



New occurrence of the Guanshan Lagerstätte (Cambrian Series 2, Stage 4) in the Kunming area, Yunnan, southwest China, with records of new taxa

Jun Zhao, Yujing Li , Paul A. Selden , and Peiyun Cong

ABSTRACT

As a classic Burgess-Shale-Type Konservat-Lagerstätte, the Guanshan biota is well known for its abundant soft-bodied fossils with high taxonomic diversity. Here, we report a new locality of the Guanshan biota in the Kunming area, Yunnan, South China with several new forms being first documented. In particular: a naraoiid euarthropod, the dorsal exoskeleton of which has characters of both naraoiids and *Emucaris*; and a discoidal animal, identified as a small eldonioid-like metazoan, which has a counterpart from the Emu Bay Shale Lagerstätte of South Australia, and which further strengthens the biogeographic connection between the early Cambrian biotas of South China and Australia. Our new discoveries not only expand the palaeogeographic distribution of the Guanshan biota, but also reveal that its biodiversity is much higher than previously thought, and can be justifiably regarded as a community successor to the Chengjiang biota.

ARTICLE HISTORY

Received 20 January 2020
Revised 2 June 2020
Accepted 8 June 2020

KEYWORDS

The Guanshan biota, early Cambrian, naraoiid, medusiform metazoan, biogeographic connection

Jun Zhao [zhaojunpaleo@126.com], Yunnan Key Laboratory for Palaeobiology, Institute of Palaeontology, Yunnan University, Kunming, Yunnan, 650091, China; Yunnan Key Laboratory of International Rivers and Transboundary Eco-Security, Yunnan University, Kunming 650091, China; MEC International Joint Laboratory for Palaeobiology and Palaeoenvironment, Institute of Palaeontology, Yunnan University, Kunming, Yunnan, 650091, China; Yujing Li [yujingli@ynu.edu.cn], Yunnan Key Laboratory for Palaeobiology, Institute of Palaeontology, Yunnan University, Kunming, Yunnan, 650091, China; MEC International Joint Laboratory for Palaeobiology and Palaeoenvironment, Institute of Palaeontology, Yunnan University, Kunming, Yunnan, 650091, China; Paul A. Selden [selden@ku.edu], Department of Geology, University of Kansas, 1457 Jayhawk Boulevard, Lawrence, KS 66045, USA; Natural History Museum, Cromwell Road, London SW7 5BD, UK; Peiyun Cong [cong@ynu.edu.cn], Yunnan Key Laboratory for Palaeobiology, Institute of Palaeontology, Yunnan University, Kunming, Yunnan, 650091, China; MEC International Joint Laboratory for Palaeobiology and Palaeoenvironment, Institute of Palaeontology, Yunnan University, Kunming, Yunnan, 650091, China.

HITHERTO, the Guanshan biota, one of the classic Burgess-Shale-type (BST) Konservat Lagerstätten in China, has already produced *ca* 75 taxa assigned to more than 10 metazoan groups (e.g., Steiner *et al.* 2012, Hu *et al.* 2013, Liu *et al.* 2015, Hu *et al.* 2017, Zeng *et al.* 2018, Zhao *et al.* 2018). Chronologically the Guanshan lies between some early Cambrian biotas, e.g., the Chengjiang, Xiaoshiba and Malong biotas and middle Cambrian BST assemblages, e.g., the Kaili biota and the Burgess Shale Fauna (Hopkins *et al.* 2017, Chen *et al.* 2019) (Fig. 1), and thus it is an important window into the ‘Cambrian Explosion’ and forms a link in the history of the early evolution of marine animals (Hu *et al.* 2013, Liu *et al.* 2015, 2016). Eleven fossil sites of the Guanshan biota have been reported in the literature, most of which are located in Kunming and the surrounding areas (Hu *et al.* 2013, Liu *et al.* 2016, Chen *et al.* 2019). To date, only eight sites still produce fossils (Fig. 2), while others have already disappeared because of the construction of residential areas. Recently, an occurrence of the Guanshan assemblage with soft-bodied fossils was discovered at the Kanfuqing section, Malong County, eastern Yunnan (Chen *et al.* 2019), where the soft-bodied fossils of the Guanshan biota have been found on both sides of the Xiaojiang Fault.

Characterized by the tagmosis of a head shield and a trunk shield, naraoiids are an abundant group of non-bio-mineralized trilobitomorph arthropods, ranging from the

early Cambrian to the late Silurian (Mayers *et al.* 2019, Zhai *et al.* 2019). Ten valid species have been assigned to Naraoiidae Walcott, 1912 (Mayers *et al.* 2019), and with exquisite preservation of soft tissues, these taxa are of special interest for studies of marine arthropods. The life habits of naraoiids remain controversial although, after reconstructing the appendages of *Naraoia spinosa* Zhang & Hou, 1985 from the Chengjiang biota, Zhai *et al.* (2019) proposed a detritus-feeding strategy for juveniles and a predatory/scavenging behaviour for adults.

Predominantly occurring in early and middle Cambrian strata across the globe, eldonioids are a group of enigmatic medusiform metazoans, characterized by the presence of circumoral tentacles, radial structures, concentric ornaments, and dorsal and ventral discs with coiled digestive organs enclosed in between (Schroeder *et al.* 2018). The affinity and ecology of this group still remains problematic, although recently Zhao *et al.* (2018) discussed four types of interrelationships between an eldonioid from the Kaili biota, *Pararotadiscus guizhouensis* Zhao & Zhu, 1994 and associated fossils, providing some palaeoecological insights into the group.

Naraoiids have never been discovered from the Guanshan biota, and eldonioids were once reported (Hu *et al.* 2013) but lack detailed descriptions. Here, we briefly report a new locality of this Lagerstätte by listing some typical representatives and introducing two taxa which are rare in the Guanshan biota: a naraoiid euarthropod and an eldonioid-like animal. These new discoveries not only expand the

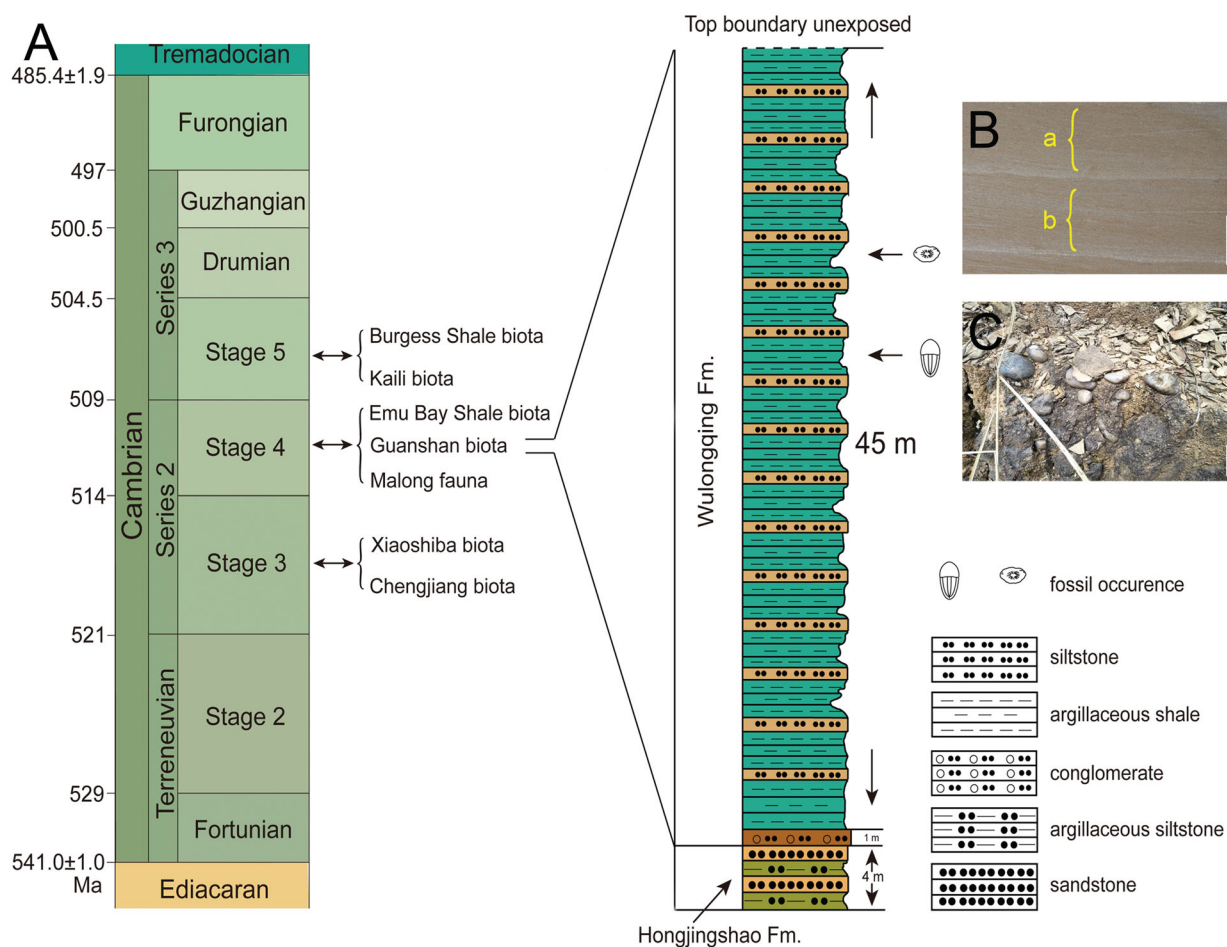


Figure 1. Changchunshan section, Kunming, Yunnan. **A**, major fossil Lagerstätten in the Cambrian (left) and the simplified schematic stratigraphic column of the Changchunshan (right). **B**, polished slab from the argillaceous shale from this section; brackets (a) and (b) refer to the graded mudstone beds yielding most of the Guanshan fossils, including the two unnamed taxa. **C**, the conglomerates intercalated between the Hongjingshao Formation and the Wulongqing Formation. Scale bars = 5 mm for B and 30 mm for C.

palaeogeographic distribution of the Guanshan biota, but also provide new materials for the studies of marine animals in the early Cambrian. Similar representatives of the two taxa were once documented from the Emu Bay Shale Fauna of South Australia (Paterson *et al.* 2010, 2016, Schroeder *et al.* 2018). Paterson *et al.* (2015) discussed the biogeographic connections between the early Cambrian biotas of Australia and South China and with the documentation herein of similar taxa with similar features, the biogeographic connections between the two assemblages are further strengthened.

New occurrence of the Guanshan biota in Kunming

Geological setting. The Changchunshan section (25.00331°N, 102.81020°E) (Fig. 2) is *ca* 10.8 km southeast from the downtown area of Kunming and *ca* 6 km north of the well-known Gaoloufang village, an important section for the Guanshan fossils. The Cambrian succession in Changchunshan is composed of the Hongjingshao Formation (upper part) and the overlying Wulongqing Formation (lower-middle part), intercalated with layers of conglomerates. The underlying Hongjingshao Formation has

a thickness of *ca* 4 m and consists of dark brown sandstones and grey argillaceous siltstones, with no fossils yet discovered. The Wulongqing Formation (*ca* 45 m in thickness) is mostly composed of greyish-yellow silty mudstones (the main layers producing soft-bodied fossils) interbedded with dark brown siltstones. The top boundary of the Wulongqing Formation is not exposed in this section.

Abundance of fossils, composition of the ecologic community and preservation of specimens. Extensive excavation only recently commenced at this fossil section, and a total of over 700 specimens have been obtained. Although we feel that such numbers do not warrant a detailed statistical analysis yet, we have outlined the current diversity, abundance and the range of ecological categories present at the new Guanshan biota locality in Table 1. To date, nine metazoan groups have been discovered in this section, including arthropods, brachiopods, priapulids, vetulicolians, anomalocaridids, hyoliths, chancelloriids, sponges and echinoderms (Figs. 3, 4). In terms of abundance, trilobites and brachiopods, represented by *Palaeolenus lantenoisi* Mansuy, 1912, *Redlichia mansuyi* Resser and Endo, 1937 and *Diandongia* sp. Hu *et al.* 2013 dominate the fauna, accounting for 81%; non-trilobite arthropods, represented by *Isoxys minor* Luo &

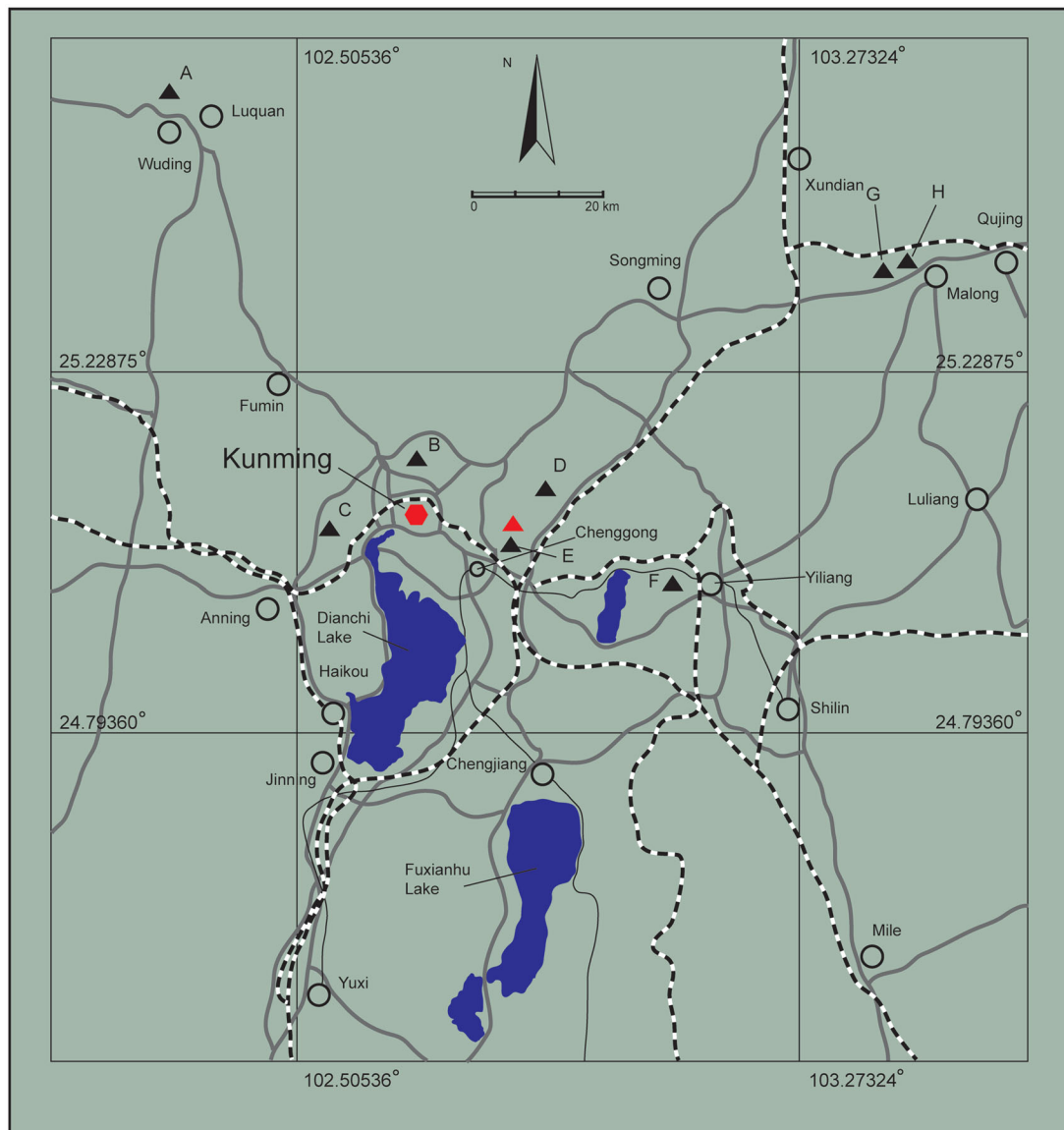


Figure 2. The main fossil sites of the Guanshan biota in Eastern Yunnan. A, Shijiangjun. B, Gangtoucun. C, Baimei. D, Dabanqiao. E, Gaoloufang. F, Lihuazhuang. G, Wulongqing. H, Kanfuqing. Red triangle is the Changchunshan section.

Table 1. Taxonomic diversity, specimen abundance and ecological composition of the Guanshan biota from the Changchunshan section.

Ecological composition	Taxonomy diversity	Specimen abundance
Pelagic metazoans	<i>Tuzoia sinensis</i> P'an, 1957	10
	<i>Tuzoia tylodesa</i> Luo & Hu, 2006	12
	<i>Isoxys minor</i> Luo & Hu, 2008	15
	elodonoid-like metazoan	16
	<i>Redlichia mansuyi</i> Resser & Endo, 1937	100
Nektobenthos	<i>Palaeolenus lantenoisi</i> Mansuy, 1912	300
	<i>Panlong tetranodusa</i> Liu & Luo, 2006	15
	<i>Guangweicaris spinatus</i> Luo et al. 2007	13
	anomolocarid	2
Vagile epibenthos	vetulicolian	18
	naraoiid	3
	<i>Linevitus malongensis</i> Yu, 1974	4
Sessile epibenthos	<i>Wudingecrinus rarus</i> Hu et al. 2010	2
	<i>Allonnia tenuis</i> Zhao et al. 2018	9
	<i>Crumillospongia biporosa</i> Rigby, 1986	4
Infauna	<i>Wudingscolex sapushanensis</i> Hu et al. 2012	12
	<i>Guanduscolex minor</i> Hu et al. 2010	8
	<i>Diandongia</i> sp. Hu et al. 2013	208



Figure 3. Some arthropods of the Guanshan biota from the Changchunshan section. **A**, *Redlichia mansuyi* Resser & Endo, 1937 (YKLP 13351). **B**, *Palaeolenus lantenoi* Mansuy, 1912 (YKLP 13391), preserved with antennae. **C**, *Palaeolenus lantenoi* Mansuy, 1912 (YKLP 13353), preserved in groups. **D**, *Panlongia tetranodusa* Liu & Luo in Liu *et al.* 2006 (YKLP 13354). **E**, *Guangweicaris spinatus* Luo *et al.* 2007 (YKLP 13356). **F**, *Tuzoia sinensis* P'an, 1957 (YKLP 13357). **G**, *Isoxys minor* Luo & Hu, 2008 (YKLP 13358). **H**, *Tuzoia tylodesa* Luo & Hu in Luo *et al.* 2006 (YKLP 13359). Scale bars = 5 mm for A, C, E, F and 3 mm for B, D, G, H.

Hu in Luo *et al.* 2008, *Tuzoia sinensis* P'an, 1957 and *Guangweicaris spinatus* Luo *et al.* 2007, account for 9%; a range of other metazoans constitute the remaining 10%. Soft-bodied fossils, such as priapulids and vetulicolians, are

few and only account for 5% of the total specimens. The naraoiid and eldonioid-like metazoans described below are very rare, accounting for *ca* 0.4% and *ca* 4.3% respectively. Taxa from this section can be placed in a variety of

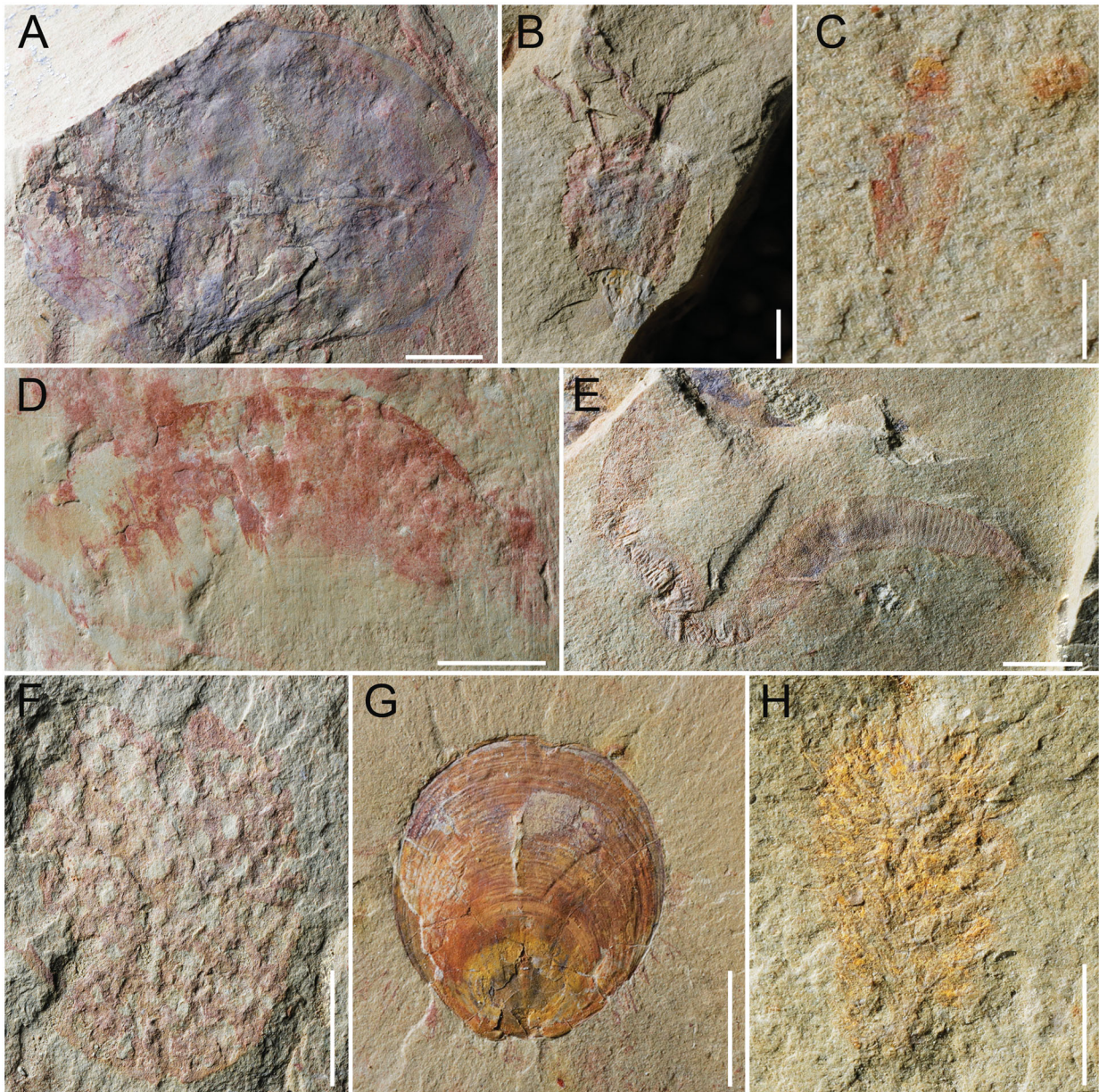


Figure 4. Some non-arthropod metazoans of the Guanshan biota from the Changchunshan section. **A**, an anterior part of a vetulicolian (YKLP 13394). **B**, *Wudingeocrinus rarus* Hu & Luo in Luo *et al.* 2008 (YKLP 13364). **C**, *Lineivitus malongensis* Yu, 1974 (YKLP 13392). **D**, An anomalocaridid frontal appendage (YKLP 13360). **E**, *Wudingscolex sapushanensis* Hu *et al.* 2012 (YKLP 13361). **F**, *Crumillospongia biporosa* Rigby, 1986 (YKLP 13362). **G**, *Diandongia* sp. Hu *et al.* 2013 (YKLP 13363), preserved with setae. **H**, *Allonnia tenuis* Zhao *et al.* 2018 (YKLP 13393). Scale bars = 5 mm for A, D, F, 3 mm for B, E, G, H and 1 mm for C.

ecological categories, such as the sessile epibenthos (e.g., *Wudingeocrinus rarus* Hu & Luo in Luo *et al.* 2008), vagile epibenthos (e.g., *Lineivitus malongensis* Yu, 1974), nektobenthos (e.g., anomalocaridid), infauna (e.g., *Wudingscolex sapushanensis* Hu *et al.* 2012) and pelagic (e.g., *Tuzoia sinensis* P'an, 1957). All fossils are oriented parallel or sub-parallel to the bedding planes, with most being preserved as individuals (e.g., Fig. 3A), with accumulations of individual specimens rarely found (e.g., Fig. 3C). Due to weathering and diagenetic processes, most fossils show a reddish-brown or greyish-white staining on the body surface due to the presence of iron oxide and clay minerals, which contrasts sharply with the greyish-yellow matrix, a preservation style typical of Guanshan fossils at other localities (Hu *et al.* 2013). Soft tissues of the arthropods from this section are

scarcely present, and only a few trilobites and the naraoiid described below preserved some soft parts, such as antennae. Bivalved arthropods, such as *Tuzoia* and *Isoxys*, only have the valves preserved, without any soft part preservation (Fig. 3F–H). Based on the specimens at hand, the frequency of soft tissue preservation and the abundance and variety of soft-bodied fossils, comparatively speaking this section seems to be slightly inferior to Gaoloufang, the classic quarry of the Guanshan biota.

Materials and methods

All the fossils described below were collected in the first three months of 2019. Some were prepared using a needle under a Nikon SMZ 800 N, revealing parts covered by matrix. Digital

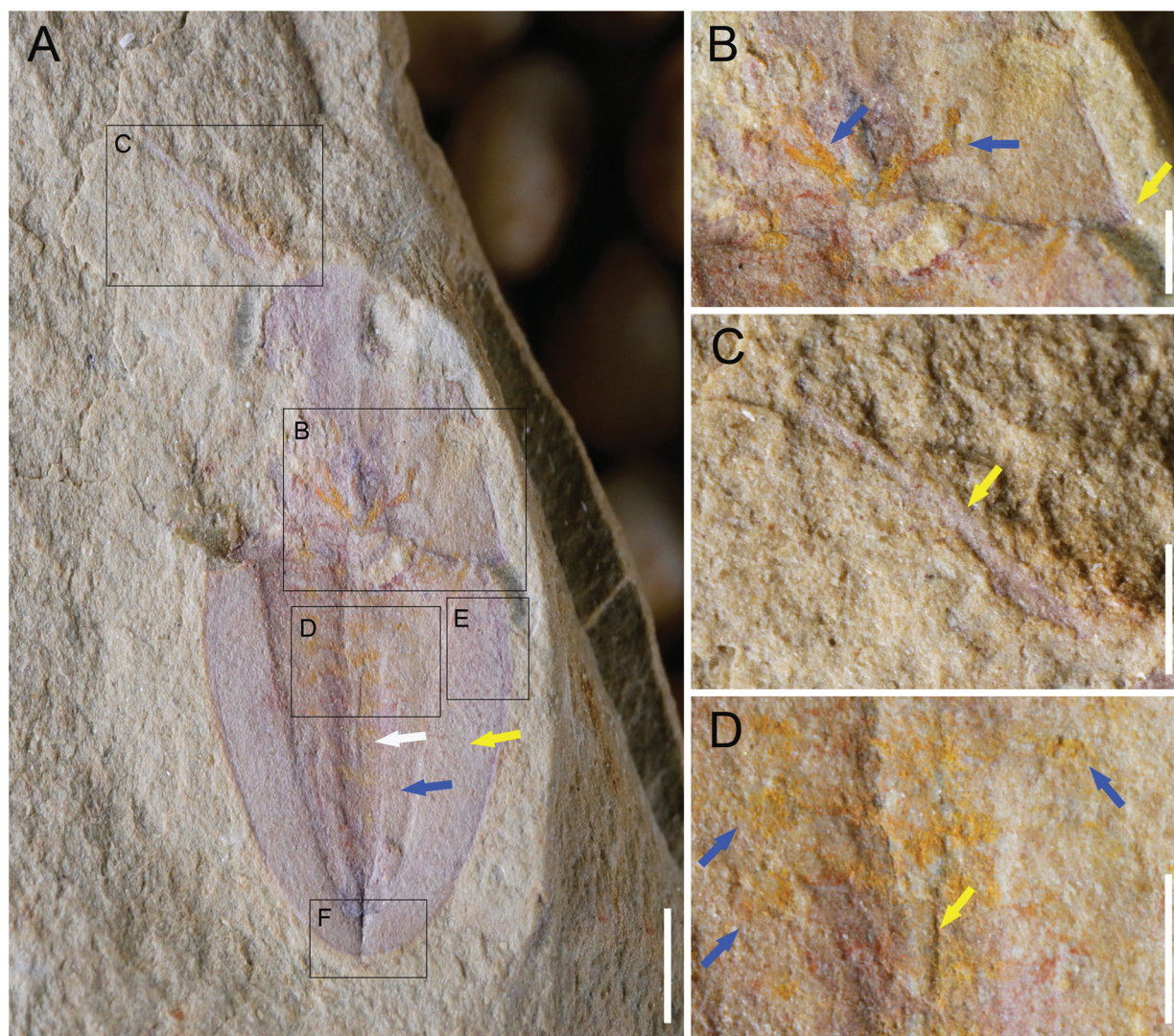


Figure 5. The unnamed naraoid euarthropod (YKLP 13365). **A**, the overall morphology of the euarthropod. This being the counterpart, the positions and orientations of the characters should be reversed when referring to the part. Yellow arrow points to the marginal zone and blue arrow points to the pleural field and white arrow points to the axial region. **B**, detail of (A) (position marked by frame B), yellow arrow points to the genal spine and blue arrows point to the dendritic structures. **C**, detail of (A) (position marked by frame C), yellow arrow points to the antenna. **D**, detail of (A) (position marked by frame D), yellow arrow points to the possible gut and blue arrows point to the presumed inflated gut diverticula. Scale bars = 1 mm for A and 0.5 mm for B, C, D.

photographs were taken using a Canon EOS 5D SR camera mounted with a Canon MP-E 65 mm (1–5 \times) macro lens, under cross-polarized light and processed in Adobe Photoshop CS 5. Line drawings were made using Adobe Illustrator CS 5. Terminology follows Zhu *et al.* (2002), Paterson *et al.* (2010), Hou *et al.* (2017) and Schroeder *et al.* (2018). All the specimens are housed at the Yunnan Key Laboratory for Palaeobiology, Yunnan University (YKLP).

Specimens of the unnamed euarthropod in the Guanshan biota are fairly rare, and only three have been obtained, all of which contrast distinctly to the matrix in colour: the dorsal exoskeleton and antenna of YKLP13365 (Fig. 5) are purple, whereas the traces of soft tissues are preserved in light yellow. This specimen is just a counterpart, but almost complete; whereas the part was highly weathered and collapsed into pieces, and was impossible to repair for photography. YKLP 13366 (Fig. 6C) (also a counterpart) is an incomplete specimen with most of the headshield missing. Traces of intersegmental furrows and the dorsal exoskeleton are

preserved in grey white. YKLP 13367 (Fig. 7A) is also incomplete, with the headshield and parts of the trunk missing. The surface of the trunk is preserved in grey-white while the border is a dark-brown. The variety of colours observed in these specimens is most likely due to weathering processes. Specimens of eldonioid-like metazoans (Figs 8–10) are comparatively abundant, with 16 slabs (YKLP 13368–13383) bearing more than 30 individuals.

Systematic palaeontology

Order Nektaspida Raymond, 1920

Family Naraoidae Walcott, 1912

Genus and species uncertain

Figs 5–7

Description. Body suboval (Fig. 5A), sagittal length (excluding antenna) *ca* 7 mm. Maximum width of dorsal

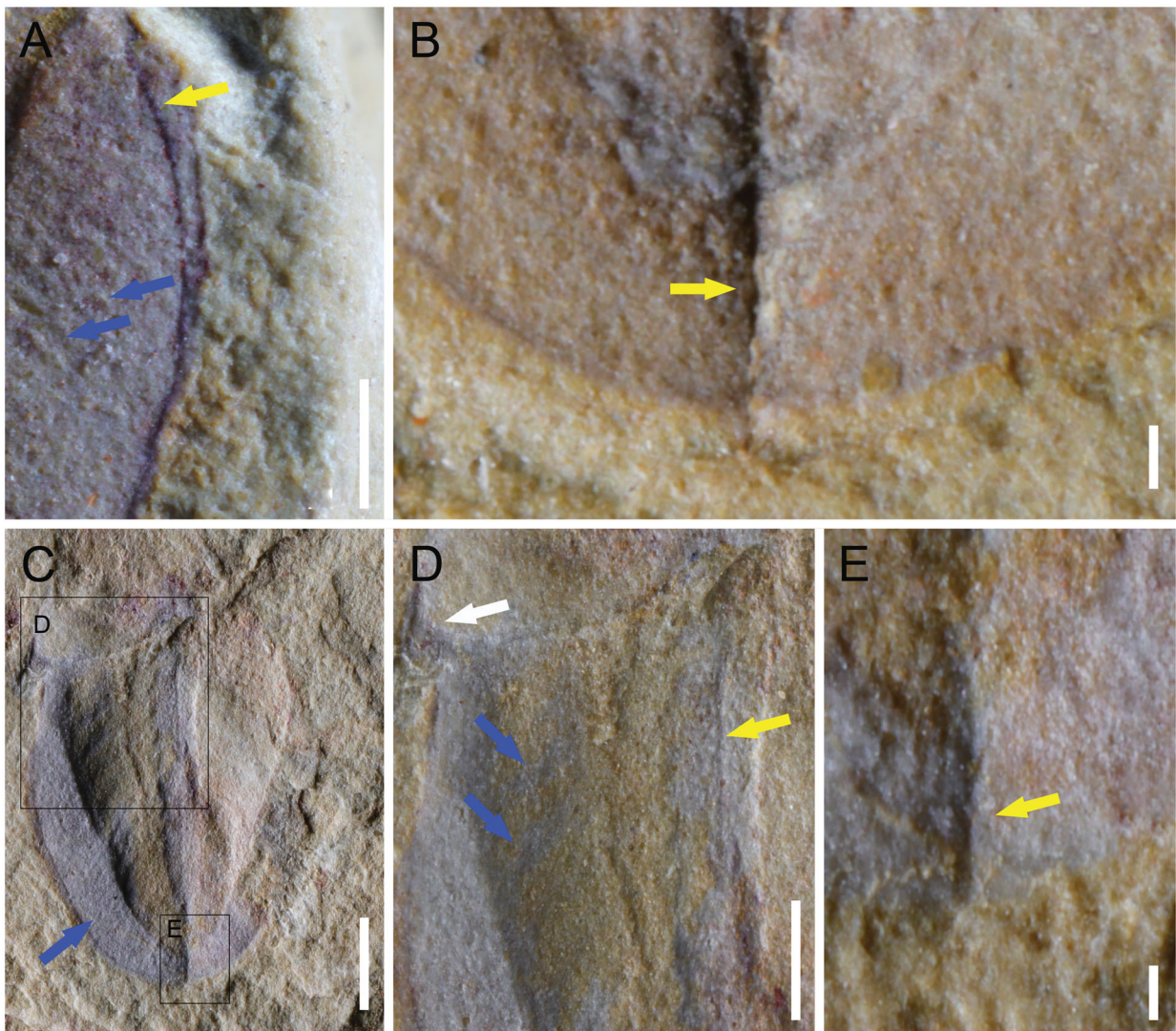


Figure 6. The unnamed naraoiid euarthropod. A, detail of (Fig. 5A) (position marked by frame E), yellow arrow points to the doublure and blue arrows point to the polygonal ornaments. B, detail of (Fig. 5A) (position marked by frame F), yellow arrow points to the postaxial ridge. C, YKLP 13366, blue arrow points to the polygonal ornaments in the marginal zone. D, detail of (C) (position marked by frame D), yellow arrow points to the possible gut and white arrow points to the genal spine and blue arrows point to the possible intersegmental furrows. Scale bars = 1 mm for C, 0.5 mm for A, D and 0.1 mm for B, E.

exoskeleton, located anterior part of trunk, *ca* 57% of sagittal length. Cephalic shield with 2 small, blunt, subtriangular genal spines (Fig. 5B), possibly semielliptical in outline. Sagittal length *ca* 43% of dorsal exoskeleton length, *ca* 75% of width. Antenna slender, tapering distally, extending laterally beyond anterior margin of cephalic shield (Fig. 5C). Dendritic structures (Fig. 5B), possibly traces of post-antennal appendages, project both antero-left and antero-right, preserved on posterior part of cephalic shield, and bounded by its axis. No podomeres visible on presumed appendages.

Trunk subtriangular in profile, composed of axial region, pleural field and marginal zone (e.g., Fig. 5A). Sagittal length *ca* 57% of that of dorsal exoskeleton. Axial region subconical, evenly tapering posteriorly. Convex, tube-like structure (presumed gut) runs along midline of axial region (Figs 5D, 6D). Several pairs of transverse structures aligned on both sides of gut, their distal ends inflated into subcircular structures, possibly gut diverticula (Fig. 5D). Some oblique, weakly impressed furrows (Fig. 6D) preserved on pleural field, possibly intersegmental furrows. Marginal zone (Fig.

6A, C) evenly tapering posteriorly, covered by rectangular and pentagonal ornament. Doublure (Fig. 6A), slightly narrower than margin, runs approximately parallel to margin, except in anteriormost region of trunk where it diverges inward from lateral margins. Postaxial ridge (Figs 6B, E, 7B), narrow, tapering posteriorly, extending from rounded posterior end of axial region, cutting across most of marginal zone behind.

Discussion. The dorsal exoskeleton of the euarthropod described above is composed of an anterior and a posterior shield without any body segments in between, which accords with the diagnosis of Naraoiidae Walcott, 1912. Three kinds of naraoiids have been identified from the older Chengjiang biota: *Naraoia halia* Simonetta and Delle Cave, 1975, *Naraoia spinosa* Zhang & Hou, 1985 and *Misszhouia longicaudata* (Zhang & Hou, 1985). Both *N. spinosa* and *M. longicaudata* are relatively abundant and well preserved in the Chengjiang biota, allowing us to make detailed comparisons in overall morphology with the euarthropod documented here.

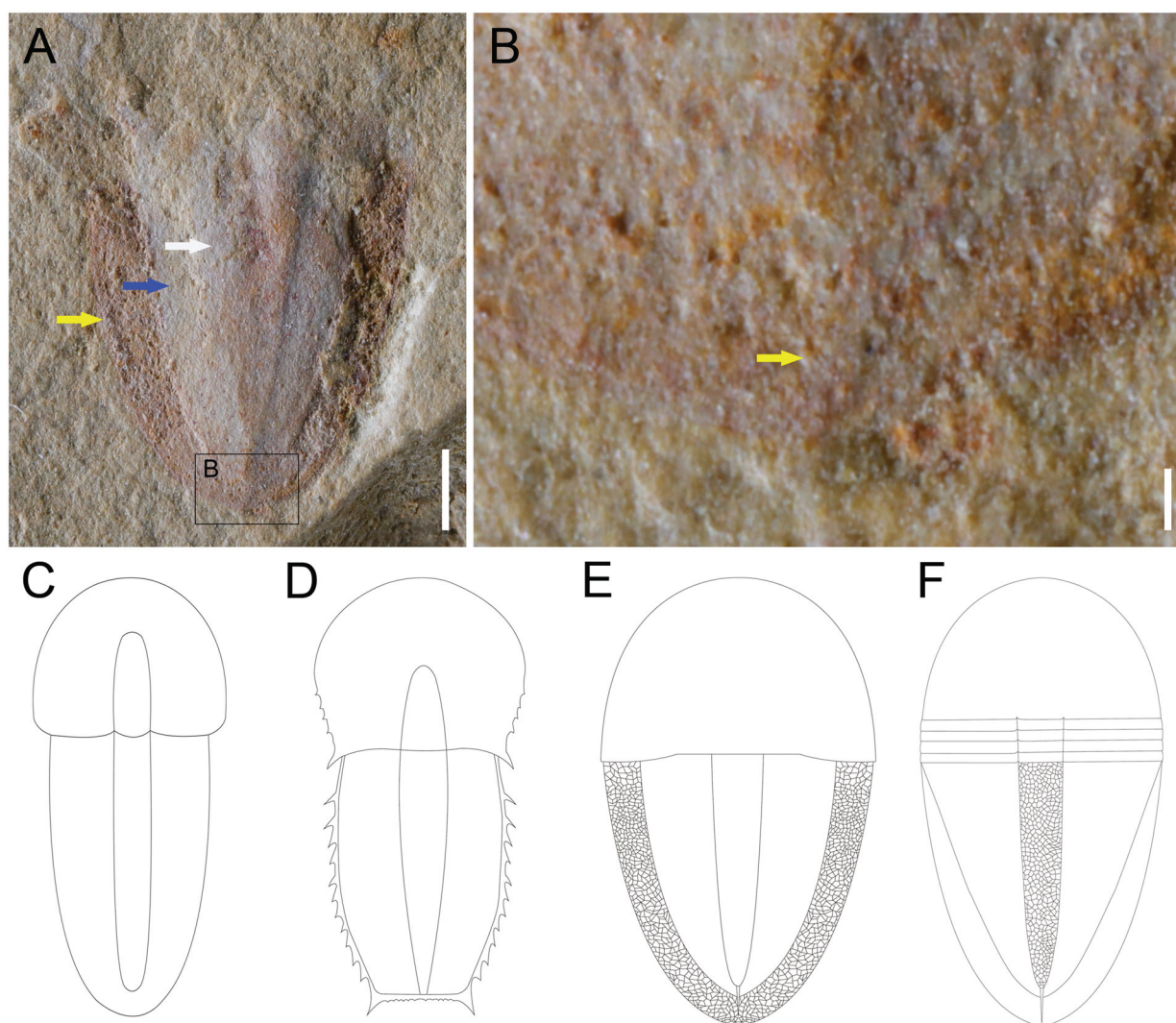


Figure 7. The unnamed naraoiid euarthropod and reconstruction of the dorsal exoskeleton of some euarthropods from early Cambrian. **A**, YKLP 13367, yellow arrow points to the marginal zone and blue arrow points to the pleural field and white arrow points to the axial region. **B**, detail of (A) (position marked by frame B), yellow arrow points to the postaxial ridge. **C**, *Misszhouia longicaudata* Zhang & Hou, 1985 (revised from Hou et al. 2017). **D**, *Naraoia spinosa* Zhang & Hou, 1985 (revised from Hou et al. 2017). **E**, The unnamed euarthropod from the *Guanshan biota*. **F**, *Emucaris fava* Paterson et al. 2010 (revised from Paterson et al. 2010). Scale bars = 1 mm for A and 0.1 mm for B.

The obvious similarity between the two naraoiids and the unnamed taxon is the tagmosis of the dorsal exoskeleton (Fig. 7C–E), which consist of only a cephalic shield and a trunk. The difference is that the trunk components of the unnamed taxon, including the postaxial ridge and polygonal ornaments, are clearly absent in the naraoiids. Paterson et al. (2010) erected the Family Emucarididae to accommodate two nektaspid euarthropods from the Emu Bay Shale Fauna of South Australia: *Emucaris* and *Kangacaris*, both of which are characterized by the tagmosis of a cephalic shield, a thorax and a pygidium. The obvious similarity between the unnamed taxon and emucaridids, especially *Emucaris*, is the overall morphology, and components of the trunk of the former and pygidium of the latter (Fig. 7E, F). Both are elongate and subtriangular, with the sagittal length being longer than that of cephalic shield, and both possess an axial region, pleural field, marginal zone with a doublure, and a postaxial ridge. Some differences also exist: the axial region

of the specimens herein lacks polygonal ornaments, whereas the marginal zone is ornamented with many rectangles and pentagons. In addition, the marginal zone and doublure do not have the same dimensions, which is different from *Emucaris*. The biggest difference between the unnamed taxon and *Emucaris* is the absence of free thoracic segments, which leads to a bipartite body plan for the former and a tripartite body for the latter.

The tagmosis of the described euarthropod, the bipartite body without free thoracic segment, strongly indicates a close relationship with naraoiids, and thus we tentatively assign it to the family Naraoiidae, while its trunk components show some resemblances with *Emucaris*. Therefore, the overall morphology of the dorsal exoskeleton of the unnamed taxon seems to have characters from both naraoiids and *Emucaris*, which could see this taxon erected as a new genus within the order Nektaspida Raymond, 1920, but, a more detailed morphological description and possibly a

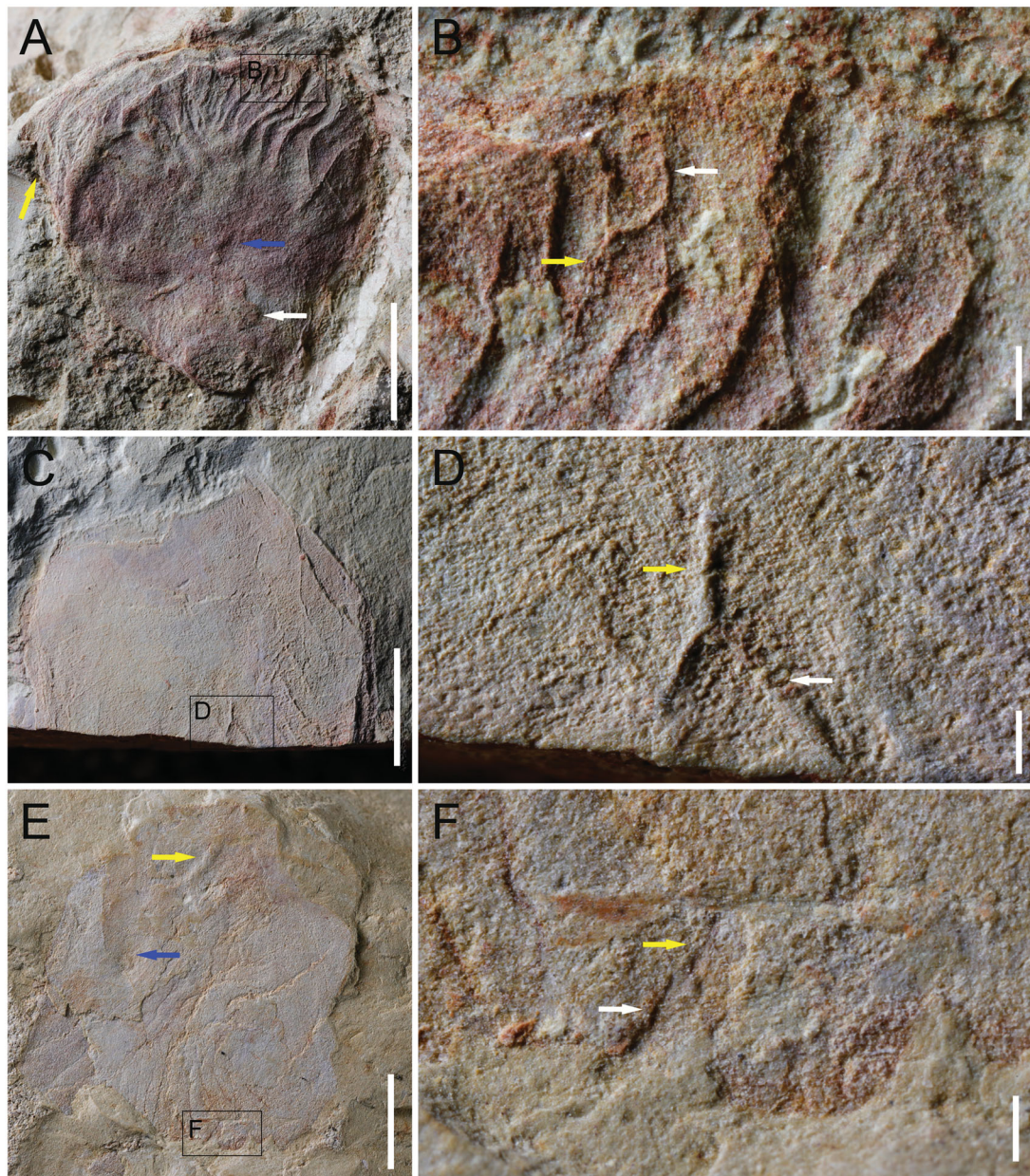


Figure 8. The unnamed eldonioid-like metazoan. **A**, YKLP 13368, yellow arrow points to the folds of the disc, and white and blue arrows point to the relief and the depression on the disc respectively. **B**, detail of (A) (position marked by frame B), yellow and white arrows point to the primary and secondary bifurcations of the radiating lobe respectively. **C**, YKLP 13369. **D**, detail of (C) (position marked by frame D), yellow and white arrows point to the primary and secondary bifurcations of the radiating lobe respectively. **E**, YKLP 13373, yellow and blue arrows point to the relief and the depression on the disc respectively. **F**, detail of (E) (position marked by frame F), yellow and white arrows point to the primary and secondary bifurcations of the radiating lobe respectively. Scale bars = 5 mm for A, C, E and 0.5 mm for B, D, F.

phylogenetic analysis of well-preserved specimens, especially those with soft tissues, is needed before this new genus is erected. Due to the scarcity and poor preservation of the specimens, the taxon is left under open nomenclature here.

? Family Eldoniidae Walcott, 1911

? Family Rotadiscidae Dzik, 1911

Figs 8–10

Description. Body eldonioid-like, disc diameter 11 mm–24 mm. Radial lobes with primary and secondary bifurcations (e.g., Fig. 8B, D, F). Dark stains preserved on some discs (Fig. 9), possibly remains of coiled sac with

presumed anterior end (Fig. 9A) and distal end (Fig. 9B). Concentric corrugations absent on most specimens, vague imprints observed on presumed coiled sac surface of YKLP 13375 (Fig. 9B). Plastic deformation such as folds, creating positive relief and depressions are constantly present on the discoidal surfaces of the Guanshan specimens (e.g., Fig. 8A, E).

Discussion. Radial lobes with bifurcations, although few, are clearly preserved on the discs of some specimens, which we consider to be morphological structure of this metazoan, not post-mortem deformation. With assumed anterior and distal ends, the coiled sac of the Guanshan specimens are located

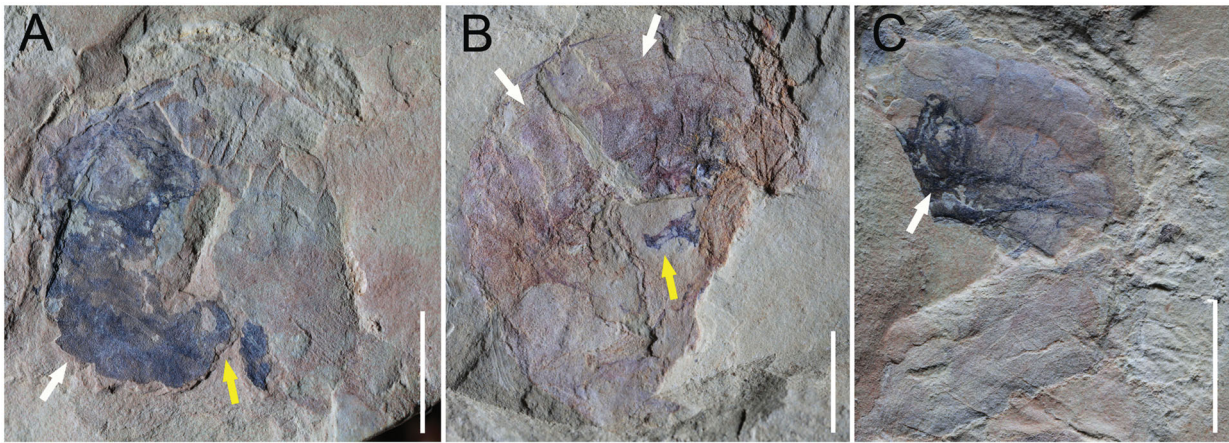


Figure 9. The unnamed eldonioid-like metazoan. **A**, YKLP 13374, white arrow points to the remains of the coiled sac and yellow arrow points to the presumed anterior end. **B**, YKLP 13375, white arrows point to the concentric corrugations near the disc margin and yellow arrow points to the presumed posterior end. **C**, YKLP 13376, white arrow points to the remains of the coiled sac. Scale bars = 5 mm.

at the centre of the disc and are preserved as a comparatively darker colour than other parts of the organism. These features are seen as important diagnostic features of eldonioids (e.g., *Eldonia ludwigi* Walcott, 1911, *Eldonia eumorphus* (Sun & Hou 1987), *Pararotadiscus guizhouensis* (Zhao & Zhu 1994)), and the presence of these features in the Guanshan specimens indicates a close relationship. Folds, relief and depressions can be observed on almost all the Guanshan specimens, indicating a flexible and nonbiomineralized disc. Compared to YKLP 13368, the folds of the disc margin of an individual on YKLP 13377 (Fig. 10B) are regularly arranged and closely spaced, which may not indicate simple plastic deformation, but its identity cannot be confirmed based on the specimens here.

Hu *et al.* (2013) first reported medusiform fossils from the Guanshan biota (abbreviated as GS below), and assumed them to be eldonioids, but did not provide detailed descriptions due to the scarcity and poor preservation of the material. From the overall morphology of those specimens (e.g., fig. 208, Hu *et al.* 2013), they possibly represent the metazoan described above. Paterson *et al.* (2015) and Schroeder *et al.* (2018) reported rotadiscids from the Emu Bay Shale (abbreviated as EBS below) and claimed that they showed similarities with *Pararotadiscus guizhouensis* Zhao & Zhu, 1994 from the middle Cambrian Kaili biota of South China. The similarities between the rotadiscid from the EBS and the medusiform metazoan from the GS are the small size of the disc (both less than 25 mm in diameter), radial lobes with bifurcations and concentric corrugations although the imprints of the corrugations are weak on GS specimens. The differences between the taxa are the presence and absence of strong plastic deformations (Fig. 8), coiled sac (Fig. 9) and trace fossils on the disc (e.g., fig. 1, Schroeder *et al.* 2018). Based on the overall morphology and characters preserved on the specimens from both EBS and GS, the two medusa-like metazoans may belong to the same taxon. Similar to those of the EBS, the specimens documented herein do not show any sign of circumoral tentacles, central ring and central cavity, some defining characters of eldonioids, and hence the phylogenetic position of these medusiform

metazoans still remains obscured and need to be confirmed by more evidence.

Based on the discussion above, we tentatively regard the two small medusiform metazoans from both the EBS and the GS as an eldonioid-like metazoan.

Reinforced biogeographic links

Paterson *et al.* (2015) discussed the biogeographic links between the early Cambrian biotas of Australia and South China based on several shared arthropod taxa, such as *Squamacula* (Zhang *et al.* 2004), *Kangacaris* Paterson *et al.* 2010, *Tuzoia* Walcott, 1912 and *Tanglangia* Luo & Hu in Luo *et al.* 1999. Most of the documented taxa from South China are components of the Chengjiang biota. Our study shows that the Guanshan biota, several million years younger than Chengjiang, also yields taxa which are comparable to those from the Emu Bay Shale. The euarthropod from Guanshan is assigned to the Naraoiidae Walcott, 1912 based on the tagmosis, but its trunk components and ornaments are rather similar to *Emucaris* Paterson *et al.* 2010 from the EBS, indicating the potential of some taxonomic relationship between the two taxa. The eldonioid-like animal from the GS shares important features with that of the EBS creature, especially the primary and secondary bifurcations of the radiating lobes. These taxonomic similarities possibly indicate that the EBS is comparable to both early Cambrian Burgess-Shale-type biotas from South China (Chengjiang and GS), sharing an increasing number of taxa across arthropods and non-arthropod animals, reinforcing the biogeographic connection between Australia and South China during the early stages of the Cambrian.

The Guanshan biota, a community successor of the Chengjiang

Stratigraphically, the Chengjiang biota belongs to Cambrian Series 2, Stage 3, while the Guanshan is slightly younger, belonging to Cambrian Series 2, Stage 4.

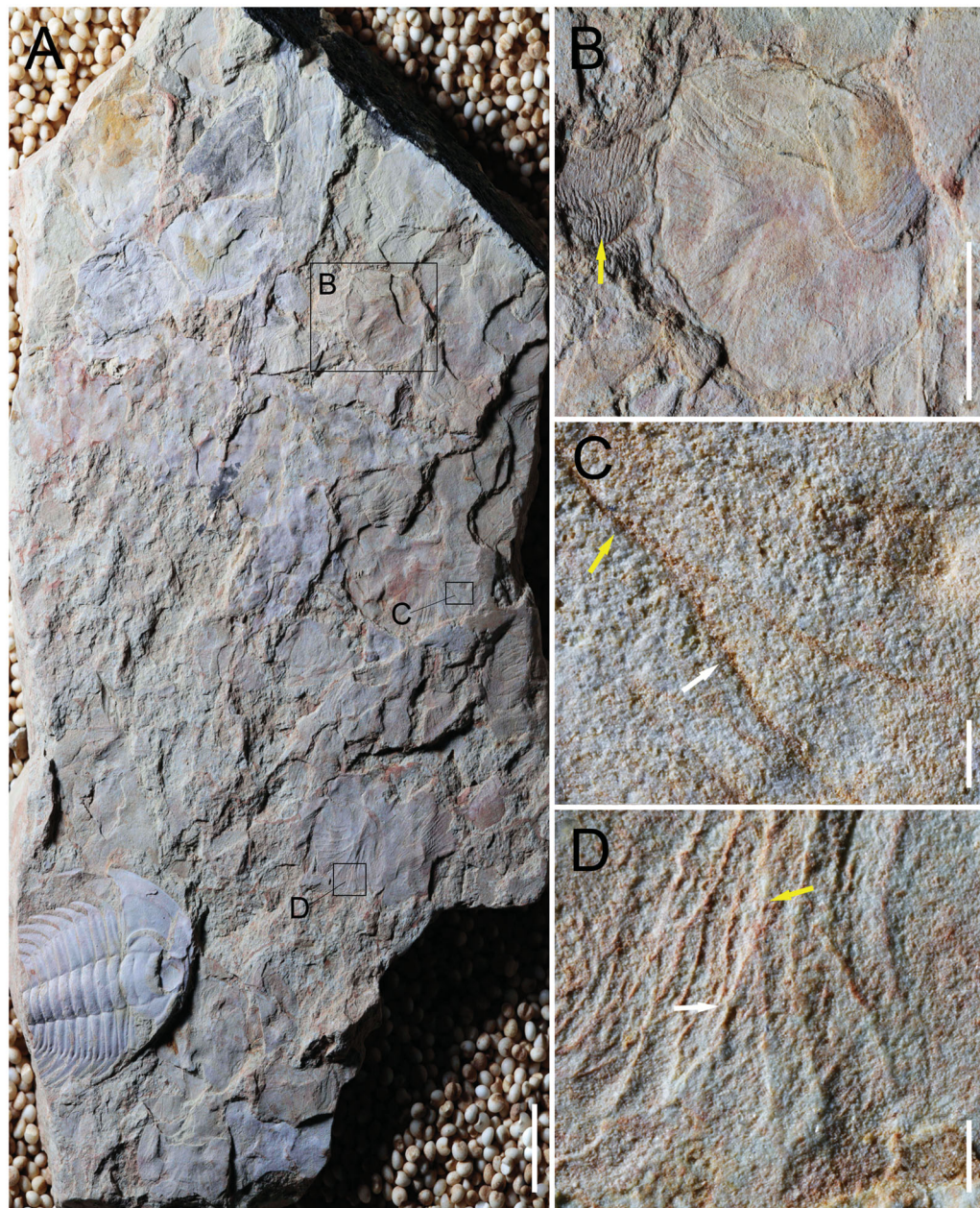


Figure 10. The unnamed eldonioid-like metazoan. **A**, the slab (YKLP 13377) bearing several individuals. **B**, detail of (A) (position marked by frame B), yellow arrow points to the regularly arranged folds on the disc. **C**, detail of (A) (position marked by frame C), yellow and white arrows point to the primary and secondary bifurcations of the radiating lobe respectively. **D**, detail of (A) (position marked by frame D), yellow and white arrows point to the primary and secondary bifurcations of the radiating lobe respectively. Scale bars = 10 mm for A, 5 mm for B and 0.5 mm for C, D.

Palaeogeographically, the main fossil sites of the Chengjiang are situated in Chengjiang, Jinning, Haikou and Anning, areas, all of which are located in Kunming and its surrounding areas (Hou *et al.* 2017, Chen *et al.* 2019), in a similar modern geographic region as the Guanshan biota. In addition, the Chengjiang has yielded 19 metazoan groups, plus animals of uncertain affinity which are ecologically divided into nektobenthos, infauna, epibenthos and pelagic animals (Hou *et al.* 2017), and after the discovery of an annelid animal (Liu *et al.* 2015), the Guanshan biota has already produced 16 metazoan groups plus problematic fossils, with most taxa being comparable to the Chengjiang. The new discovery of the naraoiid euarthropod and the eldonioid-like

metazoan in the Guanshan further strengthens this comparison in taxa with the Chengjiang, and strongly indicates that it is a community successor of the latter.

Acknowledgements

We appreciate the constructive comments from the reviewers and the editor that helped to improve the manuscript significantly. We thank L. Fei for the assistance during fieldwork.

Disclosure statement

No potential conflict of interest was reported by the author(s).

Funding

This research was supported by National Natural Science Foundation of China [No: 41572015] and CAS Pilot Research Programme XDB26000000.

ORCID

Yujing Li  <http://orcid.org/0000-0002-9554-5948>

Paul A. Selden  <http://orcid.org/0000-0001-7454-4260>

Peiyun Cong  <http://orcid.org/0000-0001-9910-6478>

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