

# A new euarthropod from the Cambrian Stage 4 Guanshan Biota of South China

DE-GUANG JIAO and KUN-SHENG DU



Jiao, D.-G. and Du, K.-S. 2022. A new euarthropod from the Cambrian Stage 4 Guanshan Biota of South China. *Acta Palaeontologica Polonica* 67 (4): 969–974.

A new small euarthropod *Astutuscaris bispinifer* gen. et sp. nov. is described from the early Cambrian Stage 4 Guanshan Biota in Yunnan, China. This new euarthropod possesses a wide head shield, a pair of possible eyes, paired frontalmost appendages located antero-medially, 11 imbricated tergites most of which have backward-directed tergopleura ending in almost posteriorly oriented spines, and two well-marked wide spines. The affinity of *Astutuscaris* among euarthropods is uncertain because of the undefined nature of its frontalmost appendages, the incomplete head shield, the anterior trunk tergites, and the limbs. There are about 24 species of non-trilobite euarthropods reported from the Guanshan Biota to date, the documentation of this new taxon expands the biological diversity of euarthropods from this important biota in Yunnan, China.

**Key words:** Arthropoda, evolution, Cambrian, Guanshan Biota.

*De-Guang Jiao* [dgjiao@yxnu.edu.cn] and *Kun-Sheng Du* [kunshengdu@qq.com] (corresponding author), Research Center of Paleobiology, Yuxi Normal University, 134 Phoenix Road, Yuxi, Yunnan, 653100, China; Institute of Paleontology, Yunnan University (Chenggong), Kunming, 650091, China.

Received 21 August 2021, accepted 16 June 2022, available online 21 October 2022.

Copyright © 2022 D.-G. Jiao and K.-S. Du. This is an open-access article distributed under the terms of the Creative Commons Attribution License (for details please see <http://creativecommons.org/licenses/by/4.0/>), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

## Introduction

The knowledge on Cambrian arthropods is essential for resolving the phylogenetic relationships and evolutionary history of extinct and extant arthropods (Yang et al. 2013; Daley et al. 2018; Giribet and Edgecombe 2019). Euarthropods are the most diverse group among the typical Burgess Shale-type Cambrian-aged Guanshan Biota (Hu et al. 2010, 2013). There are many euarthropods (e.g., trilobites, radiodonts, and bivalved euarthropods) described from this famous biota (Hu et al. 2010, 2013; Liu et al. 2012; Chen et al. 2019; Jiao et al. 2021a, b). Except the above mentioned groups there are only a few other taxa reported (Hu et al. 2010, 2013; Zhao et al. 2020; Jiao et al. 2021a, 2022), i.e., *Guangweicaris spinatus*, *Panlongia tetranodusa*, *Longquania bispinosa*, *Leancoilia* sp., *Sinoburium* sp., the unnamed naraoiid, *Alacaris?* sp., *Lihuacaris ferox*, and *Bailongia longicaudata*. In this contribution we describe a new and rare euarthropod with an elongated exoskeleton from the Cambrian Stage 4 Guanshan Konservat-Lagerstätte.

**Institutional abbreviations.**—RCP, Research Center of Paleobiology, Yuxi Normal University, Yuxi, China.

**Other abbreviations.**—en, endopod; ex, exopod; ey, eye; fa, frontal appendage; gut, digestive tract; hs, head shield; lim, limb; p1–p5, podomeres 1–5; st, stalk; T1–T13, tergites 1–13; ts, terminal spine.

**Nomenclatural acts.**—This work and the nomenclatural acts it contains, have been registered in ZooBank: urn:lsid:zoobank.org:pub:7396B74C-AE35-450C-90FA-27A9A609DAAD

## Material and methods

The sole and articulated specimen (RCP 0002) of *Astutuscaris bispinifer* gen. sp. nov. and two specimens (RCP 0003 and RCP 0004) belonging to *Guangweicaris spinatus* were collected from Yiliang County which already provided exquisitely preserved fossils in the past (Jiao et al. 2016, 2021b). The fossils are housed at the Research Center of Paleobiology, Yuxi Normal University.

All the specimens were photographed with a LEICA DFC 500 digital camera mounted on a Stereoscope LEICA M205 C. The single specimen of *Astutuscaris bispinifer* gen. sp. nov. was photographed with a LEICA DFC7000 T monochrome digital camera attached to a LEICA M205 FA fluo-

rescence stereomicroscope, and also scanned with a Zeiss Xradia 520 Versa X-ray Microscope.

## Systematic palaeontology

Clade Euarthropoda Lankester, 1904

Class, order, and family uncertain

Genus *Astutuscaris* nov.

Zoobank LCID: urn:lsid:zoobank.org:act:8B855A7C-119F-4DDC-BE27-9AECF99CC735

*Etymology*: From latin *astutus*, flexible; and *caris*, shrimp; referring to its arthropod affinities.

*Type species*: *Astutuscaris bispinifer* sp. nov. by monotypy, see below.

*Diagnosis*.—As for the type species.

*Astutuscaris bispinifer* sp. nov.

Figs. 1, 2A<sub>1</sub>, A<sub>2</sub>, B<sub>1</sub>–B<sub>3</sub>.

Zoobank LCID: urn:lsid:zoobank.org:act:D09B7A08-1422-484C-A6AD-0204E2E9F55C

*Etymology*: From Latin *bispinifer*, two-spined; referring to its two terminal spines on the end of the body.

*Holotype*: RCP 0002, an articulated specimen (Fig. 1).

*Type locality*: The outcrop near Lihuazhuang village (see Jiao et al. 2021b: fig. 1), Yiliang, Kunming, Yunnan, China.

*Type horizon*: Lower part of Wulongqing Formation, *Palaeolenus* Biozone, Cambrian Series 2, Stage 4 (Hu et al. 2010; Jiao et al. 2021b).

*Material*.—Type material only.

*Diagnosis*.—Small elongate euarthropod with a pair of prominent and bull-horn-like first appendages without sturdy spines and elbow articulations, a wide head shield potentially possessing a pair of antero-median eyes, an elongated thorax consisting of eleven imbricated and homonomous tergites, second to eighth thoracic tergites having lateral doublures and pleural spines, and two long separate spines attached to the last tergite.

*Description*.—The single nearly complete specimen, dorso-ventrally compressed, has a length of 8.6 mm (excluding the first appendage pair), and a width of 2.2 mm (Fig. 1A<sub>1</sub>–A<sub>3</sub>, B<sub>1</sub>–B<sub>4</sub>). The body is about four times as long as wide in dorsal view. The dorsal exoskeleton consists of a wide head shield and 11 imbricated tergites, and terminates with two sturdy separate spines which are maybe modified, posteriorly directed appendages of the terminal somite (Figs. 1A<sub>1</sub>, A<sub>2</sub>, B<sub>1</sub>–B<sub>4</sub>, 2A<sub>1</sub>, A<sub>2</sub>, B<sub>1</sub>–B<sub>3</sub>). The wide cephalon is incomplete, but it may have a semi-elliptical outline (Figs. 1A<sub>1</sub>–A<sub>4</sub>, B<sub>1</sub>–B<sub>4</sub>, 2A<sub>1</sub>, A<sub>2</sub>, B<sub>1</sub>–B<sub>3</sub>). The black carbonaceous structure preserved as a circular shape and located in the anterior and middle part of head is here interpreted as an uncertain structure given that it locates on a different level than the rest of the structures (Figs. 1B<sub>1</sub>, B<sub>2</sub>, B<sub>6</sub>, 2A<sub>1</sub>, A<sub>2</sub>, B<sub>1</sub>–B<sub>3</sub>). The left frontalmost appendage seems to be an antenna although having no distinct segments, while the right one is likely to be a great appendage for some small and medial spines on its

possible last podomere (Fig. 1A<sub>1</sub>–A<sub>4</sub>, B<sub>1</sub>–B<sub>4</sub>). Considering that the anterior sclerite of fuxianhuids and some bivalved euarthropods is a complete structure (Fu et al. 2018; Jin et al. 2021), two disjunct, elliptical structures located anterior to the proximal articles of frontalmost appendages are likely to be the eyes for the oval structures and elongate structures which here are respectively interpreted as possible eyes and stalks (Fig. 1A<sub>1</sub>–A<sub>4</sub>, B<sub>1</sub>–B<sub>4</sub>).

There are 11 imbricated tergites (T<sub>n</sub>) behind the head (Figs. 1A<sub>1</sub>, A<sub>2</sub>, B<sub>1</sub>–B<sub>4</sub>, 2A<sub>1</sub>, A<sub>2</sub>, B<sub>1</sub>–B<sub>3</sub>). Incomplete anterior margin of T<sub>1</sub>, having a similar curvature to that of the successive tergites, is preserved on both part and counterpart (Fig. 1A<sub>1</sub>, A<sub>2</sub>, B<sub>1</sub>–B<sub>4</sub>, B<sub>8</sub>). Anterior margin of T<sub>3</sub> is straight, and posterior margins of T<sub>5</sub>–T<sub>9</sub> and T<sub>11</sub> are straight (Fig. 1A<sub>1</sub>, A<sub>2</sub>, B<sub>1</sub>–B<sub>4</sub>). The tergopleura of T<sub>3</sub>–T<sub>8</sub> curve backwards, and their pleural spines are almost posteriorly oriented (Fig. 1A<sub>1</sub>, A<sub>2</sub>, B<sub>1</sub>–B<sub>5</sub>). The tergopleura of T<sub>2</sub>–T<sub>8</sub> have narrow doublures (Fig. 1A<sub>1</sub>, A<sub>2</sub>, B<sub>1</sub>–B<sub>5</sub>). T<sub>2</sub>–T<sub>10</sub> have a similar length. T<sub>11</sub> is slightly longer than the preceding tergites and lacks pleural spines (Figs. 1A<sub>1</sub>, A<sub>2</sub>, B<sub>1</sub>–B<sub>4</sub>, B<sub>9</sub>, 2A<sub>1</sub>, A<sub>2</sub>, B<sub>1</sub>–B<sub>3</sub>). One robust endopod underneath the head shield preserves at least five conical podomeres (Fig. 1A<sub>3</sub>, A<sub>4</sub>, A<sub>6</sub>). Four elongate, red structures (“en” in Figs. 1A<sub>1</sub>, A<sub>2</sub>, B<sub>1</sub>–B<sub>4</sub>, B<sub>7</sub>, B<sub>8</sub>, 2A<sub>1</sub>, A<sub>2</sub>, B<sub>1</sub>–B<sub>3</sub>), represent trunk endopods, although they do not display obvious segments. These endopods, one located underneath T<sub>1</sub> and T<sub>2</sub>, and two beneath T<sub>3</sub> (Fig. 2A<sub>1</sub>, A<sub>2</sub>, B<sub>1</sub>–B<sub>3</sub>), indicate there is one pair limb belonging to each of these three tergites. The smaller structure, relative to the endopod, of the limb beneath T<sub>3</sub> is tentatively interpreted as exopod (Figs. 1B<sub>7</sub>, 2A<sub>2</sub>, B<sub>2</sub>, B<sub>3</sub>), further clarification of its morphology is contingent on the discovery of additional specimens. The irregular line passing along the entire length of the body may represent the gut (Fig. 1A<sub>1</sub>, A<sub>2</sub>, B<sub>1</sub>–B<sub>4</sub>).

*Remarks*.—The elongate exoskeleton, the possible eyes and the first pair of appendages located antero-medially on the head, and the curvature of the first appendages are also observed in the great-appendage euarthropods (Haug et al. 2012b; Aria et al. 2020; Liu et al. 2020). The morphology of the frontalmost appendages, 11 trunk tergites, the narrow doublures of tergites, and the two terminal spines of *Astutuscaris* contribute to distinguish this new euarthropod genus from *Yohioia* (Haug et al. 2012b). The morphology of the first appendage of *Astutuscaris* and the pair of posterior terminal spines differ from those of other megacheirans, e.g., leanchoilids and jianfengiids (Haug et al. 2012a, b; Aria et al. 2020; Liu et al. 2020)

*Astutuscaris* is distinguishable from *Guangweicaris* by its curving frontalmost appendages, and elongate exoskeleton without medial axial spines and distinct sections (e.g., the abruptly reduced abdomen). *Guangweicaris* possesses a wide head shield with a pair of long antennae, a thorax composed of three small tergites and five normal tergites, and an abruptly reduced abdomen (Fig. 2C, D) consisting of seven tergites all bearing a axial spine (Luo et al. 2007; Yang et al. 2008; Wu and Liu 2019; Chen et al. 2020). The curving first appendages

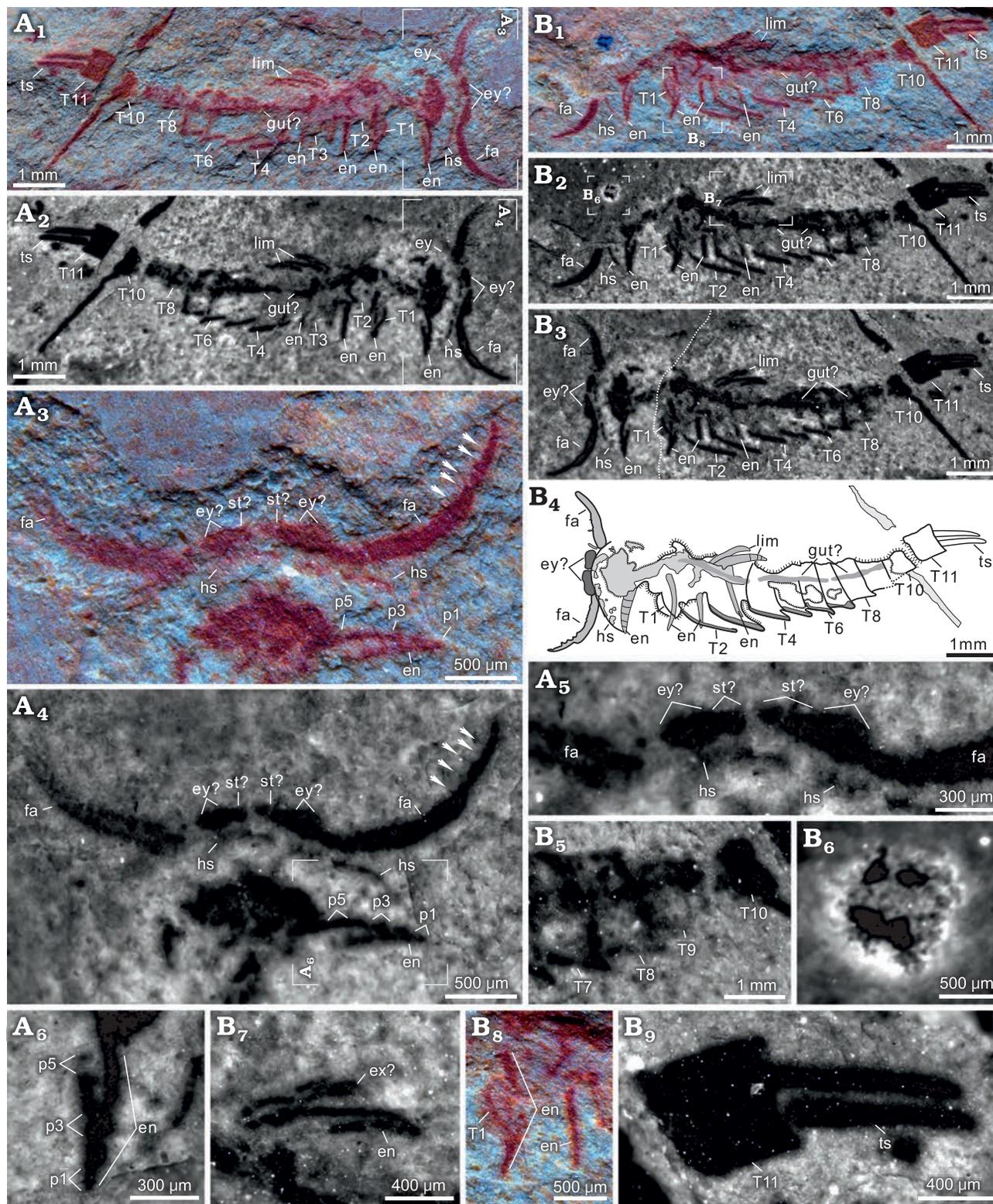


Fig. 1. Euarthropod *Astutuscaris bispinifer* gen. et sp. nov. from the Cambrian Stage 4 Guanshan Biota, Lihuazhuang village, Yunnan, China. **A.** RCP 0002a, part of the sole specimen; showing the head shield, 11 imbricated tergites most with pleural spines, and two terminal spines (A<sub>1</sub>, A<sub>2</sub>); possible eyes (A<sub>3</sub>, A<sub>4</sub>, A<sub>5</sub>); first appendages with small spines (A<sub>3</sub>, A<sub>4</sub>, white arrows); endopod with at least five podomeres (A<sub>6</sub>). **B.** RCP 0002b, counterpart of the sole specimen; note the 11 imbricated tergites and trunk limbs (B<sub>1</sub>, B<sub>2</sub>); restored specimen by digitally combining the part and counterpart, the dashed line indicating the contact (B<sub>3</sub>); interpretive drawing of the narrow doublures of thoracic tergites marked in dark grey (B<sub>4</sub>); T7–T10 and pleural spines (B<sub>5</sub>); detail of the unknown structure (B<sub>6</sub>); the limb with an endopod and a possible exopod (B<sub>7</sub>); single endopod under T1 and T2 respectively (B<sub>8</sub>); T11 and two separate spines being marked (B<sub>9</sub>). Natural light photographs (A<sub>1</sub>, A<sub>3</sub>, A<sub>4</sub>, B<sub>1</sub>, B<sub>8</sub>); fluorescent photographs (A<sub>2</sub>, A<sub>5</sub>–A<sub>6</sub>, B<sub>2</sub>, B<sub>3</sub>, B<sub>5</sub>–B<sub>7</sub>, B<sub>9</sub>). Abbreviations: en, endopod; ex, exopod; ey, eye; fa, frontal appendage; gut, digestive tract; hs, head shield; lim, limb; p1–p5, podomeres 1–5; st, stalk; T1–T11, tergites 1–11; ts, terminal spine.

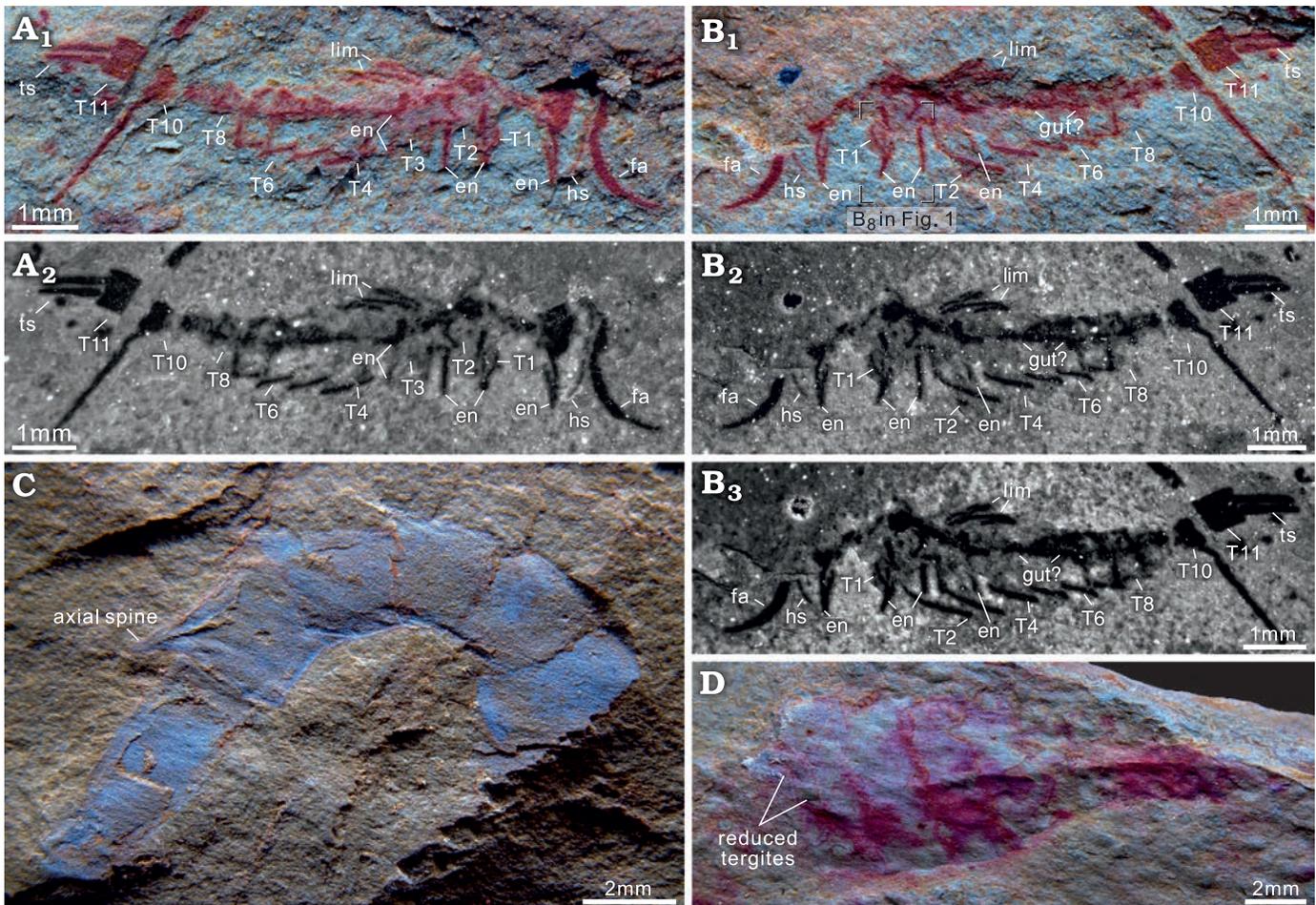


Fig. 2. Euarthropods *Astutuscaris bispinifer* gen. et sp. nov. (A, B) and *Guangweicaris spinatus* Luo, Fu, and Hu, 2007 (C, D) collected from Cambrian Guanshan Biota, Lihuazhuang village, Yunnan, China. A. RCP 0002a, specimen before preparation. B. RCP 0002b, specimen before preparation (B<sub>1</sub>, B<sub>2</sub>) and after preparation (B<sub>3</sub>). C. RCP 0003, a small and incomplete specimen about 16 mm in length. D. RCP 0004, a small specimen about 17 mm in length. Natural light photographs (A<sub>1</sub>, B<sub>1</sub>, C, D); fluorescent photographs (A<sub>2</sub>, B<sub>2</sub>, B<sub>3</sub>). Abbreviations: en, endopod; ex, exopod; ey, eye; fa, frontal appendage; gut, digestive tract; hs, head shield; lim, limb; p1–p5, podomeres 1–5; st, stalk; T1–T11, tergites 1–11; ts, terminal spine.

of *Astutuscaris* are different from the long antennae (at least 21 podomeres) of *Guangweicaris* (Yang et al. 2008; Chen et al. 2020). Unlike the trunk of *Guangweicaris* including a suddenly reduced abdomen (Yang et al. 2008; Wu and Liu 2019; Chen et al. 2020), *Astutuscaris* has a trunk gradually tapering backward. The last tergite of *Guangweicaris* bears an axial spine (Yang et al. 2008; Chen et al. 2020), while, *Astutuscaris* has no axial spines. The posterior end of *Astutuscaris* composes of two isolated spines, and the tail of *Guangweicaris* possesses a ventral medial extension and two lateral processes (Chen et al. 2020).

*Astutuscaris bispinifer* gen. et sp. nov. is different from the stages 8 and 9 of *Fuxianhuia protensa* Hou, 1987, by its at least 11 trunk tergites, one pair endopod under normal tergites two and three respectively, and last tergite carrying two long and separate spines. The juveniles (stages 8 and 9) of *F. protensa* are about 11 mm to 15 mm long, and consist of eight or nine trunk tergites which have a pattern of segmental mismatch in thoracic region and a terminal telson with paired caudal flukes (Fu et al. 2018).

## Concluding remarks

The curvature and insertion of first appendages, the location of the possible eyes, and the elongate body of *Astutuscaris bispinifer* gen. et sp. nov. are similar to the Cambrian megacheiran, such as species of *Fortiforceps*, *Jianfengia*, *Sklerolibyon*, and *Yohioia*. Similarities of *A. bispinifer* and *Yohioia tenuis* from the Cambrian Burgess Shale are particularly marked for the elongate exoskeleton and the tergopleura with pleural spines (Haug et al. 2012b; Aria et al. 2020). The smallest *Y. tenuis* is about 6 mm in length, and bears thirteen trunk tergites and a paddle-like telson with eight marginal spines (Haug et al. 2012b), while *A. bispinifer* is about 8.6 mm in length, possesses eleven trunk tergites and two terminal spines. The thorax with eleven tergites of *A. bispinifer* is the same as that of the leanchoilid megacheiran arthropods, like species of *Leanchoilia* and *Alalcomenaeus* (Edgecombe et al. 2011; Hu et al. 2013; Aria et al. 2020; Liu et al. 2020). Evidently, the frontalmost appendage without sturdy spines of this new taxon differs

quite considerably from the multisegmented sub-chelate appendages of megacheirans. The pair of terminal spines are another character differentiating *A. bispinifer* from typical megacheirans (Edgecombe et al. 2011; Hu et al. 2013; Aria et al. 2020; Liu et al. 2020). The prominent and curving frontalmost appendages are also found in some bivalved euarthropods (Fu et al. 2014; Yang et al. 2016; Hou et al. 2017; Jin et al. 2021), e.g., *Pectocaris inopinata*, *Isoxys inopinata*, and *Clypeocaris serrata*.

The incompletely preserved walking leg with conical podomeres under the head resembles the limbs of *Chengjiangocaris kunmingensis* from the Xiaoshiba Biota (see Yang et al. 2013: fig. 1f), but, one pair of limbs beneath each of the first three tergites and the two long terminal spines of *Astutiscaris bispinifer* gen. et sp. nov. support it is not a fuxianhuiid which have a thorax with ventral segmental mismatch and a terminal tailspine with paired caudal flukes (Fu et al. 2018).

The two sturdy separate spines of *Astutiscaris bispinifer* gen. et sp. nov. are possibly the modified, posteriorly directed appendages of the terminal somite that is a common character of vicissicaudates a major clade of artiopods (Van Roy 2005; Lerosey-Aubril et al. 2017). If this interpretation is correct, then *A. bispinifer* might be a vicissicaudate-like euarthropod. Nevertheless, its curving frontalmost appendages and possible anterior and middle eyes still separate it from the vicissicaudates.

The nature of the first curving appendage without obvious segments of *Astutiscaris bispinifer* gen. et sp. nov. is contingent on the discovery of new specimens, although it's possible to be an antenna for lacking the typical elbow joints or articulations. Together with the incomplete head, anterior trunk tergites, and limbs, the affinity of *A. bispinifer* among euarthropods remains unclear until new material that could provide more key taxonomic characters is found. So far, about 24 non-trilobite euarthropod species were reported from Guanshan Biota, i.e., four radiodont species (Jiao et al. 2021b), two fuxianhuiid species (Jiao et al. 2021a), 11 species of bivalved euarthropods (Hu et al. 2013; Wu and Liu 2022), five non-trilobite artiopod species (Hu et al. 2013; Zhao et al. 2020; Jiao et al. 2022), *Leancoilia* sp. (Hu et al. 2013), and *Lihuacaris ferox* (Jiao et al. 2021a). Accordingly, this new taxon increases the species diversity of the typical Burgess Shale-type Guanshan Biota, especially that of euarthropods.

## Acknowledgments

We thank Peter Van Roy (Ghent University, Belgium) and one anonymous reviewer for their critical reviews. Special acknowledgements are given to Xi-Guang Zhang, Jie Yang, Tian Lan, Jin-Bo Hou, and Jia-Lin Du (all Yunnan University, Kunming, China) for assistance in fieldwork. This work was supported by the National Natural Science Foundation of China (41730318) and the Innovative Research Fund of Yuxi Normal University (KSD, grant number 202111390020 and 2020B49).

## References

- Aria, C., Zhao, F.C., Zeng, H., Guo, J., and Zhu, M.Y. 2020. Fossils from South China redefine the ancestral euarthropod body plan. *BMC Evolutionary Biology* 20: 4.
- Chen, F.Y., Zhang, Z.F., Betts, M.J., Zhang, Z.L., and Liu, F. 2019. First report on Guanshan Biota (Cambrian Stage 4) at the stratotype area of Wulongqing Formation in Malong County, Eastern Yunnan, China. *Geoscience Frontiers* 10: 1459–1476.
- Chen, H., Legg, D., Liu, Y., and Hou, X.G. 2020. New data on the anatomy of fuxianhuiid arthropod *Guangweicaris spinatus* from the lower Cambrian Guanshan Biota, Yunnan, China. *Acta Palaeontologica Polonica* 65: 139–148.
- Daley, A.C., Antcliffe, J.B., Drage, H.B., and Pates, S. 2018. Early fossil record of Euarthropoda and the Cambrian Explosion. *Proceedings of the National Academy of Sciences of the United States of America* 115: 5323–5331.
- Edgecombe, G.D., García-Bellido, D.C., and Paterson, J.R. 2011. A new leancoiliid megacheiran arthropod from the lower Cambrian Emu Bay Shale, South Australia. *Acta Palaeontologica Polonica* 56: 385–400.
- Fu, D.J., Ortega-Hernández, J., Daley, A.C., Zhang, X.L., and Shu, D.G. 2018. Anamorphic development and extended parental care in a 520 million-year-old stem-group euarthropod from China. *BMC Evolutionary Biology* 18: 147.
- Fu, D.J., Zhang, X.L., Budd, G.E., Liu, W., and Pan, X.Y. 2014. Ontogeny and dimorphism of *Isoxys auritus* (Arthropoda) from the Early Cambrian Chengjiang biota, South China. *Gondwana Research* 25: 975–982.
- Giribet, G. and Edgecombe, G.D. 2019. The phylogeny and evolutionary history of arthropods. *Current Biology* 29: R592–R602.
- Haug, J.T., Briggs, D.E., and Haug, C. 2012a. Morphology and function in the Cambrian Burgess Shale megacheiran arthropod *Leancoilia superlata* and the application of a descriptive matrix. *BMC Evolutionary Biology* 12: 162.
- Haug, J.T., Waloszek, D., Maas, A., Liu, Y., and Haug, C. 2012b. Functional morphology, ontogeny and evolution of mantis shrimp-like predators in the Cambrian. *Palaeontology* 55: 369–399.
- Hou, X.G., Siveter, D.J., Siveter, D.J., Aldridge, R.J., Cong, P.Y., Gabbott, S.E., Ma, X.Y., Purnell, M.A., and Williams, M. 2017. *The Cambrian Fossils of Chengjiang, China: The Flowering of Early Animal life*. John Wiley & Sons, Kunming.
- Hu, S.X., Zhu, M.Y., Luo, H.L., Steiner, M., Zhao, F.C., Li, G.X., Liu, Q., and Zhang, Z.F. 2013. *The Guanshan Biota* [in Chinese, with English abstract]. 204 pp. Yunnan Science and Technology Press, Kunming.
- Hu, S.X., Zhu, M.Y., Steiner, M., Luo, H.L., Zhao, F.C., and Liu, Q. 2010. Biodiversity and taphonomy of the Early Cambrian Guanshan biota, eastern Yunnan. *Science China Earth Sciences* 53: 1765–1773.
- Jiao, D.G., Du, K.S., Zhang, X.G., Yang, J., and Eggink, D. 2022. A new small soft-bodied non-Trilobite artiopod from the Cambrian Stage 4 Guanshan Biota. *Geological Magazine* 159: 730–734.
- Jiao, D.G., Pates, S., Lerosey-Aubril, R., Ortega-Hernández, J., Yang, J., Lan, T., and Zhang, X.G. 2021a. New multipodomeric appendages of stem-group euarthropods from the Cambrian (Stage 4) Guanshan Konservat-Lagerstätte. *Royal Society Open Science* 8: 211134.
- Jiao, D.G., Pates, S., Lerosey-Aubril, R., Ortega-Hernández, J., Yang, J., Lan, T., and Zhang, X.G. 2021b. The endemic radiodonts of the Cambrian Stage 4 Guanshan biota of South China. *Acta Palaeontologica Polonica* 66: 255–274.
- Jiao, D.G., Yang, J., and Zhang, X.G. 2016. A superarmoured lobopodian from the Cambrian Stage 4 of southern China. *Science Bulletin* 61: 1372–1376.
- Jin, C.F., Mai, H.J., Chen, H., Liu, Y., Hou, X.G., Wen, R.L., and Zhai, D.Y. 2021. A new species of the Cambrian bivalved euarthropod *Pectocaris* with axially differentiated enditic armatures. *Papers in Palaeontology* 7: 1781–1792.
- Lerosey-Aubril, R., Zhu, X.J., and Ortega-Hernández, J. 2017. The Vicis-

- sicaudata revisited—Insights from a new aglaspidid arthropod with caudal appendages from the Furongian of China. *Scientific Reports* 7: 11117.
- Liu, J.N., Ou, Q., Han, J., Zhang, Z.F., He, T.J., Yao, X.Y., Fu, D.J., and Shu, D.G. 2012. New occurrence of the Cambrian (stage 4, series 2) Guanshan Biota in Huize, Yunnan, South China. *Bulletin of Geosciences* 87: 125–132.
- Liu, Y., Ortega-Hernández, J., Zhai, D.Y., and Hou, X.G. 2020. A reduced labrum in a Cambrian great-appendage euarthropod. *Current Biology* 30: 3057–3061.
- Luo, H.L., Fu, X.P., Hu, S.X., Li, Y., Hou, S.G., You, T., Pang, J.Y., and Liu, Q. 2007. A new arthropod, *Guangweicaris* Luo, Fu et Hu gen. nov. from the Early Cambrian Guanshan Fauna, Kunming, China. *Acta Geologica Sinica-English Edition* 87: 1–7.
- Van Roy, P. 2005. An aglaspidid arthropod from the Upper Ordovician of Morocco with remarks on the affinities and limitations of Aglaspidida. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* 96: 327–350.
- Wu, Y.C. and Liu, J.N. 2019. Anatomy and relationships of the fuxianhuiid euarthropod *Guangweicaris* from the early Cambrian Guanshan Biota in Kunming, Yunnan, Southwest China revisited. *Acta Palaeontologica Polonica* 64: 543–548.
- Wu, Y.C. and Liu, J.N. 2022. New data on the bivalved arthropod *Tuzoia* from the Cambrian ( Series 2 , Stage 4 ) Guanshan Biota in Kunming, Yunnan, Southwest China. *Frontiers in Earth Science* 10:862679.
- Yang, J., Hou, X.G., and Dong, W. 2008. Restudy of *Guangweicaris* Luo, Fu et Hu, 2007 from the lower Cambrian Canglangpu formation in Kunming area. *Acta Palaeontologica Sinica* 47: 115–122.
- Yang, J., Ortega-Hernández, J., Butterfield, N.J., and Zhang, X.G. 2013. Specialized appendages in fuxianhuiids and the head organization of early euarthropods. *Nature* 494: 468–471.
- Yang, J., Ortega-Hernández, J., Lan, T., Hou, J.B., and Zhang, X.G. 2016. A predatory bivalved euarthropod from the Cambrian (Stage 3) Xiaoshi-ba Lagerstätte, South China. *Scientific Reports* 6: 27709.
- Zhao, J., Li, Y.J., Selden, P.A., and Cong, P.Y. 2020. New occurrence of the Guanshan Lagerstätte (Cambrian Series 2, Stage 4) in the Kunming area, Yunnan, southwest China, with records of new taxa. *Alcheringa* 44: 343–355.