

Ventral Morphology and Ecological Implications of *Cindarella eucalla* (Artiopoda, Xandarellida) from Chengjiang Biota, China

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Abstract

Artiopoda, an early arthropod group, displays post-antennal appendages resembling trilobite limbs, but relationships with other early arthropods remain enigmatic. Limited studies and morphological details hinder the understanding of internal relationships within Artiopoda. Recently, exceptionally well preserved arthropod fossils from the Chengjiang Biota were studied using X-ray computed tomography, revealing detailed morphologies. In this study, *Cindarella eucalla*, a xandarellid from the Chengjiang Biota, was re-investigated using X-ray computed tomography and fluorescent microscopy to reconstruct its morphology and understand its phylogeny and ecology. This study successfully reconstructed a three-dimensional model of *Cindarella eucalla*, revealing features, such as spindle-shaped trunk tergites with the anterior six covered by the head shield and axial spines extending from the last four, natant hypostome, four post-antennal cephalic appendage pairs, dorsoventral mismatch existed between trunk tergites and limb pairs. This research suggests that *Cindarella eucalla* could escape in a very short time when it encounters an enemy, and it probably lived in muddy environments with ample light. Phylogenetic analysis indicates that Xandarellids may have close relationship with conciliterga or a clade composed of Nektaspida + (Conciliterga + (*Phytophilaspis pergamena* + Trilobita)).

eLife Assessment

The study presents a very well-illustrated specimens of the artiopodan *Cindarella eucalla* from the Chengjiang Biota, using computer tomography (CT) scanning to illustrate multiple specimens with preserved appendages, a rarity in artiopodans. The description of these fossils is **important** for expanding our understanding of this taxon and its relatives. The imaging and morphological description are followed by a discussion of how this morphology relates to other Cambrian arthropods and its potential ecological function. The evidence provided in this section about resulting function and ecology is presently **incomplete** and the conclusions are put forward too strongly. This assessment could be improved if the work is revised with more careful wording and additional data.

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Introduction

Artiopoda is an extinct group of early arthropods containing Vicissicaudata, Protosutura, Trilobites, and other non-biomineralized arthropods (mainly referring to Conciliterga, Nectopleura, Petalopleura and other arthropods with similar dorsal exoskeleton morphology to that of trilobites) (Hou and Bergström, 1997 [↗](#); Du et al., 2019 [↗](#); Mayers et al., 2019 [↗](#)). All post-antennal appendages are similar. Some analyses suggested that Artiopoda are paraphyletic with Panchelicerata and Total-group Mandibulata, while some resolved artiopoda as a sister group with Panchelicerata in Total-group Chelicerata, and other studies considered it as a sister group with the Total-group Mandibulata (Stein et al., 2013 [↗](#); Ortega-Hernández et al., 2013 [↗](#); Aria et al., 2020 [↗](#); Aria, 2022 [↗](#); Edgecombe, 2020 [↗](#); Zeng et al., 2020 [↗](#)). Opinions on the relationship of animals within and out of this clade vary (Lerosey-Aubril et al., 2017 [↗](#); Schmidt et al., 2022 [↗](#); Zhang et al., 2022 [↗](#)a; Zhu et al., 2023 [↗](#)). Apart from trilobites, most artiopods are only reported to preserve incomplete dorsal exoskeletons (Ortega-Hernández et al., 2013 [↗](#); Hou et al., 2017 [↗](#); Berks et al., 2023 [↗](#)). In recent years, detailed ventral morphology of several artiopods was revealed with X-ray computed tomography (Chen et al., 2019 [↗](#); Zhai et al., 2019 [↗](#)a; Schmidt et al., 2021 [↗](#), 2022 [↗](#); Zhang et al., 2022 [↗](#)a; Du et al., 2023 [↗](#)). *Cindarella eucalla*, a xandarellid (Petalopleura, Artiopoda) only reported from Chengjiang Biota, was considered as a predator or scavenger for its advanced visual system (Hou and Bergström, 1997 [↗](#); Ramsköld et al., 1997 [↗](#); Hou et al., 2017 [↗](#); Chen et al., 2019 [↗](#)). However, the inferences on ecology and its relationship with other Xandarellids were analyzed on limited details, and the phylogenetical results varied in different research when analyzed with parsimony or Bayesian inference (Ramsköld et al., 1997 [↗](#); Legg et al., 2013 [↗](#); Hou et al., 2017 [↗](#); Lerosey-Aubril et al., 2017 [↗](#); Chen et al., 2019 [↗](#); Du et al., 2019 [↗](#); Berks et al., 2023 [↗](#); Zhu et al., 2023 [↗](#)). This animal's further details on endopods and exopods, natant hypostome and gut, dorsoventral mismatch between trunk tergites and limbs, axial spines are unknown when we try to understand its phylogeny and ecology. Hence, this research applied X-ray computed tomography and 3D rendering software Drishti2.4 to illustrate the ventral morphology of *C. eucalla*, reanalyzed the relationship with other artiopods by parsimony and Bayesian inference, and made further comparisons with close groups and some extant arthropods.

Results

Systematic Palaeontology

Euarthropoda [Lankester, 1904](#) ([Lankester ER, 1904](#))

Artiopoda [Hou & Bergström, 1997](#) ([Hou and Bergström, 1997](#))

Xandarellida Chen, Ramsköld, Edgecombe & Zhou in [Chen et al., 1996](#) ([Chen et al., 1996](#))

Constituent taxa

Cindarella eucalla Chen, Ramsköld, Edgecombe & Zhou in [Chen et al., 1996](#) ([Chen et al., 1996](#)), *Xandarella spectaculum* Hou, Ramsköld & Bergström, 1991 ([Hou et al., 1991](#)), *Xandarella mauretanica* Ortega-Hernández et al., 2017 ([Ortega-Hernández et al., 2017a](#)), *Sinoburius lunaris* Hou, Ramsköld & Bergström, 1991 ([Hou et al., 1991](#); [Chen et al., 2019](#); [Schmidt et al., 2021](#)), *Luohuilinella rarus* Zhang, Fu, & Dai, 2012 ([Zhang et al., 2012](#)), *Luohuilinella deletres* Hou et al., 2018 ([Hou et al., 2018](#)), *Zhugeia acuticaudata* Zhu et al., 2023 ([Zhu et al., 2023](#)).

Emended diagnosis

Xandarellida is a clade in Artiopoda. Examination of the available materials reveals that this taxon is mostly preserved in a dorsoventrally flattened state, with a broad, semicircular head shield that has stalked eyes originating from the ventral side. The head shield has dorsal exoskeleton bulges or notches that accommodate the eyes, or the eyes simply extend out from the lateral edge of the head shield. The natant hypostome, a pair of uniramous antennae, and three to five pairs of biramous appendages are covered by the head shield. In some genera, the antenna attaches with one to two antennal scales. The head shield extends posteriorly, covering several thoracic tergites or is closely followed by a reduced thoracic tergite. The middle and/or posterior trunk tergites have variable patterns of dorsoventral mismatch relative to the ventral biramous appendage pairs. Each of some trunk tergites generally covers more than one limb pair. The endopods have spiny or small endites, or none at all ([Ramsköld et al., 1997](#); [Hou et al., 2018](#); [2017](#); [Chen et al., 2019](#)).

Remarks

This taxon comprised six genera: *Cindarella*, *Xandarella*, *Luohuilinella*, *Sinoburius*, *Zhugeia*. The updated information primarily relies on recent studies ([Ortega-Hernández et al., 2017a](#); [Hou et al., 2018](#); [Chen et al., 2019](#)) and new data regarding *Cindarella eucalla* in this research. The dorsal exoskeleton bulges or eye notches on head shield have been reported in *Xandarella spectaculum*, *Sinoburius lunarius*, *Luohuilinella deletres*, and *Luohuilinella ramus*, but not in *Cindarella eucalla* ([Hou et al., 1991](#); [Chen et al., 1996](#); [Hou and Bergström, 1997](#); [Hou et al., 1999](#); [Chen, 2004](#); [Hou et al., 2004](#); [Zhang et al., 2012](#); [Hou et al., 2017](#); [2018](#); [Chen et al., 2019](#); [Schmidt et al., 2021](#)). Natant hypostome have been reported in all Xandarellid species except *Luohuilinella ramus* ([Hou et al., 1991](#); [Hou and Bergström, 1997](#); [Luo et al., 1997](#); [Hou et al., 1999](#); [2004](#); [2018](#); [Chen, 2004](#); [Chen et al., 2019](#); [Schmidt et al., 2021](#)). *Phytophilaspis pergamena* was not resolved in the Xandarellid clade (**Figure 9**; **SFigure 7**). No antennal scale was mentioned in previous studies or in this research on *Xandarella spectaculum*, *Xandarella mauretanica*, *Luohuilinella* ([Zhang et al., 2012](#); [Ortega-Hernández et al., 2017a](#); [Hou et al., 2018](#)), but one on the inner side of *Sinoburius lunaris* and *Cindarella eucalla* revealed in this research ([Chen et al., 2019](#); [Schmidt et al., 2021](#)). The number of post-antennal cephalic appendage pairs ranges from three to five: Three pairs in *Luohuilinella deletres*, four pairs in *Cindarella eucalla*, *Xandarella mauretanica* and *Sinoburius lunaris*, five pairs in

Xandarella spectaculum (Hou et al., 2017 [↗](#); Ortega-Hernández et al., 2017 [↗](#); Hou et al., 2017 [↗](#), 2018 [↗](#); Chen et al., 2019 [↗](#); Schmidt et al., 2021 [↗](#)). The head shield in *Xandarella spectaculum*, *Luohuilinella* and *Sinoburius* closely followed by a small tergite without pleural elongations, but in *Cindarella eucalla*, the head shield extended posteriorly like a folded carapace to cover the anterior six trunk tergites (Ramsköld et al., 1997 [↗](#); Zhang et al., 2012 [↗](#); Hou et al., 2017 [↗](#), 2018 [↗](#); Chen et al., 2019 [↗](#); Schmidt et al., 2021 [↗](#)). The dorsoventral segmental mismatch between trunk tergites and ventral limb pairs displayed various patterns: 1. The last four tergites lengthened with an increase in appendage numbers posteriorly in *Xandarella spectaculum*; 2. The last thoracic tergite covers two ventral appendage pairs in *Sinoburius lunaris* (Chen et al., 2019 [↗](#); Schmidt et al., 2021 [↗](#)); 3. Tergites posterior to the sixth trunk tergite and appendage pairs underneath in *Cindarella eucalla* (Hou et al., 2017 [↗](#)). The endites on the inner side of endopods vary: *Sinoburius lunaris* has no endites but gnathobases with blunt spines at the proximal of protopodites, in *Xandarella spectaculum*, endites on endopod podomeres are unclear; and *Cindarella eucalla* has a cluster of blunt spines on each endopod podomere; In *Luohuilinella deletres*, a pair of sharp spines on each endopod podomere (Hou et al., 2018 [↗](#); Chen et al., 2019 [↗](#); Schmidt et al., 2021 [↗](#)). *Sinoburius lunaris* and *Xandarella spectaculum* have distinctive pygidiums larger than its previous tergites, while *Luohuilinella ramus*, *Luohuilinella deletres* and *Cindarella eucalla* do not. Individuals with distinctive large pygidiums have a median spine and two lateral spine pairs (e.g., in *Sinoburius lunaris*) or only a median spine (e.g., in *Xandarella spectaculum*), and four (in *Cindarella eucalla*) or more (in *Luohuilinella deletres*) axial spines on posterior tergites in these who lack an obvious pygidium. Therefore, this research updated the diagnosis of Xandarellida as described above.

Description

Genus *Cindarella* Chen, Ramsköld, Edgecombe & Zhou in Chen et al., 1996 [↗](#)

Emended diagnosis

The whole body is divided into two tagmata: the cephalon and the trunk with the anterior six tergites covered by the extensions of the head shield. The dorsal exoskeleton in the trunk, consisting of 22 to 32 tergites, is spindle-shaped, with the ninth tergite being the widest. The terminal four tergites show extensions of median ridge into long wide spines. All tergites are in equal length. The cephalic appendages include a pair of large, stalked compound eyes, a pair of multi-annulate antennae, and four pairs of biramous appendages with a similar morphology to those of the trunk. The cephalic appendages become stronger and larger from anterior to posterior. Each of the anterior six tergites in the trunk covers a pair of biramous appendages, and each of the following tergites covers more than one pair, indicating a decoupling of tergites and ventral appendage pairs. All trunk appendages are biramous and share a similar morphology. Each biramous appendage consists of a protopodite with gnathobasic bulges, a six-podomere endopod with a cluster of spines on each podomere, an exopod with dozens of lamellae on a paddle-like shaft, and a rod-like exite.

Cindarella eucalla Chen, Ramsköld, Edgecombe & Zhou in Chen et al., 1996 [↗](#)

1996 *Cindarella eucalla* Chen et al., Taiwan Museum of Natural Science, pp. 160–162, Figures 208–210.

1997 *Almenia spinosa* Hou and Bergström, Scandinavian University Press, pp. 81–83, Figures 71–73.

1997 *Cindarella eucalla* Ramsköld et al., Transactions of the Royal Society of Edinburgh-Earth Sciences, **Figures 1–14** [↗](#).

1999 *Cindarella eucalla* Luo et al., Yunnan Science and Technology Press, pp. 49, plate 6, **Figure 4** [↗](#).

2004 *Cindarella eucalla* Hou et al., Blackwell Publishing Ltd., pp. 170–171, Figures 16.57–16.58.

2013 *Cindarella eucalla* Zhao et al., Scientific Reports, **Figures 1** [↗](#)–**2** [↗](#).

2017 *Cindarella eucalla* Hou et al., John Wiley & Sons Ltd., pp. 206–207, Figures 20.37–20.38. Diagnosis: As for genus.

Dorsal exoskeleton

The exoskeleton was non-biomineralized and most specimens preserved dorsoventrally flattened (**Figures 1** [↗](#) A, B, D; 6 A; 7 A, C; 8A; **SFigures 1** [↗](#); 6 A, C), only a few specimens preserved laterally (YKLP 17369 in **Figure 3** [↗](#) and **SFigure 4** [↗](#), YKLP 17366 in **SFigure 2** [↗](#) A). Complete specimens, excluding appendages, measured from the anterior margin of the cephalon to the rear end of the last tergite, ranged from 11.60 to 90.25 mm in length along the sagittal axis. The length could reach up to 130 mm in Hou et al., (2017) [↗](#). The dorsal exoskeleton was divided into two tagmata: a large semi-elliptical head shield and the trunk with 22 to 32 tergites (YKLP 17361 in **Figure 6** [↗](#) A shows 32 tergites, YKLP 17374 in **SFigure 6** [↗](#) C shows 28 tergites; YKLP 17360 in **Figure 1** [↗](#) A shows 24 tergites; ELRC 18505 shows 24 tergites, ELRC 18502 shows 22 tergites in Ramsköld et al., (1997) [↗](#)). No ornaments were observed on the dorsal exoskeleton (**Figures 1** [↗](#) A, B; 6 A, 7 A, C; **SFigures 1** [↗](#) A, B; 2 A–F; 6 C). The head shield had no sharp genal spines but blunt lateral margins (**Figures 1** [↗](#) A, B; 3 A; 6 A; 7 A, C; 8A; **SFigures 1** [↗](#) A, B; 2 B; 6 C). Its length (measured from the anterior margin to the posterior margin of head shield) was 33.68%–46.89% of the body length, ranging from 8.79 to 59.80 mm in this study. The maximum width (which is also the width of the head shield) was 84.17%–145.30% of the length, ranging from 10.46 to 71.86 mm. The posterior extension of the head shield covered the first six trunk tergites (**Figures 1** [↗](#) A, B, D; 3 A, C; 6 A, B; **SFigures 1** [↗](#) A, B; 6 C). The dorsal trunk exoskeleton was spindle shaped, with the anterior nine tapering anteriorly and the others tapering posteriorly. All tergites were in equal lengths (**Figures 1** [↗](#) A, C; 3 A; 6 A; 7 A, C; **SFigures 1** [↗](#) A, B; 2 A, B, F; 6 C). Median ridges of the last four tergites extended into axial spines (**Figure 7** [↗](#) B, D).

Gut and diverticulae

The gut extends from the hypostome to the terminal tergite (**Figures 1** [↗](#) B, C, D; 5 A, B; 6 A; **SFigures 1** [↗](#); 2 B, D–F), and in YKLP 17363a, about 40% of the hypostome's length is covered dorsally by the gut (**Figure 1** [↗](#) B, C). The diverticulae resembles to those of *Naraoia spinosa*, but the branch pattern is simpler (**Figures 1** [↗](#) B; 6 A; **SFigure 1** [↗](#) A, B).

Anterior sclerite and hypostome

There is a small sclerite located in front of the hypostome (**Figure 3** [↗](#) E, E1, E2; 5 A, B). It is narrower and shorter than the hypostome. The hypostome is connected to the pleura (**Figure 3** [↗](#) E, E1, E2; 5 A, B). The hypostome is rectangular, and covers the anterior gut (**Figures 1** [↗](#) B, C, D; 6 A; **SFigure 1** [↗](#) A, C). There is a putative moth near the posterior margin of the hypostome (**Figure 5** [↗](#) B).

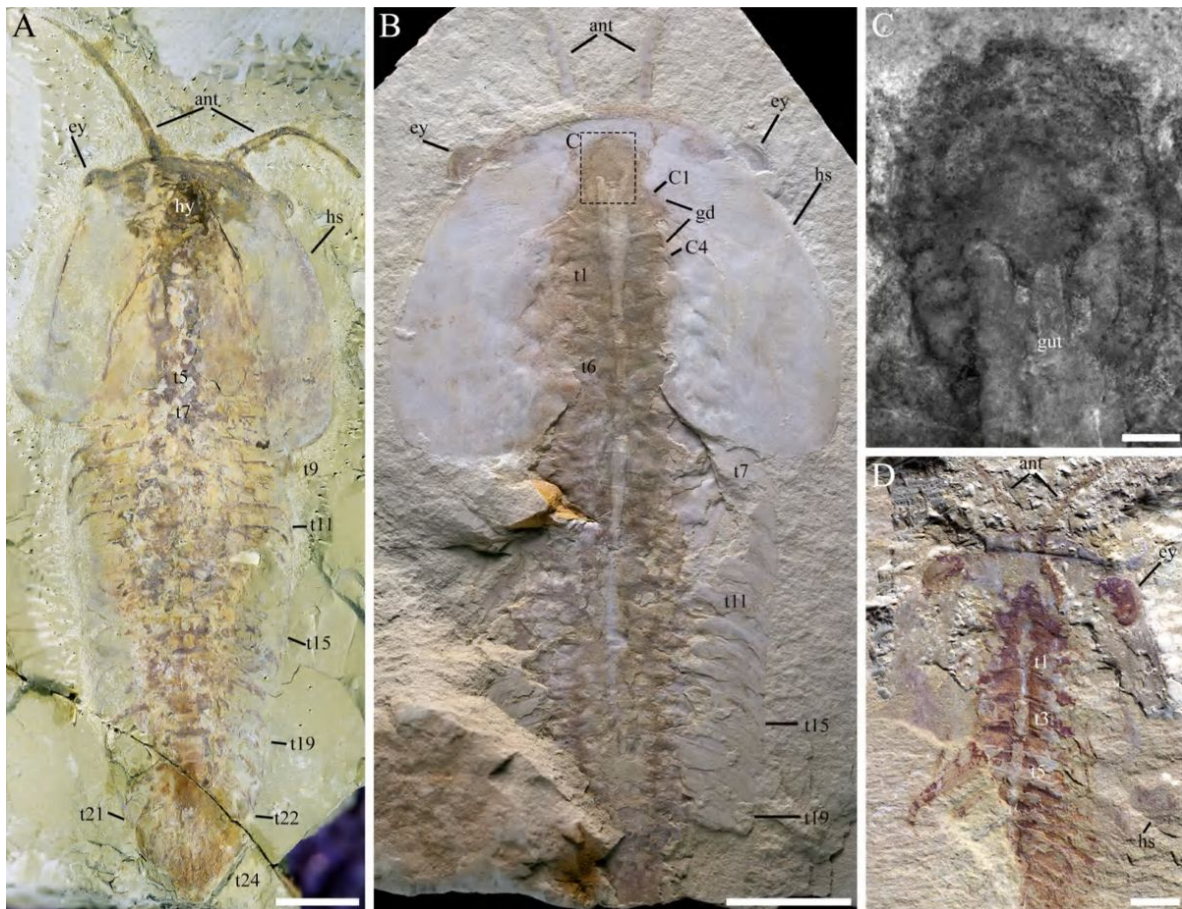


Figure 1.

Macro-photographic (A, B, D) and fluorescent (C) images of *Cindarella eucalla*. A Dorsal view of YKLP 17360. B Dorsal view of YKLP 17363a. C Close-up of hypostome in B. D Ventral view of YKLP 17373. Abbreviations: ant, antenna(e); ca, caeca; el, exopod lobe (shaft); *Cn*, Post-antenna cephalic appendage number; exo, exopod; ey, eye(s); gut, gut content/trace; hs, head shield; *tn*, tergite number. Scalebar: 1 cm in A and B, 2 mm in D, 1 mm in C. **Figure 1—figure supplement 1**. Macro-photographic images of *Cindarella eucalla*. A Dorsal view of YKLP 17363b. B Dorsal view of YKLP 17364. C Dorsal view of YKLP 17375. Abbreviations: ant, antenna(e); *Cn*, post-antenna cephalic appendage number; ey, eye(s); gut, gut content/trace; hs, head shield; *tn*, tergite number; *r*, right; *l*, left. Scalebar: 5 mm.

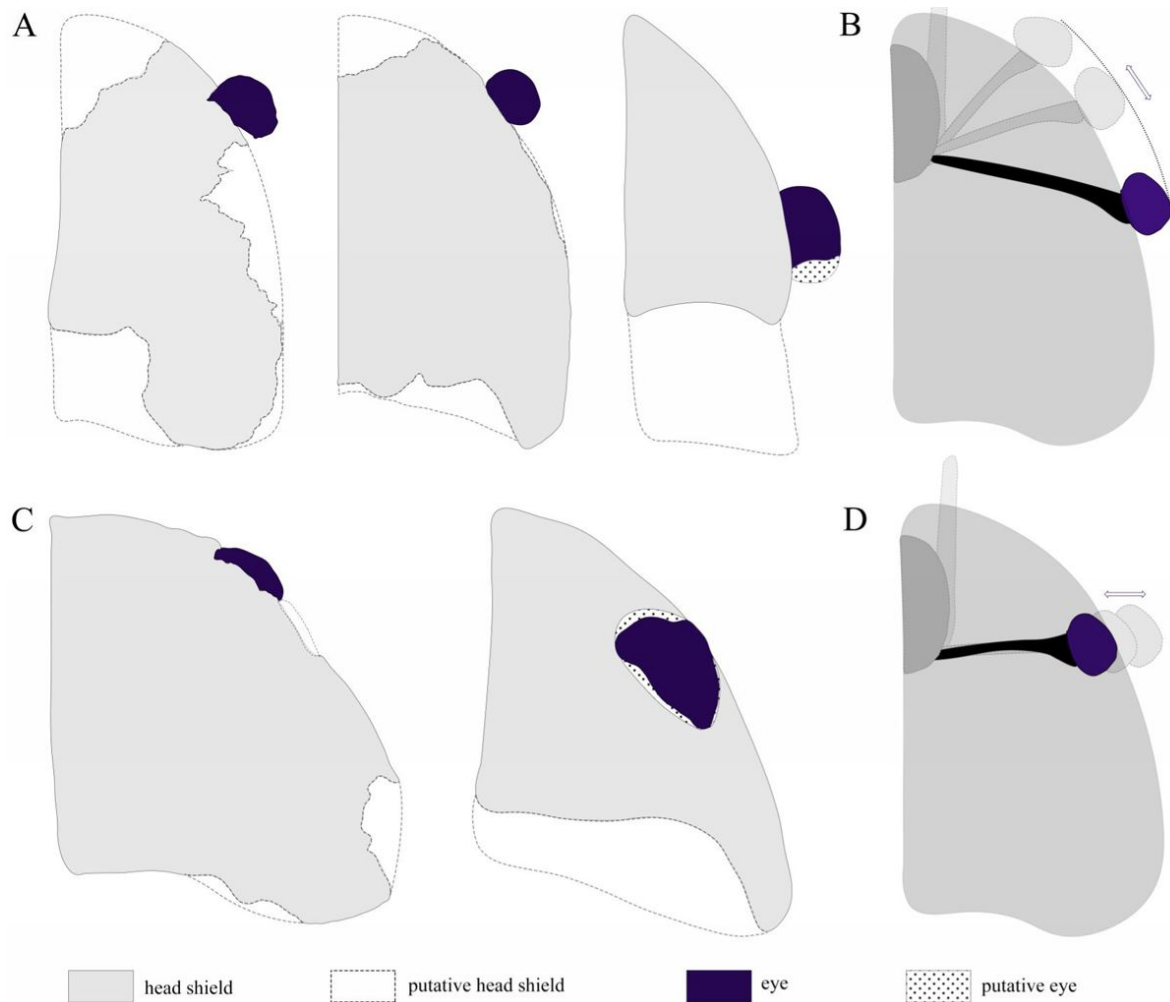


Figure 2.

Schematic diagram of eye movements in *Cindarella eucalla*. Gray area indicates head shield, dashed line indicates putative head shield, deep purple area indicates eye, dotted area indicates putative eye in A and C. A Outline of head shield and eyes in three specimens of *Cindarella eucalla* (Left to right): YKLP 17371, YKLP 17368 and YKLP 17366. B Schematic diagram of eye movements in A. C Outline of head shield and eyes in two specimens of *Cindarella eucalla* (Left to right): YKLP 17365, YKLP 17368. D Schematic diagram of eye movements in A and C. Not to scale. **Figure 2—figure supplement 1** [↗](#). Head shield and eyes of *Cindarella eucalla*. A YKLP 17366, Dorsal view. B YKLP 17368, dorsal view. C YKLP 17367, dorsal view. D YKLP 17365, dorsal view. E YKLP 17376, dorsal view. F YKLP 17373, dorsal view. G YKLP 17372, dorsal view. Scalebar: 2 mm in G, 5 mm in A, D and F, 1 cm in B, C and E. **Figure 2—figure supplement 2** [↗](#). Outline of head shield (half) and eyes in *Cindarella eucalla* specimens. Gray area indicates head shield, dashed line indicates putative head shield, deep purple indicates eye, dotted area indicates putative eye. A YKLP 17371. B YKLP 17368. C. YKLP 17366. D YKLP 17362 (flipped horizontal). E YKLP 17367. F YKLP 17376 (flipped horizontal). G YKLP 17365. H YKLP 17373. I YKLP 17372 (flipped horizontal). Not to scale.

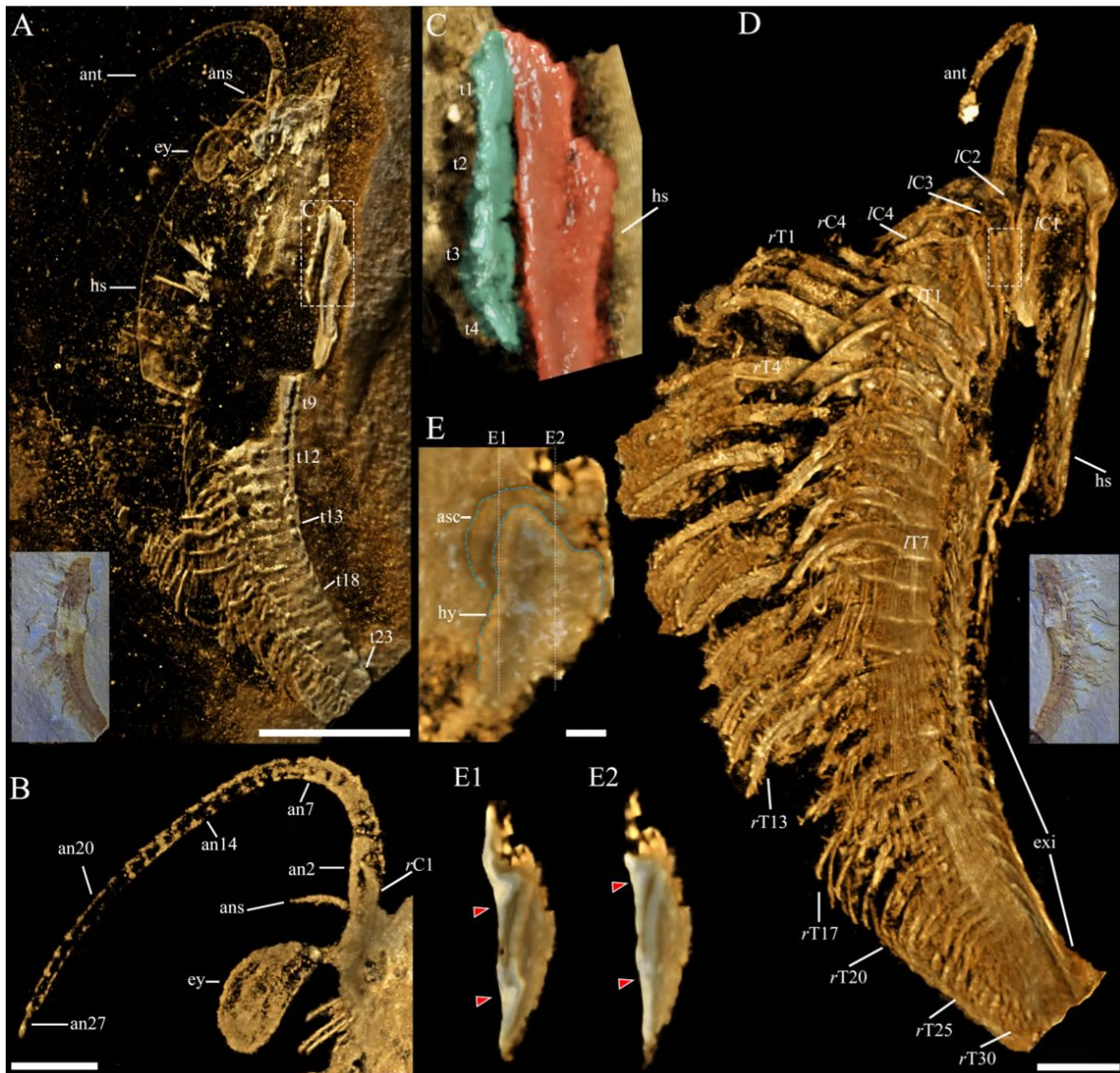


Figure 3.

Digital anatomy of *Cindarella eucalla* (YKLP 17369) based on X-ray tomographic data processed in Drishti v2.4. A YKLP 17369a, dorsal view. B YKLP 17369a, left antenna and eye, dorsal view. C overlap of head shield (in red) and trunk tergites (in cyan) within the dashed box in A. D YKLP 17369b, Ventral view, body and appendages digitally extracted from rocks. E Anterior sclerite and hypostome within the dashed box in D with the second and third left cephalic appendages removed, ventral view (flipped horizontally). The dashed lines indicate two longitudinal sections in E1 and E2. E1–E2 two longitudinal sections (flipped horizontally) indicated in E. The arrowheads indicate separated sclerites posited anterior to first post-antennal appendage pair. Abbreviations: *ann*, antennal segment number; *ant*, antenna(e); *ans*, antennal scale; *asc*, anterior sclerite; *Cn*, post-antennal cephalic appendage number; *exi*, exite(s); *ey*, eye(s); *hs*, head shield; *tn*, tergite number; *Tn*, trunk appendage number; *l*, left; *r*, right. Scalebar: 5 mm in A, 2 mm in D, 1 mm in B, 0.2 mm in E, no scalebar in C, E1 and E2.

Figure 3—figure supplement 1. Macro-photographic (A and C) and fluorescent (B and D) images of *Cindarella eucalla* (YKLP 17369). A and B YKLP 17369a, dorsal view. C and D YKLP 17369b. Abbreviations: *tn*, tergite number. Scalebar: 5 mm.



Figure 4.

Digital anatomy of *Cindarella eucalla* (YKLP 17369b) based on X-ray tomographic data processed in Drishti v2.4. A Dorsal view of the first right trunk appendage. B Dorsal view of the third left trunk appendage, red arrows indicate spines on terminal claw of endopods. C Dorsal view of the seventh left trunk appendage, red arrows indicate spines on terminal claw of endopods. D Ventral view of the eleventh right trunk appendage. E Dorsal view of left posterior trunk appendages. Abbreviations: el, exopod lobe; en, endopod; lm, lamella(e); exi, exite(s); hs, head shield; pd n , endopod podomere number; pt, protopodite; st, seta(e); tc, terminal claw; tn, tergite number; T n , trunk appendage number; l, left; r, right. Scalebar: 1 mm in A–E. **Figure 4—figure supplement 1** [↗](#). Macro-photographic (A, C) and fluorescent (B, D) images of *Cindarella eucalla* (YKLP 17369). A YKLP 17374, dorsal view. B close-up of trunk appendages within the dashed box in A. C YKLP 17362, dorsal view. D close-up of a trunk exopod within the dashed box in C. Abbreviations: el, exopod lobe/shaft; ey, eye; hs, head shield; lm, lamella(e); T n , trunk appendage number; tn, Tergite number; l, left; r, right. Scalebar: 1 cm in A, 5 mm in C, 2 mm in B, 1 mm in D.

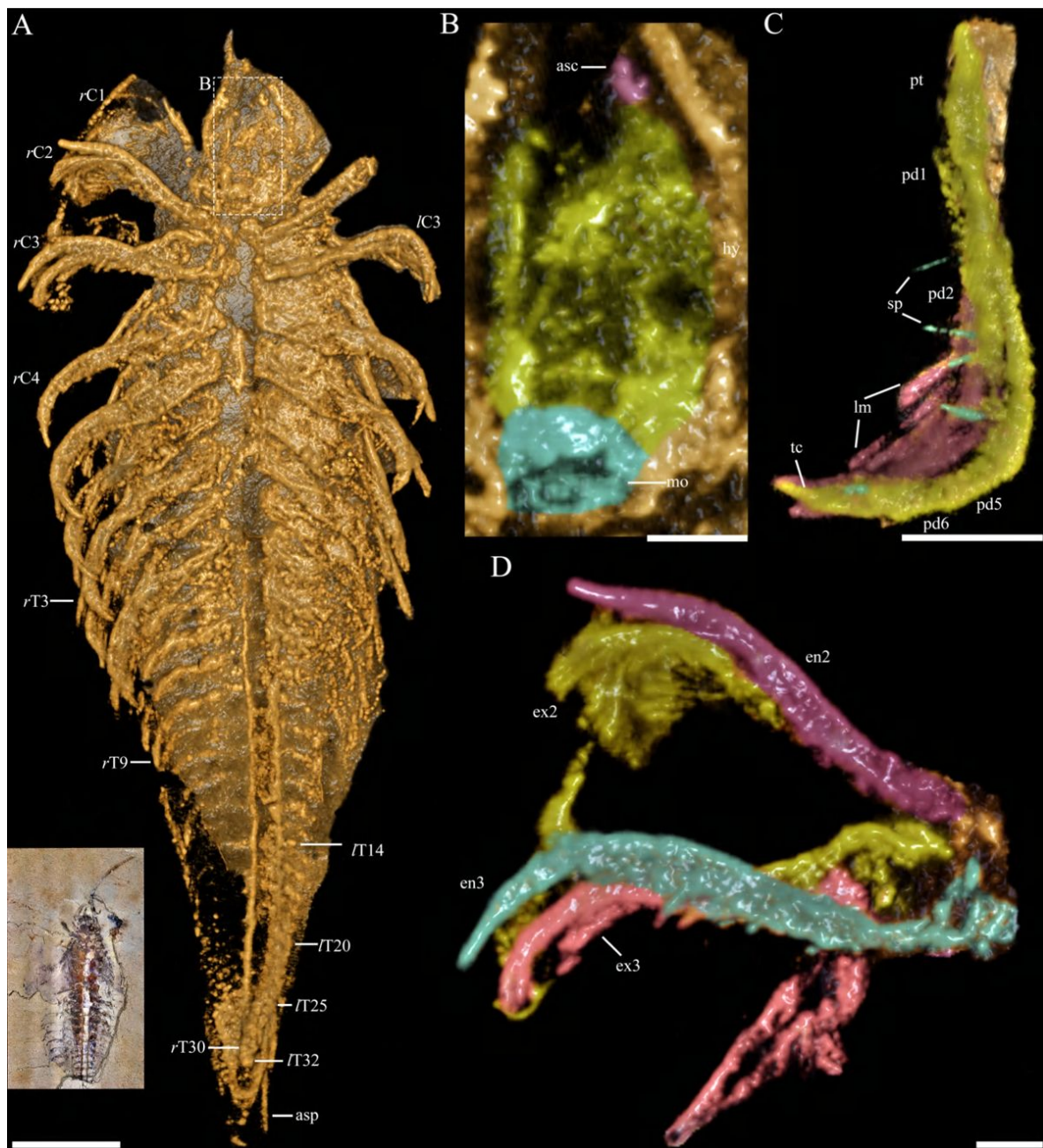


Figure 5.

Digital anatomy of *Cindarella eucalla* (YKLP 17370) based on X-ray tomographic data processed in Drishti v2.4. A Overview, ventral, with dorsal exoskeleton partially removed. B anterior structures beneath the head shield within the dashed box in A, with anterior sclerite, hypostome and mouth painted in different colours respectively. C Ventral view of the third left cephalic appendage. D Ventral view of the second and third right cephalic appendages, with the exopods and endopods painted in different colours. Abbreviations: ant, antenna(e); asp, axial spine(s); Cn, post-antennal cephalic appendage number; hy, hypostome; pdn, endopod podomere number; lm, lamella(e); pt, protopodite; sp, spine(s); tc, terminal claw; Tn, trunk appendage number; l, left; r, right. Scalebar: 2 mm in A and B, 1 mm in C, 0.5 mm in D.

Cephalic appendages

A pair of large, stalked compound eyes made up of many ommatidia protrude out of the anterolateral margin of the head shield (**Figure 1** [A, B, D; 3 A, B; 6 A, B; 7 C; 8 A, B, F; SFigure 1](#) [A; 2; 5 C](#)). These eye stalks can move flexibly, backward or forward, and they can extend out from or contract under the head shield (**Figure 1** [A, B, D; 2; 3 A, B; 6 A; 7 C; 8 A, B; SFigure 1](#) [A–3 C](#)). It seems more likely that the eyes are unsegmented. These eyes originate ventrally, anterior to the antennae (**Figure 3** [A, B](#)). The multi-annulated antenna is slender and long, with over 30 annulae (**Figures 1** [A; 3 A, B, D; 7 A; 8 A, B; SFigure 1](#) [A; 2 C, F, G; 5 C](#)). The annulae decrease slowly in length and width from the proximal to the distal (**Figures 1** [A; 3 B; SFigure 1](#) [B, C; 2 C, F, G](#)). An antennal scale attaches at the rear end of the first annula or the base of the second one, extending laterally from probably the inner side (**Figure 3** [B](#)). Behind the antennae are four appendage pairs identified from the trunk appendages with the anterior margin of the first trunk tergite (**Figures 1** [A, B, D; 3 A, C](#)). The appendages are biramous, in similar morphology but increased in size posteriorly (**Figures 3** [D; 5 A, D; 6 A, B; 8 B](#)). The morphology of cephalic appendages is similar to these of trunk, especially the anterior trunk appendages (**Figures 3** [D; 5 A, C, D; 6 B; 8 A, B](#)). Cephalic appendages are small compared to the anterior trunk appendages, tapering anteriorly (**Figures 3** [D; 5 A, D; 6 B; 8 A, B](#)). The last cephalic appendage pair is smaller than the first trunk appendage pair (**Figures 3** [D; 5 A; 6 B; 8 B](#)).

Trunk appendages

All trunk appendages are biramous and share a similar morphology. Each appendage consists of a protopodite with gnathopod bulges, a six-podome endopod with spines on each podome, an exopod with dozens of lamellae attached to the paddle-shaped shaft, and a rod-like exite (**Figures 3** [D; 4; 5 C, D; 6 B, C; 8 C, D; SFigure 6](#) [B, D](#)). Each of the first six anterior trunk tergites beneath the posterior extension of the head shield covers a pair of biramous appendages (**Figures 1** [A, B, D; 3 A, C; 6 B](#)). The first or second trunk appendage pair is the largest among all trunk appendage pairs, and the following three or more pairs are of similar size (**Figures 3** [D; 4; 5 A; 6 B](#)). All trunk appendages taper posteriorly, and only limb buds could be observed underneath the last several tergites (**Figures 3** [D; 4 E; 5 A; 6 B; 8 B, F](#)). Behind the sixth trunk tergite, this animal shows a decoupling of tergites and appendage pairs (**Figures 3** [D; 6 A, B; 8 B](#)). Tergites posterior to the sixth trunk segment cover an increasing number of appendage pairs, lacking correspondence between tergite boundaries and limb boundaries (**Figures 3** [D; 6 A, B; 8 A, B; SFigure 1](#) [C; 5 A, C; 6](#)). Variation is observed among different specimens (**Figures 3** [D; 5 A; 6 A, B; SFigure 1](#) [C; 5 A, C; 6](#); and **Figures 5** [C](#) and **9** [C](#) in [Ramsköld et al., 1997](#) [C](#)).

Discussion

Synonym

Almenia spinosa [Hou and Bergström, 1997](#) [C](#) was previously considered to be synonymous with *Cindarella eucalla* ([Hou and Bergström, 1997](#) [C](#); [Ramsköld et al., 1997](#) [C](#); [Edgecombe and Ramsköld, 1999](#) [C](#); [Hou et al., 2004](#) [C](#), [2017](#) [C](#)). However, our analysis suggests that *Almenia spinosa* is actually synonymous with *Xandarella spectaculum*, not *Cindarella eucalla*. Here follows the reasons:

1. The edges of *Almenia spinosa*'s head shield are relatively sharp, and its posterolateral corner that extends into a pointed genal angle — a feature more similar to *Xandarella spectaculum* than *Cindarella eucalla*, which has a blunt and rounded head shield without a distinct genal angle.

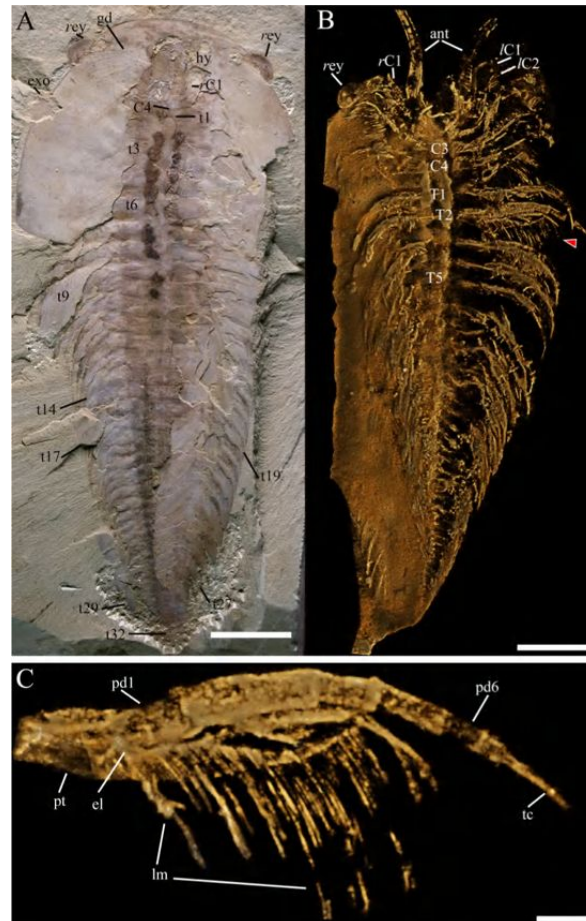


Figure 6.

Macro-photographic picture (A) and results from X-ray tomographic data processed in Drishti v2.4 (B, C), YKLP 17361. A Overview, dorsal. B Overview, ventral. C Ventral view of the second left trunk appendage. Abbreviations: ant, antenna(e); Cn, post-antennal cephalic appendage number; el, exopod lobe (shaft); ey, eye(s); gd, gut diverticula(e); hy, hypostome; pdn, endopod podomere number; pt, protopodite; sp, spine(s); tc, terminal claw; Tn, appendage number; tn, tergite number; l, left; r, right. Scalebar: 1 cm in A and B, 2 mm in C. **Figure 6—figure supplement 1**. Outline of trunk tergites and ventral segments (gut trace or appendage boundaries). A YKLP 17361. B YKLP 17362. C ELRC 18505. Abbreviations: tn, tergite number. Scalebar: not to scale.

2. The number of post-antennal cephalic appendage pairs in *Almenia spinosa*—six or more—is consistent with *Xandarella spectaculum*, unlike *Cindarella eucalla*, which has only four pairs.
3. *Almenia spinosa* has eleven trunk tergites, possibly followed by a small tergite close to the head shield—similar to *Xandarella spectaculum*. In contrast, *Cindarella eucalla*'s head shield covers six anterior trunk tergites, followed by 16 to 26 trunk tergites.
4. The last four tergites of *Almenia spinosa* are of subequal length, gradually lengthening towards the rear (as seen in Hou and Bergström, 1997 [DOI](#), Figures 75, 76). This pattern is similar to *Xandarella spectaculum*, while all trunk tergites of *Cindarella eucalla* are nearly in the same length.

Dorsal exoskeletal

Cindarella eucalla's exoskeleton is divided into a head shield and trunk, with the anterior six trunk tergites covered by the posterior of head shield. There was no evidence of overlap between the anterior six trunk tergites and the head shield (Chen et al., 1996 [DOI](#); Chen, 2004 [DOI](#); Ramsköld et al., 1997 [DOI](#); Hou et al., 2004 [DOI](#), 2017 [DOI](#)). The anterior six trunk tergites have small or no pleurae (Figure 1 [DOI](#) B; 3 C). This is unlike other Xandarellid species (*Xandarella spectaculum*, *Sinoburius lunaris*, *Luohuilinella*, etc.) which have a small tergite closely following the posterior margin of head shield (Zhang et al., 2012 [DOI](#); Hou et al., 2017 [DOI](#), 2018 [DOI](#); Chen et al., 2019 [DOI](#); Schmidt et al., 2021 [DOI](#)). No obvious pygidium can be distinguished in this animal. *Xandarella spectaculum*'s body is divided into a head shield and trunk. The head shield may be composed of two fused or separated tergites. Following the head shield is a small tergite and a series of trunk tergites, mostly preserved in dorsal-ventral compression (Hou et al., 1991 [DOI](#), 1999 [DOI](#), 2004 [DOI](#), 2017 [DOI](#); Chen et al., 1996 [DOI](#); Chen, 2004 [DOI](#); Hou and Bergström, 1997 [DOI](#)). *Sinoburius lunaris* shows a similar dorsal exoskeleton to *Xandarella spectaculum* (Chen et al., 2019 [DOI](#); Schmidt et al., 2021 [DOI](#)). At least two thoracic tergites of *Zhugeia acuticaudata* are covered by its head shield (Zhu et al., 2023 [DOI](#)). According to the morphology of the dorsal exoskeleton, none of these species exhibit a distinct reduction of the trunk, and there are no obvious adaptations for suspension feeding on the head shield as trilobites live such a lifestyle (Fortey and Owens, 1999 [DOI](#)). In contrast to typical suspension-feeding trilobites, none of the Xandarellid species has a specialized head shield for this lifestyle.

Eye slits and exoskeletal bulges

Cindarella eucalla lacks the eye slits present in *Xandarella spectaculum* and *Phytophilaspis pergamena*, as well as the lateral notches found in *Luohuilinella ramus* and *Luohuilinella deletres* (Ivantsov, 1999 [DOI](#); Hou et al., 2017 [DOI](#), 2018 [DOI](#)). *Xandarella spectaculum* has distinct eye slits extending from the eyes to the lateral margin of the head shield, dividing it into two parts (Hou et al., 1991 [DOI](#); Hou and Bergström, 1997 [DOI](#); Chen, 2004 [DOI](#); Hou et al., 1999 [DOI](#), 2004 [DOI](#), 2017 [DOI](#)). *Phytophilaspis pergamena* is considered to have eye slits (open sutures in Ivantsov, 1999 [DOI](#)) that run across the segments transversely. A hypothesis posits that the notches found within Xandarellid species (*Cindarella*, *Luohuilinella*, *Xandarella* and *Phytophilaspis*, *Sinoburius*) reflect a progressive involution of the perforations accommodating the ventral stalked eyes (Chen et al., 2019 [DOI](#)).

Ventral compound eyes

Cindarella eucalla's eyes are particularly prominent among Artiopods, with stalks long enough to extend the entire eye pair beyond the edge and retract fully under the head shield, and can also move back and forth freely (Figures 1 [DOI](#) A–C; 2; 3 A; 6 A; 7 C; S Figures 1 [DOI](#)–3 [DOI](#)). This expands the visual field and safeguards the eyes (by retracting under the head shield). The largest compound eyes of *Cindarella eucalla* reach 5.36 mm in an incomplete specimen (YKLP 17367). Stalked compound eyes of *Xandarella spectaculum* protrude from the dorsal exoskeletal bulges of the head shield, indicating a limited range of motion within the eye bulges. *Xandarella spectaculum* has

smaller eyes than *Cindarella eucalla* when their body length is the same. One study estimated that *Cindarella eucalla* has more than 2000 ommatidia (the maximum diameter of the measured individual's eye is about 3.8 mm) (Zhao et al., 2013 [DOI](#)). *Xandarella spectaculum* has a pair of eyes in middle size compared to *Cindarella*, *Luohuilinella*, *Zhugeia* and *Sinoburius*. *Luohuilinella deletres* has a pair of ventral stalked eyes, with a maximum eye diameter of 4.45 mm in a 84.96 mm-long specimen (YKLP 11120) (Hou et al., 2018 [DOI](#)). The eyes of *Sinoburius lunaris*, which belongs to the same order as *Xandarella spectaculum*, appear to be smaller, consistent with morphological analysis results.

The living environment of this animal may be broader than that of *Luohuilinella deletres*, *Xandarella spectaculum*, *Zhugeia acuticaudata*, and *Sinoburius lunaris*. Its visual system is more advanced than other Xandarellids. Some researches indicated that this animal could be a predator with acute vision (Zhao et al., 2013 [DOI](#)). Though acute vision is helpful for predation when feeding, acute vision is not a sufficient and necessary condition for predation. It could be a predator or not.

Anterior sclerite

Cindarella eucalla has an anterior sclerite in front of the hypostome (Figure 3 [DOI](#) E). This anterior sclerite has been observed in numerous extinct and extant euarthropods, including Radiodontans (*Lyrarapax unguispinus*, *Anomalocaris saron*, *Anomalocaris canadensis*, *Hurdia victoria*, *Amplectobelua symbrachiata*) (Ortega-Hernández, 2015 [DOI](#); Daley and Edgecombe, 2014 [DOI](#); Zeng et al., 2018 [DOI](#)), Fuxianhuiids (*Fuxianhuia protensa*, *Fuxianhuia xiaoshibaensis*, *Apankura machu*, *Alacaris mirabilis*, *Chengjiangocaris longiformis*, *Xiaocaris luoi*, *Guangweicaris spinatus*) (Budd, 2008 [DOI](#); Wu and Liu, 2019 [DOI](#); Liu et al., 2020 [DOI](#) a; Aria et al., 2021 [DOI](#)), Megacheirans (*Kootenichela deppi*, *Worthenella cambria*, *Jianfengia multisegmentalis*) (Legg et al., 2013 [DOI](#); Aria et al., 2021 [DOI](#); Zhang et al., 2022 [DOI](#) b), as well as a branch between Radiodontans and Megacheirans (*Kylinxia zhangii*), Artipodans (*Misszhouia longicaudata*, *Helmetia expanse*) (Zeng et al., 2020 [DOI](#); O'Flynn et al., 2023 [DOI](#)), *Kuamaia lata*) (Ortega-Hernández, 2015 [DOI](#); Budd, 2008 [DOI](#)), Myriapoda (*Paralamyctes subicolous*) (Aria et al., 2021 [DOI](#)), Crustaceans (*Bathynomus*) (Aria et al., 2021 [DOI](#)). This anterior sclerite has not been reported in other artipods except for Helmetiids and some Naraoids (*Misszhouia longicaudata*) (Budd, 2008 [DOI](#); Ortega-Hernández, 2015 [DOI](#); Park, 2023 [DOI](#)). *Cindarella eucalla* serves as another example of an Artipod possessing an anterior sclerite positioned at the base of the eye stalks. Some studies suggest that the anterior sclerite and labrum fused into a hypostome in trilobites (Park, 2023 [DOI](#)). Our findings indicate that *Cindarella eucalla* (an Artipoda) possesses both a hypostome and an anterior sclerite.

Natant hypostome

The hypostome plays a pivotal role in the evolution, ecology, and classification of early arthropods (Scholtz and Edgecombe, 2005; Liu et al., 2016 [DOI](#), 2020 [DOI](#) b; Ortega-Hernández et al., 2017 [DOI](#) b, 2019 [DOI](#); Budd, 2021 [DOI](#)). Different types of hypostome serve diverse functions, with most playing a crucial role in feeding and digestion, particularly in trilobites (Fortey, 1990; Fortey and Owens, 1999 [DOI](#); Fortey, 2014 [DOI](#)). Three types of hypostome were identified in trilobites: natant, conterminant, and impendent (Fortey, 1990). The hypostome's attachment, morphology, and other features generally determine its function, with the mouth located at or near the posterior edge (Fortey, 1990; Fortey and Owens, 1999 [DOI](#); Fortey, 2014 [DOI](#)). The hypostomes of *Cindarella eucalla* and *Xandarella spectaculum* are natant. There is no conclusive evidence of the connection between the hypostome and cephalic duoblure in these species, and it is less likely that the hypostome and cephalic duoblure are connected in examined specimens in this research. Most previous researches on the evolution and phylogeny of the hypostome in artipods have been based on comparison with trilobites, suggesting that the hypostome covers the esophagus and midgut, receiving food transmitted by the limb base and delivering it to the mouth (Fortey, 1990; Fortey and Owens, 1999 [DOI](#); Fortey, 2014 [DOI](#)). When dealing with bulky food, trilobite predators/scavengers rely on larger hypostomes that are closely connected to the duoblure to provide more space to accommodate captured prey in front of the mouth and push food into the esophagus. Therefore,

conterminant hypostomes are considered to be an essential feature of predatory or scavenging trilobites (Fortey and Owens, 1999 [\[1\]](#)). Among the Xandarellids, *Cindarella eucalla*, *Xandarella spectaculum* and *Sinoburius lunaris* have typical natant hypostomes (Figure 1 [\[1\]](#) C, D) (Hou et al., 1991 [\[2\]](#); Hou and Bergström, 1997 [\[3\]](#); Hou et al., 1999 [\[4\]](#), 2004 [\[5\]](#), 2017 [\[6\]](#)). *Cindarella eucalla*'s hypostome is rectangular in shape, and its midgut extends from the posterior third of the hypostome to the rear of the body (Figure 1 [\[1\]](#) C, D), indicating that the midgut opening is located under the hypostome, while the mouth opening is likely at the end of the gut margin covered by the hypostome. *Xandarella spectaculum* has a subelliptic hypostome (Hou and Bergström, 1997 [\[3\]](#)), while *Sinoburius lunaris* has a natant hypostome with a sharp anterior end and a long, oval-shaped posterior end (Chen et al., 2019 [\[7\]](#)). Natant hypostomes in trilobites have been highly conserved from the Cambrian to Carboniferous periods, consistent with their particle-feeding habits and lack of significant posterior differentiation (Fortey and Owens, 1999 [\[1\]](#); Fortey, 2014 [\[8\]](#)). This type of hypostome is usually small and semicircular, resembling a plate that is separate from the doublure. Similarly, in Xandarellids that preserved natant hypostomes, there is no evidence of any connection between the hypostome and cephalic doublure on either side, nor any significant posterior differentiation. These animals likely had a particle diet.

Antennae and antennal scale

The antennae of Artiopods are typically uniramous, long, soft, and multi-segmented. With some species possessing setae on the segments (Hou et al., 2017 [\[6\]](#); Zeng et al., 2017 [\[9\]](#); Leroosey-Aubril and Ortega-Hernández, 2019 [\[10\]](#); Holmes et al., 2020 [\[11\]](#); Zhang et al., 2021 [\[12\]](#), 2022 [\[13\]](#) b). In extant arthropods, antennae serve mechanical functions, interacting with the surrounding water, processing food, or cleaning the body (Vogel, 1983 [\[14\]](#); Hou and Bergström, 1997 [\[3\]](#); Schneider et al., 1998 [\[15\]](#); Spaethe et al., 2007 [\[16\]](#); Symonds et al., 2012 [\[17\]](#); Johnson et al., 2017 [\[18\]](#)). The antennae of *Cindarella eucalla* and *Sinoburius lunaris* differ from other Artiopods, such as *Eoredlichia intermedia* and *Retifacies abnormalis*, in terms of length and antennal scales at the base (Hou et al., 2017 [\[6\]](#); Chen et al., 2019 [\[7\]](#); Schmidt et al., 2021 [\[19\]](#); Zhang et al., 2022 [\[13\]](#) a). *Cindarella eucalla* has one antennal scale on the outside of the first segment, and *Sinoburius lunaris* has one antennal scale on the inner side of the second or sixth segment. In extant arthropods, such as male moths, antennal scales on the segments enhance their ability to detect signals (Wang et al., 2018 [\[20\]](#)). The antennae of crustaceans have various functions, such as the antennal scale of juvenile shrimp being an integral part of the second antennae and assisting in or enhancing locomotion (Herberholz et al., 2019 [\[21\]](#)). The nature of antennal scales in Xandarellids is more likely to be similar to male moths' antennal scales in terms of attachment position and quantity, and they may also have a signal detection function. Furthermore, bristles on their antennae were not prominent in *Cindarella eucalla*, *Xandarella spectaculum*, *Sinoburius lunaris* and *Luohuilinella deletres*. We suggest that antennal scales may play a role similar to bristles, but not limited to this, requiring further research.

Post-antennal cephalic appendages

The morphology of post-antennal cephalic appendages is crucial for studies of arthropod evolution, classification, and ecology (Briggs and Whittington, 1997 [\[22\]](#); Whittington, 1980; Wills, 1998 [\[23\]](#); Waloszek et al., 2005 [\[24\]](#); Lamsdell et al., 2013 [\[25\]](#); Yang et al., 2013 [\[26\]](#); Du et al., 2023 [\[27\]](#)). Cambrian arthropods' postantennal cephalic appendages suggest a close connection to feeding (Hou and Bergström, 1997 [\[3\]](#); Waloszek et al., 2007 [\[28\]](#); Hou et al., 2017 [\[6\]](#)). The gnathobase of protopodite or the endites on the inner side of endopod podomeres can relay food from the food grooves formed by the trunk appendages to the mouth (Fortey and Owens, 1999 [\[1\]](#)). *Luohuilinella deletres*, *Cindarella eucalla*, *Sinoburius lunaris* and *Xandarella spectaculum* have 3, 4, 4, and 6 post-antennal cephalic appendage pairs, respectively (Hou et al., 2017 [\[6\]](#), 2018 [\[29\]](#); Chen et al., 2019 [\[7\]](#); Schmidt et al., 2021 [\[19\]](#)). The post-antennal cephalic appendages of these four species show a trend of increasing size from anterior to posterior, and show morphological differentiation in *Sinoburius lunaris* (exopod and endopod podomere number varied towards the posterior of the body). The

cephalic appendages of these animals may be adapted for gathering food around the head shield or delivering food transmitted from the trunk appendages. These appendages are not strong, and their functions do not seem to be closely related to predation.

Trunk appendages

Trunk limbs

Trunk appendages are typically of two types in arthropods, uniramous and biramous (Boxshall, 2004; Zhang and Briggs, 2007; Briggs et al., 2012). The majority of known trunk appendages in arthropods are biramous (Hou and Bergström, 1997; Hou et al., 2017). *Misszhouia longicaudata* and *Cindarella eucalla* have biramous appendages with similar morphology, though their descriptions are not identical (Chen et al., 1996; Hou and Bergström, 1997; Zhang and Briggs, 2007; Hou et al., 2017). These biramous appendages consist of a protopodite, an endopod with six podomeres and clusters of spines, an exopod with a shaft fringed by lamellae and a distal large lamella with marginal setae (Figures 3 D; 4; 5 A, C, D; 6 C; 8 B, C, D; SFigure 5 B, D in this study; Figures 4, 5, 8, 9–13 in Chen et al., 1997). phylogenetic analyses indicates that trunk appendages of some trilobites possess gnathobase at their base, an endopod with clusters of spines on its podomeres, and a forked terminal claw (Whittington, 1980; Fortey, 2014). These trilobite appendages likely functioned as a food sorting device, with the gnathobase and clusters of spines on the endopod podomeres forming a food groove that propelled food forward to the cephalic appendages, which then passed the food to the mouth (Fortey and Owens, 1999). The gnathobase of *Cindarella eucalla* appears to be less robust than that of *Limulus polyphemus* or *Sidneyia inexpectans* (Bicknell et al., 2018). Differences in the trunk endopod of *Xandarella spectaculum*, *Cindarella eucalla*, and *Luohuilinella deletres* mainly involve the number of podomeres, the presence of endites and gnathobase. Several studies suggest that these flap-like structures in horseshoe crabs can be used for respiration (Gray, 1957; Henry et al., 1996; Suzuki et al., 2008). The trunk endopods of *Cindarella eucalla* and *Luohuilinella deletres* are relatively strong, and no distinct gnathobase has been observed in available material, but there are clusters or pairs of spines on the endopod segments (Figure 3 D; 4 D; 5 B, C; 6 B). Each endopod podomere of *Cindarella eucalla* possesses a cluster of spines, while each endopod podomere of *Luohuilinella deletres* may bear one or a pair of sharp spines, and no gnathobase or spines on endopod podomeres have been observed in *Sinoburius lunaris* (Hou et al., 2018; Chen et al., 2019). The clustered spines on the endopod podomeres of *Cindarella eucalla* presumably enhance walking, cleaning, and stirring the muddy bottom to facilitate food sorting before transportation to the mouth. The paired or single spines on the endopod podomeres of *Luohuilinella deletres* may not be highly effective for cleaning and stirring the muddy bottom, but they can still grasp food and transport it to the mouth. *Cindarella eucalla* likely lives in muddy environments with abundant sedimentation and engage in predation or scavenging from this perspective. *Luohuilinella deletres* and *Sinoburius lunaris* inhabit sediment-poor or non-sediment environments and do not engage in predation or scavenging.

Exite

Epipodite is a lateral outgrowth on the base of protopodite in crustacean, typically found on the post-maxillary trunk limbs in branchiopods and on the thoracopods (maxillipeds and pereopods) in Malacostraca (Minelli et al., 2013). This structure is rare in other arthropods except for crustaceans and pancrustaceans, making it considered as a unique feature of crustacean appendages (Zhang et al., 2007; Eoff et al., 2009; Zhai et al., 2019b). However, Liu et al. (2021) reported the presence of exites in Megachyerians (*Leanchoilia illecebrosa*, *Leanchoilia obesa*) and Arthropods (*Naraoia spinosa*, and *Retifacies abnormalis*). Based on the similar morphology of exite and its position on the protopodite, the authors suggested that exite in these groups is homologous to epipodite of crustaceans (Liu et al., 2021), thereby tracing the origin of

this structure back to earlier than the origin of crustacean appendages. *Cingdarella eucalla* has a small rod-shaped exite (**Figure 3** [D](#), [4 E](#)). The presence of exite in *Cindarella eucalla* supports this view.

Segmental mismatch

The mismatch of the posterior trunk tergites and ventral limbs in this species differs from that of Fuxianhuiids (each tergite covers two to four appendage pairs in opisthothorax of *Fuxianhuia protensa* Hou, 1987, *Chengjiangocaris longiformis* Hou & Bergström, 1991), other Artiopods (One of the thoracic tergites covers two appendage pairs in *Sinoburius lunaris* Hou, Ramsköld & Bergström, 1991; The last four tergites cover two, three, five, twelve appendage pairs respectively in *Xandarella spectaculum* Hou, Ramsköld & Bergström, 1991), and various forms of segmental mismatch in most extant arthropods (Hou et al., 1991 [B](#); Hou, 1987; Hou and Bergström, 1997 [B](#); Luo et al., 1997 [B](#); Hou et al., 1999 [B](#); Chen, 2004 [B](#); Hou et al., 2004 [B](#); Minelli et al., 2013 [B](#); Hou et al., 2017 [B](#); Chen et al., 2019 [B](#); Schmidt et al., 2021 [B](#)).

Phylogenetic analysis

The maximum parsimony (equal weight) analysis resolved Xandarellida a sister-group to a clade comprising Nektaspida + (Conciliterga + (Trilobita + phytophilaspis pergamena)), the position of *Cindarella eucalla* was recovered as the earliest branch of *Xandarella spectaculum* + (*Zhugeia actica data* + *Sinoburius lunaris*) (**Figure 9** [A](#)).

Implied weights ($k = 3, 4, 5, 10$) consistently recovered Conciliterga a sister-group of Xandarellids (**Figure 9** [B](#), [C](#)), which is distinct with other analyses of Artiopoda (Chen et al., 2019 [B](#); Du et al., 2019 [B](#); Mayers et al., 2019 [B](#); Berks et al., 2023 [B](#); Zhu et al., 2023 [B](#)). And *Cindarella eucalla* was resolved as part of a clade alongside *Xandarella spectaculum* and *Sinoburius lunaris* (**Figure 9** [B](#), [C](#)). This is distinguished from most previous researches primarily, especially these published in recent years based on updated character matrix (Ortega-Hernández et al., 2013 [B](#); Chen et al., 2019 [B](#); Du et al., 2019 [B](#); Mayers et al., 2019 [B](#); Berks et al., 2023 [B](#); Zhu et al., 2023 [B](#)). In previous studies, Xandarellids were generally resolved as part of a clade alongside *Luohuilinella deletres* and *Luohuilinella ramus*, or as sister-group to *Luohuilinella* when maximum parsimony analysis was performed (Chen et al., 2019 [B](#); Du et al., 2019 [B](#); Mayers et al., 2019 [B](#); Berks et al., 2023 [B](#); Zhu et al., 2023 [B](#)).

Bayesian inference produced a less resolved overall topology for Artiopoda, but provided a support for the clade of Xandarellida (**Figure 9** [D](#)). Here, *Cindarella eucalla* also forms a clade with *Xandarella spectaculum*, *Luohuilinella deletres*, *Luohuilinella ramus*, and a clade comprising *Zhugeia actica data* and *Sinoburius lunaris*.

The analyses indicate that Xandarellida consists of at least six reported species, including *Cindarella eucalla*, *Xandarella spectaculum*, *Luohuilinella deletres*, *Luohuilinella ramus*, *Sinoburius lunaris* and *Zhugeia actica data*. Xandarellids, Conciliterga, Trilobita, Nektaspida, *phytophilaspis pergamena* and *Tonglailia bispinosa* form a relative stable clade in both equal weight and implied weight of the maximum parsimony analyse (**Figure 9** [A](#), [B](#), [C](#)).

Ecology

The dorsal exoskeleton indicates that *Cindarella eucalla* could not serve a suspension-feeding. It has large compound eyes and could be a predator or not. The natant hypostome is not helpful for predation, but probably indicates detritivorous habit similar to trilobites with natant hypostome (Fortey and Owens, 1999 [B](#)). The strong trunk endopods with clusters of spines suggest a mud-rich living environment and efficient movement in life.

Conclusions

Almenia spinosa is synonymous with *Xandarella spectaculum*, not *Cindarella eucalla*. This research elucidated the ventral organization of *Cindarella eucalla*, including its anterior sclerite, appendage morphology, axial spines and segmental mismatch, with the employment of X-ray computed tomography. It may live a particle diet in muddy environment with ample light, and can survive from large predators by escaping with fast movement. Similarly, other xandarellids likely subsist on particle diet, albeit in distinct environments. This animal might not be close to *Luohuilinella*, and Xandarellids may have closer relationships with *Concilliterga* than other artiopods.

Methods

Materials

17 specimens of *Cindarella eucalla* deposited at the Yunnan Key Laboratory for Palaeobiology, Yunnan University were collected in this study. All specimens were collected from the following places: Haikou, Jinning and Anning in Kunming. They stratigraphically belong to the *Eoredlichia-Wutingaspis* biozone of Yu'an-shan Member, Chiungchussu Formation (Cambrian Series 2, Stage 3).

Observation and documentation

Macrophotography was captured in Canon EOS 5DS R camera (DS126611, Canon Inc., Tokyo, Japan) with MACRO PHOTO LENS MP-E 65 mm, with directional illumination provided by a LEICA LED5000 MCITM (Leica Microsystems, Wetzlar, Germany) (**Figures 1** [A, B, D](#); **6 A**; **7 A, C**; **SFigures 1** [A, B, D](#); **2**; **4 A, C**; **5 A, C**). Fluorescence microscopic images were photographed with a Leica DFC7000T CCD linked to a Leica M205 FA fluorescent microscope (Leica Microsystems, Wetzlar, Germany) (**Figures 1** [C](#); **SFigures 4** [B, D](#); **5 B, D**). All Images were processed and arranged into figures with Adobe Photoshop CC 2018.

X-ray computed tomography and 3D rendering

X-ray computed tomography were performed on a Zeiss Xradia 520 Versa (Carl Zeiss X-ray Microscopy, Inc., Pleasanton, CA, USA) at the Yunnan Key Laboratory for Palaeobiology, Institute of Palaeontology, Yunnan University, Kunming, China (YKLP 17369, YKLP 17370, YKLP 17361 and YKLP 17371). All TIFF stacks were processed with software Drishti (Version 2.4) to enable digital dissections of various structures (**Figures 3** [A–C](#); **5** [A, B, C](#); **6 B, C**; **7 B, D**).

3D modelling

Complete 3D models of *Cindarella eucalla* (**Figure 8** [A](#)) were reconstructed in Blender 2.9 by starting with basic meshes such as spheres and cubes, then refining their shapes using the sculpting tool.

Phylogenetic analysis

The character matrix employed in the phylogenetic analyses encompasses 71 taxa and 93 characters, as detailed in the character matrix. This study utilizes an updated iteration of the dataset previously employed by Zhang et al. (2022) [A](#), incorporating additional information in this study and six species that have been recently documented by Berks et al. (2023) [A](#) and Zhu et al. (2023) [A](#). Parsimony analyses were run in TNT1.5 under New Technology Search, using Driven Search with Sectorial Search, Ratchet, Drift and Tree fusing options activated with standard

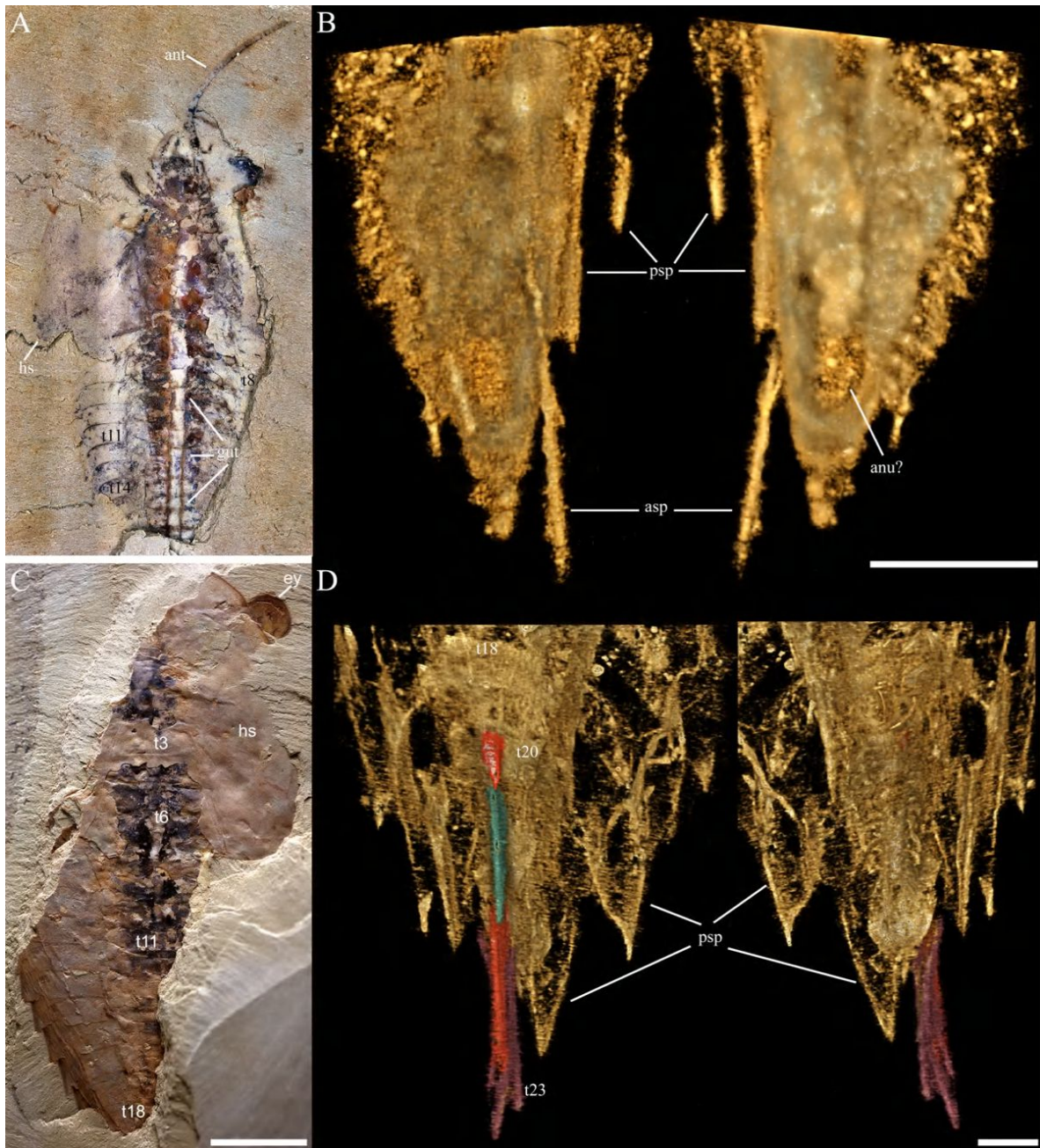


Figure 7.

Macro-photographic picture (A, C) and results from X-ray tomographic data processed in Drishti v2.4 (B, D). A Overview of YKLP 17370, dorsal view. B Dorsal (left) and ventral (right) views of the posterior trunk in A hide in the rock. C Overview of YKLP 17371, dorsal view. D Dorsal (left) and ventral (right) views of posterior trunk in C hide in the rock. Abbreviations: ant, antenna(e); anu?, putative anus; asp, axial spine(s); Cn, post-antennal cephalic appendage number; ey, eye(s); gut, gut content/trace; hs, head shield; psp, pleural spine(s); Tn, tergite number. Scalebar: 1 cm in C, 2 mm in A, 1 mm in B and D.

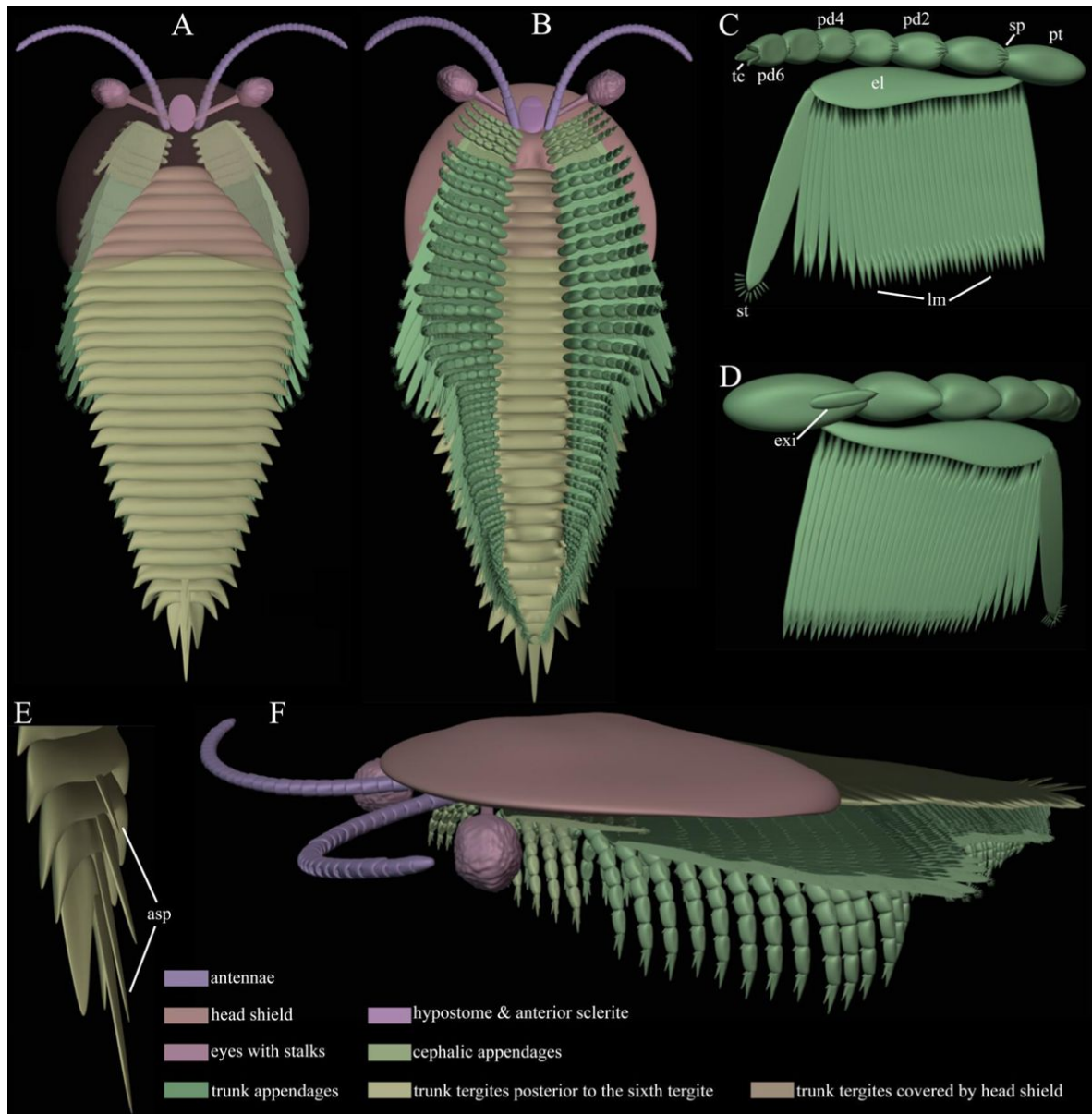


Figure 8.

Three-dimensional Blender model of *Cindarella eucalla*. A Overview in dorsal view with the head shield transparent. B Overview in ventral view. C Biramous appendage in ventral view. D Biramous appendage in ventral view. E Last four trunk tergites with axial spines in antero-lateral oblique view. F Overview in lateral left view. Not to scale.

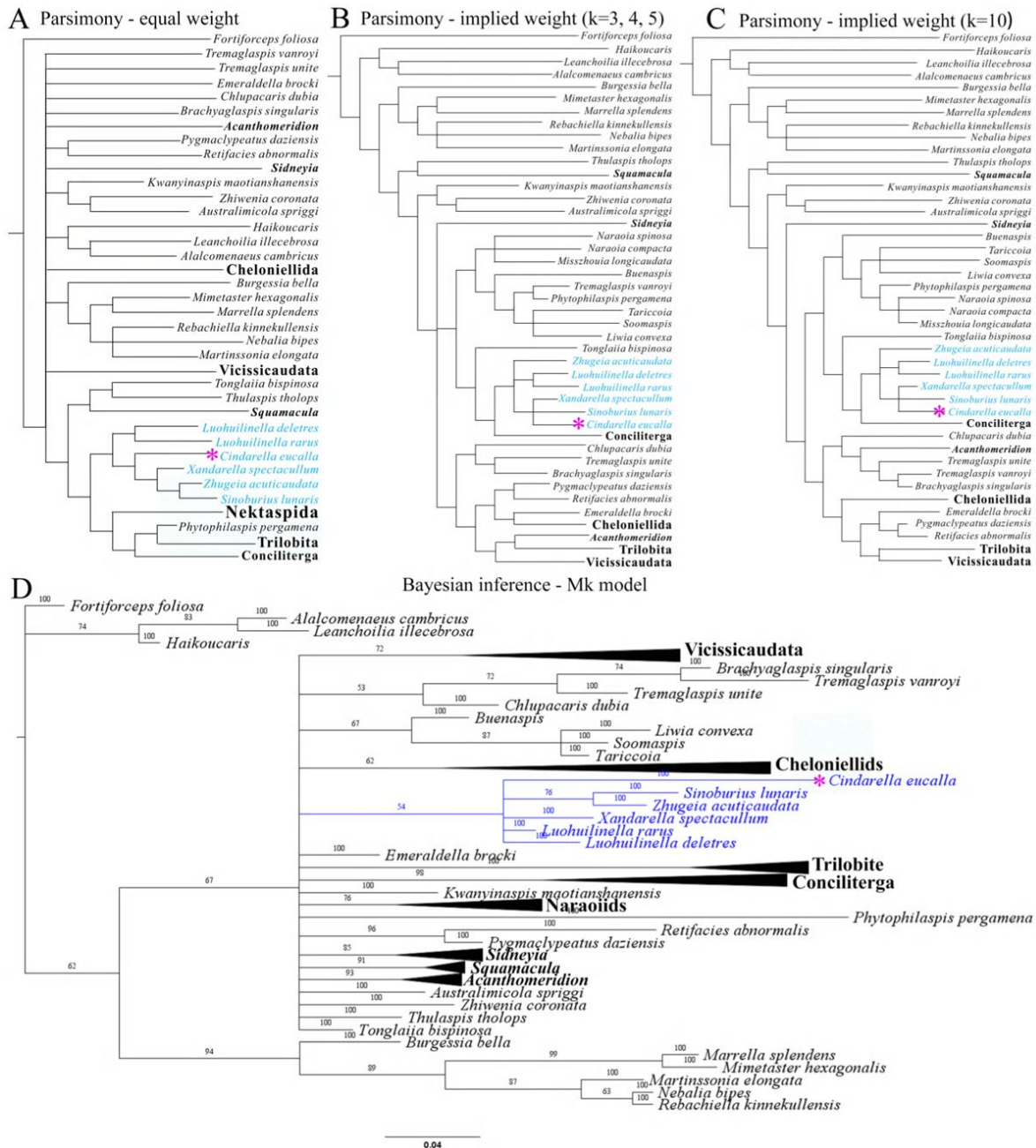


Figure 9.

Results of parsimony and Bayesian phylogenetic analyses. All trees depict a strict consensus. Multiple species within the same genus are indicated as a single genus and marked in bold, Xandarellids are in blue, purple asterisks indicate *Cindarella eucalla*. A Equal weight parsimony, 159 most-parsimonious trees, 274 steps, consistency index (CI) = 0.391, retention index (RI) = 0.712. B Implied weight parsimony, k = 3, 4, 5, 281 steps, CI = 0.381, RI = 0.700. C Implied weight parsimony, k = 10, 40 most-parsimonious trees, 276 steps, CI = 0.388, RI = 0.709. D MrBayes. Setting: Mk model, four runs, 10 000 000 generations, 1/1000 sampling resulting in 10 000 samples, 25% burn-in resulting in 7500 samples retained. **Figure 9—figure supplement 1**. Strict consensus trees from parsimony analyses on Artiopoda showing common synapomorphies mapped. The numbers 0 to 92 below the branches represent 93 characters sequentially used for phylogenetic analysis. A Equal weight, 159 trees, CI=0.391, RI=0.712, 274steps. B Implied weight, k=3, 43 trees, CI=0.381, RI=0.700, 281 steps. C Implied weight, k=10, 40 trees, CI=0.388, RI=0.709, 276steps.

settings (Goloboff, 1999 [↗](#); Goloboff et al., 2008 [↗](#); Goloboff and Catalano, 2016 [↗](#); Nixon, 1999 [↗](#)). The analysis was set to find the minimum tree length 100 times. All characters were treated as unordered. For comparative purposes, analyses were performed under equal (EW) and implied weights (IW; $k = 3, 4, 5, 10$) to test the effect of homoplasy penalization on the position of *Cindarella eucalla* and the robustness of the dataset. Bayesian analysis was run in MrBayes 3.2 using the Monte Carlo Markov chain model for discrete morphological characters.

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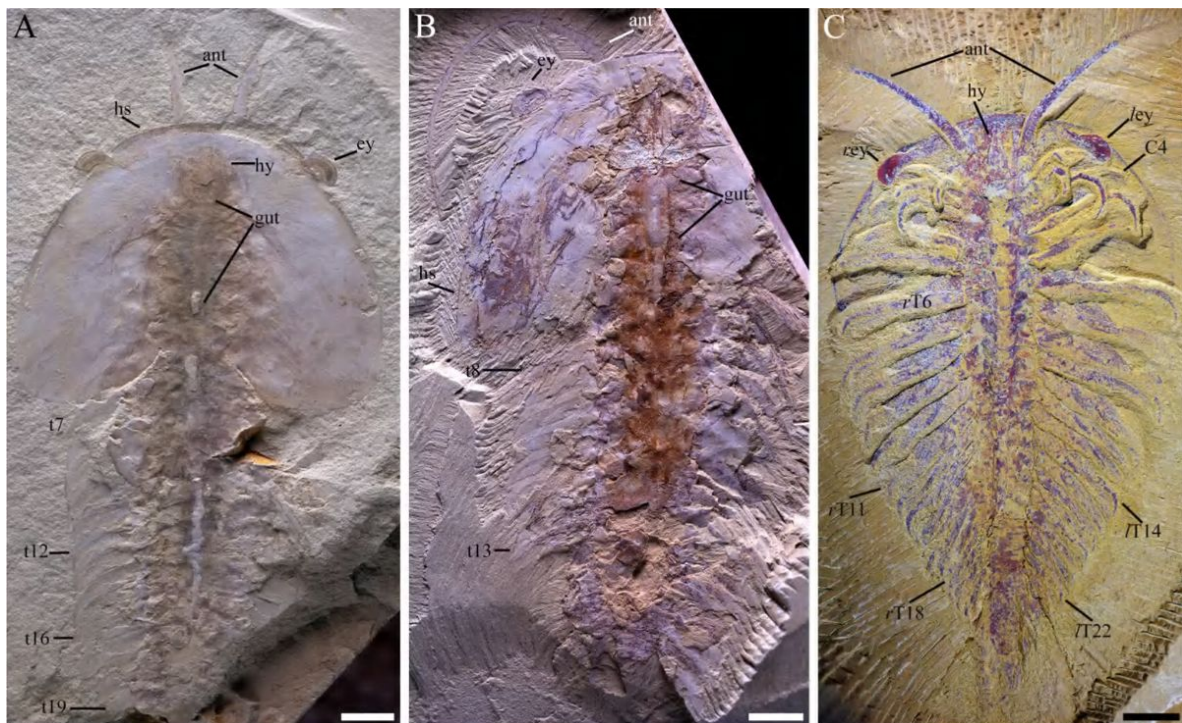


Figure 1—figure supplement 1.

Macro-photographic images of *Cindarella eucalla*. A Dorsal view of YKLP 17363b. B Dorsal view of YKLP 17364. C Dorsal view of YKLP 17375. Abbreviations: ant, antenna(e); Cn, post-antenna cephalic appendage number; ey, eye(s); gut, gut content/trace; hs, head shield; tn, tergite number; r, right; l, left. Scalebar: 5 mm.

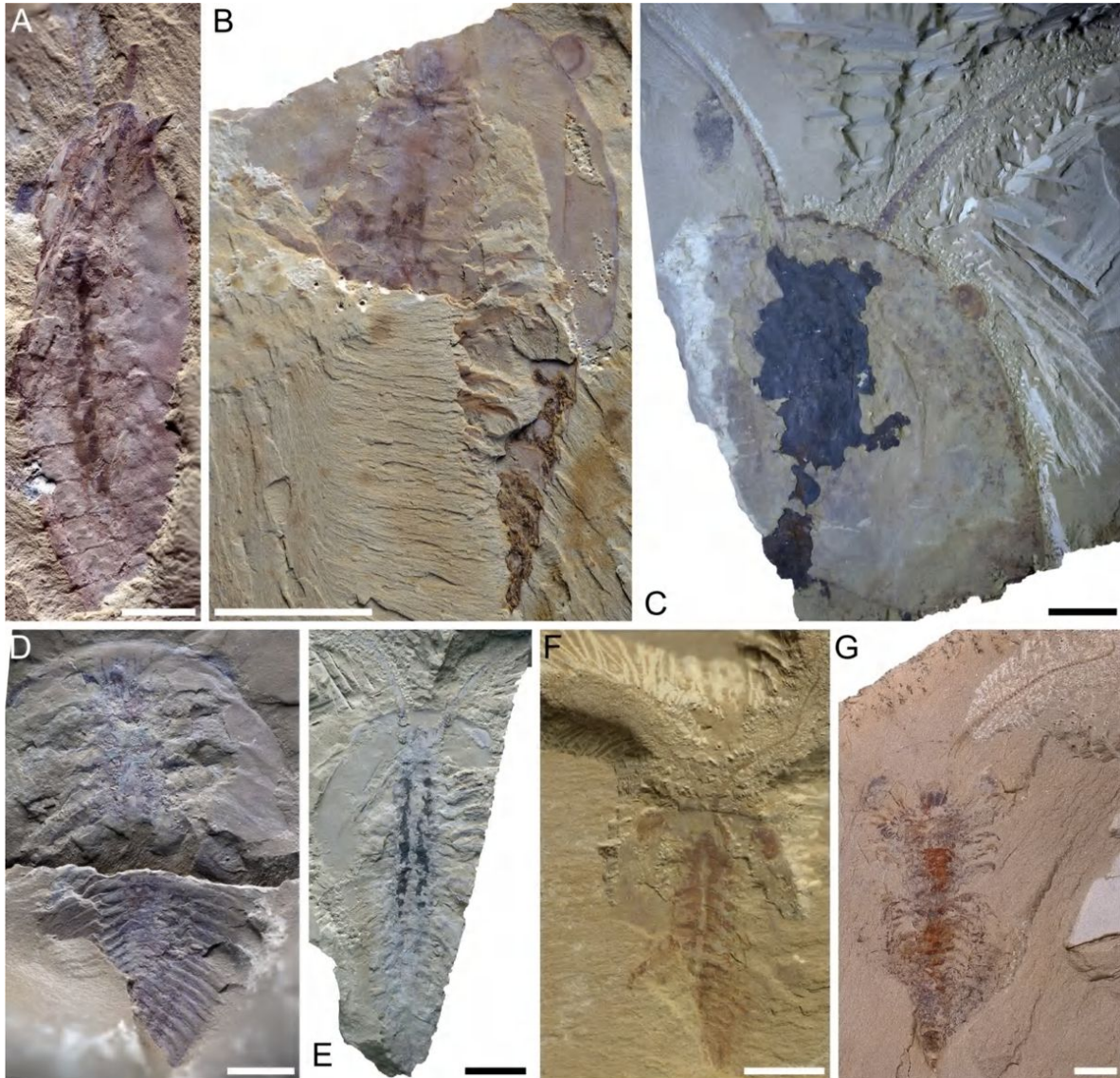


Figure 2—figure supplement 1.

Head shield and eyes of *Cindarella eucalla*. A YKLP 17366, Dorsal view. B YKLP 17368, dorsal view. C YKLP 17367, dorsal view. D YKLP 17365, dorsal view. E YKLP 17376, dorsal view. F YKLP 17373, dorsal view. G YKLP 17372, dorsal view. Scalebar: 2 mm in G, 5 mm in A, D and F, 1 cm in B, C and E.



Figure 2—figure supplement 2.

Outline of head shield (half) and eyes in *Cindarella eucalla* specimens. Gray area indicates head shield, dashed line indicates putative head shield, deep purple indicates eye, dotted area indicates putative eye. A YKLP 17371. B YKLP 17368. C. YKLP 17366. D YKLP 17362 (flipped horizontal). E YKLP 17367. F YKLP 17376 (flipped horizontal). G YKLP 17365. H YKLP 17373. I YKLP 17372 (flipped horizontal). Not to scale.

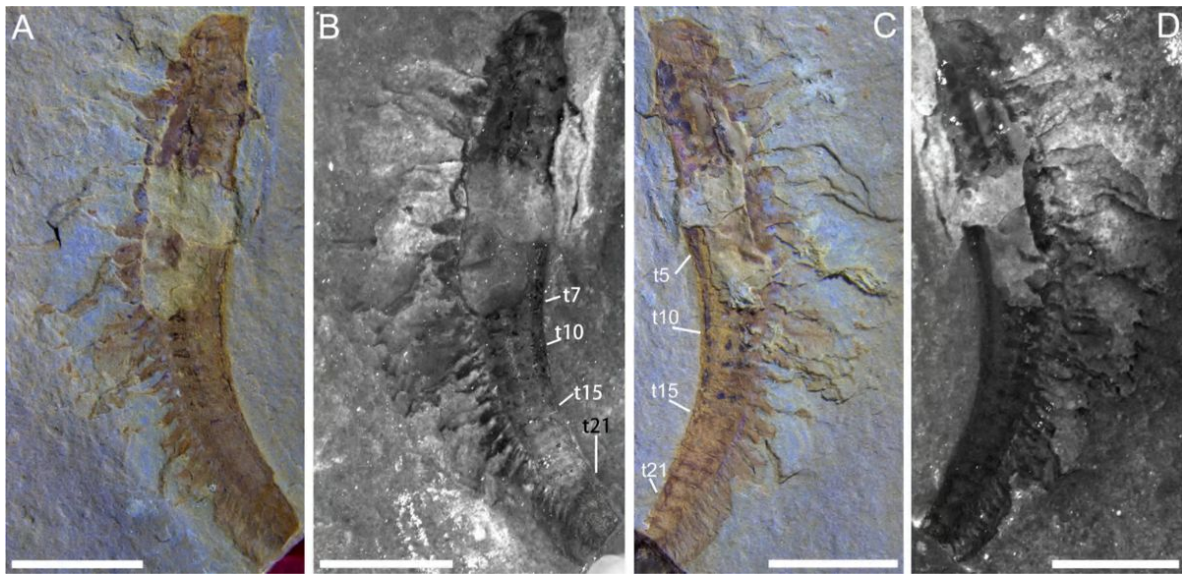


Figure 3—figure supplement 1.

Macro-photographic (A and C) and fluorescent (B and D) images of *Cindarella eucalla* (YKLP 17369). A and B YKLP 17369a, dorsal view. C and D YKLP 17369b. Abbreviations: *tn*, tergite number. Scalebar: 5 mm.



Figure 4—figure supplement 1.

Macro-photographic (A, C) and fluorescent (B, D) images of *Cindarella eucalla* (YKLP 17369). A YKLP 17374, dorsal view. B close-up of trunk appendages within the dashed box in A. C YKLP 17362, dorsal view. D close-up of a trunk exopod within the dashed box in C. Abbreviations: el, exopod lobe/shaft; ey, eye; hs, head shield; lm, lamella(e); Tn, trunk appendage number; tn, Tergite number; l, left; r, right. Scalebar: 1 cm in A, 5 mm in C, 2 mm in B, 1 mm in D.

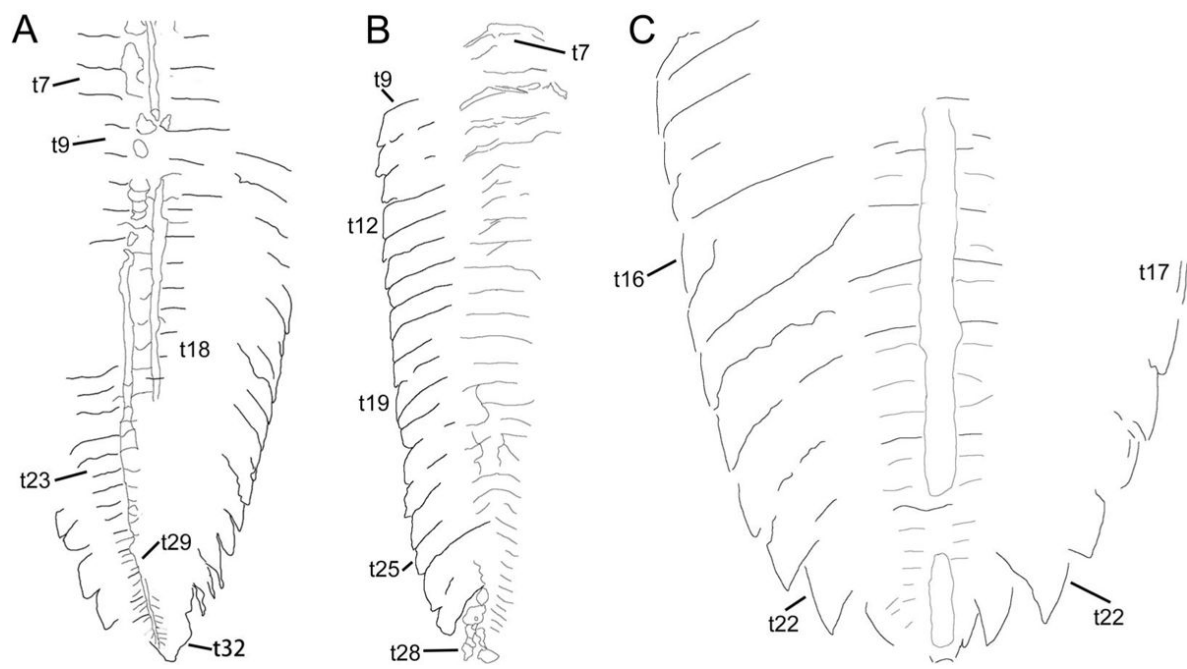


Figure 6—figure supplement 1.

Outline of trunk tergites and ventral segments (gut trace or appendage boundaries). A YKLP 17361. B YKLP 17362. C ELRC 18505. Abbreviations: *tn*, tergite number. Scalebar: not to scale.

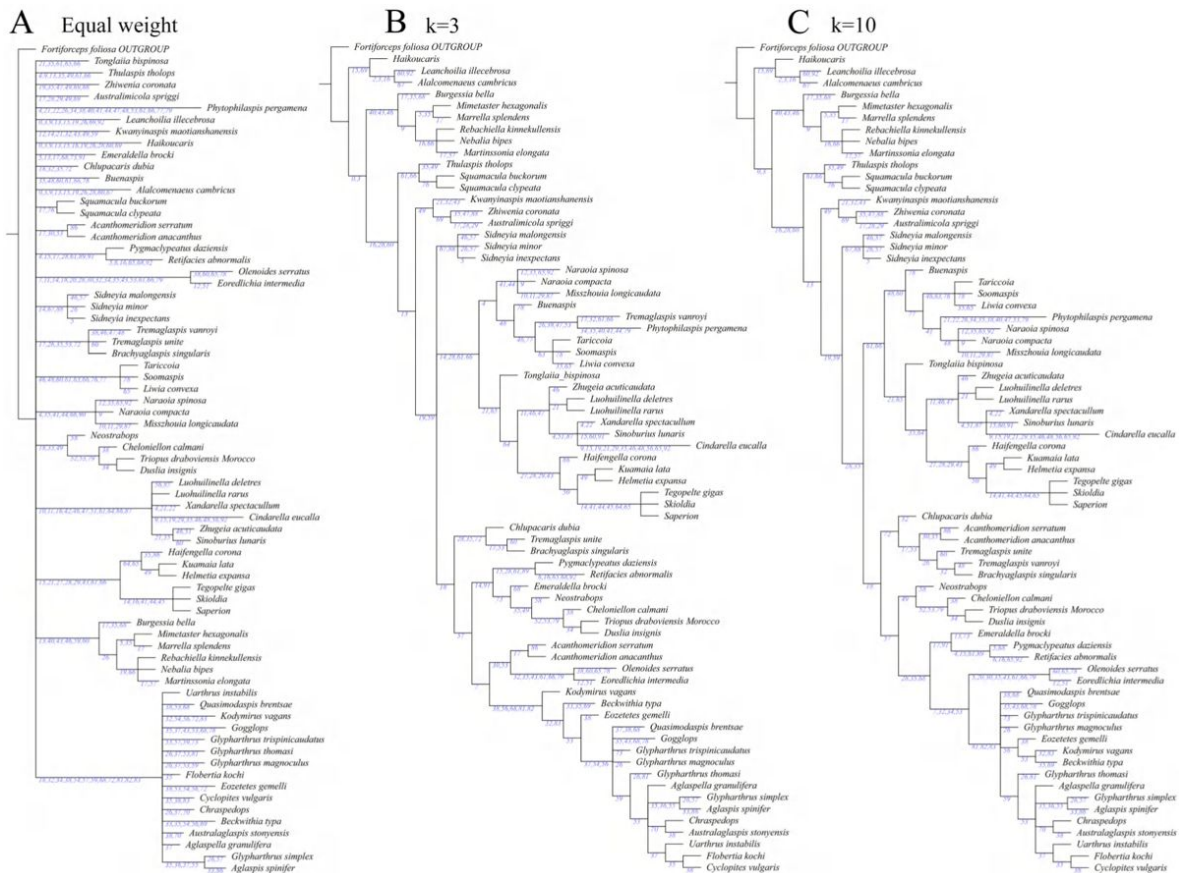


Figure 9—figure supplement 1.

Strict consensus trees from parsimony analyses on Artipoda showing common synapomorphies mapped. The numbers 0 to 92 below the branches represent 93 characters sequentially used for phylogenetic analysis. A Equal weight, 159 trees, CI=0.391, RI=0.712, 274steps. B Implied weight, k=3, 43 trees, CI=0.381, RI=0.700, 281 steps. C Implied weight, k=10, 40 trees, CI=0.388, RI=0.709, 276steps.

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Zhu Y, Zeng H, Liu Y, Zhao F (2023) **New Artiopodan Euarthropods from the Chengjiang Fauna (Cambrian Stage 3) at Malong, Yunnan, China** *Acta Palaeontologica Polonica* **68** <https://doi.org/10.4202/app.01080.2023>

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Reviewer #1 (Public review):

Summary:

The manuscript by Zhang et al. analyzed 17 specimens of *Cindarella eucalla* with 3D technology and discussed the anatomical findings, the relationship to other artiopods, and the ecology of the animal. The results are excellent and the findings are very interesting. However, the discussion needs to be extended, as the point the authors are trying to make is not always clear. I also recommend some restructuring of the discussion. Overall this is an important manuscript, and I'm looking forward to reading the edited version.

Strengths:

The analyses, the 3D data is excellent and provides new information.

Weaknesses:

The discussion - the authors provide information for the findings, but do not discuss them in detail. More information is needed.

<https://doi.org/10.7554/eLife.100729.1.sa3>

Reviewer #2 (Public review):

Summary:

Zhang et al. present very well-illustrated specimens of the artiopodan *Cinderella eucalla* from the Chengjiang Biota. Multiple specimens are shown with preserved appendages, which is rare for artiopodans and will greatly help our understanding of this taxon. The authors use CT scanning to reveal the ventral organization of this taxon. The description of the taxon needs some modification, specifically expansion of the gut and limb morphology. The conclusion that *Cinderella* was a fast-moving animal is very weak, comparisons with extant fast animals and possibly FEA analyses are necessary to support such a claim. Although the

potential insights provided by such well-preserved fossils could be valuable, the claims made are tenuous and based on the available evidence presented herein.

Strengths:

The images produced through CT scanning specimens reveal the very fine detail of the appendages and are well illustrated. Specimens preserve guts and limbs, which are informative both for the phylogenetic position and ecology of this taxon. The limbs are very well preserved, with protopodite, exopodite, and endopodites visible. Addressing the weaknesses below will make the most of this compelling data that demonstrates the morphology of the limbs well.

Weaknesses:

Although this paper includes very well-illustrated fossils, including new information on the eyes, guts, and limbs of *Cinderella*, the data are not fully explained, and the conclusions are weakly supported.

The authors suggest the preservation of complex ramifying diverticular, but it should be better illustrated and the discussion of the gut diverticulae should be longer, especially as gut morphology can provide insights into the feeding strategy.

The conclusion that *Cinderella eucalla* was fast, sediment feeding in a muddy environment, is not well supported. These claims seem to be tenuously made without any evidence to support them. The authors should add a new section in the discussion focused on feeding ecology where they explicitly compare the morphology to suspension-feeding arthropods to justify whether it fed that way or not. To further explore feeding, the protopodite morphology needs to be more carefully described and compared to other known taxa. The function of endites on the endopodite to stir up sediment for particle feeding in a muddy environment would also need to be more thoroughly discussed and compared with modern analogs. The impact of their findings is not highlighted in the discussion, which is currently more of a review of what has been previously said and should focus more on what insights are provided by the great fossils illustrated by the authors.

The authors argue that their data supports fast escaping capabilities, but it is not clear how they reached that conclusion based on the data available. Is there a way this can be further evaluated? The data is impressive, so including comparisons with extant taxa that display fast escaping strategies would help the authors make their case more compelling. The authors also claim that the limbs of *Cinderella* are strong, again this conclusion is unclear. Comparison with the limbs of other taxa to show their robustness would be useful. To actually test how these limbs deal with the force and strain applied to them by a sudden burst of movement, the authors could conduct Finite Element Analyses.

<https://doi.org/10.7554/eLife.100729.1.sa2>

Reviewer #3 (Public review):

This paper provides an interesting description of the ventral parts of the Cambrian xandarellid *Cindarella eucalla*, derived from exceptionally preserved specimens of the Chengjiang Biota. These morphological data are useful for our broad understanding and future research on Xandarellida, and are generally well-represented in the description and accompanying figures. The strengths of this work rest in this morphological description of exceptional fossil material, and this is generally well supported. In addition, the authors put this description in the context of the morphology of other xandarellids and Cambrian arthropod groups, with most of these parallels being useful and reasonably supported, though in several places homology is assumed and this currently lacks evidence. The

manuscript goes on to use these morphological data and comparisons to other groups (particularly trilobites) to make suggestions for the ecology of *Cindarella eucalla* and other xandarellids. The majority of my comments on this work relate to this latter aim - the ecological conclusions drawn are generally derived through morphological comparisons, where a specific morphology has been suggested as an adaption to a particular ecological function in another extinct arthropod group. However, the original suggestions for ecological function are untested, and so remain hypotheses. Despite this, they are frequently presented as truisms to enable ecological conclusions to be drawn for *Cindarella eucalla*. I have listed my comments and queries on the study below for the authors to address or respond to, and I hope they are useful to the authors.

Comments:

There are a number of ecological and functional morphology conclusions stated that seem put too strongly to be considered sufficiently supported by the evidence given. These relate to both the description of *C. eucalla*, and comparisons to other extinct arthropod taxa (notably trilobites). Many of these latter statements are assumptions of functional morphology, and should not be repeated as truisms, rather than they represent suggested functions and ecologies based on the known morphological descriptions. This aspect occurs throughout the article, and, for me, is the primary concern.

<https://doi.org/10.7554/eLife.100729.1.sa1>

Author response:

Reviewer #1 (Public review):

Summary:

The manuscript by Zhang et al. analyzed 17 specimens of Cindarella eucalla with 3D technology and discussed the anatomical findings, the relationship to other artiopods, and the ecology of the animal. The results are excellent and the findings are very interesting. However, the discussion needs to be extended, as the point the authors are trying to make is not always clear. I also recommend some restructuring of the discussion. Overall this is an important manuscript, and I'm looking forward to reading the edited version.

Strengths:

The analyses, the 3D data is excellent and provides new information.

Weaknesses:

The discussion - the authors provide information for the findings, but do not discuss them in detail. More information is needed.

We are committed to enhancing the quality of our manuscript further and, in response to your comments, will implement the following improvements:

- (1) Comparative Analysis of Eyes: We will expand our discussion to include a detailed comparative analysis of the eyes of *Cindarella eucalla* with those of other artiopods (e.g. Xandarellids, trilobites, living insects), focusing on morphology, size, and other relevant characteristics.
- (2) Segmental Mismatch Discussion: We will provide an in-depth exploration of the specifics and significance of the segmental mismatch to offer a clearer understanding of its

implications. We will also compare the characteristics of this mismatch in our focal species with those observed in extant arthropods, such as spiders and myriapods. This comparison will be further enriched by integrating our phylogenetic analysis, thereby providing a broader evolutionary context.

(3) Methodological Clarity: We will provide more detailed information on the parameters used for the analyses in the Methods section, especially the phylogenetic sections and the X-ray tomography section.

(4) Phylogenetic Analysis: We will engage in a more in-depth discussion of certain characters (e.g. anterior sclerite, hypostome, endopodite, segmental mismatch, etc.) within our phylogenetic analyses to clarify their relevance and contribution to our findings.

Reviewer #2 (Public review):

Summary:

Zhang et al. present very well-illustrated specimens of the artiopodan Cinderella eucalla from the Chengjiang Biota. Multiple specimens are shown with preserved appendages, which is rare for artiopodans and will greatly help our understanding of this taxon. The authors use CT scanning to reveal the ventral organization of this taxon. The description of the taxon needs some modification, specifically expansion of the gut and limb morphology. The conclusion that Cinderella was a fast-moving animal is very weak, comparisons with extant fast animals and possibly FEA analyses are necessary to support such a claim. Although the potential insights provided by such well-preserved fossils could be valuable, the claims made are tenuous and based on the available evidence presented herein.

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previously said and should focus more on what insights are provided by the great fossils illustrated by the authors.

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Here are the key points we plan to address:

- (1) Gut and Limb Morphology: We will expand our description of the gut and limb morphology of *C. eucalla*, providing a more detailed comparison and analysis. This will include a revised discussion on the function and ecological implications of these features.
- (2) Fast-Moving Animal Claim: We acknowledge your concern about the conclusion that *C. eucalla* was a fast-moving animal. We will conduct a more detailed comparison among *C. eucalla* and other Cambrian arthropods and living arthropods, focusing on morphological and functional aspects. We will also reconsider our claim and will be more cautious in our conclusions. If the comparison proves insufficient, we will remove this assertion from the manuscript. But we may no longer conduct Finite Element Analysis, as a comprehensive and cautious analysis would require a massive project to complete.
- (3) Sediment Feeding in a Muddy Environment: We will revise the section discussing the feeding ecology of *C. eucalla*. We will enhance this section by comparing the morphology of *C. eucalla* to that of suspension-feeding arthropods, which will help to substantiate our claims. Additionally, we will expand the discussion to include a more detailed examination of endites, gnathobases, and other relevant anatomical structures.
- (4) Impact of Findings: We will endeavor to highlight the impact of our findings in the discussion, focusing on the insights provided by the well-preserved fossils illustrated in our study.

Reviewer #3 (Public review):

This paper provides an interesting description of the ventral parts of the Cambrian xandarellid Cinderella eucalla, derived from exceptionally preserved specimens of the Chengjiang Biota. These morphological data are useful for our broad understanding and future research on Xandarellida, and are generally well-represented in the description and accompanying figures. The strengths of this work rest in this morphological description of exceptional fossil material, and this is generally well supported. In addition, the authors put this description in the context of the morphology of other xandarellids and Cambrian arthropod groups, with most of these parallels being useful and reasonably supported, though in several places homology is assumed and this currently lacks evidence. The manuscript goes on to use these morphological data and comparisons to other groups (particularly trilobites) to make suggestions for the ecology of Cinderella eucalla and other xandarellids. The majority of my comments on this work relate to this latter aim - the ecological conclusions drawn are generally derived through morphological comparisons, where a specific morphology has been suggested as an adaption to a particular ecological function in another extinct arthropod group. However, the original suggestions for ecological function are untested, and so remain hypotheses. Despite this, they are frequently presented as truisms to enable ecological conclusions to be drawn for Cinderella eucalla. I have listed my comments and queries

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We plan to address the following points in upon revision:

- (1) Homology Assumptions: You pointed out that we have assumed homology in certain instances without sufficient evidence. We will revise the manuscript to include a more detailed analysis of the anterior sclerite and exite, considering phylogenetic relationships and morphological comparisons to provide a more robust discussion.
- (2) Ecological and Functional Morphology: We acknowledge that our conclusions regarding the ecological function were presented with too much certainty. We will adopt a more cautious approach in our discussion, ensuring that our ideas are clearly labeled as such and are supported by a comparison of relevant studies on Cambrian arthropods and extant arthropods, including fluid dynamics, functional morphology, etc. We will re-evaluate the ecological function section, and if it does not add value and clarity to the manuscript—our speculations do not contribute to the understanding of the specimen or may lead to misunderstandings—we will remove the relevant parts. We believe future changes reflect a more cautious and rigorous approach to the ecological and functional interpretations of *C. eucalla*.

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