

The endemic radiodonts of the Cambrian Stage 4 Guanshan Biota of South China

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The Guanshan Biota (South China, Cambrian, Stage 4) contains a diverse assemblage of biomineralizing and non-biomineralizing animals. Sitting temporally between the Stage 3 Chengjiang and Wuliuan Kaili Biotas, the Guanshan Biota contains numerous fossil organisms that are exclusive to this exceptional deposit. The Guanshan Konservat-Lagerstätte is also unusual amongst Cambrian strata that preserve non-biomineralized material, as it was deposited in a relatively shallow water setting. In this contribution we double the diversity of radiodonts known from the Guanshan Biota from two to four, and describe the second species of *Paranomalocaris*. In addition, we report the first tamisiocaridid from South China, and confirm the presence of a tetradial oral cone bearing small and large plates in “*Anomalocaris*” *kunmingensis*, the most abundant radiodont from the deposit. All four radiodont species, and three genera, are apparently endemic to the Guanshan Biota. When considered in the wider context of geographically and temporally comparable radiodont faunas, endemism in Guanshan radiodonts is most likely a consequence of the shallower and more proximal environment in which they lived. The strong coupling of free-swimming radiodonts and benthic communities underlines the complex relationship between the palaeobiogeographic and environmental distributions of prey and predators. This local adaptation of radiodonts to their prey is highlighted by the frontal appendage morphology of the two species of *Paranomalocaris*, apparently specialised to different feeding modes, while the recognition of the limited geographic range of some radiodont faunas highlights the importance of exploring as many deposits as possible to fully understand this group.

Key words: Amplectobeluidae, Anomalocarididae, Tamisiocarididae, *Paranomalocaris*, Burgess Shale-type exceptional preservation, shallow water, Cambrian, China.

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Introduction

South China is crucial for our understanding of the early evolution of animal life, as it is home to numerous Cambrian deposits that preserve non-biomineralized fossils (Steiner

et al. 2005; Zhang et al. 2008; Gaines 2014; Muscente et al. 2017). The most prolific of these Burgess Shale-type (BST) deposits (e.g., Chengjiang, Fandian, Qingjiang, Xiaoshiba) belong to the Cambrian Stage 3 (Zhang et al. 2001, 2008; Hu et al. 2010b; Hou et al. 2017; Fu et al. 2019; Du et al.

2020). The Cambrian (Stage 4) Wulongqing Formation, which hosts the Guanshan Biota, falls stratigraphically between these fossil sites and another prolific Cambrian BST deposit, the Wuliuan Kaili Formation (Zhao et al. 2011). As such, it complements the South Chinese fossil record of Cambrian non-biomineralizing organisms, and allows the evolution of marine palaeocommunities to be examined at a high temporal resolution (Hu et al. 2010b, 2013; Hopkins et al. 2017; Chen et al. 2019; Zhang et al. 2008; Zhao et al. 2020; Du et al. 2020). In South China, the Guanshan Biota is sub-contemporaneous to the less diverse Balang (Peng et al. 2005) and Shipai faunas (Zhang and Hua 2005). It is also roughly temporally equivalent to several assemblages of exceptionally preserved fossils from around the world (Hu et al. 2013), such as the Emu Bay Shale Biota of East Gondwana (Paterson et al. 2016), the Sinsk Biota of Siberia (Ivantsov et al. 2005), or the Indian Spring (English and Babcock 2010) and Kinzers (Skinner 2005) biotas of Laurentia. This facilitates intercontinental faunal comparisons. For instance, like other Cambrian BST biotas in South China, the Guanshan fauna shows palaeobiogeographic affinities with the Emu Bay Shale fauna in East Gondwana. These similarities are interpreted as evidence for close proximity between these two palaeocontinents during the early Cambrian (Paterson et al. 2015; Holmes et al. 2018; Zhao et al. 2020).

The Guanshan Konservat-Lagerstätte is also important in its own right. It is a Tier 2 BST deposit (sensu Gaines 2014), which has yielded nearly 100 species from over 10 different sites (Liu et al. 2012, 2016; Hu et al. 2013; Chen et al. 2019; Zhao et al. 2020). Importantly, the abundant trace fossils and sedimentological evidence both suggest deposition in a relatively shallow-water shelf environment (Hu et al. 2013; Chen et al. 2019, 2020a; Ding et al. 2018, 2020), in striking contrast with the quiet, deep-water depositional settings inferred for most Cambrian Konservat-Lagerstätten (Gaines 2014). Non-biomineralizing components of the Guanshan fauna include ctenophores, eldoniids, poriferans, scalidophorans, vetulicolians, and a great diversity of panarthropods, such as lobopodians, radiodonts, artiopods, euarthropods with bivalved or folded carapaces, fuxianhuiids, and megacheirans (e.g., Luo et al. 2007; Hu et al. 2010b, 2012, 2013; Wang et al. 2013; Huang and Wang 2014; Li et al. 2015, 2017; Liu et al. 2016; Zeng et al. 2018a; Wu and Liu 2019; Chen et al. 2019, 2020b; Zhao et al. 2020). Exceptional preservation of non-biomineralized structures has also been documented in brachiopods (e.g., pedicle, setae, Hu et al. 2010a; Zhang et al. 2011; Hu et al. 2013; Chen et al. 2019) and trilobites (e.g., appendages, gut, Hu et al. 2013; Hopkins et al. 2017).

The Radiodonta from Guanshan Biota were represented so far by two species, *Anomalocaris kunmingensis* Wang, Huang, and Hu, 2013, and *Paranomalocaris multisegmentalis* Wang, Huang, and Hu, 2013, that were first described from a handful of isolated frontal appendages (Wang et al. 2013). The holotype of *A. kunmingensis* was subsequently re-illustrated by Liu et al. (2018: sup. fig.

3C), while Zeng et al. (2018a) described a well-preserved isolated oral cone that they tentatively assigned to the same species. This assignment was based on the much greater abundance of this taxon in the Wulongqing Formation compared to *P. multisegmentalis*, the authors noting that more than 100 frontal appendages of *A. kunmingensis* have been collected (Zeng et al. 2018a). More recently Zhao et al. (2020: fig. 4D, table 1) illustrated an incomplete frontal appendage and mentioned another radiodont fossil, both collected from a new Guanshan section, assigning both to an undetermined anomalocaridid species. In summary, despite the abundance of radiodont fossils in the Guanshan Konservat-Lagerstätte, only a handful of them have been illustrated to date: the five specimens composing the type material of *A. kunmingensis*, three additional frontal appendages figured by Hu et al. (2013), and the single oral cone tentatively assigned to *A. kunmingensis* by Zeng et al. (2018a), the incomplete holotype of *P. multisegmentalis*, and the recently illustrated frontal appendage from the Changchunshan section.

In the present contribution we describe new radiodont fossils from the Guanshan Konservat-Lagerstätte. This new material allows the description of two new taxa, including the first representative of the family Tamisiocarididae in South China, and confirms the presence of an oral cone in *Anomalocaris kunmingensis*. This newly documented diversity of the radiodont fauna from Guanshan is compared to that reported from other Cambrian Stage 4 BST deposits globally. The completely endemic fauna of Guanshan radiodonts suggests a strong influence of the benthic environment and its communities on the composition of these presumed free-swimming predators.

Institutional abbreviations.—YKLP, Key Laboratory for Palaeobiology, Yunnan University, Kunming, China.

Other abbreviations.—aux, auxiliary spine; BST, Burgess Shale-type; co, central opening of oral cone; ds, dorsal spine; en, endite; la, left appendage; lp, left large plate; oc, oral cone; om, organic matter; pd, podomere; pp, posterior plate; ra, right appendage; rp, right large plate; s, shaft podomere; sp, small plate; ts, terminal spine; w, ecdysozoan worm.

Nomenclatural acts.—This published work and the nomenclatural acts it contains, have been registered in ZooBank: urn:lsid:zoobank.org:pub:5FCBD9DE-C9BE-4A8F-9C68-0232D9829401

Overview of radiodont anatomy

Radiodonts are among the latest diverging members of the lower stem-group euarthropods (Daley et al. 2009; Ortega-Hernández 2016). Their body consists of a head region (typically equipped with dorsal and lateral sclerites, a pair of compound eyes, a circlet of sclerotized plates surrounding the mouth, a pair of protocerebral frontal appendages) and a

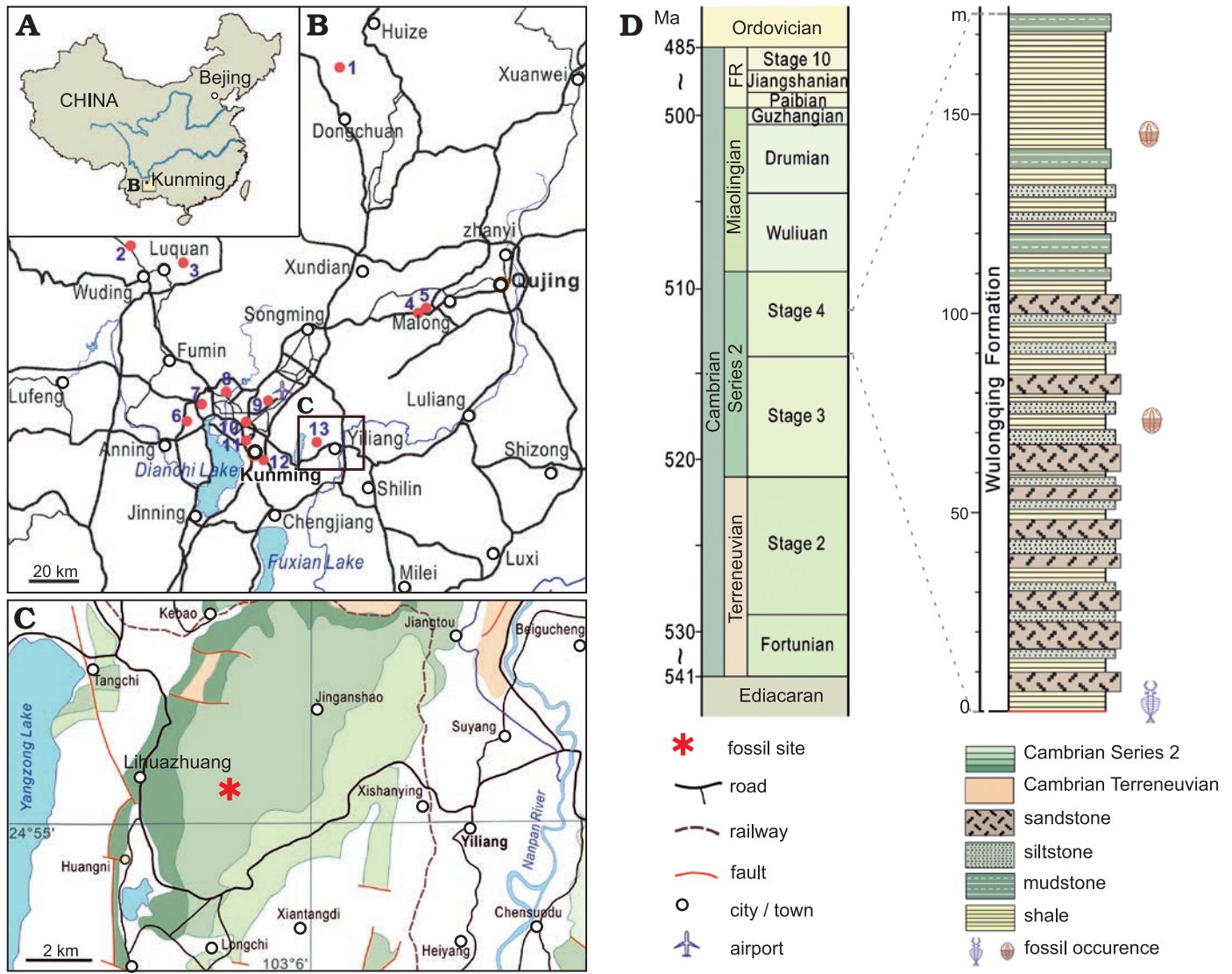


Fig. 1. **A.** Map of China showing location of the studied area. **B.** Map showing thirteen sites where fossil assemblages assigned to the Cambrian (Stage 4) Guanshan biota have been found: 1, Dahai (Liu et al. 2012); 2, Shijiangjun (Luo et al. 2008); 3, Xinlongcun (Liu et al. 2016); 4, Wulongqing (Luo et al. 2008); 5, Kanfuqing (Chen et al. 2019); 6, Baimei (Liu et al. 2016); 7, Qiongzhusi (Luo et al. 2008); 9, Dabanqiao (Luo et al. 2008); 10, Changchunshan (Zhao et al. 2020); 11, Gaoloufang (Luo et al. 2008; Hu et al. 2010); 12, Chenggongxincheng (Hu et al. 2013); 13, Lihuazhuang (Jiao et al. 2016; this study). **C.** The location of the Lihuazhuang section in (asterisk). **D.** Stratigraphic column showing the occurrence of the fossils reported in this study.

trunk region made of poorly-differentiated segments (Whittington and Briggs 1985; Daley et al. 2009; Paterson et al. 2011, 2020; Cong et al. 2014; Ortega-Hernández et al. 2017). The trunk bears one or two sets of paired swimming flaps laterally, which are considered as homologous to the biramous appendages of the more crown-ward deutero-pods (Van Roy et al. 2015). The frontal appendages attached adjacent to the ventral oral cone anteriorly, and were used for feeding following different strategies. These strategies include prey capture (e.g., Daley and Budd 2010; Daley and Edgecombe 2014; Liu et al. 2018), sediment sifting (e.g., Daley et al. 2013a; Moysiuk and Caron 2019) and even suspension feeding (e.g., Vinther et al. 2014; Van Roy et al. 2015; Lerosey-Aubril and Pates 2018). The frontal appendages consist of a series of well-sclerotized podomeres, sepa-

rated from one another by arthrodial membranes, and carrying endites of varied morphologies. Typically centimetric, these appendages were larger and more heavily sclerotized than the remains of most co-occurring non-biomineralizing organisms, which may partly explain the ubiquity of radiodonts in Cambrian BST deposits. Radiodont frontal appendages also provide a multitude of characters for phylogenetic analyses and systematics, which usually allow assignment of taxa up to the family level. Four families are currently recognized: Amplectobeluidae, Anomalocarididae, Hurdiidae, and Tamisiocarididae. Amplectobeluids, anomalocaridids, and tamisiocaridids have paired endites on their podomeres, differentiating them from hurdiids, which possess a single endite per podomere (with the sole exception of *Ursulinacaris*, see Pates et al. 2019a). Tamisiocaridids

bear slender endites that are typically longer than the height of their corresponding podomere, and are subequal in length along the appendage. In ampletobeluids and anomalocaridids, the endites are approximately the same length or usually shorter than the height of their corresponding podomere, and they alternate long/short on adjacent podomeres. Most ampletobeluids bear a distinctive hypertrophied endite in the proximal part of the appendage. Ampletobeluids may also differ from anomalocaridids in the presence of gnathobase-like structures posterior to the mouth, as-yet only documented in *Ampletobelua* and *Ramskoeldia* (Cong et al. 2017, 2018), and a possibly tetraradial, rather than triradial organization of the oral cone (Liu et al. 2018).

Geological setting

The Guanshan Biota is known from over 10 localities (Zhao et al. 2020) in the Wulongqing Formation in East Yunnan (Hu et al. 2013). This lithostratigraphic unit is comprised of sandstone, siltstone, and mudstone beds, with the lower part of the sequence deposited in a deeper-water environment than the higher levels (Hu et al. 2013; Chen et al. 2020). Exceptionally preserved fossils are most often retrieved from mudstone layers with minimal bioturbation, which probably represent rapid burial event beds according to sedimentological and taphonomic analyses (Hu et al. 2013; Forchielli et al. 2014). Sedimentological characteristics and ichnofossils both suggest deposition of the Guanshan Konservat-Lagerstätte in shallower settings compared to most other Cambrian BSTs, with the possible exception of the Emu Bay Shale, Australia (Hu et al. 2013; Paterson et al. 2016; Ding et al. 2018; Chen et al. 2019, 2020a).

The fossils described in this contribution originate from a locality c. 2.5 km southeast of the village of Lihua (Fig. 1). The Cambrian succession is well exposed along a valley, with the exception of the oldest part that is truncated by a fault (Fig. 1C). The succession exposed at the Lihuazhuang section is composed of brownish siltstone and quartzose sandstone beds with subordinate thin-bedded muddy shale, which belong to the Cambrian (Stage 4; Canglangpuan regional stage, *Palaeolenus*–*Megapalaeolenus* trilobite zones) Wulongqing Formation (Hu et al. 2013; Jiao et al. 2016). The diverse radiodonts reported here are found alongside numerous brachiopod valves (Zhang et al. 2011).

Material and methods

Digital images for all specimens were captured under bright-field illustration using a Leica M205-C stereomicroscope fitted with a Leica DFC 500 digital camera. Figured images were processed with Adobe Photoshop CS 4. Figures were constructed using Inkscape 1.0. Digital measurements were taken from photographs using ImageJ2 (Schneider et al. 2012; Rueden et al. 2017).

All studied fossils are deposited at the Key Laboratory for Palaeobiology, Yunnan University, Kunming, China.

The terminology for isolated radiodont appendages follows the terms used by Daley and Edgecombe (2014) and Guo et al. (2019). The proximal-most podomeres of the frontal appendage are referred to as the “shaft”. Articulations between podomeres in the shaft are more weakly defined than those of the “distal articulated region”, the more distal part of the appendage bearing most of the endites, the outgrowths projecting from the ventral margin, and associated with articulating membranes. In addition, a change in slope on the dorsal margin, or “dorsal kink”, often separates these two regions. The “height” of a podomere refers to the distance between its ventral and dorsal margins, while its “length” describes its extent along the proximo-distal axis of the appendage. The term “auxiliary spines” describes the small spines that project from the endite margins either distally or proximally (i.e., towards the distal or proximal end of the appendage). The position of auxiliary spines on endites is described in reference to the base or the tip of the endite to which they are attached (i.e., towards the insertion site of the endite on the podomere, or opposite to it). The arrangement of these spines can either be pectinate or radiating, depending on whether they are parallel to or diverging from one another, respectively.

Systematic palaeontology

Clade Panarthropoda Nielsen, 1995

Order Radiodonta Collins, 1996

Family Ampletobeluidae Pates, Daley, Edgecombe, Cong, and Lieberman, 2019b

Type genus: Ampletobelua Hou, Bergström, and Ahlberg, 1995.

Genera included: Type genus, *Lyrarapax* Cong, Ma, Hou, Edgecombe, and Strausfeld, 2014, and *Ramskoeldia* Cong, Edgecombe, Daley, Guo, Pates, and Hou, 2018, and “*Anomalocaris*” *kunmingensis* Wang, Huang, and Hu, 2013.

Remarks.—“*Anomalocaris*” *kunmingensis* was one of only a handful of radiodont taxa at the time when it was formally described (Wang et al. 2013). It was assigned to *Anomalocaris* based on the number of podomeres in the frontal appendage and the alternation of long and short endites on subsequent podomeres (Wang et al. 2013), characters shared with species of *Anomalocaris*, such as *A. canadensis*, *A. pennsylvanica*, and *A. saron* (Briggs 1979; Whittington and Briggs 1985; Chen et al. 1994; Hou et al. 1995). Our understanding of radiodont diversity and their internal relationships has substantially increased in recent years, and all phylogenetic analyses including this taxon aimed at understanding the interrelationships of radiodont taxa have retrieved “*Anomalocaris*” *kunmingensis* as a member of Ampletobeluidae rather than Anomalocarididae (Vinther et al. 2014; Cong et al. 2014; Van Roy et al. 2015; Lerosey-Aubril and Pates 2018; Liu et al. 2018). Additional support for the assignment of this taxon

to Amplectobeluidae rather than Anomalocarididae comes from the relative lengths of the endites on the fifth and third podomeres in the distal articulated region, which has been proposed as diagnostic for this family (Cong et al. 2018). In most amplectobeluids, the endite is distinctively longer on the fifth podomere than the third—as seen in a previously described specimen of this taxon (Wang et al. 2013: fig. 1g) — while in Anomalocarididae the endite is longer on the third than the fifth (e.g., Daley and Edgecombe 2014).

Vinther et al. (2014) referred “*Anomalocaris*” *kunmingensis* as *Amplectobelua kunmingensis*, but more recent studies have simply treated this taxon as either *Anomalocaris kunmingensis* or “*Anomalocaris*” *kunmingensis* (e.g., Cong et al. 2014; Van Roy et al. 2015; Lerosey-Aubril and Pates 2018; Liu et al. 2018; Zeng et al. 2018a; Guo et al. 2019; Lerosey-Aubril et al. 2020). The Guanshan taxon comprises 13 podomeres in the distal articulated region, whereas the two species currently assigned to *Amplectobelua* have 12 podomeres. The recently described amplectobeluid *Ramskoeldia* has 13 podomeres in its distal articulated region, a less hypertrophied endite than *Amplectobelua* or *Lyrarapax*, and endites with multiple auxiliary spines which face both proximally and distally (Cong et al. 2018), all characters exhibited by “*Anomalocaris*” *kunmingensis*. However, the amplectobeluid appendage from Guanshan also exhibits notable differences compared to *Ramskoeldia*, such as a particularly weak distal tapering or the presence of an unusually well-developed shaft endite projecting ventro-proximally. The latter character could suggest closer affinities with *Laminacaris* (Guo et al. 2019), another possible amplectobeluid from Chengjiang (Lerosey-Aubril and Pates 2018). “*Anomalocaris*” *kunmingensis* also differs from *Ramskoeldia* species in the presence of an oral cone (sensu Liu et al. 2018; Zeng et al. 2018a; this study) and the absence of gnathobase-like structures (Cong et al. 2018). Thus, if “*Anomalocaris*” *kunmingensis* can be confidently re-assigned to the family Amplectobeluidae, it remains unclear whether it would warrant the creation of a new genus or could be accommodated within an existing one. Study of the abundant material mentioned by Zeng et al. (2018a) will allow a formal revision of this species.

Genus uncertain

“*Anomalocaris*” *kunmingensis* Wang, Huang, and Hu, 2013

Figs. 2–4.

- 2013 *Anomalocaris kunmingensis* sp. nov.; Wang et al. 2013: 3938–3939, fig. 1.
 2013 *Anomalocaris kunmingensis* Wang et al. 2013; Hu et al. 2013: 137, fig. 181.
 2014 *Anomalocaris kunmingensis* Wang et al. 2013; Cong et al. 2014: ext. data fig. 4.
 2014 *Amplectobelua kunmingensis* Wang et al. 2013; Vinther et al. 2014: fig. 3
 2015 *Anomalocaris kunmingensis* Wang et al. 2013; Van Roy et al. 2015: ext. data fig. 10.
 2018 *Anomalocaris kunmingensis* Wang et al. 2013; Cong et al. 2018: 619.

- 2018 *Anomalocaris kunmingensis* Wang et al. 2013; Lerosey-Aubril and Pates 2018: fig. 2, sup. figs. 4, 5.
 2018 “*Anomalocaris*” *kunmingensis* Wang et al. 2013; Liu et al. 2018: sup. figs. 2, 3C.
 2018 *Anomalocaris kunmingensis* Wang et al. 2013; Zeng et al. 2018a: 41, 42, 46.
 2018 Radiodontan gen. indet. sp. indet.; Zeng et al. 2018a: figs. 2, 3.2.
 2020 “*Anomalocaris*” *kunmingensis* Wang et al. 2013; Lerosey-Aubril et al. 2020: 506.

Material.—A pair of frontal appendages associated with an oral cone (YKLP 12414), and tentatively one partial frontal appendage (YKLP 12415) from Lihuazhuang section, locality c. 2.5 km southeast of the Lihuazhuang village, China (Fig. 1). Cambrian (Stage 4), lower part of Wulongqing Formation, *Palaeolenus* Biozone (Hu et al. 2010b).

Description.—The first specimen considered here (YKLP 12414) represents a pair of frontal appendages (Fig. 2: la, ra) anterior to an oral cone (Fig. 2: oc), surrounded by disarticulated material, including an ecdysozoan worm (Fig. 2: w). At least 13 podomeres can be tentatively identified in the left appendage (11 mm along dorsal margin, Fig. 2: la) by counting podomere boundaries and/or paired endites (Fig. 3A₂: pd). A break in the rock separates a poorly preserved area, which could represent the proximal part of the distal articulated region or part of the shaft (Fig. 3A₂: s?), from the oral cone and the right appendage. Endites are approximately the same length as the height of the podomere to which they attach (Fig. 3A₂: en). Up to two small protrusions, which may represent auxiliary spines, are seldom visible on some proximal endites. The distalmost part of the appendage is more crudely preserved ventrally, but a long dorsal spine that curves to follow the dorsal margin of the appendage is visible in this region (Fig. 3A₂: ds). Two protrusions of a similar size in more proximal parts of the appendage may represent dorsal spines, or the remains of the dorsal margin that is otherwise missing in this part of the appendage (Fig. 3A₂: ds?). The number of podomeres in the preserved part of the right appendage (Fig. 2: ra; 7 mm along the dorsal margin) cannot be counted with certainty due to poor preservation distally, but it seems to be close to 11. Boundaries can be clearly seen in the more proximal region, and the podomeres have a shape similar to those of the left appendage. Each podomere bears a robust, but incomplete, endite.

Both appendages converge proximally toward a partially preserved oral cone (Fig. 3A₃, A₄). The latter structure can be orientated anterior-posterior and left-right by comparing to the location of the associated frontal appendages, which sit antero-lateral to it in situ position. A large area between the right appendage and the partial oral cone is covered with orange/red material, where no discernible features can be observed (Fig. 2: om). The oral cone consists of plates of apparently three different sizes arranged around an approximately rectangular opening. Most of the plates are thin and wedge shaped, wider at the outer margin of the cone than the inner. Some display furrows parallel to the slightly curved plate boundaries, but otherwise lack ornamentation (Fig. 3A₄: sp).

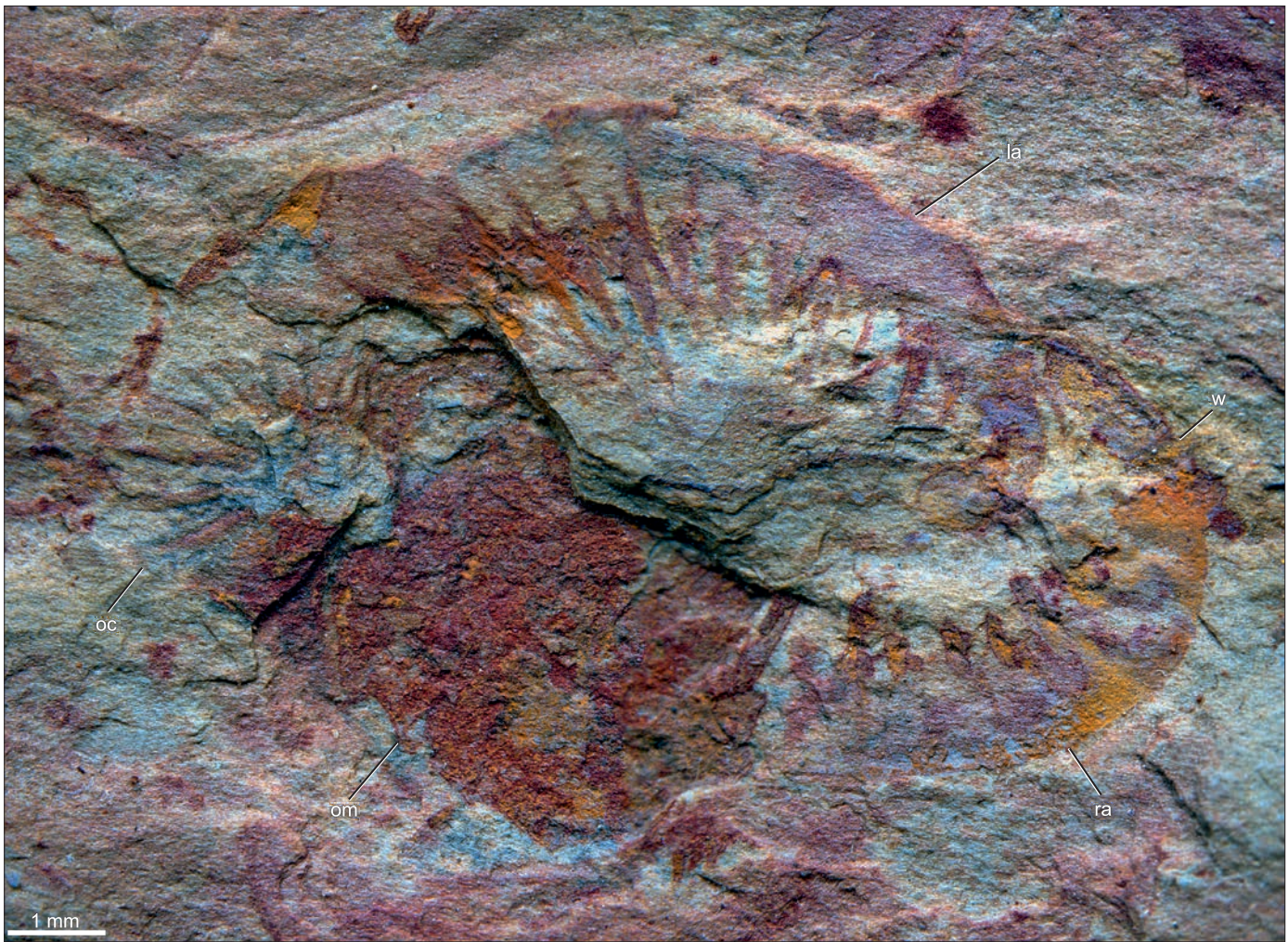


Fig. 2. Amplectobeluid radiodont “*Anomalocaris*” *kunmingensis* Wang, Huang, and Hu, 2013, from the Cambrian (Stage 4) Guanshan Biota, Lihuazhuang section, Yunnan, China. YKLP 12414, a pair of frontal appendages and associated oral cone. Abbreviations: la, left appendage; oc, oral cone; om, organic matter; ra, right appendage; w, ecdysozoan worm.

At the midpoint of the posterior margin of the central opening, one plate extends further into the opening than the other ones; this longer plate is tentatively identified as the posterior plate (Zeng et al. 2018a; Fig. 3A₄: pp?). One node-bearing larger plate occurs on each side of the oral cone (Fig. 3A₄: lp?, rp). Both face one another and their long axes are orientated normal to that of the posterior plate, which allows their identification as the left (incomplete) and right large plates of Zeng et al. (2018a). Both lateral margins of the right plate are clearly delineated by straight margins, and it extends further into the central opening than the plates to either side. The anterior part of the oral cone is missing.

A second specimen (YKLP 12415), a partial frontal appendage of at least nine podomeres that measures 15 mm along the dorsal margin, is tentatively assigned to the same taxon (Fig. 4). Podomere proportions slightly change along the appendage, from noticeably taller than long to roughly as tall as long distally (Fig. 4: pd). The proximal-most six podomeres bear large elongate spiniform endites, which are longer than the height of the podomere to which they attach. One auxiliary spine is present on the proximal margin and

up to two can be observed with confidence on the distal margin of these endites (Fig. 4: aux). Endites alternate long/short on subsequent podomeres and reduce in length along the appendage. The distalmost three podomeres bear shorter spiniform endites apparently devoid of auxiliary spines. Elongate dorsal spines curved to follow the outline of the appendage are present on the distalmost four podomeres (Fig. 4: pd). These dorsal spines look paired at least on the distalmost two podomeres. The appendage terminates in a short straight terminal spine (Fig. 4: ts).

Remarks.—The morphology of the endites with multiple auxiliary spines, shape of proximal podomeres, curvature of dorsal spines, and number of podomeres in the distal articulated region are all consistent with interpretation of these three appendages as belonging to “*Anomalocaris*” *kunmingensis*, which is reported to be by far the most abundant radiodont from the Guanshan Biota (Wang et al. 2013; Zeng et al. 2018a). The oral cone and associated frontal appendages are considered to belong to the same animal. Similar examples of these three structures found together

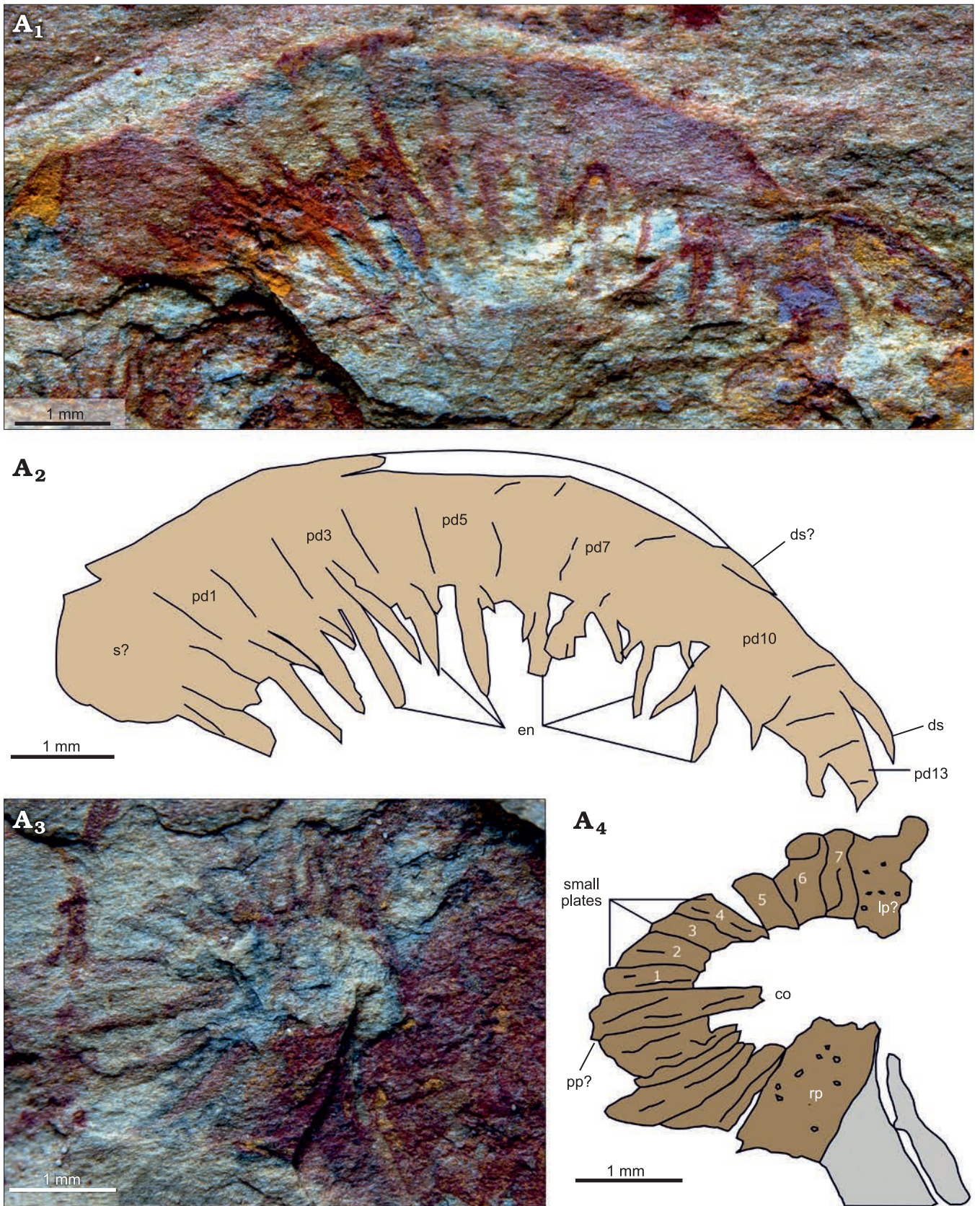


Fig. 3. Amplectobeluid radiodont “*Anomalocaris*” *kunmingensis* Wang, Huang, and Hu, 2013, from the Cambrian (Stage 4) Guanshan Biota, Lihuazhuang section, Yunnan, China. YKLP 12414, details of left frontal appendage (A₁, A₂), details of oral cone (A₃, A₄). Photographs (A₁, A₃) and explanatory drawing (A₂, A₄). Abbreviations: co, central opening; ds, dorsal spine; en, endite; lp?, putative left large plate; pd, podomere; pp? putative posterior plate; rp, right large plate; s?, shaft podomere; sp, small plate. Numbers indicate individual small plates between posterior and left plates.

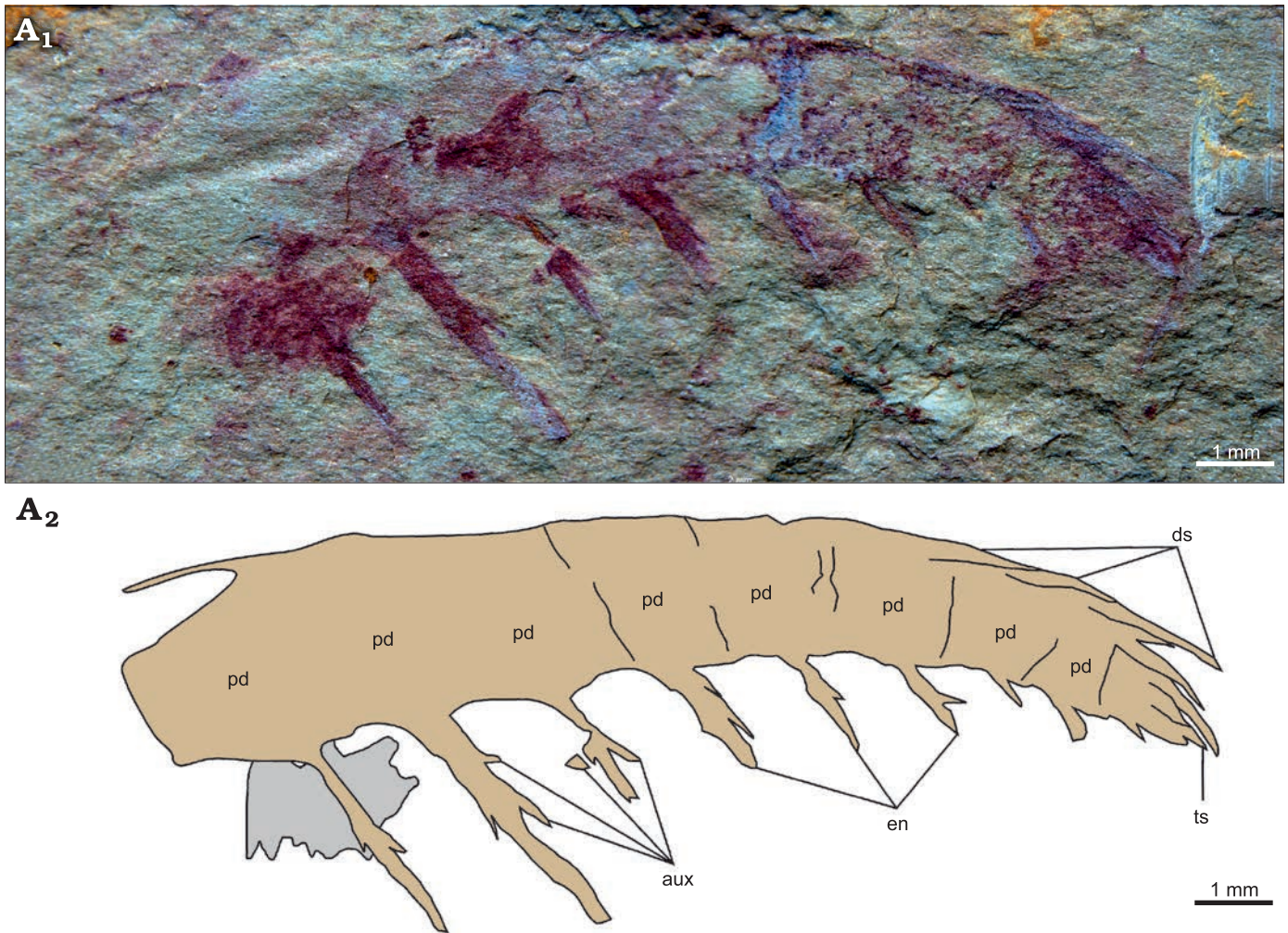


Fig. 4. Amplectobeluid radiodont “*Anomalocaris*” *kunmingensis* Wang, Huang, and Hu, 2013, from the Cambrian (Stage 4) Guanshan Biota, Lihuazhuang section, Yunnan, China. YKLP 12415, a partial frontal appendage. Photograph (A₁) and explanatory drawing (A₂). Abbreviations: aux, auxiliary spine; ds, dorsal spine; en, endite; pd, podomere; ts, terminal spine.

and dissociated with the rest of the body have been reported in several taxa (e.g., *Cambroraster*, *Hurdia*, and *Stanleycaris*; Caron et al. 2010: sup. mat. 5, pl. 1; Daley et al. 2013a: figs. 22D, 24A; Moysiuk and Caron 2019: fig. 2j), although the anatomical or taphonomic reasons for this recurrent association remain unclear. The oral cone shows multiple similarities to the single isolated Guanshan oral cone tentatively assigned to this taxon by Zeng et al. (2018a). Both specimens share a combination of features unique amongst radiodonts: a tetradial organization, in which the posterior plate is the smallest of the four large plates; the presence of both nodes and furrows; and a central opening elongate rectangular in outline and apparently devoid of inner tooth rows. Despite the absence of the anterior plate in the new specimen, the alignment of the two lateral plates strongly suggests a tetradial organization for the larger plates. Likewise, slightly more than the posterior half of the central opening is preserved; when complete the outline of this opening was likely closer to an antero-posteriorly elongate rectangle, rather than a square as in some hurdiids, although deformation cannot be entirely ruled out

in this case. An association of furrows and nodes has as-yet only been observed in the Guanshan oral cone described by Zeng et al. (2018a), and triradially arranged oral cones of *Anomalocaris*. Nodes were also described in a juvenile of the amplectobeluid *Lyrarapax* (Liu et al. 2018), but the preservation did not allow the observation of folds (if originally present). Nodes have also been reported in some hurdiid oral cones (Pates et al. 2018: fig. 2.6; Sun et al. 2020a), but not in association with folds. The nodes in the new specimen are only visible on the large lateral plates, not all plates as in the other oral cone from Guanshan (Zeng et al. 2018a), but this may be the result of poorer preservation. Lastly, the larger plates are separated from one another by sets of seven small plates in all previously described, tetradially arranged oral cones, which is the case for this new specimen between the posterior plate and left plate. The number of plates between the posterior plate and right plate cannot be counted with certainty.

The presence of an oral cone associated with frontal appendages that are both consistent with material assigned to “*Anomalocaris*” *kunmingensis*, supports the conclusions

of Zeng et al. (2018a) that this taxon possesses an oral cone. The position of the oral cone relative to the appendages supports the interpretation of Zeng et al. (2018a), that the smallest of the larger plates was at the posterior of the oral cone, and the largest plates were positioned laterally. This is the second report of a tetradial oral cone in an amplexobeluid radiodont, following a single juvenile specimen of *Lyrarapax unguispinus* (Liu et al. 2018). Poor preservation and small size prevented the observation of folds (if present) in the latter specimen. Accordingly, it remains unclear whether the combination of a tetradial organization, nodes, and folds is unique to “*Anomalocaris*” *kunmingensis* or could represent an additional diagnostic character for Amplexobeluidae.

Stratigraphic and geographic range.—Gaoloufang village and Lihuaazhuang sections, Yunnan, China, Wulongqing Formation (*Palaeolenus* and *Megapalaeolenus* zones), Cambrian (Stage 4).

Family Anomalocarididae Raymond, 1935

Type genus: *Anomalocaris* Whiteaves, 1892.

Genera included: Type genus and *Paranomalocaris* Wang, Huang, and Hu, 2013.

Remarks.—*Paranomalocaris* was originally described as a monospecific genus within the family Anomalocarididae. All phylogenetic analyses attempting to resolve the internal relationships of radiodonts to date have failed to resolve the family Anomalocarididae or even genus *Anomalocaris* (even excluding “*Anomalocaris*” *briggsi* and “*Anomalocaris*” *kunmingensis* which are not considered members of the genus) as a monophyletic group. Analyses either returned a paraphyletic grade towards monophyletic Amplexobeluidae, or a polytomy with the latter group (e.g., Cong et al. 2014; Vinther et al. 2014; Van Roy et al. 2015; Lerosey-Aubril and Pates 2018; Moysiuk and Caron 2019). Only Liu et al. (2018) retrieved a clade Anomalocarididae (*A. kunmingensis* and *A. briggsi* excluded) in one of their analyses, which recovered *Paranomalocaris* as sister to a clade uniting Anomalocarididae to Amplexobeluidae. In summary, there is no strong phylogenetic support for assigning *Paranomalocaris* to Anomalocarididae, but this is also the case of all the species of *Anomalocaris*. Future work may support the erection of a distinct family for *Paranomalocaris*, but for now we retain this genus within the family as originally described.

Genus *Paranomalocaris* Wang, Huang, and Hu, 2013

Type species: *Paranomalocaris multisegmentalis* Wang, Huang, and Hu, 2013; Gaoloufang Village, Kunming, Yunnan, China, Wulongqing Formation (*Palaeolenus* and *Megapalaeolenus* zones), Cambrian (Stage 4).

Diagnosis (emended from Wang et al. 2013).—Radiodont with slender frontal appendages, which comprise at least 17 podomeres; proximal podomeres have a tall rectangular lateral outline, which changes to approximately square dis-

tally; endites alternate long/short on subsequent podomeres, and reduce in length along the appendage; small triangular terminal spine on distalmost podomere.

Paranomalocaris multisegmentalis Wang, Huang, and Hu, 2013

Fig. 5.

2013 *Paranomalocaris multisegmentalis* sp. nov.; Wang et al. 2013: 3940, figs. 2, 3.

2013 *Paranomalocaris multisegmentalis* Wang et al. 2013; Hu et al. 2013: 137, 192, fig. 181.

2014 *Paranomalocaris multisegmentalis* Wang et al. 2013; Cong et al. 2014: ext. data fig. 4.

2014 *Paranomalocaris multisegmentalis* Wang et al. 2013; Vinther et al. 2014: fig. 3.

2015 *Paranomalocaris multisegmentalis* Wang et al. 2013; Van Roy et al. 2015: ext. data fig. 10.

2018 *Paranomalocaris multisegmentalis* Wang et al. 2013; Lerosey-Aubril and Pates 2018: fig. 2, sup. figs. 4, 5.

2018 *Paranomalocaris multisegmentalis* Wang et al. 2013; Liu et al. 2018: sup. fig. 2.

2018 *Paranomalocaris multisegmentalis* Wang et al. 2013; Zeng et al. 2018a: 41, 42, 46.

Holotype: NIGP154564, an incomplete frontal appendage compressed laterally (Wang et al. 2013).

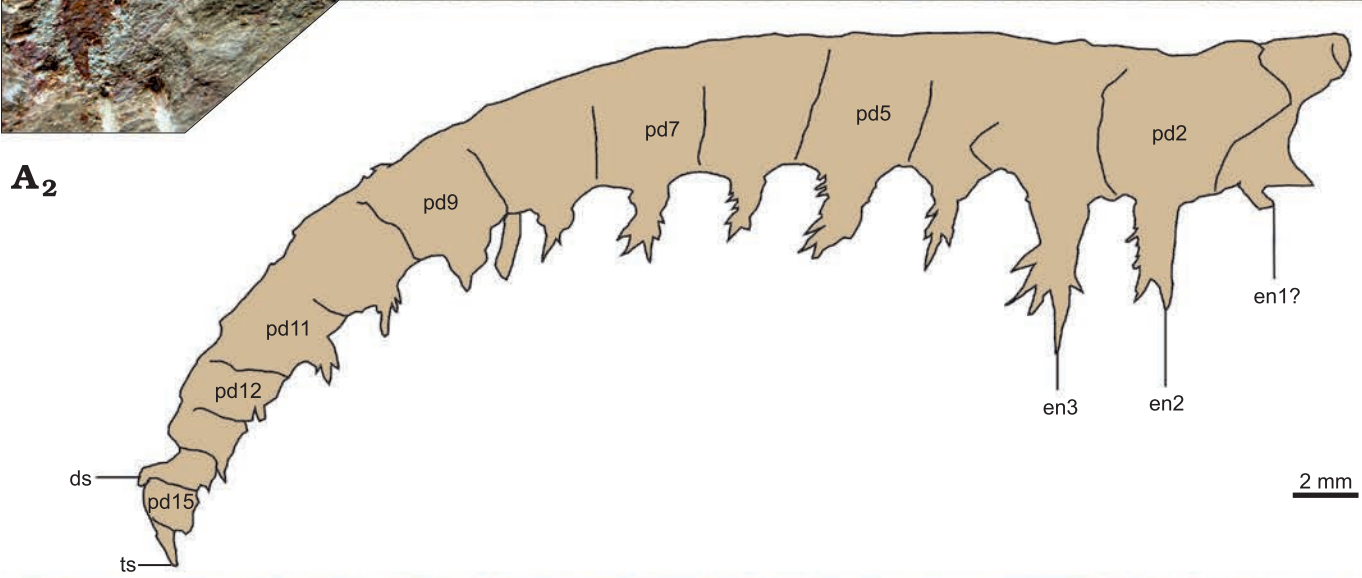
Type locality: Gaoloufang village, Kunming, East Yunnan, China (Wang et al. 2013).

Type horizon: Wulongqing Formation (*Palaeolenus* and *Megapalaeolenus* Zone), Cambrian (Series 2, Stage 4) (Wang et al. 2013).

Material.—Type material and YKLP 12416, a partial frontal appendage compressed laterally from Lihuaazhuang section, near Lihua village, about seven kilometres northwest of the Yiliang county in Yunnan, China (Fig. 1), Cambrian (Stage 4), lower part of Wulongqing Formation, *Palaeolenus* Biozone (Hu et al. 2010b).

Diagnosis (emended from Wang et al. 2013).—*Paranomalocaris* with short, plate-like proximal endites, each bearing a spiniform termination and at least three distally facing auxiliary spines; serrated dorsal spines.

Description.—YKLP 12416 is incomplete proximally, consists of 15 podomeres (Fig. 5: pd1–15) and a terminal spine, and measures 45 mm along the dorsal margin. The appendage curves ventrally with a slight dorsal kink visible at the midpoint of the second podomere (Fig. 5A₁). Most podomeres are approximately square shaped, being slightly taller than long in the proximal part and slightly longer than tall towards the middle, except for the four distal ones that are notably taller than long. Endites are present on every podomere (Fig. 5A₂: en). No second row of endites is observed. On pd1, the endites are not well preserved. A single outgrowth from the ventral surface close to the proximal margin might represent a broken endite base (Fig. 5A₂: en1) orientated towards the proximal part of the appendage. The endite on pd2 is broadly rectangular in outline (3 × 1 mm), with an incomplete spiniform termination, and bears three auxiliary spines on its distal margin (Fig. 5A₃). En3, the longest endite (Fig. 5A₂), measures c. 4.5 mm from base to tip,



and is also rectangular in outline, except for a robust spiniform termination that slightly curves towards the distal portion of the appendage. Three robust and elongate auxiliary spines radiate ventro-distally from the middle third of the distal margin of en3, and a single, much smaller one project from its proximal margin (Fig. 5A₃). En4 is much smaller than En3, but exhibits similar shape and distribution pattern of auxiliary spines. En5–11 bear three to six auxiliary spines on both margins, which follow a mostly pectinate arrangement and project at an angle of c. 130° (distal ones) or c. 150° (proximal ones) with the long axes of the endites (Fig. 5A₃). The size of the spiniform termination relative to the rest of the endite tends to decrease from en4–11. The preservation of en12–15 is poorer, but en13–15 appear to be short, project distally, and devoid of auxiliary spines. A small dorsal spine may occur on pd14, and a single, robust terminal spine is visible on pd15 (Fig. 5A₂: ds, ts).

Remarks.—While the broad shape of en3–11 and their pattern of numerous distal and proximal facing auxiliary spines bear similarity to both *Paranomalocaris multisegmentalis* and *Ramskoeldia platyacantha*, the relative length and morphology of en2–7 provide strong support for the interpretation of this specimen as the distal 15 podomeres of a *P. multisegmentalis* appendage.

The alternation in size of the endites of adjacent podomeres and their overall reduction in length along the appendage are characters known in all anomalocaridids. While members of the *Anomalocaris* have 13 podomeres in the distal articulated region, all 15 podomeres of the new specimen are considered to belong to the distal articulated region, a number only known in the *Paranomalocaris* and *Tamisiocaris* (Daley and Peel 2010; Wang et al. 2013; Vinther et al. 2014). Affinities with the latter genus can be discarded, as endites of *Tamisiocaris* are all of subequal length, a character that currently distinguishes Tamisiocarididae from Amplectobeluidae and Anomalocarididae.

Under a hypothesis that would interpret this specimen as *Ramskoeldia platyacantha*, the distal 13 podomeres of YKLP 12416 would represent the distal articulated region, with pd1 and pd2 comprising the shaft. The slight dorsal kink in pd2 could be interpreted as supporting this arrangement, however its presence within a podomere, rather than at the boundary of two adjacent podomeres, suggests that this feature is due to a slight twist of the appendage during compression and does not represent a biological feature. Two further observations allow us to reject the assignment of this specimen to *R. platyacantha*, in favour of *Paranomalocaris*. Firstly, the endites decrease in length along the whole appendage with no exception, while an en7 longer than en5 characterizes the amplectobeluid genera *Amplectobelua* and *Ramskoeldia*. Secondly, the distalmost shaft podomere bears

a small and simple spiniform endite at its distal margin in *R. platyacantha*, while the specimen described herein would exhibit an elongate endite with auxiliary spines at this position (Fig. 5: en2), if interpreted as a sub-complete appendage of this species. For the specimen under consideration, en2 is smaller than, but morphologically similar to en3, as would be expected from the endites of adjacent podomeres in the distal articulated region of *Paranomalocaris*.

Some characters diagnostic for *Paranomalocaris multisegmentalis* cannot be observed in YKLP 12416. The serrated appearance of the distal dorsal margin of the holotype appendage, resulting from the presence of half a dozen dorsal spines, is not observed in the new specimen due to the poor preservation/incomplete exposition of this part of the fossil. Likewise, the proximal part is missing in the new specimen, which therefore only preserves 15 podomeres, whereas Wang et al. (2013) described the holotype specimen to possess “at least 22 podomeres”. We can confirm at least 17 podomeres from the figured specimen (Wang et al. 2013: figs. 2, 3), but since this previously illustrated specimen is clearly incomplete, a higher podomere number must characterize the genus *Paranomalocaris*. Of note, YKLP 12416 shows that the proximal endites (Fig. 5: en2, en3) differ from the more distal ones in having a single proximally facing auxiliary spine each (rather than multiple ones), a detail that could not be observed in the holotype due to preservation.

Stratigraphic and geographic range.—Gaoloufang village and Lihuazhuang section, Yunnan, China, Wulongqing Formation (*Palaeolenus* and *Megapalaeolenus* zones), Cambrian (Stage 4).

Paranomalocaris simplex sp. nov.

Fig. 6.

Zoobank LCID: urn:lsid:zoobank.org:act:F79695F0-AF05-4A3A-B326-A6516936F3B2

Etymology. From Latin *simplex*, simple; emphasising the simple morphology of endites and dorsal spines in the new species, which contrast to the complex endites and serrated dorsal spines of the type species.

Type material. Holotype: YKLP 12417, a laterally compressed frontal appendage; paratype: YKLP 12418a, a partial laterally compressed frontal appendage from the type locality.

Type locality. Lihuazhuang section, locality c. 2.5 km southeast of the Lihua village, China (Fig. 1).

Type horizon. Lower part of Wulongqing Formation, *Palaeolenus* Biozone, Cambrian (Stage 4) (Hu et al. 2010b).

Material.—Type material only.

Diagnosis.—*Paranomalocaris* with long needle-like endites, some exceeding in length the height of the podomere to which they attach; non-serrated dorsal spines present on every podomere.

← Fig. 5. Anomalocaridid radiodont *Paranomalocaris multisegmentalis* Wang, Huang, and Hu, 2013, from the Cambrian (Stage 4) Guanshan Biota, Lihuazhuang section, Yunnan, China. YKLP 12416, incomplete frontal appendage (proximalmost region missing); general view (A₁), white arrow indicates fold in dorsal margin; details of the proximal preserved endites (A₂, A₃), white arrows, distally facing auxiliary spines; black arrows, proximally facing auxiliary spines. Photographs (A₁, A₃) and explanatory drawing (A₂). Abbreviations: ds, dorsal spine; en, endite; pd, podomere; ts, terminal spine.

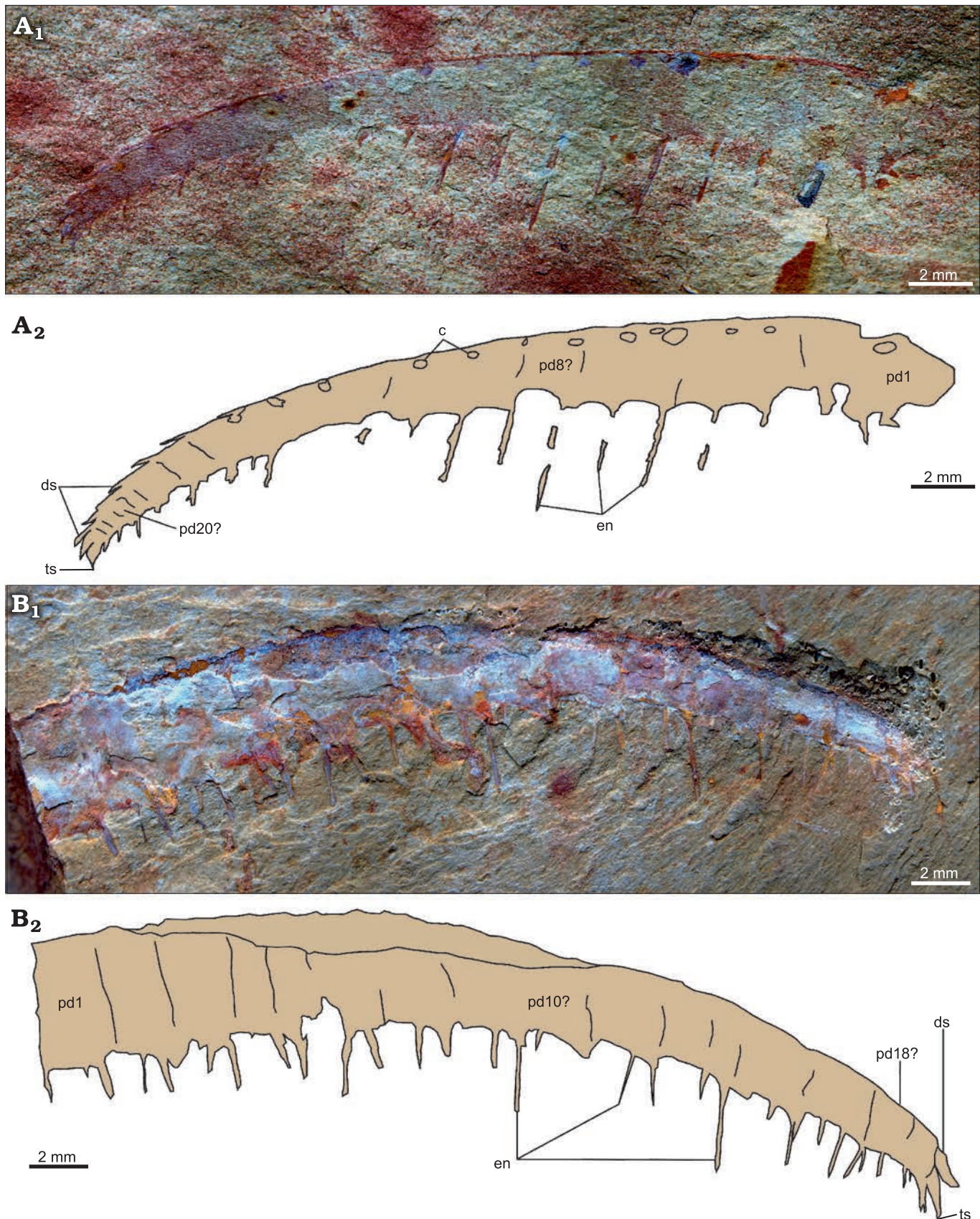


Fig. 6. Anomalocaridid radiodont *Paranomalocaris simplex* sp. nov. from the Cambrian (Stage 4) Guanshan Biota, Lihuazhuang section, Yunnan, China. **A.** YKLP 12417, a near complete frontal appendage. **B.** YKLP 12418, distal portion of a frontal appendage. Photographs (A₁, B₁) and explanatory drawings (A₂, B₂). Abbreviations: c, circular attachment point for dorsal spine; ds, dorsal spine; en, endite; pd, podomere; ts, terminal spine.

Description.—Two isolated near-complete frontal appendages laterally compressed (YKLP 12417, 12418a) measuring 32 mm and 33 mm along the dorsal margin, respectively (Fig. 6). At least 20 podomeres can be identified for each appendage, changing in lateral outline from tall rectangles proximally to square shapes distally (Fig. 6: pd). Podomeres can be identified from their boundaries, visible as simple lines on the surface of the appendage, and/or from the pair of endites projecting ventrally.

Both specimens bear needle-like endites, one pair per podomere, which reduce in length toward the distal tip of the appendage, and alternate long/short on adjacent podomeres (Fig. 6: en). In the holotype (YKLP 12417; Fig. 6A), thin and short auxiliary spines might occur on the distal margin, at an angle of c. 140° with the long axis, on some endites. Other endites appear to lack auxiliary spines. No auxiliary spines are visible on any endites of the paratype (Fig. 6B). Dorsal spines are visible on every podomere in the holotype, either as spines in its distal third (Fig. 6A₂: ds) or as circular attachment points in its more proximal region (Fig. 6A₂: c). A single spine in the distal region of YKLP 12418a may be a dorsal spine, but most of the dorsal surface of this specimen is poorly preserved. One small and curved terminal spine is visible on each specimen (Fig. 6: ts).

Remarks.—The type species and hitherto only species of *Paranomalocaris*, namely *Paranomalocaris multisegmentalis*, was distinguished from other members of Anomalocarididae by its high number of podomeres, the morphology of its proximal endites (plate-like and bearing at least five auxiliary spines on both proximal and distal margins), and the presence of serrated dorsal spines.

Among radiodonts only *Paranomalocaris* and *Tamisiocaris* possess such a high number of podomeres in the distal articulated region. As discussed above, this feature is combined with an alternation in endite length along the appendage only in *Paranomalocaris*, allowing a confident assignment of the new taxon to this genus. *Paranomalocaris simplex* can be easily differentiated from *P. multisegmentalis* by the slender morphology of its endites, and the absence of serration on the dorsal spines.

Stratigraphic and geographic range.—Lihuazhuang section, Yiliang county, Yunnan, China, Wulongqing Formation (*Palaeolenus* Biozone), Cambrian (Stage 4).

Family Tamisiocarididae Pates and Daley, 2019

Type genus: *Tamisiocaris* Daley and Peel, 2010.

Genera included: Type genus and “*Anomalocaris*” *briggsi* Nedin, 1995.

Tamisiocarididae indet.

Fig. 7.

Material.—A single partial frontal appendage (YKLP 12419) from Lihuazhuang section, locality c. 2.5 km southeast of Lihua village, China (Fig. 1), Cambrian (Stage 4), lower part of Wulongqing Formation, *Palaeolenus* Biozone (Hu et al. 2010).

Description.—This near complete appendage is composed of 15 approximately square podomeres (counted from the number of endites and rarely observed podomere boundaries), and measures c. 50 mm along the dorsal margin (Fig. 7). The appendage lacks both proximal and distal ends, but the preserved portion tapers distally (Fig. 7A₃, A₄). Each podomere bears an elongate and slender endite, subequal in size along the appendage (Fig. 7: en). The best preserved of these endites are longer than the height of the podomere to which they attach and are slightly curved towards the proximal end of the appendage (e.g., Fig. 7A₄: en9). Endites bear short and delicate auxiliary spines, c. 0.5–1 mm apart, that project at an angle of 120–150° relative to the long axis, from both the proximal and distal margins following a pectinate arrangement (Fig. 7: aux). The presence of dorsal spines cannot be determined, as the dorsal margin of the appendage is not well preserved, especially distally.

Remarks.—YKLP 12419 possesses well-differentiated podomeres bearing endites with auxiliary spines, which is a combination of characters solely known in radiodonts and the recently described deuteropod *Kylinxia* (Zeng et al. 2020). The presence of numerous elongate endites, similar in size and morphology in the entire distal articulated region allows a confident assignment of this fossil to the radiodont family Tamisiocarididae. Indeed, endites alternate long/short on adjacent podomeres in ampletobeluids, anomalocaridids, and *Kylinxia*, while there is a marked difference in size and morphology between the proximal and distal (when present) endites of the distal articulated region in hurdiids. A lack of functional articulation and therefore of distal articulated region characterizes the atypical radiodont genus *Caryosyntrops*.

As only a single row of endites can be observed, the pairing of endites cannot be ascertained in this new taxon. However, it is well-documented from other radiodonts known from many more frontal appendages, such as *Anomalocaris canadensis*, that the second series of endites often remains concealed within the sediment (Daley and Edgecombe 2014). Moreover, frontal appendages of hurdiids, the one family with unpaired endites, bear auxiliary spines on the distal margin of endites only, and typically have fewer than 14 podomeres. The presence of auxiliary spines on both distal and proximal faces of endites, and the high podomere count, allow a confident assignment of this new material to the family Tamisiocarididae.

The presence of fine auxiliary spines on both proximal and distal margins of endites is known in the two formally described tamisiocaridid taxa, “*Anomalocaris*” *briggsi* and *Tamisiocaris borealis* (Daley et al. 2013b; Vinther et al. 2014). However, the Guanshan specimen notably differs from both these taxa in the outline of its podomeres, which are square in lateral view, rather than tall and rectangular. We leave this incomplete appendage in open nomenclature as important features, such as the total number of podomeres or the presence of dorsal and terminal spines, cannot be determined. However, we recognize that it rep-

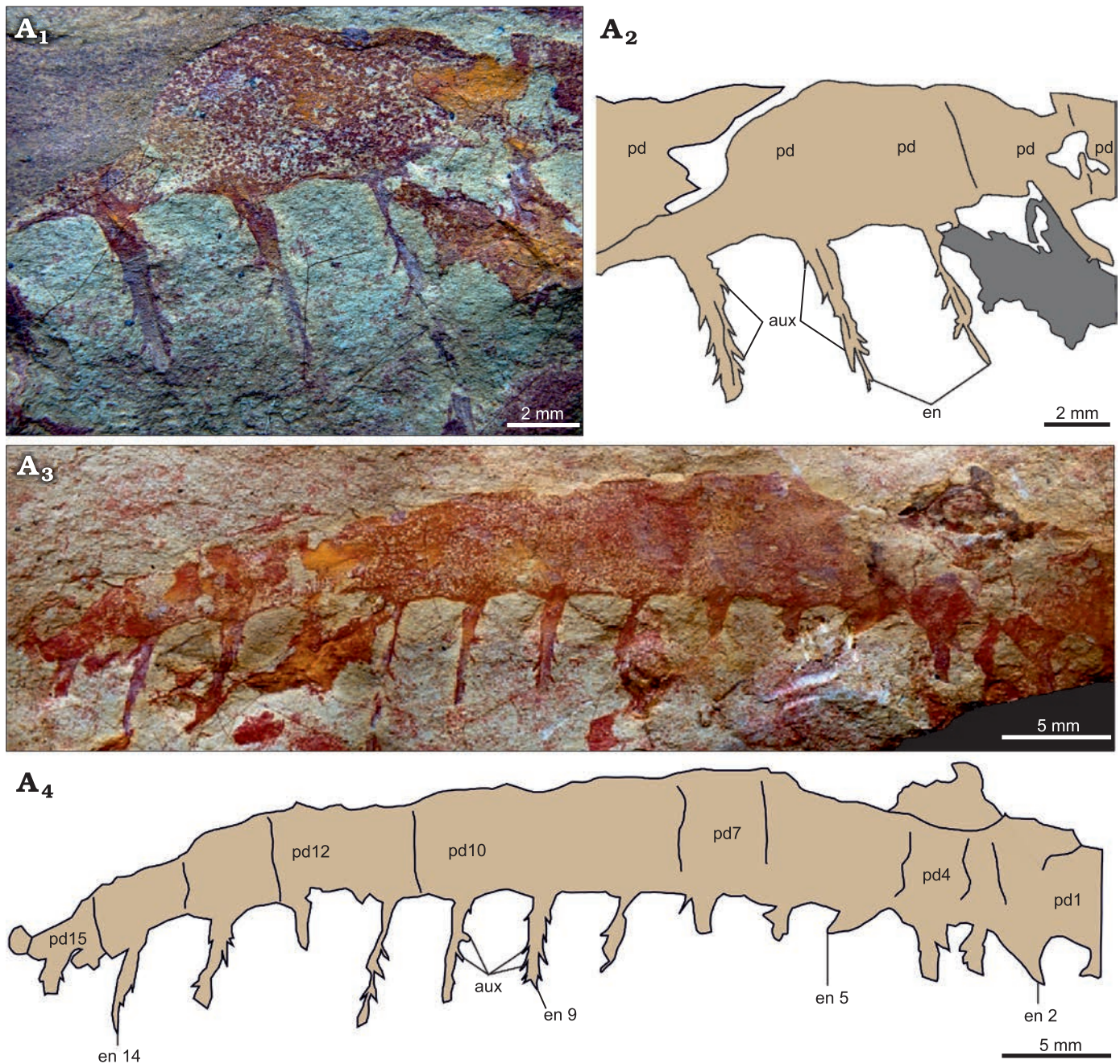


Fig. 7. Tamisiocarididae indet. from the Cambrian (Stage 4) Guanshan Biota, Lihuazhuang section, Yunnan, China. YKLP 12419, a partial frontal appendage. Counterpart (A₁, A₂), part (A₃, A₄). Photographs (A₁, A₃) and explanatory drawings (A₂, A₄). Abbreviations: aux, auxiliary spine; en, endite; pd, podomere.

represents a new species and probably a new genus of tamisiocaridid radiodont. As such, this specimen extends the palaeogeographic range of the family to the South China palaeocontinent. Other tamisiocaridids are known from the Cambrian, Stage 3 of Laurentia (*Tamisiocaris borealis*, Buen Formation; Daley and Peel 2010; Vinther et al. 2014) and Stage 4 of Gondwana (*Anomalocaris briggsi*, Emu Bay Shale; Daley et al. 2013b) and Laurentia (*Tamisiocaris* aff. *borealis*, Kinzers Formation; Pates and Daley 2019).

Stratigraphic and geographic range.—Lihuazhuang section, Yiliang county, Yunnan, China. Wulongqing Formation (*Palaeolenus* Biozone), Cambrian (Stage 4).

Discussion

Endemism in Guanshan radiodonts: geographic and environmental considerations.—The new material from the Lihuazhuang section increases our knowledge of the diversity of these stem-group euarthropods in the Wulongqing Formation, the Cambrian of South China, and even to some extent the Cambrian Stage 4 worldwide. This study doubles the known diversity of radiodont species in the Guanshan Biota (2–4 or 3–5, if the new material illustrated in Zhao et al. 2020 represents a distinct species) and extends the known palaeogeographic range of the family Tamisiocarididae to

South China. All four recognized radiodont families are now known from this palaeocontinent, as amplexobeluids, anomalocaridids, and hurdiids have all been previously reported from multiple BST deposits in the region (Chen et al. 1994; Hou et al. 1995; Liu 2013; Wang et al. 2013; Cong et al. 2014, 2016; Zeng et al. 2018b; Liu et al. 2020). *Caryosyntrips*, an atypical radiodont genus that may belong to its own family, remains solely known from Gondwana and Laurentia (Daley and Budd 2010; Pates and Daley 2017; Lerosey-Aubril et al. 2020; Pates et al. 2021).

The global distribution of radiodont families contrasts with the apparent endemism of the Guanshan radiodont fauna at the genus and species levels. For example, all four Guanshan radiodont species, and the genus *Paranomalocaris* Wang, Huang, and Hu, 2013, as a whole, are only known from the Wulongqing Formation. Indeed, if “*Anomalocaris*” *kunmingensis* Wang, Huang, and Hu, 2013, represents a new genus, then all four genera are endemic. The absence of any of the nine, possibly eleven radiodont species present in the Chengjiang Lagerstätte is striking. Several of these species have been reported in other, less prolific (i.e., Tier 3 of Gaines 2014) Cambrian BST deposits in South China (Table 1) and the genera *Amplexobelua*, *Anomalocaris*, *Cambroraster*, and *Ramskoeldia*, also occur in Cambrian Stage 3–Miaolingian BST deposits of North China (Sun et al. 2020a) and Laurentia (e.g., Daley and Budd 2010; Daley and Edgecombe 2014; Moysiuk and Caron 2019; Lerosey-Aubril et al. 2020; Pates et al. 2019b, 2021). This indicates that the marked compositional dissimilarity between the Chengjiang and Guanshan radiodont faunas cannot simply be explained by differences in the palaeogeographical distribution or stratigraphic age. We propose that the endemic nature of the Guanshan radiodonts is best explained by the different environment in which they lived. Both sedimentological and ichnological evidence support a more proximal, possibly more energetic depositional setting above storm wave-base for the Wulongqing Formation, although the reconstructed palaeoenvironment varies from anywhere between the shoreface and a tidal flat (Ding et al. 2018; Chen et al. 2019; see also Chen et al. 2020a for possible variations from a section to another). This contrasts with the quiet, relatively deep-water environment near the shelf break and a fluctuating oxycline proposed for most BST deposits (Gaines 2014). Considering that most radiodonts were capable swimmers (see Moysiuk and Caron 2019 and Liu et al. 2020 for a possible exception), it might be expected that their geographic range was less constrained by the spatial variation of environmental conditions on the seafloor than that of most benthic organisms. This assumption finds support in the intercontinental palaeogeographic distributions of many radiodont genera. However, the high endemism of the Guanshan radiodont fauna at the genus level illustrates that these animals could also be tightly connected to the benthic environments, and the prey animals that lived in them. In this regard, suspension feeding radiodonts (Vinther et al. 2014; Lerosey-Aubril and Pates 2018; Paterson et al.

2020) and a few other metazoans (e.g., some ctenophores and cnidarians) likely represented rare exceptions of truly pelagic animals, at a time when macroscopic life is thought to have remained largely confined to the hyperbenthic realm 1–10 meters off the bottom of the oceans (Vannier 2009). The ecological coupling of radiodonts and benthic communities might have been more pronounced in proximal shelf environments, hence its clearer expression in the Guanshan Lagerstätte. The combination of this ecological coupling with challenges posed by life in physically (e.g., energetic regime, temperature, turbidity) and chemically (e.g., oxygenation) different environments may explain not only the endemism of the Guanshan radiodont fauna, but also contribute to the apparently complex palaeobiogeographic patterns exhibited by the members of this group, even at regional or intracontinental scales (Pates et al. 2021).

Diversity of feeding strategies in radiodont assemblages.—Co-occurring radiodont taxa display adaptations in their frontal appendages and other feeding structures (e.g., gnathobase-like structures and oral cones) that suggest different ecological specializations (Daley and Budd 2010; Cong et al. 2017, 2018). Taxa with prominent triangular membrane between podomeres, relatively short endites with robust auxiliary spines, and prominent dorsal spines in the distal region, are generally considered raptorial predators (e.g., *Anomalocaris canadensis*, *Lyrarapax unguispinus*; Daley and Edgecombe 2014; Cong et al. 2014; Liu et al. 2018), while those with more elongate endites tend to be interpreted as sweep feeders (e.g., *Hurdia victoria*; Daley et al. 2013a) or sediment sifters (e.g., *Cambroraster falcatus*; Moysiuk and Caron 2019). A small number of radiodonts with microscopic distances between auxiliary spines or setae on their endites were most likely suspension feeders (e.g., *Pahvantia hastata*, *Tamisiocaris borealis*, and probably “*Anomalocaris*” *briggsi*; Vinther et al. 2014; Lerosey-Aubril and Pates 2018).

Two of the four radiodonts in the Guanshan Biota appear suited for raptorial predation, a hypothesis supported by the relatively short and spinose endites of *Paranomalocaris multisegmentalis* and “*Anomalocaris*” *kunmingensis*. The distinct form of their endites, broad, stubby, and spinose in the former, trident-like in the latter, suggests a specialization for different prey types. The other two Guanshan radiodonts appear more suited for sweep feeding, the elongate and slender endites of *Paranomalocaris simplex* sp. nov. and the new tamisiocaridid taxon. Parallels can be drawn between the inferred feeding ecologies of components of diverse radiodont assemblages. This is exemplified by comparison to other Cambrian Stage 4 deposits with their different taxonomic makeup (Tables 1, 2). Two taxa in the Kinzers Formation, *Amplexobelua* aff. *symbrachiata* and *Anomalocaris pennsylvanica*, show adaptations for raptorial predation, while *Laminacaris?* sp. and *Tamisiocaris* aff. *borealis* both display long endites more indicative of sweep feeding (Pates and Daley 2019). Again, in the Emu Bay Shale, *Anomalocaris* cf. *canadensis* shows adaptations for raptorial predation, and

Table 1. Taxonomic diversity of the radiodont faunas from the Cambrian Konservat-Lagerstätten of South China. Radiodonts have also been reported from the Qingjiang Biota, South China (Shuijingtuo Formation, Stage 3), but specimens are yet to be formally described (Fu et al. 2019). An isolated hurdiid lateral carapace element has also been reported from this formation (Daley et al. 2013a). * The radiodont material from the Kaili Formation is in need of revision; the specimens illustrated by Zhao et al. (2005, 2011) might be better regarded as belonging to an amplectobeluid, possibly the *Amplectobelua*. ** *Cucumericrus* and *Zhenghecaris* may not represent true radiodonts.

Stage	Stage 3			Stage 4		Wuliuan	Furongian
Lagerstätte	Chengjiang	Malong	Zunyi	Balang	Guanshan	Kaili	Guole
<i>Amplectobelua</i>	<i>Amplectobelua symbrachiata</i> (Hou et al. 1995; Cong et al. 2017)	–	<i>Amplectobelua symbrachiata</i> (Steiner et al. 2005)	–	–	–	–
<i>Anomalocaris</i>	<i>Anomalocaris saron</i> (Hou et al. 1995); cf. <i>Anomalocaris canadensis</i> (Wu et al. 2021)	<i>Anomalocaris saron</i> (Zhang et al. 2001; Luo et al. 2008)	–	<i>Anomalocaris</i> sp. (Liu 2013)	–	<i>Anomalocaris saron</i> * (Zhao et al. 2005; Zhao et al. 2011)	–
“ <i>Anomalocaris</i> ” Amplectobeluidae	–	–	–	–	“ <i>Anomalocaris</i> ” <i>kunmingensis</i> (Wang et al. 2013; Zeng et al. 2018; this study)	–	–
<i>Cambroraster</i>	<i>Cambroraster</i> sp. nov. A (Liu et al. 2020)	–	–	–	–	–	–
<i>Lenisicaris</i>	<i>Lenisicaris lupata</i> (Wu et al. 2021)	–	–	–	–	–	–
<i>Lyrarapax</i>	<i>Lyrarapax trilobus</i> (Cong et al. 2016), <i>Lyrarapax unguispinus</i> (Cong et al. 2014)	–	–	–	–	–	–
<i>Peytoia</i>	–	–	–	cf. <i>Peytoia nathorsti</i> (Liu, 2013)	–	–	–
<i>Paranomalocaris</i>	–	–	–	–	<i>P. multisegmentalis</i> (Wang et al. 2013), <i>P. simplex</i> (this study)	–	–
<i>Ramskoeldia</i>	<i>Ramskoeldia consimilis</i> , <i>Ramskoeldia platyacantha</i> (Cong et al. 2018)	–	–	–	–	–	–
Anomalocarididae	–	–	–	–	Anomalocarididae indet. (Zhao et al. 2020)	–	–
Hurdiidae	–	–	–	–	–	–	Hurdiidae indet. (unpublished data)
Tamisiocarididae	–	–	–	–	Tamisiocarididae indet. (this study)	–	–
<i>Cucumericrus</i> **	<i>Cucumericrus decorates</i> (Hou et al. 1995)	–	–	–	–	–	–
<i>Zhenghecaris</i> **	<i>Zhenghecaris shankouensis</i> (Zeng et al. 2018)	–	–	–	–	–	–

“*Anomalocaris*” *briggsi* to suspension feeding (Daley et al. 2013b), and in the Pioche Formation the raptorial predator *Anomalocaris magnabasis* and likely sweep-feeder *Hurdia* sp. co-occur (Pates et al. 2019b). Closer geographically to the Guanshan Biota, the two radiodont taxa from the Balang Formation, one species of *Anomalocaris* and *Peytoia*, both left in open nomenclature, also appear specialized for distinct feeding ecologies (Liu 2013). A similarly important diversity of feeding ecologies has been inferred for younger radiodont assemblages, such as those of the Burgess Shale

and Marjum Lagerstätten (Daley and Budd 2010; Pates et al. 2021). More subtle differences in the endite morphology within radiodont genera, for example, *Anomalocaris*, could indicate specializations of individual species to different types of local prey (Pates et al. 2019b). The numerous morphological differences exhibited by radiodont feeding appendages, even in taxa from a given locality, evidences the great ability of these organisms to adapt to new food sources in each area they colonized, and further illustrates their strong connection to local, mostly benthic faunas.

Table 2. Taxonomic diversity of radiodont faunas from Cambrian: Stage 4 Konservat-Lagerstätten. Radiodont material has also been recovered from the Cambrian: Stage 4 Poleta Formation (Laurentia), but these specimens remain unidentified beyond the family level (English and Babcock 2010). **Anomalocaris magnabasis* is known from both the Comet Shale Member and Combined Metals Member of the Pioche Formation, *Hurdia* sp. is only known from the Combined Metals Member. ** note that we do not follow Wu et al.’s (2021) reassignment of this species to their new genus *Lenisicaris*.

Palaeocontinents	Gondwana		Laurentia				South China		
Lagerstätte	Emu Bay Shale	Valdemiedes Formation	Carrara Formation, Pyramid Shale Member	Eager Formation	Kinzers Formation	Latham Shale	Pioche Formation*	Guanshan	Balang
<i>Amplectobelua</i>	–	–	–	–	aff. <i>Amplectobelua symbrachia-ta</i> (Pates and Daley 2019)	–	–	–	–
<i>Anomalocaris</i>	cf. <i>Anomalocaris canadensis</i> (Daley et al. 2013b)	–	<i>Anomalocaris magnabasis?</i> (Pates et al. 2019b)	<i>Anomalocaris canadensis</i> (Briggs 1979; Daley and Edgecombe 2014)	<i>Anomalocaris pennsylvanica</i> (Briggs 1979; Pates and Daley 2019)**	–	<i>Anomalocaris magnabasis</i> (Pates et al. 2019b)	–	<i>Anomalocaris</i> sp. (Liu 2013)
“ <i>Anomalocaris</i> ” Amplectobeluidae	–	–	–	–	–	–	–	“ <i>A.</i> ” <i>kunmingensis</i> (Wang et al. 2013; Zeng et al. 2018; this study)	–
“ <i>Anomalocaris</i> ” Tamisiocarididae	“ <i>Anomalocaris</i> ” <i>briggsi</i> (Daley et al. 2013b)	–	–	–	–	–	–	–	–
<i>Caryosyntrips</i>	–	cf. <i>Caryosyntrips camurus</i> (Pates and Daley 2017)	–	–	–	–	–	–	–
<i>Hurdia</i>	–	–	–	–	–	–	<i>Hurdia</i> sp. (Pates et al. 2019b)	–	–
<i>Laminacaris?</i>	–	–	–	–	<i>Laminacaris?</i> sp. (Pates and Daley 2019)	–	–	–	–
<i>Lenisicaris</i>	–	–	–	–	<i>Lenisicaris pennsylvanica</i> (Briggs 1979; Pates and Daley 2019; Wu et al. 2021)	–	–	–	–
<i>Paranomalocaris</i>	–	–	–	–	–	–	–	<i>Paranomalocaris multisegmentalis</i> (Wang et al. 2013), <i>P. simplex</i> (this study)	–
<i>Peytoia</i>	–	–	–	–	–	–	–	–	cf. <i>Peytoia nathorsti</i> (Liu 2013)
<i>Ramskoeldia</i>	–	–	–	–	–	<i>Ramskoeldia consimilis?</i> (Pates et al. 2019b)	–	–	–
<i>Tamisiocaris</i>	–	–	–	–	<i>Tamisiocaris</i> sp. (Pates and Daley 2019)	–	–	–	–
Tamisiocarididae	–	–	–	–	–	–	–	Tamisiocarididae indet. (this study)	–

Conclusions

Recent collecting efforts and redescriptions placing accessioned material in a modern systematic context have revealed that radiodonts in the Cambrian Stage 4 were more diverse than previously appreciated. In this study we report two new radiodont taxa, doubling the known diversity of this group from the Guanshan Biota. The new radiodont data includes the first tamisiocaridid from South China, a second species of *Paranomalocaris*, and confirms the presence of a tetradial oral cone in “*Anomalocaris*” *kunmingensis*. All four radiodont taxa are only known from the Guanshan Biota, which further illustrates the differences between its taxonomic composition compared to the Chengjiang Biota, and other Cambrian exceptionally preserved faunas of South China. This unique taxonomic composition is likely a consequence of the Guanshan radiodonts inhabiting a more proximal, shallow-water environment compared to other radiodonts. This in turn implies a strong coupling between the free-swimming radiodont fauna, and the local benthic communities. The importance of these trophic relationships is further illustrated by the numerous morphological adaptations that radiodonts evolved in response to access to different prey locally. In the Guanshan Biota, this local evolution is particularly well exemplified by the endemic genus *Paranomalocaris*, which is represented by two species specialized for different feeding modes. The endemism of Guanshan radiodonts underscores the importance of exploring as many deposits as possible to gain as complete an understanding of Cambrian total-group euarthropod biodiversity as possible.

Authors’ contributions

JY, TL, and XGZ designed the project. DGJ and XGZ photographed material. DGJ, XGZ, and SP prepared figures with input from RL-A and JO-H. DGJ, JY, TL, and XGZ performed fieldwork, collected and prepared the material. SP and RL-A interpreted the data, and wrote the manuscript with input of all co-authors. All authors performed research, discussed, and approved the final manuscript.

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