Soft-part anatomy of the Early Cambrian bivalved arthropods *Kunyangella* and *Kunmingella*: significance for the phylogenetic relationships of Bradoriida

Xianguang Hou^{1,*}, Mark Williams², David J. Siveter²,
Derek J. Siveter^{3,4}, Richard J. Aldridge² and Robert S. Sansom²

¹Yunnan Key Laboratory for Palaeobiology, Yunnan University, Kunming 650091,
Yunnan Province, People's Republic of China

²Department of Geology, University of Leicester, University Road, Leicester LE1 7RH, UK

³Geological Collections, University Museum of Natural History, Oxford OX1 3PW, UK

⁴Department of Earth Sciences, University of Oxford, Parks Road, Oxford OX1 3PR, UK

Bradoriids are small bivalved marine arthropods that are widespread in rocks of Cambrian to Early Ordovician age. They comprise seven families and about 70 genera based on shield ('carapace') morphology. New bradoriid specimens with preserved soft-part anatomy of *Kunmingella douvillei* (Kunmingellidae) are reported from the Early Cambrian Chengjiang Lagerstätte of China together with, for the first time to our knowledge, a second bradoriid species with preserved soft parts, *Kunyangella cheni* (Comptalutidae). *Kunmingella douvillei* has a 10-segmented limb-bearing body with uniramous ninth and tenth appendages and a series of homogeneous, apparently (proximal parts not preserved) unspecialized post-antennal biramous limbs with setose leaf-shaped exopods. Each endopod consists of five podomeres. A presumed penultimate instar of *Ky. cheni* preserves remnants of three head and two trunk appendages, and the adult is reconstructed as having four head appendages. This material allows testing of the affinity of the Bradoriida. *Kunmingella* is identified as a stem crustacean in character-based analyses, through both morphological comparisons and cladistic reconstructions. Global parsimony analysis recovers a monophyletic Bradoriida as the sister group to crown crustaceans.

Keywords: Arthropoda; Bradoriida; Cambrian; Chengjiang Lagerstätte; China; exceptional preservation

1. INTRODUCTION

Bradoriida are a prolific group of Cambrian and Early Ordovician marine arthropods that form an important component of the Cambrian ecosystem (Williams *et al.* 2007). They had a worldwide distribution and occur in most of the major Cambrian lagerstätten (Hou *et al.* 1996, 2002, 2004; Siveter *et al.* 1996; Siveter & Williams 1997; Shu *et al.* 1999). They first appear in the fossil record slightly earlier than trilobites of the Early Cambrian *Parabadiella* Biozone in south China (Hou *et al.* 2002), and using bivalved shield (i.e. 'carapace') morphology alone have been resolved into at least seven families (Williams *et al.* 2007). In having a bivalved shield, bradoriids resemble the ostracod crustaceans, a group that ranges from at least the Ordovician to Recent (Salas *et al.* 2007; Siveter 2008; Williams *et al.* 2008). Ostracods are the most prolific arthropods represented in the fossil record and the taxon to which bradoriids were traditionally assigned (e.g. Sylvester-Bradley 1961). Elucidating the systematic affinities of the Bradoriida is hampered by limited evidence of their soft anatomy, which until now has been

known only from *Kunmingella douvillei* (Mansuy 1912) from the Lower Cambrian of China (Hou *et al.* 1996; Shu *et al.* 1999) and from one specimen of an undescribed species from the Middle Cambrian of Australia (Hinz-Schallreuter 1993). The previously documented anatomical evidence suggested that *Kunmingella*—and by implication bradoriids in general—is not an ostracod; that it probably lies at a level low on the stem line of Crustacea (Hou *et al.* 1996; Shu *et al.* 1999); and that it is not closely related to the Phosphatocopida, the other widespread group of Cambrian bivalved arthropods that were also once thought to be ostracods (e.g. Müller 1979; cf. Siveter *et al.* 2001, 2003a; Maas *et al.* 2003).

Shield morphology is a poor means of establishing the affinity of bivalved arthropods because the bivalved shield is a feature prone to evolutionary convergence (Walossek 1993, p. 112). Even before the soft parts of bradoriids were known, Jones & McKenzie (1980) had already suggested that the group represented an artificial taxon. As Siveter *et al.* (2003b, 2007) and Siveter (2008) have indicated with respect to ostracods, viable affinity of such bivalved fossil material can only be tested by reference to specimens with soft-part anatomy preserved. Newly discovered specimens described here of the bradoriid *Km. douvillei* (Kunmingellidae) and *Kunyangella cheni* (Comptalutidae) from Yunnan Province, southern China,

* Author for correspondence (xghou@ynu.edu.cn).

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provide a much expanded dataset by which to assess bradoriid palaeobiology. Our new morphological data reveal the adult *Km. douvillei* to possess a 10-segmented body with the last three trunk segments, together with the associated appendages, extending beyond the posterior margin of the shield, a long antenna inserted posterior of the eye and uniramous ninth and tenth appendages. In addition, we show that *Ky. cheni* bears at least five pairs of appendages. We use these data, in conjunction with those reported by Hou *et al.* (1996) and Shu *et al.* (1999), to examine the systematic affinity of two bradoriid families, and thereby examine the phylogenetic relationships of the group itself. Kunmingellids are known from the Cambrian of China and Siberia, and comptalulitids are documented from the Cambrian of China, central Asia, Siberia and Australia (Jones & Laurie 2007; Williams *et al.* 2007).

2. MATERIAL AND METHODS

As with other exceptionally preserved fossils of the Chengjiang Konservat-Lagerstätte (Hou *et al.* 2004), the material described here is preserved as two-dimensional specimens or, more rarely, with weak three dimensionality. The taphonomic pathway involves pyrite replacement, later pseudomorphed by iron oxides, within clay-rich host sediment (Gabbott *et al.* 2004). Specimens were prepared mechanically using fine needles. Images were captured using a Canon five-dimensional DSLR Camera attached to Leitz Aristophot and Nikon Multiphot macrophotographic equipment. All material was collected from the Lower Cambrian of the Chengjiang and the Haikou (Kunming) areas, Yunnan Province, and is deposited in the Yunnan Key Laboratory for Palaeobiology (YKLP), Yunnan University, Kunming, China.

3. SYSTEMATIC PALAEONTOLOGY

Phylum: Arthropoda, Subphylum and Class uncertain.
Order: Bradoriida Raymond, 1935?

Remarks. As there is no information on the soft-part anatomy of the type genus *Bradoria* Matthew, 1899, herein *Kunmingella* and *Kunyangella* are tentatively assigned to the Bradoriida.

Family: Kunmingellidae Huo & Shu, 1985

Genus: *Kunmingella* Huo, 1956

2002 *Kunmingella* Huo, 1956; Hou *et al.*, p. 358 (q.v. for full synonymy).

2007 *Kunmingella* Huo, 1956; Zhang, p. 113

Diagnosis. Kunmingellids with adults having five limb-bearing segments in both the head and trunk; uniramous antenna inserted posterior of the eye; biramous second to eighth appendages, each bearing a leaf-shaped exopod; and uniramous ninth and tenth appendages. Shield with a broad anterodorsal lobe; posterior lobe elongate, straight to weakly crescent shaped, tapering, extends from just behind valve centre to immediately in front of the posterior cardinal corner. Broad, shallow depression occurs between anterodorsal and posterior lobes, deepest mid-dorsally. A low, narrow latero-admarginal ridge is entire between cardinal corners. Valves smooth to finely granulose.

Species: *Kunmingella douvillei* (Mansuy, 1912).

2002 *Kunmingella douvillei* (Mansuy, 1912); Hou *et al.*, p. 359, figs 11a–k, 12a–j, 13a–h (q.v. for full synonymy).

2004 *Kunmingella douvillei* (Mansuy, 1912); Hou *et al.*, p. 114, fig. 16.13

2007 *Kunmingella douvillei* (Mansuy, 1912); Zhang, p. 115, pl. 1, figs 1–13, pl. 2, figs 1–18, pl. 5, figs 1–11, text-figs 3A, 5A.

2007 *Kunmingella douvillei* (Mansuy); Williams *et al.*, figs 2.4–6

2007 *Kunmingella douvillei* (Mansuy 1912); Vannier, fig. 5i.

2008 *Kunmingella douvillei* (Mansuy 1912); Siveter, pl. 1, figs 4, 6

2008 *Kunmingella douvillei* (Mansuy 1912); Williams *et al.*, text-fig. 2.3

Diagnosis. *Kunmingella* with shield lacking a posteroventral spine.

Syntypes. Shields and valves on a slab of mudstone (Mansuy 1912, p. 22, pl. 1, fig. 8). Kebaocun section, Yiliang County, Yunnan Province; Heilinpu Formation, Lower Cambrian. The repository for this material is unknown.

Material. Countless thousands of specimens are known from numerous localities in Sichuan and especially Yunnan provinces, southern China (see Hou *et al.* (2002) and Zhang (2007) for details), but individuals with preserved soft-part anatomy are extremely rare. Previously figured specimens with soft parts are detailed in Hou *et al.* (1996, 2002, 2004), Shu *et al.* (1999), Gabbott *et al.* (2004), Williams *et al.* (2007, 2008) and Siveter (2008). The 32 newly collected specimens documented here, many together with their counterparts, all bear soft-part anatomy: YKLP10988–94, 10996–11001, 11003–18 and (formerly RCCBYU) 10196 and 10258–59. Shields are 1.25–6 mm long (a greater range than that recorded by Hou *et al.* (2002): 1.76–5.24 mm); those over 3.5 mm long are regarded as adults (see §3b).

In the following description, we refer to only those specimens that most clearly exhibit a particular feature.

(a) Adults

The morphology of the shield is given in the diagnosis of the genus. The assumed division between the head and the trunk is indicated by the disposition of appendages: trunk appendages point backwards, head appendages forward (e.g. figure 1d, f, g). The body has 10 limb-bearing segments, five each in the head and the trunk, each bearing a single pair of appendages, the limb bases of which are not preserved (figure 1g, o). The adult body has a maximum width of about 1.5 mm and narrows posteriorly from the sixth segment. Segments 2–8 are typically 0.5 mm long axially (figure 1g). The posterior-most segments, including the tiny triangular-shaped tail-piece, form a cone-shaped termination to the trunk that protrudes beyond the posterior margin of the shield (figure 1g).

A pair of lateral eyes occurs just in front of the insertion point of the first appendage (antenna) at the site of the anterodorsal node of the shield (figure 1a, m). The first, uniramous appendage is about 2.5 mm long, tapers distally and consists of five podomeres, of which typically the distal three protrude beyond the shield

Figure 1. Bradoriida with soft-part anatomy preserved, Yu'anshan Member, Heilipu Formation, Lower Cambrian, Haikou, Kunming area and Chengjiang area, Yunnan Province, South China; (*a,c-f,h-k,n*) from Ercaicun, Haikou, Kunming area; (*b,l,m*) from Mafeng, Haikou, Kunming area; (*g,o*), from Xiaolantian, Chengjiang area. (*a,d-o*) *Kunmingella douvillei*: (*a*) YKLP (formerly RCCBYU) 10259, fully open shield, dorsal view, $\times 6.25$; (*d_{j,n}*) YKLP 10994, (*d*) fully open shield, dorsal view, $\times 6.6$, (*j*) posterior part, dorsal view, $\times 8$, (*n*) anterior part, dorsal view, $\times 11$; (*e*) YKLP10993 fully open shield, dorsal view, $\times 6$; (*f*) YKLP10998, fully open shield, dorsal view, $\times 7.4$; (*g,o*) YKLP10988b, (*g*) fully open shield, dorsal view (1–10: body segmentation), $\times 5.5$, (*o*) posterior part, dorsal view, $\times 10$; (*h,i*) YKLP (formerly RCCBYU) 10258, (*h*) fully open shield, dorsal view, $\times 6$; (*i*) posterior part, dorsal view, $\times 10$; (*k*) YKLP11001a, juvenile, right lateral view, with left valve behind soft parts, $\times 24$; (*l*) YKLP11000, juvenile, lateral view of posterior part of excavated closed shield (1–5: podomeres of endopod), $\times 13$; (*m*) YKLP10990a, fully open shield, dorsal view of anterior part, $\times 10$. (*b,c*) *Kunyangella cheni*: (*b*) YKLP 11003, right lateral view, $\times 18.5$; (*c*) YKLP 11002, left lateral view, with right valve behind soft parts, $\times 21.5$. Abbreviations: a1–a5, head appendages; a6–a10, trunk appendages; en, endopod; ex, exopod; rv, right valve; lv, left valve; td, terminal limb-bearing division; tp, tail piece; 1–5, podomeres of the endopod.

anteriorly (figure 1*d,m*). There are five to six short, stiff setae on the outer and distal edges of the distal-most podomere (figure 1*d,n*). Podomeres 2–4, at least, each have an endite distally on their inner margins, with the endite of at least the third and fourth podomeres bearing splays of setae.

Appendages 2–8 are biramous, each having a large leaf-shaped exopod (most evident on the trunk in

figure 1*d_{f,h-j}* and on the head in YKLP 10990a) and an endopod consisting of five podomeres (e.g. figure 1*l*; also unfigured specimen YKLP 10196 and Shu *et al.* 1999, figs 1*a-c*). The four post-antennal cephalic appendages can each be traced back to a discrete body segment (figure 1*g*); each endopod bears a single elongate endite on the inner margin of each podomere (Shu *et al.* 1999), but it cannot be determined whether any of the

exopods are fringed by marginal setae (as is the case with the exopods of the trunk appendages; see below). Each endopod of trunk appendages 6–8 has a single endite on (possibly the inner margin of) each podomere (figure 1l and YKLP10196; Shu *et al.* 1999) and each exopod bears stiff and distally progressively longer setae on its distal outer and inner margins (figure 1d,j).

The ninth and tenth pairs of appendages are uniramous (figure 1a,e,f,i,o). The ninth appendage is narrow, elongate, about 2 mm long excluding the short terminal ‘claw-like’ structure and posteriorly it projects well beyond the shield (figure 1a,f,h,i). It comprises at least five podomeres, each about 0.5–0.75 mm long, with setae originating from the inner surface of each podomere; adjacent podomeres are geniculate. The tenth appendage is about 1 mm long and consists of at least three podomeres each bearing short, stiff setae, at least six of which occur on the distal-most podomere (figure 1a,h,i).

(b) *Ontogeny*

Based on isolated shields and valves, *Km. douvillei* has five ontogenetic stages (Zhang 2007). Growth stages 1 and 2 each have a tiny (*ca* 200–230 µm diameter), univalved, dome-like shield; later pre-adult growth stages each have a small bivalved shield. The anterior and posterior lobes of the shield become well developed first in growth stage 4. On these criteria, YKLP11001a (figure 1k), with soft-part anatomy, is considered to be growth stage 4. In the new material presented here, all specimens with 10 appendages (collected from various horizons) are considered to be adults, and these range from 3.5 to 6 mm long (figure 1a,d–h). YKLP11001a (figure 1k) differs principally from adults by having seven appendages and a trunk that does not appear to extend beyond the posterior margin of the shield. Its first appendage is uniramous, at least 0.55 mm long, and comprises five podomeres; no setae are determinable, but this may be a factor of preservation. Appendages 2–6 each have an endopod composed of at least four podomeres. An exopod is not discernible on the second and third appendages; appendages 4–6 each have a leaf-shaped exopod. Appendage 7, seen as a single, posteriorly projecting ramus, consists of at least three elongate podomeres.

Family: Comptalutidae Öpik, 1968

Genus: *Kunyangella* Huo, 1965

2002 *Kunyangella* Huo, 1965; Hou *et al.*, p. 387 (q.v. for full synonymy).

2007 *Kunyangella* Huo, 1965; Zhang, p. 128

Diagnosis. Comptalutids with the penultimate growth stage having three head appendages, including two post-antennal limbs each with a narrow, elongate endopod bearing at least two stout setae terminally; the endopod of each trunk appendage is broader, and each podomere has an endite with setae. Shield with mid-dorsal node, but no other lobation. A weak latero-admarginal ridge occurs between cardinal corners, demarcated from the lateral valve surface by a furrow.

Species: *Kunyangella cheni* Huo, 1965

2002 *Kunyangella cheni* Huo, 1965; Hou *et al.*, p. 387, figs 20d–k, 21a (q.v. for full synonymy).

2007 *Kunyangella cheni*; Zhang, p. 129

Diagnosis. *Kunyangella* with shield bearing a bulbous, elongate to arcuate mid-dorsal node.

Holotype. External mould of a (juvenile?) left valve, Northwest University, Xi'an, China, no. 0006; Huo, 1965, pl. 1, fig. 6. Jinning County, Yunnan Province; Heilinpu Formation, Lower Cambrian.

Material. Known from a few hundred specimens from several localities in Yunnan Province (Hou *et al.* 2002). Herein, we document the first (two) specimens with soft-part anatomy preserved, both from Haikou: YKLP11002–3. Both shields are about 2 mm long and, bearing in mind that specimens from Yunnan Province are up to 2.38 mm long (Hou *et al.* 2002), each probably represents a penultimate growth stage.

(c) *Soft-part anatomy*

There are remnants of a mass of soft tissue within the shield of YKLP 11002 (figure 1c), but no more detail of the body is preserved. YKLP 11003 (figure 1b) shows red coloration mid-posteriorly that might represent the remnants of soft tissues protruding beyond the body. However, the posteroventral position of the trunk appendages may indicate that much of the body was accommodated within the shield. An anterodorsal node (‘eye lobe’) is absent, and there is no indication of the presence of an eye.

YKLP 11002 preserves remnants of five appendage pairs, three anteriorly that project forwards on the presumed head and two behind that project posteroventrally on the presumed trunk. Given that YKLP 11002 probably represents a penultimate growth stage, it is considered that adults would have four pairs of appendages in the head (for ontogenetic patterns of segmentation in Crustacea, e.g. Waloszek & Maas 2005).

The presumed first pair of appendages (occurring in a similar position and with similar morphology to the distal end of the first appendage of *Kunmingella*) are preserved in the lateral view as two short, stout podomeres protruding from the shield mid-anteriorly (these very delicate podomeres were visible when originally observed, but subsequently they mostly flaked off from the shale matrix and therefore are not now seen clearly in figure 1c). More posteriorly, there are narrow, presumed endopods of two appendage pairs extending beyond the shield (a2, a3), each consisting of two podomeres with elongate, almost claw-like pairs of setae terminally. Remnants of two trunk appendages (a4, a5)—presumed endopods—are broader than appendages 1–3 and have stout setae terminally. The fifth appendage shows at least three podomeres, each having an endite with setae. YKLP 11003 preserves remnants of two pairs of trunk appendages (presumed a4, a5) protruding posteroventrally from a closed shield.

4. THE ANATOMY AND LIFESTYLE OF *KUNMINGELLA DOUVILLEI*

The considerably increased dataset of soft-part anatomy for *Km. douvillei* allows a revised reconstruction of the animal (figure 2). The occurrence of five limb-bearing segments in the head and five in the trunk (figure 1g,o) and the disposition of the associated appendages confirm the cephalic-trunk boundary suggested by Hou *et al.* (1996) and Shu *et al.* (1999, p. 287). However, Shu *et al.* (1999) identified only eight appendage pairs. The

Figure 2. Reconstruction of *Km. douvillei* (Mansuy 1912), based on the new material here and, in part, on evidence from Hou *et al.* (1996) and Shu *et al.* (1999). Interpretation of the morphology of the exopods and endopods of the head appendages is based on specimen YKLP 10990a and Shu *et al.* (1999), respectively. For clarity, some of the appendages have been omitted from the reconstruction. The reconstruction shows the dorsal aspect of the animal with the shield stripped away; in appendage 2, the endopod, which lies below the exopod from the dorsal aspect, is emphasized to show the five podomeres. Information on the limb bases of all appendages is lacking. Abbreviations as for figure 1, except lr, latero-admarginal ridge.

new material shows for the first time, to our knowledge, that the first appendage is long (2.5 mm) and that its insertion point is just behind that of the eye (figure 1m) and in a more posterior position than envisaged by Shu *et al.* (1999). Our material confirms the observation of the latter authors that the biramous post-antennal appendages each have an endopod comprising five podomeres, with the inner margin of each podomere bearing an endite ('lobate expansions' of Shu *et al.* 1999). Each exopod of these biramous appendages is leaf-like (YKLP11005) and, at least for appendages 6–8, is fringed by marginal setae. The new material shows that the posterior morphology of *Km. douvillei* comprises uniramous ninth and tenth appendages (equal to biramous eighth appendage and furca of Shu *et al.* 1999, fig. 6e), and that the last three trunk segments, together with the associated appendages, extend beyond the posterior margin of the shield (figure 1g,o; cf. Shu *et al.* 1999, p. 287). Our new material also shows that three appendages (and presumably three segments) are added between growth stage 4 (*sensu* Zhang 2007) and the adult stage (see above).

Kunmingella douvillei possibly crawled on and swam near the substrate, with its dorsal shield held widely open in life (Shu *et al.* 1999; Hou *et al.* 2004). Vannier (2007, fig. 3) suggested that the species may have

formed a component of the Early Cambrian meiofauna, living at the sediment–water interface, with a lifestyle and ecological niche similar to some Recent ostracods. The eyes and possibly the long first appendage would have acted as sensory devices. The leaf-shaped exopods may have aided swimming. The trailing ninth and short tenth appendages may have functioned to stabilize the animal during locomotion. An approximate morphological analogue of the ninth appendage is the antenniform cercus in the Burgess Shale trilobite *Olenoides serratus* (Whittington 1975). Remains of *Km. douvillei* shields occur in considerable numbers in elliptical aggregates interpreted as coprolites, indicating possible predation by anomalocaridids and/or unknown epibenthic predators (Vannier & Chen 2005).

5. PHYLOGENETIC POSITION OF BRADORIIDA

Bradoriida encompasses a wide range of bivalved arthropod morphologies that traditionally were regarded as ostracod or ostracod-like crustaceans (e.g. Sylvester-Bradley 1961). Previous studies based on less complete soft-part evidence concluded that *Kunmingella* was perhaps a stem-lineage crustacean (Hou *et al.* 1996; Shu *et al.* 1999). The new material described here allows testing of the systematic relationship of two bradoriid families.

Following the scheme of Waloszek and co-authors (e.g. Waloszek & Müller 1998; Waloszek 1999, 2003; Maas *et al.* 2004; Waloszek *et al.* 2005, 2007; Stein *et al.* 2005; Zhang *et al.* 2007), the series of homogeneous, unspecialized post-antennal biramous limbs with setose leaf-shaped exopods in *Km. douvillei* represent the plesiomorphic condition as in the ground plan of Euarthropoda (e.g. Waloszek 2003). Even though the proximal parts of the appendages are not preserved, the generalized, homogeneous nature of the limb rami suggests that the limb bases are also unspecialized. The endopods of *Kunmingella* each consist of five podomeres: possession of fewer than seven podomeres is characteristic of members of Crustacea (Waloszek 2003; Waloszek *et al.* 2007; Zhang *et al.* 2007; figures 1i,j and 2), while possession of five head appendages indicates a level on the crustacean stem line equivalent to that of *Henningsmoenicaris* or *Oelandocaris* (Stein *et al.* 2005, 2008) or more derived Labrophora (Zhang *et al.* 2007, fig. 3). In contrast to the morphology of *Kunmingella*, the adult growth stage of *Ky. cheni* is here considered to have only four head appendages. According to the scheme of Waloszek and others, possession of just four head segments, rather than five, would place *Kunyangella* in a more basal position than *Kunmingella*, and comptalutitids and kunmingellids would form a paraphyletic group. Alternatively, if *Kunyangella* does not belong to Crustacea, then similarities between comptalutitids and kunmingellids, such as those of the shield, would represent convergence and the Bradoriida would be polyphyletic.

However, these scenarios also require consideration in terms of global parsimony. To this end, we have coded *Kunmingella* and *Kunyangella* for inclusion in the arthropod morphological database presented and analysed by Wills *et al.* (1998): although this analysis is in need of revision, it represents the most comprehensive database of fossil arthropod characters. To ensure that we are

considering the range of previous hypotheses for bradoriid relationships, we have also included *Klausmuelleria* and *Vestrogrothia* to represent the Phosphatocopina. Heuristic search methods (see the electronic supplementary material) recovered a monophyletic Bradoriida as the sister taxon to crown-group crustaceans. The placement of the Bradoriida on the crustacean stem is supported by their possession of a mobile appendage on the terminal division of the trunk and five head segments (depending upon optimization criteria; see the electronic supplementary material), and by their lack of crown-group characters such as specialized second and third appendages. Conversely, Phosphatocopina are recovered as crown-group crustaceans on the basis of their placement relative to Remipedia (see the electronic supplementary material). The marrellomorphs are placed as sister group to the clade (Bradoriida + Eucrustacea), at the base of the crustacean stem. Alternative interpretations of arthropod phylogeny (e.g. using molecular data) can be applied using back-bone constraint trees. When the pancrustacean hypothesis of Regier *et al.* (2005) is taken into account, the same placement of Bradoriida is recovered.

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