two rows of radially aligned puncta in the ventral part of each growth band in the posteroventral part of the carapace (Figs. 3.5, 3.7, 4.8); near the ventral margin, the punctuate zone is located in the upper 1/4 to 1/5 of each growth band (Fig. 3.8).

**Distribution:** Lower Upper Jurassic Tiaojishan Formation at Daxishan, Linglongta, Jianchang, northern China.

**DISCUSSION**

In contrast to other crustaceans, spinicaudatans do not shed their dorsal carapaces during the ecdysis, a new growth band is added peripherally to each valve when they cast off a chitinous inner skeletal duplicature (Tasch 1969). Thus, the information of the entire ontogenetic development is preserved in the carapace of the individual. This may contribute to understanding the probable rate and mode of growth, and to decipher their evolution (Stigall and Hartman 2008).

The carapace ornamentation of the described new species shows clear evolutionary trend during the ontogeny. The growth bands near the umbo are ornamented with small-diameter polygonal reticulation (Figs. 3.2, 4.4). In the middle part of the carapace, growth bands are ornamented with evenly distributed puncta (Figs. 3.3, 4.5). While in the ventral part of the carapace, growth band ornamentation shows a mixed ornamentation pattern: i.e. each band being ornamented with evenly distributed puncta in its dorsal part, while the radial lirae (Figs. 3.5, 3.7) and punctate reticulation (Fig. 3.8) occurring in its ventral part. This carapace ornamentation evolutionary trend may indicate that Linglongtaestheria gen. nov. originated from an ancestor with fine reticulate carapace.

**CONCLUSIONS**

Clam shrimp are important index fossils for the subdivision and correlation of non-marine Mesozoic strata. The ontogenetic information preserved in fossil clam shrimp carapaces is helpful to decipher their phylogenetic evolution. The detailed SEM imaging method is a favorable tool for the fossil clam shrimp taxonomy. Herein described new fossil species clearly shows fine polygonal reticulation on growth bands in the dorsal part of the carapace. This may indicate that the new genus has originated from an ancestor with reticulate carapace.

**Acknowledgments:** This work, the new genus, and the new species names have been registered with ZooBank under urn:lsid:zoobank.org:pub:B455C88E-9B1B-4099-B36F-9825DCF77EB4. This study was supported by the Strategic Priority Research Program of Chinese Academy of Sciences (XDB26000000), by the National Natural Science Foundation of China (41972007, 41572006, 41688103, 91514302, 41172010), and by Major Basic Research Projects of the Ministry of Science and Technology, China (973 Project 2012CB822004). The field investigation was fulfilled by the great help of Prof. SUN Ge (College of Palaeontology, Shenyang Normal University; Key-Lab for Evolution of Past Life and Environment in Northeast Asia, Ministry of Education, Jilin University), Vice Director CHENG Shao-li (Fossil Resources Protection Bureau of Liaoning Province), Mr. WANG Xue-bing, Mr. XIANG Yong (Land Resources Bureau of Jianchang County), Mr. SUN You-li, Mr. MA Lian-hui (Linglongta Land Resources Institute), Prof. JI Qiang (Institute of Geology, Chinese Academy of Geosciences), Prof. DONG Hai-liang and Dr. HUANG Yong-jian (China University of Geosciences, Beijing). Many thanks go to Dr. M Hethke (Free University of Berlin) and an anonymous reviewer for constructive comments. This manuscript is a contribution to IGCP 679.

**Authors’ contributions:** GL collected the material and wrote the manuscript. Laboratory preparation and SEM imaging were conducted by GL.

**Competing interests:** GL declares that he has no conflict of interests.

**Availability of data and materials:** Available type materials of the new species are described in the text.

**Consent for publication:** Not applicable.

**Ethics approval consent to participate:** Not applicable.

**REFERENCES**


