Paleontological Research, vol. 26, no. 3, pp. 327–335, July 1, 2022

doi:10.2517/PR200047

A *Sidneyia*-like euarthropod from the Guanshan biota (Cambrian Series 2, Stage 4), eastern Yunnan, southwest China

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Received October 22, 2020; Revised manuscript accepted April 15, 2021; Published online July 1, 2022

Abstract. ***Sidneyia inexpectans*** **was first excavated in Laurentia, and since then** ***Sidneyia*** **and** ***Sidneyia*****-like euarthropods have been reported from different continents. Here we describe a new** ***Sidneyia*****-like euarthropod from the Guanshan biota and, its preserved dorsal exoskeleton and appendages resemble those of** ***S. inexpectans*****. The discovery in the Guanshan biota provides a new data point of** ***Sidneyia*****-like euarthropod in Cambrian Stage 4 and a second occurrence on the South China plate.**

Keywords: Cambrian Explosion, Cambrian *Lagerstätten*, Euarthropoda, *Sidneyia*, Vicissicaudata

Introduction

Sidneyia inexpectans Walcott, 1911 is an iconic and relatively large euarthropod of the middle Cambrian Burgess Shale biota from British Columbia, Canada (e.g. Stein, 2013; Zacaï *et al.*, 2016; Sun *et al.*, 2020). Hitherto, the detailed morphologies of its dorsal exoskeleton and appendages beneath the cephalic shield and trunk have been described and studied (e.g. Walcott, 1911; Bruton, 1981; Stein, 2013). The cephalic shield in dorsal view is sub-rectangular with a notch situated on each lateral margin, accommodating an eye stalk and an antenna; cephalic appendages, including antenna, are at least three; thorax is nine segmented, and thoracic appendages mainly comprise protopodite, endopod, and exopod with lamellae; abdomen is two or three segmented; caudal fan, composed of a telson and a pair of uropods, is articulated with the posteriormost abdominal segment. Recently, combined with studies of its digestive system, gut contents, and microstructures of gnathobasic spines, *S. inexpectans* has been considered a durophagous carnivore with predatory and/or scavenging habits (e.g. Stein, 2013; Zacaï *et al.*, 2016; Bicknell *et al.*, 2018a; Bicknell and Paterson, 2018; Bicknell *et al.*, 2018b; Bicknell *et al.*, 2021). The phylogenetic position of *Sidneyia* within Euarthropoda has been revised (e.g. Bruton, 1981; Boxshall, 2004; Selden *et al.*, 2015) and, recent phylogenetic analyses resolved it as the most basal Vicissicaudata within Artiopoda (based on its well-developed tergopleurae and terminal trunk segment bearing a pair of non-walking appendages) (Lerosey-Aubril *et al.*, 2017), or a possible chelicerate (based on the similarities between its exopod morphology and the gill opercula of euchelicerates) (Legg, 2014; Aria and Caron, 2017).

Sidneyia was originally described from Laurentia (Walcott, 1911), and occurrences of this genus and other *Sidneyia*-like specimens from other localities within and beyond Laurentia have also been documented (e.g. Zhang *et al.*, 2002; Briggs *et al.*, 2008; Peel, 2017; Pates *et al.*, 2018) mainly based on their similarities with *S. inexpectans* in dorsal exoskeleton (such as a cephalic shield, a thorax of nine segments and a relatively narrow abdomen with caudal fan), but most have since been rejected or doubted for the lack of some defining characters (Briggs *et al.*, 2008; Stein, 2013; Peel, 2017; Sun *et al.*, 2020). The specimen from the Mantou Formation (Cambrian Miaolingian, Wuliuan) preserved some key characters which are diagnostic of the dorsal exoskeleton of *S. inexpectans* (e.g. nearly identical trunk tagmosis, similar length-to-width ratio, cephalic shield with lateral notches and pairs of spines on posterior margin of the last abdominal segment), and was considered a possible represen-

Table 1. Examinations of *Sidneyia* and *Sidneyia*-like euarthropods in the literature in this study.

Locality	Original description	Reference for original description	This study	Reason
Burgess Shale	*Sidneyia inexpectans*	Walcott, 1911	*Sidneyia*	Type species
Kinzers Formation	*Sidneyia* sp.	Resser and Howell, 1938	Not *Sidneyia*	Fragments of posterior trunk segments, different from *Sidneyia*
Wheeler Formation	*Sidneyia*? sp.	Briggs and Robison, 1984	*Sidneyia*-like animal	Similar appendages
Spence Shale	*Peytoia* cf. *nathorsti*	Conway Morris and Robison, 1988	*Sidneyia*-like animal	Similar appendages
Chengjiang	*Sidneyia sinica*	Zhang *et al.*, 2002	*Sidneyia*-like animal	Dorsal exoskeleton similar, but lacking appendages
Spence Shale	*Sidneyia* sp.	Briggs *et al.*, 2008	*Sidneyia*-like animal	Dorsal exoskeleton similar, but lacking appendages
Kinzers Formation	Similar to *Sidneyia inexpectans*	Briggs *et al.*, 2008	*Sidneyia*-like animal	Dorsal exoskeleton similar, but lacking appendages
Sirius Passet	*Sidneyia*? sp.	Peel, 2017	*Sidneyia*-like animal	Dorsal exoskeleton similar, but lacking appendages
Mantou Formation	*Sidneyia* cf. *inexpectans*	Sun *et al.*, 2020	*Sidneyia*	Dorsal exoskeleton very similar, although lacking appendages

tative of the type species from North China plate (Sun *et al.*, 2020). In consideration of the similarities between those rejected or doubted specimens and *S. inexpectans*, describing them as *Sidneyia*-like euarthropods (a generalized term describing incompletely preserved dorsal exoskeletons and appendages that superficially resemble overall *Sidneyia* morphologies) seems reasonable (Table 1). Here, we introduce a new *Sidneyia*-like euarthropod from the Guanshan biota (Cambrian Series 2, Stage 4). Overall profile and composition of its dorsal exoskeleton, including a thorax and an abdomen with a uropod, basically resemble *S. inexpectans*.

Material and methods

All specimens are housed at Yunnan Key Laboratory for Palaeobiology, Yunnan University (YKLP). YKLP 13395 and YKLP 13396 were excavated from the Wulongqing Formation, *Palaeolenus* biozone, Gaoloufang section (24°57′32.976″N, 102°48′19.404″E) (Figure 1). YKLP 13395 was prepared using a needle under a Nikon SMZ 800N, revealing parts covered by matrix. Digital photographs were taken using a Canon EOS 5D SR camera mounted with a Canon MP-E 65 mm (1–5X) macro lens, under cross-polarized light and processed in Adobe Photoshop CS 5. Line drawings were made using Adobe Illustrator CS 5. Terminology follows Bruton (1981), Stein (2013) and Bicknell *et al.* (2018b).

Preservation of specimens.—YKLP 13395 is dorsoventrally compacted and nearly complete, although missing a possible cephalic shield. Anterior two thoracic segments are slightly disarticulated from the rest of the trunk, while middle and posterior thoracic segments are cracked along the axial region and lost, exposing appendages beneath. Lamellae under the right posterolateral thoracic segments are displaced and preserved in disorder, and no clear articulation can be observed. YKLP 13396 is separately preserved and, although the relationship with YKLP 13395 cannot be confirmed herein, its overall morphology and arrangement of its spines resemble those seen in *Sidneyia inexpectans* Walcott, 1911 (e.g. Stein, 2013, fig. 9; Bicknell *et al.*, 2018a, fig. 2), and therefore we tentatively describe and discuss it together with the *Sidneyia*-like euarthropod below.

Systematic paleontology

Phylum Euarthropoda Lankester, 1904
Subphylum Artiopoda Hou and Bergström, 1997
Superclass Vicissicaudata Ortega-Hernández *et al.*, 2013
Family Sidneyidae Walcott, 1911
Gen. et sp. indet.

Figures 2, 3, 4

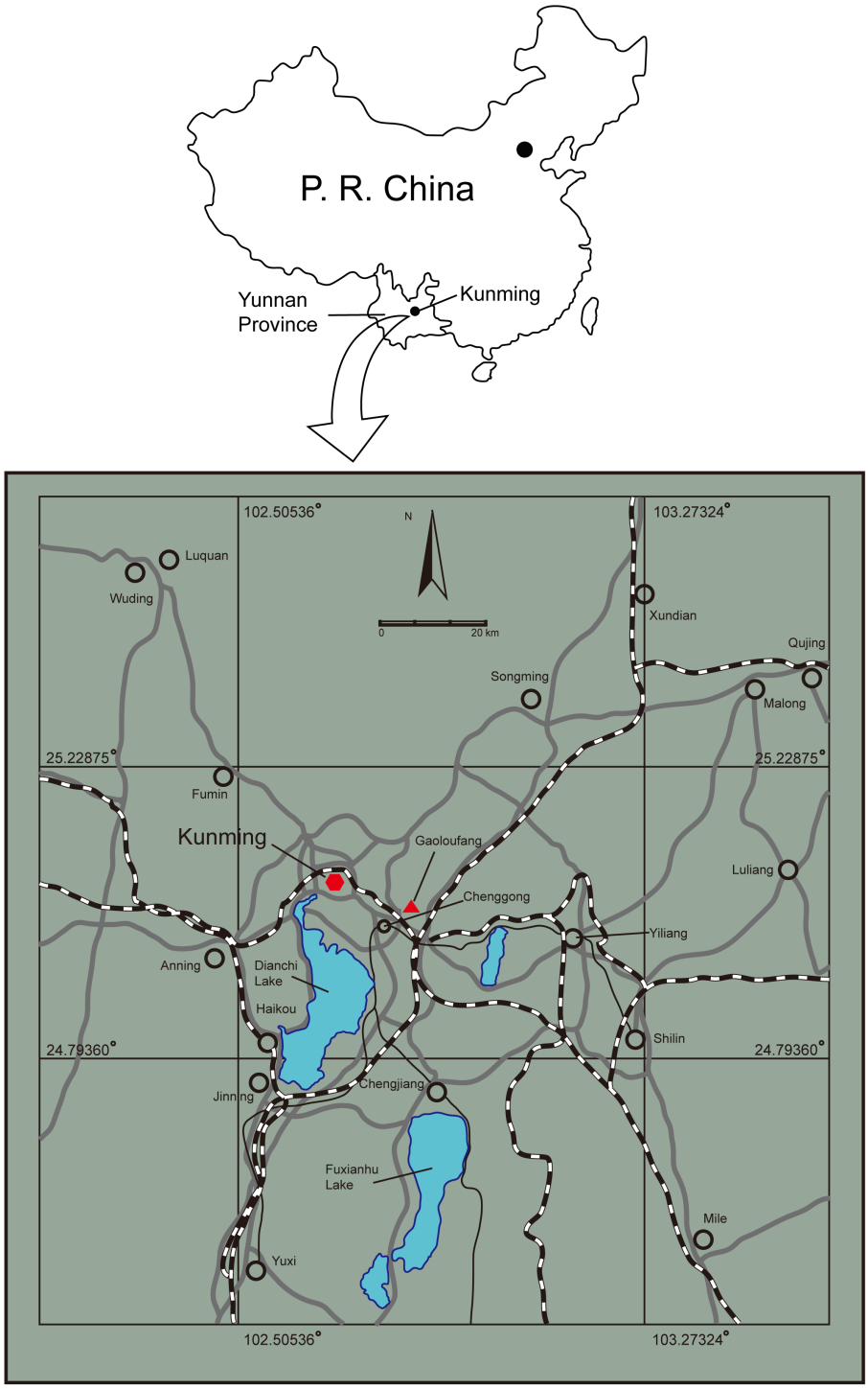

Figure 1. The location map showing the Gaoloufang section (black triangle).

Material.—YKLP 13395, a nearly complete specimen, preserved thorax, abdomen and uropod. YKLP 13396, a protopodite bearing gnathobasic spines.

Locality.—Gaoloufang section, Kunming City, Yunnan Province, Southwest China.

Horizon and age.—Wulongqing Formation (Cambrian Series 2, Stage 4).

Description.—YKLP 13395 79 mm in sagittal length,

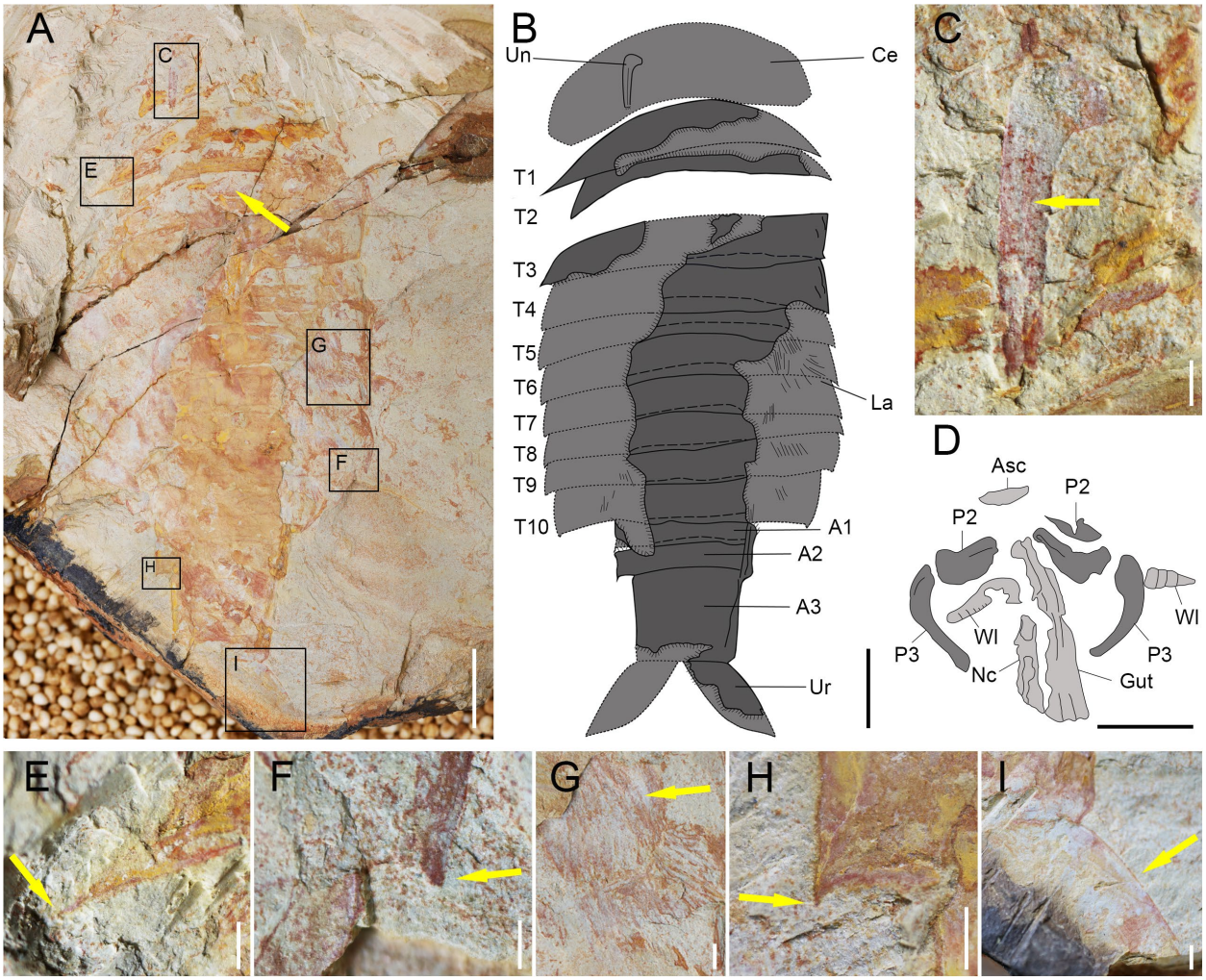

Figure 2. YKLP 13395. **A,** the overall profile of the *Sidneyia*-like euarthropod from the Guanshan biota, yellow arrow points to the disarticulation of the anterior two thoracic segments from the rest; **B,** line drawing of A, morphologies of the presumed cephalon and uropods are drawn with speculation and based on *Sidneyia inexpectans* Walcott, 1911; **C,** detail of A, yellow arrow points to the longitudinal groove; **D,** line drawing of *Chengjiangocaris kunmingensis* Yang *et al.*, 2013 (redrawn from Yang *et al.*, 2013); **E,** detail of A, yellow arrow points to the pleural tip; **F,** detail of A, yellow arrow points to the pleural tip; **G,** detail of A, yellow arrow points to the imbricated and blade-like lamellae; **H,** detail of A, yellow arrow points to the pleural tip; **I,** detail of A, yellow arrow points to the uropod. Asc, anterior sclerite; A1–A3, abdominal segments 1–3; Ce, cephalic shield; Gut, gut; La, lamellae; Nc, nerve cord; P2–P3, SPA podomere 2–3; T1–T10, thoracic segments 1–10; Un, unidentified structure; Ur, uropod; Wl, walking leg. Scale bars = 10 mm for A, 1 mm for C, E–I. Line drawing and redrawn picture not to scale.

with its maximum transverse width, located at middle part of thorax, measuring 35 mm. A sub-cylindrical structure is preserved in front of the trunk, tapering posteriorly with its anterior part diverged to the right. A narrow groove runs longitudinally along its center. Thorax 53 mm in length (sag.) and composed of ten imbricated segments. Pleural tip of anteriormost thoracic segment long and spine-like, projecting laterally, whilst those of posterior ones relatively stout, projecting posteriorly. Posterolateral sections of segment 6–10 missing, exposing underlying imbricated and blade-like lamellae. Abdomen with three segments, length (sag.) measuring 18 mm. Anterior two similar in length (sag.) and width (tr.). The 3rd slightly narrower, with its length (sag.) more than total of anterior two. Pleural tips of the first two abdominal segments short and sharp, projecting posteriorly. Uropod flap-like, with its anterior part articulated to posterior margin of the 3rd abdominal segment.

YKLP 13396: a-gnathobase-bearing protopodite, measuring 6 mm in width (tr.); dorsal margin slightly concave. At least 15 stout spines of different sizes in more or less triangle profile lined along its right margin. Two rows

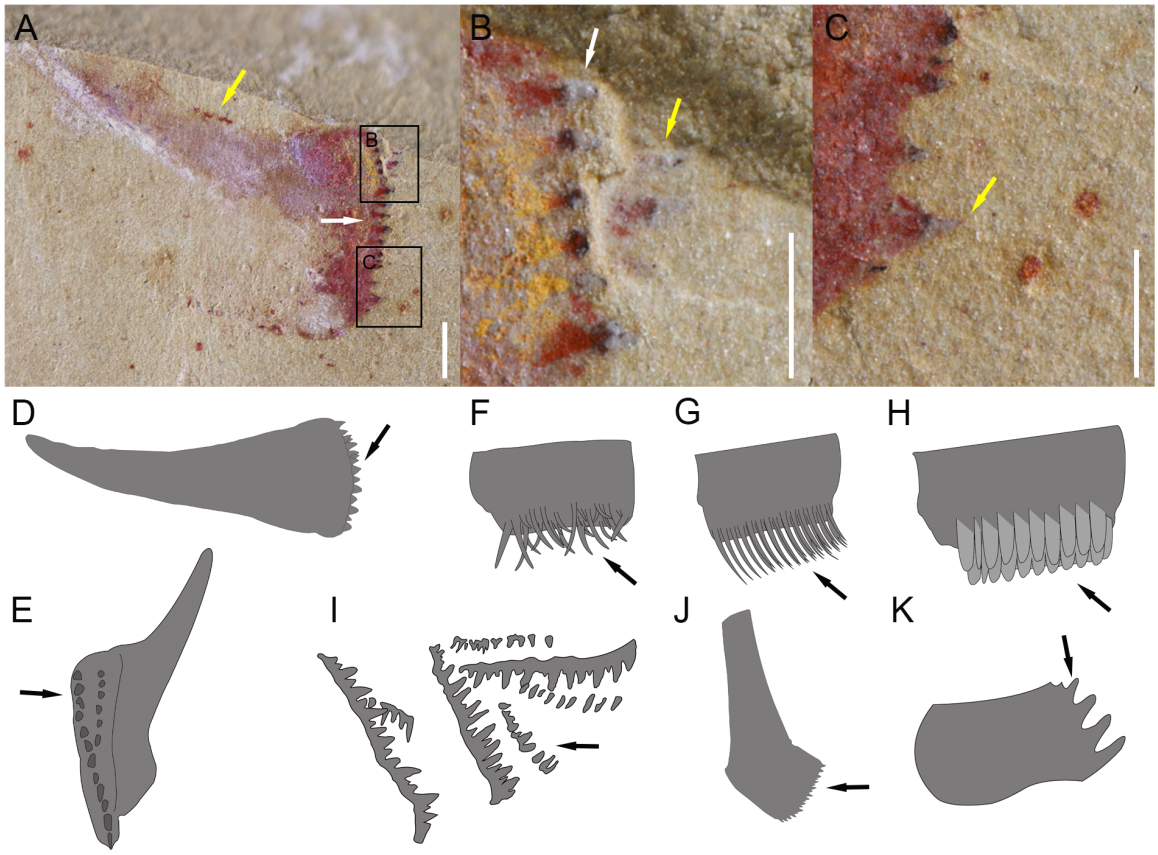

Figure 3. The gnathobasic protopodite from the Guanshan biota and gnathobases and gnathobase-like structure from some Cambrian euarthropods and an amplectobeluid (radiodont). **A,** YKLP 13396, yellow arrow points to the concavity on the dorsal margin and white arrow points to the spines lined on the right margin; **B,** close-up of A, white and yellow arrows point to the spines and the spines underneath; **C,** close-up of A, yellow arrow points to the spine accompanied by two smaller ones on both sides; **D,** protopodite of *Sidneyia inexpectans* Walcott, 1911 (redrawn from Bicknell *et al.*, 2018a); **E,** protopodite of *Sidneyia inexpectans* Walcott, 1911, showing two rows of spines on the upper part (redrawn from Bicknell *et al.*, 2018a); **F–H,** protopodites of the 2nd , 9th and 15th appendage of an adult *Naraoia spinosa* Zhang and Hou, 1985 respectively (redrawn from Zhai *et al.*, 2019); **I,** gnathobases of *Wisangocaris barbarahardyae* Jago *et al.*, 2016 (redrawn from Jago *et al.*, 2016); **J,** protopodite of *Redlichia rex* Holmes *et al.*, 2020 (redrawn from Holmes *et al.*, 2020); **K,** gnathobase-like structure of an amplectobeluid (redrawn from Cong *et al*., 2017; Cong *et al.*, 2018). Black arrows point to the gnathobases and gnathobase-like structure. Scale bars = 1 mm for A, 0.5 mm for B and C. Redrawn pictures not to scale.

of spines discerned on its upper part.

Discussion

Vicissicaudata, Sidneyidae, *Sidneyia* and *Sidneyia*-like euarthropods are erected mainly based on shared features of dorsal exoskeleton. Vicissicaudates are characterized by most of trunk segments (6–19) having wide pleurae and the posteriormost trunk segment bearing paired non-walking appendages (Lerosey-Aubril *et al.*, 2017). The Guanshan animal shows the presence of wide trunk segments' pleurae and a pair of non-walking uropods articulated to the terminal trunk segment, which fits well within Vicissicaudata (Figure 4). Key diagnostic characters of sidneyids include: a tripartite body (cephalic shield, thorax and abdomen); nine thorax segments having ventral

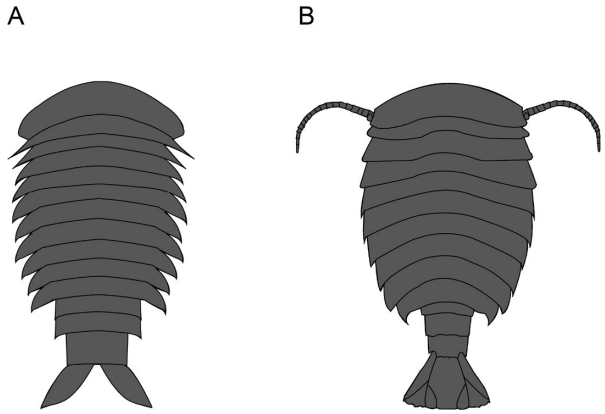

Figure 4. Reconstructions of the *Sidneyia*-like euarthropod (**A**) from the Guanshan biota and *Sidneyia inexpectans* (**B**) from the Burgess Shale (redrawn from Bruton, 1981). Not to scale.

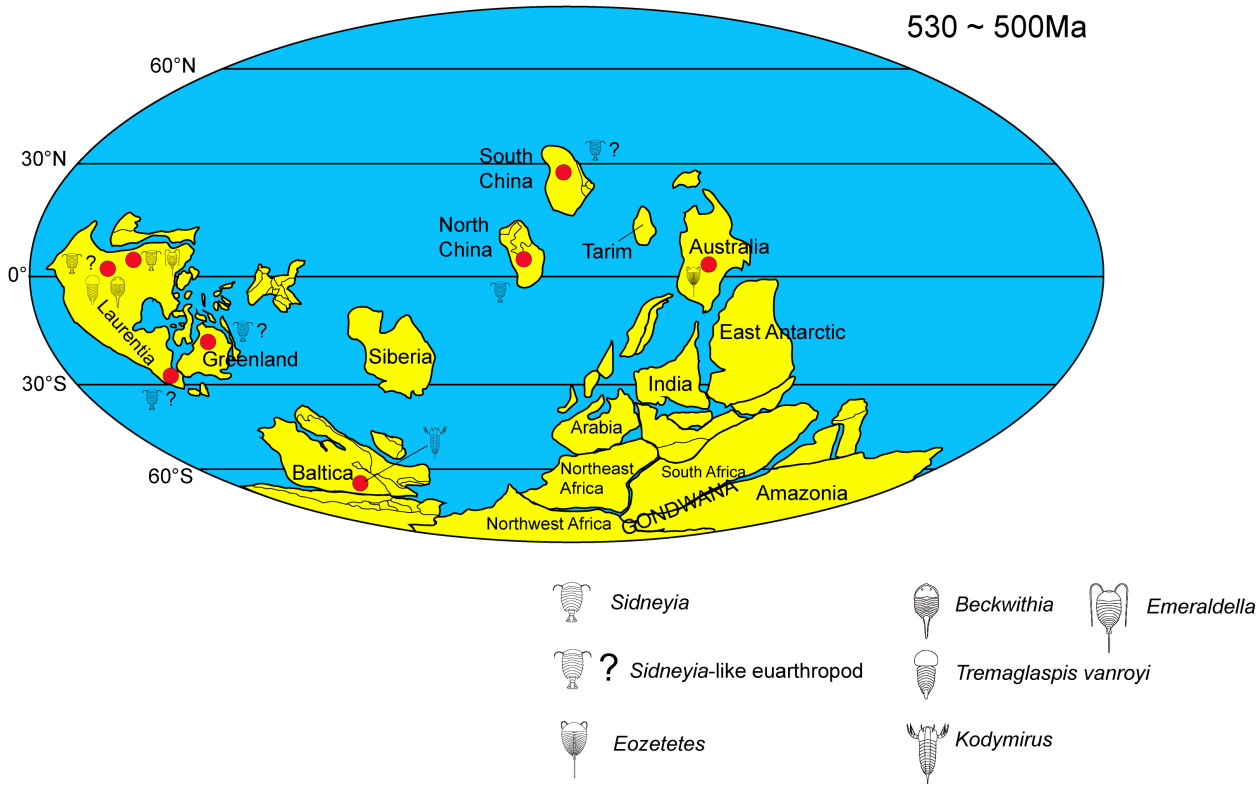

Figure 5. The palaeogeographic distributions of vicissicaudates in early and middle Cambrian. (Modified from Zhou *et al.*, 2014).

appendages; two or three abdominal segments; a terminal trunk segment articulated with paired non-walking appendages; surface of dorsal exoskeleton being smooth or ornamented by narrow and irregular ridges (e.g. Walcott, 1911; Bruton, 1981; Stein, 2013; Zacaï *et al.*, 2016; Sun *et al.*, 2020).

Comparisons with Sidneyia inexpectans *Walcott, 1911*.—Similarities: YKLP 13395 shows that the Guanshan euarthropod represents *S. inexpectans* in body plan (Figure 4), tergopleurae of middle and posterior thoracic segments, densely distributed lamellae and number of abdominal segments (Figure 2); YKLP 13396 is a gnathobasic protopodite and, its overall profile and spine arrangement more resemble *S. inexpectans* than gnathobase and gnathobase-like structures in other Cambrian euarthropods or radiodonts (Figure 3). Differences: the sub-cylindrical structure (Figure 2C) is reminiscent of the 3rd podomere of the specialized postantennal appendage (SPA) in *Chengjiangocaris kunmingensis* Yang *et al.*, 2013 (Figure 2D), whereas SPA has never been observed in *Sidneyia* specimens; the Guanshan euarthropod has ten thoracic segments, whilst *S. inexpectans* has nine.

Comparisons with other Sidneyia-*like euarthropods*.—Both the Guanshan and Chengjiang animals have a thorax and abdomen, while segment numbers are slightly different: the former has ten and three respectively and the latter has nine and two. In addition, the posteriormost appendage of the Guanshan animal arises from the posterior abdominal segment (Figure 2I), however those of the Chengjiang animal are from the rear margin of the telson (Zhang *et al.*, 2002). *Sidneyia*? sp. from the Sirius Passet biota (Peel, 2017) has a three-segmented abdomen, the same as the Guanshan animal. The difference lies in the number of thoracic segments: the former is ten, while the latter is nine. The Guanshan animal resembles *Sidneyia* sp. from the Spence Shale and YPM 94007 from the Kinzers Formation (Briggs *et al.*, 2008) in overall morphology of the thorax and thoracic segments. Specimens from the Wheeler Formation (KUMIP 204798–204799, *Sidneyia*? sp. Briggs and Robison, 1984) and the Spence Shale (KUMIP 204777–204780, *Peytoia* cf. *nathorsti* Conway Morris and Robison, 1988) are separately preserved appendages. The Guanshan specimens have poorly preserved appendages, but YKLP 13396 is similar to KUMIP 204798 (Briggs and Robison, 1984, fig. 14.3–4) in possessing gnathobasic spines.

Comparisons with other vicissicaudates.—The trunk segment number of cheloniellids ranges from eight to

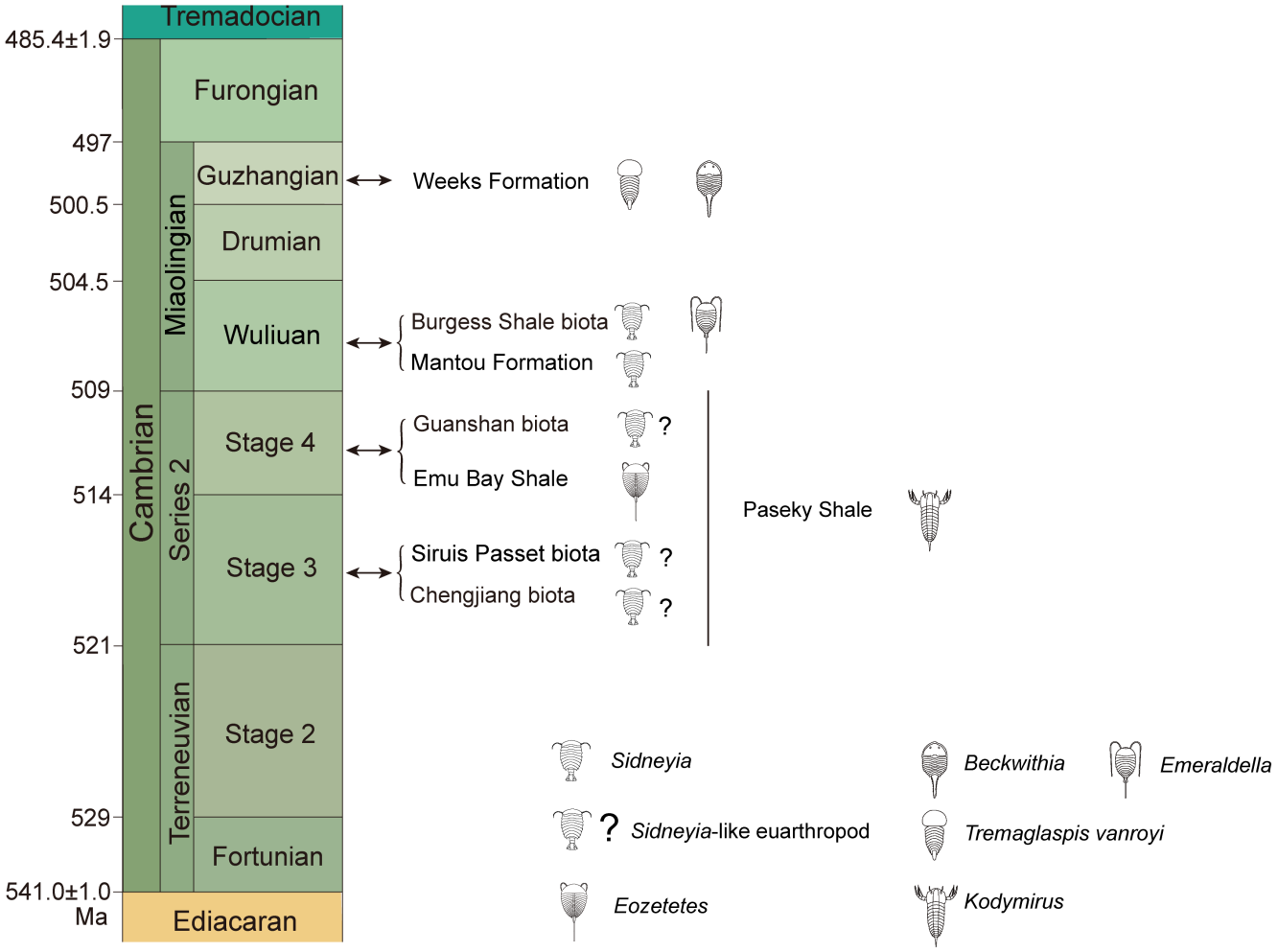

Figure 6. Early and middle Cambrian fossil *Lagerstätten* yielding vicissicaudates.

thirteen, but they differ from the Guanshan animal in the following features: pleural tips of the first two to three segments directed forward; no abdomen present; caudal region consisting of a forked segment articulated or not with elongate medial spine (Wendtruff *et al.*, 2018). *Emeraldella brutoni* has a thorax consisting of ten segments (Lerosey-Aubril and Ortega-Hernández, 2019), which is the same with the Guanshan animal, but the former has only a single cylindrical terminal segment, not a three-segmented abdomen. In addition to different caudal structures, *E. brocki* is distinguished from the Guanshan animal in having eleven thoracic segments (Bruton and Whittington, 1983; Stein and Selden, 2012). Aglaspidids are different from the Guanshan animal in having tergal processes on the trunk pleurae and a bipartite postventral plate (Lerosey-Aubril *et al.*, 2017).

Based on the comparisons above, the Guanshan specimen is more similar to *Sidneyia* in its dorsal exoskeleton than to other members within of Vicissicaudata. Until the discovery of specimens with better preservation and articulated appendages, we tentatively describe it as a *Sidneyia*-like euarthropod.

The status of Sidneyia-like euarthropods.—*Sidneyia*-like euarthropods, the Chengjiang animal (Zhang *et al.*, 2002), *Sidneyia* sp. from Spence Shale Member, Langston Formation, Utah (Briggs *et al.*, 2008) and *Sidneyia*? sp. from the Sirius Passet (Peel, 2017), resemble sidneyids in gross dorsal exoskeleton morphology, which may indicate some intrinsic affinities among them. Among these euarthropods, the Sirius Passet taxon shows more similarities with *Sidneyia inexpectans*, including the same body tagmosis, similar head shield and the same number of thoracic segments. Although having different number of thoracic segments, the Guanshan animal possesses lamellae and uropod, which are similar to *S. inexpectans*. The Chengjiang animal shares the same body tagmosis

with *S. inexpectans*, but head shield and caudal region morphologies are obviously different, indicating a relatively distant affinity with *S. inexpectans* when compared to other *Sidneyia*-like euarthropods.

Predation in the Guanshan ecosystem.—To date, predatory behaviors in the Guanshan biota have been documented on brachiopods (Zhang *et al.*, 2011) and trilobites (Hu *et al.*, 2013). Potential predators in this biota include radiodontans, cnidarians, priapulids, ctenophorans, *Redlichia* (Hu *et al.*, 2013), and *Isoxys* (Huang and Wang, 2014). YKLP13396 is a protopodite bearing gnathobasic spines, which could be used for crushing or grinding, and therefore the new *Sidneyia*-like euarthropod described above may be a durophage, like *S. inexpectans*. If so, predation in the Guanshan was more complex than previously thought, and the 'arms race' of this ecosystem might have been accelerated by the arrival of durophagous predator.

Representatives of Vicissicaudata occur worldwide in early and middle Cambrian (Figure 5); the occurrences in Laurentia (Bruton, 1981; Briggs and Robison, 1984; Conway Morris and Robison, 1988; Briggs *et al.*, 2008; Peel, 2017), North China (Sun *et al.*, 2020) and South China (Zhang *et al.*, 2002) indicate a strong dispersal ability and a wide palaeogeographic distribution of *Sidneyia* and *Sidneyia*-like euarthropods. The discovery in the Guanshan biota provides a new data point of *Sidneyia*-like euarthropods in Cambrian Stage 4 and a second occurrence on the South China plate (Figure 6).

Acknowledgements

This research was supported by National Natural Science Foundation of China (No: 41572015) and CAS Pilot Research Program XDB26000000. We thank L. Fei for assistance during field work.

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Author contributions

J. Z. and P. Y. C. designed the study. Z. X. Y. collected the fossil specimens. All authors described and interpreted the specimens. J. Z. and Y. J. L. photographed the specimens and prepared the figures. J. Z., Y. J. L. and P. A. S. wrote the first draft of the manuscript with substantial input from all co-authors.