Discovery of diverse *Pectocaris* species at the Cambrian Series 2 Hongjingshao Member Xiazhuang section (Kunming, SW China) and its ecological, taphonomical, and biostratigraphical implications

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Abstract

Pectocaris are intermediate- to large-sized Cambrian bivalved arthropods. Previous studies have documented *Pectocaris* exclusively from the Cambrian Series 2 Chengjiang biota in Yu'anshan Member, Chiungchussu Formation in SW China. In this study, we report *Pectocaris paraspatiosa* sp. nov., along with three other previously known species of this genus, from the Xiazhuang section belonging to the Hongjingshao Member of Tsanglangpu Formation in Kunming. The new species can be distinguished from its congeners by the shaped postero-dorsal corner and transverse carina of the carapace, the sparsely arranged endopodal endites, and the morphologies of the abdomen, telson, and tailfans. We interpret *P. paraspatiosa* sp. nov. as a filter-feeder and a powerful swimmer adapted to shallow, agitating environment. Comparison among the *Pectocaris* species reinforces previous view that niche differentiation had been established among the congeneric species based on morphological disparity. Our study is the first to verify the occurrence of *Pectocaris* outside the Chengjiang biota. With a review of the shared fossil taxa of Chengjiang and Xiaoshiba biota, we identify a strong biological connection between the Yu'anshan and Hongjingshao Members.

INTRODUCTION

Pectocaris were intermediate- to large-sized bivalved arthropods in the Cambrian ocean (Hou, 1999; Hou et al., 2004b; Jin et al., 2021). The genus currently comprises three species, *P. spatiosa* Hou, 1999, *P. eurypetala* (Hou & Sun, 1988), and *P. inopinata* (Jin et al., 2021). All of them are so far only known from the Cambrian Series 2 Stage 3 Chengjiang Lagerstätte in eastern Yunnan, South China. They were characterized by the large carapace covering about half length of the body, a great number of short stout body segments, densely arranged comb-like appendages with multiple podomeres and broad tailfans. They had been considered as branchiopod crustacean and resolved within Hymenocarina later, thus showing affinity with Mandibulata (Izquierdo-López & Caron, 2022). However, the key apomorphies of Mandibulata,

for instance, a third appendage specialized as the mandible, has not been found in *Pectocaris*. Therefore, their phylogenetic position within the arthropod tree remains uncertain. In terms of ecology, *Pectocaris* have been considered to be swimming species in view of the well-developed abdomen and tailfans (Hou & Sun, 1988; Hou, 1999; Hou et al., 2004b; Jin et al., 2021). Although *P. inopinata* Jin et al., 2021 was interpreted as predatory and/or scavenging (Jin et al., 2021), the other two species of the genus have been regarded as filter feeding (Hou et al., 2004b).

The geographical distribution and ecological niche of *Pectocaris* remain poorly known. A number of non-trilobite arthropods initially found in the Chengjiang Lagerstätte, including *Isoxys*, *Leanchoilia*, *Misszhouia*, *Naraoia*, and *Xandarella*, have recently been found in contemporary Lagerstätten in South China including the Qingjiang (Fu et al., 2019) and Fandian (Du et al., 2020) Lagerstätten. Some bivalved arthropods, such as *Isoxy*, have even lasted for several periods of geological history (Williams et al., 1996; Hu et al., 2007; García-Bellido et al., 2009a; García-Bellido et al., 2009b; Sun et al., 2022). In addition to retrieving bio-stratigraphical connections among the Lagerstätten, these findings would also indicate that the above arthropods were ecologically tolerant, or had strong dispersal ability, or that the related lineage (in the case of *Isoxys*) successfully evolved through time and adapted to the changing environment. But for *Pectocaris*, none of its species has previously been found outside the Chengjiang Lagerstätte, and the genus seems to be temporal–spatially restricted.

Recent research of Xiaoshiba Lagerstätte manifest that it has some arthropod genera in common with the Chengjiang Lagerstätte, such as *Fuxianhuia* and *Chengjiangocaris*, and has been considered as the continuation of the Chengjiang community (Yang et al., 2013 2016, 2018). In the Xiazhuang assemblage, which is correlated to the early phase of the Xiaoshiba Lagerstätte, (Zeng et al., 2014) that mentioned the presence of a specimen possibly belonging to *Pectocaris* and two specimens of *Jugatacaris*? sp., which is phylogenetically close to *Pectocaris* (cf., e.g., Jin et al., 2021). Therefore, it is reasonable to suspect that the *Pectocaris* species and their close relatives might have continued surviving after the Chengjiang period. Investigating the distribution of *Pectocaris* among different Cambrian Lagerstätten would reveal its temporal

and spatial distributions, and would improve the understanding of the evolution and environmental adaptation of this group and other Cambrian bivalved arthropods with similar morphologies.

In this paper, we report *Pectocaris paraspatiosa* sp. nov. along with several other previously known species of the genus, based on newly collected material from the Xiazhuang section (Fig 1). With the presence of *Pectocaris* in the Xiazhuang assemblage and the morphological difference among *Pectocaris* species, we discuss the related issues in palaeoecology, taphonomy, and biostratigraphy.

MATERIAL AND METHOD

Specimens analyzed herein were collected from the Xiazhuang section (cf. Zeng et al., 2014) that lies to the northwest of the Guanshan reservoir, Xiazhuang village, Chenggong district, Kunming, China (Fig 1). This section includes the Yu'anshan Member at its lower part and the Hongjingshao Member at its upper part, both belonging to Cambrian Series 2 (cf. Zeng et al., 2014). In the Hongjingshao Member, we obtained abundant specimens of *Hongshiyanaspis*, *Fuxianhuia*, *Kutorgina* and *Paraselkirkia*, which are characteristic elements of this member. In addition, there are 35 specimens of bivalved arthropods which we identify as *Pectocaris* and one another identified as *Jugatacaris*, which are reported here.

In the laboratory, fossil specimens were excavated with steel needles, and were then photographed with a Leica M205C fluorescence-microscope and a Canon camera equipped with a 100 mm Macro lens. Line drawings of the specimens were made with the aid of a camera lucida attached to a NIKON SMZ 1270 stereomicroscope. All the specimens analyzed in this paper have been housed at the Yunnan Key Laboratory for Palaeobiology, Institute of Palaeontology, Yunnan University.

SYSTEMATIC PALAEONTOLIGY

Phylum ARTHROPODA von Siebold, 1848

Class UNCERTAIN

Order ODARAIIDA Simonetta and Delle Cave, 1975

Family PECTOCARIDIDAE Hou, 1999

Genus PECTOCARIS Hou, 1999

Type species. *Pectocaris spatiosa* Hou, 1999.

Other species. *Pectocaris eurypetala* (Hou & Sun, 1988), *Pectocaris inopinata* Jin *et al.* 2021, *Pectocaris paraspatiosa* sp. nov.

Diagnosis (amended after Jin et al., 2021). Intermediate- to large-sized Cambrian bivalved arthropods. Carapace sub-rectangular or sub-elliptical, devoid of ornaments and marginal spines, covering slightly more than half of body length. Stalked eyes and anterior end of head usually protruding beyond carapace. Trunk usually with over 40 segments each much wider than long. Trunk appendages densely arranged, with flap-like exopods carrying short setae and multi-segmented endopods bearing setulose endites. Telson elongate, connected to a pair of broad tailfans via small sub-triangle sclerites.

Pectocaris paraspatiosa sp. nov.

Figures 2–3

Etymology: Prefixion “Para-” means the new species is similar to *Pectocaris spatiosa* Hou, 1999 in appearance.

Type specimens. Holotype: YKLP 16289 (Figs 2, 3A, B); Paratype: YKLP 16290, YKLP 16291, YKLP 16292, YKLP 16293 (Fig 3E, G, I, K).

Other material examined. YKLP 16294, YKLP 16295, YKLP 16296, YKLP 16297, YKLP 16298 (see supplementary material).

142 *Preservation*. All the 12 specimens studied herein are incomplete. The holotype (Figs 2A, B, 3A,
143 B) preserved with overall outline of carapace, about 19 trunk segments, telson, and some
144 appendages. Carapace invert by 180° relative to trunk, presumably due to taphonomic process or
145 molting behavior. Appendages somewhat dislocated yet with fine details. The other 11 ones
146 preserve the posterior part of the trunk and in some specimens also the tailfans. As to the
147 preservation aspect, the holotype has its carapace laterally compressed while the trunk
148 dorsal–ventrally compressed that judged from the shape and width of the telson and the lateral
149 position of the notches on which the tailfans should had been attached. Among the other
150 specimens, which only have trunk segments preserved, 10 are preserved in dorsal–ventral aspect
151 (Figs 3E, G, I, K and supplementary material), and one is preserved in oblique-lateral aspect that
152 judged from the width of the telson and the tailfans (see supplementary material).
153 *Remarks*. We interpret the carapace of the holotype as being invert by 180º for the following
154 reasons. Firstly, in general, the most anterior of the carapaces of the species of *Pectocaris* are
155 usually sagittal and the posterior end is broader than the left and the right end of carapace in Fig.
156 2A, 3A) than the anterior (Hou, 1999; Hou et al., 2004b; Fu & Zhang, 2011; Jin et al., 2021).
157 Secondly, the dorsal margin of the carapace of *Pectocaris* is often nearly straight while the
158 ventral margin is usually convex. Thirdly, the gently curved trunk of the holotype, which
159 overlains the anterior margin of the carapace, can be better explained as a relative rotation
160 between the trunk and the carapace (as seen in other species of *Pectocaris*), rather than a dorsal-
161 ward dislocation of the trunk.
162
163 *Diagnosis*. Intermediate-sized *Pectocaris* species. Carapace sub-rectangular, with shaped
164 postero-dorsal edge. Trunk segments sub-equal in width but progressively longer posteriorly and
165 no sudden narrowing toward to the telson. Telson flukes separated and almost straight on both
166 outsides. Endites slender, more sparsely spaced than congeners, with gap between endites sub-
167 equal to or slightly larger than width of endite.
168

Description. Carapace elongate (Fig. 2A, B). Dorsal margin comparatively straight. Anterior margin evenly curved. Posterior margin broader than anterior margin, and with shaped postero-dorsal part showing appearance of being "cut off", leaving short straight edge (black arrowheads in Figs 2A). Postero-dorsal angle about 150º. A straight rod-like structure presents in the posterior part of the carapace which connect the dorsal and ventral margin is interpreted as the ridge of the carapace. Marginal spines and ornaments absent.

About 15 trunk segments preserved in YKLP 16289a (part of holotype) while four additional anterior segments revealed in YKLP 16289b (counterpart of holotype) by manual preparation (Fig 2A, B). Fewer trunk segments preserved in other specimens. Each segment sub-rectangular or trapezoidal in shape, with no dorsal or lateral spines (Figs 2A, B, 3A, B). Segments sub-equal in width and gradually narrowed to the telson.

Telson sub-trapezoidal, with anterior part sub-equally wide to last abdominal segment, while posterior part significantly wider, interrupted by small postero-lateral notches (Figs 2B, 3B, E, G, I, K). Small sub-triangular sclerite present in each notch, connecting telson with broad, sub-divided tailfans (Fig. 3E–L). Shallow groove present on both right and left sides of telson.

Trunk appendages poorly preserved in holotype (Fig. 2, 3A–D), all being incomplete and more or less dislocated from *in vivo* positions. Longest one consisting of more than 24 podomeres (Fig. 2E). Each podomere with one sub-quadrate or slightly trapezoidal endite carrying up to six slender apical setae (Fig. 2C, F, G, I). Endite setae in proximal part of endopod (Fig. 2G, I) somewhat thicker than those in more distal part (Fig. 2C, F). Distance between endites sub-equal to, or slightly larger than width of each endite. Shape of exopod not resolved, with only some densely arranged, short marginal setae preserved (Fig. 2D, H). Head appendages not preserved.

Differential diagnosis. The present species is similar to its congeners and *Jugatacaris agilis* Fu & Zhang, 2011 in the outline of carapace (Hou, 1999; Hou et al., 2004b; Fu & Zhang, 2011; Jin et al., 2021), but can be distinguished from them by its "cut-off" shaped postero-dorsal edge.

Like other *Pectocaris* species, *P. paraspatiosa* sp. nov. lacks the dorsal fin-like structure which is the character of *J. agilis* (Fu & Zhang, 2011). The *Waptia*-like bivalved arthropod *Xiazhuangocaris chenggongensis* can be readily recognized by the prominent anterior notch and narrow anterior tip of the carapace from the same section (Zeng et al., 2020).

The abdomen of *P. paraspatiosa* sp., nov. tends to be sub-equally wide at its different parts which is different from all other *Pectocaris* species that have posteriorly tapering abdomens.

The endopods of most *Pectocaris* species and *J. agilis* all have multiple seta-bearing endites (in *P. inopinata*, the setulose endites are present in posterior trunk appendages and in proximal section of anterior trunk appendages). However, the endites of the other species compared here are more densely arranged, especially in *P. inopinata* and *J. agilis*. Moreover, the endites of *P. inopinata* are stouter and those of *P. eurypetala* are sub-trapezoidal and seem to be smaller.

Locality and horizon. Xiazhuang section of Chenggong, Kunming, China. Hongjingshao Member of Tsanglangpu Formation, Cambrian Stage 3, Series 2.

OTHER *PECTOCARIS* SPECIES FROM THE XIAZHUANG SECTION

In addition to the 12 specimens of *P. paraspatiosa* sp. nov., 22 specimens collected from the same stratum were also recognized as *Pectocaris* species, namely *P. eurypetala* (2 specimens), *P. spatiosa* (19 specimens), *P. inopinata* (1 specimen). Also, there is 1 specimen most likely belonging to *J. agilis* (Fig. 4I). All these were preserved with the posterior part of the trunks and sometimes also with the tailfans, while the anterior parts of their bodies were missing. Among the various morphological features described in previous studies (Hou & Sun, 1988; Hou, 1999; Hou et al., 2004b; Fu & Zhang, 2011, Jin et al., 2021), some were the most useful for identifying the present specimens, such as, the morphologies of the appendages, abdomen and the telson. We identify *P. eurypetala* from other species by the more widely spaced abdominal segments while distinct slender telson and the longer broad telson rami (Fig. 4G, H, 5B). Even though the endite of *P. spatiosa* is uncertain, it is still can be distinguished by the transverse

broad and significantly vertical shorter abdomen. Along with the sub-rectangular telson and the broad, paddle like telson fluke decorated with paired groove, there are typical characters for this species (Fig. 4A–F, 5C). Although there is only one specimen of *P. inopinata*, the striking absence of the presence of dorsal and lateral spines on abdominal segments in all other *Pectocaris* species is anadamant evidence to distinguish the species to its congeners (Fig. 4K, L, 5D). One specimen is identified as *J. agilis* in the reason of the undivided telson fluke which is seem to be a universal characteristic that absent in *Pectocaris* (Fig. 4I, J).

DISCUSSION

Ecology

Like other species of the genus *Pectocaris*, the strongly built multi-segmented trunk of *P. paraspatiosa* sp. nov. attached to broad tailfans (Fig. 5) suggests its capability as a good swimmer. The swim propulsion might be stronger than its congeners in view of the longer abdominal segments that could have provided greater torque for its tailfans in beating water; and the setulose exopods could as well provide propulsion, even if it is difficult to estimate due to their fragmental preservation in the present specimens. But this is a reasonable assumption and needs to be tested with biomechanical models where the function of the muscles attached to the internal surface of the exoskeletons can be analyzed, which could be left to further work.

The multi-segmented endopods of *P. paraspatiosa* sp. nov. carrying setulose endites (Fig. 2C, F, G, I), similar to *P. eurypetala*, *P. spatiosa*, and *J. agilis*, suggest a filter-feeding behavior that had been interpreted for the latter three species (Hou et al., 2004b; Fu & Zhang, 2011). The endites of *P. paraspatiosa* sp. nov. are more sparsely arranged compared with other *Pectocaris* species and *J. agilis*. This may imply the new species could filter larger food particles. In addition, the endite setae on the proximal section of the endopods of *P. paraspatiosa* sp. nov. are thicker than the more distal ones (Fig. 2I), possibly implying that the proximal endites could

process harder food particles. In *P. inopinata*, the distal six podomeres of the endopod equipped with paired strong claws were interpreted to have been used for ploughing through the sediments for food, for grasping preys, and/or for scratching tissues from carcasses (Jin et al., 2021). Such claws are not observed in *P. paraspatiosa* sp. nov. (Fig. 2E). Therefore, a filter-feeding behavior is a more appropriate explanation than a predatory or scavenging feeding for this species.

The morphological differences among *Pectocaris* species (Hou, 1999; Hou et al., 2004b; Jin et al., 2021; this study) indicate that this genus was a polymorphic group evolving towards adaptations to various ecological niches. These species differ from each other in size, carapace shape, number and length of body segments and the presence of dorsal and lateral spines on the abdominal segments, shapes of telson and tailfans, number of trunk-appendage podomeres, and details of enditic armatures (Table 1; Fig. 5).The co-occurrence of the four species of *Pectocaris* (Figs 2–4) as well as *Jugatacaris* at the Xiazhuang section reinforces previous conclusion that taxonomically close Cambrian arthropods could develop different body and appendage structures in order to establish niche differentiation and thus exploit resources provided by the competitive marine ecosystem (Jin et al., 2021; Zeng et al., 2020). *Pectocaris* spp., *Xiazhuangocaris chenggongensis*, and *Clypecaris serrata* (Yang et al., 2016; Zeng et al., 2020; this study) further showcase the morphological disparity of the so-called Hymenocarina (see e.g., Izquierdo-López & Caron, 2022) in the Hongjingshao period, which however is less diversified than the hymenocarines in the Chengjiang and the Burgess Shale faunas (Briggs, 1994; Hou et al., 2017). The only verified bivalved arthropods at the Hongjingshao Member of Xiazhuang section include the *Pectocaris* species reported in this study and *X. chenggongensis* described by Zeng et al. (2020), which are intermediate- to large-sized swimmers. Small bivalved arthropods such as bradoriids and *Clypecaris* have not been reported from this site. Considering the generally coarse lithology compared with the mudstones in the Yu'anshan Member where the Chengjiang biota is preserved, this may denote stronger hydraulic condition that was unfavourable for the living or the preservation (see below) of the smaller swimming arthropods.

278 **Taphonomic implications**

279

280 A noticeable feature of the *Pectocaris* specimens from the Xiazhuang section is that except for
281 the holotype (Fig. 2) and one *P. spatiosa* specimen (Fig. 4A, B), all other specimens only
282 preserve the posterior part of the trunk, with anterior part of the body and appendages missing.
283 Although one complete individual of *X. chenggongensis* and one specimen of *Jugatacaris*? sp.
284 preserved with carapace and appendicular details were reported from the same stratum (Zeng et
285 al., 2014, 2020), such cases have been rare. By contrast, the intermediate- and large-sized
286 hymenocarines in the Cambrian series 2 strata elsewhere, represented by the *Pectocaris* species
287 and *Jugatacaris agilis* from the Chengjiang biota (Yu'anshan Member, see Hou et al., 2004b; Fu
288 & Zhang, 2011; Jin et al., 2021), and the pectocaridid-like arthropod from the Xiaoshiba biota,
289 usually preserve both the anterior and the posterior parts of the body, although incomplete
290 specimens with only the posterior part of the trunk could also be found (e.g., the Meishucun
291 section, see Hou & Sun, 1988). We consider taphonomic explanations for these observations, as
292 detailed below.

293 The clastic sediments of Hongjingshao Member at the Xiazhuang section contain a great
294 portion of siltstone and sandstone beds, being generally coarser than the underlying Yu'anshan
295 Member that is dominated by mudstones (Zeng et al., 2014; our field observation). This
296 presumably denotes strong hydrodynamics and would result in more intensified mechanical
297 breakage of the thanatocoenosis before burial, as discovered in modern sedimentary systems
298 (e.g., Zhai et al., 2015). Meanwhile, the Hongjingshao stratum lacks the alternating background
299 and event beds, which are characteristic for the Yu'anshan Member containing soft-bodied
300 Chengjiang biota (Zeng et al., 2014). Previous investigations suggested that post-mortem
301 transport was limited in the event beds, where the thanatocoenosis probably experienced fast, *in*
302 *situ* burial (Zhao et al., 2009, 2012). We propose that the strong hydraulic disturbance and
303 unfavourable burying mode at the Xiazhuang section were the main causes for the
304 incompleteness of the *Pectocaris* specimens. By the way, the strong hydralic disturbance, which

can be inferred from both the coarse lithology and the incomplete preservation of the *Pectocaris* specimens, could support our above inference that *P. paraspatiosa* sp. nov. had been a powerful swimmer adapted to agitating environments.

Meanwhile, the selective preservation of our *Pectocaris* specimens may be due to the fact that the anterior part of their bodies is less resistant to degradation. Observations on relatively complete specimens of *P. eurypetala*, *P. inopinata*, and *P. spatiosa* from the Chengjiang biota revealed clear sclerotization of the posterior part of the trunk protruding beyond the carapace, in contrast to very faint or no sclerotization for the anterior part of the body protected by the carapace (Hou et al., 2004b; Jin et al., 2021). This is similar to other Cambrian bivalved arthropods, such as *Chuandianella ovata* Li, 1975 (Zhai et al., 2022), *Nereocaris exilis* Legg et al., 2012, and *Waptia fieldensis* Walcott, 1912 (Vannier et al., 2018), probably denoting reaction to the protective carapace for the anterior part and the need for propulsion action for the posterior part of body, respectively. The trace of the appendages and gut suggest that the carapace of *Pectocaris* was generally thin and poorly sclerotized/mineralized compared with other bivalved arthropods, such as *Chuandianella ovata*, *Ercaicunia multinodosa* Luo & Hu, 1999, and *Clypecaris* preserved in other Cambrian series 2 strata in eastern Yunnan (Yang et al., 2016; Hou et al., 2017; Zhai et al., 2019a; Liu et al., 2021). Therefore, we assume that, upon death, the *Pectocaris* individuals at the Xiazhuang section were probably exposed to certain degree of mechanical and biochemical degradations before being buried, resulting in the absence of the more tender anterior part of body in most of the specimens. Whether the transportation-accompanying size sorting had occurred for the *Pectocaris* specimens from the Xiazhuang section is uncertain, because although all the specimens we study are comparatively large late forms, those collected from the finer mudstones in Yu'anshan Member were dominated by large individuals as well.

Biostratigraphical connection between Hongjingshao and Yu'anshan Members

The Hongjingshao Member, which was originally named by Zhang (1966) with type section from the northern hillside between Canglangpu (i.e., Tsanglangpu, now known as Changlongpu) and Hongjingshao (now known as Hongjunshao Village) in Malong County, is characterized by thick sandstone beds intercalated with thin mudstones (Luo et al., 1994, Yang et al., 2013; Zeng et al., 2014). The underlying Yu'anshan Member, which was originally named with type section from Mt. Yu'anshan to the west of Kunming City, is characterized by intermediately thick mudstone beds intercalated with sandstone beds (Luo et al., 1982), and in many localities the mudstones consist of frequent alternations of dark-coloured background beds and light-coloured event beds (Zhu et al., 2001b, 2005b; Hou et al., 2017). Thereby, as the lower part of the Tsanglangpu Formation and the upper part of the Chiungchussu Formation, respectively, the Hongjingshao and the Yu'anshan Members had been originally distinguished by lithology. Meanwhile, the Yu'anshan Member yields the Chengjiang Lagerstätte (Zhang & Hou, 1985; Chen et al., 1996; Hou et al., 2004b, 2017), and the Hongjingshao Member preserves the Xiaoshiba Lagerstätte (Yang et al., 2013, 2015, 2018) and the Xiazhuang fossil assemblage (Zeng et al., 2014), which is considered contemporary to the lower part of the Xiaoshiba Lagerstätte (Zeng et al., 2017, 2020).

Previous works suggested that both the Xiaoshiba Lagerstätte and the Xiazhuang assemblage are extensions of the Chengjiang Lagerstätte in view of their shared faunal compositions especially the trilobites (Hou et al., 2017; Zeng et al., 2017b). In this study, we make a checklist of shared fossil taxa between the Yu'anshan Member and the Hongjingshao Member based on previous references (Table 2), and include the genus *Pectocaris* in this list in the light of the present study. Such a checklist showcases the biostratigraphical connection between the Hongjingshao Member (of Tsanglangpu Formation) and the Yu'anshan Member (of Chiungchussu Formation).

We concur with Zeng et al. (2014) that the Hongjingshao formation is diachronous. As litholostratigraphic units, formations and members are defined by lithology, and would basically reflect the sedimentary settings. However, because depositional process can be diachronous, the

lithostratigraphic units are not necessarily isochronic. Meanwhile, because faunal communities could potentially survive different environments with different sedimentary settings, different members or formations in the strata can have the same fossil taxa if they belonged to the same geological age. Hongjingshao Member is transitional for Cambrian marine communities, also opening up some new genera and species. The extension of some species from the Yu'anshan Member into the Hongjingshao Member indicates that these species managed to survive after the Chengjiang time period, despite changes in marine environment, as marked by the lithology (Table 2).

CONCLUSION

We report *Pectocaris paraspatiosa* sp. nov., a fourth species of the genus, from the Cambrian Series 2 Hongjingshao Member at the Xiazhuang section, Kunming, China. The new species can be distinguished from its congeners by a number of features, including the shaped posterodorsal corner of carapace, the sub-equal widths of posterior trunk segments and their greater lengths, the absence of dorsal and lateral body spines, the shape of telson, and the sparsely distributed setulose endites on the endopods. We interpret *P. paraspatiosa* sp. nov. as a powerful swimmer adapted to relatively strong hydraulic condition in shallow water, based on a combination of evidence including the broad tailfans, the strongly built limbless abdominal segments and telson, as well as the coarse lithology in which it is preserved. A filter-feeding strategy is inferred from the multi-segmented endopods carrying setulose endites, which is similar to its congeners.

Comparison among the *Pectocaris* species suggests that this genus was polymorphic and intra-genus niche differentiation was established by morphological disparity. Such inference can be supported by the co-occurrence of the various *Pectocaris* species at the Xiazhuang section. The *Pectocaris* species, along with *Xiazhuangocaris chenggongensis* previously described from the same section, may imply that the agitating environment therein favoured intermediate and large swimming hymenocarines to small bivalved arthropods.

We propose that the strong hydraulic disturbance and unfavourable burying mode at the

Xiazhuang section were the main causes for the incompleteness of the *Pectocaris* specimens. The different degrees of sclerotization of the anterior and the posterior parts of the trunk, and the weak sclerotization/mineralization of the carapace of *Pectocaris*, also played a role in selective degradation.

The discovery of *Pectocaris* species in the Xiazhuang fossil assemblage adds to the list of shared fossil taxa between the Hongjingshao Member and the underlying Yu'anshan Member, reinforcing conclusions made by previous studies that both the Xiaoshiba Lagerstätte and the Xiazhuang assemblage were continuing the Chengjiang biota.

Acknowledgements. This study is supported by Yunnan Provincial Grants 202101AT070158, 202301AS070049, YNWR-QNBJ-2019-295, "Open for collaboration" grant from Yunnan Key Laboratory for Palaeobiology, Yunnan University and High-Level Talents of Liupanshui Normal University (LPSSYKYJJ202210). We thank Prof. Peiyun Cong, Mr. Di Wu, Miss. Mengying Yin, Miss. Ting Zhao, and Dr. Yang Zhao (YKLP, Yunnan University) for attending the field work, Prof. Jie Yang, Mr. Wei Li (YKLP, Yunnan University), and Dr. Ruilin Wen (Institute of Geology and Geophysics, Chinese Academy of Sciences) for helpful discussion. Generous support for field investigation from Mr. Kunhong Chen and his colleagues at the Yuhua Subdistrict Administration Office is much appreciated.

Figure captions

Figure 1. Map showing the distribution of the strata of Cambrian Series 2 Chiungchussu Formation (light brown) and Canglangpu Formation (dark brown) in eastern-central Yunnan, China. Gray stars indicate fossil sites yielding *Pectocaris* in previous studies (Hou & Sun, 1988; Hou, 1999; Hou *et al*., 2004b; Jin *et al*., 2021). Red star indicates the fossil locality investigated in the present paper (Xiazhuang section).

Figure 2. *Pectocaris paraspatiosa* sp. nov. (YKLP 16289a and b, holotype) from the Hongjingshao Member of Tsanglangpu Formation at Xiazhuang section. A, part, overview. Note that the carapace is invert by 180º relative to the trunk, with the anterior end on the right and the dorsal margin at the bottom. Arrow indicates anterior direction of the carapace. B, counterpart, overview. C, details of two endopods (rectangle in A). Red arrowheads indicate setae on two of the endites, respectively. D, exopod setae (rectangle in A). E, trunk appendages (rectangle in B). F, details of one of the endopods (rectangle in B), showing six endites (arrowed; with two endites enlarged in the small inset). G, details of two setulose endites (small rectangle in right-upper part of B). H, exopod setae (rectangle in E). I, setulose endites of the endopod (rectangle in E). *Abbreviations*: am, anterior margin of carapace; dm, dorsal margin of carapace; en, endopod; lv, left valve; rc, ridge of carapace; rv, right valve; s*n*, the *n*th body segment (counted from posterior to anterior); st, seta(e); tpm, posterior margin of telson; ts, telson.

Figure 3. *Pectocaris paraspatiosa* sp. nov. from the Hongjingshao Member of Tsanglangpu Formation at Xiazhuang section. A, B, holotype (YKLP 16289a and b), explanatory drawings of the overviews in Fig. 2A, B, respectively. C, explanatory drawing of appendage enlarged in A (rectangle in A). D, explanatory drawing of appendage enlarged in B (rectangle in B). E, F, YKLP 16290 (paratype), light photo and explanatory drawing. A trilobite (*Hongshiyanaspis*) is preserved with this specimen (adjacent to its tailfans). G, H, YKLP 16291 (paratype), light photo and explanatory drawing. I, J, YKLP 16292 (paratype), light photo and explanatory drawing. K, L, YKLP 16293 (paratype), light photo and explanatory drawing. *Abbreviation*: sts, sub-triangular sclerite at the basal part of the tailfan.

Figure 4. Other species of the genus *Pectocaris* from the Hongjingshao Member of Tsanglangpu Formation at Xiazhuang section. Each specimen is presented with the light photo on the left and the explanatory drawing on the right. A–F, *Pectocaris spatiosa* Hou, 1999. A, B, YKLP 16299; C, D, YKLP 16300; E, F, YKLP 16301. G, H, *Pectocaris eurypetala* Hou & Sun, 1988, YKLP

16302. I, J, *Jugatacaris*? sp., YKLP 16303, note the fused left and right tailfans. K, L, *Pectocaris inopinata* Jin et al., 2021, YKLP 16304, note the lateral-dorsal abdomen spines characterizing this species. *Additional abbreviations*: an, anus.

Figure 5. Schematic drawings of the posterior part of the body of *Pectocaris* species. Based on Hou & Sun (1988), Hou (1999), Hou et al. (2004b), Jin et al. (2021), and the present study. Not to scale.

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581 International Journal for the Geo-Sciences **220**: 31–46.

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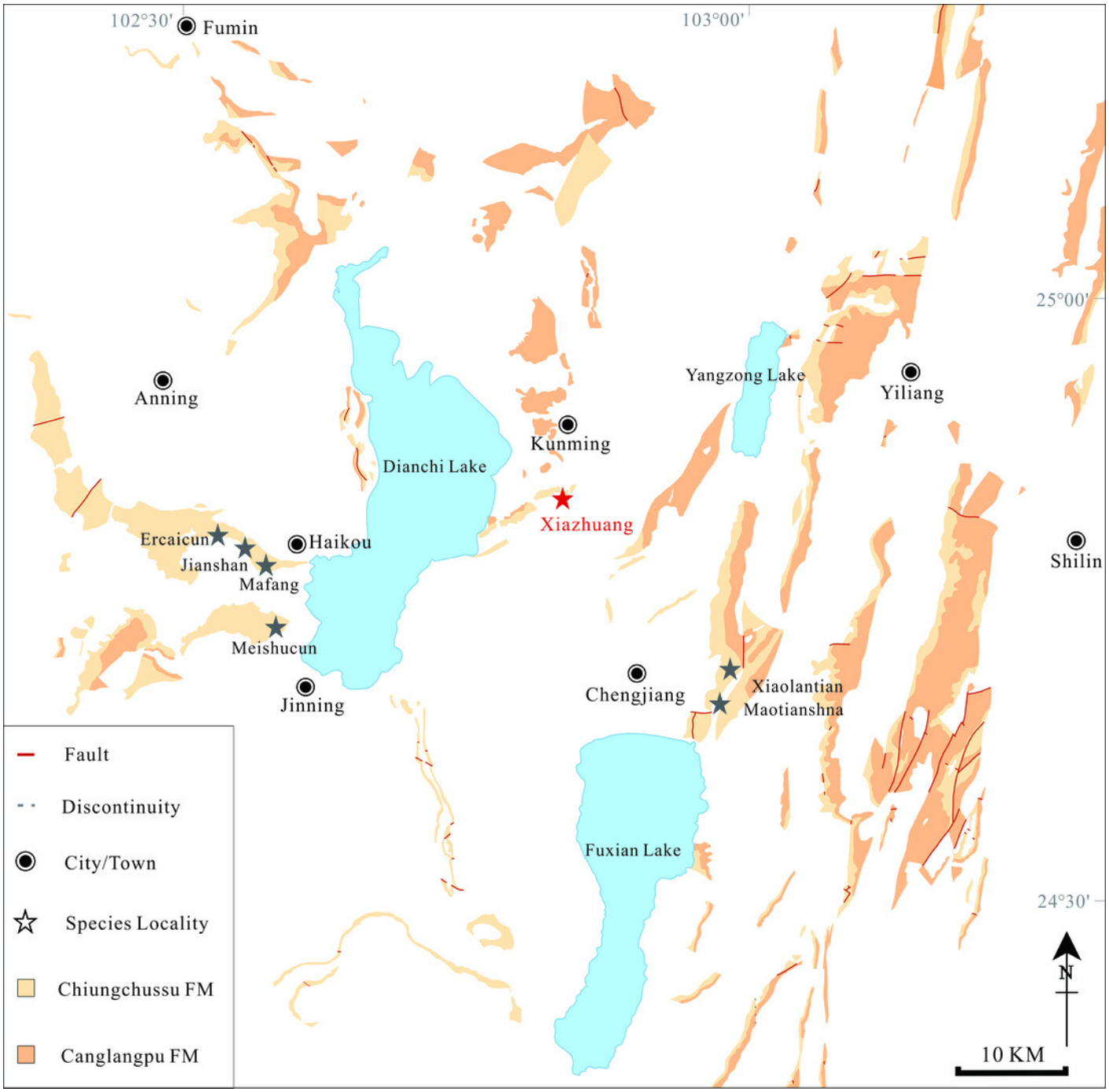
Figure 1

Map showing the distribution of the strata of Cambrian Series 2 Chiungchussu Formation (light brown) and Canglangpu Formation (dark brown) in eastern-central Yunnan, China.

Gray stars indicate fossil sites yielding *Pectocaris* in previous studies (Hou & Sun, 1988; Hou, 1999; Hou *et al*., 2004b; Jin *et al*., 2021). Red star indicates the fossil locality investigated in the present paper (Xiazhuang section).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Jianshan
Mafang
Shilin
Meishucun
Chengjiang
Xiaolantian
Maotianshna
Jinning
Fuxian Lake
24°30'
Fault
Discontinuity
City/Town
Species Locality
Chiungchussu FM
Canglangpu FM
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Figure 2

Pectocaris paraspatiosa sp. nov. (YKLP 16289a and b, holotype) from the Hongjingshao Member of Tsanglangpu Formation at Xiazhuang section.

(A) Part, overview. Note that the carapace is invert by 180º relative to the trunk, with the anterior end on the right and the dorsal margin at the bottom. Arrow indicates anterior direction of the carapace. (B) Counterpart, overview. (C) Details of two endopods (rectangle in A). Red arrowheads indicate setae on two of the endites, respectively. (D) Exopod setae (rectangle in A). (E) Trunk appendages (rectangle in B). (F) Details of one of the endopods (rectangle in B), showing six endites (arrowed; with two endites enlarged in the small inset). (G) Details of two setulose endites (small rectangle in right-upper part of B). (H) Exopod setae (rectangle in E). (I) Setulose endites of the endopod (rectangle in E). *Abbreviations*: am, anterior margin of carapace; dm, dorsal margin of carapace; en, endopod; lv, left valve; rc, ridge of carapace; rv, right valve; s*n*, the *n*th body segment (counted from posterior to anterior); st, seta(e); tpm, posterior margin of telson; ts, telson.

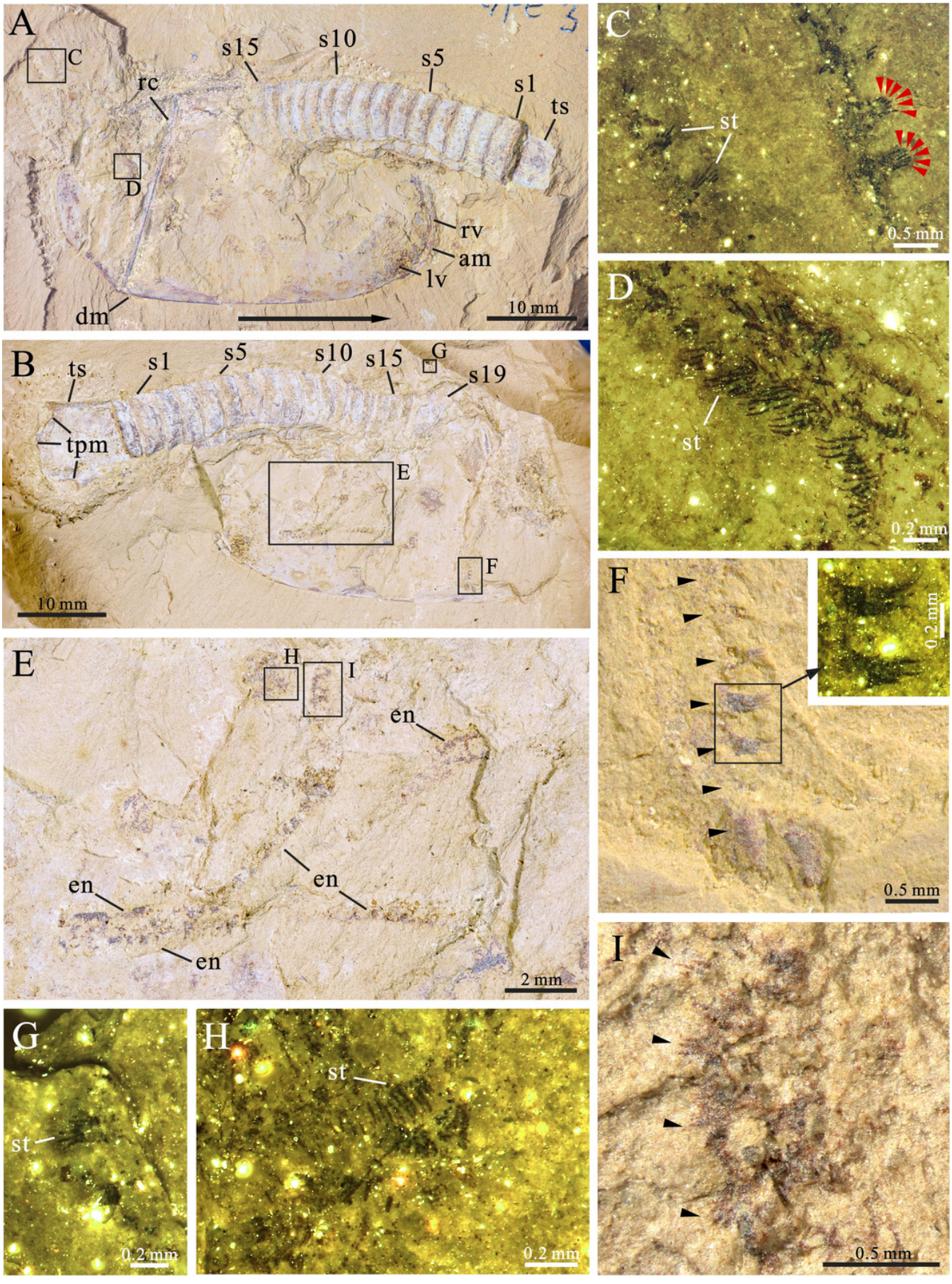
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Figure 3

Pectocaris paraspatiosa sp. nov. from the Hongjingshao Member of Tsanglangpu Formation at Xiazhuang section.

(A and B) holotype (YKLP 16289a and b), explanatory drawings of the overviews in Fig. 2A, B, respectively. (C) explanatory drawing of appendage enlarged in A (rectangle in A). (D) explanatory drawing of appendage enlarged in B (rectangle in B). (E and F) YKLP 16290 (paratype), light photo and explanatory drawing. A trilobite (*Hongshiyanaspis*) is preserved with this specimen (adjacent to its tailfans). (G and H) YKLP 16291 (paratype), light photo and explanatory drawing. (I and J) YKLP 16292 (paratype), light photo and explanatory drawing. (K and L) YKLP 16293 (paratype), light photo and explanatory drawing.
Abbreviation: sts, sub-triangular sclerite at the basal part of the tailfan.

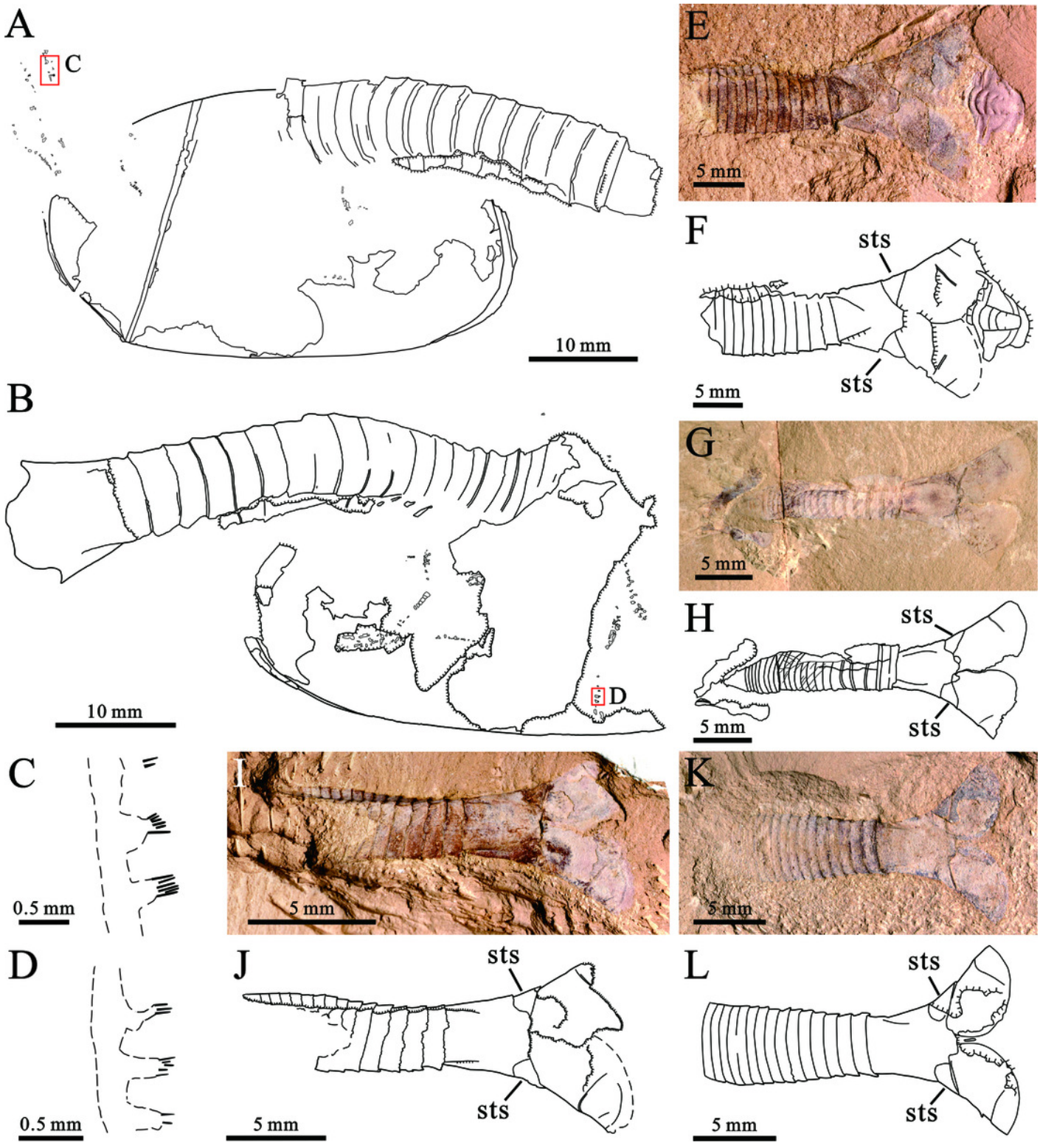
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Figure 4

Other species of the genus *Pectocaris* from the Hongjingshao Member of Tsanglangpu Formation at Xiazhuang section. Each specimen is presented with the light photo on the left and the explanatory drawing on the right.

(A–F) *Pectocaris spatiosa* Hou, 1999. (A and B) YKLP 16299; (C and D) YKLP 16300; (E and F) YKLP 16301. (G and H) *Pectocaris eurypetala* Hou & Sun, 1988, YKLP 16302. (I and J) *Jugatacaris*? sp., YKLP 16303, note the fused left and right tailfans. *(*K and L) *Pectocaris inopinata* Jin et al., 2021, YKLP 16304, note the lateral-dorsal abdomen spines characterizing this species. *Additional abbreviations*: an, anus.

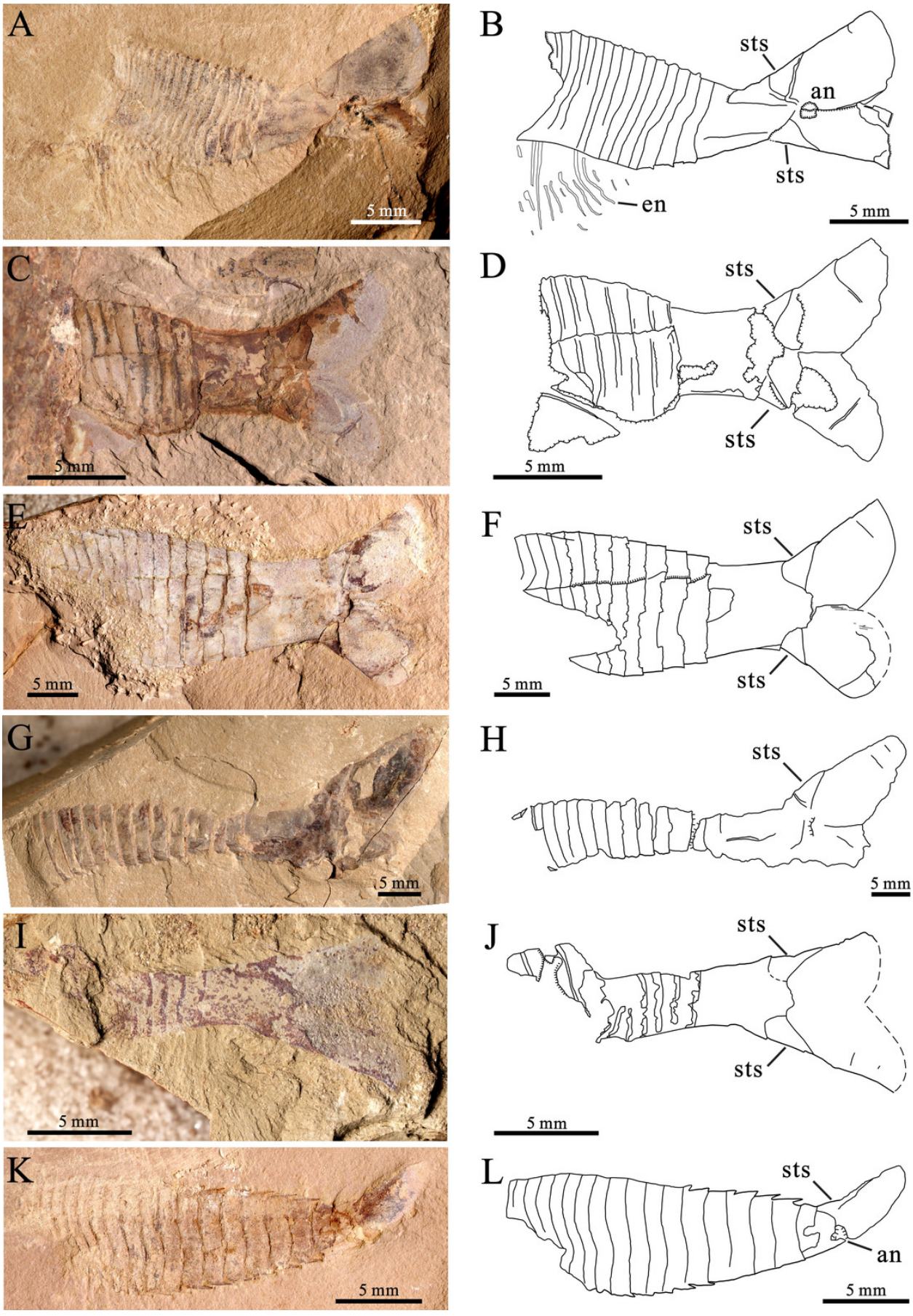
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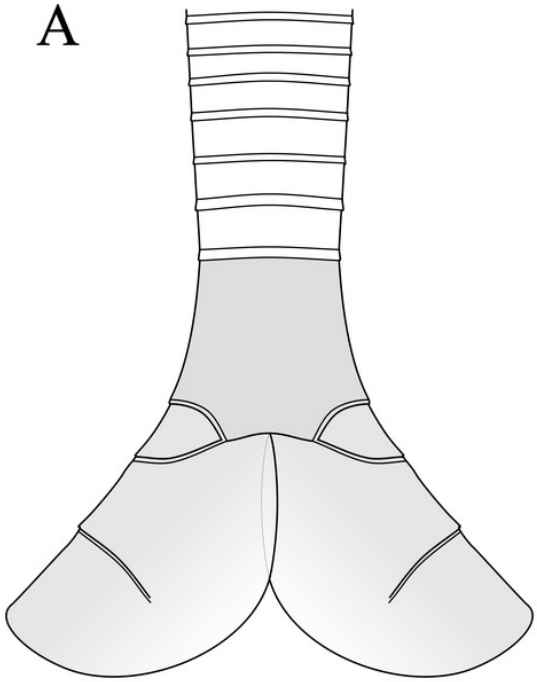
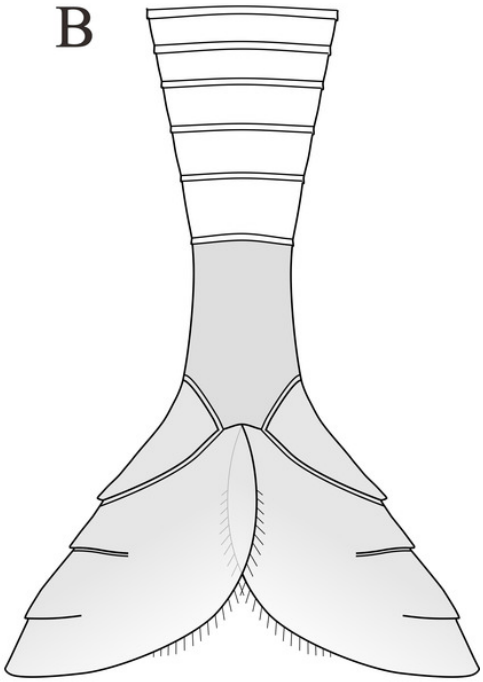
Figure 5

Schematic drawings of the posterior part of the body of *Pectocaris* species.

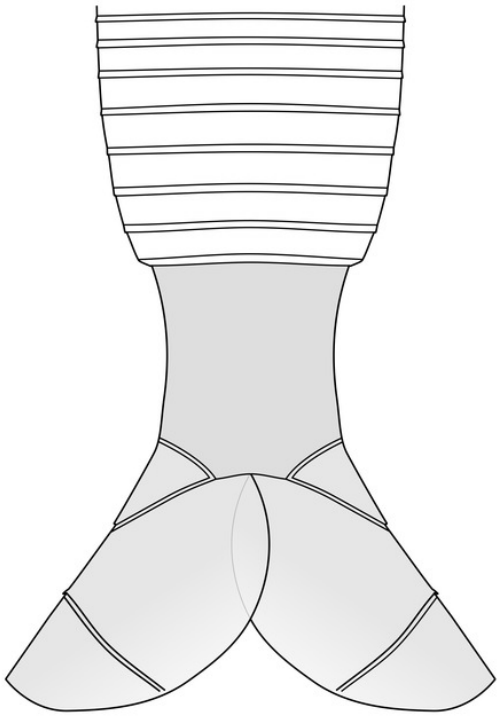
Based on Hou & Sun (1988), Hou (1999), Hou et al. (2004b), Jin et al. (2021), and the present study. Not to scale.



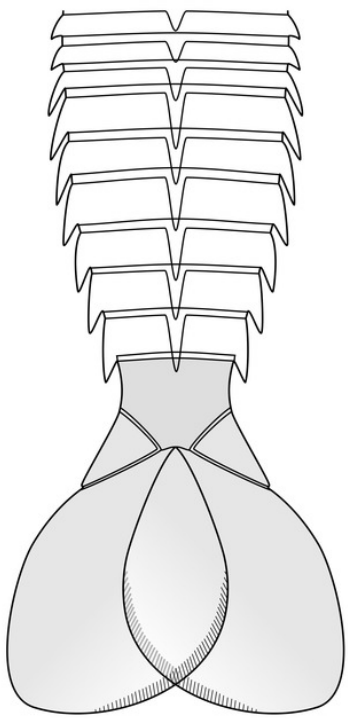
P. paraspatiosa sp. nov



P. eurypetala



P. spatiosa



P. inopinata

Table 1(on next page)

Brief comparison of the abdomen and telson morphologies of *Pectocaris*.

Species / Characters	*P. paraspatiosa* sp. nov.	*P. eurypetala*	*P. spatiosa*	*P. inopinata*
Carapace	Sub-parallelogram in lateral view	Sub-parallelogram in lateral view/ V-shaped opening in dorsal lateral view	Sub-parallelogram in lateral view	Sub-parallelogram in lateral view
n of endopodal podomeres	>24	c.40	>20	>19
Endite	Slender, sparsely spaced, with 6 spines	Slender, tightly spaced, with 6 spines	Not clear, probably tightly spaced	Stout, tightly spaced, with 6 spines
Terminal claw(s) of endopod	Nnknown	Small	Nnkown	Small, accompanied by prominent paired spines
Abdomen segments length	Sub-equal, relatively wide	Increasing posteriorly, relatively wide	Sub-equal, relatively narrow	Increasing posteriorly, relatively wide
Shape of caudal segment	Sub-trapezium, wide, middle	Sub-rectangle, narrow, long	Sub-rectangle, wide, short	Sub-square, narrow, short
Telson fluke	Blade like, broad	Blade like, slender	Blade like, broad	Paddle like, broad

Table 2(on next page)

Table 2. Summary of fossil taxa (families and lower ranks) shared by Chengjiang biota, the Yu'anshan Member (Chiungchussu Formation) and Xiaoshiba biota/Xiazhuang assemblage, the Hongjingshao Member (Tsanglangpu Formation).

Shared taxon	Species in Yu'anshan Member	Species in Hongjingshao Member
Genus *Wiwaxia* Walcott, 1911	*Wiwaxia papilio* Zhang et al., 2015 (Zhao et al., 2014)	*Wiwaxia foliosa* Yang et al., 2014
Genus *Kutorgina* Billings, 1861	*Kutorgina chengjiangensis* Zhang et al., 2007	*Kutorgina chengjiangensis* (Zeng et al., 2014)
Genus *Selkirkia* Walcott, 1911	*Selkirkia sinica* (= *Paraselkirkia sinica*) (Luo & Hu in Luo, Hu, Chen, Zhang & Tao, 1999)	*Selkirkia sinica* Luo and Hu,1999 (Lan et al., 2015)
Genus *Sicyophorus* Luo & Hu in Luo, Hu, Chen, Zhang & Tao, 1999	*Sicyophorus rarus* Luo & Hu in Luo, Hu, Chen, Zhang & Tao, 1999	*Sicyophorus* sp. (Zeng et al., 2014)
Genus *Mafangscolex* Hu, 2005	*Mafangscolex sinensis* Hou & Sun, 1988	*Mafangscolex* cf. *yunnanensis* Yang et al., 2020
Genus *Hallucigenia* Conway Morris, 1977	*Hallucigenia fortis* Hou & Bergström, 1995	*Hallucigenia*? (Zeng et al., 2014)
Family Luolishaniidae Hou and Bergström, 1995	*Luolishania longicruris* Hou & Chen, 1989	*Collinsium ciliosum* Yang et al., 2015
Genus *Pectocaris* Hou et al., 2004a	***P. eurypetala* (Hou & Sun, 1988), *P. inopinata* Jin et al., 2021, *P. spatiosa* Hou, 1999**	***P. eurypetala*, *P. paraspatiosa* sp. nov., *P. inopinata*, *P. spatiosa* (this study)**
Genus *Jugatacaris* Fu & Zhang, 2011	*Jugatacaris agilis* Fu & Zhang, 2011	*Jugatacaris*? sp. (Zeng et al., 2014)
Genus *Combinivalvula* Hou, 1987	*Combinivalvula chengjiangensis* Hou, 1987	*Combinivalvula* sp. (Zeng et al., 2014)

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Shared taxon	Species in Yu'anshan Member	Species in Hongjingshao Member
Genus Chengjiangocarididae Hou and Bergström, 1997	*Chengjiangocaris longiformis* Hou & Bergström, 1991	*Chengjiangocaris kunmingensis* Yang et al., 2013 *Alacaris mirabilis* Yang et al., 2018
Genus *Fuxianhuia* Hou, 1987	*Fuxianhuia protensa* Hou, 1987 (Hou & Bergström, 1997)	*Fuxianhuia xiaoshibaensis* Yang et al., 2013
Genus *Kuanyangia* Hupé, 1953	*Kuanyangia pustulosa* (Lu, 1941), *Kuanyangia* sp. of Hou & Bergström, 1997 (Hou et al., 2004b, 2017)	*Kuanyangia (Sapushania) granulosa* Zhang, 1966 (Zeng et al., 2014)
Genus *Yunnanocephalus* Kobayashi, 1936	*Yunnanocephalus yunnanensis* (Mansuy, 1912) (Hou et al., 2004b)	*Yunnanocephalus yunnanensis* (Mansuy, 1912) (Zeng et al., 2014)
Genus *Dolerolenus* Leanza, 1949	*Dolerolenus* (*Malungia*) *laevigata* Lu, 1961 *Dolerolenus* (*Malungia*) *malungensis* Lu, 1961	*Dolerolenus* (*Malungia*) *laevigata* Lu, 1961 *Dolerolenus* (*Malungia*) *malungensis* Lu, 1961
Genus *Chengjiangaspis* Zhang & Lin, 1980	*Chengjiangaspis chengjiangensis* Zhang & Lin, 1980	*Chengjiangaspis chengjiangensis* (Hou et al., 2019)
Genus *Hongshiyanaspis* Zhang & Lin, 1980	*Hongshiyanaspis yiliangensis* Zhang et al., 1980	*Hongshiyanaspis yiliangensis* (Hou et al., 2019)
Genus *Liangwangshania* Chen, 2005	*Liangwangshania biloba* Chen, 2005	*Liangwangshania biloba*? Chen, 2005