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First discovery of the spinicaudatan genus *Carapacestheria* Shen, 1994 in Asia

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Abstract. The rare clam shrimp (spinicaudatan) genus *Carapacestheria* Shen, 1994 was originally described from the upper Lower–lower Middle Jurassic of Antarctica. Later, it was reported from the Middle Jurassic of Argentina and the lowest Cretaceous of the United Kingdom. Here, a new species, *Carapacestheria cangshanensis* sp. nov., is described from the Upper Jurassic Penglaizhen Formation in southwestern China. The subquadrate-shaped carapace of the new species has a distinct ornamentation pattern, which transitions from medium-sized reticulations to radial lirae. There are punctae within the polygonal cells and between the lirae. According to its geological range and geographical distribution, *Carapacestheria* first occurred in Antarctica, and later appeared in the northern hemisphere during the Late Jurassic.

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Introduction

Clam shrimp, previously called conchostracans, are large branchiopod crustaceans, with a laterally compressed body enclosed by a bivalved chitinous or complex chitin-mineral carapace (Tasch, 1969; Astrop and Hegna, 2015; Hegna *et al*., 2020). Recent clam shrimp live in seasonally astatic wetlands, such as playas, vernal pools, rice fields or fishless lakes (Brendonck *et al*., 2008; Li, 2017a), and can be found on all continents except Antarctica. These living habitats are consistent with their relatively short life cycles; *Eulimnadia texana*, for example, finish their life cycles within two or three weeks (Chen and Shen, 1985). As a result, they have been, and continue to be, successful colonizers of ephemeral freshwater ecosystems that alternate between wet and dry conditions in the Earth's history. Fossil clam shrimp are commonly abundant and diverse in lacustrine deposits, and thus can be useful for biostratigraphic subdivision and correlation of nonmarine successions (Chen *et al*., 2007; Ando *et al*., 2011; Li and Matsuoka, 2012; Li *et al*., 2014, 2016; Boukhalfa *et al*., 2015; Olsen, 2016; Zhang *et al*., 2017; Scholze *et al*., 2019; Gallego *et al*., 2020; Li, 2020a).

The clam shrimp genus *Carapacestheria* Shen, 1994 was first described from the Lower and Middle Jurassic transition beds of Antarctica. Recently, it was recovered in the Middle Jurassic of Argentina (Monferran *et al*., 2020), and the lowest Cretaceous of the UK (Li *et al*., 2021). Some specimens of *Carapacestheria* were recently identified by T. A. Hegna from Africa (Liao, 2022). In this paper, the author reports the first discovery of *Carapacestheria* in the Upper Jurassic of southwestern China.

Geological setting

The well-developed non-marine Upper Jurassic and Lower Cretaceous red beds are widely distributed in the study area in the northern Sichuan basin of southwestern China (Figure 1). The Lower Cretaceous yields a *Chuanestheria* clam shrimp fauna (Figure 2), which occurs in three formations, in ascending order, the Cangxi, Bailong and Qiqusi formations [Shen and Chen, 1982; Wang and Zeng, 1982; Bureau of Geology and Mineral Resources of Sichuan Province (BGMRS), 1997]. The underlying Upper Jurassic yields an *Eosestheriopsis* clam

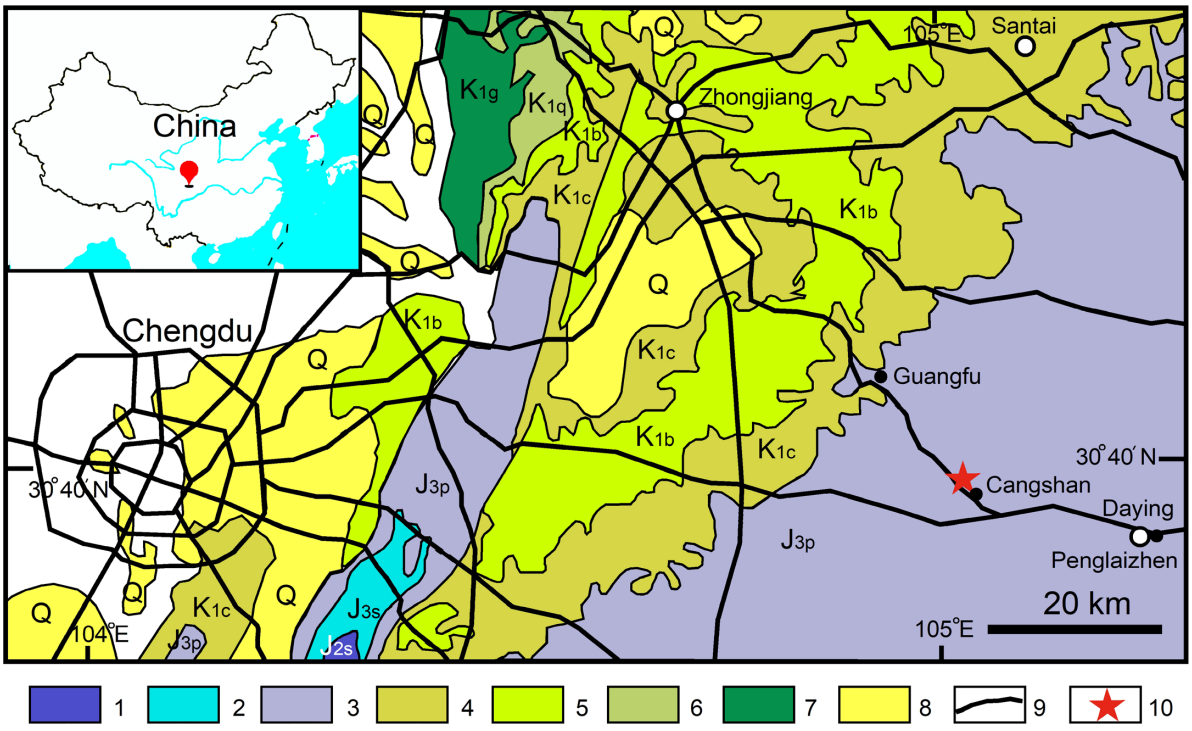

Figure 1. Geological map of the study area, showing the fossil clam shrimp locality (after BGMRS, 1991). 1, the Middle Jurassic Shaximiao Formation (J_{2s}); 2, the Upper Jurassic Suining Formation (J_{3s}); 3, the Upper Jurassic Penglaizhen Formation (J_{3p}); 4, the Lower Cretaceous Cangxi Formation (K_{1c}); 5, the Lower Cretaceous Bailong Formation (K_{1b}); 6, the Lower Cretaceous Qiqusi Formation (K_{1q}); 7, the Lower Cretaceous Gudian Formation (K_{1g}); 8, the Quaternary (Q); 9, a road; 10, the fossil clam shrimp locality.

Series	Formation	Clam shrimp fauna	
Lower Cretaceous	Gudian Fm		
	Qiqusi Fm	*Chuanestheria* fauna	
	Bailong Fm		
	Cangshan Fm		
Upper Jurassic	Penglaizhen Fm	*Eosestheriopsis* fauna	*Qinghaiestheria* assemblage
			Eosestheriopsis–Carapacestheria assemblage
	Suining Fm		*Suiningestheria* assemblage

Figure 2. The lithostratigraphic subdivision and clam shrimp faunas of the Upper Jurassic and the Lower Cretaceous of the study area in northern Sichuan Province, southwestern China (after Shen and Chen, 1982; BGMRS, 1991; Li, 2004). Fm: Formation.

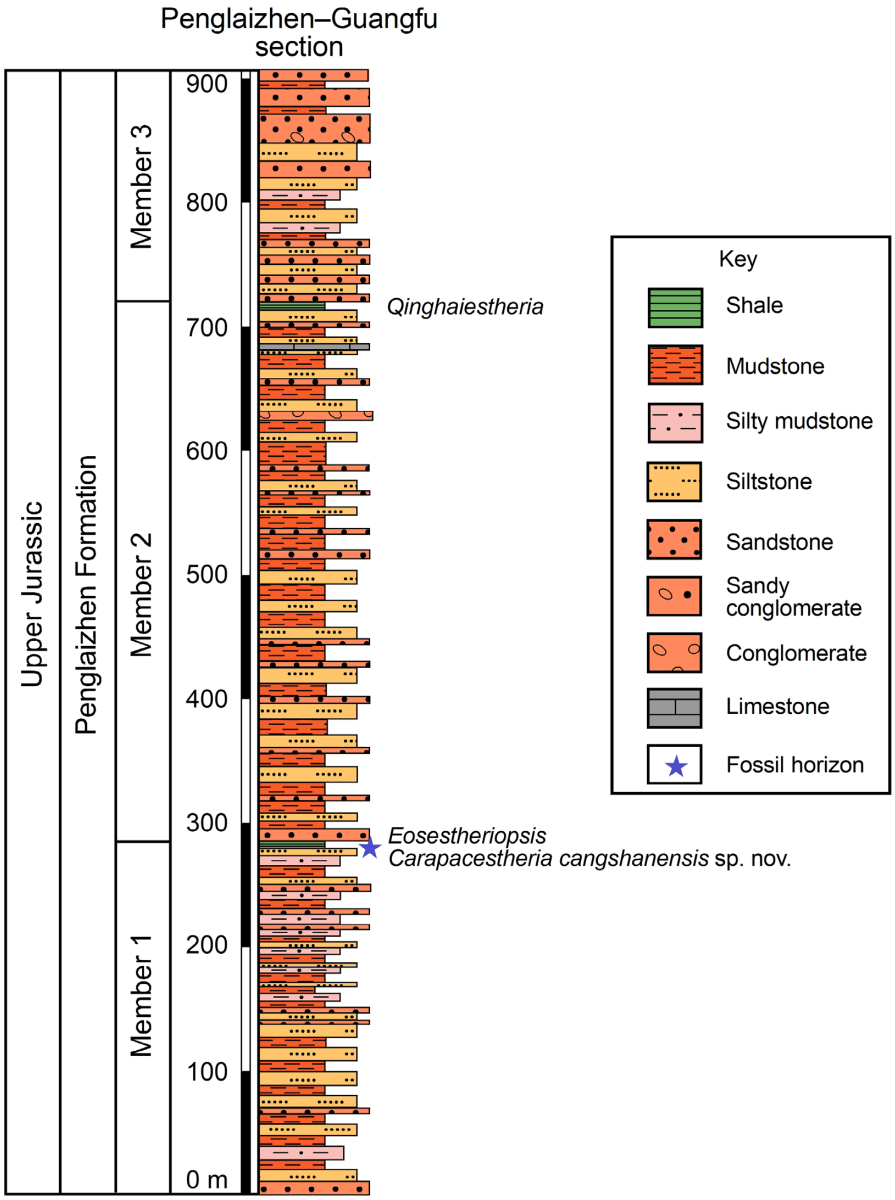

Figure 3. Columnar section of the Penglaizhen Formation from Penglaizhen town of Daying County to Guangfu Town of Zhongjiang County in northern Sichuan Province, showing the clam shrimp fossil horizons (after Shen and Chen, 1982; Xia *et al*., 1982; Li, 2004).

shrimp fauna, which occurs in two formations, the lower the Suining Formation, and the upper the Penglaizhen Formation (Wang *et al*., 2010). The Suining Formation (200–600 m thick) consists of bright red mudstones and siltstones, yielding a *Suiningestheria* clam shrimp assemblage (Shen and Chen, 1982; BGMRS, 1997). The Penglaizhen Formation is about 907 m thick along the type section from Penglaizhen of Daying County to Guangfu of Zhongjiang County (Figure 3). It is comprised of greyish purple sandstones interbedded with brownish red mudstones, intercalated with the yellowish green Cangshan shales in its lower part (yielding a *Eosestheriopsis–Carapacestheria* clam shrimp assemblage), and the Jingfuyuan shales in its upper part (yielding a *Qinghaiestheria* clam shrimp assemblage) (Figure 3) (Shen and Chen, 1982; Xia *et al*., 1982; Wang, 1983; Li, 2004, 2010).

Material and methods

The figured specimens were collected from the Cangshan shales at the top of the first member of the

Upper Jurassic Penglaizhen Formation in Cangshan town, Zhongjiang County, Sichuan Province, southwestern China (Figures 1, 3). The specimens were first prepared with needles in the laboratory, and then the carapace's delicate ornamentation was examined with a Zeiss V20 stereo light microscope and a LEO 1530 VP scanning electron microscope (SEM). Previous studies have shown that the taxonomically-important, delicate carapace microsculpture cannot be observed with a light microscope, but can be clearly seen under the SEM (Li, 2017b, c, 2020c, 2022a, b). The figured specimens are deposited in Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGPCAS).

Systematic palaeontology

The author follows the classification of spinicaudatans at the order and suborder level by Martin and Davis (2001). 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 and Shen, 1985). Scholze and Schneider (2015, table 1) proposed another system to describe the size of clam shrimp; however, the author finds that the tripartite category of Chen and Shen (1985) is easier 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

Diagnosis.—The carapace outline varies from cyziciform to cycladiform and telliniform. The umbo is small, located in the anterior or middle part of the dorsal margin. Growth bands in the dorsal part of the carapace are ornamented with polygonal reticulations, which can transition to various-sized reticulations, delicate punctae or radial lirae distally. The proportional carapace surface occupied respectively by reticulations and radial lirae is inversely related (Astrop and Hegna, 2015; Li, 2020b).

Remarks.—Chen and Shen (1985) included seven families in the superfamily Eosestherioidea, including Aquilonoglyptidae Novojilov, 1958a emend. Li, 2022a, Diestheriidae Zhang and Chen in Zhang *et al*., 1976, Eosestheriidae Zhang and Chen in Zhang *et al*., 1976, Euestheriidae Defretin-Lafranc, 1965, Loxomegaglyptidae Novojilov, 1958b emend. Li, 2020c, Orthothemosiidae Defretin, 1965, Ulugkemiida Novozhilov, 1958b. Later, seven other families were assigned to Eosestherioidea, such as Antronestheriidae Chen and Hudson, 1991, Nestoriidae Shen and Chen, 1984, Polygraptidae Novojilov, 1954 (Wang and Liu, 1980; Li, 2020b), Shipingiidae Kozur and Weems, 2005 emend. Li, 2022b, Triglyptidae Wang, 2014, Eosestheriopseiidae Niu in Niu *et al*., 2005, Jiliaoestheriidae Wang in Wang *et al*., 2004. The latter two families are characterized by having a row of small nodules along the upper margin of each growth line, but they differ in that eosestheriopseiids are small in size, while jiliaoestheriids have large carapaces (larger than 10 mm) (Niu and Xin, 2017). Further SEM morphological studies on these two families are needed in the future. Recently, Sun and Cheng (2022) also included Lioestheriidae Raymond, 1946 in Eosestherioidea in their fig. 8, but they neglected to comment in the text. In fact, after the revision of *Lioestheria* Depéret and Mazeran, 1912 by Kozur *et al*. (1981), the family Lioestheriidae was considered to include taxa with a large umbo, on which spines, nodules or fine ribs occur (Chen and Shen, 1985). Thus, it should not be assigned to Eosestherioidea.

Family Eosestheriidae Zhang and Chen in Zhang *et al*., 1976

Diagnosis.—The carapace size is small to very large. The ornamentation transitions from polygonal reticulations in the dorsal and/or antero-ventral part of the carapace to radial lirae in the ventral and/or postero-ventral part of the carapace. Polygonal cells small or large. Radial lirae fine or thick, sparse or dense, curving or branching, often intercalated with irregular short lirae. The proportional carapace surface occupied respectively by reticulations and radial lirae is inversely related (Gallego, 2010).

Remarks.—The family Eosestheriidae includes the following genera: *Abrestheria* Wang, 1981, *Allestheria* Shen and Chen in Shen *et al*., 1982, *Carapacestheria* Shen, 1994, *Eosestheria* Chen in Zhang *et al*., 1976, *Guiestheria* Shen, 1982, *Hardapestheria* Stigall in Stigall *et al*., 2014, *Menucoestheria* Gallego in Gallego and Covacevich, 1998, *Nothocarapacestheria* Rohn *et al*., 2014, *Shouchangestheria* Chen and Shen, 1982, *Turfanograpta* Novojilov, 1957, *Yanjiestheria* Chen in Zhang *et al*., 1976, *Yumenestheria* Shen and Chen in Shen *et al*., 1982.

Genus ***Carapacestheria*** Shen, 1994 here emended.

Type species.—*Cyzicus* (*Lioestheria*) *disgregaris* Tasch, 1987, from the Lower–Middle Jurassic Ferrar Group of Carapace Nunatak, Antarctica.

Included species.—*Carapacestheria disgregaris* (Tasch, 1987) emend. Shen, 1994, *C. balli* Shen, 1994, *C. taschi* (Vallati, 1986) emend. Monferran *et al*., 2020, and *C*.? *lulworthensis* Li *et al*., 2021.

Emended diagnosis.—Carapace small or moderate in size; elliptical, subovate, subcircular or subquadrate in

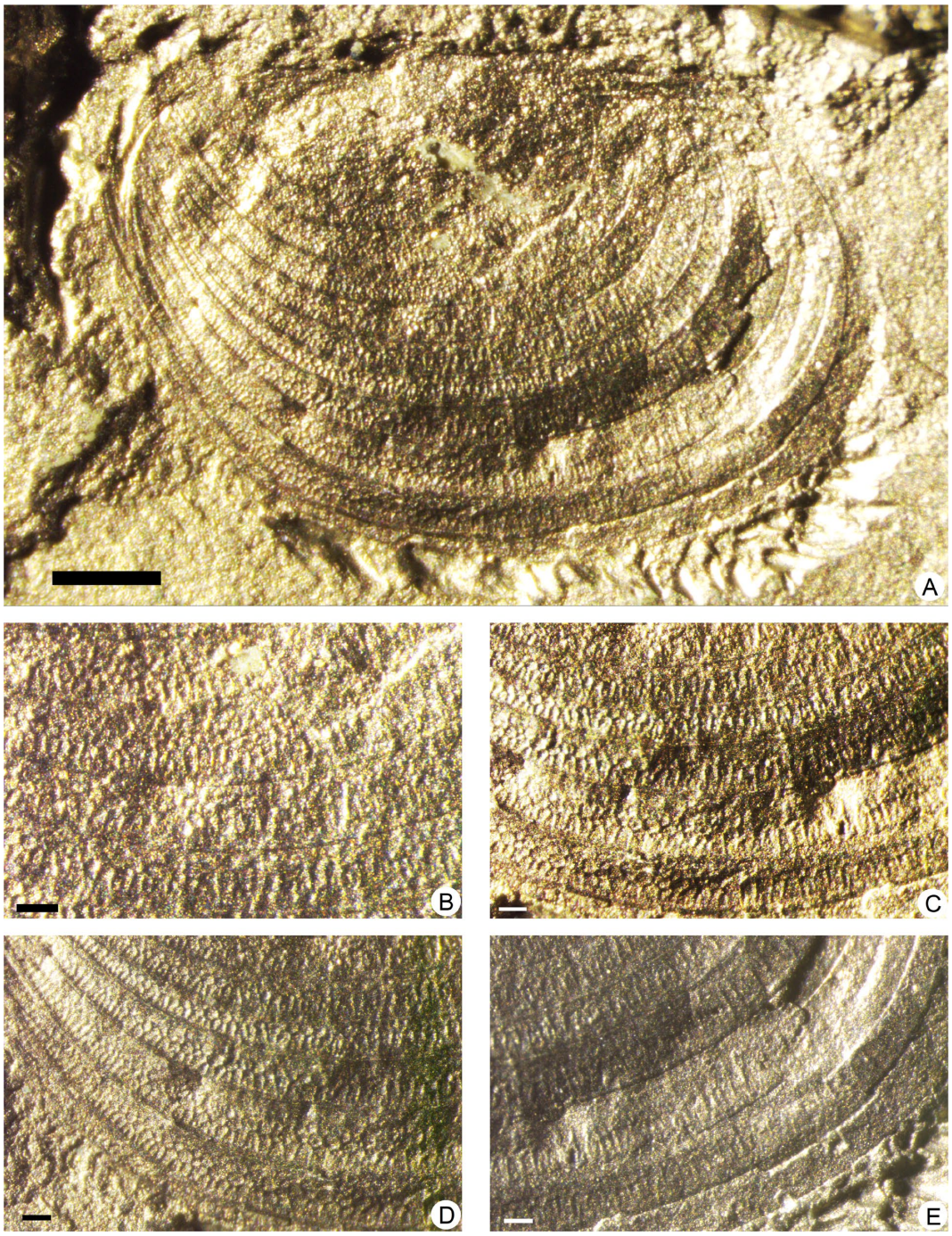

Figure 4. *Carapacestheria cangshanensis* sp. nov., holotype, left valve, NIGPCAS 180620, gold-coated. All figures are light microscopy images. **A**, whole specimen; **B**, reticulate-linear transition ornamentation in the middle part of the carapace, showing the fine polygonal reticulations in the upper part, which transform to radial lirae in the lower part of each growth band; **C**, reticulate-linear transition ornamentation in the ventral part of the carapace, showing the fine polygonal reticulations in the upper part, which transform to radial lirae in the lower part of each growth band; **D**, reticulate ornamentation on antero-ventral part of the carapace, showing the transition from polygonal reticulations in the upper part to radial lirae in the lower part of each growth band; **E**, the radial lirae on postero-ventral part of the carapace. Scale bars = 500 μm in A, 100 μm in B–E.

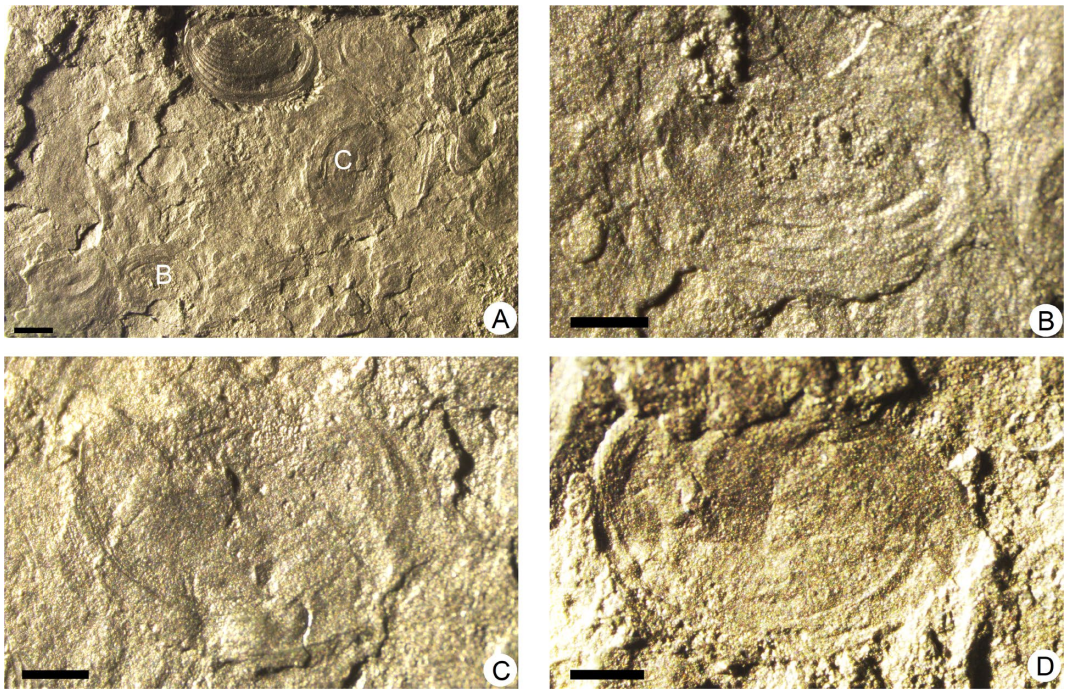

Figure 5. *Carapacestheria cangshanensis* sp. nov. All figures are gold-coated, light microscopy images. **A**, the slab contains the holotype specimen (upper middle), and the paratype specimens in B (lower left) and C (middle right); **B**, paratype, NIGPCAS 180620B, a poorly preserved left valve; **C**, paratype, NIGPCAS 180620C, a poorly preserved left valve; **D**, paratype, NIGPCAS 180620D, inner side of a right valve. Scale bars = 1 mm in A, 500 μm in B–D.

outline; growth bands ornamented with polygonal reticulations in the dorsal and antero-ventral parts of the carapace; growth bands in the ventral and postero-ventral parts of the carapace ornamented with radial lirae; carapace bearing a transitional area of two type of ornamentation; numerous minute punctae filling in polygonal cells and between the lirae; diameter of polygonal cells being 0.02–0.06 mm; radial lirae density about 30–40 per mm.

Remarks.—Shen (1994) described the genus *Carapacestheria* and mentioned that the mesh diameter is within the range from 0.02 to 0.36 mm, and the radial lirae density is about 40 per mm. In the newly described species, the diameter of some polygonal cells in the antero-ventral part of the carapace can reach 0.06 mm (Figure 4D). The radial lirae density is about 33 per mm (Figure 4A, E).

Carapacestheria was originally assigned to Eosestheriidae (Shen, 1994), because its carapace's ornamentation transitions from medium-sized reticulations to radial lirae. Later, according to the occurrence of punctae on growth bands in the middle and lower parts of the carapace, Wang (2014) inferred that *Carapacestheria* may have punctae on growth bands near the umbo, thus he re-assigned *Carapacestheria* to the family Triglyptidae. But, no SEM figure published by Shen (1994) supports Wang's assignment. The author here just follows Shen's (1994) original assignment to Eosestheriidae.

Carapacestheria cangshanensis sp. nov.
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Figures 4–6

Material.—Holotype: NIGPCAS 180620, a left valve. Paratypes: NIGPCAS 180620B, a poorly preserved left valve; NIGPCAS 180620C, a poorly preserved left valve; NIGPCAS 180620D, inner side of a right valve.

Etymology.—The species was named for the site of its collection near Cangshan town of Zhongjiang County, Sichuan Province, China.

Diagnosis.—Carapace of small size, subquadrate in outline. Growth lines smooth, about 10–16 in number. Growth bands in the middle and ventral parts of the carapace are sculptured with reticulate-linear transition ornamentation: polygonal reticulations in the upper part, which transform to radial lirae in the lower part of each growth band. The diameter of polygonal cells in the middle part of the carapace is about 20–30 μm. The polygonal cells in the antero-ventral and ventral parts of the carapace are mainly about 20–40 μm in size, few of them

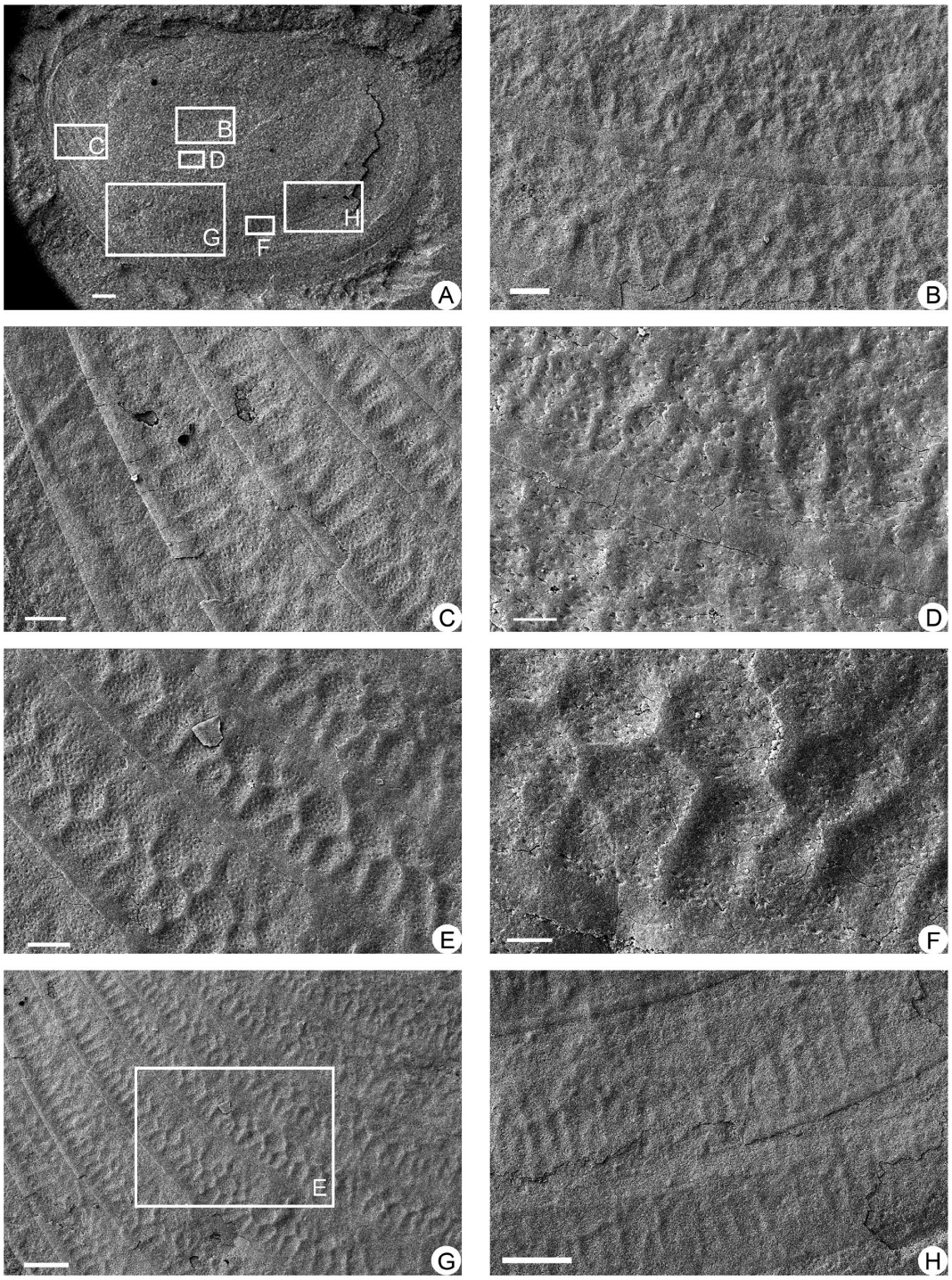

Figure 6. *Carapacestheria cangshanensis* sp. nov., holotype, NIGPCAS 180620. All figures are SEM images. **A**, a left valve; **B**, irregular reticulation and radial lirae on growth bands in the middle part of the carapace; **C**, radial lirae intercalated with punctae in the anterior part of the carapace; **D**, irregular reticulation and radial lirae in the middle part of the carapace, punctae occur within the reticulate mesh and between the radial lirae; **E**, medium sized reticulation on growth bands in the antero-ventral part of the carapace, punctae occur in the mesh; **F**, enlarged image of reticulation with punctae on a growth band in the ventral part of the carapace; **G**, reticulation and radial lirae on growth bands in the antero-ventral part of the carapace; **H**, radial lirae on growth bands in the postero-ventral part of the carapace. Scale bars = 200 μm in A, 20 μm in D, F, 40 μm in B, C, E, 100 μm in G, H.

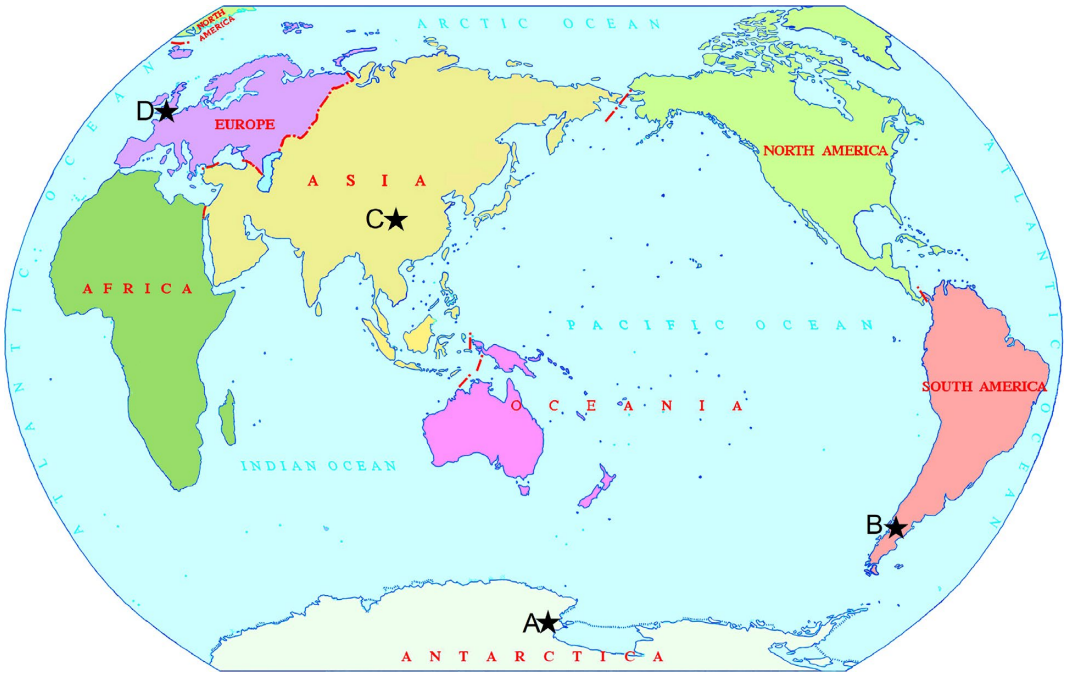

Figure 7. Global distribution of fossil clam shrimp genus *Carapacestheria*. **A**, from the Lower to Middle Jurassic of Carapace Nunatak, Antarctica (Shen, 1994). **B**, from the Middle Jurassic of Chubut Province, Argentina (Monferran *et al*., 2020). **C**, from the Upper Jurassic of Sichuan Province, China. **D**, from the lowest Cretaceous of Dorset, the United Kingdom (Li *et al*., 2021).

Table 1. Measurements of figured specimens (H=height, L=length).

Specimen number	Figure	Number of growth lines	L (mm)	H (mm)	H/L
NIGPCAS 180620	4A, 6A	16	3.5	2.4	0.69
NIGPCAS 180620B	5B	>12	2.4	1.6	0.67
NIGPCAS 180620C	5C	> 10	2.7	1.9	0.70
NIGPCAS 180620D	5D	> 9	2.5	1.9	0.76

can reach the size of 50–60 µm. Growth bands in the anterior and postero-ventral parts of the carapace ornamented with radial lirae, about 33 per mm. Punctae occur within the mesh and between the lirae.

Description.—Carapace small in size, subquadrate in outline, 2.4–3.5 mm long, 1.6–2.4 mm high, height/length ratio about 0.67–0.76 (Table 1). Umbo small, located at the anterior part of the long and straight dorsal margin. The anterior and posterior margins are widely rounded. The ventral margin is widely arched. Growth lines wide (19–23 µm) and smooth, about 10–16 in number. Growth bands widen gradually distally, and reaching the widest by the last third growth band (210 µm), although the last fifth and sixth ones become a little narrow in the holotype specimen (Figure 4A). Growth bands in the middle part of the carapace ornamented with irregular fine reticulations (mesh diameter between 20 and 30 µm), which transform to radial lirae in the lower part of each growth band (Figures 4B, 6B, D). Growth bands in the antero-ventral and ventral parts of the carapace ornamented with medium-sized polygonal reticulations in the upper part of each growth band, which change to radial lirae in the lower part of each growth band (Figures 4C, D, 6E, G). The polygonal cell diameter is mainly about 20–40 µm, few cell diameter reaches 50–60 µm (Figures 4C, D, 6E–G). Minute punctae (about 1 µm in diameter) are evenly distributed in the polygonal cells. The big cell can have more than 30 punctae (Figure 6E, F). Growth bands in the anteroior and postero-ventral parts of the carapace ornamented with radial lirae (Figures 4A, D, 6C, G, H), about 33 lirae per mm, minute punctae occur between the lirae (Figure 6C, G, H).

Occurence.—Upper Jurassic Penglaizhen Formation, Canshan town of Zhongjiang County, Sichuan Province, southwestern China.

Discussion

Four species of *Carapacestheria* have already been

described from Argentina, Antarctica and the UK (Figure 7): *Carapacestheria disgregaris* (Tasch, 1987) emend. Shen, 1994, *C. balli* Shen, 1994, *C. taschi* (Vallati, 1986) Monferran *et al*., 2020, and *C*.? *lulworthensis* Li *et al*., 2021. The former two species were recovered from the upper Lower–lower Middle Jurassic Ferrar Group of Carapace Nunatak, Antarctica. *C. disgregaris* has elliptical or subovate carapace outline, carapace height/length ratio about 0.56–0.7. *C. balli* has a rounded carapace outline, carapace height/length ratio about 0.73–0.83. They have well-developed reticulations, and are easily differentiated from the new species *C. cangshanensis* sp. nov., because the latter has mainly reticulate-linear transition ornamentation occupying the middle and ventral parts of the carapace. According to the morphometric analysis of Astrop *et al*. (2012), the elliptical *C. disgregaris* and the rounded *C. balli* may represent male and female morphotypes, respectively. But Astrop *et al*. (2012) neglected to comment on *C. balli* in their analysis.

The species, *C. taschi*, was described from the Middle Jurassic Las Chacritas Member of the Cañadón Asfalto Formation in Chubut Province of Argentina (Monferran *et al*., 2020). It has an elongated oval to round (elliptical) outline, carapace height/length ratio about 0.4–0.9. It differs from the new species by lacking punctae, and by having well-developed irregular reticulations (mesh diameter 5–30 μm) and dense radial lirae (about 50 per mm). *C*.? *lulworthensis* Li *et al*., 2021 was described from the lowest Cretaceous (?) Freshwater Beds of the Purbeck Limestone Formation of Dorset in the southern UK. It has a similar carapace outline to the new species, but differs by having relatively small-sized reticulations (mesh diameter about 25 μm). No punctae were observed in the British species, perhaps due to poor preservation. According to its limited fossil records and geological ranges, *Carapacestheria* first occurred from the southern hemisphere during the Early and Middle Jurassic transition interval, with records in the northern hemisphere since the Late Jurassic.

Conclusion

The Late Jurassic clam shrimp, *Carapacestheria cangshanensis* sp. nov., represents the first record of the genus in Asia. Its earlier occurrence in Antarctica might indicate that *Carapacestheria* first occurred in the southern hemisphere during the Early and Middle Jurassic transition interval. The records of *Carapacestheria* from China and the UK might indicate its arrival in the northern hemisphere during Late Jurassic, reaching Europe during the earliest Cretaceous.

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