

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

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Pectocaris are intermediate- to large-sized Cambrian bivalved arthropods. Previous studies have documented *Pectocaris* exclusively from the Cambrian Series 2 Stage 3 Chengjiang biota in Yu'an-shan Formation, Chiungchussu Stage in SW China. In this study, we report *Pectocaris paraspatisosa* sp. nov., and three other previously known *Pectocaris* from the Xiazhuang section in Kunming, which belongs to the Hongjingshao Formation and is a later phase within Cambrian Stage 3 than the Yu'an-shan Formation. The new species can be distinguished from its congeners by the sparsely arranged endopodal endites and the morphologies of the abdomen, telson, and telson processes. We interpret *P. paraspatisosa* sp. nov. as a filter-feeder and a powerful swimmer adapted to shallow, agitated environments. Comparison among the *Pectocaris* species reinforces previous views that niche differentiation had been established among the congeneric species based on morphological differentiation. Our study shows the comprehensive occurrences of *Pectocaris* species outside the Chengjiang biota for the first time. With a review of the shared fossil taxa of Chengjiang and Xiaoshiba biotas, we identify a strong biological connection between the Yu'an-shan and Hongjingshao Formations.

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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 Stage 3 Chengjiang biota in Yu'an-shan Formation, Chiungchussu Stage in SW China. In this study, we report *Pectocaris paraspatiosa* sp. nov., and three other previously known *Pectocaris* from the Xiaozhuang section in Kunming, which belongs to the Hongjingshao Formation and is a later phase within Cambrian Stage 3 than the Yu'an-shan Formation. The new species can be distinguished from its congeners by the sparsely arranged endopodal endites and the morphologies of the abdomen, telson, and telson processes. We interpret *P. paraspatiosa* sp. nov. as a filter-feeder and a powerful swimmer adapted to shallow, agitated environments. Comparison among the *Pectocaris* species reinforces previous views that niche differentiation had been established among the congeneric species based on morphological differentiation. Our study shows the comprehensive occurrences of *Pectocaris* species outside the Chengjiang biota for the first time. With a review of the shared fossil taxa of Chengjiang and Xiaoshiba biotas, we identify a strong biological connection between the Yu'an-shan and Hongjingshao Formations.

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. euryptala* (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, Southwest China. They were characterized by the large carapace covering about half of the body length, a great number of short stout body segments, densely arranged comb-like appendages with multiple podomeres and broad telson processes (Hou et al., 2004b). *Pectocaris* had been considered as branchiopod crustaceans and resolved within Hymenocarina later, thus showing affinity with the Mandibulata (Hou, 1999; Hou et al., 2004b; Aria & Caron, 2017;

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 a swimming species in view of the well-developed abdomen and telson processes (Hou & Sun, 1988; Hou, 1999; Hou et al., 2004b; Jin et al., 2021). Although *P. inopinata* is interpreted as a predator and/or scavenger (Jin et al., 2021), the other two species of the genus have been regarded as filter feeders (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*, *Leancoilia*, *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 *Isoxys*, are found across the Cambrian period, spanning tens of millions of years (Williams et al., 1996; Hu et al., 2007; García-Bellido et al., 2009a; García-Bellido et al., 2009b; Sun et al., 2022; Ma et al., 2023). In addition to retrieving bio-stratigraphical connections among 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 in the Xiaoshiba Lagerstätte shows that it has some arthropod genera in common with the Chengjiang Lagerstätte, such as *Fuxianhuia* and *Chengjiangocaris*, and has been considered as the temporal continuation of the Chengjiang community (Yang et al., 2013 2016; Lan et al., 2018; Yang et al., 2018). Zeng et al., (2014) reported several specimens that resembled *Pectocaris* and/or *Jugatacaris*, the latter being phylogenetically close to *Pectocaris* according to 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 community. 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 paraspatisosa* sp. nov. along with several other previously known species of the genus, based on newly collected material from the Xiazhuang section (Fig 1). Based on the presence of *Pectocaris* the Xiazhuang assemblage and the morphological difference among *Pectocaris* species, we discuss the paleoecological, taphonomic, and biostratigraphic significances of the species.

MATERIALS AND METHODS

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'an-shan Formation at its lower part and the Hongjingshao Formation at its upper part, both belonging to Cambrian Series 2 (Zeng et al., 2014). In the Hongjingshao Formation, we obtained abundant specimens of *Hongshiyanaspis*, *Fuxianhuia*, *Kutorgina* and *Paraselkirkia*, which are characteristic elements of this formation. In addition, 36 specimens of bivalved arthropods are found to co-occur with the above taxa and are reported in this study.

In the laboratory, fossil specimens were excavated with steel needles, and were 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.

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SYSTEMATIC PALEONTOLOGY

Phylum ARTHROPODA von Siebold, 1848
Class UNCERTAIN
Order PECTOCARIDIDA Simonetta and Delle Cave, 1975
Family PECTOCARIDIDAE Hou, 1999
Genus PECTOCARIS Hou, 1999

Type species. Pectocaris spatiosa Hou, 1999.

Other species. Pectocaris euryptala (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 lateral processes 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); Paratypes: YKLP 16290, YKLP 16291, YKLP 16292, YKLP 16293 (Figs 3E, G, I, K).

Other material examined. YKLP 16294, YKLP 16295, YKLP 16296, YKLP 16297, YKLP 16298, YKLP 16299, YKLP 16300 (see supplementary material).

Diagnosis. Intermediate-sized *Pectocaris* species. Carapace sub-rectangular. Trunk segments sub-equal in width but progressively longer posteriorly and without sudden narrowing towards to the telson. Telson processes separated and each almost straight on both outsides. Endites slender, more sparsely spaced than congeners, with gap between endites sub-equal to or slightly larger than width of endite.

Preservation. All the 12 specimens studied herein are incomplete. The holotype (Fig 2A, B, 3A, B) preserves the overall outline of carapace, about 19 trunk segments, telson, and some appendages. The carapace is inverted by 180° relative to trunk, presumably due to taphonomic process. The appendages are somewhat dislocated yet with fine details. The other 11 ones preserve the posterior part of the trunk and in some specimens also the telson processes.

Regarding its preservation, the holotype has the carapace laterally compressed, while the trunk is dorso-ventrally compressed, judging from the shape and width of the telson and the lateral position of the notches which would hold the telson processes if the specimen was complete. Among the other specimens, which only have trunk segments preserved, 10 are preserved in dorsal–ventral aspect (Figs 3E, G, I, K and supplementary material), and one is preserved in oblique-lateral aspect judged from the widths of the telson and the telson processes (see supplementary material, YKLP 16299).

Remarks. We interpret the carapace of the holotype as being inverted by 180° for many reasons. Firstly, in general, the most anterior of the carapace in the species of *Pectocaris* is usually sagittal and the posterior end is broader (cf. the left and the right end of carapace in Figs. 2A, 3A) (Hou, 1999; Hou et al., 2004b; Fu & Zhang, 2011; Jin et al., 2021). Secondly, the dorsal margin of the carapace of *Pectocaris* is often nearly straight while the ventral margin is usually convex. Thirdly, the gently curved trunk of the holotype, which overlains the anterior margin of the carapace, can be better explained as a relative rotation between the trunk and the carapace (as seen in other species of *Pectocaris*), rather than a dorsal-ward dislocation of the trunk.

Description. The carapace is elongate (Figs. 2A, B), with comparatively straight dorsal and ventral margins. The posterior margin has shaped postero-dorsal part showing appearance of being “cut off”, leaving short straight edge (Fig. 2A). The postero-dorsal angle is about 150°. A straight rod-like structure in the posterior part of the carapace that connects the dorsal and ventral margins is interpreted as the breakage of the carapace. Marginal spines and ornaments are absent.

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

The telson is sub-trapezoidal, with anterior part sub-equally as wide as the last abdominal segments, while its posterior part is significantly wider, interrupted by small postero-lateral notches (Figs 2B, 3B, E–L). A small sub-triangular sclerite that possibly denotes acute lateral extensions (Izquierdo-López & Caron, 2022b) is present in each notch, connecting the telson with broad, sub-divided telson processes (Figs. 3E–L). A pair of shallow grooves are present on the telson processes.

Trunk appendages are only preserved in the holotype (Figs. 2, 3A–D), all being incomplete

and more or less dislocated from *in vivo* positions, the longest one consisting of more than 24 podomeres (Fig. 2E). Each podomere bears one sub-quadrate or slightly trapezoidal endite carrying up to six slender apical setae (Figs. 2C, F, G, I). Endite setae in the proximal part of the limb (Figs. 2G, I) are somewhat thicker than those in the distal part (Figs. 2C, F). The distance between endites is sub-equal to, or slightly larger than the width of each endite (Figs 2C, F). The overall shape of the exopod is not resolved, but it can be seen to bear densely arranged, short marginal setae (Figs. 2D, H).

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), such as the sagittal anterior end and the “cut-off” shaped postero-dorsal edge. Like other *Pectocaris* species, *P. paraspatisosa* sp. nov. lacks the dorsal fin-like structure which is characteristic of *J. agilis* (Fu & Zhang, 2011). The *Waptia*-like bivalved arthropod *Xiazhuangocaris chenggongensis* from the same section (Zeng et al., 2020) can be readily recognized by the prominent anterior notch and narrow anterior tip of the carapace.

The abdomen of *P. paraspatisosa* sp., nov. tends to be sub-equally wide throughout its length 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 setae-bearing endites (in *P. inopinata*, the setulose endites are present in posterior trunk appendages and in proximal section of anterior trunk appendage). 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 Formation, Cambrian Stage 3, Series 2.

OTHER *PECTOCARIS* SPECIES FROM THE XIAZHUANG SECTION

In addition to the 12 specimens of *P. paraspatisosa* 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 trunk and sometimes also with the telson processes, 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), the most useful traits characterizing the present species include the morphology of the limbs, the abdomen, the telson and the telson processes. The comparison of *P. paraspatisosa* sp. nov. with its congeners from Chengjiang biota show that 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, shape of telson and telson processes, number of trunk-appendage podomeres, and details of enditic armatures (Table 1; Fig. 5). Based on the materials collected in Xiazhuang section, we distinguish *P. eurypetala* from other species by the more widely spaced abdominal segments while distinct slender telson and the longer broad telson processes (Figs. 4G, H, 5B). Even though the limb endites of *P. spatiosa* are poorly preserved, it can still be recognized by the broad and short abdomen. Along with the sub-rectangular telson and the broad, paddle like telson processes decorated with longer shallow groove, there are typical characters for this species (Figs. 4A–F, 5C). Although there is only one specimen of *P. inopinata*, the characteristic dorsal and lateral spines on the abdominal segments provide unambiguous evidence of its presence within the present samples (Figs. 4K, L, 5D). One specimen is identified as *Jugatacaris agilis* based on its fused telson processes, a characteristic that is absent in *Pectocaris* (Figs. 4I, J).

DISCUSSION

Ecology

Like other species of the genus *Pectocaris*, the strongly built multi-segmented trunk of *P. paraspatisosa* sp. nov. attached to broad telson processes (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 telson processes in beating water. The setulose exopods could as well provide propulsion, even if it is difficult to quantify due to their fragmental preservation in the present specimens. Such assumptions need 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. paraspatisosa* sp. nov. carrying setulose endites (Figs. 2C, F, G, I), similar to *P. euryptetala*, *P. spatiosa*, and *J. agilis*, suggest a filter-feeding behavior as had been interpreted for the latter three species (Hou et al., 2004b; Fu & Zhang, 2011). The endites of *P. paraspatisosa* sp. nov. are more sparsely arranged compared with other *Pectocaris* species and *J. agilis*. This may imply that the new species could filter larger food particles. In addition, the endite setae on the proximal section of the endopods of *P. paraspatisosa* 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. paraspatisosa* 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 adapting to various ecological niches. 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 Hymenocarina (see e.g., Izquierdo-López & Caron, 2022a) in the Hongjingshao, which however is less diversified than the hymenocarines in the Chengjiang and the Burgess Shale faunas (Briggs, 1994; Hou et al., 2017; Izquierdo-López & Caron, 2022a). The only verified bivalved arthropods at the Hongjingshao Formation 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, *Clypecaris* and *Ercaicunia* have not been reported from this site. Considering the generally coarse lithology compared with the mudstones in the Yu'an Shan Formation where the Chengjiang biota is preserved, this may denote stronger hydraulic conditions that were unfavorable for the smaller swimming arthropods.

Taphonomic implications

A noticeable feature of the *Pectocaris* specimens from the Xiazhuang section is that except for the holotype (Fig. 2) and one *P. spatiosa* specimen (Figs. 4A, B), all other specimens only preserve the posterior part of the trunk, with anterior part of the body and appendages missing. Although one complete individual of *X. chenggongensis* and one specimen of *Jugatacaris?* sp. preserved with carapace and appendicular details were reported from the same stratum (Zeng et al., 2014, 2020), such cases have been rare. By contrast, the intermediate- and large-sized hymenocarines in the Cambrian series 2 strata elsewhere, represented by the *Pectocaris* species and *Jugatacaris agilis* from the Chengjiang biota (Yu'an Shan Formation, see Hou et al., 2004b; Fu & Zhang, 2011; Jin et al., 2021), and the pectocaridid-like arthropod from the Xiaoshiba biota, usually preserve both the anterior and the posterior parts of the body, although incomplete specimens with only the posterior part of the trunk can also be found (e.g., the Meishucun

section, see Hou & Sun, 1988). Considering the combined effects of living environment, burial environment, burial process and individual size on biological preservation (Saleh et al., 2020, 2021, 2022b), our interpretations of taphonomy implications are described below.

The clastic sediments of Hongjingshao Formation at the Xiazhuang section contain a great portion of siltstone and sandstone beds, being generally coarser than the underlying Yu'an-shan Formation that is deposited as part of a delta and dominated by mudstones (Zeng et al., 2014; Saleh et al., 2022a; our field observation). This presumably denotes strong hydrodynamics and would result in more intensified mechanical breakage of the thanatocoenosis before burial, as discovered in modern sedimentary systems (e.g., Zhai et al., 2015). Meanwhile, the Hongjingshao stratum lacks the alternating background and event beds, which are characteristic of the Yu'an-shan Formation containing soft-bodied Chengjiang biota (Zeng et al., 2014). Previous investigations suggested that post-mortem transport was limited in the event beds, where the thanatocoenosis probably experienced fast, *in situ* burial (Zhao et al., 2009, 2012). 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 strong hydraulic 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. paraspatisosa* sp. nov. had been a powerful swimmer adapted to turbulent environments.

Meanwhile, the selective preservation of our *Pectocaris* specimens may be due to the fact that the anterior part of their body 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 sclerotization in 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

o 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 *Clypeocaris* 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 labile anterior part of body in most of the specimens. Whether the turbulent 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 Formation were dominated by large individuals as well.

Biostratigraphical connection between Hongjingshao and Yu'anshan Formations

The Hongjingshao (Member) Formation, 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 Formation, 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 Stage and the upper part of the Chiungchussu Stage, respectively, the Hongjingshao and the Yu'anshan Formations had been originally distinguished by lithology. Meanwhile, the Yu'anshan Formation yields the Chengjiang Lagerstätte (Zhang & Hou, 1985;

Chen et al., 1996; Hou et al., 2004b, 2017), and the Hongjingshao Formation 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'an-shan Formation and the Hongjingshao Formation 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 Formation (of Tsanglangpu Stage) and the Yu'an-shan Formation (of Chiungchussu Stage).

We concur with Zeng et al. (2014) that the Hongjingshao Formation is diachronous. As lithostratigraphic 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 in 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 Formation is transitional for Cambrian marine communities, also opening up some new genera and species. The extension of some species from the Yu'an-shan Formation into the Hongjingshao Formation indicates that these species were 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., as the fourth species of the genus, from the Cambrian Series 2 Hongjingshao Formation at the Xiazhuang section, Kunming, China. The new

species can be distinguished from its congeners by a number of features, including the sub-equal widths of posterior trunk segments and their greater length, the absence of dorsal and lateral body spines, the shape of telson, and the sparsely distributed setulose endites on the endopods. We interpret *P. paraspatisosa* sp. nov. as a powerful swimmer adapted to relatively strong hydraulic condition in shallow water, based on a combination of evidence including the broad telson processes, 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 is polymorphic and intra-genus niche differentiation was established by morphological differentiation. Such inference is 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 favored 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 Formation and the underlying Yu'anshan Formation, reinforcing conclusions made by previous studies that both the Xiaoshiba Lagerstätte and the Xiazhuang assemblage were continuing the Chengjiang biota.

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Figure captions

Figure 1. Distribution of the main localities of the Chengjiang biota, Yunnan Province and the position of the specimen in the stratum. A, Black 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 study (Xiazhuang section) (redrawn in Hou et al., 2017). B, Stratigraphic column of the Xiazhuang section (redrawn in Zeng et al., 2014). Red arrowhead indicates the position of the specimen analyzed in the present study.

Figure 2. *Pectocaris paraspatiosa* sp. nov. (YKLP 16289a and b, holotype) from the Hongjingshao Formation at Xiazhuang section. A, part, overview. Note that the carapace is invert by 180° 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 endite. D, exopod

setae (rectangle in A). E, trunk appendages (rectangle in B). F, details of one of the endopods (rectangle in B), showing seven 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; rs, rod-like structure; rv, right valve; *sn*, 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 Formation at Xiazhuang section. A, B, holotype (YKLP 16289a and b), explanatory drawings of the overviews in Figs. 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 (*Hongshiyanspis*) is preserved with this specimen (adjacent to its telson processes). 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 telson processes.

Figure 4. Other species of the genus *Pectocaris* from the Hongjingshao 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 telson processes. K, L, *Pectocaris inopinata* Jin et al., 2021, YKLP 16304, note the lateral-dorsal abdominal spines characterizing this species. *Additional abbreviations*: an, anus.

Figure 5. Schematic drawings of the posterior part of the body and the endites 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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Figure 1

Distribution of the main localities of the Chengjiang biota, Yunnan Province and the position of the specimen in the stratum.

(A) Black 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 study (Xiazhuang section) (redrawn in Hou et al., 2017). (B) Stratigraphic column of the Xiazhuang section (redrawn in Zeng et al., 2014). Red arrowhead indicates the position of the specimen analyzed in the present study.

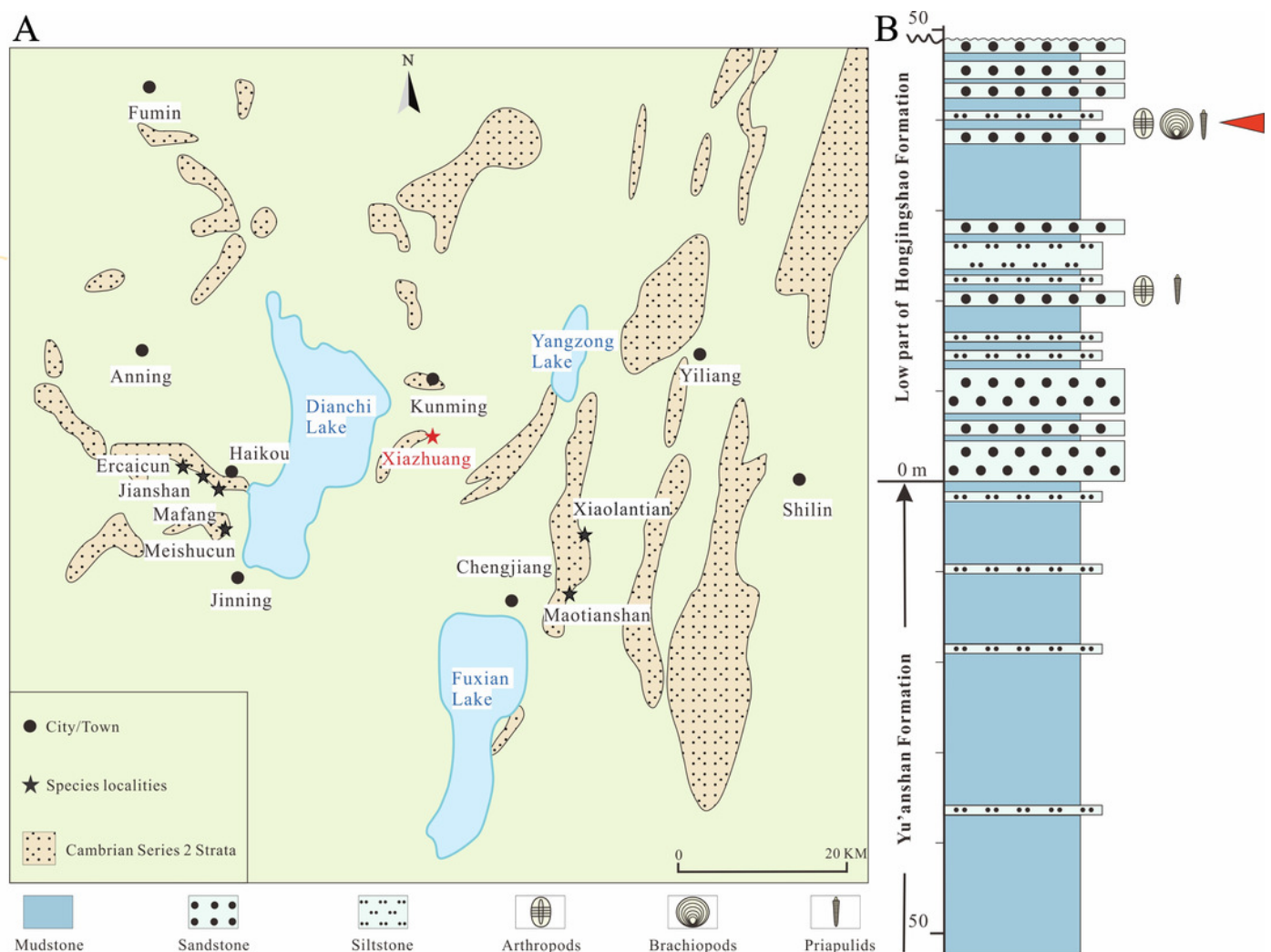


Figure 2

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

(A) part, overview. Note that the carapace is invert by 180° 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 endite. (D) exopod setae (rectangle in A). (E) trunk appendages (rectangle in B). (F) details of one of the endopods (rectangle in B), showing seven 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; rs, rod-like structure; rv, right valve; *sn*, the *n*th body segment (counted from posterior to anterior); st, seta(e); tpm, posterior margin of telson; ts, telson.

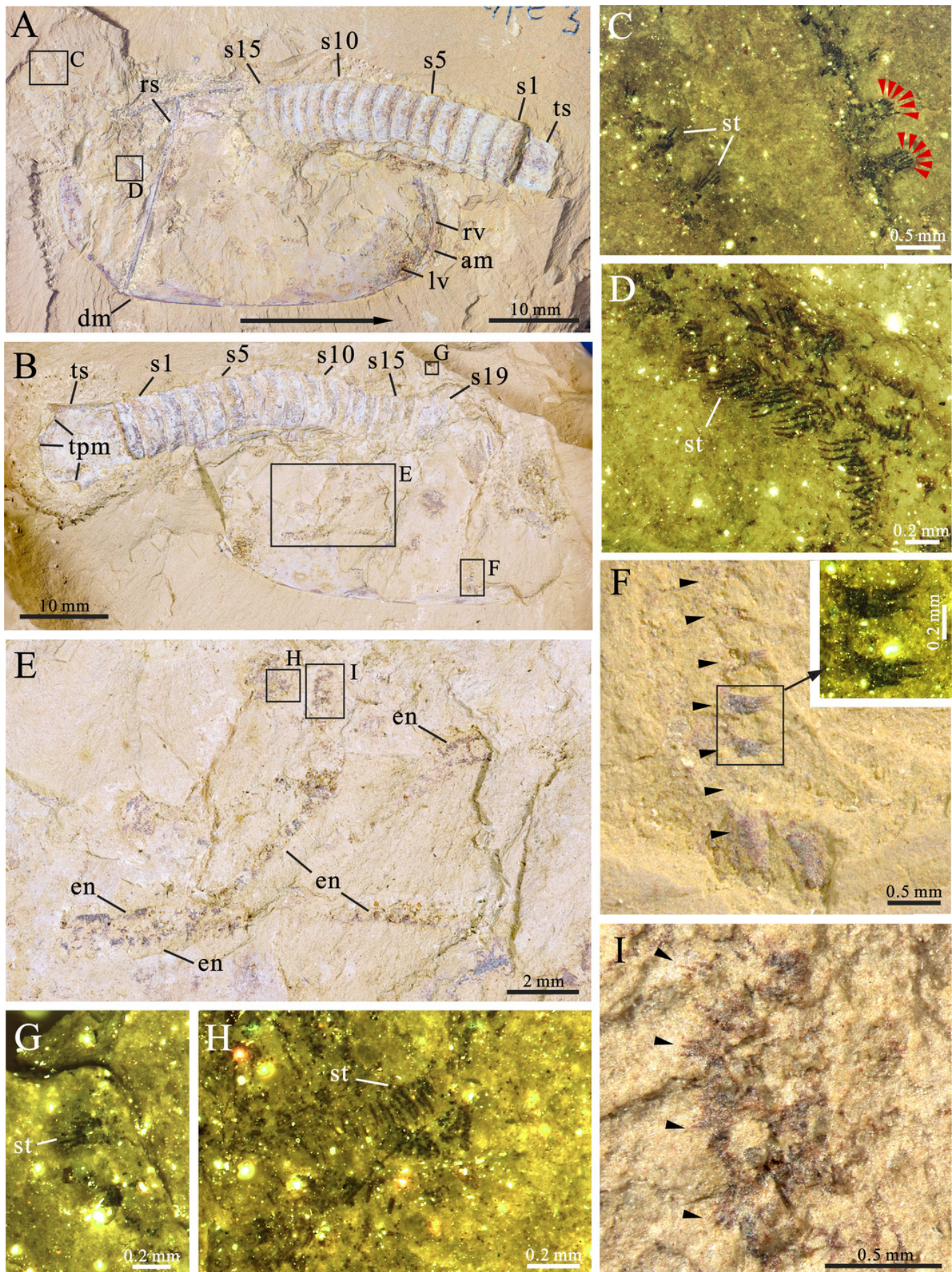


Figure 3

Pectocaris paraspatiosa sp. nov. from the Hongjingshao Formation at Xia Zhuang 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 (*Hongshiyanspis*) is preserved with this specimen (adjacent to its telson processes). (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 telson processes.

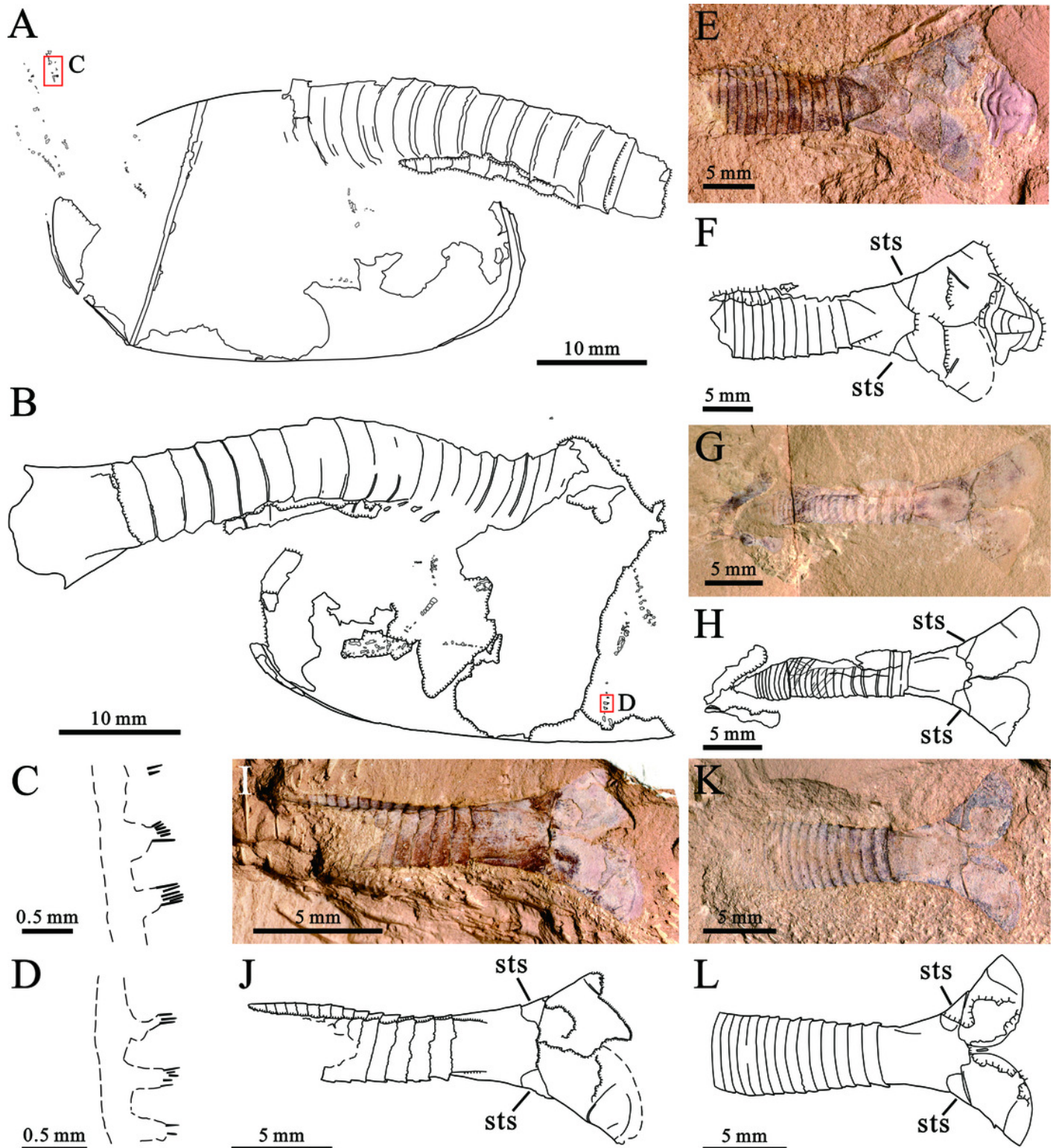


Figure 4

Other species of the genus *Pectocaris* from the Hongjingshao 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 and H), *Pectocaris eurypetala* Hou & Sun, 1988, YKLP 16302. (I and J), *Jugatacaris?* sp., YKLP 16303, note the fused left and right telson processes. (K and L) *Pectocaris inopinata* Jin et al., 2021, YKLP 16304, note the lateral-dorsal abdominal spines characterizing this species. *Additional abbreviations:* an, anus.

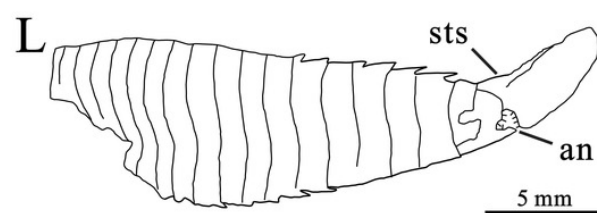
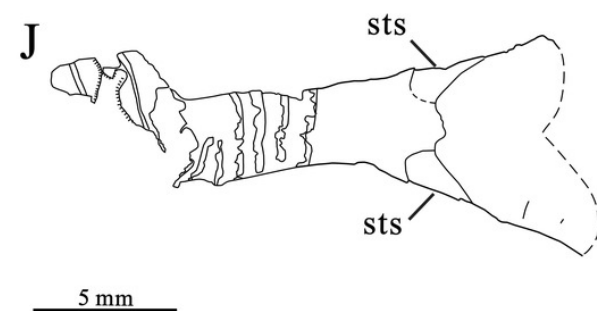
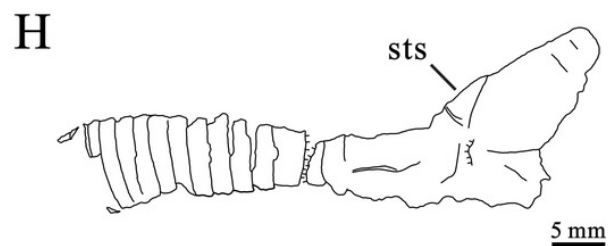
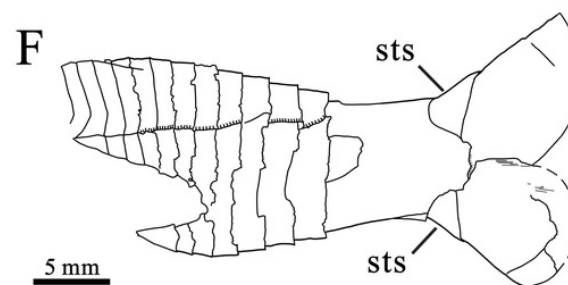
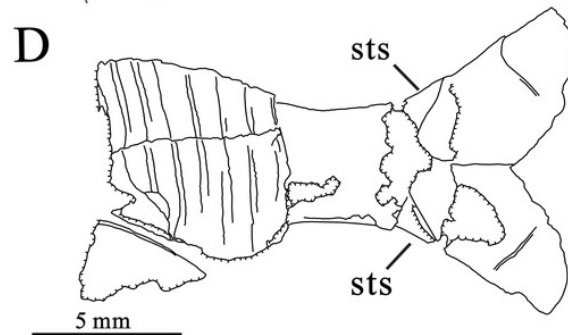
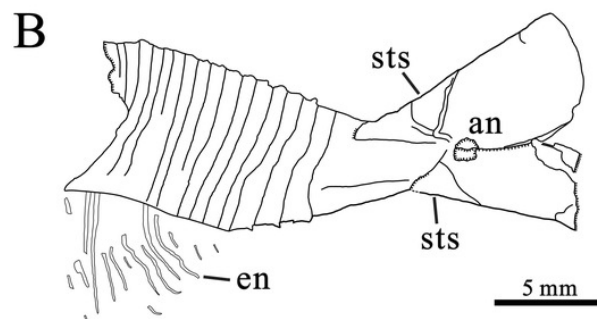
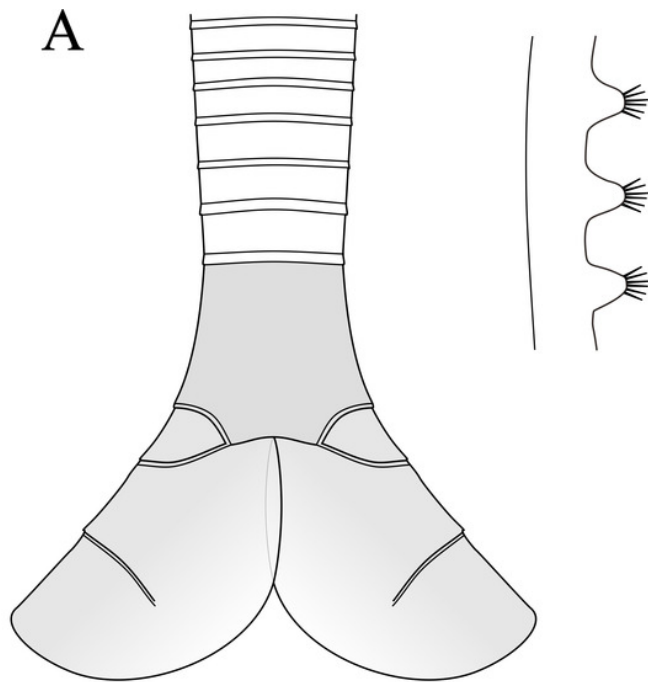


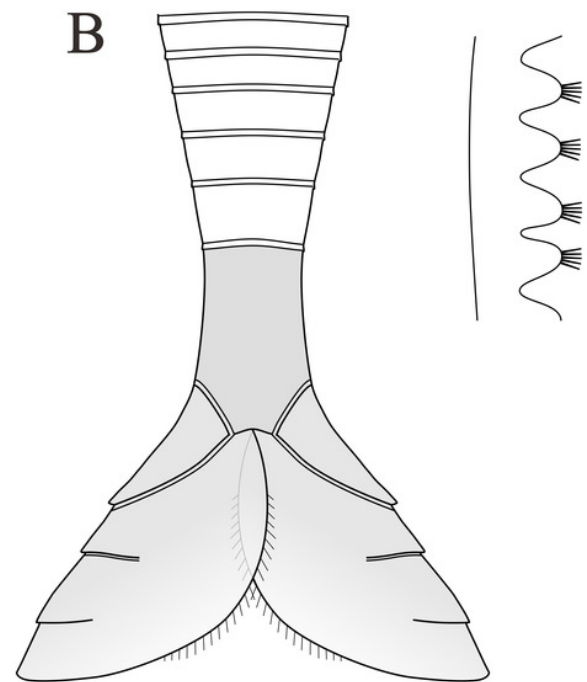
Figure 5

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

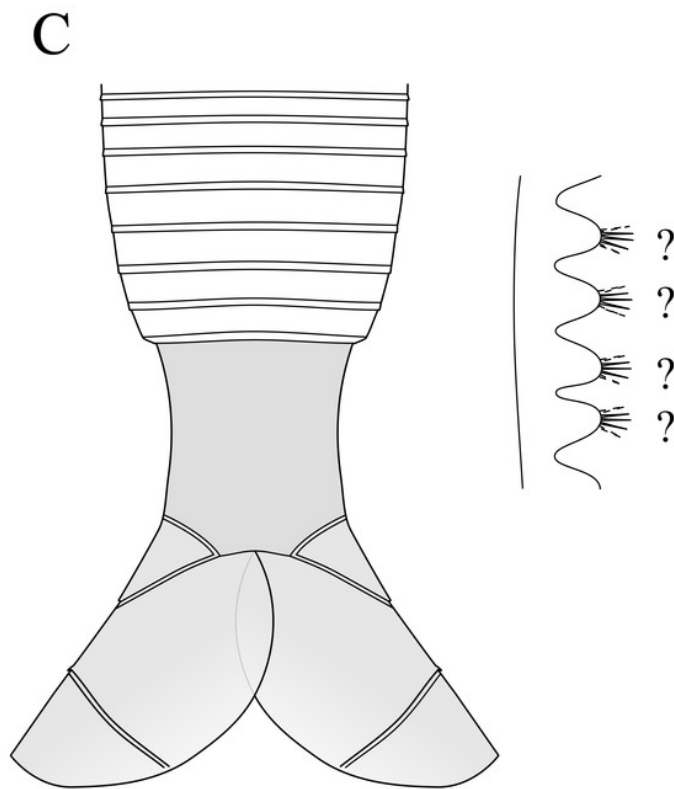
Based on Hou & Sun (1988), Hou (1999), Hou et al. (2004b), Jin et al. (2021), and the present study. Not to scale.



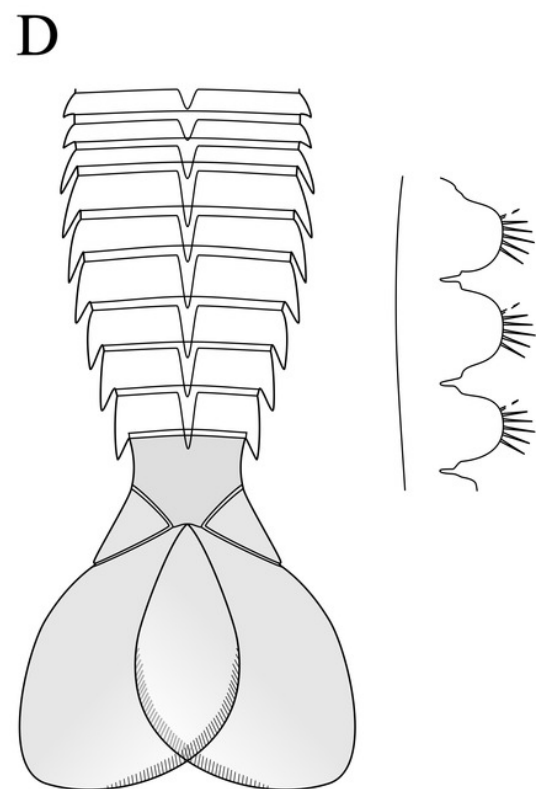
P. paraspatisosa sp. nov



P. eurypetala



P. spatiosa



P. inopinata

Table 1(on next page)

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

Species	<i>P. paraspatisosa</i> sp. nov.	<i>P. eurypetala</i>	<i>P. spatiosa</i>	<i>P. inopinata</i>
Characters				
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
<i>n</i> of endopodal podomeres	>24	c.40	>20	>19
Endite	Slender, sparsely spaced, with 6 spines	Slender, tightly spaced, with 6 spines	Slender, tightly spaced	Stout, tightly spaced, with 6 spines
Terminal claw(s) of endopod	Unknown	Small	Unkown	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 telson	Sub-trapezium, wide, middle	Sub-rectangle, narrow, long	Sub-rectangle, wide, short	Sub-square, narrow, short
Telson processes	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 Formation (Chiungchussu Stage) and Xiaoshiba biota/Xiazhuang assemblage, the Hongjingshao Formation (Tsanglangpu Stage).

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

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

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