



MULTI-SEGMENTED ARTHROPODS FROM THE MIDDLE CAMBRIAN OF BRITISH COLUMBIA (CANADA)

DAVID LEGG

Department of Earth Science and Engineering, Imperial College London, South Kensington Campus, London SW7 2AZ, UK and Department of Earth Sciences, The Natural History Museum, London SW7 5BD, UK, <d.legg10@imperial.ac.uk>

ABSTRACT—A new arthropod, *Kootenichela deppi* n. gen. n. sp., is described from the Stanley Glacier exposure of the middle Cambrian (Series 3, Stage 5) Stephen Formation in Kootenay National Park (British Columbia, Canada). This taxon possesses a number of primitive arthropod features such as an elongate, homonomous trunk (consisting of at least 29 segments), poorly sclerotised trunk appendages, and large pedunculate eyes associated with an anterior (ocular) sclerite. The cephalon encompasses a possible antenna-like appendage and enlarged raptorial appendages with a bipartite peduncle and three spinose distal podomeres, indicative of megacheiran (“great-appendage” arthropod) affinities. The relationships of megacheirans are controversial, with them generally considered as either stem-euarthropods or a paraphyletic stem-lineage of chelicerates. An extensive cladistic analysis resolved *Kootenichela* as sister-taxon to the enigmatic *Worthenella cambria* from the middle Cambrian (Series 3, Stage 5), Burgess Shale Formation in Yoho National Park (British Columbia), which is herein reinterpreted as a megacheiran arthropod. Based on their sister-group relationship, both taxa were placed in the new family Kootenichelidae, to which *Pseudoiulia* from the Chengjiang biota is also tentatively assigned. All of these taxa possess an elongate, multi-segmented body and subtriangular exopods. This family occupies a basal position within a paraphyletic Megacheira, the immediate outgroup of Euarthropoda (crown-group arthropods). The resultant topology indicates that analyses that have resolved megacheirans as stem-chelicerates have done so because they have rooted on inappropriate taxa, e.g., trilobitomorpha and marrellomorpha.

INTRODUCTION

“**G**REAT-APPENDAGE” ARTHROPODS (formally Megacheira Hou and Bergström, 1997), so-called because they possess enlarged raptorial frontal appendages, have figured prominently in discussions of arthropod phylogeny. These arthropods have generally been considered representatives of either the chelicerate stem-lineage (Cotton and Braddy, 2004; Dunlop, 2006; Haug et al., 2012b), or the euarthropod stem-lineage (Budd, 2002; Daley et al., 2009; Legg et al., 2012). The former interpretation is based on structural similarities between the “great-appendages” of megacheirans and the chelicerae of chelicerates (pycnogonids, horseshoe crabs, arachnids, and the extinct eurypterids); both of which are chelate or subchelate raptorial appendages with a distinctive elbow joint (Haug et al. 2012a, 2012b). The latter was originally proposed based on an absence of morphology characteristic of crown-group clades (Hou and Bergström, 1997), but has since found support in phylogenetic analyses (Budd, 2002; Daley et al., 2009; Legg et al., 2012). In some instances (e.g., Budd, 2002) the “great-appendage” has been compared to the enlarged frontal appendages of anomalocaridids, although they show little structural similarity. The two hypotheses are not mutually exclusive, some workers suggesting that megacheirans represent a transitional grade of organisation between anomalocaridids and chelicerates (Chen et al., 2004; Haug et al., 2012b). However, this hypothesis has not been demonstrated phylogenetically and is based on a priori assumptions of frontal limb evolution.

Herein a new “great-appendage” arthropod, *Kootenichela deppi* n. gen. n. sp., is described, from the recently studied (Caron et al., 2010) middle Cambrian (Series 3, Stage 5) Stanley Glacier exposure of the “thin” Stephen Formation in Kootenay National Park (British Columbia, Canada). This taxon shows a remarkable similarity to the putative annelid *Worthenella*

cambria Walcott, 1911, from the nearby Walcott Quarry exposure of the Burgess Shale Formation in Yoho National Park, which is herein reinterpreted as a “great-appendage” arthropod. The phylogenetic position of these taxa and their bearing on euarthropod evolution was examined by coding them into the most comprehensive cladistic analysis of fossil and recent panarthropods to date (Legg et al., 2012).

Abbreviations used in figures are as follows: an, antenna; as, anterior sclerite; atp, anterior tergal process; ca, cephalic appendage; cs, cephalic shield; dga, distal podomeres of “great-appendage”; dp, distal podomeres; en, endopod; ep, eye peduncle; ex, exopod; ga, “great-appendage”; le, lateral eye; mga, medial article of “great-appendage”; mg, midgut gland; mo, mouth; oc, ocelli; pa, peduncle article; pga, proximal “great-appendage” article; rga, right “great-appendage”; rle, right lateral eye; sf, setal fringe; t1–50, trunk somites 1–50; te, telson; tf, trace fossils; tp, telson processes.

PHYLOGENETIC METHODOLOGY

Kootenichela deppi n. gen. n. sp. has previously been included in a phylogenetic analysis of panarthropods as “Stanley Glacier” (Legg et al., 2012). This taxon was originally coded using photographs published in Caron et al. (2010) and has been modified based on direct observation of the material presented herein. Specifically, in the original analysis *Kootenichela* was coded as possessing a cephalon with four limb-bearing segments and the presence of an anterior (ocular) sclerite was coded as uncertain (see taxon description for current interpretations of these characters).

To this data set three additional taxa were added, *Worthenella*, *Jianfengia* Hou, 1987 and *Tanglangia* Luo and Hu in Luo et al., 1999. The latter two were coded based on their original descriptions, photographs in Hou et al. (2004) and additional information provided by Dr. Xiaoya Ma (The Natural History

Museum, London) and Dr. Derek Siveter (University Museum of Natural History, Oxford). Although *Pseudoiulia* Hou and Bergström, 1998, shows striking similarities to *Kootenichela* and *Worthenella* it is based on anatomically incomplete material and an examination of additional photographs of described material (provided by Dr. Derek Siveter) did not provide useful information on characters for coding.

Character 163 of Legg et al. (2012), "Shape of exopods," was modified to include the state "(3) subtriangular (fin-shaped)" to accommodate morphologies observed in both *Kootenichela* and the newly added taxa. In the original phylogenetic analysis the morphology of the exopods was coded as uncertain as they could not be determined using the previously published photographs of this taxon.

Cladistic analysis was undertaken using TNT (Tree analysis using New Technology) v. 1.1. (Goloboff et al., 2008a). The large size of the data set (176 taxa and 580 characters; see online Supplemental Data file) necessitates the use of New Technology search options. These were undertaken using 100 Random Addition Sequences with Parsimony Ratchet (Nixon, 1999), Sectorial searches, Tree Drifting and Tree Fusing (Goloboff, 1999). Experimentation was able to determine that default settings for these options were sufficient to find the most parsimonious trees. Multistate characters were treated as non-additive (unordered) and weighted using both equal weighting and implied weighting with a variety of concavity constants ($k=1, 3, \text{ and } 10$). Implied weighting is the favored weighting option from a philosophical standpoint (Legg et al., 2012), and has been shown to increase character support and reduce the sensitivity of the data set to the inclusion of additional taxa and/or characters (Goloboff et al., 2008b). Few methods of determining nodal support are unaffected by character weighting, although Symmetric Resampling is most appropriate in such instances (Goloboff et al., 2003). Symmetric Resampling used 100 replicates, using New Technology search options including Parsimony Ratchet, Sectorial searches, Tree Drifting and Tree Fusing, with a change probability of 33%. Nodal support is expressed as Group present/Contradicted (GC) frequency differences.

SYSTEMATIC PALEONTOLOGY

Phylum ARTHROPODA Siebold, 1848

Class "MEGACHEIRA" Hou and Bergström, 1997

Family KOOTENICHELIDAE new family

Type genus.—*Kootenichela* n. gen.

Included genera.—*Worthenella* Walcott, 1911, and possibly *Pseudoiulia* Hou and Bergström, 1998.

Diagnosis.—Elongate arthropods with a trunk of at least 25 somites and subtriangular exopod flaps fringed with fine setae.

Remarks.—The diagnosis of this family is based on morphological similarities between *Kootenichela* and *Worthenella*, the sister-taxon relationship of which is supported by their positions in the phylogenetic analysis performed herein. The lower Cambrian arthropod *Pseudoiulia cambriensis* Hou and Bergström, 1998, conforms to this familial diagnosis, but due to its incomplete preservation was not included in the current phylogenetic analysis and is thus only tentatively assigned to Kootenichelidae.

Genus KOOTENICHELA new genus

Type species.—*Kootenichela deppi* n. gen. n. sp. by monotypy.

Diagnosis.—Distinguished from other kootenichelids by the presence of an elongate trunk with at least 29 segments and a pair of "great-appendages" consisting of a bipartite proximal peduncle

and three spine bearing podomeres, the proximal of which is recurved and accounts for 70% of total appendage length.

Etymology.—After Kootenay National Park, where material referred to this taxon was discovered, and *chela* (Latin for "claw"), in reference to the raptorial frontal appendage.

KOOTENICHELA DEPPI new species

Figures 1–4

2010 "Great Appendage arthropod A" CARON et al., p. 813m, fig. 3F.

Diagnosis.—Short cephalon encompassing an ocular segment with a large pair of pedunculate lateral eyes, and a pair of "great-appendages," midgut glands anastomosing.

Description.—The description refers to the holotype ROM 59948 (Figs. 1.1, 1.2, 2.1, 2.2, 3), except where otherwise noted. The cephalon is 4 mm long (<10% preserved body length), measured from the anterior-most margin to the postero-dorsal margin. This is best preserved in the part (Figs. 1.1, 2.1, 3) and consists of two distinct regions: a narrow anterior (i.e., an anterior sclerite) and an expanded posterior. The anterior region bears two large pedunculate eyes 0.9 mm in diameter; a small rounded stain within the cephalon is the right eye and appears to preserve individual lenses. Individual lenses can also be distinguished on the left eye (Fig. 3) and number 50/mm². The posterior margin of the cephalon curves antero-ventrally and encompasses at least the "great-appendages" and possibly an antenna-like appendage on the ocular segment. There are no other cephalic limbs although the posterior of the cephalon appears to overlap the first trunk tergites, which led to the previous misinterpretation that it possessed four-limb bearing segments. Numerous striations in the posterior part of the cephalon (Fig. 3) may indicate that it was convex in life and was crushed post-mortem. The putative antenna is preserved as a narrow, almost filamentous staining with little structural detail. This structure is interpreted as a true biological structure rather than abiogenic staining, which is not found elsewhere in material from this horizon. Gaps in the staining may represent antennal segments. The "great-appendages" are composed of a bipartite proximal peduncle and three distal spine-bearing podomeres. Although poorly preserved in the holotype, the spines have similar proportions and degree of recurvature to those in a well-preserved isolated pair of co-occurring "great-appendages" that are herein considered conspecific (ROM 61521; Figs. 1.3, 2.5). The most proximal spine-bearing podomere has the longest spine, 11.1 mm in length (70% total appendage length), less robust than the others and slightly recurved. An anterior gut trace is preserved; this documents a ventrally directed mouth (Fig. 3) and extends into the anterior cephalic region (Figs. 1.1, 1.2, 2.1, 2.2), where the dark staining may result from gut-rupture. Midgut glands extend from the gut into the posterior cephalon and trunk (Figs. 1.1, 1.2, 2.1, 2.2) and consist of tri- or tetra-radiate finger-like projections. They extend posteriorly to (at least) segment 6, and a strand of unbranched gut is preserved between segments 8 and 15 (Figs. 1.1, 1.2, 2.1, 2.2). The preserved part of the trunk in the holotype is 43.5 mm long and consists of 29 segments; the posterior is missing, but may be preserved in ROM 61520 (Figs. 1.4, 1.5, 2.3, 2.4) where possible lateral projections are preserved at the posterior of the specimen. The latter is a dorso-ventrally preserved trunk section consisting of at least 29 segments, tapering posteriorly. Each segment bears a single pair of limbs. The limbs are poorly preserved in all specimens making identification difficult, however in the holotype stout, multi-annulated endopods are preserved underneath triangular exopods, the latter evident by their dark setal fringe (Figs. 1.1, 2.1). There is no evidence of a gnathobasic protopodite and given the extent of the annulation in the appendages it is unlikely this animal possessed them.

Etymology.—After the actor Johnny Depp for his portrayal of

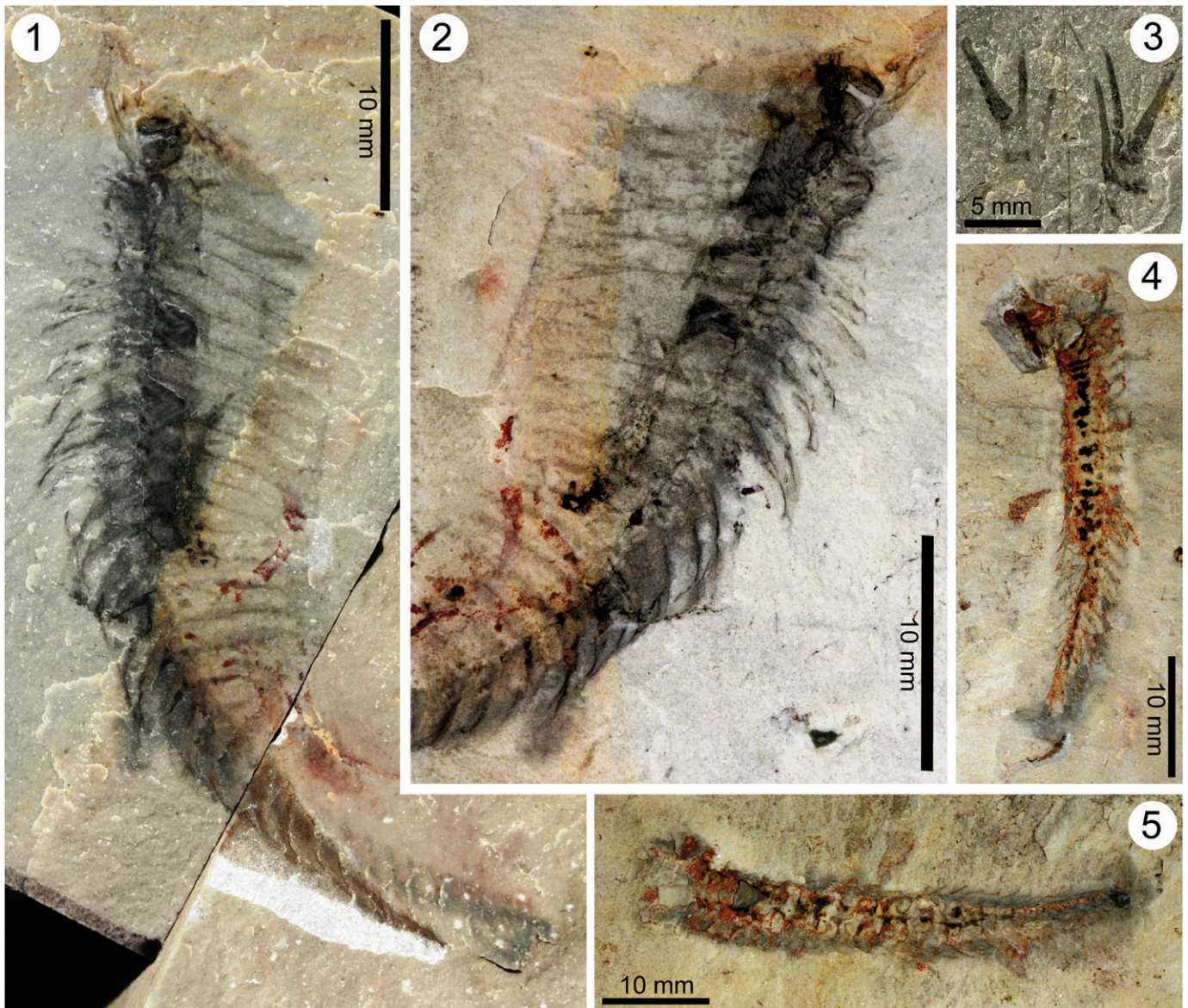


FIGURE 1—Specimens of *Kootenichela deppi* n. gen. n. sp. 1, 2, part and counterpart of the holotype ROM 59948; 3, ROM 61521, an isolated pair of “great-appendages”; 4, 5, part and counterpart of ROM 61520.

Edward Scissorhands in the 1990 film of the same name. The hands of which are reminiscent of this taxon.

Types.—Holotype, ROM (Royal Ontario Museum, Toronto, Canada) 59948 (Figs. 1.1, 1.2, 2.1, 2.2, 3), a near complete specimen preserved in an oblique-lateral orientation, consisting of a cephalon and an elongate trunk, the posterior of which is missing. Paratypes, ROM 61521 (Figs. 1.3, 2.5), a pair of isolated “great-appendages”, and ROM 61520 (Figs. 1.4, 1.5, 2.3, 2.4), an isolated trunk with poorly preserved limbs and a possible telson.

Occurrence.—Specimens were collected from the mudstone layers of Cycle 5 of the Waputik Member (Stephen Formation), Stanley Glacier locality, Kootenay National Park, British Columbia, Canada (Caron et al., 2010), stratigraphically equivalent to the Marpole Limestone Member of the Burgess Shale Formation in the nearby Yoho National Park (Cambrian, Series 3, Stage 5; *Pagetia walcotti* subzone, *Bathyriscus-Elrathia* zone).

Remarks.—The presence of a short raptorial frontal appendage in *Kootenichela* (Fig. 4) clearly indicates affinities with Megacheira. Amongst this group *Kootenichela* shows most similarities to the Chengjiang megacheirans *Fortiforceps foliosa* Hou and

Bergström, 1997, and *Jianfengia multisegmentalis* Hou, 1987. All taxa possess a long, homonomous trunk (20 segments in *Fortiforceps*, 25 in *Jianfengia*), with multi-podomerous appendages consisting of >10 segments. The Chengjiang taxa also possess telsons with modified lateral processes (Hou and Bergström, 1997; Strausfeld, 2012), making their possible presence in *Kootenichela* more plausible. *Kootenichela* differs from these taxa in possessing only three spine-bearing articles in its “great-appendage,” whereas the others have four (Haug et al., 2012b). In this regard the appendages are more like those of *Haikoucaris* (Chen et al., 2004) or *Leanchoilia* (Liu et al., 2007; Haug et al., 2012a), although few other features are common to these taxa.

Genus WORTHENELLA Walcott 1911

Type species.—*Worthenella cambria* Walcott, 1911 by monotypy.

Diagnosis.—Kootenichelid with an elongate trunk composed of 50 segments.

Remarks.—The diagnosis presented herein reflects the placement of the genus in the new arthropod family Kootenichelidae.

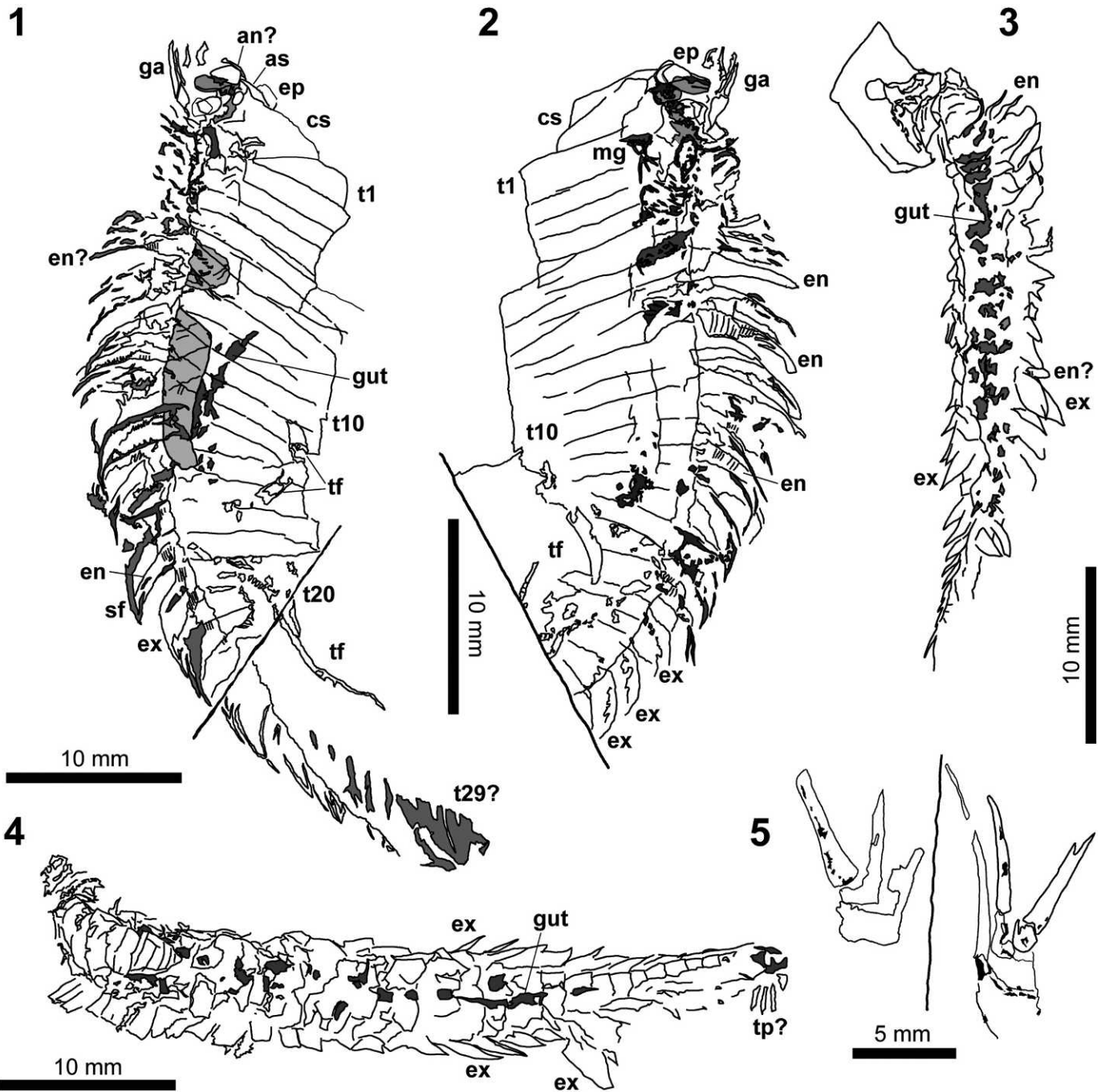


FIGURE 2.—Interpretive camera lucida drawings of *Kootenichela deppi* n. gen. n. sp. 1, 2, part and counterpart of the holotype ROM 59948; 3, 4, part and counterpart of ROM 61520; 5, ROM 61521.

WORTHENELLA CAMBRIA Walcott 1911

Figures 5, 6

- 1911 *Worthenella cambria* WALCOTT, p. 125, 153, pl. 22, fig. 2.
- 1916 *Worthenella cambria*; OSBORN, p. 1228, fig. 25.
- 1927 *Worthenella cambria*; WALTON, p. 240, 243, figs. 4, 6.
- 1942 *Worthenella cambria*; MILLER, p. 123, fig. 69B.
- 1979 *Worthenella cambria*; CONWAY MORRIS, p. 336.
- 1986 *Worthenella cambria*; BRIGGS AND CONWAY MORRIS, p. 179, fig. 16.
- 1994 *Worthenella cambria*; BRIGGS ET AL., p. 221.

Type.—Holotype and only specimen, USNM (United States National Museum of Natural History, Washington D.C., U.S.A.) 57643 (Figs. 5, 6), a near complete specimen preserved in lateral orientation.

Diagnosis.—Trunk segments with an anterior ridge and lacking extensive lateral pleura.

Description.—USNM 57643 (Figs. 5, 6) has a preserved length of 59.6 mm. The cephalic region accounts for just 5% of the entire body length (3.2 mm). In the original description of this taxon, Walcott (1911) noted the presence of a reflective spot is possibly indicative of an eye. Under direct light a single reflective spot is present on the left antero-lateral margin of the cephalon (Fig. 5.1,

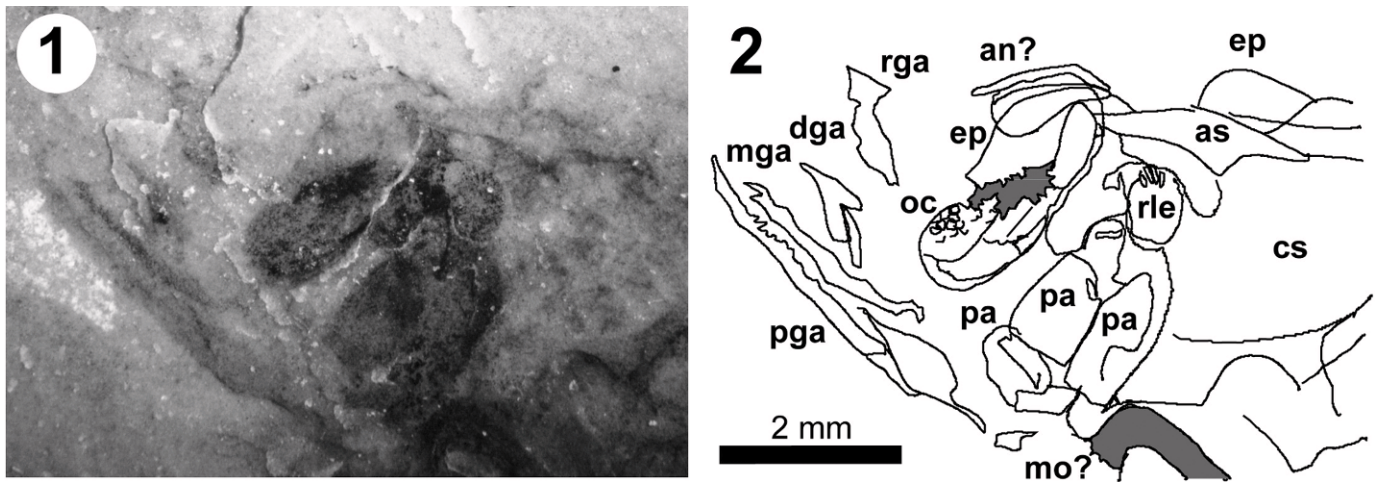


FIGURE 3—*Kootenichela deppi* n. gen. n. sp. 1, anterior head region of ROM 59948a; 2, interpretive camera lucida drawing of 1.

5.3). A second eye on the right antero-lateral margin of the cephalon, approximately 2 mm in diameter, is observable under polarized light (Fig. 5.2). A small rectangular area between the eyes may represent an anterior sclerite (Figs. 5, 6). Walcott (1911) noted the presence of two limb types in the head region which he interpreted as an anterior pair of jointed tentacles, and a posterior pair of long filamentous palps. The later structures, best observed under direct lighting, are here interpreted as part of a “great-appendage” (Figs. 5.3, 6.1). Although individual segments are indistinguishable, a distinct rounded segment may represent the proximal spinose article. Definitive structures anterior to this

antenniform appendage could not be distinguished, although a fragment of cuticle, possibly representing the basal segments of the right antenna, could be observed using polarized light (Fig. 5.2). The trunk of this taxon is clearly split into discrete articles separated by soft-tissue, i.e., arthrodized somites (Figs. 5, 6). Such segmentation is very distinct from that of annelids which lack discrete sclerotized plates. Fifty trunk segments could be distinguished (Figs. 5.1, 5.2, 6), four more than indicated by Walcott (1911). Some somites possess distinctive ridges. These structures can best be seen on somites 3 and 4 (Figs. 5.1, 5.3, 6). The trunk tapers towards the posterior with the anterior somites (represented by somite 6) measuring 4.6 mm high and 1.5 mm long, and the posterior somites (represented by somite 39) measuring 1.07 mm by 0.71 mm. The structures formally identified as bipartite parapodia on somites 9–35 are clearly evident under direct light; under polarized light however these can be seen to represent instead the most proximal elements of arthropodized limbs. Each appendage is tapered, indicative of trunk endopods. Reflective areas at the posterior of the trunk may represent exopods (Fig. 5.1, 5.2, 6). If so they are sub-triangular, almost fin-shaped, and reminiscent of *Kootenichela*. A gap between the trunk somites and the trunk limbs was originally interpreted as an enteric canal. This structure has the same composition as the surrounding matrix (Fig. 5.2) and most likely represents a preservational artifact.

Occurrence.—The only specimen of *Worthenella* was collected from middle Cambrian (Series 3, Stage 5; *Pagetia bootes* subzone, *Bathyriscus-Elrathia* zone) Walcott Quarry Shale Member of the Burgess Shale Formation, exposed along Fossil ridge, between Mouth Wapta and Mount Field in Yoho National Park, British Columbia, Canada.

Remarks.—*Worthenella cambria* was originally considered a polychaete annelid of uncertain affinities (Walcott, 1911). The ventrolateral appendages were interpreted as bipartite parapodia, an interpretation followed by some subsequent workers (e.g., Walton, 1927). Osborn (1916) compared *W. cambria* to the extant polychaetes *Nereis virens* and *Arabella opalina* and speculated that it may have lived in a similar habit to these taxa. This species was largely ignored in subsequent works except for the occasional reference to miscellaneous polychaetes from the Burgess Shale (e.g., Miller, 1942; Ushakov, 1974). Conway Morris (1979) rejected polychaete affinities for this taxon, instead considering it a vermiform organism of uncertain affinities, or a possible uniramous arthropod (Briggs and Conway Morris, 1986) although later stating that it had a body plan prohibiting assignment to any known phylum (Conway Morris, 1989). The segmentation of the

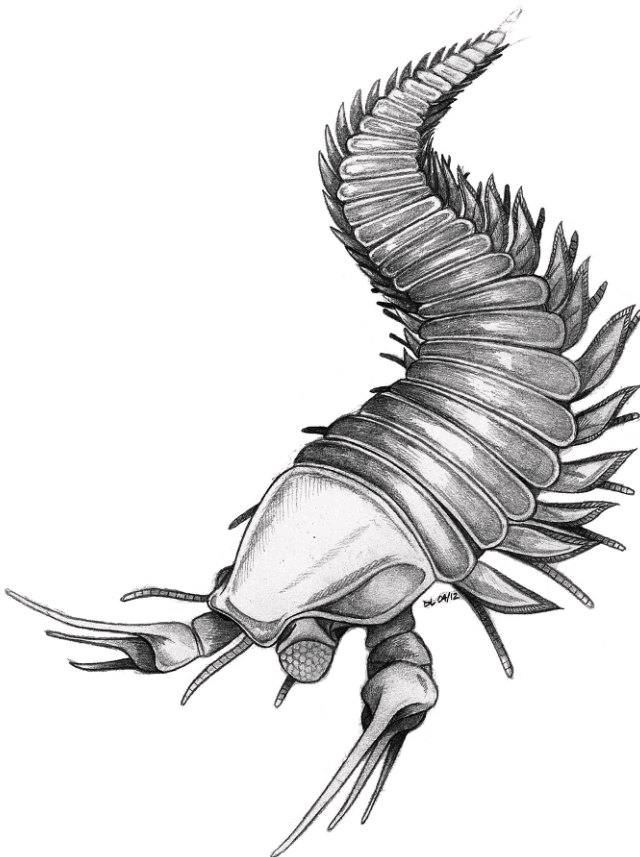


FIGURE 4—Reconstruction of *Kootenichela deppi* n. gen. n. sp.

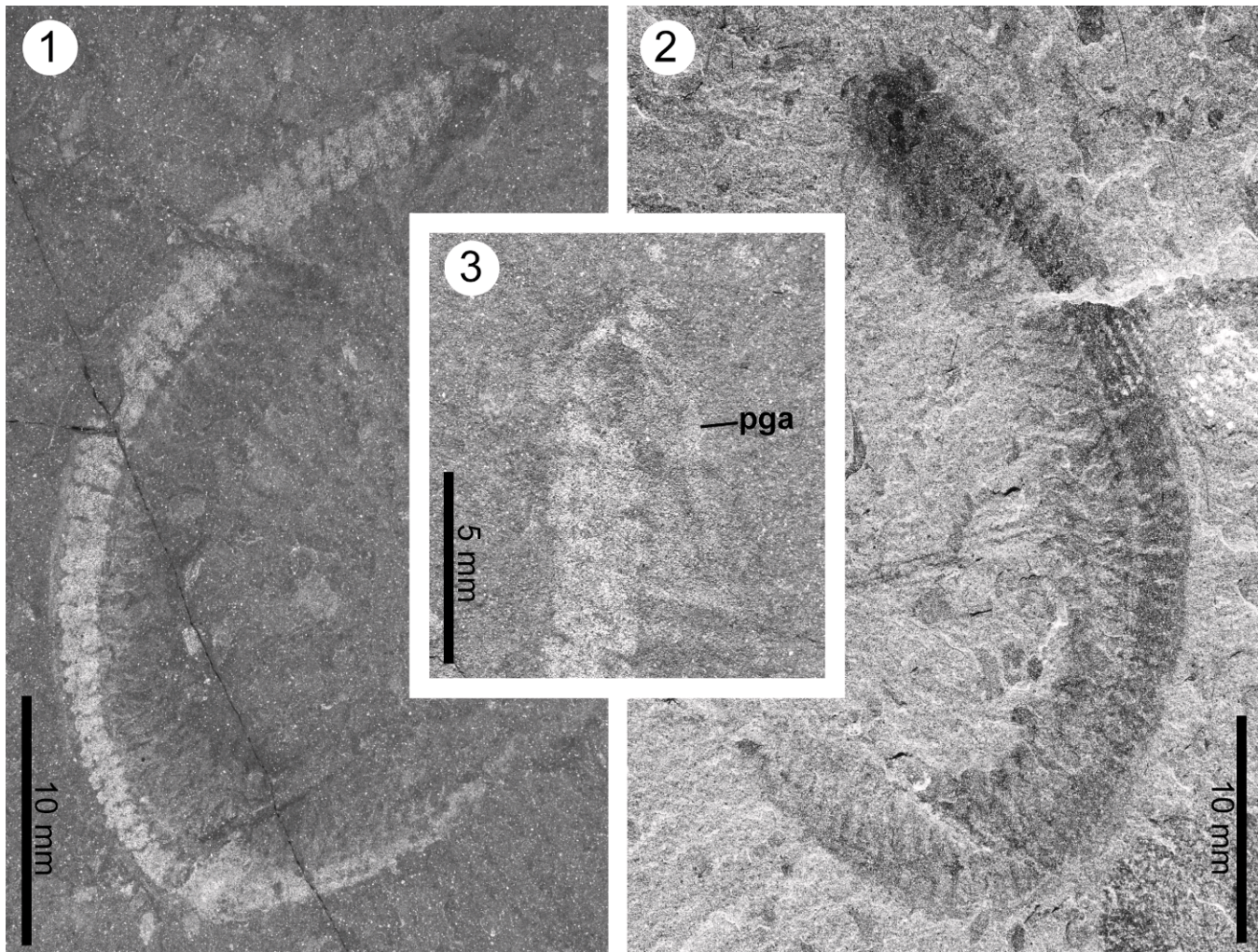


FIGURE 5—The type and only specimen of *Worthenella cambria* Walcott, 1911, USNM 57643. 1, part, in direct light; 2, counterpart, in cross-polarized light; 3, detailed view of the cephalic region of the part showing possible proximal “great-appendage” article (pga).

main body axis into discrete plates, i.e., arthrodisation, is instead indicative of arthropod affinities and is the interpretation favored herein. The long multisegmented trunk of *W. cambria* is reminiscent of a number of Cambrian arthropod taxa, such as *Pseudoiulia cambriensis* Hou and Bergström, 1998 and *Xanthomyria spinosa* Budd et al. 2001. These taxa have been allied to the Myriapoda (Budd et al., 2001), based on the shared presence of a long body with homonymous segments. This interpretation has been questioned because these taxa lack autapomorphies of Myriapoda (Edgecombe, 2004). Furthermore, a large number of segments appears to be a common feature amongst Cambrian arthropods, with many taxa possessing over 20 segments, e.g., *Fuxianhuia protensa* Hou, 1987, *Jianfengia multisegmentalis*, and *Fortiforceps foliosa*. In this regard *W. cambria* is unlike any other taxon from the Burgess Shale Formation, except *Kootenichela deppi*; both taxa possess a tapered, elongate and multisegmental trunk, subtriangular exopods and large pedunculate eyes. This morphology is also common amongst taxa from the earlier Chengjiang biota of southwest China. A long, slender and tapering trunk is prevalent in the so called “great-appendage” arthropods such as *Fortiforceps*, *Tanglangia* and *Jianfengia* (Hou et al., 2004). Amongst them, *W. cambria* most closely resembles *Jianfengia multisegmentalis*. Both taxa possess trunk somites which appear to lack extensive lateral pleura and possess ridged tergites.

DISCUSSION

Mode of life.—The presence of well-developed midgut glands in *Kootenichela* indicates either a predatory or scavenging mode of life (Butterfield, 2002). In extant arthropods midgut glands act as a phosphate storage. The midgut glands of *Kootenichela* are poorly phosphatized in the holotype which may indicate that this individual had gone a considerable time without food and had used up its phosphate stores (García-Bellido and Collins, 2007). Other evidence for a predatory lifestyle in megacheirans includes the possession of robust gnathobasic trunk appendages and well developed eyes. Although the latter are present in *Kootenichela* the former appear absent. Instead the enlarged frontal appendage may have been used to grasp and manipulate prey items, although how food was moved to the mouth is unclear.

Although megacheirans have traditionally been considered benthic (e.g., Bruton and Whittington, 1985) many later workers have considered them nektobenthic and capable of prolonged periods of swimming (e.g., García-Bellido and Collins, 2007; Haug et al., 2012a). Whereas it seems very likely that these organisms spent some time swimming in the water column, as many marine arthropods do, it seems unlikely this was the primary source of locomotion. Many extant benthic arthropods employ short bursts of swimming as an escape mechanism but spend the majority of their time amongst the benthos. This was also likely the case for the kootenichelids which show little if any

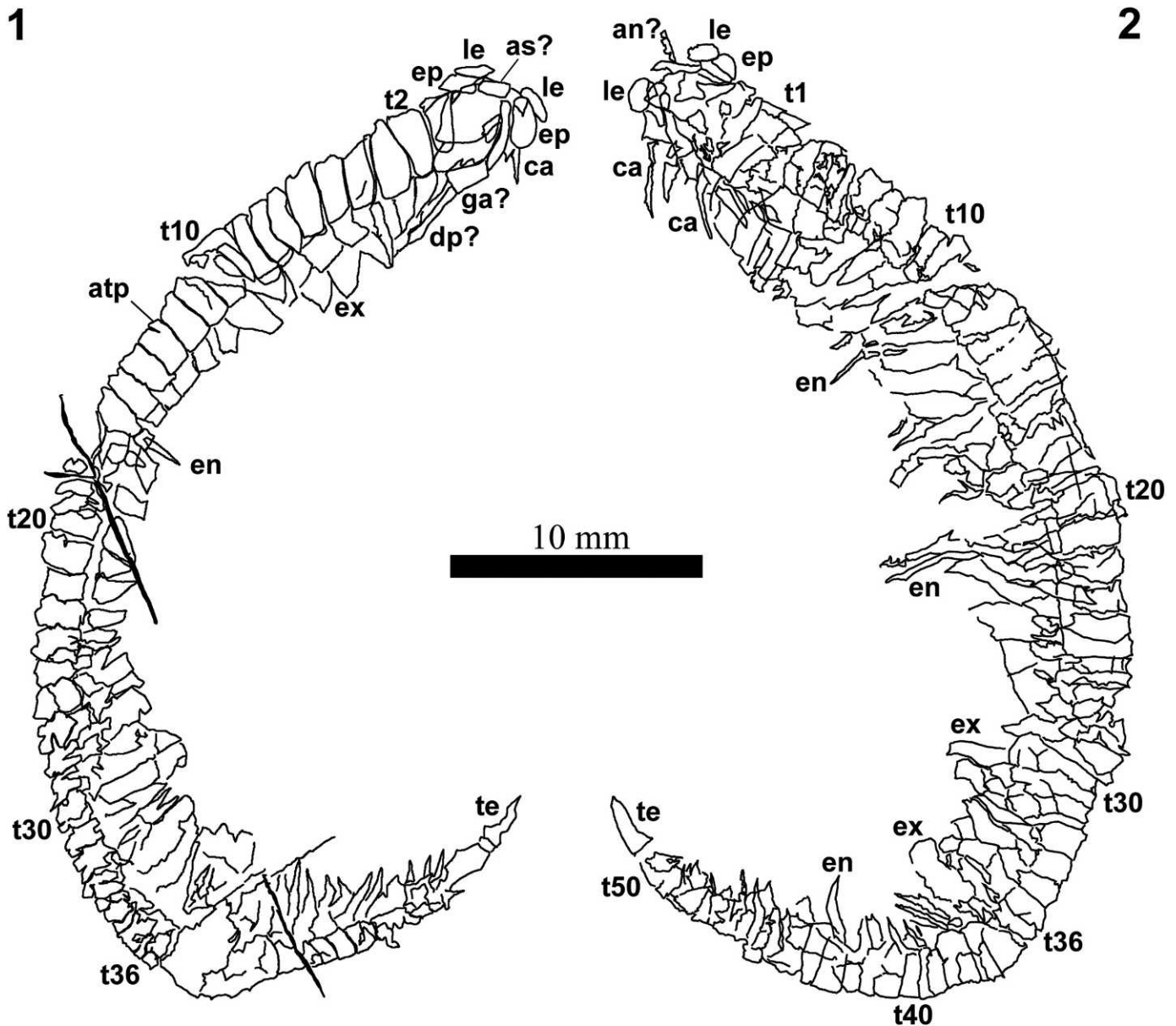


FIGURE 6—Interpretive camera lucida drawings of *Worthenella cambria* Walcott, 1911. 1, 2, part and counterpart of USNM 57643.

adaptations for a nektonic lifestyle however in the absence of direct evidence these any hypotheses regarding lifestyle will remain speculative.

Affinities and the status of Megacheira.—Relationships amongst the euarthropod stem-lineage were stable under different search parameters and character weighting schemes producing three MPTs (Most Parsimonious Trees) under Implied Weighting options ($k=1, 3,$ and 10), with character fits of 153.90476 (CI=0.559; RI=0.860), 92.07607 (CI=0.565; RI=0.864) and 40.48612 (CI=0.567; RI=0.865) respectively, and 83 MPTs of 1257 steps (CI=0.568; RI=0.866) under equal weighting. *Kootenichela* and *Worthenella* resolved as sister-taxa (Fig. 7), which in turn resolved as the basal-most representatives of a paraphyletic megacheiran clade. The current analysis resolved megacheirans as the paraphyletic outgroup of Euarthropoda (Fig. 7), broadly consistent with other phylogenetic analyses (e.g., Daley et al., 2009), although notably different from that of (Budd, 2002) which resolved megacheirans as the basal-most arthropod

group. The latter considered the “great-appendage” homologous to the labrum of later arthropods, and therefore derived from the protocerebral somite; this analysis also considered the “short great-appendages” of megacheirans homologous to the “long great-appendages” of anomalocaridids, a possible arthropod ancestor (Daley et al., 2009). This view is challenged herein. The “great-appendage” of megacheirans and the chelicerae of chelicerates possess a number of similarities, notably chelate or subchelate spines on the dorsal margin of their distal podomeres and a distinctive elbow joint (Haug et al., 2012a, 2012b); whereas the “great-appendage” of anomalocaridids is elongate (~14 podomeres), almost antenniform in some taxa (e.g., *Anomalocaris*), and possesses short spines that project perpendicular to the ventral appendage axis. A key taxon in this argument is *Parapeytoia*. This taxon was originally considered an anomalocaridid (Hou et al., 1995), but a number of studies have cast doubt on its affinities (e.g., Daley et al., 2009; Stein, 2010). A study of high quality photographs of this taxon (provided by Dr. Derek

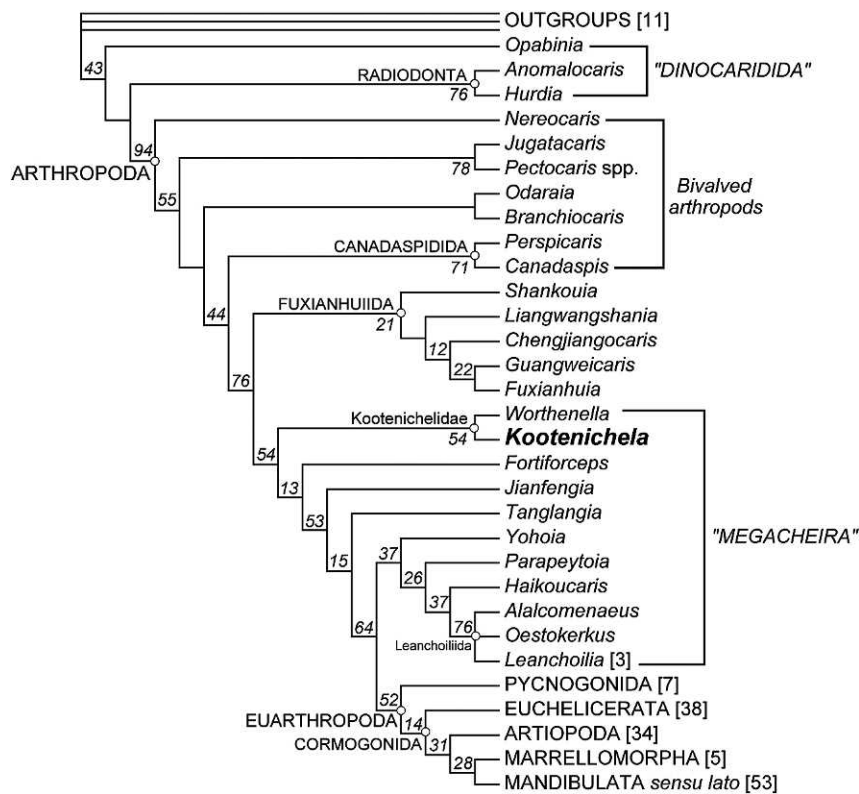


FIGURE 7—The phylogenetic position of *Kootenichela*, *Worthenella* and other stem-lineage euarthropods. Numbers above nodes are GC support values, taken for $k=3$ (which differ little from those of other k values). Numbers next to taxon names indicate the number of terminal taxa they encompass.

Siveter) was unable to identify any of the supposed anomalocaridid features originally described for this taxon, namely lanceolate blades and a Peytoia-like oral cone (Hou et al., 1995; Collins, 1996). The “great-appendages” of this taxon are also unlike those of anomalocaridids; with their reduced number of podomeres and subchelate dorsal spines they are more like those of megacheirans, and resolved as such in this analysis (Fig. 7). Coding this taxon as possessing the supposed anomalocaridid features did not change its position but expectedly increased tree length and increased levels of homoplasy. I therefore suggest that the “great-appendages” of anomalocaridids and megacheirans may not be homologous. It should also be noted that other studies that have supported a close relationship between anomalocaridids and megacheirans have not employed cladistic analysis (e.g., Chen et al., 2004), with some even claiming that phylogenetic analysis is un-parsimonious (Haug et al., 2012b). In the latter study the proposed relationships amongst “great-appendage” arthropods induce considerable amounts of homoplasy amongst included taxa and relied on ad hoc hypotheses of frontal appendage evolution. How this could be considered a more parsimonious approach to determining relationships is unclear. The claim that phylogenetic analysis is unparsimonious compared to ad hoc hypotheses of relationships shows a misunderstanding of both cladistic methodology and the principle of parsimony (Farris, 1983).

In the current analysis the chelicerates s.l. resolve as paraphyletic in that pycnogonids are instead the sister-taxon to all other euarthropods (=Cormogonida). This would indicate that a raptorial deutocerebral appendage is symplesiomorphic for euarthropods and is indeed present in the nearest outgroup, the megacheirans. Arguably studies that have resolved megacheirans as stem-lineage chelicerates differ little from the current topology but have used an inadequate root for their trees. For instance

Cotton and Braddy (2004) used marrellomorphs to root their phylogeny, and Edgecombe et al. (2011) used a trilobitomorph. Both these clades are crown-group arthropods in the present analysis, more specifically they are stem-group mandibulates, and therefore rooting a tree with them would result in the stem-lineage, i.e., megacheirans, being pulled crownwards towards the nearest non-mandibulate taxa, i.e., chelicerates. It would also produce a monophyletic Chelicerata, a result that was not obtained herein. This analysis employed a number of non-arthropod outgroups, preventing this effect and is therefore likely to be a more accurate depiction of megacheirans and euarthropod relationships.

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ACCESSIBILITY OF SUPPLEMENTAL DATA

Supplemental data deposited in Dryad repository: <http://dx.doi.org/10.5061/dryad.41r04>.

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