



Clam shrimp assemblage from Daohugou: A link correlating northern Hebei and western Liaoning

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Abstract

The clam shrimp species, *Triglypta pingquanensis* Wang, 1984, is reported in the Middle Jurassic Daohugou beds from two localities in Inner Mongolia. The species is predominant in the Middle Jurassic Longmen Formation in Yingzi Village, Pingquan City, northern Hebei. This discovery significantly strengthens the correlation between the Haifanggou and Longmen formations. The clam shrimp of the Haifanggou and Longmen formations are dominated by *T. haifanggouensis* Chen, 1976 and *T. pingquanensis*, respectively. The clam shrimp assemblage from the Daohugou beds serves as a crucial link for correlating the Middle Jurassic in northern Hebei and western Liaoning, and it represents the early assemblage of the Yanliao biota. Moreover, a new species, *T. hebeiensis* Liao & Huang **sp. nov.**, is described in the uppermost layer of the Longmen Formation in this study.

Keywords: clam shrimp, Jurassic, *Triglypta haifanggouensis*, *Triglypta pingquanensis*, Yanliao biota

Introduction

The renowned Yanliao biota is a Jurassic terrestrial biota known for its rich diversity of diverse salamanders, pterosaurs, feathered dinosaurs, early mammals, insects, spiders, branchiopods, and plants. The term “Yanliao biota” originated from the Yanliao entomofauna, characterized by fossil insects from the Haifanggou Formation near to Haifenggou Village, Beipiao City, western Liaoning, and the “Jiulongshan” Formation (equivalent to Longmen Formation in this study) near to

Zhouyingzi Village, Luanping County, northern Hebei (Hong, 1983). The border region between Hebei Province, Liaoning Province, and Inner Mongolia constitutes the core area of the Yanliao Biota (Fig. 1). The biota has gained international recognition due to the discovery of diverse, well-preserved fossils, including salamanders, feathered dinosaurs, early mammals, insects, spiders, clam shrimps, and plants (e.g., Wang *et al.*, 2000; Ji *et al.*, 2006; Meng *et al.*, 2006, 2015; Luo *et al.*, 2007, 2015; Zhang *et al.*, 2008; Huang *et al.*, 2012, 2013; Zhou *et al.*, 2013; Sullivan *et al.*, 2014; Huang, 2016, 2019) from the fossil-bearing Daohugou beds near to Daohugou Village, Wuhua Town, Ningcheng County, Inner Mongolia (Fig. 1, locality 3; Fig. 3C), since the early 21st century.

Clam shrimps, one of the most common invertebrates in the Yanliao biota, are widely distributed across various localities (Fig. 1; Fig. 3). Early studies on the Daohugou beds initially classified all clam shrimps under the genus *Euestheria* (Ji & Yuan, 2002; Ren *et al.*, 2002; Zhang, 2002). Shen *et al.* (2003) identified them as four species: *Euestheria ziliujingensis* Chen, 1976, *E. haifanggouensis* Chen, 1976, *E. jingyuanensis* Chen, 1976, and *E. luanpingensis* Zhang, Shen & Niu, 1987, based on subtle differences in shape and growth line number among individuals. The four species are all members of the famous *E. ziliujingensis* assemblage, which was established by Zhang *et al.* (1976) and considered as the most common clam shrimp assemblage of the Middle Jurassic in China (Zhang *et al.*, 1976). However, recent studies suggest that only one species, *Triglypta haifanggouensis*, exists in the Daohugou locality (Liao *et al.*, 2017; Liao, 2022). It is also the predominant species in the Haifanggou Formation in Beipiao City, Liaoning Province (Zhang *et*

al., 1976; Liao *et al.*, 2017; Liao, 2022). The presence of this species provides significant evidence supporting the correlation between the Daohugou beds in Inner Mongolia and the Haifanggou Formation in western Liaoning (Huang *et al.*, 2017; Liao *et al.*, 2017; Liao, 2022). The Longmen Formation (previously referred to as “Jiulongshan Formation”), which is exposed in Pingquan City and Luanping County of northern Hebei, share similar fossil content with the Haifanggou Formation (Huang *et al.*, 2017; Huang, 2019). Despite the similarities in fossil content, some previous studies suggested the two formations were of different ages owing to the difference of fossil insects (Zhang, 2006, 2015; Zhang *et al.*, 2015). In this study, clam shrimp from the Longmen Formation near to Yingzi Village in northern Hebei (Fig.1, locality 2; Fig. 3B) and the Daohugou beds in Inner Mongolia are compared, and the relationship between the Longmen and Haifanggou formations is discussed. Moreover, a new species from the uppermost layer of the Longmen Formation is described.

Geological setting

The Daohugou beds, exposed in the southeastern marginal area of the Ningcheng Basin, Inner Mongolia, comprise

terrestrial sediments resting unconformably on Archean gneisses and are overlain unconformably by the Late Jurassic Tiaojishan Formation (Fig. 2; Fig. 3C, E). Most of the sediments are lacustrine with horizontal bedding, which are composed mainly of gray tuffs interbedded mainly with white-grayish and brown-grayish fine-grained tuffaceous shales (Fig. 2). In addition to Daohugou Village, outcrops have been found at Zhujiagou (Fig. 1, locality 4; Fig. 3D), Xigou, Jiangzhangzi (Fig.1, locality 5; Fig. 3E) and Chentaizi villages of Wuhua Town, Ningcheng County, Inner Mongolia, and Reshuitang near to Wubaiding Village, Lingyuan City, Liaoning Province. Clam shrimps were primarily discovered in the middle-upper fossil-bearing layers of the Daohugou beds. In addition, abundant cladocerans and anostracans have been found in the Daohugou beds (Huang, 2015, 2019; Huang *et al.*, 2015). Presence of these branchiopods indicates that the lake system was broad with relatively shallow water (Huang, 2015). There were controversies about the age and stratigraphic placement of the Daohugou beds (*e.g.*, Ren *et al.*, 2002; Zhang, 2002; Liu *et al.*, 2006a, 2012). However, it is widely accepted that the fossil content of Daohugou and adjacent localities belongs to the Yanliao biota and is a typical representative of the biota in recent years (*e.g.*, Huang, 2016, 2019; Liao *et al.*, 2017; Xu *et al.*, 2017).

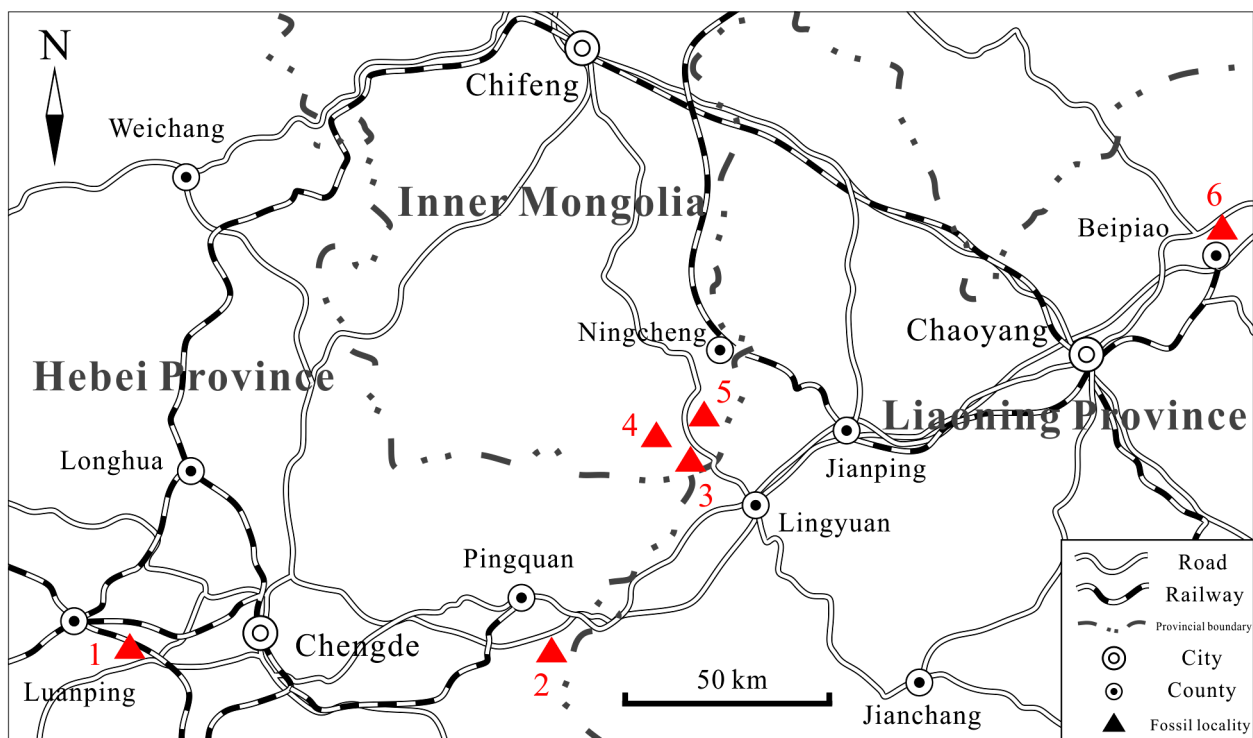


FIGURE 1. Clam shrimp fossil localities of the early assemblage of the Yanliao biota. 1, Zhouyingzi Village, Zhangbaiwan Town, Luanping County, Hebei Province (N40.97°, E117.60°). 2, Yingzi Village, Songshutai Town, Pingquan City, Hebei Province (N40.90°, E118.87°). 3, Daohugou Village, Wuhua Town, Ningcheng County, Inner Mongolia (N41.32°, E119.23°). 4, Zhujiagou Village, Wuhua Town, Ningcheng County, Inner Mongolia (N41.38°, E119.15°). 5, Jiangzhangzi Village, Wuhua Town, Ningcheng County, Inner Mongolia (N41.40°, E119.26°). 6, Haifenggou Village, Beipiao City, Liaoning Province (N41.84°, E120.80°).

The Jiulongshan Formation originally referred to a set of non-coal-bearing sediments which disconformably overlies the Longmen Formation in western Beijing (Bureau of Geology and Mineral Resources of Beijing Municipality, 1991). Its stratotype section, primarily composed of purple-green sandstones, mudstones, and conglomerates, is located at Yuejiapo, Mentougou District, Beijing (Bureau of Geology and Mineral Resources of Beijing Municipality, 1991). Few fossils were discovered in the section. Huang (1954, 1960) considered that it was actually a synonym of the Tiaojishan Formation. Isotope chronological studies confirmed this by indicating that the Jiulongshan and Tiaojishan formations were of the same age (Liu *et al.*, 2006b; Li *et al.*, 2014). However, the so-called “Jiulongshan” Formation in northern Hebei actually refers to the sediments that mainly consist of conglomerates, sandstones, and mudstones, which are disconformably overlain by the Tiaojishan Formation. Diverse fossils including clam shrimps, insects, bivalves and plants were found in the upper part of the “Jiulongshan” Formation in northern Hebei. Huang (2019) suggested that the so-called “Jiulongshan” Formation in northern Hebei could be correlated to the Haifanggou Formation in western Liaoning or the Longmen Formation in western Beijing based on lithology, isotopic ages, and fossil content. We follow this view and use the term “Longmen Formation” to refer to the fossil-bearing sediments overlain by the

Tiaojishan Formation in northern Hebei. The correlation between the Haifanggou and the Longmen formations has been demonstrated in previous studies (Huang, 2015, 2019; Huang *et al.*, 2017; Zhao, 1990; Zhang *et al.*, 2013). The presence of a regional unconformity under the two formations (Fig. 2) indicates the prelude of the Yanshan Movement (Huang, 2015, 2019; Huang *et al.*, 2017). In northern Hebei, the Longmen Formation is mainly exposed in Luanping, Pingquan and Qinglong. It is a set of terrestrial clastic sediments interbedded with tuff which are composed mainly of greenish-yellow or greenish-grey conglomerates, sandstones, siltstones and mudstones (Fig. 2). The section near to Yingzi Village, Pingquan City is well-exposed (Fig. 1, locality 2; Fig. 3B). It unconformably lies on the sandstones of the Upper Triassic Liujiagou Formation, and is disconformably overlain by volcanic rocks of the Upper Jurassic Tiaojishan Formation (Fig. 2). Clam shrimp were primarily found in tuffaceous mudstones of the uppermost fossil-bearing layers of the formation.

The Longmen Formation in northern Hebei shares similar fossil content with the Haifanggou Formation in western Liaoning and Inner Mongolia. *Ferganoconcha sibirica*, recovered from the Longmen Formation (Second Regional Geological Survey Team of Hebei Provincial Bureau of Geological Survey, 1976), is also the predominant species of the Haifanggou Formation (Liaoning Provincial Bureau of Geology and Minerals, 1989; Jiang, 2006).

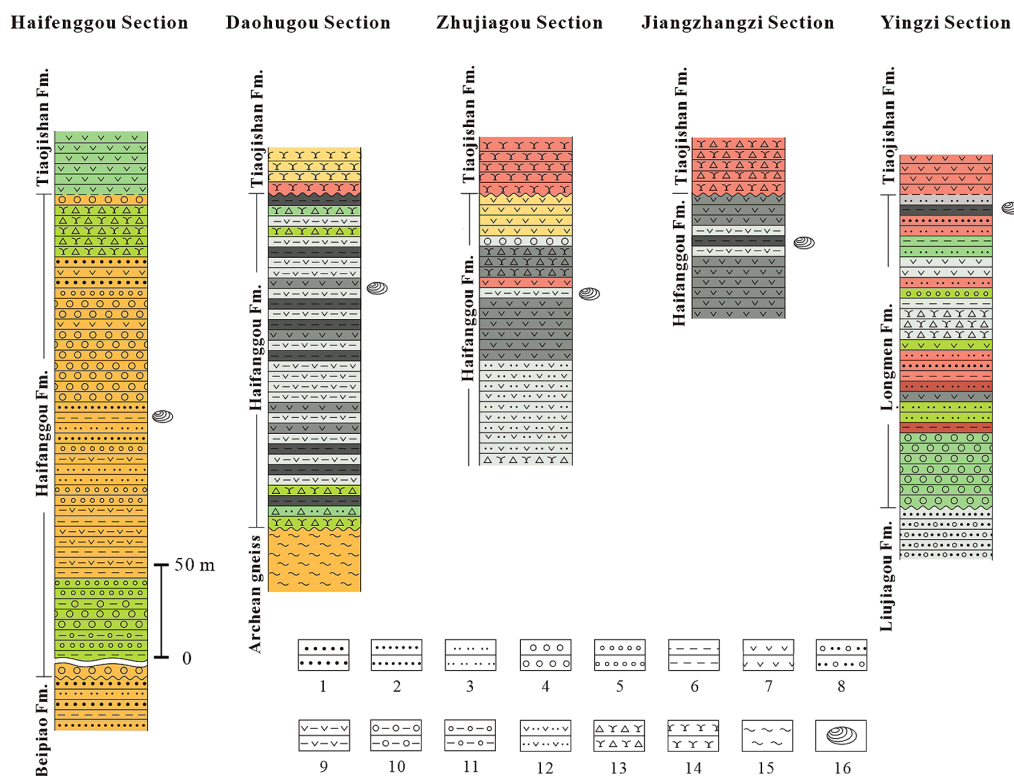


FIGURE 2. Columns of the Haifanggou and Longmen formations. Lithology: 1. gritstone; 2. sandstone; 3. siltstone; 4. conglomerate; 5. fine conglomerate; 6. mudstone; 7. tuff; 8. sandstone with gravels; 9. tuffaceous mudstone; 10. mudstone with gravels; 11. mudstone with fine gravels; 12. tuffaceous gritstone; 13. volcanic breccia; 14. andesite; 15. gneiss; 16. clam shrimp.

The representative insect *Yanliaocorixa chinensis* from the Haifanggou Formation (including the Daohugou beds) was initially found in the Longmen Formation near to Zhouyingzi Village, Luangping County, Hebei Province (Hong, 1983; Fig. 1, locality 1). Hong (1983) identified a rove beetle from the Longmen Formation as *Prostaphylinus mirus*, previously named by Lin (1976) in the Haifanggou Formation. A subsequent study indicated that it was probably the same species with some common rove beetles in the Daohugou beds (Cai & Huang, 2010). However, it should be noted that some researchers have different views on the similarity of insects between the Haifanggou and Longmen formations. Zhang *et al.* (2015) and Zhang (2010, 2015) argued that the identification of some insects in the Daohugou beds were questionable,

and there were actually no common species between the two formations. Additionally, Zhang (2006) suggested that the Haifanggou and Longmen formations possessed different mayflies in the generic and even familial level.

Material and methods

Specimens of *Triglypta pingquanensis* were collected from the mudstones and tuffaceous mudstones in the Middle Jurassic Longmen Formation near to Yingzi Village, Pingquan City, Hebei Province, and the Middle Jurassic Daohugou beds (Haifanggou Formation) near to Jiangzhangzi and Zhujiagou villages, Wuhua Town, Ningcheng County, Inner Mongolia, respectively.

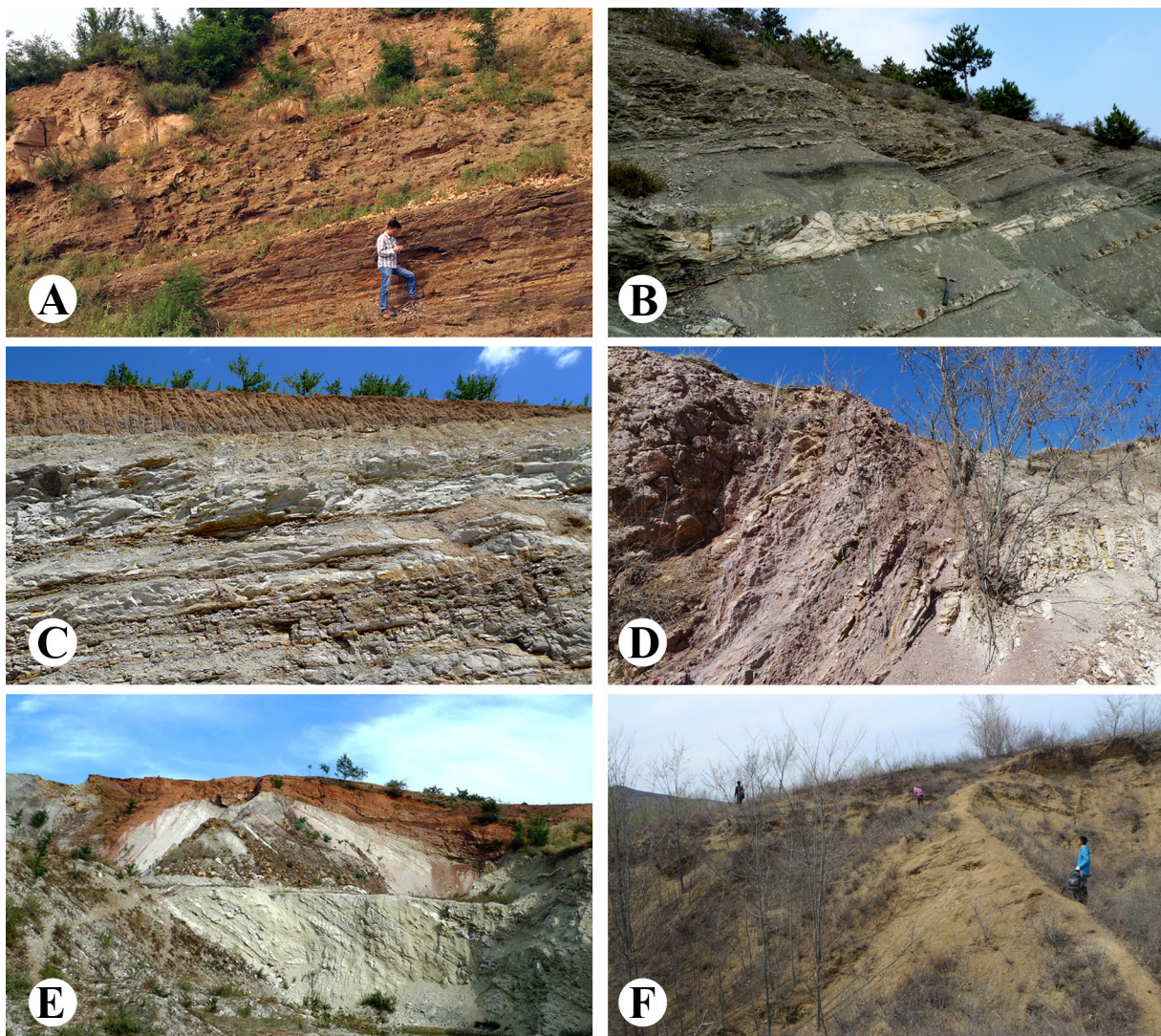


FIGURE 3. Sections of the Haifanggou and Longmen formations. **A**, The upper fossil bearing layers of the Longmen Formation at Zhouyingzi locality. **B**, The uppermost fossil bearing layers of the Longmen Formation at Yingzi locality. **C**, The fossil bearing layers of the Haifanggou Formation overlain by the red andesites of the Tiaojishan Formation at Daohugou locality. **D**, The fossil bearing layers of the Haifanggou Formation overlain by the red andesites of the Tiaojishan Formation at Zhujiagou locality. **E**, The middle–upper fossil bearing layers of the Haifanggou Formation overlain by the red andesites of the Tiaojishan Formation at Jiangzhangzi locality. **F**, The fossil bearing layers of the Haifanggou Formation at Haifenggou locality.

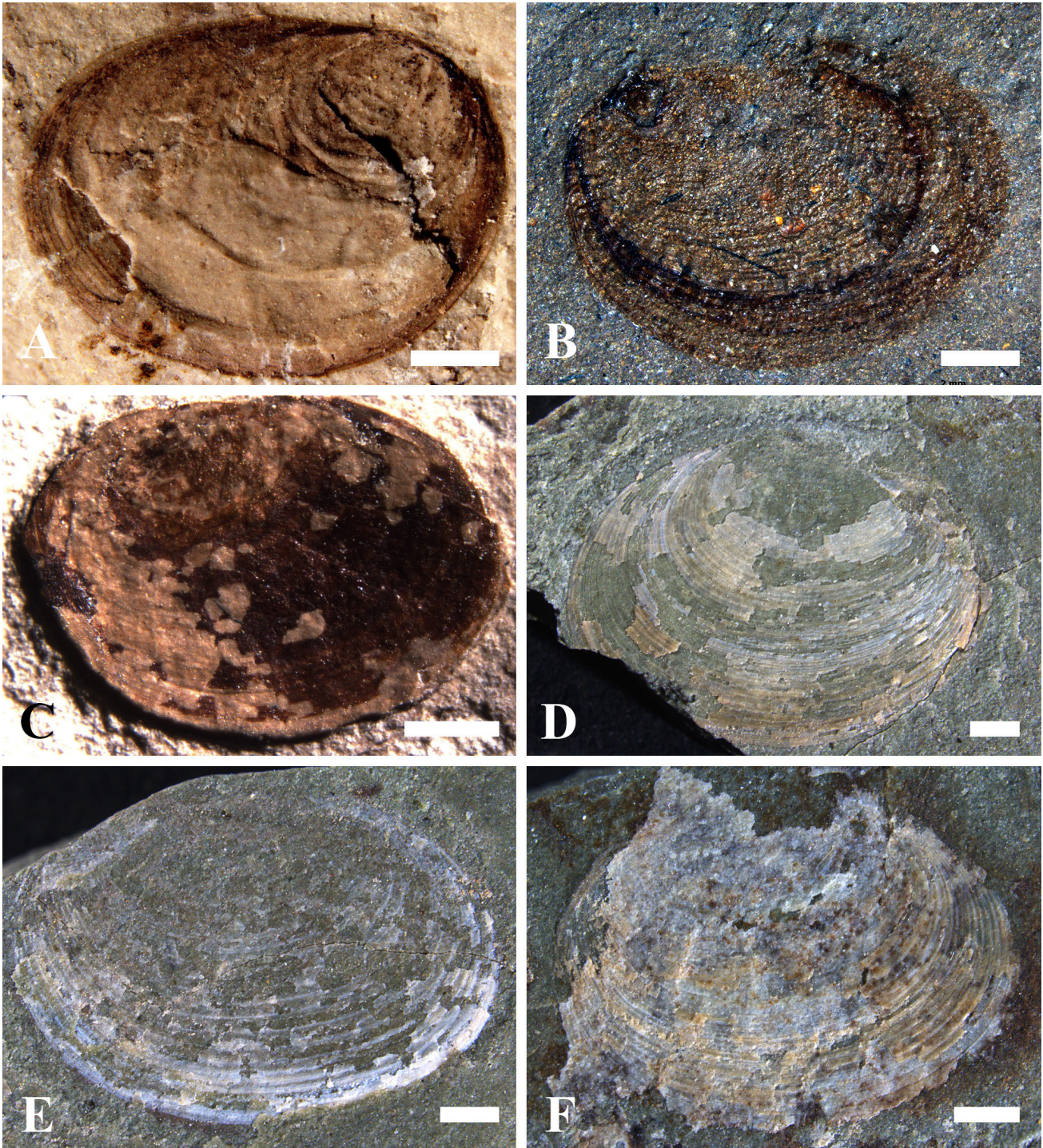


FIGURE 4. Carapaces of *Triglypta pingquanensis* (A–C) and *T. hebeiensis* sp. nov. (D–F) from the Longmen and Haifanggou formations. **A**, A whole carapace from the Haifanggou Formation at Zhujiagou locality NIGP204094. **B**, A whole carapace from the Longmen Formation at Yingzi locality NIGP178172. **C**, A whole carapace from the Haifanggou Formation at Jiangzhangzi locality NIGP204095. **D**, A whole carapace from the Longmen Formation at Yingzi locality NIGP204096. **E**, A whole carapace from the Longmen Formation at Yingzi locality NIGP204097. **F**, A whole carapace from the Longmen Formation at Yingzi locality NIGP204098. Scale bars = 1 mm.

Specimens of *T. hebeiensis* sp. nov., were collected from the uppermost of the Longmen Formation near to Yingzi Village. A total of more than ten individuals on several slabs were collected.

A Zeiss Discovery V20 microscope was used to investigate and photograph the outline and other macroscopic features of the specimens, and a LEO 1530VP Scanning Electron Microscope (SEM) was used

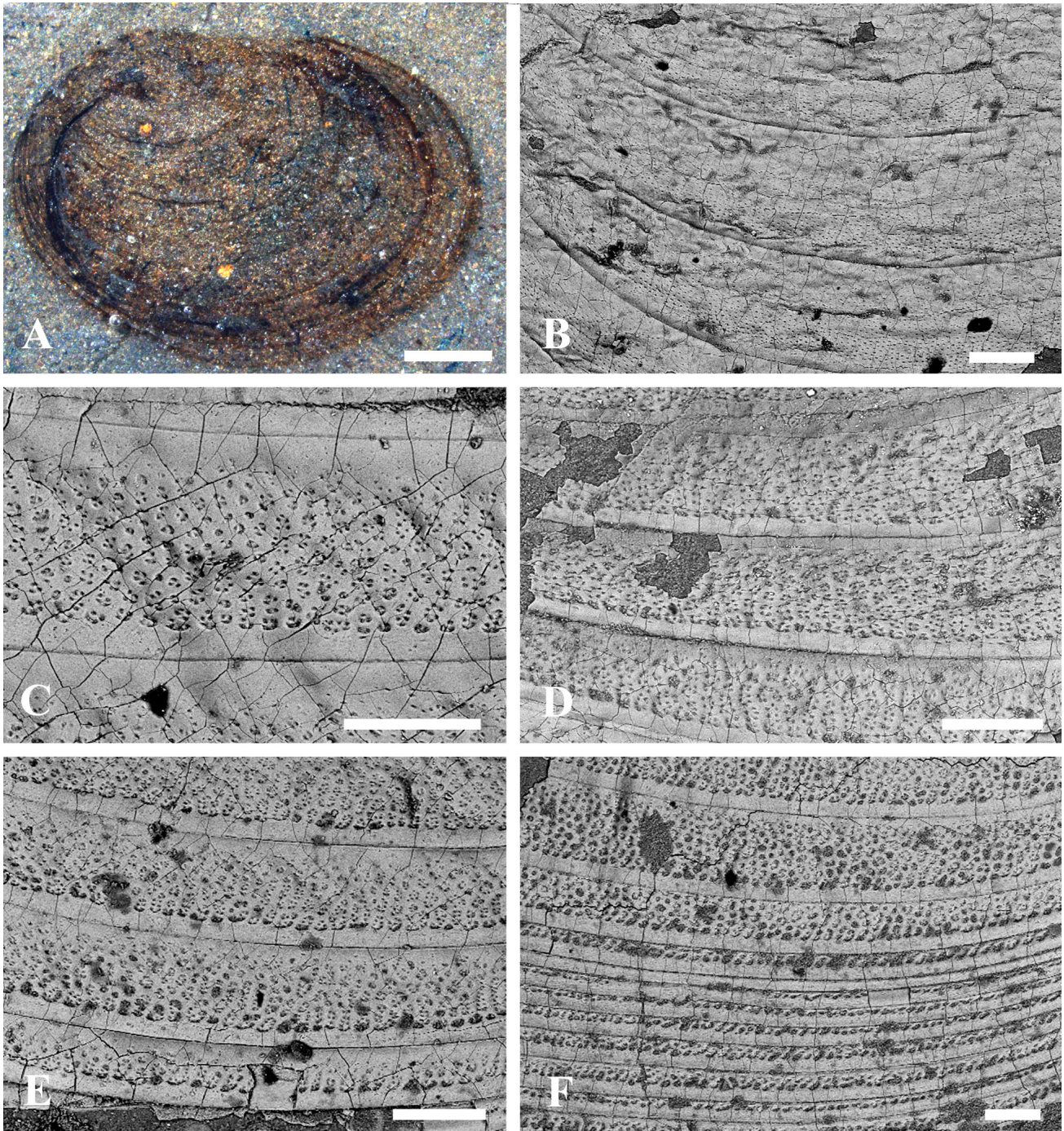


FIGURE 5. Carapace and ornamentations of *Triglypta pingquanensis* from the Longmen Formation in Yingzi Village, Pingquan, Hebei Province. **A**, A whole carapace NIGP178170. **B**, Punctae at the dorsal-median area of the carapace NIGP178170. **C**, Punctae-formed reticulations at the median area of the carapace NIGP178171. **D**, Punctae-formed reticulations transform to linear arrangements at the anterior-median area of the carapace NIGP178172. **E**, Punctae-formed reticulations transform to linear arrangements at the median ventral area of the carapace NIGP178170. **F**, Punctae-formed reticulations and linear arrangements at the posterior ventral marginal area of the carapace NIGP178170. Scale bars = 1 mm in (A) and 100 μ m in (B–F).

to investigate and photograph the micro-ornamentations. All the specimens are housed in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences.

We follow the recent classification of spinicaudatans by Martin & Davis (2001), and the fossil classification by Zhang *et al.* (1976), combining the proper terms of Wang (1983, 1984, 1985, 2014), and Scholze & Schneider (2016).

Results

In our previous studies (Huang, 2016, 2019; Liao *et al.*, 2017), only one species, *Triglypta haifanggouensis*, was found at Daohugou and adjacent localities. The type specimens of this species were obtained from the Haifanggou Formation near to Haifenggou Village, Beipiao City, Liaoning Province (Zhang *et al.*, 1976; Fig. 1, locality 6; Fig. 2). Consequently, this species was considered as the sole and the predominant species of the Haifanggou Formation in Inner Mongolia and western Liaoning (Liao *et al.*, 2017; Huang, 2019). However, until the present study, the correlation between the Haifanggou and Longmen Formations had not been supported by clam shrimp fossils owing to the absence of shared species. Clam shrimps from the Daohugou beds of Jiangzhangzi and Zhujiagou localities are mainly *T. haifanggouensis*. Moreover, abundant specimens of *T. pingquanensis* are also found in the two localities. *Triglypta pingquanensis* was initially found and named from the Longmen Formation in Yingzi Village, Pingquan City, Hebei Province (Wang, 1984). This species exhibits an oval to elongated oval carapace (Fig. 4A–C), characterized by well-developed “flower-shaped” punctae-formed reticulations on its carapace (Fig. 5, 6). The presence of *T. pingquanensis* in the Daohugou beds supports the notion that the Longmen Formation in northern Hebei can be correlated to the Haifanggou Formation in western Liaoning and Inner Mongolia.

It is noteworthy that Wang *et al.* (1984) described a species, *T. yingziensis*, from the Longmen Formation at Yingzi locality. However, it only differs from *T. pingquanensis* in its rounder outline (Wang *et al.*, 1984). We assume that it may be a synonym of *T. pingquanensis*. *T. luanpingensis* from the Longmen Formation in Zhouyingzi locality, Hebei Province (Fig. 1, locality 1; Fig. 3A) shares a similar ornamentation layout with *T. haifanggouensis*, but its punctae on its carapace are special polygonal-shaped (Liao *et al.*, 2017). The five species *T. haifanggouensis*, *T. pingquanensis*, *T. yingziensis*, *T. luanpingensis*, and *T. hebeiensis* Liao & Huang **sp. nov.** (Fig. 4D–F, 7) from the Haifanggou and Longmen formations constitute the early clam shrimp assemblage of the Yanliao biota. They differ from the late assemblage of the Yanliao biota in the Upper Jurassic Tiaojishan Formation, which includes *Liaoxiestheria linglongtaensis* Liao *et al.*, 2017, *Linglongtaestheria daxishanensis* Li, 2020, *L. qinglongensis* Teng *et al.*, 2022, and *Tianzhuestheria jianchangensis* Wang *et al.*, 2014. In recent years, more and more species of the “*E. ziliujingensis*” assemblage have been proved to belong to the genera *Triglypta*, *Qaidamestheria*, *Linglongtaestheria* and *Tianzhuestheria*, etc. (e.g., Wang, 1998, 2014; Li, 2022; Liao, 2022; Liao *et al.*, 2017, 2023). *Euestheria* likely does not exist in the Jurassic of China. In addition,

the apparent differences of clam shrimps between the late Middle Jurassic and early Late Jurassic have been found in several regions (Liao *et al.*, 2017, 2023; Li, 2022), just like the Yanliao biota. The so-called “*E. ziliujingensis*” assemblage may be equivalent to the *Triglypta-Qaidamestheria* assemblage established by Wang (1998). This clam shrimp assemblage, endowed with important biostratigraphic significance, is widely distributed in the Middle–Late Jurassic of China. Further investigations into these Jurassic species are critical to better understand the Jurassic stratigraphic correlation of China.

Systematic palaeontology

Order Diplostraca Gerstaecker, 1866

Suborder Spinicaudata Linder, 1945

Superfamily Eosestherioidea Zhang & Chen, 1976

Family Triglyptidae Wang, 2014

Genus *Triglypta* Wang, 1984

Type species. *Triglypta pingquanensis* Wang, 1984, from the upper part of the Middle–Late Jurassic Longmen Formation near the Yingzi Village, Pingquan City, Hebei Province, by original designation.

***Triglypta hebeiensis* Liao & Huang sp. nov.**

Materials. Holotype, NIGP204101; paratypes, NIGP204096–204098, 204101–204103;

Etymology. After the Hebei Province, from where the specimens were collected.

Diagnosis. Carapace oval or elongate oval, moderate to large in size (7.5–8.8 mm in length); dorsal margin short; larval valve small; umbo in medial to marginal position; growth bands abundant in number, ornamented with micro punctae; punctae gathered together at mid-anterior and the median ventral areas, and gradually transform to well-developed linear arrangements and radial lirae forwards and downwards.

Type locality and horizon. Middle Jurassic Longmen Formation near the Yingzi Village, Pingquan City, Hebei Province; uppermost Middle Jurassic (Callovian).

Description. Carapace oval to elongated oval in outline, 7.5–8.8 mm in length and 5.4–6.7 mm in height (Fig. 4D–F, 7A); dorsal margin short, straight or slightly curved; larval valve small, umbo locates at medial to marginal position (Fig. 4D–F, 7A); both the anterior and the posterior margins sharply curved; growth lines fine, 23 to more than 30 in number; growth bands ornamented with dense punctae (Fig. 7B–E); each three to five punctae gather together on several growth bands at the mid-anterior to the median areas of the carapace (Fig. 7B); gathered punctae gradually transform to linear

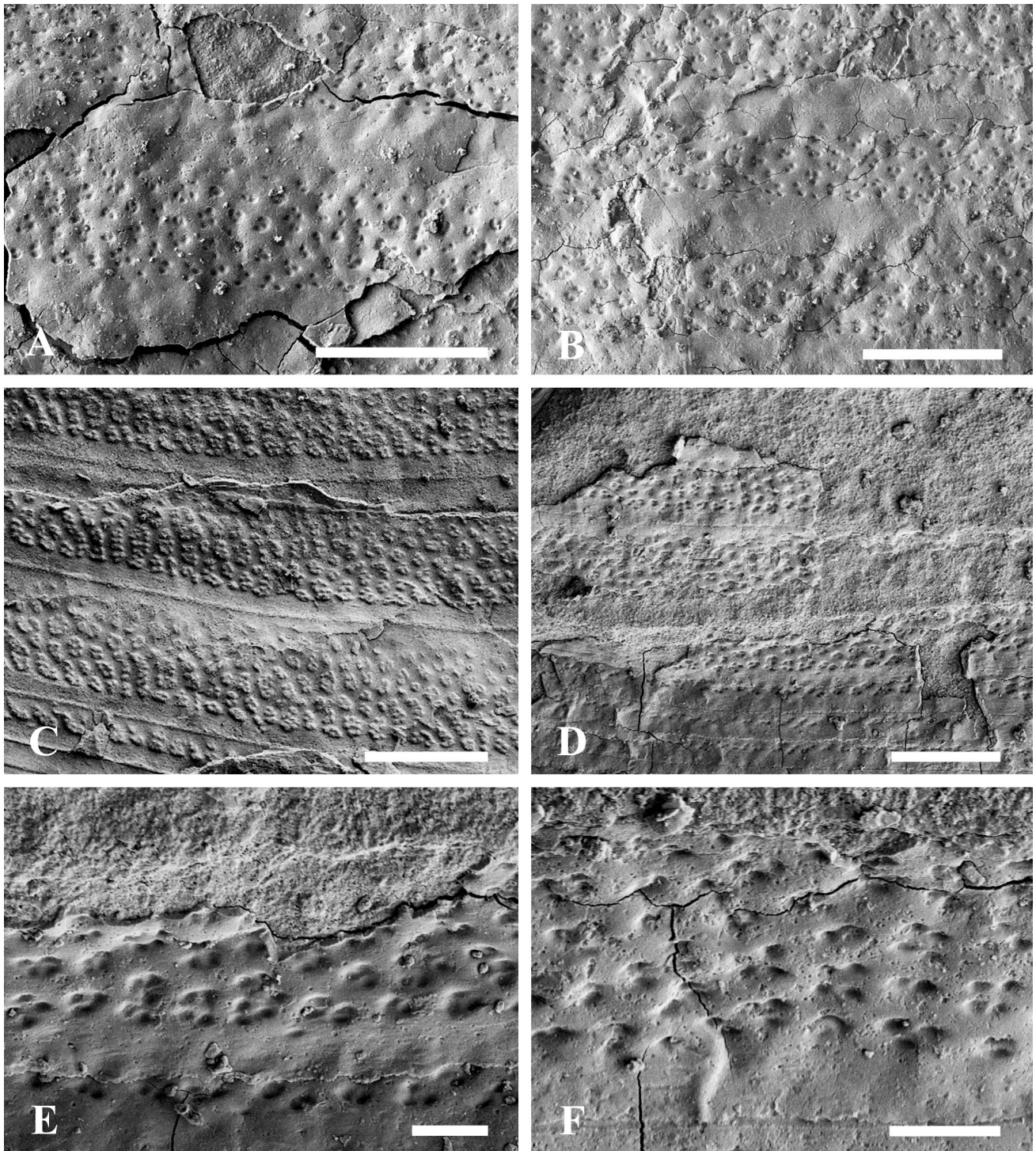


FIGURE 6. Ornamentations on carapaces of *Trigypta pingquanensis* from the Haifanggou Formation (Daohugou beds) at Jiangzhangzi and Zhujiagou localities in Ningcheng County, Inner Mongolia. **A–C**, NIGP204099. **A**, Punctae-formed reticulations at median-anterior area of carapace. **B**, Punctae-formed reticulations at median-posterior area of carapace. **C**, Imprints of punctae-formed reticulations transform to linear arrangements at median-anterior area of carapace on external mold. **D–F**, NIGP204100. **D**, Punctae-formed reticulations at median-ventral area of carapace. **E**, Enlargement of **D**. **F**, Punctae-formed reticulations at median area of carapace. Scale bars = 100 μm in (**A–D**) and 20 μm in (**E**, **F**).

arrangements, and extremely prominent at the anterior areas; linear arrangements relatively straight, each one arranged by one or two lines of punctae (Fig. 7C–F); radial lirae present between linear arrangements; space between

two arrangements 35–60 μm wide; punctae disappear and linear arrangements totally transform to lirae on several very narrow growth bands at the marginal areas (Fig. 7F).

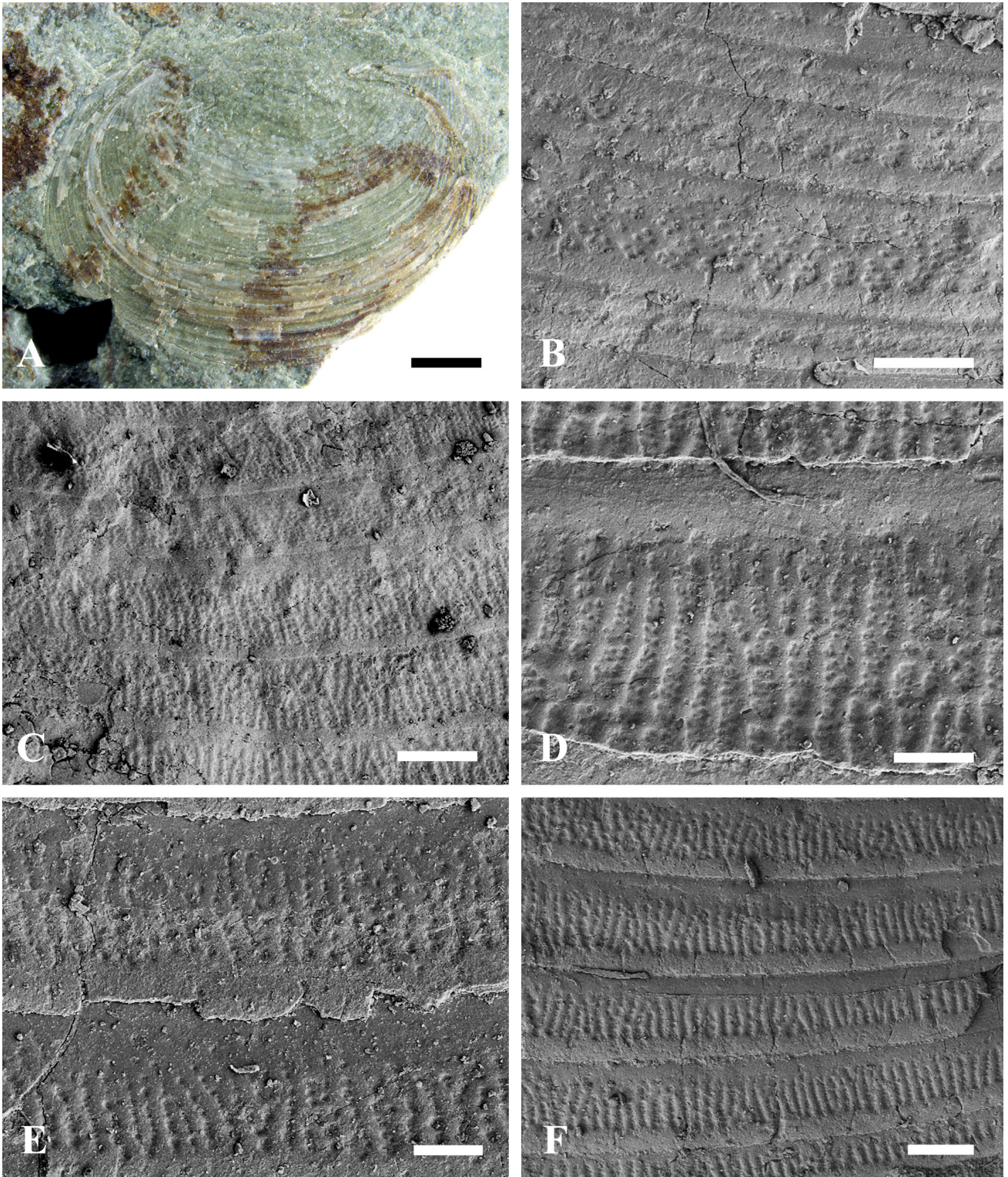


FIGURE 7. Carapace and ornamentations of *Triglypta hebeiensis* **sp. nov.** from the Longmen Formation in Yingzi Village, Pingquan City, Hebei Province. **A**, A whole carapace, right valve, holotype, NIGP204101. **B**, Gathered punctae at the mid-anterior area of carapace, NIGP204098. **C**, Gathered punctae transform to linear arrangements at the anterior-median area of the carapace, NIGP204102. **D**, Enlargement of linear arrangements of punctae at the median area of carapace, NIGP204097. **E**, Linear arrangements of punctae at the anterior median area of carapace, NIGP204103. **F**, Linear arrangements transform to lirae at the ventral marginal area of the carapace, NIGP204103. Scale bars = 1 mm in (A), 50 μ m in (B, D, E), and 100 μ m in (C, F).

Measurements.

Specimen	Fig.	Growth bands number	L (mm)	H (mm)	H/L
NIGP204096, paratype	4D	>30	8.80	6.67	0.76
NIGP204098, paratype	4F	>25	7.80	5.48	0.70
NIGP204097, paratype	4E	>23	8.41	5.68	0.68
NIGP204101, holotype	7A	≈30	8.14	5.58	0.69
Non-type		>23	7.60	5.96	0.78

Remarks. The new species possesses a significantly larger carapace (average length≈8 mm; average height≈6 mm) and relatively more growth bands compared to all other species in the genus. Moreover, it is also distinguished from other species by its umbo which is located close to the median of the dorsal margin. This species is mainly ornamented with punctae, punctae linear arrangements, and radial lirae. This combination of characters makes it readily distinguished from *T. pingquanensis*, *T. haifanggouensis*, *T. yingziensis*, *T. luanpingensis*, *T. manasica* Wang, 1985, *T. tianshanensis* Wang, 1985, *T. ovata* Wang, 1985, *T. yingzuigouensis* Wang, 1985, *T. eedemtensis* Li *et al.*, 2014, and *T. yabraiensis* Wang, 2014, which possess prominent and abundant reticulations formed by gathered punctae but lacks well-developed radial lirae on their carapaces. Its well-developed linear arrangements and radial lirae resemble the ornamentations of *T. jianchangensis* Wang, 2014 and *T. jiyuanensis* Liao & Huang, 2023. But it possesses several gathered punctae at the mid-anterior to the median ventral areas, which are not prominently observed on the carapace of *T. jianchangensis* and *T. jiyuanensis*. Considering that this species was found in the uppermost layer of the Middle Jurassic Longmen Formation, we believe its ornamentation might represent a transitional type from the latest Middle Jurassic to the earliest Late Jurassic.

Conclusion

Triglypta pingquanensis is reported in the Middle Jurassic Daohugou beds near to Zhujiagou and Jiangzhangzi localities. This discovery reinforces the previous notion that the Haifanggou Formation can be correlated to the Longmen Formation. In addition, a new species *T. hebeiensis* Liao & Huang **sp. nov.** is described from the uppermost layer of the Longmen Formation. The clam shrimp assemblage from Daohugou serves as a crucial link for correlating the Haifanggou and Longmen formations. The clam shrimp of the Haifanggou and Longmen formations in northern Hebei, western Liaoning and Inner Mongolia comprise five species: *T. haifanggouensis*, *T. pingquanensis*, *T. yingziensis*, *T. luanpingensis*, and *T.*

hebeiensis Liao & Huang **sp. nov.** These species constitute the early clam shrimp assemblage of the Yanliao biota and are distinctly different to the late assemblage from the Tiaojishan Formation.

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