

A new euarthropod with ‘great appendage’-like frontal head limbs from the Chengjiang Lagerstätte, Southwest China

Robert J. O’Flynn, Denis Audo, Mark Williams,
Dayou Zhai, Hong Chen, and Yu Liu

ABSTRACT

Bushizheia yangi gen. et sp. nov. is a euarthropod species from the Cambrian (Series 2, Stage 3) Chengjiang Lagerstätte, Southwest China. Sclerotised dorsal tergites, sclerotisation of post-frontal head limb appendages, and no isolated cephalic sclerite support the euarthropod affinities of *B. yangi* gen. et sp. nov. However, the frontal head limbs resemble in morphology the anteroventral raptorial appendage of radiodonts. Although, due to the absence of critical soft anatomy, we cannot elucidate the exact segmental affinities of these raptorial appendages, the possession of ‘great appendage’-like frontal head limbs is important for assessing the range of limb morphology evolved by early euarthropods.

Robert J. O’Flynn. Yunnan Key Laboratory for Palaeobiology, Institute of Palaeontology, Yunnan University, 650500 Kunming, China and MEC International Joint Laboratory for Palaeobiology and Palaeoenvironment, Yunnan University, 650500 Kunming, China. liangwangshania@126.com
<http://orcid.org/0000-0001-9939-6321>

Denis Audo. Yunnan Key Laboratory for Palaeobiology, Institute of Palaeontology, Yunnan University, 650500 Kunming, China and MEC International Joint Laboratory for Palaeobiology and Palaeoenvironment, Yunnan University, 650500 Kunming, China. denis.audo@edu.mnhn.fr
<http://orcid.org/0000-0003-3486-3552>

Mark Williams. School of Geography, Geology and the Environment, University of Leicester, University Road, Leicester, LE1 7RH, UK and MEC International Joint Laboratory for Palaeobiology and Palaeoenvironment, Yunnan University, 650500 Kunming, China. mri@leicester.ac.uk

Dayou Zhai. Yunnan Key Laboratory for Palaeobiology, Institute of Palaeontology, Yunnan University, 650500 Kunming, China and MEC International Joint Laboratory for Palaeobiology and Palaeoenvironment, Yunnan University, 650500 Kunming, China. dyzhai@ynu.edu.cn

Hong Chen. Yunnan Key Laboratory for Palaeobiology, Institute of Palaeontology, Yunnan University,

<http://zoobank.org/A1DFE048-F763-4B75-9EF0-A20B9B8CD619>

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650500 Kunming, China and MEC International Joint Laboratory for Palaeobiology and Palaeoenvironment, Yunnan University, 650500 Kunming, China. chenhong3397258@126.com
Yu Liu. Yunnan Key Laboratory for Palaeobiology, Institute of Palaeontology, Yunnan University, 650500 Kunming, China and MEC International Joint Laboratory for Palaeobiology and Palaeoenvironment, Yunnan University, 650500 Kunming, China. yu.liu@ynu.edu.cn <http://orcid.org/0000-0002-2346-740X>

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INTRODUCTION

Over 250 species have been recorded from the Cambrian Series 2, Stage 3 Chengjiang biota of Yunnan Province, China, with arthropods representing *circa* 33% of these species (Hou et al., 2017). These include taxa with soft anatomy preservation that are instrumental to elucidating early euarthropod evolution (e.g., Hou and Bergström, 1997; Stein and Selden, 2011; Chen et al., 2019). Among these, arthropods with a grasping appendage, the so-called great or frontal appendages, are iconic animals of the Chengjiang biota (e.g., Chen et al., 2004; Liu et al., 2007; Fu et al., 2011; Legg and Vannier, 2013; Cong et al., 2014).

Here we describe the euarthropod *Bushizheia yangi* gen. et sp. nov. from the Chengjiang biota. This species is known only from a single specimen with a well-preserved dorsal exoskeleton that is divided into head, thorax, and pygidium (Figure 1A–B), but is most notable for its long frontal appendages that resemble those of radiodonts and the euarthropod *Kiisortoqia soperi* Stein, 2010 (see Stein, 2010, figure 7B). We discuss what happened to the 'great appendage' with reference to two possibilities for the evolution of the primary antennae or 'great appendage': (1) that limb-like 'great appendages' evolved to form chelicerae (Chen et al., 2004), i.e., innervated from the deutocerebrum (see Park et al., 2018); or (2) that the labrum represents the transformed frontal 'great appendage' (see Budd, 2002; Eriksson et al., 2003; Scholtz and Edgecombe, 2006), i.e., innervated from the protocerebrum (see Park et al., 2018).

We also provide a detailed description of *Bushizheia yangi* gen. et sp. nov. and discuss its palaeoecology.

MATERIALS AND METHODS

A single specimen of *Bushizheia yangi* gen. et sp. nov. was recovered from the Yu'an-shan Member, Chiungchussu Formation at Jiucun Town (24°41'33" N, 102°59'26" E) (see Du et al., 2018,

figure 1), Chengjiang County. The Yu'an-shan Member is informally divided stratigraphically into four lithologically and palaeontologically distinctive parts (Zhu et al., 2001). *B. yangi* gen. et sp. nov. was recovered from the third stratigraphic interval of the Yu'an-shan Member from laminated mudstones of the early Cambrian (Series 2, Stage 3). It is deposited in the Yunnan Key Laboratory for Palaeobiology (YKLP 11421) at Yunnan University, Kunming.

The specimen was prepared mechanically with a mounted steel needle under a binocular microscope, where only a small amount of matrix was required to be removed by a gentle scraping action.

Fluorescence microscopy and photography (a Leica DFC7000 T linked to a Leica M205 FA fluorescence stereo microscope) were used to increase the contrast between the specimen (not autofluorescent) and the matrix (weakly autofluorescent). For photographs in natural colour, we captured several images with a Digital SLR Camera (a Canon EOS 5DS R and a Nikon D700) fitted with a 100 mm and a 105 mm macro lens, respectively, with extension rings for magnification factors above 1:1. The photographs were mostly captured in cross-polarised light to limit reflection of light and increase contrast (Bengtson, 2000). We also captured photographs with cropped light (light coming from a low vertical angle, highlighting structures at the surface) from various angles (default: from the top left) to reveal the micro relief of the fossil. The specimen was also investigated with Computed Tomography using a ZEISS Xradia 520 Versa, but no additional structures were revealed using this method.

Measurements were made on digital photographs using the image processing software ImageJ (Schneider et al., 2012). Morphological characters measured include: (1) the total length, measured from the anterior margin of the head shield to the posterior termination of the tailspine; (2) the head, measured from the anterior margin to

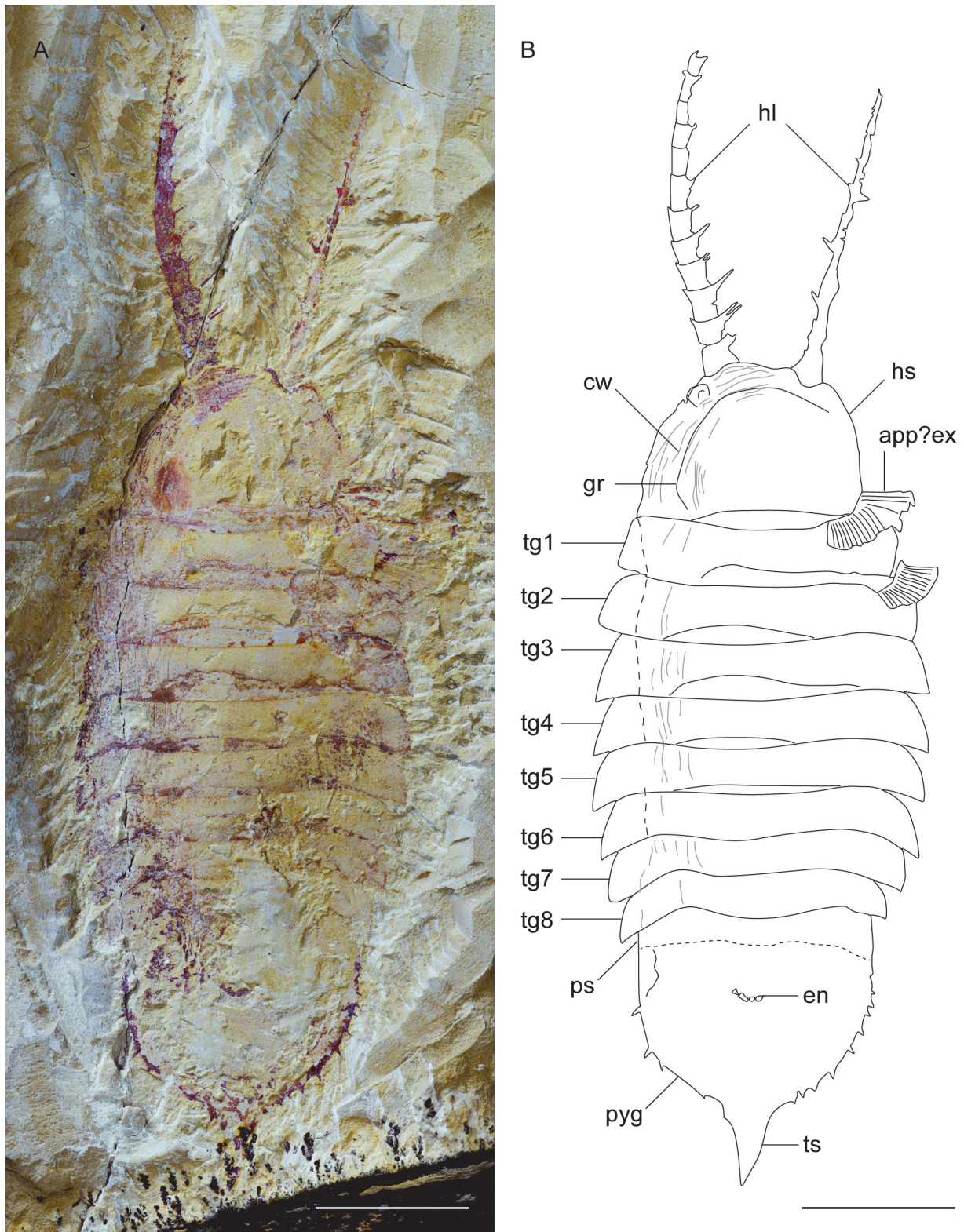


FIGURE 1. *Bushizheia yangi* gen. et sp. nov. (YKLP 11421). **A**, photograph of dorsal view; **B**, composite line drawing of dorsal view. Both scale bars are 10 mm. Abbreviation: app?ex, exopod of a post-frontal head limb appendage; cw, compression wrinkle; en, endopod; gr, groove; hl, frontal head limbs; hs, head shield; ps, pygidial segment; pyg, pygidium; tg1-8, tergites 1 through 8; ts, tailspine.

the posterior margin of the head shield; (3) tergites one through eight, measured from the anterior margin to the posterior margin of the tergite; (4) the frontal head limb, measured from the distal termination to the proximal margin of the podomeres; and (5) the pygidium, measured from the posterior margin of the posterior-most tergite to the posterior termination.

SYSTEMATIC PALAEONTOLOGY

Phylum EUARTHROPODA Lankester, 1904

Class *incertae sedis*

Order *incertae sedis*

Family *incertae sedis*

Genus *Bushizheia* O'Flynn and Liu, gen. nov.

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Type species. *Bushizheia yangi* gen. et sp. nov., by monotypy.

Diagnosis. As for type species, by monotypy.

Etymology. Bǔshízhě is Mandarin for predator: an allusion to *Kiisor-toqia* Stein, 2010, from the Kalaallisut (Greenlandic) word *kiisor-toq*, meaning predator (see Stein, 2010).

Remarks. *Bushizheia* gen. nov. is ascribed to the total group Euarthropoda – as defined by the presence of fully arthrodised bodies and limbs (Aria, 2019), because it has sclerotised trunk tergites, sclerotisation of post-antennal appendages (see Cotton and Brady, 2004), and does not have any isolated tergites in the cephalic segments (see Ortega-Hernández, 2014).

It features a long, frontal grasping appendage that is morphologically like that of radiodonts, but in combination with a completely arthrodised body organisation; this distinguishes *Bushizheia* gen. nov. from all other euarthropods, except *Kiisor-toqia*.

Bushizheia gen. nov. and *Kiisor-toqia* appear allied to each other by the possession of frontal 'great appendage'-like head limbs (Figure 2A-D). However, *Bushizheia* gen. nov. is sufficiently distinct to warrant erection of a monospecific genus. It differs from *Kiisor-toqia* by: (1) *Bushizheia* gen. nov. has a large pygidium with paired short falcate spines and a terminal tailspine (Figure 3A); *Kiisor-toqia* has a small tail shield with neither spines nor a tailspine and twice the number of thoracic tergites; see Figure 4B and also Stein, 2010, p. 482-483, figures 4B, 5B-C); (2) trilobation of thoracic tergites effaced; (3) dorsal spine is present on each podomere of the frontal head limb (see Daley and Edgecombe, 2014).

Bushizheia yangi O'Flynn and Liu, sp. nov.

Figures 1A-B, 2A-D, 3A-B, 4A

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Type material. Holotype YKLP 11421 (Figure 1A) from the Cambrian, Series 2, Stage 3, *Eoredlichia-Wutingaspis* trilobite biozone, Nangoan Stage of regional Chinese usage, Yu'an-shan Member, Chiungchussu Formation (Repository: YKLP).

Diagnosis. Euarthropod with a semi-circular head shield lacking dorsal compound eyes, eight thoracic tergites, and a large, semi-circular pygidium. Frontal head limbs *circa* 33% of body length, strong, composed of ≥ 12 podomeres, each with paired spines laterally.

Etymology. Yangi, after Mr Zhixin Yang, who recovered and prepared the fossil.

Description. Dorsal aspect of the head shield, trunk, and pygidium (Figures 1A-B, 2C-D, 3A, 4A): *Bushizheia yangi* gen. et sp. nov. is *circa* 54 mm long. The habitus is sub-elliptical in dorsal aspect, with a length (anterior margin of the head shield to the posterior termination of the tailspine) of *circa* 250% of the width (maximum width in the anterior half of the body at the third and fourth tergites) (Figures 1A-B, 4A). The length of the head shield is *circa* 20% of the total length. The trunk tapers from the fourth tergite backwards to a large pygidium (the tail shield of the exoskeleton covering the fused posterior segments of the body). The pygidium's margin is spinose (Figures 1A-B, 3A, 4A).

The head shield is a simple, semi-circular shield, with smoothly rounded posterolateral margins, and the length is *circa* 70% of its width.

The trunk consists of eight tergites. The anterior-most three tergites are virtually of equal length; the length is *circa* 20% of the width. Tergites 3-4 are widest; the width and length of tergites subsequently decrease posteriorly in width and length (Figures 1A-B, 4A). Axially, the posterior border of each tergite overhangs the following tergite by *circa* 17% of its length, but by less abaxially. The first, second, and third tergites are reflexed anteriorly, whereas tergites posterior to that are transverse or reflexed posteriorly. The tergopleurae of the first and second tergites terminate bluntly posterolaterally. The tergopleurae of tergites 3-8 are extended into posterolateral projections (Figures 1A-B, 4A).

The pygidium is a semi-circular shield and its length is *circa* 70% of its width; the margins bear eight paired short falcate spines, which curve very slightly posteriorly (Figures 1A-B, 3A, 4A). The pleural regions of the pygidium's anterior-most segment are effaced, but a transverse furrow is vis-

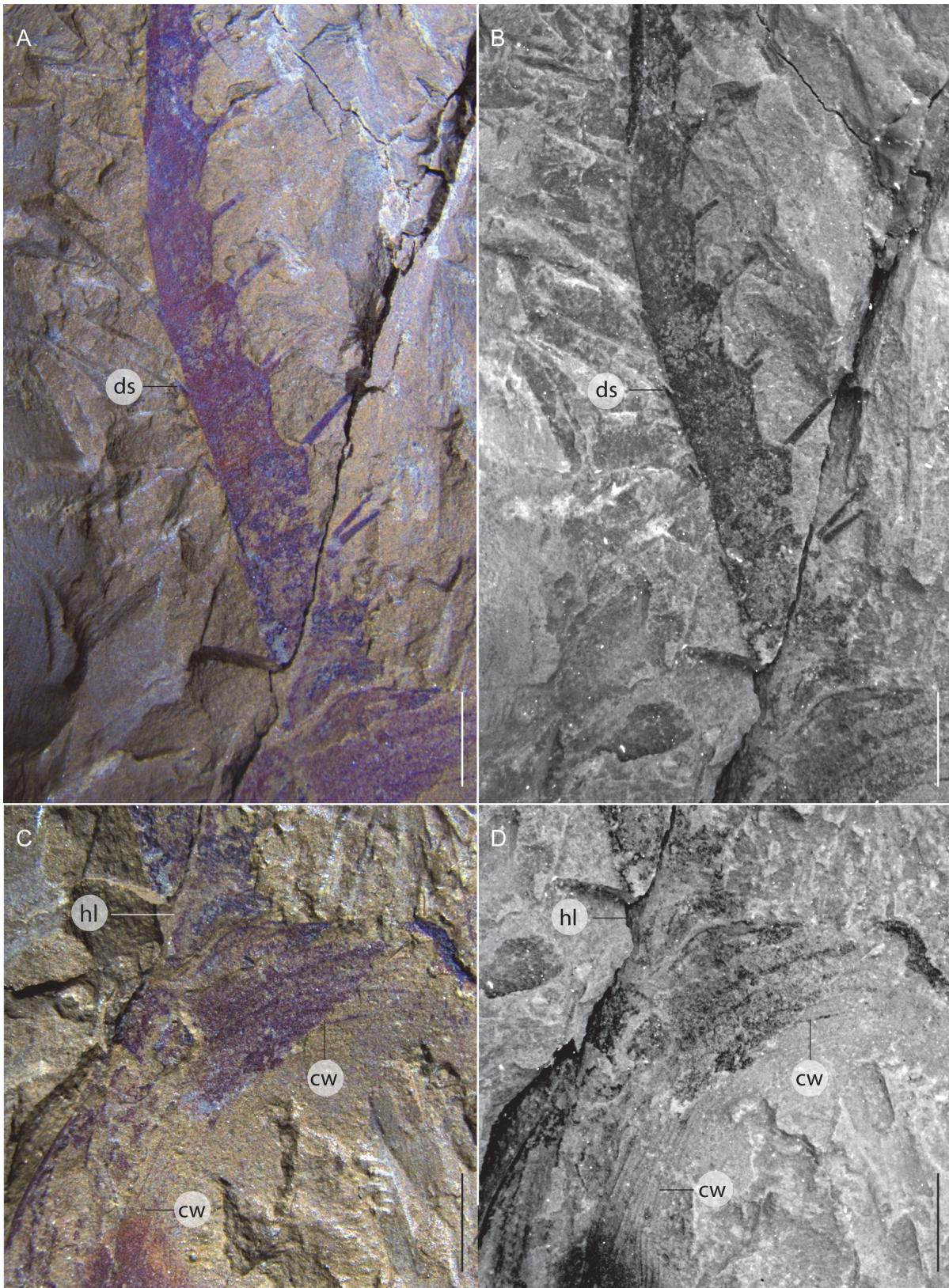


FIGURE 2. *Bushizheia yangi* gen. et sp. nov. (YKLP 11421). **A, C**, tungsten photography lighting of left frontal head limb and dorsal view of head shield, respectively; **B, D**, fluorescent photography lighting of the same. All scale bars are 2 mm. Abbreviation: cw, compression wrinkles; ds, dorsal spines; hl, frontal head limb.

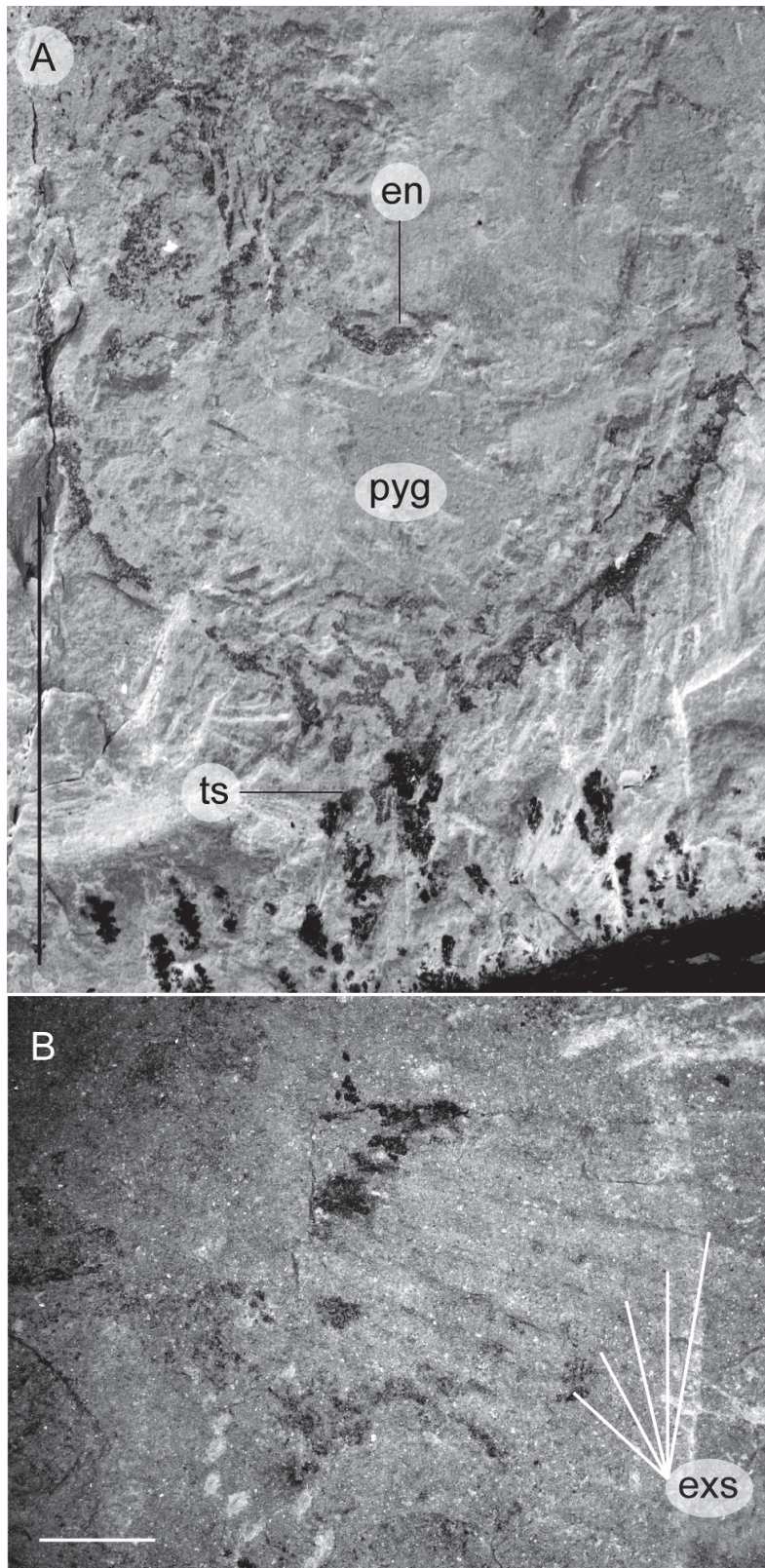


FIGURE 3. *Bushizheia yangi* gen. et sp. nov. (YKLP 11421). **A-B**, enlarged from Fig. 1A; **A**, detail of pygidium; **B**, detail of exopod setae. Scale bar 3A is 10 mm. Scale bar 3B is 1 mm. Abbreviation: en, endopod; exs, exopod setae; pyg, pygidium; ts, tailspine.

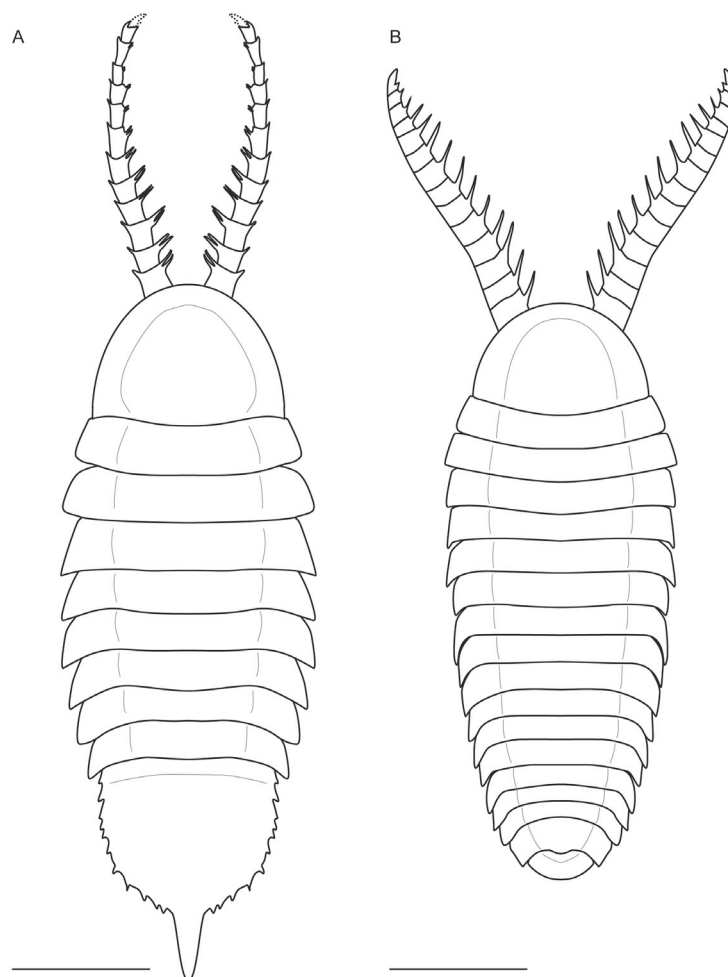


FIGURE 4. Reconstruction of **A**, *Bushizheia yangi* gen. et sp. nov. juxtaposed with **B**, *Kiisortoqia soperi* Stein 2010 (modified from Stein, 2010) in dorsal view. Both scale bars are 10 mm.

ible axially. The tailspine is sub-triangular and incompletely articulated; it is as wide as long, *circa* 8% of the total length, and *circa* 30% of the total length of the pygidium.

Appendages (Figures 1A-B, 2A-D, 4A): The frontal head limbs reach a length of *circa* 33% of the total length of the body: 12 podomeres extend beyond the head shield, each with lateral endites that bear two inward facing setae, and terminal setae that are outward facing. Podomeres 2-7 are of equal length but decrease in width distally (Figures 1A-B, 2A-B, 4A).

All visible post-frontal head limb appendages consist of either an endopod or an exopod. The one (incompletely) preserved endopod comprises four narrow podomeres (Figures 1A-B, 3A). The two preserved exopods are paddle-shaped flaps, fringed with setae (Figures 1A-B, 3B). Stein (2010), in his description of *Kiisortoqia soperi*, identified

four cephalic appendiferous segments (a head incorporating the antennular plus three post-antennular limb-bearing segments), considered to be part of the ground pattern of Euarthropoda (Waloszek et al., 2007). The distal exopod of the anterior-most post-frontal head limb appendage of *Bushizheia yangi* gen. et sp. nov. appears beneath the head shield, and may, based on its position, be the fourth cephalic appendage. The limb immediately posterior of this, adjacent to the first trunk tergite, appears to be the first trunk appendage.

Remarks. *Bushizheia yangi* gen. et sp. nov. is dorsoventrally compressed and lies parallel to lamination; its well-articulated nature (i.e., tergites preserved attached, exopods preserved *in situ*). This state of preservation, especially the presence of articulated frontal head limbs, suggests limited post-mortem transportation: in, e.g., extant crustaceans, antennae can easily disarticulate (but see

Allison, 1986). Compression wrinkles in the head shield that parallel its margin (Figures 1A-B, 2A-D), suggest localised, weak sclerotisation. It is, therefore, presumed that the head shield was a simple, convex shield, sclerotised but without substantial biomineralization.

As a result of the state of preservation, not all podomeres of the frontal appendages are accessible for a straightforward description. The exact number of podomeres cannot be established; some are obscured by sediment. Lateral endites can be confirmed for at least podomeres 2-7, 9, 11, 12, and medial endites bearing two firm setae at their tips can be confirmed for at least 4, 5, 7, 11, and 12 (Figure 2A-B). Rotation of podomere 2 evinces widely spaced double rows of endites (Figures 1A-B, 2A).

Limbs with exopod setae are visible to the right of the two anterior-most thoracic tergites; the exopod of the posterior-most cephalic limb protrudes from beneath the head shield directly adjacent to the border of the head shield and first tergite, and is significantly rotated posteriorly, as is, albeit to a lesser extent the exopod of the first trunk limb. Only a single posteriorly situated endopod is, due to a degradation or complete absence of the overlying tergite, visible. No additional limbs were revealed by palaeontological techniques. The exact number of podomeres in the frontal appendages cannot be ascertained due to poor preservation of the distal-most ones. The proximal portions of the exopods are unavailable for description, so it cannot be established as to whether they were bipartite and divided into proximal and distal portions as in *Leancoilia illecebrosa* (see Liu et al., 2007).

DISCUSSION

Frontal Appendages

Bushizheia yangi gen. et sp. nov. and *Kiisor-toqia soperi* possess a long, grasping frontal appendage very similar to that of the radiodonts. However, neither of these two species closely resemble radiodonts. Could the presence of raptorial appendages in *B. yangi* gen. et sp. nov. and *K. soperi* be symplesiomorphic, shared by *B. yangi* gen. et sp. nov. and *K. soperi* - but also with radiodonts linked earlier in the clade, to which Stein (2010) alluded? Or are they an interesting case of convergence in organisms that are not closely related (not monophyletic), which independently evolved similar traits as a result of having to adapt to similar life habits?

It is beyond the scope of this article to attempt to solve the arthropod head problem. Indeed, the preservation of *Bushizheia yangi* gen. et sp. nov. does not allow assessment of the neurological connection of the raptorial appendage. Hence, we can only compare them to other appendages based on their morphology. Therefore, we explore the significance of the raptorial appendage of *B. yangi* gen. et sp. nov. and *K. soperi* in the context of some current interpretations of the homology of cephalic arthropodan appendages; more precisely, the interpretation of the nature of the 'great appendage' of radiodonts.

For Chen et al. (2004), Waloszek et al. (2005), Vannier et al. (2009), Haug et al. (2012a, 2012b), and Tanaka et al. (2013), the radiodonts, and other 'great appendage' arthropods belong to the lineage leading to chelicerates, and the 'great appendage' is homologous to the chelicera. Following this line of reasoning, the presence of the 'great appendage' in *Bushizheia yangi* gen. et sp. nov. and *K. soperi* would, in this case, most likely be homologous to the 'great appendage' of radiodonts. The presence of this 'great appendage' would tie *B. yangi* gen. et sp. nov., *K. soperi*, and 'great appendage' and 'short-great appendage' arthropods together. More precisely, within this group, *B. yangi* gen. et sp. nov., *K. soperi* and radiodonts would be one of the sister groups of chelicerates and 'short-great appendage' arthropods. The problem being to reconcile the apparently primitive scarcity of sclerites displayed by radiodonts with them being included in Euarthropoda, especially when considering that *B. yangi* gen. et sp. nov. and *K. soperi* are fully sclerotised. One solution to this problem would be to consider that radiodonts subsequently lost part of their tergites, perhaps due to their nektobenthic life habits. The sclerotisation of *B. yangi* gen. et sp. nov. and *K. soperi* in this scenario would then represent a primitive trait.

Another, currently more widely held view, is that radiodonts are not euarthropods, but belong to a series of sister groups to euarthropods (so called 'stem-group'), which documents the progressive transition from weakly sclerotised, segmented animals resembling lobopodians to fully sclerotised animals, the euarthropods (Waloszek et al., 2005). However, the results of two important phylogenies (Daley et al., 2009, Kühl et al., 2009) supporting this theory were criticised by Haug et al. (2012b) due to apparent discrepancies in the coding of some characters and taxa. The debate on the nature of radiodonts is not closed yet: the phylogenetic analyses of Legg and Vannier, (2013), Vin-

ther et al. (2014), Yang et al. (2015, 2018), Moysiuk and Caron (2019) and Aria et al. (2020) support a 'stem-group' affinity for radiodonts. In this scheme, *Bushizheia yangi* gen. et sp. nov. and *K. soperi* clearly belong to euarthropods, as explained above, and in this scenario the appendage similarity is either a convergence with the 'great appendage' of radiodonts, or, the 'great appendage' was retained in early euarthropods, and lost, or modified beyond recognition in most lineages of euarthropods.

The convergence hypothesis agrees with the interpretation of Budd (2002), who considered the 'great appendage' to represent a pre-antennular appendage that was transformed into the labrum (see Scholtz and Edgecombe, 2006; Cong et al., 2014; Ortega-Hernández et al., 2017; Daley et al., 2018; Park et al., 2018) in the group including euarthropods (see also Eriksson et al., 2003) for which there are lines of evidence *pro* (e.g., Siewing, 1969; Lauterbach, 1973; Rempel, 1975), *et contra* (e.g., Walossek and Müller, 1998; Wolff, 2004; Mayer et al., 2014; Aria, 2020). If we subscribe to the hypothesis that the 'great appendage' was lost or reduced into the labrum, then the presence of 'great appendage'-like frontal head limbs require convergence. Such convergence can be easily explained if *Bushizheia yangi* gen. et sp. nov. and *K. soperi* used their frontal head limbs in a fashion like predatory radiodonts.

Contrary to this last hypothesis, the composition and morphology of the raptorial appendage of *Bushizheia yangi* gen. et sp. nov. bears a striking resemblance to the plesiomorphic state of the raptorial appendage within radiodonts (i.e., the predatory, microphagous species). Other, probably distantly related species also have a seemingly similar raptorial appendage, e.g., the bradoriid *Kunmingella douvillei* (Mansuy, 1912) (see Zhai et al., 2019). This could give credence to the hypothesis that the great appendage was not reduced in a group including euarthropods, but rather was lost or reduced in a group within euarthropods.

In the case of *Bushizheia yangi* gen. et sp. nov., since we do not have access to the ventral surface of the animal, we cannot describe the position of the raptorial appendage. This prevents observation of the connection of this appendage to the head, and its exact nature. We can only hope that better preserved specimens may help us understand this animal better, and perhaps lead to a better understanding of the arthropod head.

Pygidium

Despite its overall similarity to *Kiisortoqia soperi* and the morphological similarity of its appendages with those of the radiodonts, the posterior of the animal is quite different. Disparity between *Bushizheia yangi* gen. et sp. nov. and *K. soperi* in this regard may well indicate that these are not closely related organisms. On a similar line of thought, similitude between *B. yangi* gen. et sp. nov. and trilobitomorpha due to the presence of a pygidium could have been acquired by convergent evolution, an allusion to the conspicuous resemblance of the appendages of aglaspidid-like arthropods with those of the nektaspid *Naraoia spinosa* Zhang and Hou, 1985 (Zhang and Shu, 2005). Alternatively, a plesiomorphic pygidium was retained in various arthropod groups (see Ortega-Hernández, 2013); such a scenario conflicts with Edgecombe and Ramsköld (1999), Cotton and Braddy (2004), and Paterson et al. (2010, 2012) in which the presence of the pygidium is synapomorphic for a clade composed by Xandarellida, Nektaspida, Conciliterga, and Trilobita.

Artiopoda Hou and Bergström, 1997 (e.g., Xandarellida, Nektaspida, Conciliterga and Trilobita) are arthropods with filiform antennulae (see Stein and Selden, 2011). *Bushizheia yangi* gen. et sp. nov. is *ipso facto* outside Artiopoda, *ergo* the presence of the pygidium is not synapomorphic for a clade composed by the aforementioned groups. If the interpretation of a plesiomorphic pygidium is correct, this would indicate that this structure was retained in some arthropod groups (e.g., *B. yangi* gen. et sp. nov. and Trilobitomorpha) but lost in many others.

PALAEOECOLOGY

A variety of arthropods from the Chengjiang biota were most likely predators (Vannier and Chen, 2002; Chen et al., 2004). The frontal head limbs of *Bushizheia yangi* are sturdy, predatory appendages, reminiscent of the 'great appendage' of radiodonts. The presence of limbs posterior of these frontal head limbs that bear paddle-shaped exopods suitable for swimming could be indicative of a nektobenthic habit (Stein, 2010). No eyes could be found in the specimen. If the eyes in *B. yangi* gen. et sp. nov. were situated under the anterior border of the head shield, as in e.g., *Leandrocholla illecebrosa* (Hou, 1987), it is possible that they, together with the other ventral features of that area, were not preserved. The alternative hypothesis is that *B. yangi* gen. et sp. nov. was blind.

Although visual perception in animals plays an important role in prey detection, other senses are used by animals in pinpointing their prey; the absence of eyes does not preclude *B. yangi* gen. et sp. nov. from being a predator. In the case where visual perception is lacking, *B. yangi* gen. et sp. nov. may have been an ambush predator, lying in wait, and catching unsuspecting prey with its anteroventral raptorial appendage.

CONCLUSION

Bushizheia yangi gen. et sp. nov. possesses a fully arthrodised body and limbs and consequently rests comfortably within the Euarthropoda (Aria, 2019). The present data neither confirms nor refutes any of the current interpretations of the homology of cephalic arthropodan appendages and although the phylogenetic position of *B. yangi* gen. et sp. nov. is difficult to resolve because few ventral structures are visible, the many euarthropod plesiomorphies possessed by the taxon may indicate a basal position of the species, and it demonstrates the importance of fossils in characterising ground patterns, as mentioned by, amongst other authors, Stein (2010).

The dorsoventrally flattened exoskeleton and paddle-shaped exopods that are suitable for swim-

ming suggest a nektobenthic mode of life and *Bushizheia yangi* gen. et sp. nov. likely used its 'great appendage'-like frontal head limbs for predation.

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