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A restudy of the Burgess Shale (Cambrian) arthropod *Emeraldella brocki* and reassessment of its affinities

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A restudy of the Burgess Shale arthropod *Emeraldella brocki* suggests novel interpretations of its morphology. We show that the morphology is more plesiomorphic than previously assumed, particularly regarding tagmosis. The cephalon probably only incorporates three limb-bearing postantennular segments. The trunk is not differentiated and consists of 12 tergite-bearing segments and a styliform telson. Limb structure is generally similar to that of other artiopods except for a tripartite exopod and a high degree of differentiation of podomere proportions along the body. A phylogenetic analysis of 20 fossil arthropod taxa based on 36 characters renders *E. brocki* as a basal taxon within a monophyletic group that comprises all artiopods included. Autapomorphies of this taxon are a filiform antennula and a bilobate exopod that carries lamellae proximally. Trilobites are nested within a group of artiopods sharing a pygidium. *Agnostus pisiformis* is retrieved as the sister taxon to the stem-lineage crustacean *Oelandocaris oelandica*, and both constitute the sister taxon of Artiopoda. 'Great appendage' arthropods, traditionally included in the Arachnomorpha, are retrieved as sister to the Crustacea *sensu lato* + Artiopoda clade, which contradicts the arachnomorph concept.

Keywords: *Emeraldella brocki*; Euarthropoda; 'arachnomorphs'; Artiopoda

Introduction

Emeraldella brocki Walcott, 1912 from the Burgess Shale of British Columbia has usually been affiliated with the large group of fossil arthropods that includes the trilobites, variously called Arachnata, Arachnomorpha or Lamellipedia. All of these concepts assume close relationships of trilobites and their allies with Chelicerata, a view that has recently been challenged (Chen *et al.* 2004; Scholtz & Edgecombe 2005; Hughes *et al.* 2008). *Emeraldella brocki* is an interesting taxon because some recent analyses (e.g. Cotton & Braddy 2004) have suggested a more recent shared ancestry with the Chelicerata than the remainder of the artiopods. There have been a number of uncertainties, though, regarding the morphology of *E. brocki*, in particular regarding limb morphology (Hou & Bergström 1997; Edgecombe & Ramsköld 1999). Since the last thorough treatment of the material by Bruton & Whittington (1983) is now almost 30 years old, the aim of the present paper is to restudy the available material and use the retrieved data in a phylogenetic analysis to reassess the relationships of the species.

Methods

All photographs were taken with a Canon EOS 5D Mk II on a macro stand using Canon compact-macro EF 50 mm 1:2.5 and Canon macro MP-E 65 mm 1:2.8 lenses with a polarizing filter and a polarized light source. All specimens were photographed with crossed polarizers (cf. Bengtson 2000) either dry or immersed in water. Extended depth of field images (cf. Haug *et al.* 2009a) were created from stacks of photographs in Adobe Photoshop CS4 using the autoblending of layers. Where the 65 mm lens was used, due to its narrow field of view, panoramas were stitched together from multiple extended depth of field images in Photoshop CS4. Measurements were taken in Macnification 1.7.1.

Terminology follows Stein *et al.* (2008). The term limb axis is here used for the compound of basipod and endopod. The reconstruction was created using Blender 2.49 (e.g. Stein *et al.* 2008).

The taxon–character matrix includes 36 characters coded for 20 taxa (see Online Supplementary Material). Many characters are similar or identical to characters used by Edgecombe & Ramsköld (1999) and Cotton & Braddy (2004). This is indicated in the discussion of the characters. The analysis was carried out in TNT (Goloboff *et al.* 2008; made available with the sponsorship of the Willi Hennig Society) using implicit enumeration. Multi-state characters were treated as unordered. Jackknifing (Farris *et al.* 1996) and Bremer support (Bremer 1994) values were calculated in TNT. The consistency and retention

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indices were calculated in Mesquite 2.73 (Maddison & Maddison 2010).

Systematic palaeontology

Artiopoda Hou & Bergström, 1997

Emended diagnosis. Arthropods with filiform antennulae and postantennular limbs with a bilobate exopod with lamella-bearing elongate proximal portion and setiferous paddle-shaped distal portion. Endopod of seven podomeres (possible plesiomorphy) with podomeres one through four enditic, five and six stenopodous. Plesiomorphies in ground pattern helpful for diagnosis in combination with above: head shield incorporates antennulae and at least three postantennular limbs, little or no differentiation of postantennular limbs, broad paratergal folds contributing to dorsoventrally flattened appearance.

Emeraldella Walcott, 1912

Type species. *Emeraldella brocki* Walcott, 1912. Monospecific.

Emended diagnosis. Artiopod of up to at least 60 mm total length excluding telson. Head incorporating antennular and three limb-bearing postantennular segments (plesiomorphy). Trunk of 12 segments, 12th segment is elongate with reduced tergopleurae, carries caudal flaps ventrally. Telson styliform, reaching length of trunk, lateroventrally flanked by caudal flaps. Antennulae reaching length of trunk, composed of more than 80 articles. Strong differentiation of proportions of endopod podomeres along body; endopod curves outward proximally, downward at short, knee-like, fifth podomere. Sixth podomere long, distinctly stenopodous. Exopod tripartite; proximal and middle parts articulated with basipod and first podomere respectively. Lamellae on proximal part wide with fine setules distally. First postantennular limb with reduced number of podomeres, no exopod.

Occurrence. Cambrian stage 3, Burgess Shale Formation, Walcott Quarry Member, Fossil Ridge, British Columbia, Canada. Possibly also in the Wheeler Shale Formation, Drum Mountains, western Utah, USA.

Remarks. Briggs & Robison (1984) described a single specimen from the Marjum Formation in the House Range, western Utah, as an indeterminate species possibly belonging to *Emeraldella*. The specimen (KUMIP 204791, part and counterpart, deposited in the University of Kansas Natural History Museum and Biodiversity Research Center) is poorly preserved and it is difficult to discern diagnostic characters. The specimen is here regarded as indeterminate. Another, as yet undescribed specimen from the Wheeler Shale in the Drum Mountains of western Utah may represent *Emeraldella*.

Emeraldella brocki Walcott, 1912
(Figs 2–12)

1911 *Sidneya inexpectans* Walcott: 26, pl. 2, figs 2, 3.
1912 *Emeraldella brocki* Walcott: 153, pl. 30, fig. 2; text-fig. 8.
1912 *Sidneya inexpectans* Walcott; Walcott: 205, text-fig. 10.
1959 *Emeraldella brooki* Walcott; Størmer: fig. 17.
non 1983 *Emeraldella brocki* Walcott; Bruton & Whittington: 555, fig. 53, pl. 9, figs 57, 59.

Diagnosis. As for genus.

Material. All studied specimens of *Emeraldella brocki* Walcott, 1912 are deposited at the National Museum of Natural History, Smithsonian Institution, Washington, DC. The single specimen stored at the Royal Ontario Museum (R.O.M. 37850; Bruton & Whittington 1983) has not been studied. The provenance and preservation of the material are described by Bruton & Whittington (1983). The lectotype, USNM 57702, was designated by Bruton & Whittington (1983). Of the 24 other specimens, 23 are here considered conspecific: USNM 57488, 136439–136442, 144917–144924, 144926–144930, 144932–144934, 250227 and 250230. Among these, there is considerable variation in the ratio of cephalic length to width (0.30–0.55). The values could only be measured for eight specimens; others were either incomplete or too distorted. Distortion generally is a problem and may have contributed in some degree to the variation. Specimens are similar in morphology apart from the length/width ratios and are therefore considered conspecific.

USNM 144925, the holotype of *Emeraldoides problematicus* Simonetta, 1964, was included by Bruton & Whittington (1983) in *Emeraldella brocki* but is here excluded from this species. The spine-like projection in the posterior portion of the counterpart (Fig. 1B, arrow), interpreted by Bruton & Whittington (1983) as the telson, seems to be part of a larger fan-like structure. This structure appears to be on a slightly different shale surface and it is not entirely clear if it belongs to the specimen. The podomeres of the endopod do not seem to be differentiated in length, as is characteristic for *E. brocki*, and the exopods, seen in the part (Fig. 1A), are almost equal in length to the endopods.

Occurrence. As for genus.

Description. The head shield is semielliptical in outline, wider than long, without marked trilobation. The posterior border of the head shield is nearly straight. The number of limb-bearing postantennular segments in the head is hard to assess from the limbs directly because the proximal portions

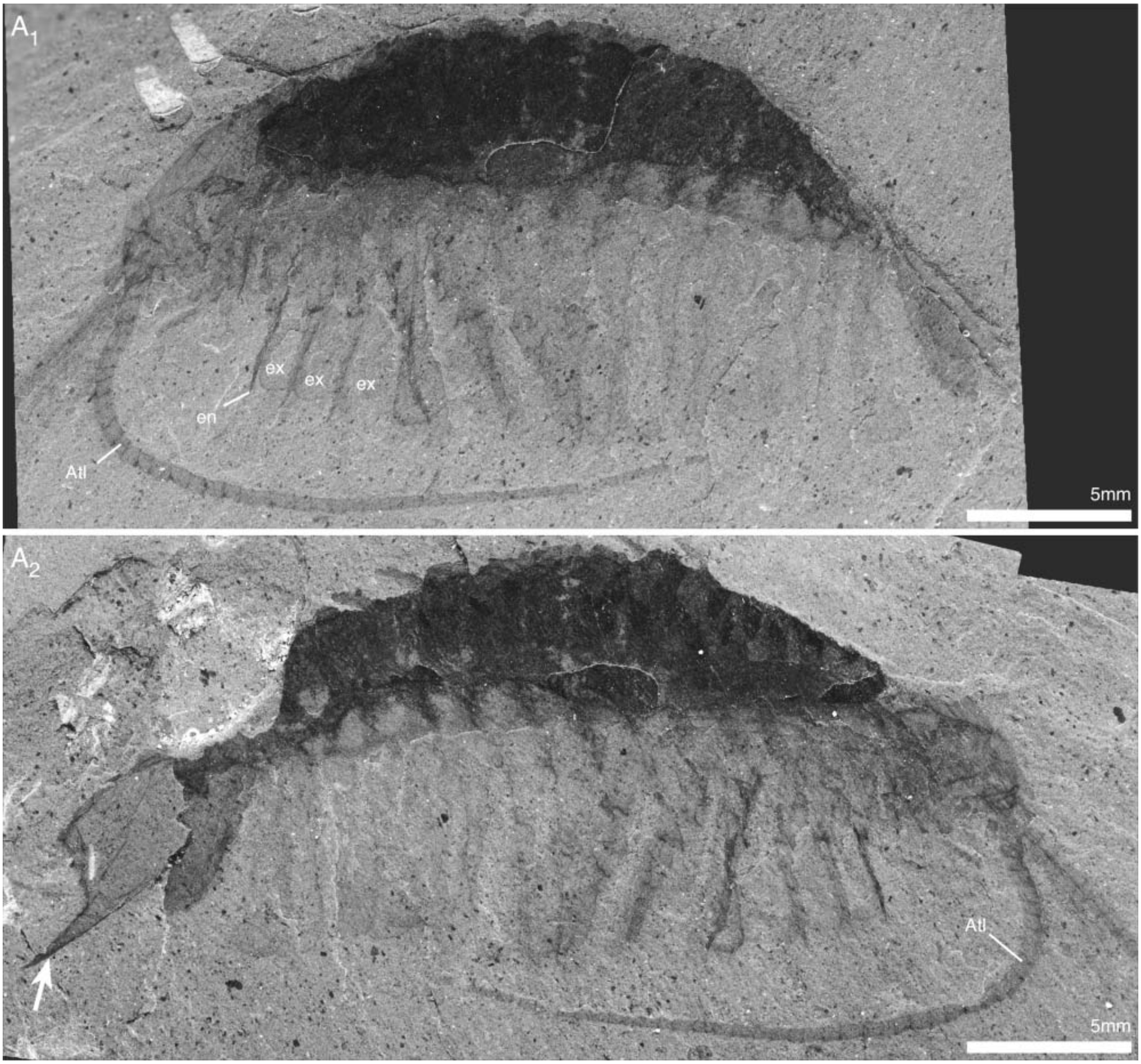

Figure 1. *Emeraldoides problematicus* Simonetta, 1964, USNM 144925: **A$_1$,** part; **A$_2$,** counterpart. Arrow points to spine-like projection that seems to be part of the tail. Abbreviations: Atl, antennula; en, endopod; ex, exopod.

of the cephalic limbs are poorly known. The midgut diverticula give a proxy. There are four pairs of diverticula in the head (Fig. 2), the most anterior of which probably belongs to the antennular segment (see below), indicating the presence of three postantennular segments.

The trunk has 12 tergite-bearing segments plus the telson. The tergites are trilobate, but trilobation may be obscured by flattening. There is some indication that trilobation continued at least into the posterior quarter (sag.) of the head shield (Fig. 2). The axis constitutes roughly one third the width of the tergites. The posterior margin of the tergites is nearly straight across the axis, bending posteriorly at the tergopleura (Fig. 3A, B1). The last tergite is elongated (sag.) and has strongly reduced tergopleurae (Fig. 3).

The posterior margin of each individual tergite is more strongly arched backwards than its anterior one. The tergites are thus longest (sag.) close to their lateral extremities. Also, overlap with the succeeding posterior tergite is strongest at the tergopleurae, reaching about one quarter the length of the tergites. Backward curvature of the tergites increases gradually toward the posterior; the tergopleurae of the first tergite arch backward less than one half the length of the second tergite, the tergopleurae of the 10th tergite arch back over more than twice the length of the 11th.

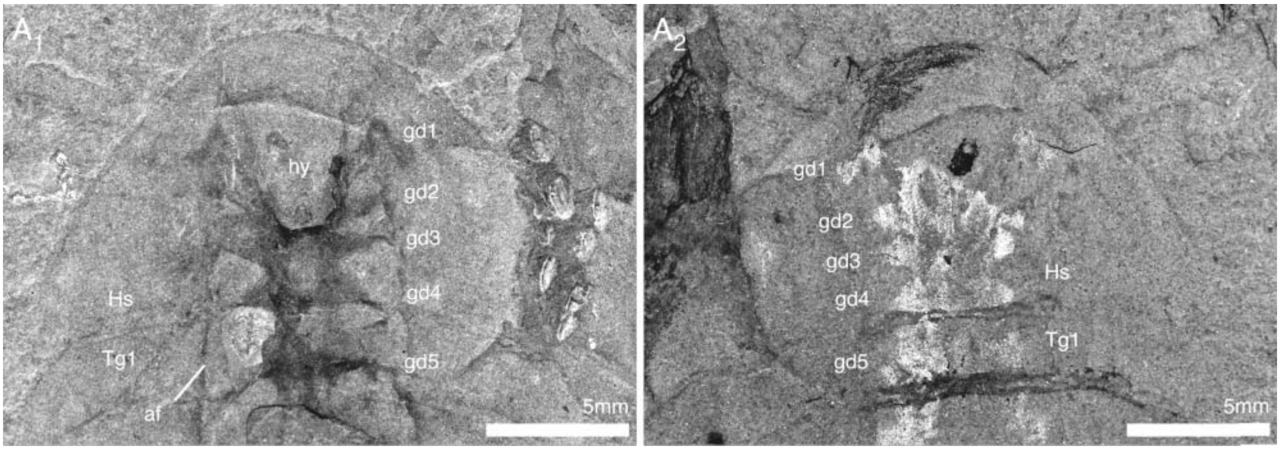

Figure 2. *Emeraldella brocki* Walcott, 1912, USNM 136439, midgut diverticula in head shield and anterior trunk: **A$_1$,** counterpart; **A$_2$,** part. Abbreviations: gd1–5, midgut diverticula 1–5; af, axial furrow; Hs, head shield; hy, hypostome; Tg1, first trunk tergite.

Parallel to the anterior margin of the tergites there is a ridge which extends across the whole tergite (Fig. 4A, B). The ridge is roughly at the position of the overlapping posterior edge of the preceding tergite and appears to be an articulation device, possibly preventing inadvertent excessive overlap, similar to the articulating step or ridge in aglaspidids (cf. Hesselbo 1992).

The telson is styliform and equals roughly the length of the trunk excluding the telson (Fig. 3). The base, where it articulates with the 12th tergite, is wide. Ventrally, the sclerotized cuticle covers everything except for a short, semicircular area under the base (Fig. 3B$_2$). The anus was situated in this area, as indicated by the gut traces (see below). The telson narrows rapidly from the base to just behind this area, more evenly posterior to that.

The attachment of the hypostome is not entirely clear. Anterolaterally, it expands distinctly where it meets the anterior cephalic shield margin. In some specimens the anterior margin of the hypostome seems to extend beyond the anterior margin of the head shield (Fig. 4A, B), but in others (Fig. 4C) the hypostome seems to curve back from the narrow doublure. It is unclear whether the hypostome abuts directly onto the anterior part of the cephalic doublure, or whether there is a narrow transverse rostral plate set off between hypostome and head shield as in the artiopod *Pygmaclypeatus daziensis* Zhang *et al*., 2000.

The sternites are known from a single specimen (USNM 144928, Fig. 5). They are hourglass-shaped and seem to be strengthened laterally. Only about eight sternites are preserved and they belong to the posterior segments of the trunk. There is a change in shape from anterior to posterior, with the anterior ones being more square and the posterior ones distinctly longer than wide and more constricted medially.

The length of the antennula reaches that of the body excluding the telson in larger individuals (Fig. 3), and exceeds it in smaller ones (Fig. 6). The proximal portions are not well known, but the insertion was behind the wing-like anterior expansion of the hypostome (Fig. 4C). The antennula consists of more than 80 articles; a count beyond 80 was not possible because the distal articles are so small that joints are no longer preserved, but the 80th article was counted at about five-sixths of the length in USNM 144923 (Fig. 6A), which suggests a much larger number. Proximally, the antennula reaches considerable width, comparable to the width of the third endopod podomere of the second postantennular limbs. The relative length of the articles varies, such that longer articles are intercalated between sequences of shorter ones (Figs 4C, 6B). The width of the articles decreases from the most proximal to the most distal. The general morphology of the articles is constant along the appendage where it can be discerned; there is a slight expansion of each article mediodistally, where a pair of setae inserts (Figs 4B, C, 6B).

The basipod is never fully exposed in the material. Most commonly, the median edge with its massive spines is visible. The size of the spines varies but there is a tendency for an increase in size distally, with prominent spines inserting close to the mediodistal edge (Fig. 7). Whether or not the spines were arranged biserially is unclear. Proximal to the median edge, the arthrodial membrane forms annulations. The lateral edge of the basipod (exposed only in USNM 136440), which is articulated with the exopod, extends far proximolaterally (Fig. 8A$_1$, 9), and thus contributes much to the length of the basipod which constitutes almost one third of the length of the entire limb axis.

The first podomere of the endopod inserts in the distal (ventral) side of the basipod (Figs 7, 8A, B, 9). Its median side is longer than the lateral, giving it a slightly trapezoidal outline which results in an outward splay of the endopod. The median side carries spines similar to but smaller than those on the basipod (Figs 8A, 9). Laterally,

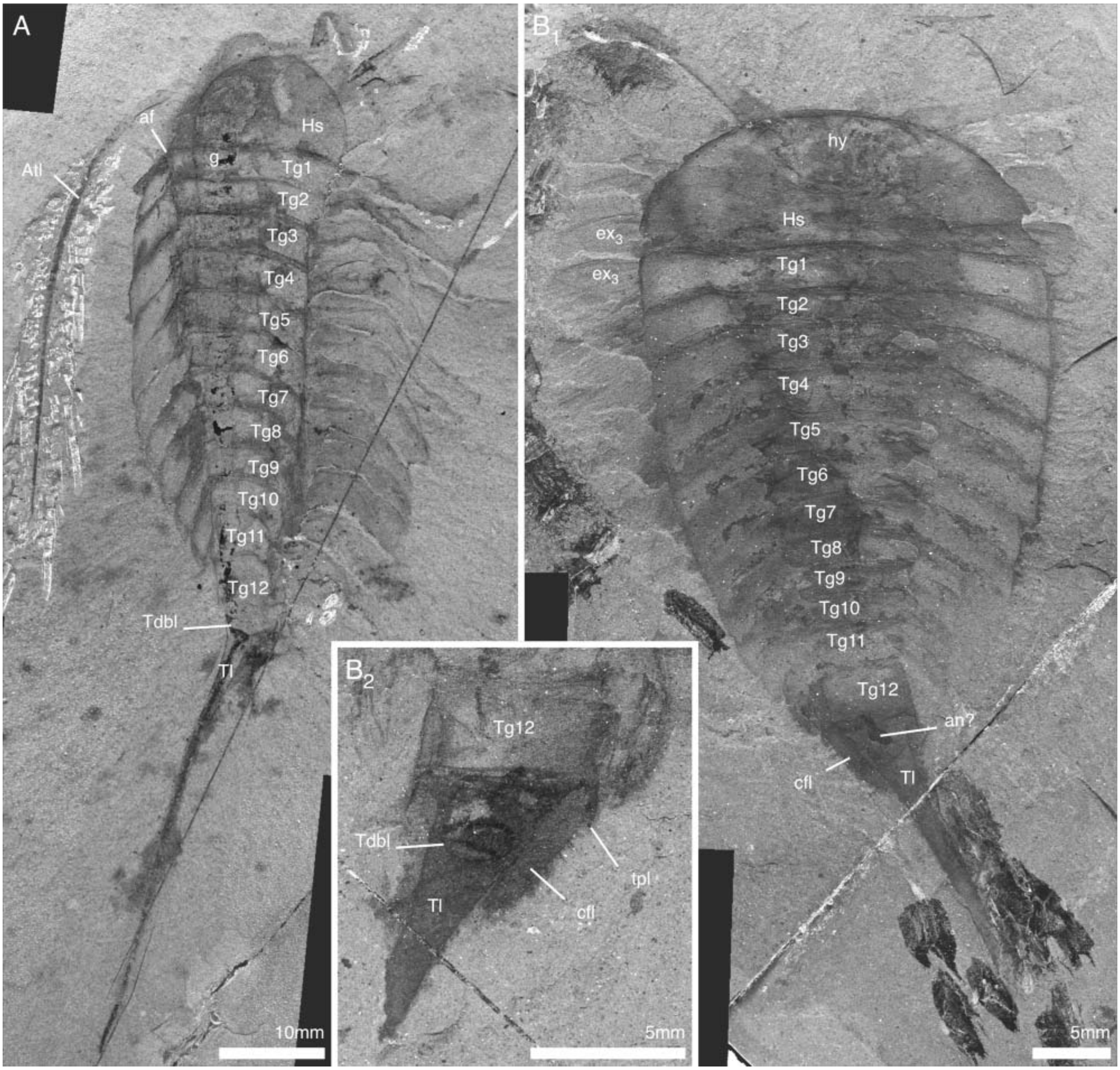

Figure 3. *Emeraldella brocki* Walcott, 1912. **A,** USNM 57702 (lectotype); **B,** USNM 136641; **B$_1$,** counterpart; **B$_2$,** part, detail of last trunk tergite and base of telson. Abbreviations: an?, anus; Cfl, caudal flaps; ex3, third part of exopod; g, gut; Tdbl, recess of sclerotised cuticle around the membranous cuticle surrounding the anus; Tg2–12, second to twelfth trunk tergite; Tl, telson; tpl, tergopleura.

the first podomere is jointed with the exopod. The second podomere is the first free podomere, i.e. it is not articulated with the exopod. Otherwise it is of similar morphology and also contributes to the outward splay of the distal part of the endopod.

The third and fourth podomeres are of similar structure. The spines on the median edge occur in well-separated pairs or groups on the more anterior limbs, and on medially drawn out endites in the more posterior ones (see below). The third podomere is slightly longer than the second (except in the most posterior limbs) and connected to it by a pivot joint (Fig. 4B, arrow). The median and lateral sides are of equal length, giving a rectangular outline. Spines insert along the median edge in three well-separated pairs. There is possibly an additional single spine distally. The spines point distally. The fourth podomere is longer than the third (except in the most posterior limbs) and connected to it by a pivot joint. There is a single spine proximally and two pairs of spines well spaced in the proximal two-thirds of the median edge (Fig. 4B); all point mediodistally or medially. Mediodistally, close to the insertion of the fifth podomere, there is a group of two to four spines which all point distally.

Figure 4. *Emeraldella brocki* Walcott, 1912. **A,** USNM 136642, head shield and anterior part of trunk; the tergites have been pushed into each other as is evident by the large overlap; multiple limbs overlying each other protrude from under the anterolateral margins of the head shield. **B,** USNM 144933, head shield and anterior part of trunk. **C,** USNM 57488 part, stars mark antennular insertion. Abbreviations: ar, articulating ridge; Cdbl, cephalic doublure; Cl1En–Cl3en, endopods of first, second, and third postantennular cephalic limbs; en$_{3-7}$, endopod podomeres 3–7; ex1–3, exopod parts 1–3; rp?, rostral plate; Tl1en, endopod of first trunk limb.

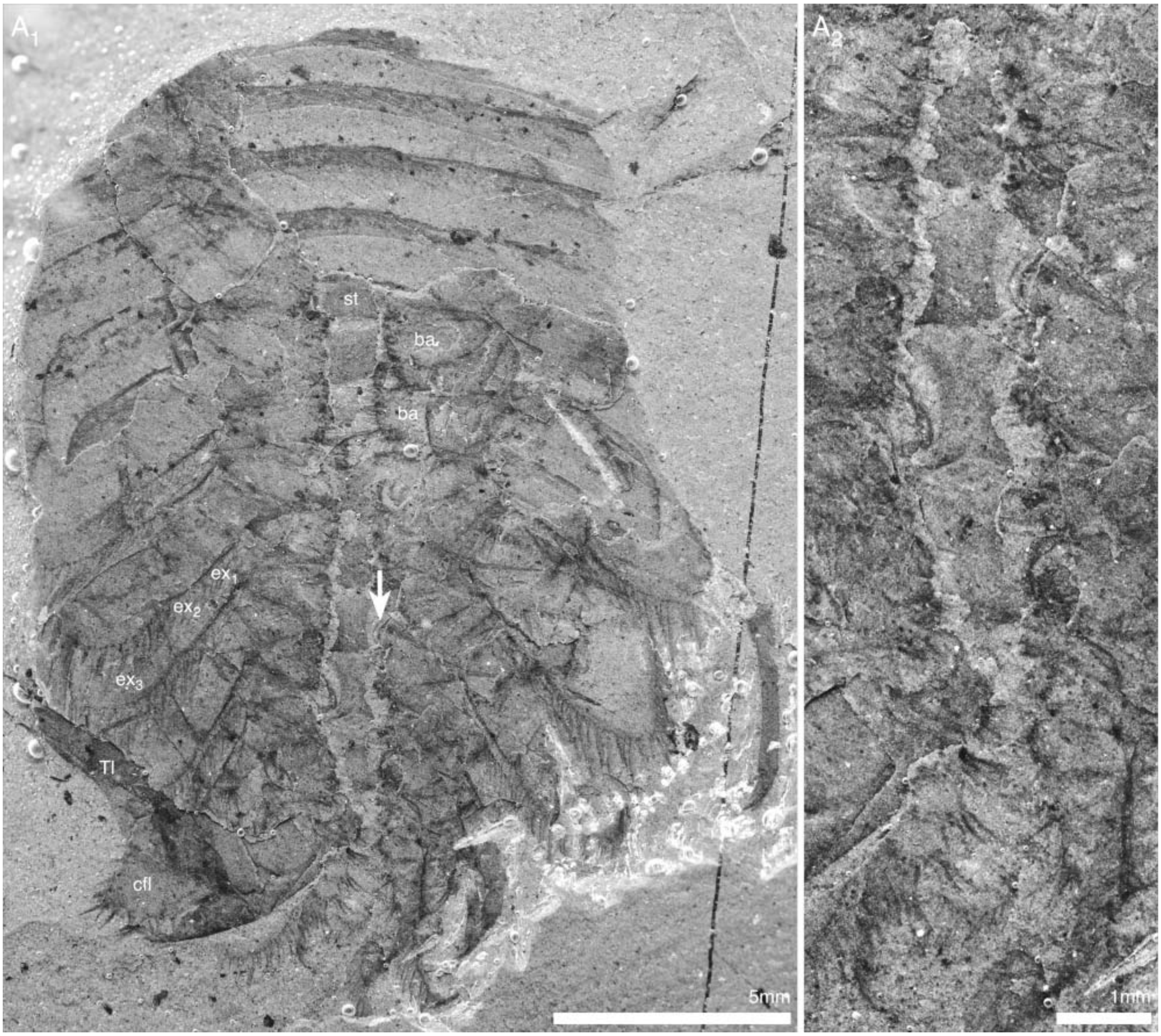

Figure 5. *Emeraldella brocki* Walcott, 1912, **A$_1$,** USNM 144928 counterpart, arrow points to sclerotized ridges in arthrodial membrane; **A$_2$,** close-up on sternites and endopods of posterior limb pair. Abbreviations: ba, basipod; st, sternite.

The fifth and sixth podomeres are considerably more slender than the first to fourth and carry spines only mediodistally, close to the insertion of the subsequent podomere. The fifth podomere is shorter than both the fourth and the sixth; most distinctly so in the mid to anterior trunk limbs where it forms a knee (Figs 7, 9C; cf. Manton 1977, p. 200, though *Emeraldella brocki* does not have a hanging stance). The distinctly stenopodous sixth podomere is of roughly equal width as the fifth but is considerably longer except in the posterior and anterior-most limbs.

The seventh, terminal, podomere (Figs 6B, 7) is short, more or less conical, and extends into a central spine, flanked by a pair of spines arising proximally from the medial and lateral sides. The spine on the medial side is smaller than the central and lateral, which are of nearly equal size. All three spines curve medially in a hook-like manner. There is considerable variation in the splay of the spines, indicating movability.

The anteroposteriorly flattened exopod is tripartite. The proximal part is shaft-like, carries lamellae on its lateral edge, and is articulated with the lateral edge of the basipod along its median edge (Figs 8A$_1$, arrow, 9B–E). The joint is hinge-like, but it is not clear whether it was functional. The lamellae are dorsoventrally flattened and thin. Their width increases laterally, where they reach almost half the width of the proximal part (Fig. 8C). Their length increases distally, with the lamellae inserting close to the joint and the middle

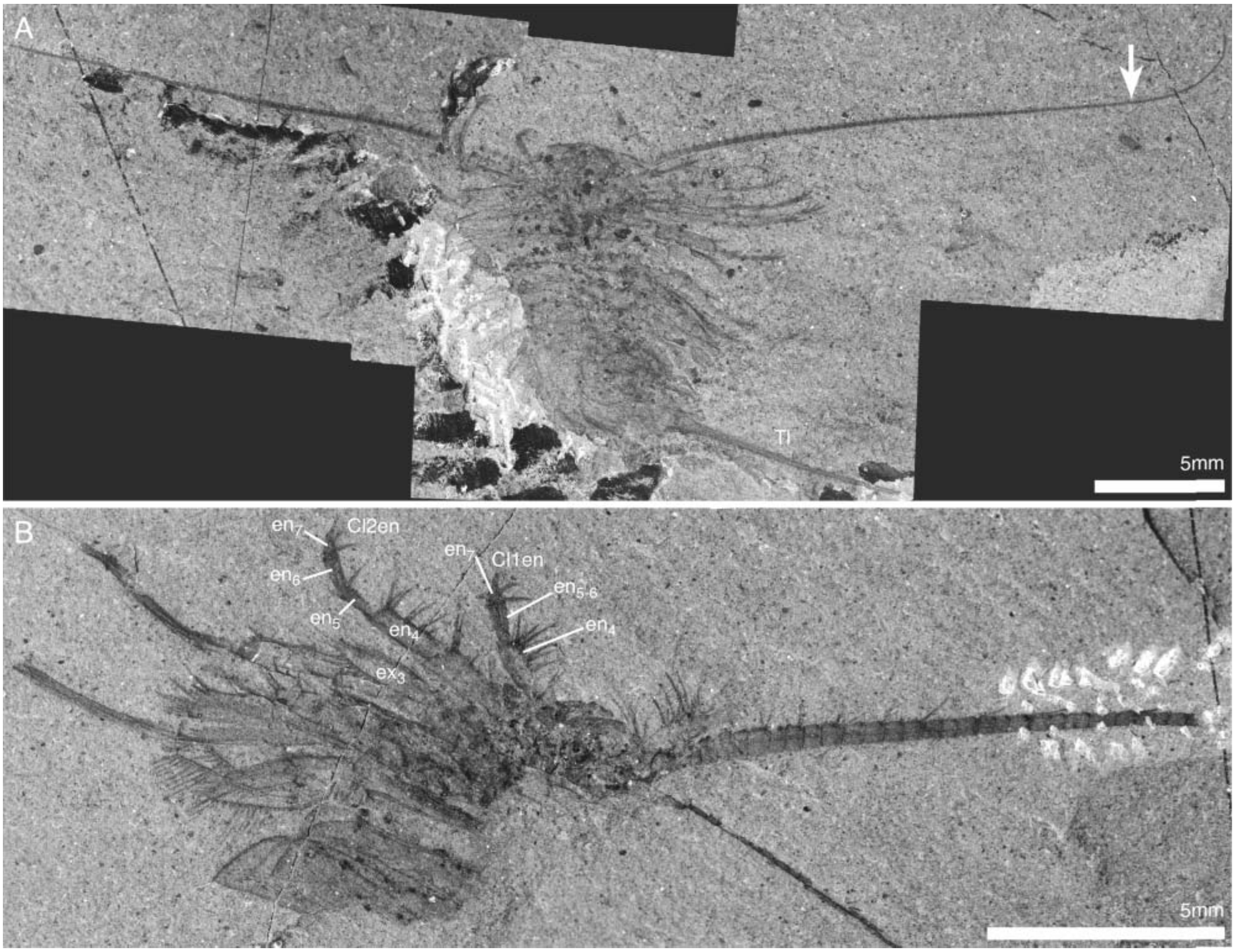

Figure 6. *Emeraldella brocki* Walcott, 1912. **A,** USNM 144923 part, arrow marks approximate position of 80th antennular article; **B,** USNM 144924 counterpart.

part reaching the combined length of the middle and distal parts. Along their rounded distal edge, the lamellae carry spinules.

The middle part of the exopod is triangular in outline. The proximal side is articulated with the proximal part of the basipod in a hinge-like joint; part of the median side articulates with the lateral side of the first podomere of the endopod. The basipod–exopod and endopod–exopod joints do not continue in one line, but are at an angle to each other, with the endopod–exopod joint inclining slightly outwards. Only the proximal quarter to third of the median side constitutes the joint with the endopod, the remainder is free and carries short setae that point towards the endopod (Figs 7, 9B–E). The distal side is articulated in another hinge-like joint with the distal part. Laterally, the joint meets with the joint between the proximal and middle parts, giving a triangular outline.

The distal part is paddle-shaped and points outwards due to its oblique joint with the triangular middle part. Its dorsal side is straight and parallel to the lamellae of the proximal part. Distally it curves downwards and continues straight until it reaches the apex on the distal side. The ventral side is more curved. Except for the straight dorsal side, the whole margin carries setae. The setae are longest on the distal side dorsal to the apex (Fig. 8C).

While their composition appears similar except for the first one, all postantennular limbs change in shape and orientation along the anterior–posterior axis. The most posterior limbs have a pendent orientation and podomeres one to four are enditic (Figs 5, 7, 9D, E), as is known from some trilobites (Whittington & Almond 1987; Ramsköld & Edgecombe 1996).

The most noticeable differentiation is in the proportions of the endopods (Edgecombe & Ramsköld 1999), and also in the proportions of the exopods relative to the endopods (Fig. 9). In the most posterior limbs, the first endopodal podomere is the longest, with the subsequent podomeres decreasing in length distally. All podomeres are more or less rectangular in shape.

The endopod of the first postantennular limb appears to be at least one podomere shorter than all other limbs. The proximal podomeres are not visible, but the fourth

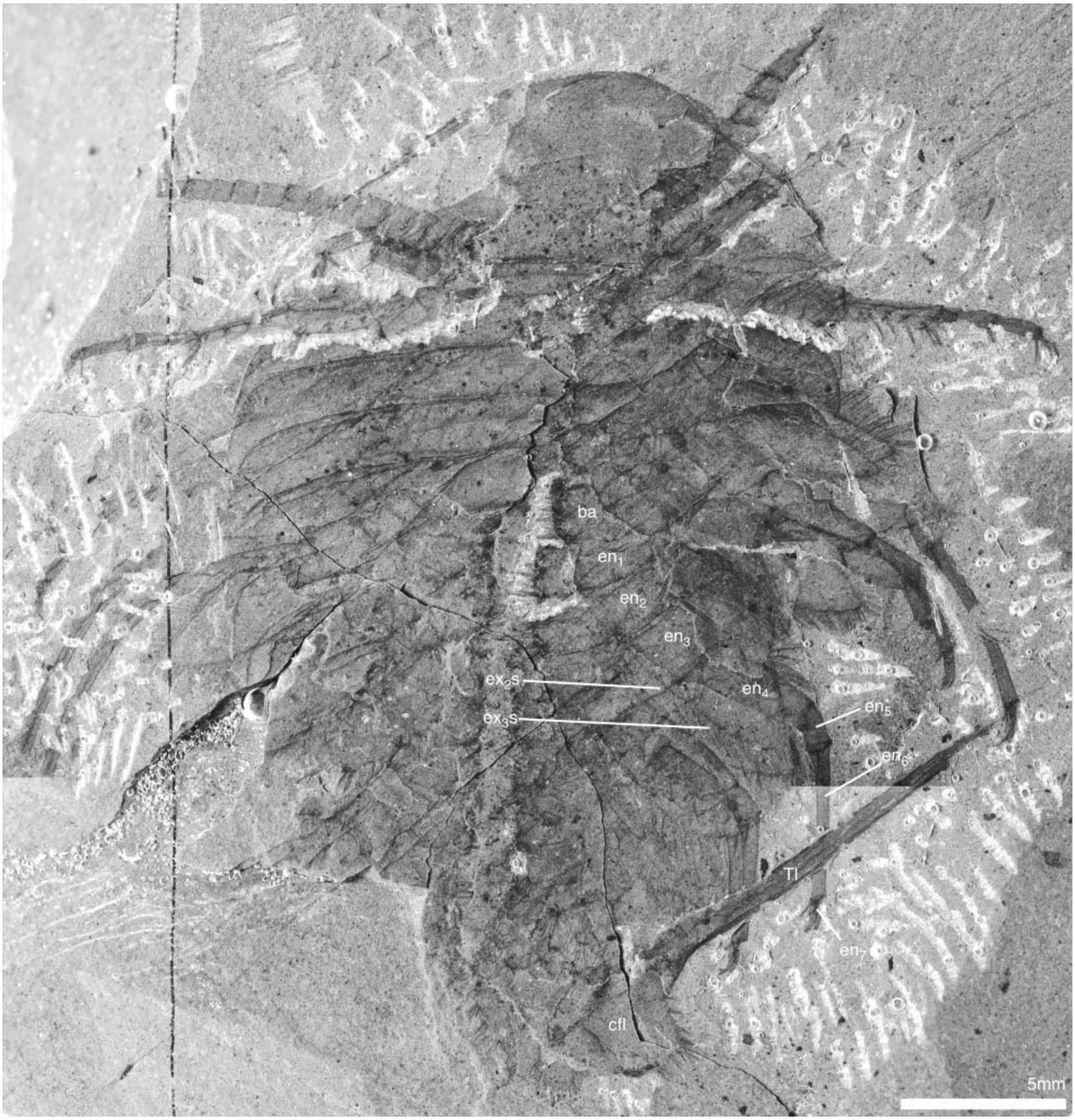

Figure 7. *Emeraldella brocki* Walcott, 1912, USNM 144928 part. The horizontal dark stripe to the right, crossing en6 of the labelled limb and the telson is an artefact from the panorama stitching.

podomere can be identified by its armature (Figs 4A, 6B). Distal to that, there are only two podomeres, one carrying two spines (Fig. 4A), and the distal podomere being a claw-like prong. The presence of two spines in this podomere may indicate that it represents the fifth and sixth podomere, the joint between which is not expressed. There is no evidence of an exopod in the first postantennular limb, but it is not clear whether this is merely preservational.

The proximal portions of the second postantennular to the first trunk limbs are not visible, but the following changes in the distal parts are observable: (*en3*, *en4*) the fourth podomere increases somewhat in length relative to the third and becomes more rectangular in shape (Fig. 6B); (*en5*) the fifth podomere decreases in length relative to the sixth and fourth, gaining the knee-like attributes; (*en6*) the sixth podomere increases significantly in length relative to the

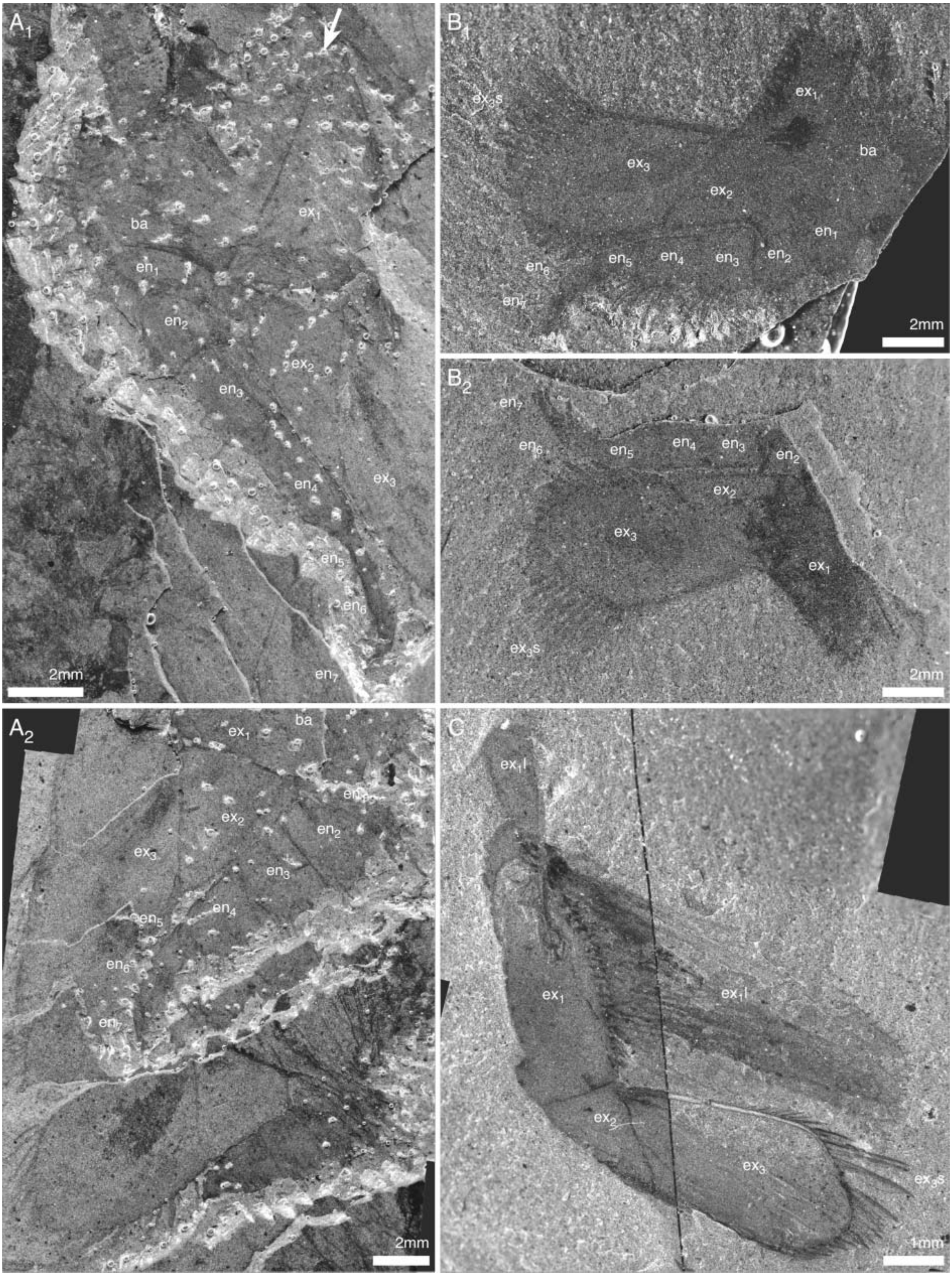

Figure 8. *Emeraldella brocki* Walcott, 1912. **A,** USNM 136440; **A1,** detail of appendage on right side in posterior half of trunk, arrow points to hinge-like joint between basipod and endopod; **A2,** detail of appendage on left side in posterior third of trunk. **B,** USNM 155636, isolated limb from posterior part of thorax, part and counterpart. **C,** USNM 250228, isolated exopod; note that one lamella is flipped up, showing the width of the lamellae. Abbreviations: en_{1-7}, endopod podomeres 1–7; ex_1l, lamellae of first exopod part; ex_3s, setae of third exopod part.

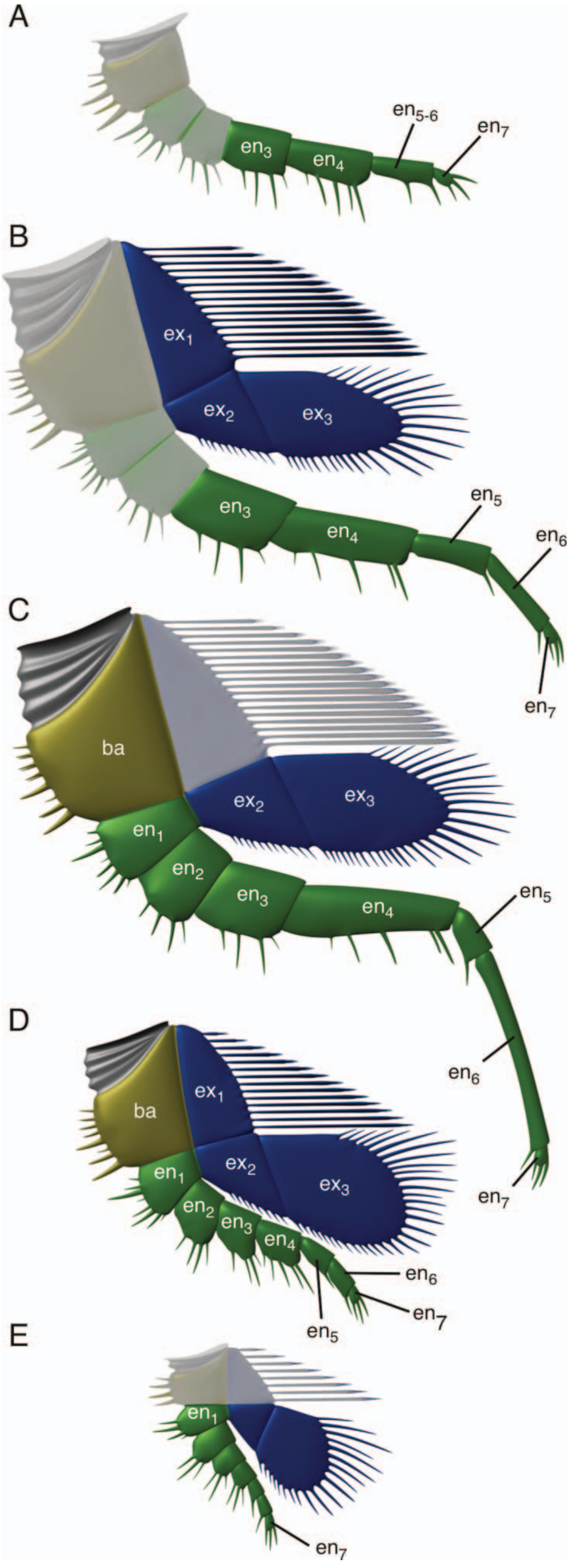

Figure 9. Reconstruction of limbs of *Emeraldella brocki* Walcott, 1912. **A,** first postantennular cephalic limb; **B,** third postantennular cephalic limb; **C,** second trunk limb; **D,** ninth trunk limb; **E,** eleventh trunk limb. Translucent portions are not known. Yellow portions are basipod, green portions endopod, and blue portions exopod.

fifth; (*ex3*) the distal part of the exopod increases in relative size to the remainder of the limb. The shape changes from triangular or elliptical to a more rounded outline (Fig. 3B$_1$).

Differentiation of the trunk limbs is expressed through increasingly differentiated podomere proportions from posterior to anterior. From the most posterior towards the second trunk limb, which is the largest limb in the whole series, the following changes in the endopod occur (Fig. 7): (*en1*, *en2*) the first and second podomeres remain relatively short and the first one in particular becomes increasingly trapezoidal, giving the middle part of the endopod an increasingly outward pointing stance; these podomeres seem to remain more or less enditic; (*en3, en4*) the third and fourth podomeres increase in length and lose their endites; the median spines insert in well-separated pairs along the median edge. Increase in length is much larger in the fourth podomere, which reaches about twice the length of the third; it also changes in shape from enditic with the endite closer to the distal end to widest proximally narrowing towards the distal end; (*en5*) the fifth podomere becomes relatively shorter and forms a knee at which the distal part of the endopod points ventrally; (*en6*) the sixth podomere increases massively in length until it reaches about the combined length of the third and fourth podomeres; it also becomes slightly downward bent; (*ex3*) the distal part of the exopod decreases in relative size to the remainder of the limb and becomes less rounded and more triangular to elliptic in outline.

The telson is flanked ventrally by a pair of flap-like structures (Figs 3B, 5A, 7, 10A) originating from the 12th trunk segment. Their distal part is paddle-shaped, resembling the distal part of the exopod (Fig. 10A$_2$). It carries setae along its lateral and distal and mediodistal margins. The setae are shorter, more robust, and more widely spaced than those of the exopod (Fig. 5A$_1$).

Traces of the alimentary canal are preserved in many specimens as dark stains. The backward-facing mouth must have been situated under the hypostome, but it is not preserved. The anterior part of the alimentary canal must have curved dorsally and posteriorly from there. The dorsal part of the anterior section is preserved in USNM 136442 as a narrower part of the gut trace in front of the first pair of midgut diverticula (Fig. 4A). It extends to the insertion of the hypostome or potential rostral plate.

There are four pairs of midgut diverticula in the head (Fig. 2), the most anterior of which is larger than the remainder. It is backwardly curved (Figs 2, 10B) and can take on a geniculate, limb-like appearance (Fig. 4A). A similar morphology of diverticula is found in the early Cambrian euarthropod stem-lineage derivative *Fuxianhuia protensa* Hou, 1987a (Waloszek *et al*. 2005).

Posteriorly, the alimentary canal can be traced backwards to the base of the telson, where the anus is assumed to open in a membranous area in a ventral recess of the more strongly sclerotized cuticle of the telson (Figs 3B, 10A, B).

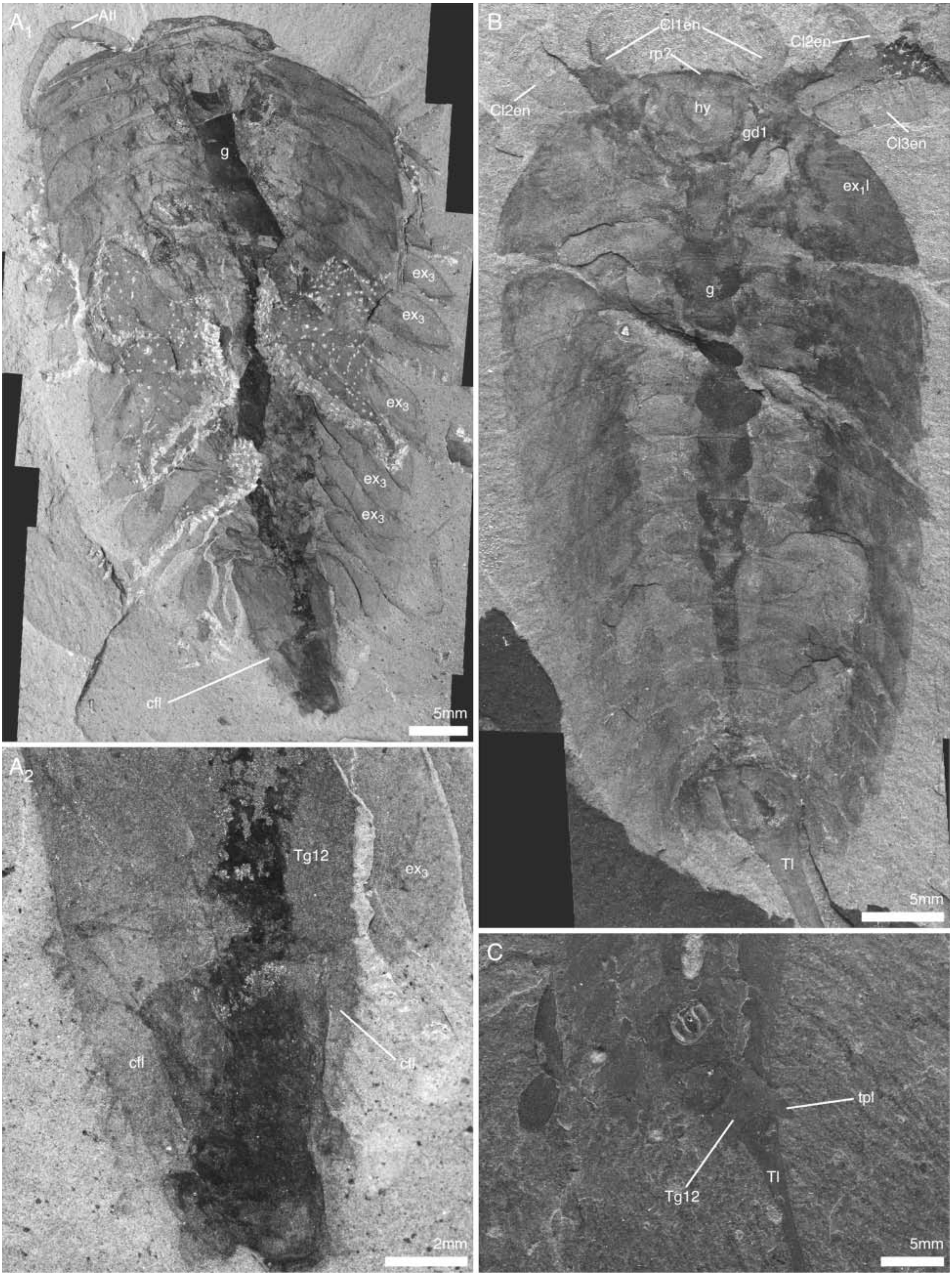

Figure 10. *Emeraldella brocki* Walcott, 1912. **A_1,** USNM 136440; **A_2,** close-up on twelfth tergite with caudal flap and base of telson, showing the complexity of the caudal flaps. **B,** USNM 144917. **C,** USNM 136439 (specimen is not immersed in water) close-up on 12th tergite and telson; the tergopleurae are plied open, demonstrating that this is not a tubular segment.

The morphology as understood herein is summarized in the reconstruction shown in Fig. 11.

Remarks. The synonymy list given above is complementary to Bruton & Whittington (1983). Størmer (1944) considered the tergites of *Emeraldella brocki* to be trilobate. Bruton & Whittington (1983) regarded this trilobation to be an artefact due to resistance of the gut infilling to compaction. While there is evidence of an inflated (cf. Lin 2006) gut in some specimens which contributes to greater relief, the evidence of trilobation is manifestly too lateral and not affected by the gut; a sharp crease exsagittally (Figs 2, 3A) and a coincident distinct bend of the tergites (Figs 3A, B1, 10B), particularly in the more posterior trunk segments, demarcate the axis.

Bruton & Whittington (1983) assumed a 90° outward flexure of the limb at the basipod, resulting in the endopod inserting laterally rather than ventrally. This kind of morphology was also assumed by Hou & Bergström (1997), while Edgecombe & Ramsköld (1999) did not make any assumptions on the most proximal part of the basipod. There is good evidence for a straight, ventrally pointing basipod with the endopod inserting in the distal (ventral) edge from USNM 144928 (Figs 5, 7). While there is some outward flexure of the limb, it is achieved in the first and second endopod podomeres, and is not consistent along the body, but reaches its maximum in the anterior trunk and possibly the cephalic limbs. The arthrodial membrane of the body–limb joint contained partly sclerotized annulations (Chen *et al.* 1997; Hou & Bergström 1997) also known from other artiopods (Ramsköld & Edgecombe 1996; Ramsköld *et al.* 1997; Edgecombe & Ramsköld 1999) and the 'great appendage' arthropod *Leanchoilia illecebrosa* (Hou, 1987b) (Liu *et al.* 2007). This is inferred to have allowed for flexibility in movement of the limb, including an outward swing with the limb axis and exopod moving as a single unit (Ramsköld & Edgecombe 1996; Chen *et al.* 1997; Liu *et al.* 2007), as in early derivatives of the crustacean stem lineage (Stein *et al.* 2008, although the partly sclerotized annulations are absent in the latter).

The limbs are considerably longer and more flexible than assumed by most previous authors (e.g. Bruton & Whittington 1983). When flipped backwards or forwards to rest on the sediment, they extend across multiple segments. The laterally flexed part of the endopod can therefore be exposed next to the margins of a tergite which belongs to a segment that is several segments more posterior or anterior to the one to which the limb belongs. This is illustrated by USNM 144928 in which one almost fully-exposed anterior trunk limb on the right side (the labelled limb in Fig. 7) extends almost across half the length of the trunk excluding the telson.

Bruton & Whittington (1983) considered the distal claw-like prong as spines arising from the distal podomere, not as a podomere. Accordingly, the endopod in their description and reconstruction comprised only six podomeres. That this terminal element is a short podomere can be seen in specimens USNM 144923, 144924, 144926, 144928. Edgecombe & Ramsköld (1999) did not discuss the endopod morphology, but provided a reconstruction of a limb based on an isolated appendage (USNM 155636, a posterior trunk limb according to the endopod proportions). This reconstruction showed only six podomeres including the distal claw-like one. Reinvestigation of the material shows another joint proximally, which is the joint between the basipod and the endopod. An endopod of seven podomeres can therefore be established for this limb. Bruton & Whittington (1983) considered the endopods of the most posterior limbs to possibly be one podomere shorter, but given that none of the posteriormost limbs is fully exposed from insertion to tip, or well enough preserved, this can be neither confirmed nor rejected.

The most recent interpretation of the exopod structure in *Emeraldella* was given by Edgecombe & Ramsköld (1999), and is largely in accord with the present interpretation except that the joint separating the middle from the proximal part was not recognized in that study. Evidence for this joint and the tripartition of the exopod is available from USNM 136642, 144928 and 250228. Hou & Bergström (1997) were the first to notice the joint in the latter specimen but interpreted it as a taphonomic fold. The straight line along which the 'filaments' attach, according to Hou & Bergström's reinterpretation (1997, their quotation marks) of Bruton & Whittington's photographs (1983), is the continued median margin of the middle and distal parts of the exopod; the 'filaments' are the setae along that margin. Hou & Bergström (1997) further interpreted the setae along the distal part as lamellae. The blade-like appearance on which they based this is curious but occurs only in the setae dorsal to the apex of the distal part of the exopod. It can be clearly seen in USNM 250228 and possibly in 144928. The setae are very different though from the lamellae of the proximal part of the exopod and it seems more reasonable to homologize the latter with the lamellae of other artiopods, based on structure and position. Whether blade-like setae could be a precursor of the lamellae is an interesting speculation but cannot be further corroborated at present.

Walcott (1912, p. 158), in his original paper, listed *Emeraldella brocki* in a table on segmentation as having only one postantennular limb-bearing segment incorporated into the head. Raymond (1920) mentioned four but, since the revisions by Simonetta (1964) and Bruton & Whittington (1983), the presence of five postantennular limb-bearing segments seemed established. That number was also coded in subsequent phylogenetic analyses of 'arachnomorphs' (Edgecombe & Ramsköld 1999; Cotton & Braddy 2004; Paterson *et al.* 2010). Given that the proximal portions of the limbs and their insertions are not accessible in the head, this high count of limbs seems to rest largely on the distal

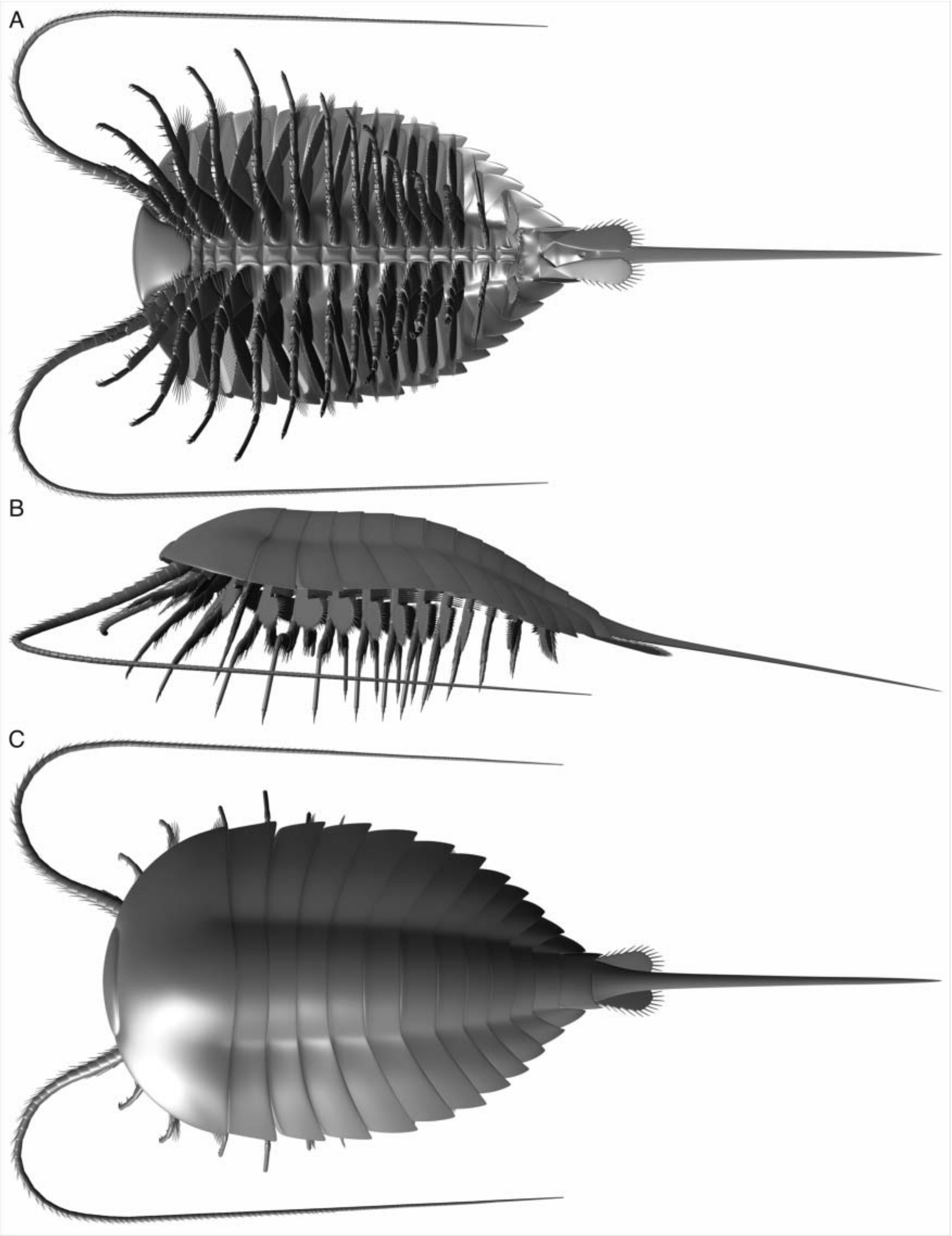

Figure 11. Reconstruction of *Emeraldella brocki* Walcott, 1912. **A,** ventral view; **B,** lateral view; **C,** dorsal view.

parts of limbs projecting beyond the margin of the head shield. As indicated above, that count is unreliable because of the great length of the limbs, and the anterior trunk limbs, when flipped forward upon collapse of the animal on the sediment, would have projected beyond the anterolateral margin of the head shield (Fig. 12). A count of the total number of limbs in the body is not practical because the whole limb series is not preserved in any of the available specimens. Bruton & Whittington (1983) in their description claimed 16 limb pairs to be present, but that seems to

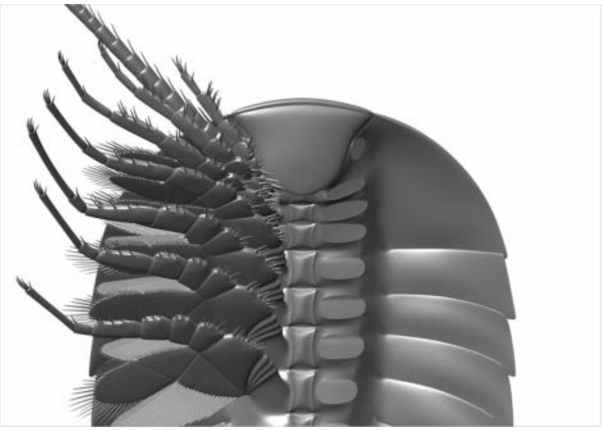

Figure 12. Reconstruction *Emeraldella brocki* in ventral view with anterior limbs flipped forward as seen in some of the specimens. The distal parts of the first and second trunk limbs would protrude from underneath the head shield, even in this pose, which is not fully flipped as expected from specimens that lie flat on the sediment surface. The left limb series is omitted to show the tergite boundaries.

have been inferred from the number of trunk tergites and number of limbs extending beyond the head shield.

Given these factors of uncertainty, the number of midgut diverticula is taken herein as an indicator of segment numbers. Assuming that the large, curved, anteriormost diverticula belong to the antennular segment, as in *Fuxianhuia protensa* (Waloszek *et al.* 2005), there would be three postantennular segments incorporated into the head. Support for the assumption that this pair of diverticula belongs to the antennular segment is given by its position in the head. Only the posterior two (i.e. the third and fourth pairs) are clearly posterior to the posterior margin of the hypostome, indicating a post-oral position. The second pair is found lateral or just anterior to the posterior margin of the hypostome. If the mouth was situated at the posterior margin of the hypostome, the second pair of diverticulae would be in a para-oral position. The first pair, which, is anterior to the posterior margin of the hypostome, roughly in the presumed position of the antennular insertion (Fig. 4C), would have belonged to a pre-oral segment. The antennular segment is the only appendage-bearing pre-oral segment. The positions of the first postantennular limbs are known to be para-oral in *Agnostus pisiformis* (Walossek & Müller 1987) and the artiopods *Triarthrus eatoni* (Hall 1838) (Cisne 1981; Whittington & Almond 1987) and *Misszhouia longicaudata* (Zhang & Hou 1985) (Zhang *et al*. 2007). In *Naraoia spinosa* Zhang & Hou, 1985 and *Misszhouia longicaudata* (Zhang & Hou 1985) there is also a one-to-one correspondence between pairs of gut diverticula and appendage-bearing segments including the antennula (Zhang *et al.* 2007). Assuming such one-to-one correspondence for *E. brocki* would lend further support for the presence of only three appendage-bearing postantennular segments in that species, regardless of the uncertain position of the mouth.

Differentiation of the cephalic limbs was recognized by Simonetta (1964) and Bruton & Whittington (1983). In both studies, the first postantennular limb was considered to be lacking an exopod and composed of fewer podomeres, though Simonetta considered it to be shortened by only one podomere. Bruton & Whittington (1983) described that limb as consisting of only three podomeres (excluding the distal one which they did not regard as a podomere, see above). Given that the proximal parts of that limb are not preserved or visible, the exact number of podomeres cannot be established but, as described above, shortening by at least one podomere is documented, and by more is possible.

The endopod of the second postantennular limb was considered to consist of only five podomeres (excluding the terminal one) by Bruton & Whittington (1983). In specimen USNM 144928 (Fig. 7), on which that interpretation was mainly based, the head is transversely folded, resulting in the antennular insertion and at least two pairs of limbs underlying the head–trunk boundary. The proximal portions of the limbs overlying each other are not discernible and the number of podomeres in that limb cannot be counted.

Bruton & Whittington (1983) found no evidence for the proximal part of the exopod (‘gb’) in the second and third postantennular appendages. The part of USNM 136441 and the part of USNM 144917 (Fig. 10B) both show traces of lamellae impressed under the right side of the head, which seem to be associated with the second or third postantennular limbs. The part of USNM 136442 shows three or four lamellae associated with the most anterior limbs on the left side.

The trunk was previously considered to consist of an 11-segmented thorax and a short, limbless abdomen of one (Simonetta 1964) or two (Walcott 1912; Bruton & Whittington 1983) tubular segments. The first 11 tergites all have well-developed tergopleurae. Posterior to these there is unequivocal evidence for a more elongate segment with reduced tergopleurae. In USNM 57702 (Fig. 3A) and 136441 (Fig. 3B), there appears to be another joint. The margins of the part anterior to it are confluent with the telson, and it is here interpreted as the basis of the telson. The apparent segmental boundary between this part and the telson in USNM 55702 seems to be the margin where the sclerotized cuticle is recessed around the membranous cuticle surrounding the anus. In USNM 136441, the supposed segmental boundary coincides with this margin, but is superimposed onto it and defines a transversely oval structure (Fig. 3B$_2$) that is also seen in USNM 136440 (Fig. 10A$_2$) where it was considered to be a segmental boundary by Bruton & Whittington (1983). It is possible that this oval structure is associated with the anus. The 12th segment, therefore, is here interpreted as the last true segment (somite). There is further evidence that this segment was not tubular, but bore a tergite, albeit with reduced tergopleurae. The tergopleurae are seen as projections flanking the telson in UNSM 136439, 136441, 250227. In USNM 136439 the lateral margins with their projections are plied open (Fig. 10C), which is considered as evidence against a tubular segment.

There is evidence for an unsclerotized ventral surface left out by the sclerotized cuticle of the telson, and that the anus is situated in this area comparable to the derivative of the crustacean stem-lineage *Sandtorpia vestrogothiensis* Haug *et al*., 2009b (Haug *et al*. 2009b, fig. 21B). Together with the fact that this caudal section is limbless, this is taken as evidence that this truly represents the telson in agreement with Simonetta (1964) but not with Bruton & Whittington (1983).

The paired flaps lateroventral to the telson were considered to represent limbs by early authors (Raymond 1920), later to be a 'bilobate ventral plate' (Simonetta 1964; Bruton & Whittington 1983). Subsequent authors again implied that it was a modified limb (Hou & Bergström 1997). The limb interpretation has its merits. Similarities with the exopods of the preceding limb pair are particularly striking in USNM 250227. The structure of the proximal part seems complex (Fig. 10A_2), but is not sufficiently well preserved to allow interpretation. It seems to insert under the 12th trunk tergite, and it is possible that these are the modified limbs of that segment.

Phylogenetic analysis

Previous work

The main focus of this analysis is to establish the position of *Emeraldella brocki* within a group of trilobites and allied euarthropods. The old Trilobitomorpha Størmer, 1944 included taxa whose close relationship with Trilobita is not supported (Hou & Bergström 1997). Hou & Bergström (1997) introduced the new taxon Lamellipedia (Marrellomorpha Beurlen, 1934 + Artiopoda Hou & Bergström, 1997). These authors placed *E. brocki* in Xenopoda Raymond, 1920, an ingroup of their Artiopoda, but they considered Xenopoda to share a more recent ancestry with Chelicerata than with the remainder of Artiopoda, which renders both Artiopoda and Lamellipedia as defined by these authors non-monophyletic. The Xenopoda + Chelicerata in Hou & Bergström (1997) were deeply nested within the artiopods. Subsequent analyses of 'lamellipedian' phylogeny by Edgecombe & Ramsköld (1999) and Paterson *et al.* (2010) rendered *E. brocki* as a basal artiopodan. The analyses by Cotton & Braddy (2004) and Hendricks & Lieberman (2008) sampled a wider range of taxa spanning the old Arachnomorpha ('trilobitomorphs' + Chelicerata). The former study retrieved a clade of chelicerate-allied taxa including 'great appendage' arthropods independently considered to be derivatives of the chelicerate stem-lineage by Maas *et al*. (2004) and Chen *et al.* (2004). Similarly to Hou & Bergström (1997), a clade closely corresponding to Xenopoda, including *E. brocki* (Cotton & Braddy 2004, clade 5 in fig. 8), was resolved as the sister group to the clade of chelicerates and allies, not the clade of trilobites and allies. In contrast to Hou & Bergström (1997), and in correspondence with Edgecombe & Ramsköld (1999) and Paterson *et al.* (2010), all non-xenopod artiopods were rendered monophyletic. Support for a similar clade, albeit excluding *Retifacies abnormalis* Hou *et al*., 1989, was also found in all three analyses of Hendricks & Lieberman (2008). Those authors did not find support for Xenopoda.

Generally, there appears to be good support for a monophyletic group of non-xenopod artiopods, notwithstanding the debated position of *Retifacies abnormalis*. Scholtz & Edgecombe (2005) proposed autapomorphies relating to exopod structure for that group. Not all are shared by *R. abnormalis*. Hughes *et al.* (2008) added antennular morphology, which would also be shared by *R. abnormalis*.

Within this taxon, four monophyletic groups were retrieved in most analyses: Nectaspidida Raymond, 1920 (Emucarididae Paterson *et al*., 2010 + (Naraoiidae Walcott, 1912 + Liwiidae Dzik & Lendzion, 1988)), Helmetiida Novozhilov, 1960, Petalopleura Hou & Bergström, 1997 (Xandarellida Chen *et al*. in Chen *et al*., 1996 + *Sinoburius lunaris* Hou *et al*., 1991), and Trilobita Walch, 1771. Relationships between these remain largely unresolved (Edgecombe & Ramsköld 1999; Hendricks & Lieberman 2008; Paterson *et al.* 2010).

Included taxa

Out-group taxa. *Shankouia zhenghei* Chen *et al*. in Waloszek *et al*., 2005 was selected as the outgroup for the tree search in TNT. The similar *Fuxianhuia protensa* Hou, 1987a was also included in the analysis because it is better known than *S. zhenghei* and allowed for more complete coding (coding sources: Chen *et al*. 1995; Hou & Bergström 1997; Waloszek *et al*. 2005; Bergström *et al*. 2008). Both are considered to be derivatives of the euarthropod stem-lineage (= early representatives of Arthropoda *s. str.*), whereas all ingroup taxa apart from *F. protensa* are considered to represent Euarthropoda. Given that some of the ingroup taxa (great-appendage arthropods, helmetiids) have been assigned to the euarthropod stem-lineage by some authors (e.g. Budd 2008), undisputed stem-lineage taxa were selected as outgroups for this analysis. *S. zhenghei* was selected as outgroup over *F. protensa* because for characters 2, 13, and 37, the latter has states that, by comparison with another similar taxon, *Chengjiangocaris longiformis* Hou & Bergström, 1991, do not appear to represent plesiomorphic character states.

Ingroup taxa. Two species of great-appendage arthropods, *Leanchoilia illecebrosa* (Hou, 1987a) (coding sources: Hou

& Bergström 1997; Liu *et al*. 2007), and *Haikoucaris ercaiensis* Chen *et al*., 2004, both from the Cambrian Series 2 of China, are included, as is the great-appendage arthropod-like *Kiisortoqia soperi* Stein, 2010.

Oelandocaris oelandica Müller, 1983 (coding source: Stein *et al*. 2008) from the Furongian of Sweden has been included as an early representative of the eucrustacean stem-lineage. *Agnostus pisiformis* (Wahlenberg, 1821) from the late Cambrian Series 3 of the same region has been included as well (coding source: Müller & Walossek 1987). This has been regarded as a trilobite (e.g. Fortey 2001; Cotton & Fortey 2005), or as an early derivative of the crustacean stem-lineage (Walossek & Müller 1990; Stein *et al.* 2005). *A. pisiformis* is included, acknowledging that limb morphology is only known from up to the earliest holaspid but not later stages. Whether the largest available stage of *O. oelandica* represents an immature stage is not known (Stein *et al*. 2008). Neither taxon shows dramatic morphological change throughout their known development. A radically different morphology in the adults of these species seems unlikely, unless very abrupt change between the latest known instars and the adult are postulated, for which there is no obvious evidence.

Apart from *Emeraldella brocki* Walcott, 1912, *Siriocaris trollae* Lagebro *et al*., 2009 is included as another artiopod taxon that lacks a pygidium. No aglaspidids are included because very little of their limb morphology is known.

Nectaspidida is represented by the naraoiids *Naraoia compacta* Walcott, 1912 (coding sources: Whittington 1977; Zhang *et al*. 2007) and *Misszhouia longicaudata* (Zhang & Hou, 1985) (coding sources: Chen *et al*. 1997; Hou & Bergström 1997; Zhang *et al.* 2007). Neither Liwiidae nor representatives of the newly established Emucarididae are included because detailed information on limb morphology is not available for any of the species belonging to these taxa.

Helmetiida is represented by *Kuamaia lata* Hou, 1987a, *Saperion glumaceum* Hou *et al*., 1991 (coding sources for both taxa: Hou & Bergström 1997; Edgecombe & Ramsköld 1999; Hou *et al.* 2004), *Skioldia aldna* Hou & Bergström, 1997 (coding sources: Hou & Bergström 1997; Hou *et al.* 2004), and *Kwanyinaspis maotianshanensis* Zhang & Shu, 2005.

Petalopleura is represented by *Xandarella spectaculum* Hou *et al*., 1991 (coding sources: Hou & Bergström 1997, Hou *et al.* 2004) and *Cindarella eucalla* Chen *et al*. in Chen *et al*., 1996. *Sinoburius lunaris* Hou *et al*., 1991 is not included because no detailed information on its ventral morphology is available.

Trilobita is represented by *Eoredlichia intermedia* (Lu, 1940) (coding source: Hou *et al*. 2009), *Olenoides serratus* (Rominger, 1887) (coding sources: Whittington 1975, 1980), and *Triarthrus eatoni* (Hall, 1838) (coding source: Cisne 1981; Whittington & Almond 1987).

Results

The analysis yielded seven equally parsimonious trees of 82 steps (Consistency Index 0.74, Retention Index 0.80). The topologies of the strict consensus and majority rule consensus trees are identical. The strict consensus tree has been rerooted in Mesquite with both *Shankouia zhenghei* and *Fuxianhuia protensa* as outgroups (Fig. 13). *Kiisortoqia soperi* is resolved as sister taxon of the remainder of the ingroup taxa. If the 'great appendage' arthropods (Fig. 13, node 4) are considered to represent the stem-lineage of the Chelicerata (Maas *et al*. 2004; Chen *et al*. 2004), then node 3 would represent Euarthropoda and *K. soperi* would be a derivative of the euarthropod stem-lineage, but support for node 3 is weak. In fact, the only autapomorphy of node 3 would be character 12 (transverse tergite margins in the anterior trunk segments, with a reversal for helmetiids). Within node 3, the 'great appendage' arthropods are resolved as the sister group to a clade (Fig. 13, node 5) comprising representatives of the crustacean stem-lineage (Fig. 13, node 6) and the artiopods (Fig 13, node 7). Support for node 5 is low; autapomorphies are an endopod of seven podomeres (character 25), differentiated podomeres of the endopod (character 26, with a reversal for helmetiids), and endites on podomeres 1–4 (character 27). Support for node 6 is similarly weak. Synapomorphies are the absence of the sclerotized ridges in the body–limb joint (character 23), insertion of the cephalic exopods in the basipod only whereas trunk exopods insert in the basipod and first podomere of the endopods (31), and multiarticulate cephalic exopods (character 34). Node 7 is better supported though most autapomorphies refer to antennular morphology (composition, gross morphology, and armature; characters 19, 20 and 21, respectively). Further autapomorphies are the bilobate exopod gross morphology (character 29), and the presence of exopod lamellae (character 32). Resolution within node 7 is poor. There is weak support for a clade of taxa sharing a pygidium (character 1; Fig. 13, node 8). Within this clade, the four artiopod groups found in most analyses (Edgecombe & Ramsköld 1999; Cotton & Braddy 2004; Hendricks & Lieberman 2008; Paterson *et al*. 2010) are retrieved, though support for the nectaspidids and helmetiids is weaker than in previous studies. The present study resolves *Emeraldella brocki* in a polytomy at the base of the artiopods (node 7). In contrast to Cotton & Braddy (2004), no support is found for closer affinities with the 'great appendage' arthropods. This also supports monophyly of Artiopoda (Fig. 13, node 7) and the name Artiopoda Hou & Bergström, 1997 is here formally adopted.

Discussion

Helmetiida

While Helmetiida was retrieved in all of the shortest trees, support is weak. Budd (2008) tentatively suggested that

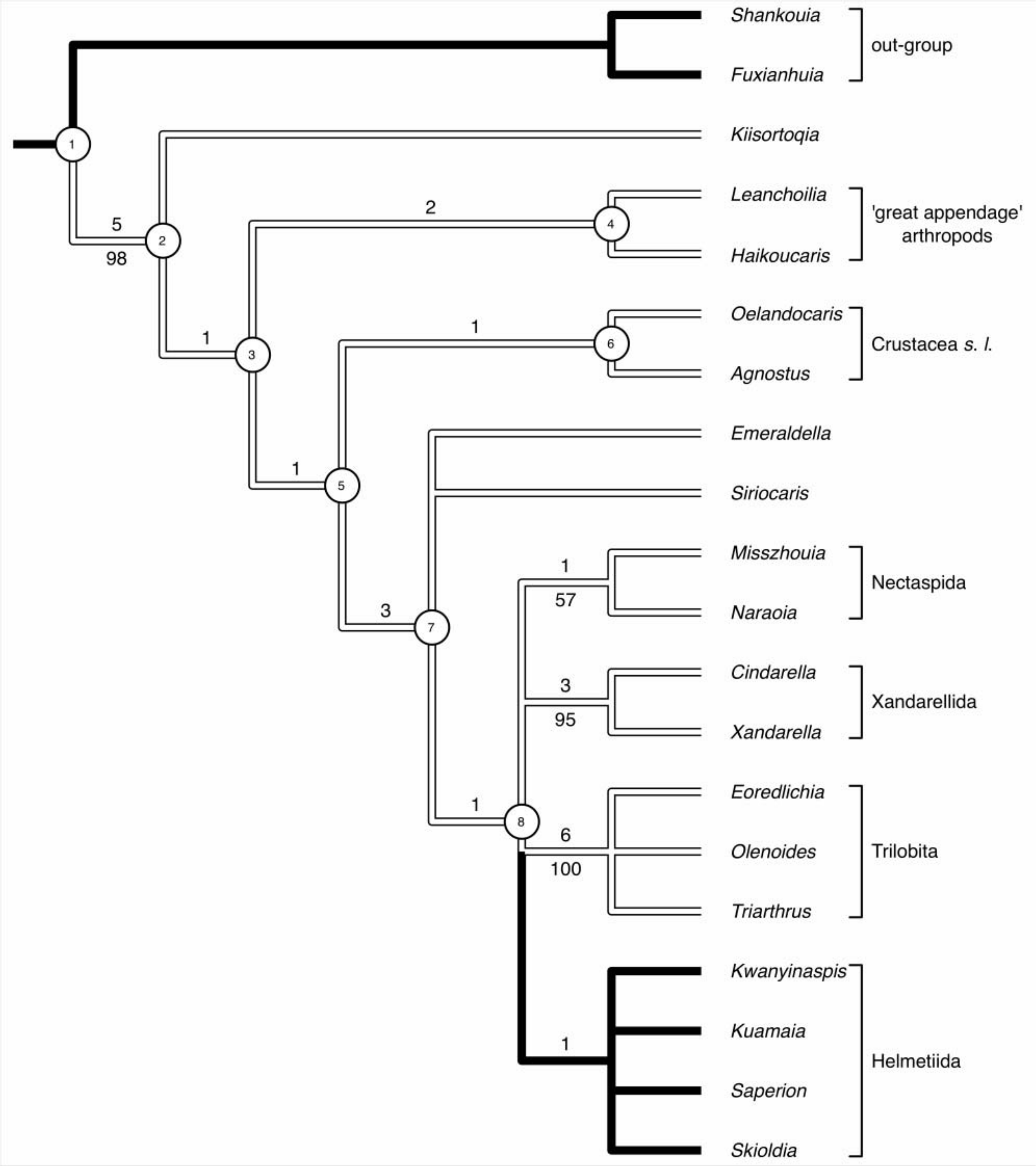

Figure 13. Strict consensus of seven equally parsimonious trees. Numbers above branches are Bremer support values, numbers below branches jackknife support values greater than 50. The solid black branches mark the occurrence of a free anterior sclerite in front of the head shield or tergite.

'lamellipedians' might be paraphyletic and derivatives of the euarthropod stem lineage or basal euarthropod taxa. This was based on the presence of an anterior sclerite in helmetiids (see discussion below) and, by implication, helmetiids should be basal within the grade of 'lamellipedians' (discussed in Paterson *et al*. 2010). In the present analysis, Helmetiida are consistently placed in a clade of artiopods with a pygidium (Fig. 13, node 8), though support for that node is fairly weak. The pygidium is further problematical as it is not known whether such a tagma was present in *Kwanyinaspis maotianshanensis* (see discussion of character 2). Coding character 2 with state 0 rather than unknown for *K. maotianshanensis* results in 19 shortest trees, with lengths of 83 steps. There is a marked loss in resolution as the helmetiids are no longer retrieved and nodes 2, 3 and 5 collapse (Fig. 14). Even in this analysis, the helmetiid taxa are nested in an 'artiopod' clade and not basal to the other euarthropods included in the analysis. There are some character states in some helmetiids that could be interpreted as plesiomorphic. Thus, *Kuamaia lata* and *Saperion glumaceum* lack the medially drawn out endite on the basipod, but it is present in *K. maotianshanensis*, the only taxon that may be lacking a pygidium. *S. glumaceum* has an antennula comprising fewer than 16 articles, but *K. lata* has a long filiform antennula of more than 20 articles. Interestingly, helmetiids seem to lack the differentiation of the endopod podomeres present in the other 'artiopods' and the Crustacea *sensu lato*.

Anterior sclerite

An anterior sclerite associated with the pre-antennular ocular segment is now identified in a number of derivatives of the euarthropod stem lineage (Waloszek *et al.* 2005; Budd 2008), though there is some semantic dispute about whether or not it is a tergite (Bergström *et al.* 2008). Budd (2008) homologized this sclerite with the anterior sclerite of helmetiids, which does seem to be associated with the lateral eyes even in these taxa (e.g. Edgecombe & Ramsköld, figs 3.2, 5). This homology was rejected by Paterson *et al.* (2010) on the grounds of tree topology, and the results of the present analysis seem to corroborate that at least the anteriorly exposed position of this sclerite may be homoplastic (Fig. 13). It seems possible though that the sclerite itself is homologous, but has been ventralized and incorporated in the head shield as a rostral plate in artiopods (cf. Bergström *et al.* 2008). Homology of the helmetiid sclerite with the rostral plate of trilobites had previously been refuted by Edgecombe & Ramsköld (1999, discussion of their character 11). They regarded the latter as a section of doublure set off by sutures, although this should not necessarily exclude homology. The rostral plate is not restricted to trilobites; *Pygmaclypeatus daziensis* has a short but relatively wide rostral plate from which the hypostome is separated by a suture. As in trilobites, the rostral plate is separated from the doublure by sutures. A similar rostral plate could be present in *Retifacies abnormalis*. In the specimen figured by Hou *et al.* (2004, fig. 16.48a) the anterior part of the hypostome or doublure is set off. In another specimen figured by Hou *et al.* (2004, fig. 16.48b) the axial portion of the anterior margin of the head seems set off by a suture. *R. abnormalis* and *P. daziensis* are considered closely related and both are regarded as basal 'artiopods' (Paterson *et al.* 2010). The putative eyes of *R. abnormalis* figured by Hou & Bergström (1997, fig. 48A) seem to be associated with the far anterior part of the hypostome, where the rostral plate should be. A similar rostral plate and hypostome complex may be present in *Emeraldella brocki*, although the evidence remains inconclusive. The configuration of doublure and ventral sclerites in trilobites is quite similar to that found in *P. daziensis* and *R. abnormalis*, though it is currently unclear whether the hypostome was attached to the rostral plate in the ground pattern of Trilobita as inferred by Fortey (1990). Jell (2003) argued for a detached condition in the ground pattern, though that argument was based on the width of the preglabellar field on the dorsal side and other proxies, as little direct evidence is currently available. Even in helmetiids the anterior sclerite is in close association with the hypostome, though it seemed not to have been attached to it (Edgecombe & Ramsköld 1999). In artiopod taxa where the hypostome is fully detached from the doublure, there often is no rostral plate, as in nectaspidids. The same is true for *Agnostus pisiformis* and *Oelandocaris oelandica* (Fig. 13, node 6), as well as *Leanchoilia illecebrosa* ('great appendage' arthropods, Fig. 13, node 10). In the latter, the lateral eyes insert in the area between the hypostome and the anterior margin of the head. An anterior sclerite associated with the eyes was reported from the 'great appendage' arthropod *Yohoia tenuis* Walcott, 1912 (Whittington 1974, pls 2:2, 12:4, 5, 'median frontal lobe', labeled m), which could hint at an independent loss of the sclerite in 'great appendage' arthropods. On the other hand, no anterior sclerite is known in *Kiisortoqia soperi*, but no ventral structures other than the protruding appendages are known from that taxon. Such ventralization would not necessarily have to be achieved through incorporation into the doublure as in some artiopods. It could be simply overgrown anteriorly by the head shield. But even if it were assumed that the anterior sclerite was ventralized to some degree in the ground pattern of Euarthropoda (Fig. 13, node 1), that explanation would suffer from some degree of homoplasy. On the one hand independent reduction or loss would have to be invoked for several taxa; on the other hand, the sclerite at least twice independently would be secondarily moved into an exposed position in a recess of the anterior margin of the head shield, in the helmetiids and in *Yohoia tenuis*. With the limited taxon sample used in this analysis, it is impossible to assess further the plausibility of this homoplasy.

Tergite articulations of *Emeraldella brocki*

The only taxon included in the present analysis that has an articulating ridge parallel to the anterior tergite margins is *Emeraldella brocki*. Similar articulating devices are found in aglaspidids and *Molaria spinifera* Walcott, 1912 (Whittington 1981). Both are broadly similar to *E. brocki*, but for neither are the appendages known in any detail. In addition to the articulating ridges, they also share with *E. brocki* a styliform telson, though it is supposed to be articulated in *M. spinifera*. In the latter, as in *E. brocki*, the

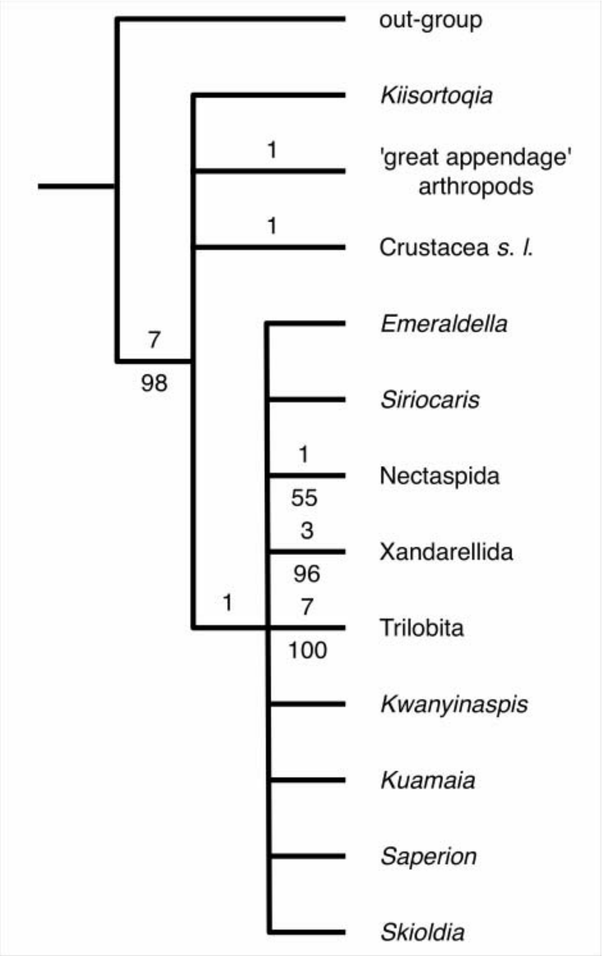

Figure 14. Strict consensus of 19 equally parsimonious trees from the re-run of the analysis with an alternative coding of character 2 for *Kwanyinaspis maotianshanensis*. Numbers above branches are Bremer support values, numbers below branches jackknife support values greater than 50.

posteriormost trunk tergite is relatively elongated and has reduced tergopleurae. It is not known whether it had lateroventral paired flaps flanking the telson like *E. brocki*. Aglaspidids do have a paired 'ventral plate' that may be homologous. Only distal parts of the postantennular limbs of *M. spinifera* are known. While the exopod flaps could represent the distal parts of a bilobate exopod as in *E. brocki*, there is no positive evidence of lamellae. The antennula identified by Whittington (1981) may pose problems though, as it seems short and rather limb-like. Of the antennulae of *Aglaspis spinifer* Raasch, 1939 only the most proximal articles are known and the morphology of the postantennular limbs are poorly known (Briggs *et al.* 1979). They are supposed to consist of the basipod and only four podomeres, while exopods are unknown.

The position of *Agnostus*

The present analysis affiliates *Agnostus pisiformis* with the early stem-lineage crustacean *Oelandocaris oelandica* and resolves them outside Artiopoda. This is in accord with Stein *et al*. (2005) but contradicts trilobite affinities (Fortey 2001; Fortey & Theron 1994; Cotton & Fortey 2005). Proponents of trilobite affinities often point out that no appendages of immature trilobites are known and, conversely, no appendages of fully grown agnostids (e.g. Bruton & Nakrem 2005). But, as indicated above, the known ontogeny is gradual with no dramatic morphological changes from instar to instar, so there is little reason to assume such radical morphological change between the last known meraspis and the adult (appendage morphology of the earliest holaspid is only partly known; Müller & Walossek 1987). In particular, a change from a head with specialized postantennular limbs to one with secondarily undifferentiated limbs of trunk morphology late in ontogeny would have to be postulated. The only artiopod species for which differentiation of cephalic limbs could be proven so far is *Emeraldella brocki*, and differentiation there differs from both *A. pisiformis* and *O. oelandica*. In *E. brocki* the exopod of the first postantennular limbs may be reduced, whereas it is the dominant ramus in that limb in both of the latter taxa (Müller & Walossek 1987; Stein *et al.* 2008). Homology seems thus questionable.

The morphological differences between *A. pisiformis* and trilobites have also been dismissed as phylogenetically uninformative autapomorphies of the former (Fortey & Theron 1994). While this may be true for the bulk of dorsal characters, it can be shown that some of the ventral characters are shared with *Oelandocaris oelandica* and thereby may be synapomorphies with Crustacea *sensu lato*. Notably, these include specific modifications of the first and second postantennular exopods which, in contrast to the exopods of the trunk limbs, are multiarticulate and insert in the lateral edge of the basipod only. These modified exopods seem to be a morphological specialization of the evolving cephalic feeding system of Crustacea *sensu lato* (Waloszek *et al*. 2007). A putative synapomorphy that was not considered here is the absence of a sternite of the segment of the first postantennular limb. Such a sternite is present in *Misszhouia longicaudata* (Chen *et al.* 1997), and the trilobite *Placoparia cambriensis* Hicks, 1875 (Edgecombe & Ramsköld 1999). The state is not known for any of the other taxa included here, which is why it is not coded. On balance, because of the absence of material of directly comparable ontogenetic stages, the affinities of agnostids remain questionable, but the present analysis fails to yield support for their trilobite affinities.

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