



## Revising some fossil clam shrimps (Branchiopoda: Diplostraca: Spinicaudata) from the Upper Triassic in Yunnan Province and Chongqing City, southwestern China

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### Abstract

Abundant Triassic spinicaudatans from China have been commonly assigned to the genus *Euestheria* Depéret & Mazeran. However, recent SEM-based studies have revealed that many of them do not belong to euestherids, as evidenced by their distinctive micro-ornamentations, revealed by scanning electron microscopy (SEM). In this study, we describe two spinicaudatan species, *Polygrapta yipinglangensis* **comb. nov.** and *P. dazuensis* **comb. nov.**, which were previously identified as members of *Euestheria* from the Upper Triassic Ganhaizi and Xujiahe formations in south-western China. The carapace ornamentations of these species exhibit fine polygonal reticulations in the upper parts, which gradually transform to linear arrangements and radial lirae at the ventral regions. Based on these features, they are classified into *Polygrapta* Novojilov. Although the two species exhibit morphological similarities, they can be distinguished by variations in reticulation size and the width of linear arrangements in their marginal areas.

**Key words:** conchostracan, *Polygrapta*, *Euestheria*, Crustacea, Euestheridae

### Introduction

Clam shrimps, commonly known as “conchostracans,” are large branchiopod crustaceans. Global fossil records demonstrate that their evolutionary history can be traced back to the Early Devonian (Emsian) (Gross, 1934; Maillieux, 1939; Raymond, 1946; Defretin, 1950; Novojilov, 1961; Cuvelier *et al.*, 2015; Hegna & Astrop, 2020; Liao & Shen, 2022). As one of the most common

and representative invertebrates in non-marine strata, they possess significant biostratigraphic value (*e.g.*, Novojilov, 1946; Zhang *et al.*, 1976; Chen & Shen, 1985; Kozur & Weems, 2010; Ghosh, 2011; Gallego *et al.*, 2020; Li, 2020; Liao & Shen, 2022).

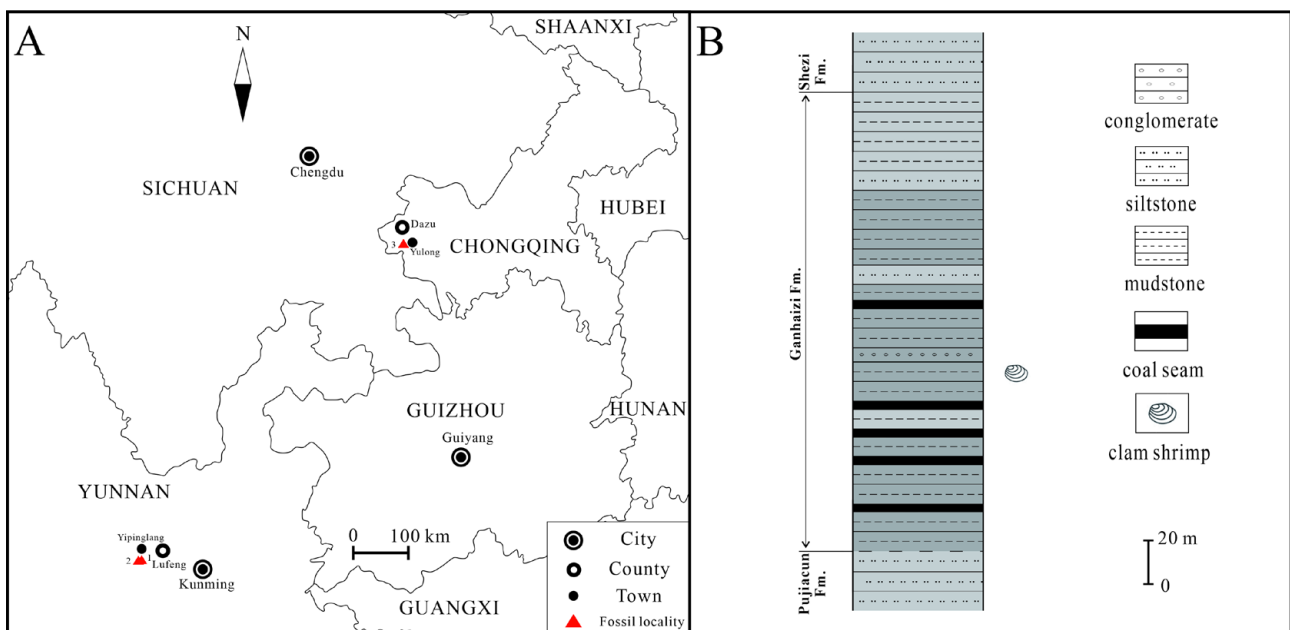
The genus *Euestheria* Depéret & Mazeran, 1912 represents the most prevalent taxon in the Mesozoic of China (Zhang *et al.*, 1976; Fang & Liao, 2024). The type species, *E. minuta* Zieten, 1833 from the Triassic of Germany, is characterized by an oval carapace ornamented with small reticulations (Depéret & Mazeran, 1912; Gross, 1934; Reible, 1962; Chen & Shen, 1985; Geyer & Kelber, 2018). This genus has been widely recognized in various regions, including China, the Germanic Basin of Germany, the Moscow Basin of Russia, and the Gondwana Basin in India (Zhang *et al.*, 1976; Ghosh, 2012; Scholze *et al.*, 2015; Scholze *et al.*, 2016; Geyer & Kelber, 2018). Previous studies on these clam shrimps were primarily conducted under optical microscopy, often failing to adequately identify the micro-ornamentations, particularly in small, poorly-preserved specimens. Consequently, numerous specimens with non-reticulate or unknown ornamentations were classified as *Euestheria* based solely on their small oval carapaces, fine growth lines, and small larval valves, rendering the genus a taxonomic “dumping ground” (Raymond, 1946; Fang & Liao, 2024).

The taxonomic “dumping ground” issue of *Euestheria* has become increasingly apparent in recent years (*e.g.*, Liao *et al.*, 2014; 2017, 2023; Liao, 2022; Huang, 2015; Huang & Cai, 2017). *Euestheria* and *Polygrapta* Novojilov, 1946 exhibit remarkable similarities in carapace size and shape, complicating their differentiation when ornamentation details are obscure or absent. The type species, *Polygrapta chatangensis*

Novojilov, 1946, was first discovered from the Upper Permian Tatarian (upper Guadalupian–Lopingian) on the southern coast of Khatanga Bay, north-eastern Russia (Novojilov, 1946; Okuyucu *et al.*, 2017; Li, 2020). This species possesses a small, oval carapace with small reticulations on the upper portion and radial lirae on the middle-ventral portion (Li, 2020). *Polygrapta* has been widely documented from various regions and periods, including the upper Permian in Liaoning Province (Shen & Li, 1986) and Xinjiang Uygur Autonomous Region (Liu, 1985, 1987, 1993), the Lower and Middle Triassic in Shanxi Province (Wang & Liu, 1980; Shen *et al.*, 1982), the Upper Triassic in Sichuan Province (Zhang *et al.*, 1976), and the Upper Triassic in Chile (Gallego 2005).

Through scanning electron microscopy (SEM) analysis of “*Euestheria*” specimens from the Upper Triassic Ganhaizi Formation (Yunnan Province) and Xujiahe Formation (Chongqing City), we demonstrate that these specimens should be taxonomically reassigned to *Polygrapta* based on diagnostic ornamentations.

Sheng *et al.* (1962) reclassified the three members from the bottom to top as the Pujiacun Formation, Ganhaizi Formation, and Shezi Formation. Among these, the Ganhaizi Formation represents the main coal-bearing strata among the three formations. It overlies conformably the Pujiacun Formation and is conformably overlain by the Shezi formation (Nanjing Institute of Geology and Palaeontology, 1975; Yunnan Provincial Bureau of Geology and Mineral Resources of Yunnan Province, 1990). This formation consists of a set of non-marine clastic sediments, predominantly composed of grey and yellow-greenish siltstones inter-bedded with coarse sandstones, mudstones, shales, and coal seams, representing an inland river, lake, and swamp environments. The age of the Ganhaizi Formation has been determined to be from the Norian to Rhaetian (Yunnan Provincial Bureau of Geology and Mineral Resources, 1996). Abundant bivalves, ostracods, clam shrimps, insects, and plants have been documented in the formation (Yunnan Provincial Bureau of Geology and Mineral Resources, 1996). The plant



**FIGURE 1.** Map of the fossil localities and the column of the Ganhaizi Formation in Yipinglang Town, Lufeng City, Yunnan Province. **A.** Map of the fossil localities: 1, Dawo locality; 2, Xingwujing locality; 3, Yulong locality. **B.** Column of the Ganhaizi Formation.

## Geological setting

The Yipinglang Coal Measure (or Yipinglang Formation), initially proposed by Wang & Lu (1936), comprises a series of Late Triassic coal-bearing sediments primarily distributed in Yimen County, Yuxi City and Yipinglang Town, Lufeng City, in central Yunnan Province, south-west China. Chen (1943) divided the Yipinglang Coal Measure into three members from the bottom to top.

assemblage of the formation is recognized as a part of the well-known Yipinglang flora. This flora, geographically constrained and floristically characterized, was formally defined as a biostratigraphic unit by Lee *et al.* (1976), who systematically described more than 60 plant species in 34 genera from the Yipinglang Coal Field. It is an important representative of the “southern type” flora (*Dictyophyllum-Clathropteris* flora) of the Late Triassic in southwestern China. Clam shrimps were predominantly

preserved in the greyish black mudstones in the middle part of the formation (Fig. 1). These fossils were originally identified as *Euestheria* in previous studies (Chen, 1974; Zhang *et al.*, 1976), and this taxonomic assignment has been widely accepted in later studies.

The Xujiuhe Formation, spanning from the Norian to Rhaetian (Lee, 1964; Wu, 1983; Sun *et al.*, 1995; Wu, 1999), comprises a series of coal-bearing fluvial-lacustrine sediments predominantly composed of yellow and grey sandstones, grey mudstones, and black carbonaceous shales (Wang *et al.*, 2010). The formation is extensively distributed in the Sichuan Basin. In Chongqing, the Xujiuhe Formation overlies the Middle Triassic Leikoupo Formation and is conformably overlain by the Lower Jurassic Zhenzhuchong Formation (Wang *et al.*, 2010). Clam shrimps from the Xujiuhe Formation studied herein were collected from the Yulong Subdistrict, Dazu District, Chongqing City (Fig. 1). The Xujiuhe Formation is particularly notable for its abundant fossil assemblages, including diverse clam shrimps, bivalves, and plants (Wang *et al.*, 2010). The plant fossils constitute a typical “southern-type” flora (*Dictyophyllum-Clathropteris* flora) of the Late Triassic in southwestern China, which is also called the “Xujiuhe flora” (Lee, 1964; Wu, 1983; Sun *et al.*, 1995; Wu, 1999). The Xujiuhe flora and the Yipinglang flora are considered to be of the same age (Lee, 1964; Wu, 1983; Sun *et al.*, 1995; Wu, 1999).

## Material and methods

Specimens of *Polygrapta yipinglangensis* **comb. nov.** were collected from the greyish black mudstones in the middle part of the Ganhaizi Formation at Xingwujing and Dawo near Yipinglang Town, Lufeng City, Yunnan Province (Fig. 1). A total of hundreds of individuals preserved on tens of rock surfaces were collected (Fig. 2E–H). Additionally, type specimens of the species from the Ganhaizi Formation in Yipinglang Town (Chen, 1974; Zhang *et al.*, 1976) were re-examined. However, no well-preserved ornamentation was found on these specimens. The type specimen of *P. dazuisensis* **comb. nov.** (Accession Number: NIGP20022) was collected from an unknown horizon of the Xujiuhe Formation near Yulong Subdistrict, Dazu District, Chongqing City (Fig. 1; Zhang *et al.*, 1976). All the specimens with NIGP accession numbers are housed in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (Nanjing, Jiangsu Province, China). These specimens, which have been previously described by Chen (1974) and Zhang *et al.* (1976), are designated as type specimens. Furthermore, specimens marked with the YNUPB are all housed at the Palaeobotanical Collections of the Institute

of Palaeontology, Yunnan University (Kunming, Yunnan Province, China).

For pre-experiment preparation, selected specimens from Yipinglang were soaked in a saturated ammonium chloride solution. This treatment effectively lightened the colour of the otherwise dark fossils, significantly improving their visibility for observation and microscopic photography. For morphological analysis, a Zeiss Discovery V20 microscope was used to examine and photograph the outline and macroscopic features of the specimens, while a Thermo Scientific Quattro S scanning electron microscope (SEM) was employed to investigate and document the micro-ornamentations.

## Systematic palaeontology

**Class Branchiopoda Latreille, 1817**  
**Order Diplostraca Gerstaecker, 1866**  
**Suborder Spinicaudata Linder, 1945**  
**Familiy Polygraptidae Novojilov, 1954**

### **Genus *Polygrapta* Novojilov, 1946**

**Type species.** *Polygrapta chatangensis* Novojilov, 1946, from the upper Permian Tatarian (upper Guadalupian–Lopingian), on the southern coast of the Khatanga Bay, northeastern Russia.

**Diagnosis.** Carapace large and oval in outline, ornamented with both single and branching radial striae, striae made up of tightly packed particles; interval between striae also ornamented with particles. The ribs of each growth band are separated by growth marks (Novojilov, 1946).

**Emended 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 (Li, 2020).

### ***Polygrapta yipinglangensis* **comb. nov.****

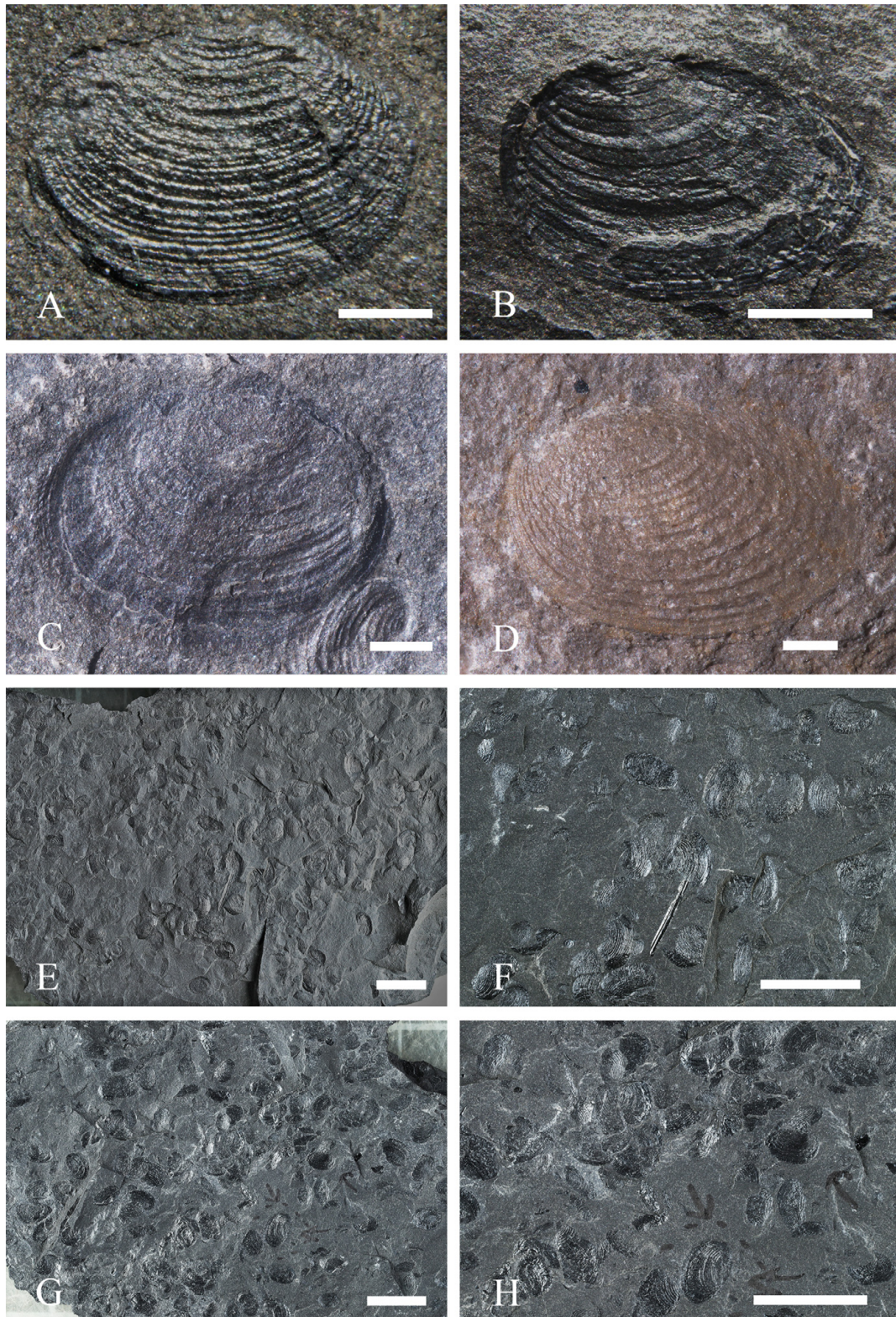
(Figs 2A–C, E–H, 3)

1974 *Euestheria yipinglangensis* Chen, p. 319, pl. 170, fig.3 in Chen, 1974

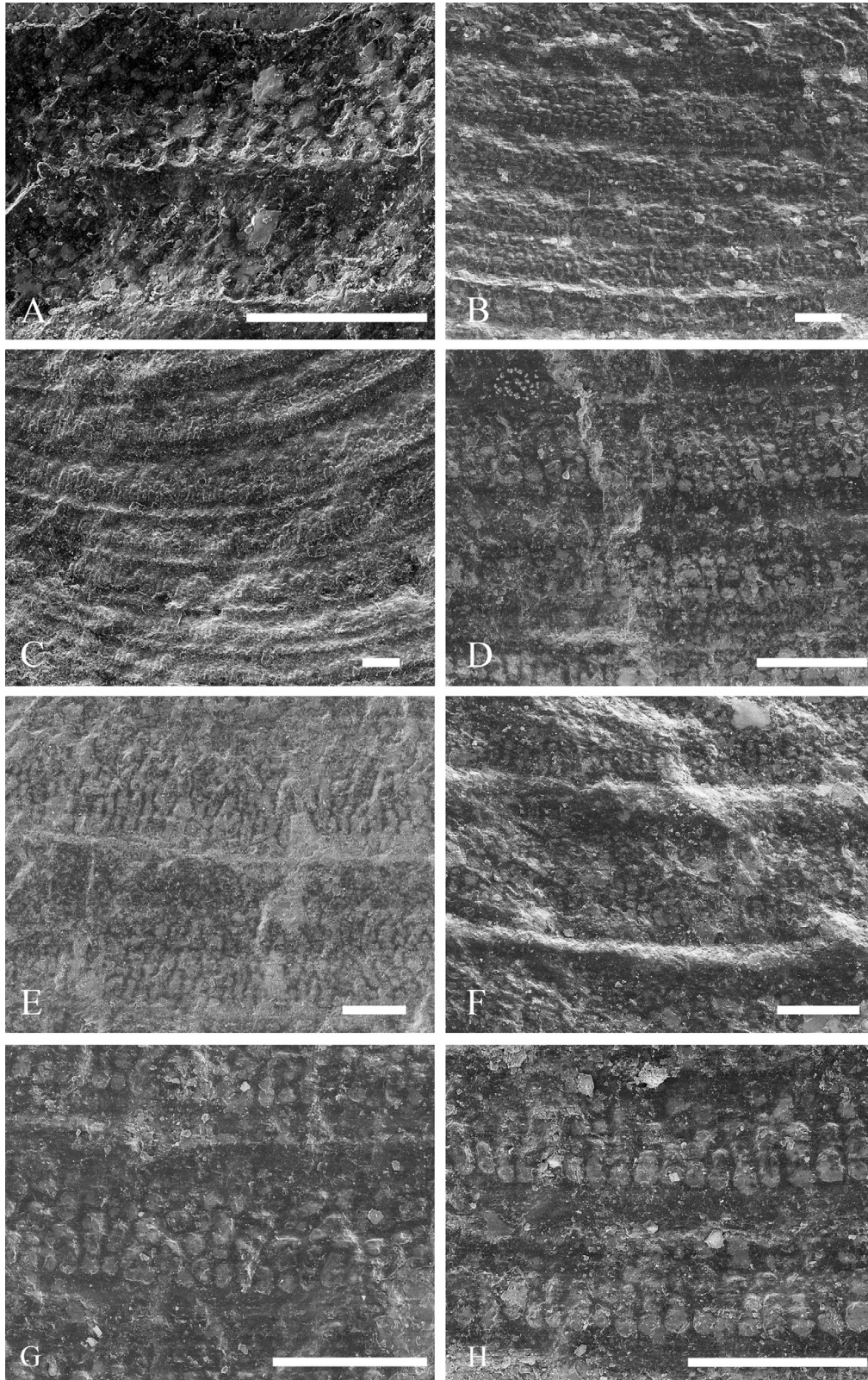
**Material.** NIGP26935, YNUPB20003–20012

**Locality and horizon.** Middle fossil-bearing layers of the Upper Triassic Ganhaizi Formation in Dawo and Xingwujing, Lufeng City, Yunnan Province.

**Description.** Carapace 3–5 mm in length (L), 2.5–4 mm in height (H), oval to elliptical in outline; growth bands 20–25 in number; larval valve small; dorsal margin



**FIGURE 2.** Carapaces of *Polygrapta yipinglangensis* **comb. nov.** (A–C, E–H) and *P. dazuensis* **comb. nov.** (D). **A**, An individual (right valve) from the Ganhaizi Formation at Dawo locality near to Yipinglang Town, Lufeng City, Yunnan Province (YNUPB20003). **B**, An individual (left valve) from the Ganhaizi Formation at Xingwujing locality near to Yipinglang Town, Lufeng City, Yunnan Province (YNUPB20004). **C**, An individual (right valve) from the Ganhaizi Formation in Yipinglang Town, Lufeng City, Yunnan Province (NIGP26935). **D**, An individual (left valve) from the Xujiahe Formation in Yulong Subdistrict, Dazu District, Chongqing City (holotype, NIGP20022). **E**, Abundant individuals densely preserved on greyish black mudstones of the Ganhaizi Formation at Dawo locality (YNUPB20005). **F**, Enlargement of **E**. **G**, Abundant individuals densely preserved on greyish black mudstones of the Ganhaizi Formation at Xingwujing locality (YNUPB20006). **H**, Enlargement of **G**. Scale bars = 1 mm in (A–D) and 10 mm in (E–H).

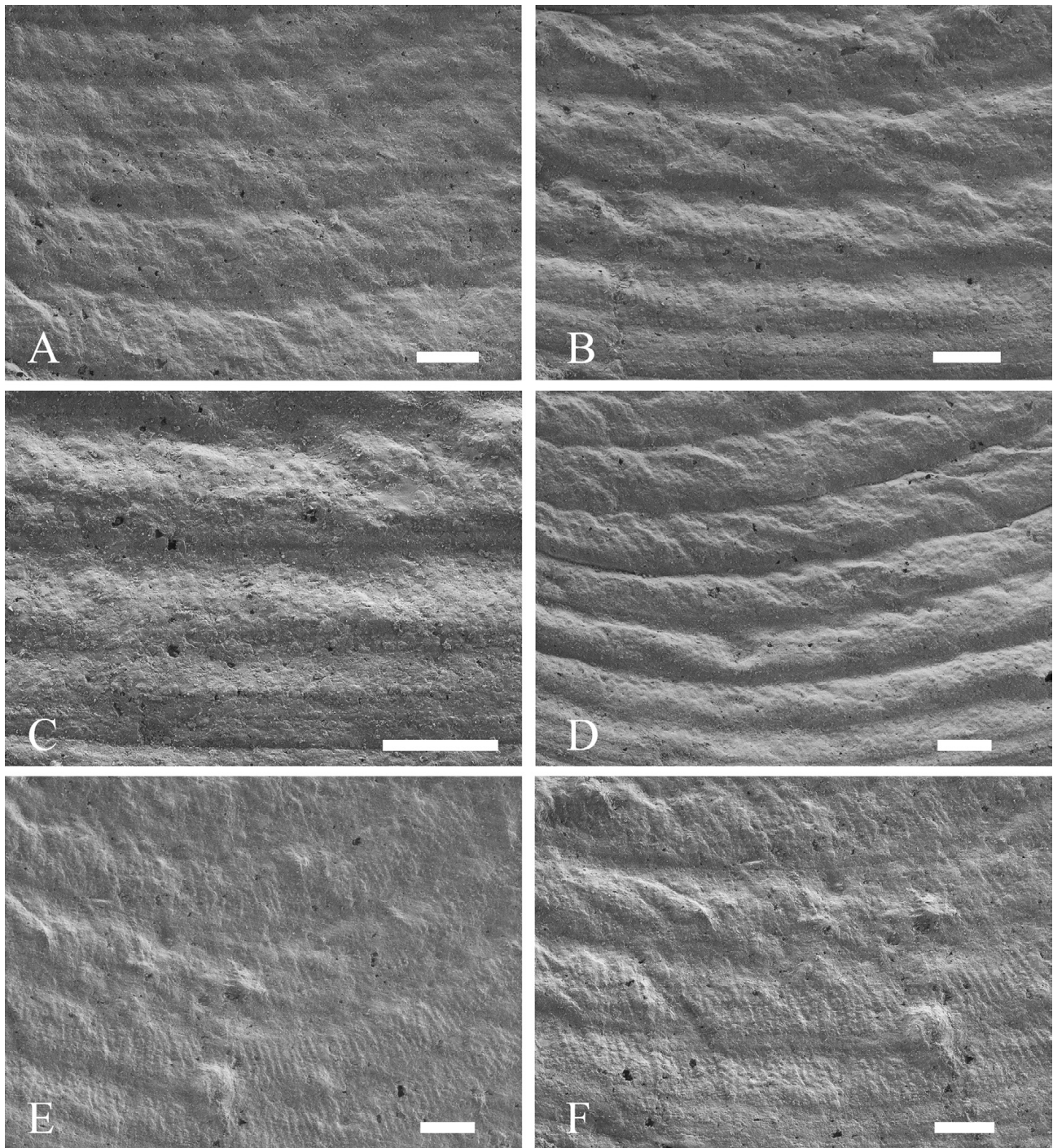


**FIGURE 3.** Ornamentations on the carapaces of *Polygrapta yipinglangensis* **comb. nov.** from the Ganhaizi Formation at Dawo (A–E, G–H) and Xingwujing (F) localities near to Yipinglang Town, Lufeng City, Yunnan Province. **A**, Reticulations at the upper part of the carapace, YNUPB20007. **B**, Reticulations at the upper to middle part of the carapace, YNUPB20008. **C**, Linear arrangements of reticulations at the anteroventral part of the carapace, YNUPB20009. **D**, Linear arrangements of reticulations at the ventral part of the carapace, YNUPB20010. **E**, Linear arrangements of reticulations at the posterior part of the carapace, YNUPB20010. **F**, Linear arrangements at the anteroventral part of the carapace, YNUPB20011. **G**, Linear arrangements at the posteroventral part of the carapace, YNUPB20012. **H**, Linear arrangements at the posterior part of the carapace, YNUPB20012. Scale bars = 100  $\mu$ m.

long and straight, slightly arched; umbo situated between the median and antero-terminal of the dorsal margin; anterior and ventral margins rounded (Fig. 2A–C); growth bands at the upper part ornamented with small polygonal reticulations (Fig. 3); reticulation approximately 15  $\mu\text{m}$  in diameter (Fig. 3D, G, H); growth bands near the middle-ventral parts ornamented with linear arrangements

of reticulations or lirae (Fig. 3C, D, G, H); each linear arrangement generally formed by a single row of 4 to 9 small reticulations longitudinally; lirae formed by intervals between linear arrangements (Fig. 3D, E, G, H).

**Remarks.** This species differs from the type species of the genus, *P. chatangensis*, from the upper Permian in Russia, in its carapace size, and characteristic of



**FIGURE 4.** Ornamentations on the carapace of *Polygrapta dazuiensis* **comb. nov.** from the Xujiache Formation in Yulong Subdistrict, Dazu District, Chongqing City, NIGP20022. **A**, Reticulations and linear arrangements of reticulations at the middle part of the carapace. **B**, Linear arrangements at the ventral part of the carapace. **C**, Linear arrangements of reticulations at the ventral-marginal part of the carapace. **D**, Linear arrangements at the anterior part of the carapace. **E**, Linear arrangements at the posterior part of the carapace. **F**, Linear arrangements at the postero-ventral part of the carapace. Scale bars = 100  $\mu\text{m}$ .

reticulations and linear arrangements. The carapace of this species is obviously smaller than that in *P. chatangensis*. The reticulations at the upper to middle parts of this species (approximately 15 µm in diameter) are generally smaller than those of *P. chatangensis* (15–30 µm in diameter; Li, 2020). Nevertheless, reticulations that form linear arrangements at the middle to lower parts of this species (approximately 15 µm in diameter) are generally bigger than those of *P. chatangensis* (6–10 µm in diameter; Li, 2020). In addition, each linear arrangement of this species is formed by a single row of 4 to 9 small reticulations, while the maximum reticulation number of *P. chatangensis* that formed the linear row could reach to 16. The ornamentation pattern of this species is similar to the genus *Anyuanestheria* Zhang & Chen, 1976 (in Zhang *et al.*, 1976) in some degree. Both of them possess reticulations and linear arrangements on their growth bands. However, the reticulation diameter of *Anyuanestheria* is generally much larger (up to about 80 µm; Li, 2023) and more irregularly arranged, and shows a greater variation in size within the same individual. Additionally, on each growth band of the ventral part of *Anyuanestheria*, the upper part displays linear ornamentations while the lower part features reticulations (Li, 2023). This characteristic was not observed on our specimens. Li (2020) mentioned that on the upper edge of each growth line (or the lower edge of each growth band) of *P. chatangensis*, there is a distinct ridge formed by the connection of crossbars of reticulations. However, such ridge was not observed in our specimens. Specimens of Li (2020) were collected from the Triassic of the Ordos Basin and exhibit well-preserved chitinous layers, whereas the specimens in this study are poorly preserved, lacking well-preserved chitinous layers. This is likely the primary reason why the ridge was not observed in our specimens.

***Polygrapta dazuensis* comb. nov.**

(Figs 2D, 4)

1974 *Euestheria dazuensis* Chen, p. 318, pl. 170, fig.6.

**Material.** Holotype NIGP20022, housed in Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences.

**Locality and horizon.** Middle fossil-bearing layers of the Upper Triassic Xujiahe Formation in Yulong Subdistrict (Town), Dazu District, Chongqing City.

**Description.** Carapace medium in size with an elliptical outline, 3.5 mm in length (L) and 2.5 mm in height (H), with 21 growth bands; dorsal margin straight, slightly arched; larval valve small; umbo situated between the median and antero-terminal of the dorsal margin; anterior and ventral margins rounded (Fig. 2D); growth

bands near the upper part ornamented with small polygonal reticulations (Fig. 4); reticulations approximately 20 µm in diameter (Fig. 4A–C); growth bands near the middle and ventral parts ornamented with linear arrangements of reticulations or lirae (Fig. 4B, D, E, F); each linear arrangement generally formed by a single row of 4–7 small reticulations arranged longitudinally; lirae formed by intervals between linear arrangements (Fig. 4B, C, E, F).

**Remarks.** This species can be distinguished from *Polygrapta yipinglangensis* **comb. nov.** primarily by its umbo position being closer to the median of the dorsal margin and its strongly posteriorly expanded posteroventral margin. In addition, compared with *P. yipinglangensis* **comb. nov.**, its reticulations are larger, and its linear arrangements near the posteroventral margin are much more developed.

## Discussion

*Euestheria* is one of the most widely distributed taxa that has been documented across all seven continents. Its type species, *E. minuta* Zieten, 1833, from the Triassic of Germany, is characterized by an oval carapace ornamented with minute polygonal reticulations (or irregular lirae). Early investigations of clam shrimps in most previous studies were primarily predominately relied on optical microscopy, which often failed to reveal the micro-ornamentations, particularly in small, poorly-preserved specimens. As a result, numerous species exhibiting non-reticulate or indeterminate ornamentations were indiscriminately assigned to *Euestheria* based solely on their small oval carapaces, fine growth lines, and diminutive larval valves, thereby rendering the genus a taxonomic “dumping ground” (Raymond, 1946; Fang & Liao, 2024). Recent studies based on SEM have revealed that an increasing number of purported ‘euestherids’ actually possess diverse non-reticulate ornamentations that markedly different from the reticulate patterns observed in the type species. This has led to significant taxonomic revisions, particularly among the Jurassic euestherids from China, which have been systematically emended and reassigned into several genera, including *Qaidamestheria* Wang, 1983; *Tianzhuestheria* Shen, Li & Chen, 2002; and *Triglypta* Wang, 1984. These re-classifications have been accompanied by substantial modifications to their taxonomic status and morphological descriptions (Wang, 2014; Liao *et al.*, 2017; Zhang *et al.*, 2017; Li, 2022; Liao, 2022; Liao *et al.*, 2023).

Clam shrimps are widely distributed in non-marine sediments of the Triassic in China. Many of them possess small oval carapaces, and have been traditionally classified

as *Euestheria* (e.g., Chen, 1974; Zhang *et al.*, 1976; Wang & Liu, 1980; Wang *et al.*, 2010; Fang & Liao, 2024). Numerous clam shrimps from the Upper Triassic Ganhaizi and Xujiuhe formations were previously assigned to *Euestheria* (Chen, 1974; Zhang *et al.*, 1976). Species from the Ganhaizi Formation include *E. yipinglangensis* (Chen, 1974), *E. minuta* (Zhang *et al.*, 1976), and *E. lata* (Zhang *et al.*, 1976), while species from the Xujiuhe Formation include *E. dazuensis* (Chen, 1974), *E. tianquanensis* (Zhang *et al.*, 1976), *E. atsuensis* (Zhang *et al.*, 1976), and *E. yanjingxiensis* (Zhang *et al.*, 1976), respectively. In this study, we re-examined the *Euestheria* specimens from the Upper Triassic Ganhaizi and Xujiuhe formations of Yunnan Province and Chongqing City, southwestern China, using SEM. Our investigation revealed that all specimens exhibit polygonal reticulations and linear arrangements of reticulations or lirae on their growth bands. These diagnostic characters provide compelling evidence for their taxonomic reclassification into *Polygrapta*, rather than their previous assignment to *Euestheria*.

*Polygrapta yipinglangensis* **comb. nov.** represents the only known species in the Ganhaizi Formation at Xingwujing and Dawo in Yipinglang Town, Lufeng City, Yunnan Province. *P. dazuensis* **comb. nov.** is a predominant species of the Xujiuhe Formation in Yulong Subdistrict (Town), Dazu District, Chongqing City. Despite our re-examination of the type specimens of *E. tianquanensis* and *E. yanjingxiensis* from Dazu, the carapaces unfortunately lack diagnostic ornamentation features. *Polygrapta* is widely distributed geologically and chronologically. Its type species, *P. chatangensis*, was initially described from the upper Permian of Russia (Novojilov, 1946). Subsequent records of this genus have also been documented from the upper Permian and Triassic in China (Zhang *et al.*, 1976; Shen & Li, 1986; Liu, 1985; Wang & Liu, 1980; Shen *et al.*, 1982) and the Upper Triassic in Chile (Gallego *et al.*, 2005). Extensive studies have consistently demonstrated that the carapace of this genus possess reticulations, with linear arrangements and lirae formed by these reticulations (Liu, 1985; Gallego *et al.*, 2005; Li, 2020).

The earliest known record of *Polygrapta* in China is represented by two species from the upper Permian Wutonggou Formation in Dalongkou, Jimsar County, Xinjiang (Liu, 1985). Our study indicates that Triassic euestherids in China, similar to the Jurassic species, may require significant taxonomic revisions. A comprehensive taxonomic reassessment is urgently required to advance our understanding of Triassic clam shrimp diversity and to facilitate global stratigraphic correlations. The two emended species exhibit strikingly similar morphological characters, providing critical evidence to support the stratigraphic correlation between their respective host

formations. This conclusion aligns with the latest stratigraphic framework of the Triassic in China that the Ganhaizi Formation correlates with the lower part of the Xujiuhe Formation (Tong *et al.*, 2019).

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