

The early Cambrian *Kuamaia lata*, an artiopodan euarthropod with a raptorial frontal appendage

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Non-technical Summary.—*Kuamaia lata*, an arthropod (jointed limbs and repeated body segments) from the Cambrian (approximately 518 million years ago) Chengjiang biota, China, belongs to a group of extinct arthropods that includes trilobites (i.e., Artiopoda). Computed tomography (CT) scans of new specimens of *Kuamaia lata* reveal a six-segmented head and predatory frontal appendages, the latter contrasting with sensory antennae considered to be a diagnostic character of Artiopoda. Evolutionary trees demonstrate that a predatory frontal appendage is ancestral for euarthropods but evolved secondarily in *Kuamaia lata* from an antenna within Artiopoda. The evolutionary position of *Kuamaia lata* adds support to a six-segmented head being ancestral for arthropods.

Abstract.—Phylogenetic analysis demonstrates that *Kuamaia lata*, a helmetiid euarthropod from the lower Cambrian (Series 2, Stage 3) Chengjiang Konservat-Lagerstätte, nests robustly within Artiopoda, the euarthropod clade including trilobitiforms. Microtomography of new specimens of *K. lata* reveals details of morphology, notably a six-segmented head and raptorial frontal appendages, the latter contrasting with filiform antennae considered to be a diagnostic character of Artiopoda. Phylogenetic analyses demonstrate that a raptorial frontal appendage is a symplesiomorphy for upper stem-group euarthropods, retained across a swathe of tree space, but evolved secondarily in *K. lata* from an antenna within Artiopoda. The phylogenetic position of *K. lata* adds support to a six-segmented head being an ancestral state for upper stem- and crown-group euarthropods.

Introduction

Helmetiidae Simonetta and Delle Cave, 1975, which are non-biomineralized Cambrian arthropods that are considered closely related to trilobites (Edgecombe and Ramsköld, 1999; Cotton and Braddy, 2004; Stein et al., 2013; Du et al., 2019), is represented by four genera (Zhao et al., 2014): *Haifengella* Zhao et al., 2014; *Helmetia* Walcott, 1918; *Kuamaia* Hou, 1987a; and *Rhombicalvaria* Hou, 1987a. *Helmetia* is known from the Burgess Shale of western Canada, and the other three genera are known from the Chengjiang Lagerstätte of southern China. Among Chengjiang arthropods, *Kuamaia lata* Hou, 1987a, is a well-documented helmetiid species (e.g., Hou, 1987a; Shu and Zhang, 1996; Hou and Bergström, 1997; Edgecombe and Ramsköld, 1999; Hou et al., 1999).

Descriptions of *Kuamaia lata* have presented inconsistencies with respect to the morphology of the anterior cephalic

appendage, and the number of head segments is undetermined. It has been noted, for example, that “tiny segments of the antennae” bear long setae and that the head shield may bear at least “three pairs of biramous limbs” (Hou et al., 2017). Alternatively, Shu and Zhang (1996), attributed a predatory function to the antennae of *K. lata*, and they bear a striking resemblance to robust frontal appendages found in *Kiisortoqia soperi* Stein, 2010, and *Bushizheia yangi* O'Flynn and Liu in O'Flynn et al., 2020 (see also Zeng et al., 2020). Indeed, *K. lata* occupies a curious position in arthropod evolution because despite its frontal appendage morphology it nests comfortably within Artiopoda Hou and Bergström, 1997—a euarthropod clade defined by the presence of filiform antennae (Stein and Selden, 2012). Microtomographic study of new specimens of *K. lata* refines and corrects previous interpretations of head structures in this species. We use new observations on the morphology of the frontal appendages and number of head segments in *K. lata* to assess the evolutionary histories of these traits across the euarthropod stem- and crown-groups.

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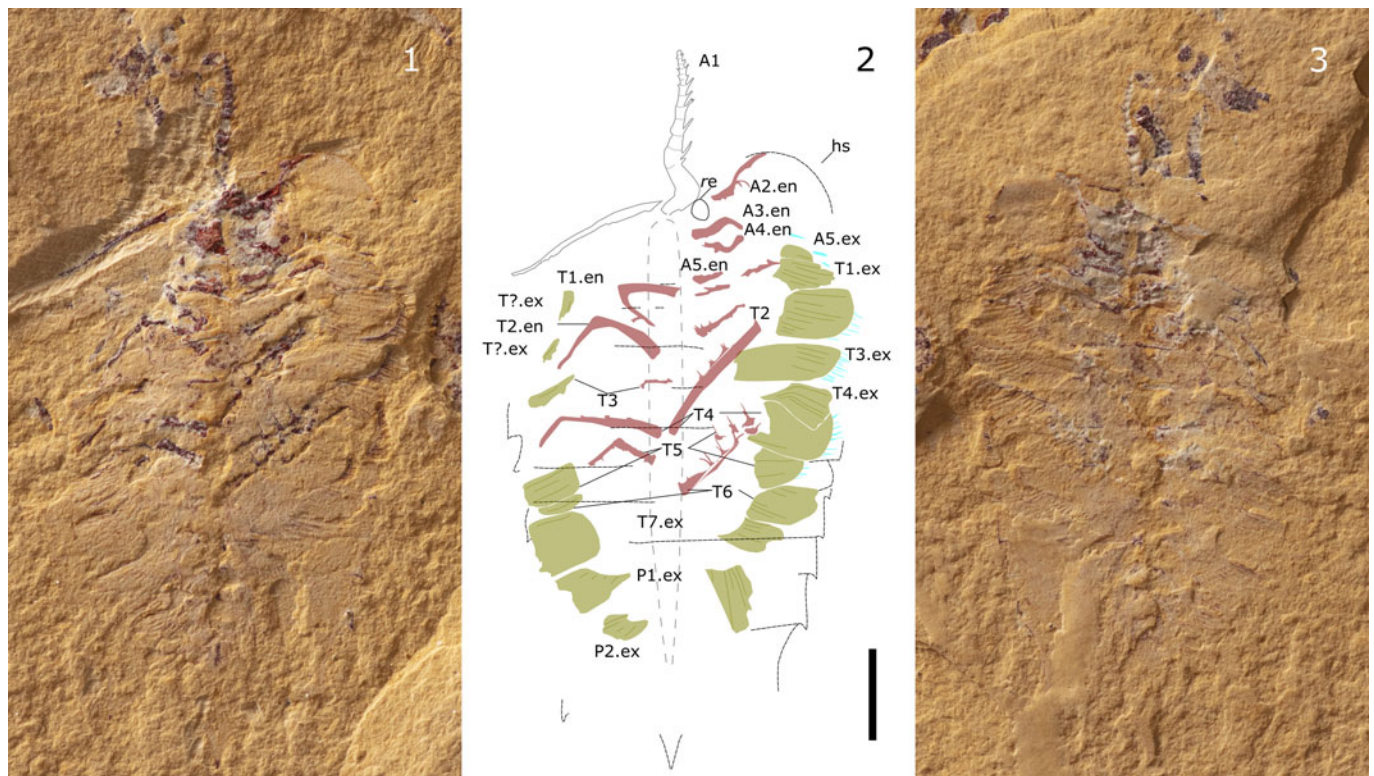


Figure 1. *Kuamaia lata* Hou, 1987a (YKLP 17295): (1) photograph of dorsal view of part; (2) composite line drawing of dorsal view; (3) photograph of dorsal view of counterpart. Abbreviations: A1 (FA) = frontal appendage; An.en = endopod of head appendage (*n*); An.ex = exopod of head appendage (*n*); re = right eye; hs = head shield; Pn.ex = exopod of pygidial appendage (*n*); Tn = thoracic appendage (*n*); Tn.en = endopod of thoracic appendage (*n*); Tn.ex = exopod of thoracic appendage (*n*). Scale bar is 2 mm.

Materials and methods

Material.—Five new specimens of *Kuamaia lata* were recovered from the Cambrian, Series 2, Stage 3, *Eoredlichia*–*Wutingaspis* trilobite biozone, Yu'an-shan Member, Chiungchussu Formation (24°41'33"N, 102°59'26"E). The specimens are deposited in the Yunnan Key Laboratory for Palaeobiology (YKLP 17295–17298) and the Chengjiang Fossil Museum of the Management Committee of the Chengjiang Fossil Site World Heritage (CJHMD 00064). When necessary, the specimens were prepared mechanically with a mounted steel needle under a binocular microscope.

Photography and CT imaging.—Several images were captured with a Digital SLR Camera (a Canon EOS 5DS R) fitted with a Canon EF 100 mm F/2.8L Macro IS USM. The photographs were mostly taken in cross-polarized light to limit reflection of light and increase contrast (Bengtson, 2000). We also captured photographs with cropped light from various angles to reveal the micro relief of the fossil. YKLP 17296, YKLP 17298, and CJHMD 00064 were also investigated with computed tomography (CT) using a ZEISS Xradia 520 Versa (beam strength: 70kV/6W, voxel size: 23.22 µm, number of TIFF images: 2834 for Fig. 2.3; beam strength: 80kV/7W, voxel size: 29.45 µm, number of TIFF images, 2765 for Fig. 4.3; beam strength: 70kV/6W, voxel size: 22.41 µm, number of TIFF images, 3190 for Fig. 5.3). We used Drishti software (Version 2.4) to generate three-dimensional (3-D) models of

the fossils, from which high-resolution screenshots were then generated and figured.

Measurements.—Measurements were made on digital photographs using the processing software ImageJ (Schneider et al., 2012).

Phylogenetic analyses.—The phylogenetic position of *Kuamaia lata* was inferred using the data matrix of O'Flynn et al. (2024) (itself modified from Zeng et al., 2020). This matrix includes 283 characters and 85 taxa (Supplementary Data Set 1). The data matrix was constructed in WinClada 1.00.08 (Nixon, 2002), and parsimony analyses were performed with Tree analysis using New Technology (TNT) 1.5 (Goloboff and Catalano, 2016). The software was set to retain 99,999 trees in memory and perform 10,000 replications. Each analysis included a traditional search with tree bisection and reconnection, a random seed of one and 1000 trees saved per replicate. Jackknife supports (under equal weights), and group present/contradicted (GC) frequency differences (under implied weights) of nodes on the trees were calculated by resampling using 1000 replicates of traditional search, with a change probability of 36% and 33%, respectively, for the two types of nodal supports. We also explored character optimization with TNT and WinClada.

Repositories and institutional abbreviations.—Specimens examined in this study are deposited in the following institutions: the Yunnan Key Laboratory for Palaeobiology

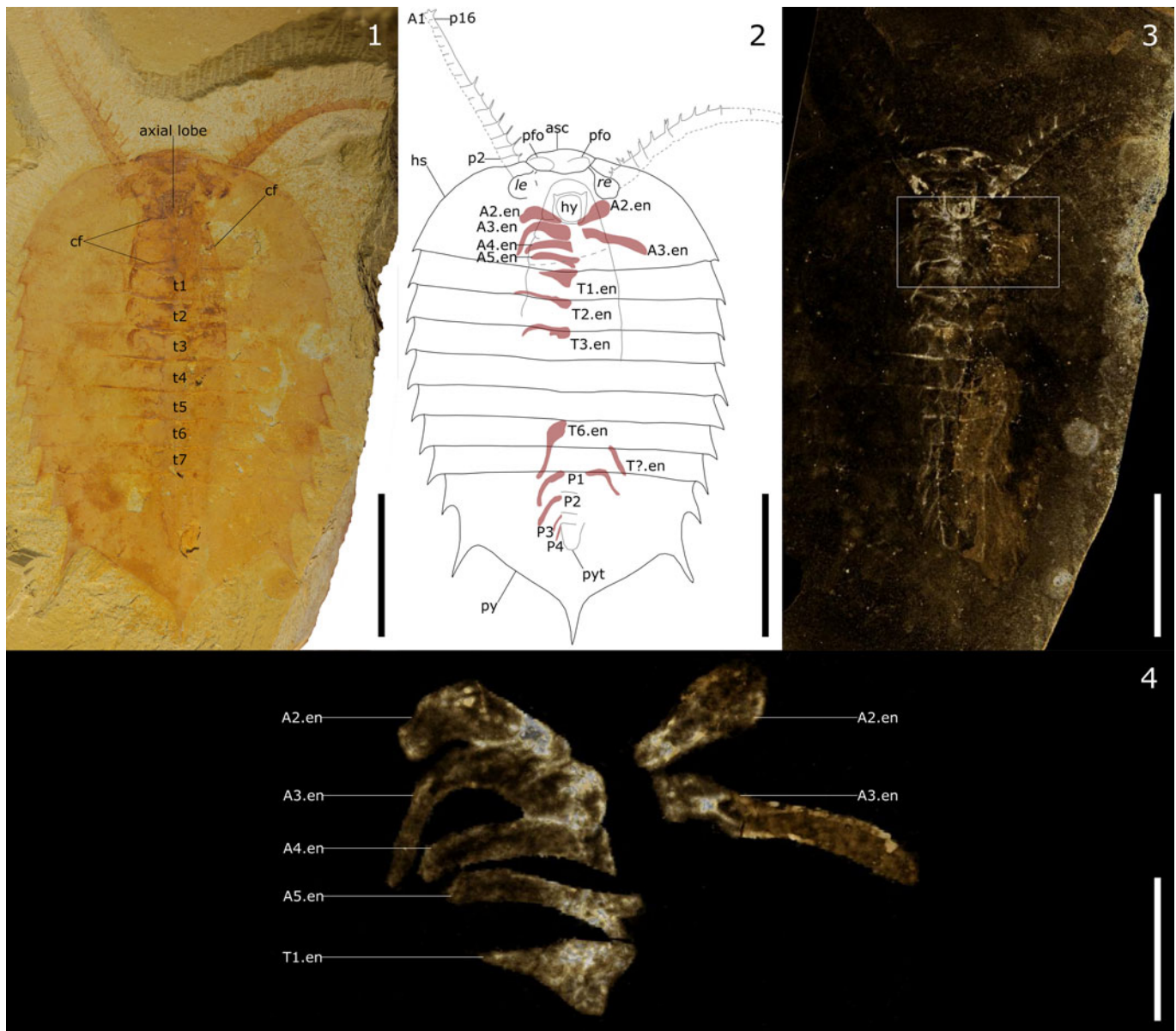


Figure 2. *Kuamaia lata* Hou, 1987a (YKLP 17296): (1) photograph of dorsal view; (2) composite line drawing of dorsal view; (3) tomographic model of dorsal view, rectangle indicates field of view in (4); (4) post-A1 head appendages dissected. Abbreviations: A1 (FA) = frontal appendage; An.en = endopod of head appendage (n); asc = anterior sclerite; le = left eye; re = right eye; hs = head shield; hy = hypostome; Pn = pygidial appendage (n); pn = frontal appendage podomere (n); pfo = protocerebral frontal organ; py = pygidium; pyt = terminus of pygidial axis; Tn.en = endopod of thoracic appendage (n); tn = tergite (n). Scale bars are 10 mm (1–3); 2.5 mm (4).

(YKLP) and the Management Committee of the Chengjiang Fossil Site World Heritage (CJHMD)

Systematic paleontology

Phylum Euarthropoda Lankester, 1904
 Class Artiopoda Hou and Bergström, 1997
 Subclass Conciliterga Hou and Bergström, 1997
 Order Helmetiida Novozhilov, 1960
 Family Helmetiidae Simonetta and Delle Cave, 1975
 Genus *Kuamaia* Hou, 1987

Type species.—*Kuamaia lata* Hou, 1987a (CN 100128) from Maotianshan, level M2.

Kuamaia lata Hou, 1987
 Figures 1–5

- 1987a *Kuamaia lata* Hou, p. 283–284, figs. 3, 4.
 1991 *Kuamaia lata*; Hou and Bergström, p. 183, figs. 57–60.
 1991 *Kuamaia lata*; Delle Cave and Simonetta, p. 201, fig. 6E.
 1996 *Kuamaia lata*; Shu and Zhang, pl. 1, 2.
 1997 *Kuamaia lata*; Luo et al., pl. 2, fig. 3.
 1999 *Kuamaia lata*; Edgecombe and Ramsköld, p. 270, fig. 5.
 1999 *Kuamaia lata*; Hou et al., p. 119–120, figs. 169, 171.
 2002 *Kuamaia lata*; Chen et al., pl. 4, fig. 4.
 2017 *Kuamaia lata*; Hou et al., p. 215, fig. 20.45.
 2020 *Kuamaia lata*; Zeng et al., extended data fig. 7P, Q.

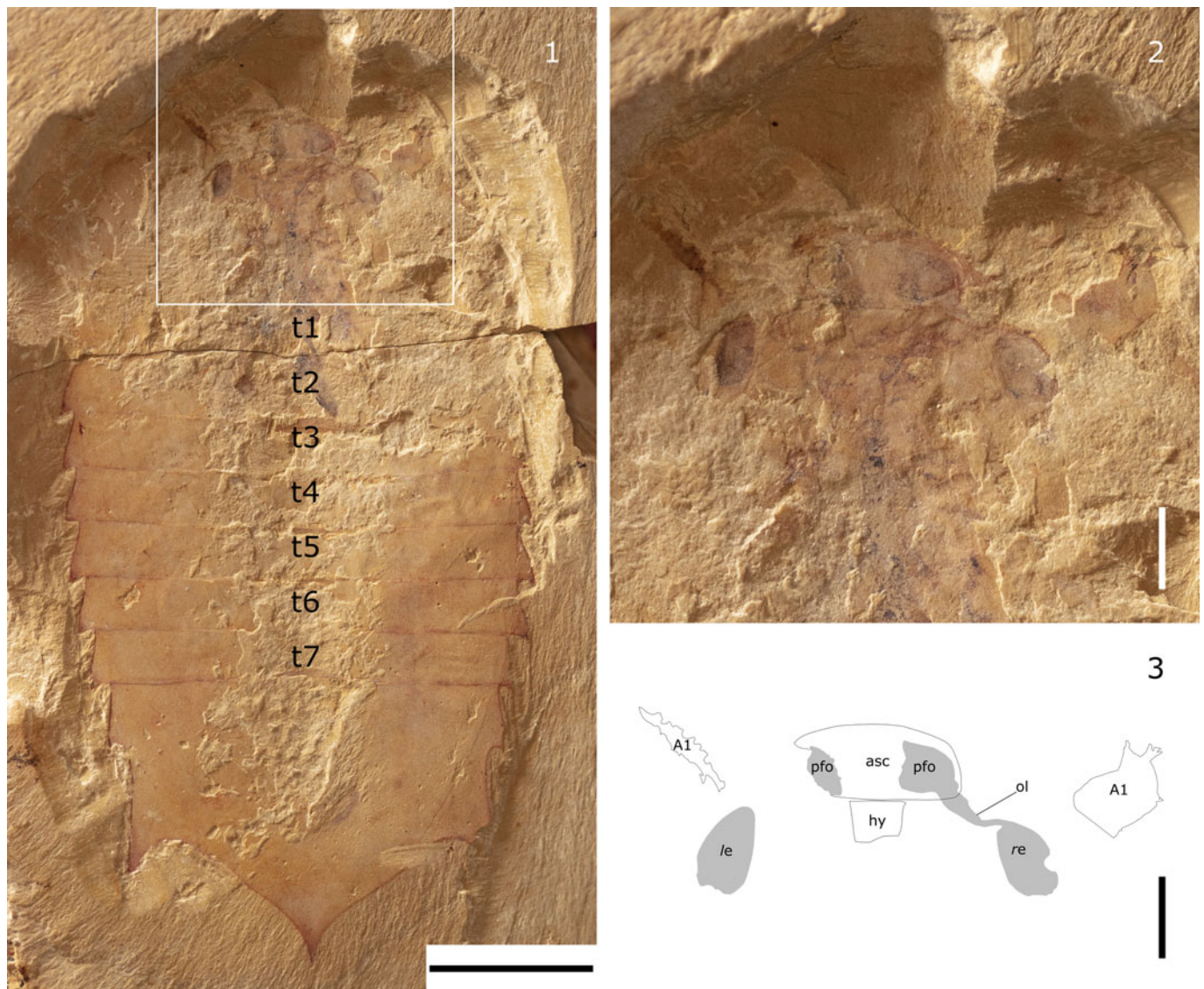


Figure 3. *Kuamaia lata* Hou, 1987a (YKLP 17297): (1) photograph of overall dorsal view, square indicates field of view in (2); (2) photograph of head; (3) line drawing of head. Abbreviations: A1 (FA) = frontal appendage; asc = anterior sclerite; le = left eye; re = right eye; hy = hypostome; ol = optic lobe; pfo = protocerebral frontal organ; tn = tergite (n). Scale bars are 10 mm.

Holotype.—Incomplete specimen (CN 100128 housed in the Museum of the Nanjing Institute of Geology and Palaeontology) from Maotianshan (Hou, 1987a, pl. 23, figs. 1, 2).

Diagnosis.—Emended after Hou and Bergström (1997). Six cephalic segments covered by head shield; from anterior to posterior, these are: protocerebral/ocular segment that carries paired optic lobes/eyes; post-ocular segment with paired raptorial deutocerebral frontal appendages (A1); and four subsequent segments each bearing a biramous appendage pair. A1 anterolaterally orientated, consisting of ≥ 16 podomeres that bear paired inward-facing spines that decrease in length gradually towards tip. Thorax comprises seven tergites with short pleural spines, each thoracic segment with one pair of biramous appendages. Large pygidium with a terminal tail spine and two pairs of marginal spines. Axis terminates in posterior half of pygidium.

Remarks.—There are features observable in the new specimens that are not observable in specimens described to date (cf., Hou and Bergström, 1997). Collectively, our new material identifies: (1) a six-segmented head; (2) frontal organs within the anterior sclerite associated with the attachment site of the optic lobes on the protocerebral segment (see also Ortega-Hernández, 2015, for the closely allied *Helmetia expansa* Walcott, 1918); (3) raptorial rather than sensory A1 on the deutocerebral segment; and (4) four pairs of post-A1 head appendages (A2–A5).

Results

Dorsal aspect of the head shield, thorax, and pygidium (Figs. 1–5).—The five observed specimens, measured from the anterior margin of the anterior sclerite to the posterior termination of the pygidium's terminal spine, are approximately 14 mm, 35 mm, 52 mm, 54 mm, and 79 mm

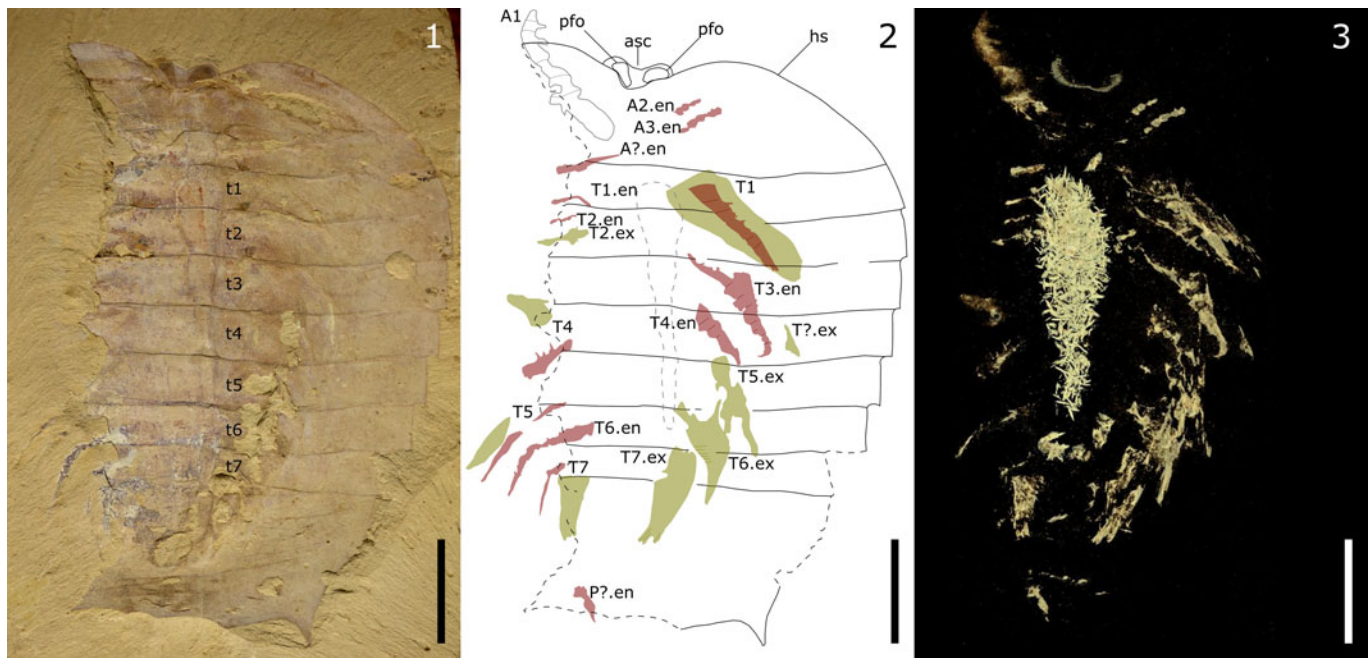


Figure 4. *Kuamaia lata* Hou, 1987a (YKLP 17298): (1) photograph of dorsal view; (2) composite line drawing of dorsal view; (3) tomographic model of dorsal view. Abbreviations: A1 (FA) = frontal appendage; An.en = endopod of head appendage (*n*); asc = anterior sclerite; hs = head shield; Pn.en = pygidial appendage (*n*); pfo = protocerebral frontal organ; Tn = thoracic appendage (*n*); Tn.en = endopod of thoracic appendage (*n*); Tn.ex = exopod of thoracic appendage (*n*); tn = tergite (*n*). Scale bar is 10 mm.

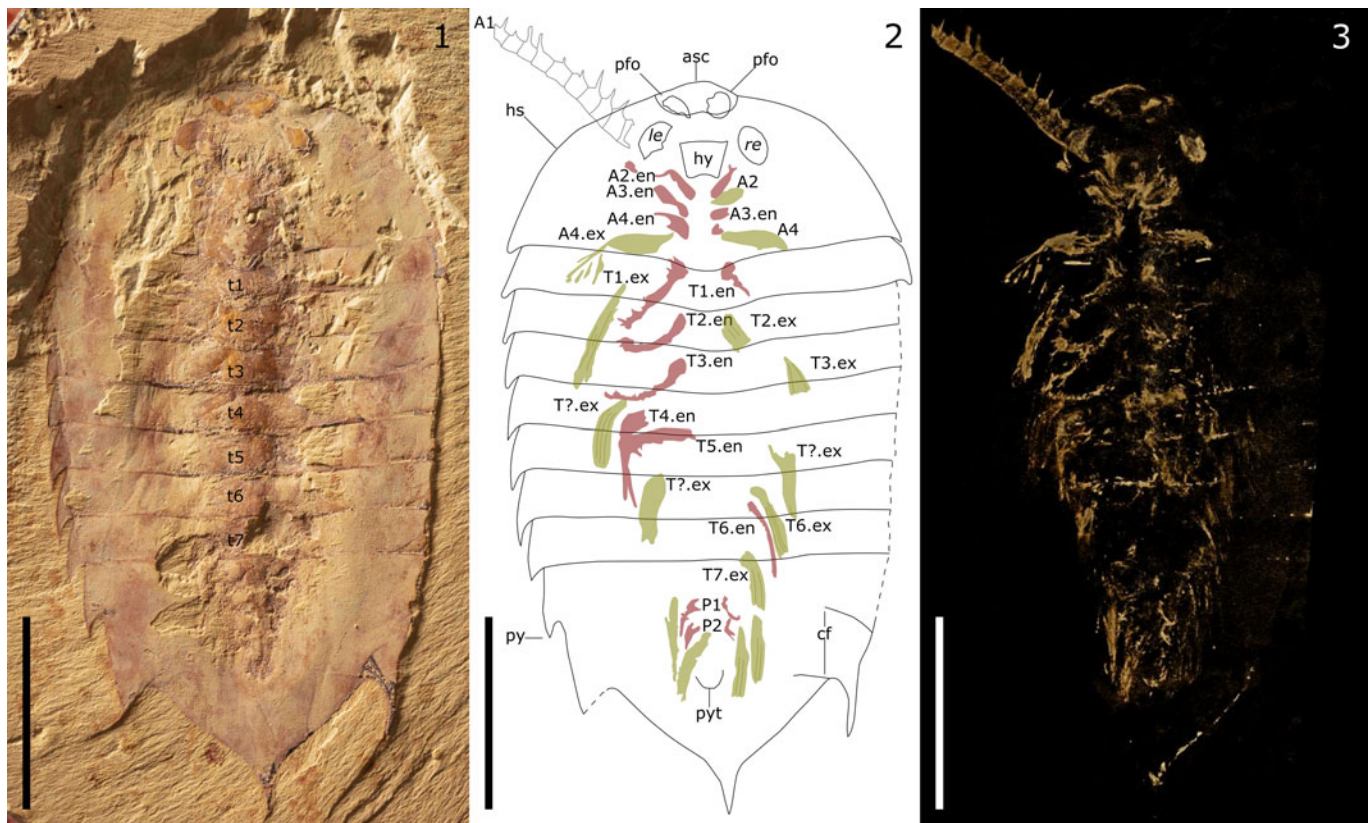


Figure 5. *Kuamaia lata* Hou, 1987a (CJHMD 00064): (1) photograph of dorsal view; (2) composite line drawing of dorsal view; (3) tomographic model of dorsal view. Abbreviations: A1 (FA) = frontal appendage; An = head appendage (*n*); An.en = endopod of head appendage (*n*); An.ex = exopod of head appendage (*n*); asc = anterior sclerite; cf = compactional fold; le = left eye; re = right eye; hs = head shield; hy = hypostome; Pn = pygidial appendage (*n*); pfo = protocerebral frontal organ; py = pygidium; pyt = terminus of pygidial axis; Tn.en = endopod of thoracic appendage (*n*); Tn.ex = exopod of thoracic appendage (*n*); tn = tergite (*n*). Scale bars are 20 mm.

(Figs. 1–5, respectively). Previously described, complete specimens, are approximately 32–59 mm (Hou and Bergström, 1997). They are dorso-ventrally compressed and lie parallel to lamination. The five specimens have similar morphologies in that each has seven tergites irrespective of ontogenetic stage, and each tergite of each specimen accounts for approximately 14% of the length of the thorax. The varying state of preservation impedes collection of all measurements from each specimen (Table 1).

Revised head organization (Figs. 1–5).—Photographs and CT data show that the head bears paired eyes with optic lobes that extend to the frontal organs within the anterior sclerite (Figs. 2, 3). The A1 inserts ventrally, behind the optic lobes and is therefore interpreted to be associated with the deutocerebral segment (Figs. 2, 4, 5). The frontal appendages (A1) are anterolaterally orientated in their proximal part (Figs. 2, 4, 5), with 16 podomeres evident in the portion of their limbs that extend beyond the head shield (Fig. 2). Podomeres 2–9 are of equal length but decrease in width distally (Figs. 2, 5). Each bears paired, well-developed, inward-facing spines, the basal attachment of which is located distally on each podomere (Figs. 2, 5). Spines are at least as long as each podomere is wide (Figs. 2, 4, 5) and decrease in length gradually towards the tip. Figures 1 and 2 illustrate A2–A5 (four post-A1 cephalic limbs, each with an endopod that consists of an indeterminate number of podomeres that bear endites); A2, A4 (Fig. 5), and A5 (Fig. 1) each possesses a paddle-shaped exopod. Figure 5 also illustrates A2–A4; A5 is absent or poorly preserved, but the space for insertion of the limb is evident between A4 and T1.

Gut content (Fig. 4).—The center of the thorax of YKLP 17298 possesses a convexity that runs longitudinally. This may be due to preserved gut content. This preservation appears as 3-D, spinose structures or elongated elements that show no preferential orientation (Fig. 4.3).

Post-A5 appendages.—Endopods, which consist of an indeterminate number of podomeres, gradually shorten posteriorly from T5. No appendages are observed posterior to P4 (Fig. 2); pygidial endopods are considerably shorter than those of the thorax (P1 is less than half the length of T6). Each exopod is flap-shaped, lamellate (Figs. 1, 5), and setose (Fig. 1).

Table 1. Measurements from each specimen (from smallest to largest, in mm).

Morphological terms	Specimen measurements (in mm)				
	YKLP 17295	YKLP 17296	YKLP 17297	YKLP 17298	CJHMD 00064
Head (length)		8.8	10.5		19.5
Thorax (length)	5.8	14.2	23.8	31	33
Pygidium (length)	3	12.2	17.4		26.3
General habitus (length)		35.2	51.7		78.8
Tergite 1–7 (each tergite's length)	≈ 0.8	≈ 2	≈ 3	≈ 4.3	≈ 4.6
Thorax (width)	7.5	22.4	28.7		43.3
Eye (diameter)		1.5	2.4		4

Table 2. Taxa used for phylogenetic analyses

<i>Aegirocassis benmoulaei</i> Van Roy and Briggs, 2011
<i>Alacaris mirabilis</i> Yang et al., 2018
<i>Alalcomenaeus cambrius</i> Simonetta, 1970
<i>Amplectobelua symbrachiata</i> Hou et al., 1995
<i>Anomalocaris canadensis</i> Whiteaves, 1892
<i>Antennacanthopodia gracilis</i> Ou and Shu in Ou et al., 2011
<i>Artemia salina</i> Linnaeus, 1758
<i>Arthroaspis bergstroemi</i> Stein et al., 2013
<i>Aysheaia pedunculata</i> Walcott, 1911
<i>Branchiocaris pretiosa</i> (Resser, 1929)
<i>Bushizheia yangi</i> O'Flynn and Liu in O'Flynn et al., 2020
<i>Canadaspis perfecta</i> (Walcott, 1912)
<i>Cardiodictyon catenulum</i> Hou, Ramsköld, and Bergström, 1991
<i>Chengjiangocaris kunmingensis</i> Yang et al., 2013
<i>Cindarella eucalla</i> Chen et al., 1996
<i>Clypeocaris serrata</i> Yang et al., 2016
<i>Collinsium ciliosum</i> Yang et al., 2015
<i>Cricocosmia jinlingensis</i> Hou and Sun, 1988
<i>Dibasterium durgae</i> Briggs et al., 2012
<i>Eoredlichia intermedia</i> (Lu, 1940)
<i>Fengzhengia mamingae</i> O'Flynn et al., 2022
<i>Forficicaris valida</i> Hou, 1999
<i>Fortiforceps foliosa</i> Hou and Bergström, 1997
<i>Fuxianhuia protensa</i> Hou, 1987a
<i>Guangweicaris spinatus</i> Luo, Fu, and Hu in Luo et al., 2007
<i>Habelia optata</i> Walcott, 1912
<i>Haikoucaris ercaiensis</i> Chen, Waloszek, and Maas, 2004
<i>Hallucigenia fortis</i> Hou and Bergström, 1995
<i>Hallucigenia sparsa</i> Conway Morris, 1977
<i>Helmetia expansa</i> Walcott, 1918
<i>Hesslandona unisulcata</i> Müller, 1982
<i>Hongshiyanspis yiliangensis</i> Zhang and Lin in Zhang et al., 1980
<i>Hurdia victoria</i> Walcott, 1912
<i>Isoxys acutangulus</i> Walcott, 1908
<i>Isoxys auritus</i> (Jiang, 1982)
<i>Isoxys curvirostratus</i> Vannier and Chen, 2000
<i>Isoxys volucris</i> Williams, Siveter, and Peel, 1996
<i>Jianfengia multisegmentalis</i> Hou, 1987b
<i>Jugatacaris agilis</i> Fu and Zhang, 2011
<i>Kerygmachela kierkegaardi</i> Budd, 1993
<i>Kiisortoqia soperi</i> Stein, 2010
<i>Kuamaia lata</i> Hou, 1987a
<i>Kylinxia zhangii</i> Zeng, Zhao, and Huang in Zeng et al., 2020
<i>Leancoilia illecebrosa</i> (Hou, 1987b)
<i>Leancoilia superlata</i> Walcott, 1912
<i>Liangwangshania biloba</i> Chen, 2005
<i>Limulus polyphemus</i> (Linnaeus, 1758)
<i>Lyrarapax unguispinus</i> Cong et al., 2014
<i>Luolishania longicruris</i> Hou and Chen, 1989
<i>Martinsonia elongata</i> Müller and Waloszek, 1986
<i>Megadictyon haikouensis</i> Luo and Hu in Luo et al., 1999
<i>Microdictyon sinicum</i> Chen, Hou, and Lu, 1989
<i>Misszhouia longicaudata</i> (Zhang and Hou, 1985)
<i>Mollisonia plenovenatrix</i> Aria and Caron, 2019
<i>Naraoia compacta</i> Walcott, 1912
<i>Naraoia spinosa</i> Zhang and Hou, 1985
<i>Narceus americanus</i> (Palisot de Beauvois, 1817)
<i>Occacaris oviformis</i> Hou, 1999
<i>Odaraia alata</i> Walcott, 1912
<i>Offacolus kingi</i> Orr et al., 2000
<i>Olenoides serratus</i> (Rominger, 1887)
<i>Onychodictyon ferox</i> Hou, Ramsköld, and Bergström, 1991
<i>Opabinia regalis</i> Walcott, 1912
<i>Pambdelurion whittingtoni</i> Budd, 1997
<i>Paucipodia inermis</i> Chen, Zhou, and Ramsköld, 1995
<i>Peytoia nathorsti</i> Walcott, 1911
<i>Priapululus caudatus</i> Lamarck, 1816
<i>Retifacies abnormalis</i> Hou, Chen, and Lu, 1989
<i>Saperion glumaceum</i> Hou, Ramsköld, and Bergström, 1991
<i>Schinderhannes bartelsi</i> Kühl, Briggs, and Rust, 2009
<i>Scutigera coleoptrata</i> (Linnaeus, 1758)
<i>Sinoburius lunaris</i> Hou, Ramsköld, and Bergström, 1991
<i>Sklerolibyon maomima</i> Aria et al., 2020
<i>Surusicaris elegans</i> Aria and Caron in Aria et al., 2015
<i>Stanleycaris hirpex</i> Pates, Daley, and Ortega-Hernández, 2018
<i>Tanglangia caudata</i> Luo and Hu in Luo et al., 1999
<i>Tegopelte gigas</i> Simonetta and Delle Cave, 1975

Tokumia katalepis Aria and Caron, 2017
Waptia fieldensis Walcott, 1912
Xandarella spectaculum Hou, Ramsköld, and Bergström, 1991
Yawunik kootenayi Aria, Caron, and Gaines, 2015
Yicaris dianensis Zhang et al., 2007
Yohoia tenuis Walcott, 1912

Phylogeny.—To test the phylogenetic position of *Kuamaia lata*, phylogenetic analyses (Table 2) were updated to incorporate new data. Based on our observations, we recoded the following characters (numbered as in Zeng et al., 2020): (1) Number of segments in head region (character 104) to ≥ 6 ; (2) frontalmost appendages, composition of articulated podomeres (character 173) to heteronomous; (3) frontalmost appendages, antenniform (character 178) to absent; (4) frontalmost appendages, number of podomeres bearing well-expanded endites (character 188) to ≥ 8 ; (5) frontalmost appendages, differentiated main spines of endites (character 190) to present; (6) frontalmost appendages, relative length of endite to podomere height (character 191) to comparable; (7) frontalmost appendages, relative width of base of endite to podomere length (character 192) to comparable, along the entire podomere; (8) frontalmost appendages, morphology of enditic spines (character 193) to spiky; (9) frontalmost appendages, proximal podomeres differentiated and peduncle-like (character 203) to unknown; (10) number of claw elements on frontalmost appendage (character 239) to double; (11) large distal claw elements with a wide base on appendages (character 241) to present.

The following monophyletic groups are recovered: (1) pan-chelicerates + megacheirans; (2) isoxyids + ‘great-appendage’ bivalved forms; (3) artiopods; and (4) total-group mandibulates composed of fuxianhuiids, myriapods, pancrustaceans, and hymenocarines. Equal (Fig. 5) and implied (Fig. 6) character weighting resolve *Kuamaia lata* as the sister taxon to *Helmetia expansa*, and both constitute the sister taxon to *Saperion glumaceum* Hou, Ramsköld, and Bergström, 1991, and *Tegopelte gigas* Whittington, 1985.

The clade that supports *Kuamaia lata*, *Helmetia expansa*, *Saperion glumaceum*, and *Tegopelte gigas* (i.e., *Helmetiida* Novozhilov, 1960) is supported by: (1) hypostome attachment (narrow overlap with pre-hypostome); (2) ocular sclerite accommodated by notched fused head shield (present); and (3) additional anterior marginal structures of head shield (notched on single tergite)—nonhomoplasious characters 47, 73, and 96, respectively (Zeng et al., 2020). Artiopoda is supported by: (1) compound eyes accommodated by dorsal bulge on fused head shield (present); (2) optic lobes incorporated into fused head shield, forming eye ridges (present); (3) hypostome accommodating antennae and extensively covering the mouth (present); (4) ocular sclerite covered by true head shield (present); (5) post-oral appendages, endopodite, endites (serrated rows of spines); and (6) differentiation of setae along exopodite (present)—nonhomoplasious characters 23, 25, 48, 74, 251, and 269, respectively (Zeng et al., 2020).

Discussion

Phylogeny.—Equal and implied weights (Figs. 6 and 7, respectively) resolved *Kuamaia lata* within Artiopoda, and the

data provide strong support for that clade (jackknife supports of 98% under equal weights and GC frequency differences of 99% under implied weights). It may be asked whether Artiopoda should be revised to include arthropods with filiform or raptorial antennae (cf., Stein and Selden, 2012). However, considering the number of taxa with, versus those without filiform antennae, coupled with a raptorial A1 in *K. lata* being deeply nested within the artiopod clade and unambiguously optimizing as secondarily derived from ancestors with filiform antennae, we do not insist on this.

A head composed of six segments, as in extant mandibulates (Fusco and Minelli, 2013), was already acquired by other artiopods, such as the iconic trilobites (El Albani et al., 2024), isoxyids, megacheirans (Chen et al., 2019; Liu et al., 2020, 2021; Schmidt et al., 2022; Zhang et al., 2022), *Bushizheia yangi* (O’Flynn et al., 2024), and even *Kylinxia zhangii* Zeng, Zhao, and Huang in Zeng et al., 2020 (O’Flynn et al., 2023), the earliest branching deuteropod. Indeed, head segmentation is ancestral and conserved. Under the scenario in which select taxa have, for example, five-segmented heads (e.g., *Kiisortoquia soperi*), fewer head segments are likely derived. However, recent studies (cited immediately above) have shown that one or more segments have been overlooked.

Morphology.—Our new material clearly demonstrates that the A1 of *Kuamaia lata* is not filiform, as first put forth by Shu and Zhang (1996). Furthermore, its podomeres are conspicuously spinose. Each one bears a long pair of spinose endites, and the base of each paired endite is comparable to the length of its associated podomere (Zeng et al., 2020 [character list]). A raptorial-like A1 that recalls radiodont frontal appendages points to the conclusion to which Shu and Zhang (1996) alluded and we corroborate—that the A1 was not adapted to a sensory function but a predatory one.

O’Flynn et al. (2020) explored the significance of the A1 of *Bushizheia yangi* (the morphology of which bears a strong resemblance to that of *Kuamaia lata*) in the context of interpretations of the homology of cephalic appendages (see also O’Flynn et al., 2024). The resemblance of the A1 of *B. yangi* to the plesiomorphic, raptorial state within radiodonts, *Kylinxia zhangii*, and *Fengzhengia mamingae* O’Flynn et al., 2022, in combination with the segmental identity of head structures (Moysiuk and Caron 2022; Zeng et al., 2022; O’Flynn et al., 2023), gives credence to the hypothesis that the raptorial A1 is a symplesiomorphy for upper stem-group euarthropods. A structurally similar morphology was convergently evolved from an antenna within Artiopoda. Following this line of reasoning and reinforced by our phylogenetic resolution of *K. lata*, the presence of a raptorial A1 is of itself not wholly reliable phylogenetically.

Transverse lines observed in *Kuamaia lata*’s axial margin of the head shield (Fig. 2.1) may be compactional artefacts, as in *Sinoburius lunaris* Hou, Ramsköld, and Bergström, 1991 (see Luo et al., 1997) and *Arthroaspis* Stein et al., 2013. They are not sharply defined axial furrows; indeed, they are absent in all other specimens. Their inconsistent presence coupled with irregularity of linearity (Fig. 2.2) point to a taphonomic artefact.

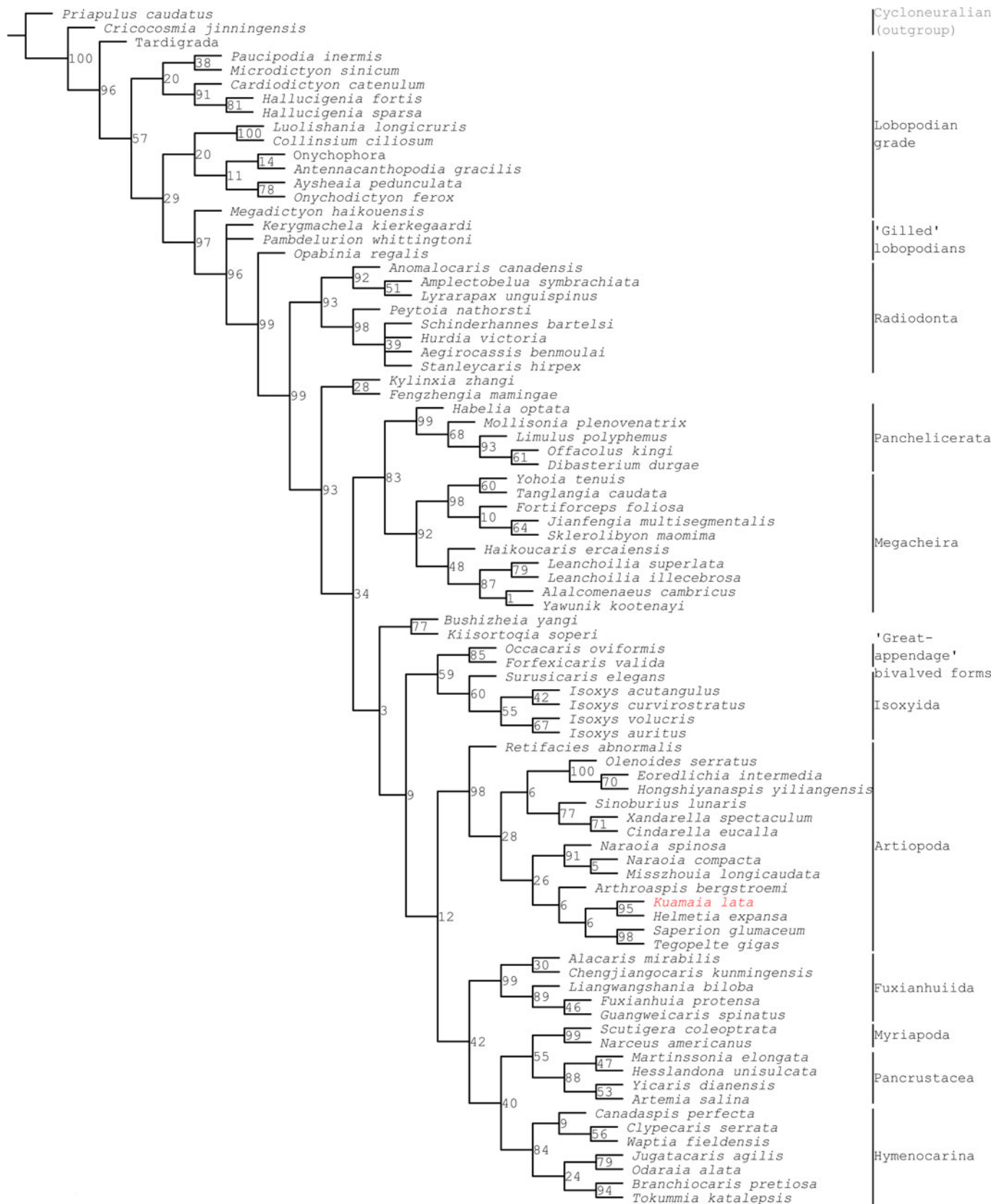


Figure 6. Consensus tree from phylogenetic analysis of panarthropod relationships based on a matrix of 283 characters and 85 taxa. Strict consensus of 60 most parsimonious trees with a score of 725 (consistency index = 0.47; retention index = 0.86) from analysis using equal weighting. *Kuamaia lata* Hou, 1987a (red) is retrieved as sister taxon to *Helmetia expansa* Walcott, 1918.

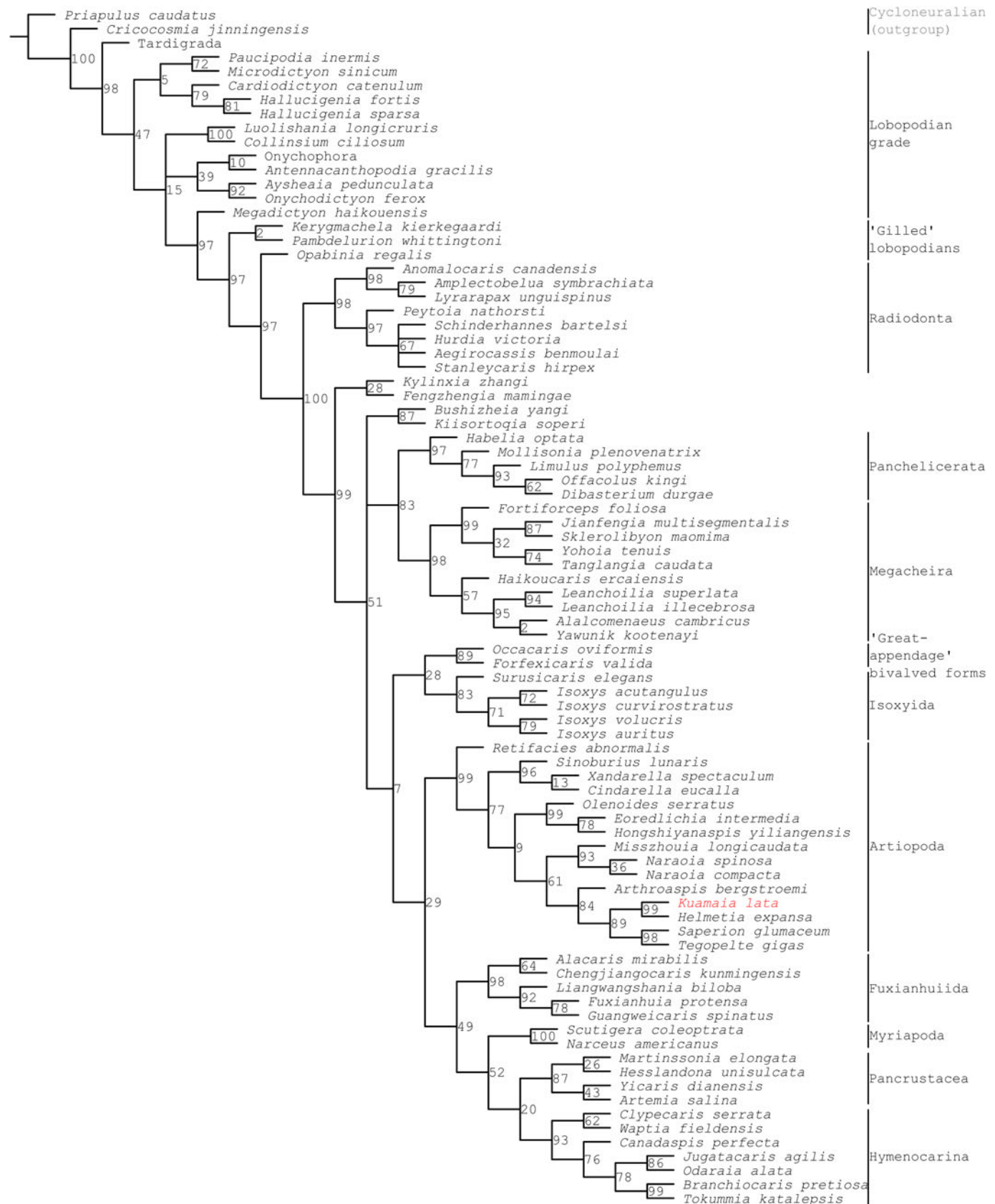


Figure 7. Consensus tree from phylogenetic analysis of panarthropod relationships based on a matrix of 283 characters and 85 taxa. Strict consensus of 3 most parsimonious trees with a score of 55.74314 (consistency index = 0.47; retention index = 0.85) from analysis using implied weighting (concavity constant $k=3$). *Kuamaia lata* Hou, 1987a (red) is retrieved as sister taxon to *Helmetia expansa* Walcott, 1918.

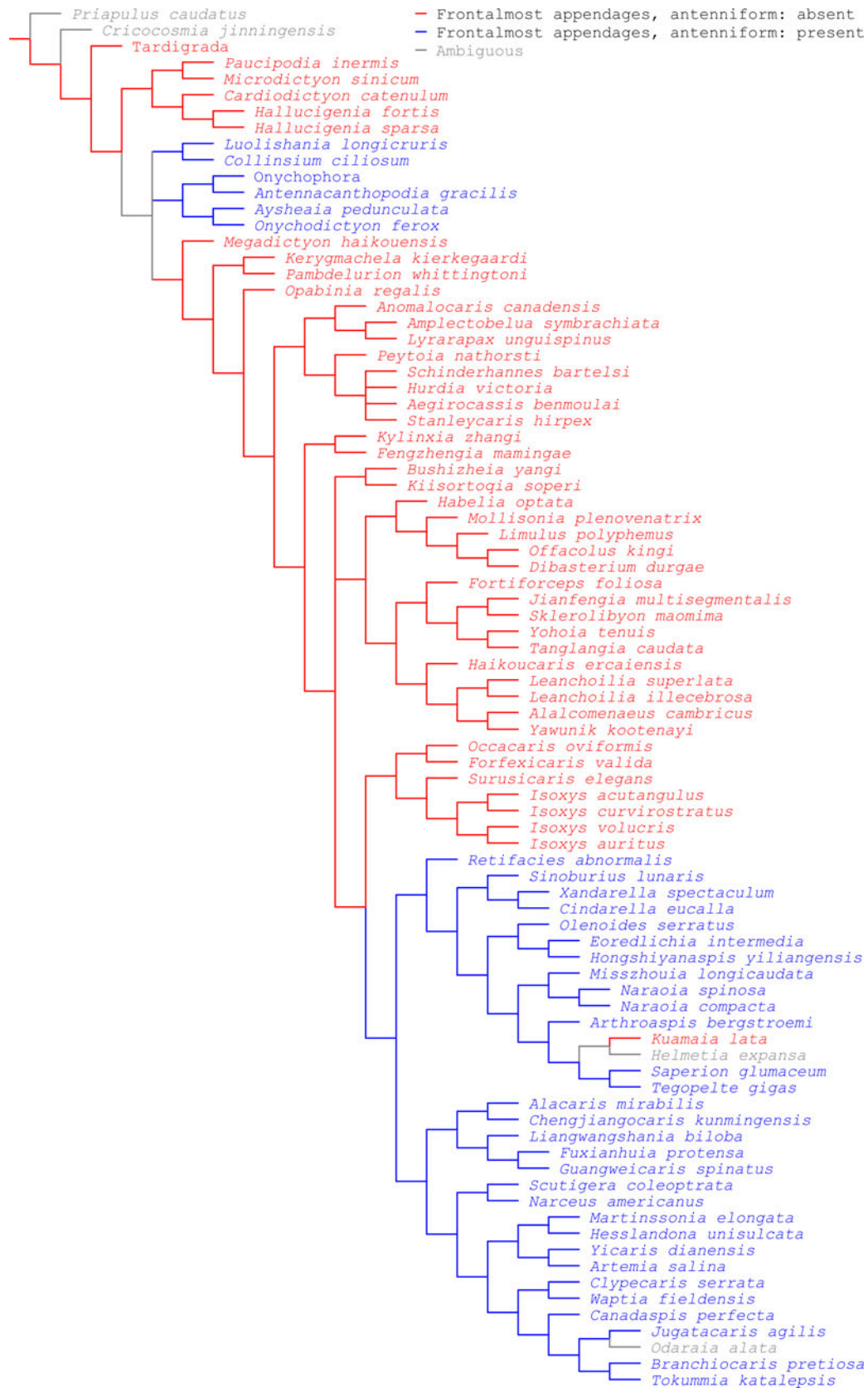


Figure 8. Cladogram of Figure 7 showing character optimization, i.e., frontalmost appendage, antenniform: absent (red); present (blue). A raptorial frontalmost appendage is a symplesiomorphy for upper stem-group euarthropods, retained across a swathe of tree space, but evolved secondarily in *Kuamaia lata* Hou, 1987a, from a filiform antenna within Artiopoda.

Gut content.—In the scenario that *Kuamaia lata* was an active feeder owing to its ability to grasp food and push it into its mouth with the aid of its raptorial A1, we submit that its gut is not sediment-filled (see also Shu and Zhang, 1996). However, the gut of YKLP 17298 is filled with a plethora of platy elements that show no preferential orientation. These platy elements bear a striking resemblance to those identified in the gut of *Megadictyon haikouensis* Luo and Hu in Luo et al., 1999, a lobopodian with a raptorial-like frontal appendage (Vannier et al., 2014, supplementary fig. 6D–J). Putative gut contents observed in *K. lata* (Fig. 4) may be due to diagenetic crystal growth in the gut, mediated by bacteria, as argued for *M. haikouensis* by Vannier et al. (2014, supplementary fig. 6E), which is suggestive of mineralization before degradational collapse.

Conclusions

Kuamaia lata is distinguished from Artiopoda as redefined by Stein and Selden (2012) by having a raptorial rather than filiform A1. However, *K. lata* possesses flattened exopod lobes with lamellae (Figs. 1, 5), endopods with at least seven podomeres (Fig. 4), and a homonomous dorsal exoskeleton with expanded tergopleurae (Figs. 1–3, 5)—and otherwise rests comfortably within Artiopoda (Stein and Selden, 2012; Du et al., 2019). Phylogenetic analyses support the hypothesis that a raptorial A1 is a symplesiomorphy for upper stem-group euarthropods (e.g., megacheirans and isoxyids), and that a structurally similar morphology was convergently evolved (a character reversal) from a secondarily filiform A1 within the artiopod clade (Fig. 8).

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Declaration of competing interests

The authors declare none.

Data availability statement

Data for this study are available in MorphoBank: <http://dx.doi.org/10.7934/P5400>. Supplementary Data Set 1. Nexus file coding.

References

Aria, C., and Caron, J.-B., 2017, Burgess Shale fossils illustrate the origin of the mandibulate body plan: *Nature*, v. 545, p. 89–92.

- Aria, C., and Caron, J.-B., 2019, A middle Cambrian arthropod with chelicerae and proto-book gills: *Nature*, v. 573, p. 586–589.
- Aria, C., Caron, J.-B., and Gaines, R., 2015, A large new leanchioliid from the Burgess Shale and the influence of inapplicable states on stem arthropod phylogeny: *Palaeontology*, v. 58, p. 629–660.
- Aria, C., Zhao, F., Zeng, H., Guo, J., and Zhu, M., 2020, Fossils from South China redefine the ancestral euarthropod body plan: *BMC Evolutionary Biology*, v. 20, no. 4, <https://doi.org/10.1186/s12862-019-1560-7>.
- Bengston, S., 2000, Teasing fossils out of shales with cameras and computers: *Palaeontologia Electronica*, v. 3, no. 1, http://palaeo-electronica.org/2000_1/fossils/issue1_00.htm.
- Briggs, D.E.G., Siveter, D.J., Siveter, D.J., Sutton, M.D., Garwood, R.J., and Legg, D., 2012, Silurian horseshoe crab illuminates the evolution of arthropod limbs: *Proceedings of the National Academy of Sciences*, v. 109, p. 15702–15706.
- Budd, G.E., 1993, A Cambrian gilled lobopod from Greenland: *Nature*, v. 364, p. 709–711.
- Budd, G.E., 1997, Stem group arthropods from the lower Cambrian Sirius Passet fauna of North Greenland, in Fortey, R.A., and Thomas, R.H., eds., *Arthropod Relationships, Systematics Association Special Volume Series*: London, Chapman & Hall, p. 125–138.
- Chen, A., 2005, A new *Fuxianhuia*-like arthropod of the early Cambrian Chengjiang fauna in Yunnan: *Yunnan Geology*, v. 24, p. 108–113.
- Chen, J., Hou, X., and Lu, H., 1989, (Early Cambrian netted scale-bearing worm-like sea animal): *Acta Palaeontologica Sinica*, v. 28, p. 1–16. [in Chinese with English summary]
- Chen, J., Zhou, G., and Ramsköld, L., 1995, A new early Cambrian onychophoran-like animal, *Paucipodia* gen. nov., from the Chengjiang fauna, China: *Transactions of the Royal Society of Edinburgh: Earth Sciences*, v. 85, p. 275–282.
- Chen, J., Zhou, G., Zhu, M., and Yeh, K., 1996, (The Chengjiang Biota. A Unique Window of the Cambrian Explosion): Taichung, China, National Museum of Natural Science, 222 p. [in Chinese]
- Chen, J., Waloszek, D., and Maas, A., 2004, A new 'great appendage' arthropod from the lower Cambrian of China and homology of chelicerate chelicerae and raptorial anteroventral appendages: *Lethaia*, v. 37, p. 3–20.
- Chen, L., Luo, H., Hu, S., Yin, J., Jiang, Z., Wu, Z., Li, F., and Chen, A., 2002, (Early Cambrian Chengjiang Fauna in Eastern Yunnan, China): Kunming, Yunnan Science and Technology Press, 199 p. [in Chinese with English summary]
- Chen, X., Ortega-Hernández, J., Wolfe, J.M., Zhai, D., Hou, X., Chen, A., Mai, H., and Liu, Y., 2019, The appendicular morphology of *Sinoburinus lunaris* and the evolution of the artiopodan clade Xandarellida (Euarthropoda, early Cambrian) from South China: *BMC Evolutionary Biology*, v. 19, no. 165, <https://doi.org/10.1186/s12862-019-1491-3>.
- Cong, P., Ma, X., Hou, X., Edgecombe, G.D., and Strausfeld, N.J., 2014, Brain structure resolves the segmental affinity of anomalocaridid appendages: *Nature*, v. 513, p. 538–542.
- Conway Morris, S., 1977, A new metazoan from the Burgess Shale of British Columbia: *Palaeontology*, v. 20, p. 623–640.
- Cotton, T.J., and Braddy, S.J., 2004, The phylogeny of arachnomorph arthropods and the origin of the Chelicerata: *Transactions of the Royal Society of Edinburgh: Earth Sciences*, v. 94, p. 169–193.
- Du, K., Ortega-Hernández, J., Yang, J., and Zhang, X., 2019, A soft-bodied euarthropod from the early Cambrian Xiaoshiba Lagerstätte of China supports a new clade of basal artiopodans with dorsal ecdysial sutures: *Cladistics*, v. 35, p. 269–281.
- Edgecombe, G.D., and Ramsköld, L., 1999, Relationships of Cambrian Arachnata and the systematic position of Trilobita: *Journal of Paleontology*, v. 73, p. 263–287.
- El Albani, A., Mazurier, A., Edgecombe, G.D., Azizi, A., El Bakhouch, A., et al., 2024, Rapid volcanic ash entombment reveals the 3D anatomy of Cambrian trilobites: *Science*, v. 384, p. 1429–1435.
- Fu, D., and Zhang, X., 2011, A new arthropod *Jugatacaris agilis* n. gen. n. sp. from the early Cambrian Chengjiang biota, South China: *Journal of Paleontology*, v. 85, p. 567–586.
- Fusco, G., and Minelli, A., 2013, Arthropod segmentation and tagmosis, in Minelli, A., Boxshall, G., and Fusco, G., eds., *Arthropod Biology and Evolution*: Berlin, Heidelberg, Springer, p. 197–221.
- Goloboff, P.A., and Catalano, S.A., 2016, TNT, version 1.5, with a full implementation of phylogenetic morphometrics: *Cladistics*, v. 32, p. 221–238.
- Hou, X., 1987a, (Three new large arthropods from lower Cambrian, Chengjiang, eastern Yunnan): *Acta Palaeontologica Sinica*, v. 26, p. 272–285. [in Chinese with English summary]
- Hou, X., 1987b, (Two new arthropods from lower Cambrian, Chengjiang, eastern Yunnan): *Acta Palaeontologica Sinica*, v. 26, p. 236–256. [in Chinese with English summary]
- Hou, X., 1999, New rare bivalved arthropods from the lower Cambrian Chengjiang fauna, Yunnan, China: *Journal of Paleontology*, v. 73, p. 102–116.

- Hou, X., and Bergström, J., 1991, The arthropods of the lower Cambrian Chengjiang fauna, with relationships and evolutionary significance, in Simonetta, A.M., and Conway Morris, S., eds., *The Early Evolution of Metazoan and the Significance of Problematic Taxa*: Cambridge, UK, Cambridge University Press, p. 179–187.
- Hou, X., and Bergström, J., 1995, Cambrian lobopodians—ancestors of extant onychophorans? *Zoological Journal of the Linnean Society*, v. 114, p. 3–19.
- Hou, X., and Bergström, J., 1997, Arthropods of the lower Cambrian Chengjiang fauna, southwest China: Fossils and Strata, no. 45, 116 p.
- Hou, X., and Chen, J., 1989, (Early Cambrian arthropod–annelid intermediate sea animal, *Luolishania* gen. nov. from Chengjiang, Yunnan): *Acta Palaeontologica Sinica*, v. 28, p. 207–213. [in Chinese with English summary]
- Hou, X., and Sun, W., 1988, (Discovery of Chengjiang fauna at Meishucun, Jinning, Yunnan): *Acta Palaeontologica Sinica*, v. 27, p. 1–12. [in Chinese with English summary]
- Hou, X., Chen, J., Lu, H., 1989, (Early Cambrian new arthropods from Chengjiang, Yunnan): *Acta Palaeontologica Sinica*, v. 28, p. 42–57. [in Chinese with English summary]
- Hou, X., Ramsköld, L., and Bergström, J., 1991, Composition and preservation of the Chengjiang fauna—a lower Cambrian soft-bodied biota: *Zoologica Scripta*, v. 20, p. 395–411.
- Hou, X., Bergström, J., and Ahlberg, P., 1995, *Anomalocaris* and other large animals in the lower Cambrian Chengjiang fauna of south-west China: *Geologiska Föreningens Stockholm Förhandlingar*, v. 117, p. 163–183.
- Hou, X., Bergström, J., Wang, H., Feng, X., and Chen, A., 1999, (The Chengjiang Fauna. Exceptionally Well-Preserved Animals from 530 Million Years Ago): Kunming, China, Yunnan Science and Technology Press, 170 p. [in Chinese with English summary]
- Hou, X., Siveter, D.J., Siveter, D.J., Aldridge, R.J., Cong, P., Gabbott, S.E., Ma, X., Purnell, M.A., and Williams, M., 2017, *The Cambrian Fossils of Chengjiang, China: The Flowering of Early Animal Life* (second edition): Chichester, UK, John Wiley & Sons Ltd., 316 p.
- Jiang, Z., 1982, Small shelly fossils, in Luo, H., Jiang, Z., Wu, X., Song, X., and Ouyang, L., eds., *The Sinian–Cambrian Boundary in Eastern Yunnan, China: Yunnan, China, People's Publishing House of Yunnan*, p. 163–199.
- Kühl, G., Briggs, D.E.G., and Rust, J., 2009, A great-appendage arthropod with a radial mouth from the Lower Devonian Hunsrück Slate, Germany: *Science*, v. 323, p. 771–773.
- Lamarck, J.-B., 1816, *Histoire Naturelle des Animaux sans Vertèbres Présentant les Caractères Généraux et Particuliers de ces Animaux, leur Distribution, leurs Classes, leurs Familles, leurs Genres, et la Citation des Principales Espèces qui s'y Rapportent*: Paris, Dunod Éditeurs, 586 p.
- Lankester, R.E., 1904, The structure and classification of the Arthropoda: *Quarterly Journal of Microscopical Science*, v. 47, p. 523–582.
- Linnaeus, C., 1758, *Systema Naturæ per Regna Tria Naturæ, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis*. 10th Edition, Volume 1: Holmiae [Stockholm], Laurentii Salvii, 702 p.
- Liu, Y., Ortega-Hernández, J., Zhai, D., and Hou, X., 2020, A reduced labrum in a Cambrian great-appendage euarthropod: *Current Biology*, v. 30, p. 3057–3061.
- Liu, Y., Edgecombe, G.D., Schmidt, M., Bond, A.D., Melzer, R.R., Zhai, D., Mai, H., Zhang, M., and Hou, X., 2021, Exites in Cambrian arthropods and homology of arthropod limb branches: *Nature Communications*, v. 12, no. 4619, <https://doi.org/10.1038/s41467-021-24918-8>.
- Lu, Y., 1940, (On the ontogeny and phylogeny of *Redlichia intermedia* Lu (sp. nov.)): *Bulletin of the Geological Society of China*, v. 20, p. 333–342. [in Chinese]
- Luo, H., Hu, S., Zhang, S., and Tao, Y., 1997, New occurrence of the early Cambrian Chengjiang fauna in Haikou, Kunming, Yunnan Province, and study on Trilobitoidae: *Acta Geologica Sinica*, v. 71, p. 122–132.
- Luo, H., Hu, S., Chen, L., Zhang, S., and Tao, Y., 1999, (Early Cambrian Chengjiang Fauna from Kunming Region, China): Kunming, China, Yunnan Science and Technology Press, 129 p. [in Chinese with English summary]
- Luo, H., Fu, X., Hu, S., Li, Y., Hou, S., You, T., Pang, J., and Liu, Q., 2007, A new arthropod, *Guangweicaris* Luo, Fu & Hu gen. nov. from the early Cambrian fauna, Kunming, China: *Acta Palaeontologica Sinica*, v. 81, p. 1–7.
- Moysiuk, J., and Caron, J.B., 2022, A three-eyed radiodont with fossilized neuroanatomy informs the origin of the arthropod head and segmentation: *Current Biology*, v. 32, p. 3302–3316.
- Müller, K.J., 1982, *Hesslandona unisulcata* sp. nov. with phosphatised appendages from upper Cambrian 'Orten' of Sweden, in Bate, R.H., Robinson, E., and Sheppard, L.M., eds., *Fossil and Recent Ostracods*: Chichester, UK, Ellis Horwood Ltd., p. 276–304.
- Müller, K.J., and Walloszek, D., 1986, *Martinsonia elongata* gen. et sp. n., a crustacean-like euarthropod from the upper Cambrian 'Orsten' of Sweden: *Zoologica Scripta*, v. 15, p. 73–92.
- Nixon, K.C., 2002, WinClada, Version 1.00.08: <https://www.scienceopen.com/document?vid=3c4c21f5-f2fc-49b1-a18e-4fba2f1337d7> (accessed March 2024).
- Novozhilov, N.I., 1960, *Klass Merostomoidea Størmer, 1944, Chlenistonogie, Trilobitoobraznye i Rakobraznye* [Arthropoda, Trilobitomorpha and Crustacea]: *Osnovy Paleontologii*, p. 195–197.
- O'Flynn, R.J., Audo, D., Williams, M., Zhai, D., Chen, H., and Liu, Y., 2020, A new euarthropod with 'great appendage'-like frontal head limbs from the Chengjiang Lagerstätte, Southwest China: *Palaeontologia Electronica*, v. 23, no. a36, <https://doi.org/10.26879/1069>.
- O'Flynn, R.J., Williams, M., Yu, M., Harvey, T.H.P., and Liu, Y., 2022, A new euarthropod with large frontal appendages from the early Cambrian Chengjiang biota: *Palaeontologia Electronica*, art. 25.1.a6, <https://doi.org/10.26879/1167>.
- O'Flynn, R.J., Liu, Y., Hou, X., Mai, H., Yu, M., Zhuang, S., Williams, M., Guo, J., and Edgecombe, G.D., 2023, The early Cambrian *Kylinxia zhang* and evolution of the arthropod head: *Current Biology*, v. 33, p. 4006–4013.
- O'Flynn, R.J., Williams, M., Yu, M., Guo, J., Audo, D., Schmidt, M., Mai, H., Liu, Y., and Edgecombe, G.E., 2024, The early Cambrian *Bushizheia yangi* and head segmentation in upper stem-group euarthropods: *Papers in Palaeontology*, v. 10, e1556, <https://doi.org/10.1002/spp2.1556>.
- Orr, P.J., Siveter, D.J., Briggs, D.E.G., Siveter, D.J., and Sutton, M.D., 2000, A new arthropod from the Silurian Konservat-Lagerstätte of Herefordshire, England: *Proceedings of the Royal Society of London B*, v. 267, p. 1497–1504.
- Ortega-Hernández, J., 2015, Homology of head sclerites in Burgess Shale euarthropods: *Current Biology*, v. 25, p. 1625–1631.
- Ou, Q., Liu, J., Shu, D., Han, J., Zhang, Z., Wan, X., and Lei, Q., 2011, A rare onychophoran-like lobopodian from the lower Cambrian Chengjiang Lagerstätte, south-western China, and its phylogenetic implications: *Journal of Paleontology*, v. 85, p. 587–594.
- Palisot de Beavois, A.M.F.J., 1805–1821, *Insectes Recueillis en Afrique et en Amérique, das les Royaumes d' Oware et de Benin, Saint-Dominique et dans les États-Unis, Pendant les Années 1786–1797*: Paris, Fain et Compagnie, 276 p.
- Pates, S., Daley, A.C., and Ortega-Hernández, J., 2018, Reply to comment on 'Aysheaia prolata from the Utah Wheeler Formation (Druman, Cambrian) is a frontal appendage of radiodontan *Stanleycaris*' with the formal description of *Stanleycaris*: *Acta Palaeontologica Polonica*, v. 63, p. 105–110.
- Resser, C.E., 1929, New lower and middle Cambrian Crustacea: *Proceedings of the United States National Museum*, v. 76, p. 1–18.
- Rominger, C., 1887, Description of primordial fossils from Mt. Stephens, North-west Territory of Canada: *Proceedings of the Academy of Sciences of Philadelphia*, v. 1887, p. 12–19.
- Schmidt, M., Hou, X., Zhai, D., Mai, H., Belojević, J., Chen, X., Melzer, R.R., Ortega-Hernández, J., and Liu, Y., 2022, Before trilobite legs: *Pygmaclipeatus daziensis* reconstructed and the ancestral appendicular organization of Cambrian artiopods: *Philosophical Transactions of the Royal Society B*, v. 377, no. 20210030, <https://doi.org/10.1098/rstb.2021.0030>.
- Schneider, C.A., Rasband, W.S., and Eliceiri, K.W., 2012, NIH Image to ImageJ: 25 years of image analysis: *Nature Methods*, v. 9, p. 671–675.
- Shu, D., and Zhang, X., 1996, *Kuamaia*, an early Cambrian predator from the Chengjiang Fossil Lagerstätte: *Journal of Northwest University*, v. 26, p. 27–33.
- Simonetta, A.M., 1970, Studies on non-trilobite arthropods from the Burgess Shale (middle Cambrian): *Palaeontographica Italica*, v. 66, p. 35–45.
- Simonetta, A.M., and Delle Cave, L., 1975, The Cambrian non-trilobite arthropods from the Burgess Shale of British Columbia. A study of their comparative morphology, taxonomy and evolutionary significance: *Palaeontographica Italica*, v. 69, p. 1–37.
- Simonetta, A.M., and Delle Cave, L., 1991, Early Palaeozoic arthropods and the problems of arthropod phylogeny; with some notes on taxa of doubtful affinities, in Simonetta, A.M., and Conway Morris, S., eds., *The Early Evolution of Metazoan and the Significance of Problematic Taxa*: Cambridge, UK, Cambridge University Press, p. 189–244.
- Stein, M., 2010, A new arthropod from the early Cambrian of North Greenland, with a 'great appendage'-like antennula: *Zoological Journal of the Linnean Society*, v. 158, p. 477–500.
- Stein, M., and Selden, P.A., 2012, A restudy of the Burgess Shale (Cambrian) arthropod *Emeraldella brocki* and reassessment of its affinities: *Journal of Systematic Palaeontology*, v. 10, p. 361–383.
- Stein, M., Budd, G.E., Peel, J.S., and Harper, D.A.T., 2013, *Arthroaspis* n. gen., a common element of the Sirius Passet Lagerstätte (Cambrian, North Greenland), sheds light on trilobite ancestry: *BMC Evolutionary Biology*, v. 13, no. 99, <https://doi.org/10.1186/1471-2148-13-99>.
- Van Roy, P., and Briggs, D.E.G., 2011, A giant Ordovician anomalocaridid: *Nature*, v. 473, p. 510–513.
- Vannier, J., and Chen, J., 2000, The early Cambrian colonization of pelagic niches exemplified by *Isoxys* (Arthropoda): *Lethaia*, v. 33, 295–311.
- Vannier, J., Liu, J., Lerosey-Aubril, R., Vinther, J., and Daley, A.C., 2014, Sophisticated digestive systems in early arthropods: *Nature Communications*, v. 5, no. 3641, <https://doi.org/10.1038/ncomms4641>.
- Walcott, C.D., 1908, Mount Stephen rocks and fossils: *The Canadian Alpine Journal*, v. 1, p. 232–248.

- Walcott, C.D., 1911, Cambrian geology and paleontology II. Middle Cambrian Merostomata: Smithsonian Miscellaneous Collections, v. 57, p. 17–40.
- Walcott, C.D., 1912, Middle Cambrian Branchiopoda, Malacostraca, Trilobita and Merostomata: Smithsonian Miscellaneous Collections, v. 57, p. 145–228.
- Walcott, C.D., 1918, Geological explorations in the Cambrian Rockies. Explorations and Fieldwork of the Smithsonian Institution in 1917: Smithsonian Miscellaneous Collections, v. 68, p. 4–20.
- Whiteaves, J.F., 1892, Description of a new genus and species of phyllocarid Crustacea from the middle Cambrian of Mount Stephen, B.C.: Canadian Record of Science, v. 5, p. 205–208.
- Whittington, H.B., 1985, *Tegopelte gigas*, a second soft-bodied trilobite from the Burgess Shale, middle Cambrian, British Columbia: Journal of Paleontology, v. 59, p. 1251–1274.
- Williams, M., Siveter, D.J., and Peel, J.S., 1996, *Isoxys* (Arthropoda) from the early Cambrian Sirius Passet Lagerstätte, North Greenland: Journal of Palaeontology, v. 70, p. 947–954.
- Yang, J., Ortega-Hernández, J., Butterfield, N.J., and Zhang, X., 2013, Specialized appendages in fuxianhuiids and the head organization of early euarthropods: Nature, v. 494, p. 468–471.
- Yang, J., Ortega-Hernández, J., Gerber, S., Butterfield, N.J., Hou, J., Lan, T., and Zhang, X., 2015, A superarmored lobopodian from the Cambrian of China and early disparity in the evolution of Onychophora: Proceedings of the National Academy of Sciences, v. 112, p. 8678–8683.
- Yang, J., Ortega-Hernández, J., Lan, T., Hou, J., and Zhang, X., 2016, A predatory bivalved euarthropod from the Cambrian (Stage 3) Xiaoshiba Lagerstätte, South China: Scientific Reports, v. 6, no. 27709, <https://doi.org/10.1038/srep27709>.
- Yang, J., Ortega-Hernández, J., Legg, D.A., Lan, T., Hou, J., and Zhang, X., 2018, Early Cambrian fuxianhuiids from China reveal origin of the gnathobasic protopodite in euarthropods: Nature Communications, v. 9, no. 47, <https://doi.org/10.1038/s41467-017-02754-z>.
- Zeng, H., Zhao, F., Niu, K., Zhu, M., and Huang, D., 2020, An early Cambrian euarthropod with radiodont-like raptorial appendages: Nature, v. 588, p. 101–105.
- Zeng, H., Zhao, F., and Zhu, M., 2022, *Innovatiocaris*, a complete radiodont from the early Cambrian Chengjiang Lagerstätte and its implications for the phylogeny of Radiodonta: Journal of the Geological Society of London, v. 180, jgs2021-164, <https://doi.org/10.1144/jgs2021-164>.
- Zhang, W., and Hou, X., 1985, (Preliminary notes on the occurrence of the unusual trilobite *Naraoia* in Asia): Acta Palaeontologica Sinica, v. 24, p. 591–595 [in Chinese with English summary].
- Zhang, W., Lu, Y., Zhu, Z., Qian, Y., Lin, H., Zhou, Z., Zhang, S., and Yuan, J., 1980, (Cambrian Trilobite Faunas of South-western China): Beijing, Science Press, 497 p. [in Chinese with English summary].
- Zhang, X., Siveter, D.J., Waloszek, D., and Maas, A., 2007, An epipodite-bearing crown-group crustacean from the lower Cambrian: Nature, v. 449, p. 595–598.
- Zhang, X., Liu, Y., O'Flynn, R.J., Schmidt, M., Melzer, R.R., Hou, X., Mai, H., Guo, J., Yu, M., and Ortega-Hernández, J., 2022, Ventral organization of *Jianfengia multisegmentalis* Hou, and its implications for the head segmentation of megacheirans: Palaeontology, v. 65, e12624, <https://doi.org/10.1111/pala.12624>.
- Zhao, F., Hu, S., Zeng, H., and Zhu, M., 2014, A new helmetiid arthropod from the early Cambrian Chengjiang Lagerstätte, Southwest China: Journal of Paleontology, v. 88, p. 367–370.

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