A new leanchoiliid megacheiran arthropod from the lower Cambrian Emu Bay Shale, South Australia

GREGORY D. EDGECOMBE, DIEGO C. GARCÍA-BELLIDO, and JOHN R. PATERSON


The Leanchoiliidae is well-known from abundant material of *Leanchoilia*, from the Burgess Shale and Chengjiang Konservat-Lagerstätten. The first Australian member of the group is *Oestokerkus megacholix* gen. et sp. nov., described from the Emu Bay Shale (Cambrian Series 2, Stage 4), at Buck Quarry, Kangaroo Island, South Australia, and is intermediate in age between the well known leanchoiliid species from the Burgess Shale and Chengjiang. Phylogenetic analysis of “short great appendage” arthropods (Megaangea) in the context of the chelicerate stem group resolves the Australian species as sister to Burgess Shale, Utah, and Chengjiang *Leanchoilia* species, but most readily distinguished from *Leanchoilia* and *Alalcomenaeus* by a different telson shape, interpreted as being forked, widening distally, and with a few dorsally curved spines at the posterior angle. Leanchoiliid interrelationships are stable to alternative character weights, and Megaangea corresponds to a clade in most analyses.

Key words: Arthropoda, Megacheira, Leanchoiliidae, Oestokerkus, Leanchoilia, Alalcomenaeus, midgut glands, phylogeny, Cambrian, South Australia.

Gregory D. Edgecombe [g.edgecombe@nhm.ac.uk], Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD, UK; Diego C. García-Bellido [Diego.GBC@geo.ucm.es], Departamento de Paleontología, Instituto de Geología Económica/Instituto de Geociencias (CSIC-UCM), José Antonio Novais 2, 28040-Madrid, Spain; John R. Paterson [jpater20@une.edu.au], Division of Earth Sciences, School of Environmental and Rural Science, University of New England, Armidale, NSW 2351, Australia.

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Introduction

“Great appendage arthropods” have figured prominently in considerations of Cambrian arthropod systematics and the assignment of early arthropod lineages to the stem groups of major extant clades. An assemblage of taxa formalised as Megaangea Hou and Bergström, 1997, has variably been regarded as belonging to the stem group of Chelicerata (Wills et al. 1998; Chen et al. 2004; Cotton and Braddy 2004) or to the stem group of all extant arthropods (Hou and Bergström 1997; Budd 2002; Daley et al. 2009). Megacheira, composed at least of the Cambrian taxa Leanchoilia, Yohoiida, and Fortiforcipida, has been depicted as a clade (Hou and Bergström 1997: fig. 87), as a polyphyletic group in different parts of the euarthropod stem group (Bergström and Hou 2005), or as an unresolved polytomyl in the chelicerate stem group (Chen et al. 2004: fig. 6). When conceived as a clade, the group is united by the “great appendage” having a few elongate spine projections, the exopods being fringed with setae, and a large telson (Hou and Bergström 1997). The extreme ends of the spectrum on the phylogenetic position of Megacheira involve whether the so-called “short great appendage” (Chen et al. 2004) is a precursor to the chelicera (Bousfeld 1995; Chen et al. 2004; Cotton and Braddy 2004; Bitsch and Bitsch 2007) or is the appendage of a segment that is anatomically anterior to the chelicera or antenna (Budd 2002).

The anatomically best understood megacheirans belong to the Order Leanchoiliida Størmer, 1944, of which the genera *Leanchoilia* Walcott, 1912, and *Alalcomenaeus* Simonetta, 1970, provide most available information. *Alalcomenaeus cambricus* Simonetta, 1970, has been revised based on Burgess Shale collections made through the 1980s and 1990s (Briggs and Collins 1999). *Alalcomenaeus* is apparently also represented in the Chengjiang fauna, based on *A. elegans* (Luo and Hu in Luo et al., 1999) (see Liu et al. 2007). The more common *Leanchoilia* has received even more study. The anatomy and taxonomy of *Leanchoilia* from both the Burgess Shale (García-Bellido and Collins 2007) and Chengjiang Lagerstätten (Liu et al. 2007) have recently been reviewed, the former updating descriptions by Bruton and Whittington (1983). Two species in the Burgess Shale (*Leanchoilia superlata* Walcott, 1912 and *Leanchoilia persephone* Simonetta, 1970) and a single species from Chengjiang (*Leanchoilia illecebrosa* [Hou, 1987]) have been redescribed based on extensive new collections. *Leanchoilia illecebrosa* subsumes several generic and specific names introduced by Luo et al. (1997) for Chengjiang material (see Liu et al. 2007...
for synonymy). \textit{Leanchoilia protogonia} Simonetta, 1970, from the Burgess Shale has been reillustrated and accepted as a valid species (Briggs et al. 2008). In addition to its Burgess Shale and Chengjiang species, \textit{Leanchoilia} has also been reported from the Spence Shale of Utah (\textit{Leanchoilia superlata}? [Briggs et al. 2008]); \textit{Leanchoilia? hanceyi} Briggs and Robison, 1984, and the Kaili Formation, Guizhou, China (\textit{Leanchoilia} sp. of Zhao et al. 2005).

Herein we add new diversity and biogeographic data for \textit{Leanchoiliidae} by documenting a new genus and species from the Emu Bay Shale, Kangaroo Island, South Australia. Earlier collections made from the Emu Bay Shale—forming the basis of previous studies (see Paterson and Jago 2006, Paterson et al. 2008 for an overview)—came from the cliff and wave-cut platform exposures outcropping on the shore-line immediately east of the mouth of Big Gully on the northeast coast of Kangaroo Island (Fig. 1). The new collections described herein come from a new inland site, Buck Quarry, the excavation of which began in 2007. The locality and elements of the arthropod fauna are documented by Paterson et al. (2008), García-Bellido et al. (2009), and Paterson et al. (2010). The Emu Bay Shale correlates with the lower Cambrian (Series 2) \textit{Pararaia janeae} Zone of the South Australian biostratigraphic scheme (Jago et al. 2006), equivalent to the early-mid Canglangpuan Stage of China and the mid–late Botoman of Siberia (Paterson and Brock 2007; Paterson et al. 2008).


\textbf{Other abbreviations.}—cn1–2, cephalic endopods; cs, cephalic shield; cx1–2, cephalic exopods; eo, excretory organ; ga, great appendage; gaf, great appendage flagellum; gap, peduncle of great appendage; L, prefix for left; mg, midgut glands; ol, overlap between adjacent trunk tergites; R, prefix for right; t1–t11, tergites of trunk segments 1–11; tn, trunk endopods; tr, reinforcing ridges on telson; ts, telson marginal spines; tx, trunk exopods; txm, trunk exopod lobe margins; vm, ventral margin of tergites.

\section*{Material and methods}

Specimen photography used a Canon EOS 5D digital camera with a Canon MP-E 65 mm 1–5× macro lens, and low angle fibro optic directional lighting from the top left (unless otherwise stated, see Figure captions). Original colour images were converted to 8-bit grey scale. Camera lucida drawings were made using a Leica MZ6 microscope at \times 16 magnification.

In the phylogenetic analysis, data were analysed using the parsimony program TNT (Goloboff et al. 2008) with an exact search (implicit enumeration). Character optimisation was explored with WINCLADA (Nixon 2002). Multistate characters were treated as unordered. Characters that have partial uncertainty (of the form “either 0 or 1 but not 2”) were treated as either of the two possible alternatives (as implemented by NONA and PeeWee). Jackknife resampling (Farris et al. 1996) and Bremer support (Bremer 1994) were used as measures of nodal support. Jackknifing used 1000 replicates with 36% deletion, each replicate a heuristic search involving 1000 random stepwise addition sequences and TBR branch swapping. Bremer support was calculated from collections of suboptimal trees obtained by exact searches. Implied weighting (Goloboff 1993) with TNT used the default concavity constant of k = 3, followed by tree search with implicit enumeration.

\section*{Systematic palaeontology}

\textbf{Phylum Arthropoda} Siebold and Stannius, 1845
\textbf{Class Megacheira} Hou and Bergström, 1997
\textbf{Order Leanchoiliida} Størmer, 1944
\textbf{Family Leanchoiliidae} Raymond, 1935
\textbf{Genus Oestokerkus} nov.

\textit{Type species:} \textit{Oestokerkus megacholix} sp. nov., see below.

\textit{Etymology:} From Greek \textit{o}ï\textit{stos}, arrow and \textit{kerkus}, tail; with reference to the forked shape of the telson.

\textit{Diagnosis.}—\textit{Leanchoiliid} with long cephalic shield, more than one-third length of trunk excluding telson; lateral eye relatively large; paratergal folds long, maximum height of thorax nearly 40% of its length; midgut glands large; two pairs in head as well developed as those in trunk; exopods fringed by long setae; telson forked, widening distally, with a few dorsally curved spines at posterior angle.
Discussion.—Membership of *Oestokerkus* in Leanchoiliidae sensu Liu et al. (2007), a group that includes the formerly recognised families Alalcomenaeidae Simonetta and Delle Cave, 1975, and Actaeidae Simonetta and Delle Cave, 1975, is clearly demonstrated by the morphology of the frontal appendage, which has greatly elongated spinose projections developed on its distal two articles and the movable finger, each projection terminating at the same length and bearing a long flagellum, presence of 11 trunk segments, anteroventrally-positioned eyes, pendant appendages that have a similar biramous structure in the cephalon and trunk, and spines fringing the margin of a long telson.

The distinction between *Alalcomenaeus* and *Leanchoilia* has most recently been reviewed by Liu et al. (2007), who emphasised the shape of the telson as a diagnostic character, that of *Leanchoilia* being pointed and that of *Alalcomenaeus* rounded. The telson of *Oestokerkus megacholix*, described below, differs substantially from the other species of both genera. The telson widens distally in the holotype of *O. megacholix* (Figs. 2, 3A, B) and is inferred to be forked. Marginal spines are confined to the posterior edge rather than being developed along the lateral margins of a lanceolate telson as in all species of *Leanchoilia*, or a paddle-shaped, posteriorly rounded telson in *Alalcomenaeus*. To date, specimens of *O. megacholix* are preserved only in lateral aspect, most likely due to gravitational settling of the body on its side—a common burial position of other leanchoiliids (Zhang and Hou 2007)—because of the deep dorso-ventral versus transversely narrow proportions of the body, thus our interpretation of the telson (see description below) has not yet been confirmed in dorsal aspect. Phylogenetic analysis (see below) resolves *O. megacholix* as sister to the widely accepted grouping of *Leanchoilia* so we have elected to erect a new genus for it rather than to widen the scope of *Leanchoilia* and be forced to rediagnose that genus using characters other than telson shape. This taxonomic framework is consistent with the generic concepts of Liu et al. (2007).

In addition to telson form, *Oestokerkus* is further distinguished from other leanchoiliid genera by relative proportions of the cephalic shield and trunk pleurotergites. The cephalic shield of *O. megacholix* occupies a greater proportion of body length than in *Leanchoilia* or *Alalcomenaeus*; the head being ca 36% the length of the trunk (excluding the telson) compared with 28% in *Alalcomenaeus cambricus*, 25% in *Leanchoilia illecebrosa*, 23% in *Leanchoilia persephone*, and 26% in *Leanchoilia superlata*. The paratergal fold in *O. megacholix* is also considerably deeper than in other leanchoiliids. The height to length ratio of ca 39% in *O. megacholix* (Fig. 2) contrasts with ca. 19–22% in the three well-known Burgess Shale and Chengjiang species of *Leanchoilia* (e.g., Liu et al. 2007: fig. 2D, E) as well as *A. cambricus*. From what is observed in other fossils from this locality—and is also the case in the Burgess Shale *Leanchoilia*—despite the fossils being compressed flat, there is little distortion. Therefore, the dimensions discussed above are not considered to deviate in any significant way from those the animals would have had in life (Fig. 7). The large midgut glands of *O. megacholix* are approached in size by some species of *Leanchoilia*, notably *L. superlata* (García-Bellido and Collins 2007: pl. 2: 5), in which their structure of radiating grooves is the same. The position and size of the lateral eye in *O. megacholix* resemble those of *A. cambricus*, in which laterally preserved specimens show the eye to be bulging at the anterolateral margin of the cephalic shield (Briggs and Collins 1999: pl. 2: 4, pl. 6: 3) but preservation in dorsoventral aspect shows that the lateral pair of eyes to be adaxial to the cephalic margin (Briggs and Collins 1999: pl. 1: 1). No evidence is available to indicate whether median eyes (either two as in *Leanchoilia* or three as in *Alalcomenaeus*) are present in *Oestokerkus* because this requires a dorsoventral aspect, though the resolution of *Oestokerkus* within Leanchoiliidae predicts the presence of this feature.

We have not coded the number of cephalic appendages in *O. megacholix* in the cladistic analysis, but the only specimen that preserves the endopods (see species description) is most consistent with two biramous cephalic appendages, as has been documented in *A. cambricus* (Briggs and Collins 1999) and in both *L. superlata* and *L. persephone* (García-Bellido and Collins 2007), and contrasting with three pairs of biramous cephalic appendages in *L. illecebrosa* (Chen et al. 2004; Liu et al. 2007). We reject the opinion of Chen et al. (2004) that Briggs and Collins (1999) probably miscounted for *Alalcomenaeus* because more recent observations on Burgess Shale *Leanchoilia* show that two pairs are indeed present in some members of Leanchoiliidae (García-Bellido and Collins 2007). The variability in this feature in a narrowly-circumscribed monophyletic group (i.e., *Leanchoilia*) indicates that it is of fairly minor taxonomic weight within this family.

*Oestokerkus megacholix* sp. nov.

Figs. 2–7.

Etymology: From Greek *mega*, large, and *cholix*, gut, in reference to the voluminous midgut glands.

Type material: Holotype: SAM P43631 a, b, part and counterpart preserved in lateral aspect (Figs. 2, 3), from the Emu Bay Shale, Buck Quarry, preserving cephalon, including spinose projections and flagella of great appendages, all 11 trunk segments, and most of telson, including a few marginal spines; midgut glands exposed in head and anterior two-thirds of trunk; some exopod setae of cephalic appendages as well as lobes and setae of those associated with entire trunk. Paratypes: All preserved in lateral aspect. SAM P45167 (Fig. 4): cephalon exposing eye and peduncle of great appendage, most of trunk with exopod setae and a few endopods. SAM P43630a, b (Fig. 5B): part and counterpart preserving cephalic shield, spinose projections of great appendage, and anterior eight trunk segments; two midgut glands and exopod setae of cephalic and trunk appendages exposed. SAM P15531 (Fig. 5A): part only, preserving cephalon, including spinose projections of great appendage, and most of trunk with midgut glands. SAM P15438 (unfigured), incomplete cephalic shield with parts of great appendage, complete trunk and apparently proximal part of telson. SAM P45168 (Fig. 6): part only, cephalon with partial great appendages, most of trunk, with midgut glands and exopod setae. SAM P45169a, b (unfigured): cephalon with partial great appendages, trunk with midgut glands. SAM P45177a, b; SAM P45178a, b (unfigured): two weathered specimens.
Fig. 2. Leanchoiliid megacheiran arthropod *Oestokerkus megacholix* gen. et sp. nov. Holotype SAM P43631a. A. Photograph. B. Interpretative camera lucida drawing. Arrows indicate tips of trunk exopod setae. Abbreviations: cs, cephalic shield; cx, cephalic exopods; ga, great appendage; gaf, great appendage flagellum; gap, peduncle of great appendage; mg, midgut glands; t1, tergite of trunk segment 1; tr, reinforcing ridges on telson; ts, telson marginal spines; tx, trunk exopods; txm, trunk exopod lobe margins; vm, ventral margin of tergites. Boundaries between trunk tergites indicated by dashed lines above dorsal margin.

Fig. 3. Leanchoiliid megacheiran arthropod *Oestokerkus megacholix* gen. et sp. nov. Holotype SAM P43631. A. P43631a. A1. Midgut glands and tergite boundaries in dorsal part of trunk. Arrows indicate furrows that may represent position of dorsal transverse tendons. A2. Telson, light from NE. A3. Spinose projections and flagella of distal articles of frontal appendage and exopod setae of cephalic and anterior trunk appendages and posterior margins of lobes of the latter. B. P43631b, telson, light from NE. Arrows indicate tips of exopod setae. Abbreviations: gaf, great appendage flagellum; mg, midgut glands; ol, overlap between adjacent trunk tergites; tr, reinforcing ridges on telson; ts, telson marginal spines; txm, trunk exopod lobe margins; vm, ventral margin of tergites.
SAM P45904a, b (unfigured): poorly-preserved cephalic shield, trunk with well-preserved midgut glands, proximal part of telson. SAM P45905a, b (unfigured): cephalic shield lacking great appendages but exposing an eye, trunk with incomplete telson. SAM P45906a, b (unfigured): great appendages with spinose projections, oriented anteriorly, trunk preserved to end of midgut glands. SAM P45908a, b (unfigured): cephalic shield, great appendages with flagella, most of trunk (telson missing), showing midgut glands and exopod setae. SAM P45909 (unfigured): small specimen with great appendages and series of mineralised midgut glands. SAM P45910a, b (unfigured): incomplete great appendages oriented anteriorly, trunk with complete series of midgut glands but indistinct appendages.

Type locality: Buck Quarry, Big Gully (Fig. 1).

Type horizon: Emu Bay Shale (Cambrian Series 2, Stage 4).

Diagnosis.—As for genus.

Description.—Cephalic shield 36% length of the trunk sagittally; dorsal margin of cephalic shield gently convex in lateral view, anteromedian margin inferred to be evenly rounded (based on comparison with lateral versus dorsal preservation of Burgess Shale *Leanchoilia* and *Alalcomenaeus*), lacking an upturned median process. Eye visible in SAM P54167 (Fig. 4A) and P45905, relatively large (20% sagittal length of cephalon), exposed under anterolateral part of cephalic shield (Fig. 4A2).
Great appendage robust, proportions of peduncle and distal spine-bearing articles as in other members of Leanchoiliidae; more commonly preserved with posterior orientation but anteriorly oriented in SAM P45906 and SAM P45910. Each of the three long spinose projections terminating at the same length, the projections evenly tapering distally, with

Fig. 6. Leanchoiliid megacheiran arthropod *Oestokerkus megacholix* gen. et sp. nov. SAM P45168. A. head and anterior part of trunk. B. Detail of spinose projections of great appendages and excretory organs (sensu Bruton and Whittington 1983). Abbreviations: cs, cephalic shield; eo, excretory organ; ga, great appendage; mg, midgut glands; tx, trunk exopods.
margins straight for much of their length or slightly curved terminally; distal spino−
se projection distinctly stouter at its base than the two more proximal projections and more markedly tapering along its length. Dark, irregular−shaped low relief lump on basal spine−bearing article of great appendages of SAM P45168 (eo in Fig. 6) and SAM P45908, corresponding to excretory organ of Bruton and Whittington (1983). Long flagella extending from each of the three spino−
se projections, seen only in SAM P43631 (Figs. 2, 3A3), of similar, narrow width along its preserved extent; annulations indistinguishable.

Trunk of 11 segments of even length. Maximum height of trunk relative to length (excluding telson) ca 39%, body deepest at tergite 4. Trunk tergite boundaries marked as narrow ridges in several specimens, corresponding to narrow band of overlap between adjacent tergites (ol in, Figs. 2, 3A1, 4A1, B). Some specimens show tergites to be bisected by a narrow but sharp furrow of uncertain identity (e.g., possibly impression of dorsal transverse tendon, cf. Stein 2010: fig. 12B, C, E) (arrows in Figs. 3A1, 4B).

Exopods with fringe of long setae on cephalic and trunk appendages (Fig. 2), setal fringe gradually shortening from about the fourth trunk segment. Setae project ventrally by more than 30% height of tergites in deepest part of trunk (Fig. 2B); setae flattened, narrow and parallel−sided along most of their length, tapering near their distal ends to terminate as a pointed tip (Figs. 2B, 3A3, arrows). Endopods exposed only in SAM P45167 (Fig. 4); two pairs associated with cephalon (Fig. 4B), those of anterior segments of trunk of similar morphology to those in cephalon, all slender, lacking obvious endites, podomere boundaries unrecognisable.

Midgut glands occupy a large extent of the dorso−
ventral height of the trunk, two midgut glands in cephalon of similar size to those in each of the first seven segments of the trunk (Figs. 3A1, 5A, 6A); all developed as radiating grooves emanating from a globular structure at their ventral edge as in

Leanchoilia superlata (García−Bellido and Collins 2007: pl. 2: 6). Foregut trace in SAM P43631 (Fig. 2) indicates that gut curves ventrally in anterior part of cephalon, mouth region not preserved. Terminal part of hindgut (in trunk segment 11) with closely spaced longitudinal lineations (Fig. 2) that apparently correspond to folds in the gut wall; hindgut terminating at base of telson.

Telson most completely preserved in holotype (SAM P43631, Figs. 2B, 3A2, B). In this specimen the telson, like rest of body, compressed in lateral aspect. Telson shows median and marginal reinforcing ridges connecting a flat triangular surface; this surface appears to be partially broken in SAM P43631, showing underlying surface of other (left) half of telson. Lateral preservation of specimen implies that top corresponds to an axial structure and bottom to a marginal one; 30−35° angle in posterior edge of vane connecting these two structures requires that in dorsal aspect, telson would appear forked and widening distally. Five stout, pointed, dorsally curved marginal spines attached to outer posterior edge on each side of telson.

Phylogenetic analysis of Leanchoiliidae

Determining the systematic position of Oestokerkus demands an appraisal of the relationships of Leanchoiliidae as a whole. Cladistic analysis including the best−known members of Megacheira, including leanchoiliids, has been conducted by Cotton and Braddy (2004) and Vannier et al. (2009). The taxonomic sampling used by Cotton and Braddy (2004) included several megacheiran genera, representative chelicera−
tes, a number of taxa representing groups that have been proposed as possible chelicere relatives (e.g., Sidneyia, Aglaspis, Chelonieniellon) in other analyses (Dunlop and Selden 1997; Hou and Bergström 1997), and members of the major lineages of the Artiopoda sensu Hou and Bergström (1997), i.e., trilobe−allied lamellipedia. Because artiopodan inter−
relations have remained quite stable through a series of phylogenetic analyses (Edgecombe and Ramsköld 1999; Cotton and Braddy 2004; Hendricks and Lieberman 2008; Paterson et al. 2010) and artiopodans are now often regarded as less closely related to Megacheira than is Chelicerata (Chen et al. 2004; Cotton and Braddy 2004; Dunlop 2006), we have reduced the sampling of Artiopoda in the present analysis. To augment the diversity of “short great appendage” arthropods, Haikoucaris is added based on the description of H. ercaiensis by Chen et al. (2004). Offacolus (Orr et al. 2000; Sutton et al. 2002) has been allied to Chelicerata and is included as a terminal. Because the present analysis is principally concerned with relationships of and within Leanchoiliidae sensu Liu et al. (2007), we follow Vannier et al. (2009) in sampling Alalcomena−

ed and Leachonolia at the species level. Within Chelicerata, Cot−
ton and Braddy (2004) and Hendricks and Lieberman (2008) sampled ancestral states in Xiphosura by coding the Devonian...
synziphosurine *Weinbergina*. Our coding for Xiphosura also employs information from extant xiphosurans because they supply more reliable information on the homology of the parts of the trunk appendages (Suzuki and Bergström 2008) and eye anatomy (Harzsch and Hafner 2006), among other character systems, than do fossils alone.

Our character set extracts characters from the matrix of Cotton and Braddy (2004) that vary in the revised taxonomic sample, reformulates some characters to accommodate revised homology concepts, and adds new characters, especially for leachioilds. In total, 32 characters are included (Table 1).

In this analysis, the primary homology of the “short great appendage” and chelicera is coded (as described by character 4), and the taxon sampling broadly constrains megacheirans as chelicerate relatives (as defended by Chen et al. 2004; Cotton and Braddy 2004) rather than testing the alternative that they could be stem group Euarthropoda (Budd 2002; Bergström and Hou 2005). A test of the two alternatives involves sampling of the entire diversity of euarthropods and a range of chelicerate relatives (as defended by Chen et al. 2004; Cotton and Braddy 2004) rather than testing the alternative that they vary in the revised taxonomic systems, than do fossils alone.

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### Table 1. Characters coded for phylogenetic analysis. Polymorphism indicated by “+”; partial uncertainty by states separated by “/”. Abbreviations: *A. Alalcomenaeus; L. Leanchoilia, O., Oestokerkus.*

<table>
<thead>
<tr>
<th>Character</th>
<th>States</th>
<th>Description</th>
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<tbody>
<tr>
<td>1. Mineralised cuticle</td>
<td>(0) absent; (1) present. For definition and discussion of this character, see Cotton and Braddy (2004: character 30) and Paterson et al. (2010: character 1).</td>
<td></td>
</tr>
<tr>
<td>2. Curvature of anterior margin of cephalic shield</td>
<td>(0) rounded or straight; (1) pointed medially; (2) with multiple spinose projections. This character codes for variability in the shape of the cephalic shield in Leanchoiliidae (state 0 and 1 sensu García-Bellido and Collins [2007: text-figs. 10 and 9, respectively]). State 2 is added to accommodate <em>Offacolus</em>; the median spine of a series that fringes the cephalic shield in Leanchoiliidae (state 0) follows García-Bellido and Collins (2007).</td>
<td></td>
</tr>
<tr>
<td>3. Number of cephalic somites/appendages</td>
<td>(0) antenna or frontal appendage only; (1) antenna or frontal appendage and two limb pairs; (2) antenna or frontal appendage and three limb pairs; (3) antenna or frontal appendage and four limb pairs; (4) antenna or frontal appendage and five limb pairs. Coding for lamellipedians and <em>Aglaspsis</em> is as discussed by Paterson et al. (2010: character 2). Coding for <em>Alalcomenaeus cambricus</em> (state 1) follows Briggs and Collins (1999), <em>Leanchoilia ilcecebrosa</em> (state 2) follows Liu et al. (2007), and <em>Leanchoilia persephone and Leanchoilia superlata</em> (state 1) follows García-Bellido and Collins (2007).</td>
<td></td>
</tr>
<tr>
<td>4. Form of first cephalic appendage</td>
<td>(0) antenna; (1) anteriorly directed raptorial appendage with reduced number of podomeres, each of the terminal podomeres bearing a spinose process on its distal margins, a geniculation between spinose podomeres and peduncle. This character is formulated to identify a homology between the frontal appendages of megacheirans and the chelicera of Chelicera, and state 1 corresponds to the putative apomorphic detail defended by Chen et al. (2004) and Cotton and Braddy (2004). Vannier et al. (2009: character 8) specify another shared property of “short great appendages” of the megacheiran (s.s.) type in their character state “bent at an angle”, referring to the geniculation between articles of the peduncle or between the peduncle and distal, spiniferous articles. This property is shared with Chelicera.</td>
<td></td>
</tr>
<tr>
<td>5. Number of spine-bearing articles on frontal appendage</td>
<td>(0) three + movable finger; (1) two + movable finger; (2) one + movable finger. The number of spine-bearing articles on the frontal appendage (exclusive of the terminal movable finger) varies from three in <em>Yoyoia</em> (Whittington 1974: pl. 6: 1–3, pl. 7: 3–6, pl. 9: 4–6) and <em>Fortiforcps</em> (Hou and Bergström 1997: figs. 31C, D, 32A, 33B, C, E) to two in <em>Haikoucaris</em> (Chen et al. 2004: fig. 2A, B) and <em>Leanchoiliidae</em>, or only one, the last being a chelicera.</td>
<td></td>
</tr>
<tr>
<td>6. Long spinose projections on distal part of terminal three podomeres of frontal appendage bearing a flagellum</td>
<td>(0) absent; (1) present. The morphology of the great appendage in <em>Leanchoiliidae</em> is coded here. We have not coded the length of the spinose projections and the presence of a flagellum as two independent characters; Cotton and Braddy’s (2004) character 6, state 2 (“spines” longer than the entire podome series) and character 8, state 1 (presence of an annulated flagellum) are thus grouped as a single trait here.</td>
<td></td>
</tr>
</tbody>
</table>
7. Length of flagellate great appendage: (0) flagella terminating at midlength of trunk; (1) flagella extending to end of body. Coding is applicable to Leancochiidae only, distinguishing some Leancohiia species that resemble Alalcomenaeus in having relative short great appendages (state 0) versus the longer appendages in L. superlata and L. illecebrosea.

8. Position of lateral faceted eyes: (0) ventral; (1) dorsal, sessile; (2) absent. Variation in Lamellipedia and several other taxa coded herein follows Paterson et al. (2010: character 3).

9. Four or five ventral eyes arranged in a subtransverse band across head shield: (0) absent; (1) present. A band of ventral eyes is shared by the best known species of Leancochiidae. The distinction between three median eyes in Alalcomenaeus cambriicus (Briggs and Collins 1999) and two in Leancohiia illecebrosea (Liu et al. 2007) and both Leancohiia superlata and L. persephone (García-Bellido and Collins 2007) is uninformative for the taxon sample here.

10. Bulge in exoskeleton accommodating drop-shaped ventral eyes: (0) absent; (1) present. This character follows Edgecombe and Ramsköld (1999: character 6) and Paterson et al. (2010: character 5).

11. Dorsal median eyes: (0) absent; (1) present. Coding for an absence of dorsal median eyes in fossil taxa considers the absence of either paired ocelli or a median eye tubercle, and the character is scored as a chelicerate autapomorphy (see Cotton and Braddy 2004: character 24).

12. Width of doublure on cephalic shield: (0) narrow or moderately wide; (1) entire ventral side of head covered by expansion of doublure. The interpretation of state 1 in Sidneyia and Squamacula is discussed by Cotton and Braddy (2004) and Paterson et al. (2010: characters 12 and 29).

13. Mouth covered by hypostome: (0) absent; (1) present. No “short great appendage” arthropods have been shown to possess a hypostome, and a reconstruction of a small labrum in Alalcomenaeus (Briggs and Collins 1999) was admitted conjectural. The absence of a conspicuous hypostome contrasts with its ubiquitous presence in lamellipedians and several putative chelicerate-allied taxa that have antennae (such as aglaspidids and Emeraldella). Chelicerates have a small epistome-labrum (Bitsch and Bitsch 2007), but like Cotton and Braddy (2004: character 27, state 4), we code a hypostomal sclerite as lacking. Kwanyinspis has a large hypostome similar to that found in aglaspidids (photograph of the holotype of Kwanyinspis mtawanishanensis shown to us by Javier Ortega-Hernández [personal communication, 2010]).

14. Tergite articulations: (0) extensive overlap of tergites; (1) edge to edge articulations. This character follows Edgecombe and Ramsköld (1999: character 18) and Paterson et al. (2010: character 20).

15. Number of trunk segments: (0) nine; (1) 11; (2) 12; (3) 13; (4) 20; (5) 21 or 22. Coding is confined to taxa that do not possess a pygidium because the precise number of somites associated with pygidia can sometimes not be determined with confidence. Codings for Xiphosura and Eurypterida use opisthosomal somite numbers following Shultz (2007: character 95).

16. Exoskeletal boundaries of anterior trunk segments: (0) boundaries transverse or reflexed posterolaterally; (1) reflexed anterolaterally. This character follows Edgecombe and Ramsköld (1999: character 19) and Paterson et al. (2010: character 21).

17. Trunk tergites with serrate lateral margins: (0) absent; (1) present. Liu et al. (2007: fig. 2C) documented a row of marginal spines on the tergites of Leancohiia illecebrosea, a featured shared by Leancohiia superlata (e.g., García-Bellido and Collins 2007: pl. 1: 7) but not other terminals coded here.

18. Differentiation in width of trunk tergites: (0) trunk with gradational narrowing posteriorly; (1) abrupt narrowing at boundary between prothorax and opisthothorax. An abrupt contraction in width between the boundary of the pro- and opisthothorax is observed in Emeraldella and Sidneyia. Yohoia has been reconstructed as having a pronounced break in the shape of the trunk tergites behind segment 10 (Whittington 1974: text-fig. 2), the point at which the paratergal folds lose their spinose tips and appendages are lacking. Specimens preserved in dorsal aspect (Whittington 1974: pl. 10) suggest that the width of the opisthothorax is rather less abruptly narrowed and we code Yohoia as state 0.

19. Appendages of posterior trunk segments: (0) all trunk tergites bearing appendages; (1) one or more posterior trunk segments lacking appendages. Coding corresponds to Cotton and Braddy’s (2004) character 43, “postabdomen of segments lacking appendages”.

20. Paired tergal carinae: (0) absent; (1) present. Liu et al. (2007: 265: fig. 2F) recorded the presence of tergal carinae in Leancohiia illecebrosea, shared with L. superlata (e.g., Bruton and Whittington 1983: pl. 17: 106; García-Bellido and Collins 2007: pl. 1: 5).

21. Pygidium: (0) absent; (1) present. Coding of the pygidium in many terminals herein was discussed by Paterson et al. (2010: character 22).

22. Telson: (0) absent; (1) present. Following Hendricks and Lieberman (2008), a telson is a post-segmental terminal structure that lacks appendages. Dunlop and Selden (1997) considered a telson to be absent in Cheloniellon, but we identify the conical projection posterior to the ultimate leg pair and cerci (Stürmer and Bergström 1978: figs. 2, 3, 10, 11) as being most consistent with an identity as a telson.

23. Telson shape: (0) styliform; (1) flap-like; (2) lanceolate; (3) short, conical. The outline of the telson in Haikoncaris ercaiensis is incompletely known, but the most complete specimen (Chen 2004: fig. 472) constrains it as either state 1 or state 2. A partial uncertainty coding is thus employed. A unique state for Cheloniellon (state 3) is based on the interpretation in character 22.

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24. Telson fringed with spines: (0) spines absent; (1) spines present. Presence of telson spines was introduced as a character by Hendrichs and Lieberman (2008: character 34).

25. Paired flaps lateral to telson: (0) absent; (1) present. This character describes the post-ventral plates of several taxa (see Edgecombe and Ramsköld 1999: character 25). Cotton and Braddy (2004: character 54) raised the possibility that the cerchi of Cheloniellon could be homologous with post-ventral plates (see also Hou and Bergström 1997: 93) because they are similarly paired structures derived from the segment immediately anterior to the telson. We have not coded for this homology because the cerchi of Cheloniellon originate dorsally rather than ventrally.

26. Midgut glands with submillimetric lamellae: (0) absent; (1) present. Midgut glands in some stem group arthropods and early crown group arthropods are metamerie reniform organs with a characteristic lamellar structure (Butterfield 2002). Their morphology is identical in Leanchoilia and Oestokerkus, notably including grooves that radiate from a ventral median node (Figs. 3A, 6A). The gut of Alalcomenaeus cambriicus is more tubular (Briggs and Collins 1999: text-figs. 10, 11), and though an anterior six segments may display phosphatised lateral projections that likely represent gut diverticula (Wilson 2006, they have not been shown to have the detailed morphology of Leanchoilia-type midgut glands. Butterfield (2002: 164) cited a figure from Bruton (1981: fig. 96) in support of “lamellar” midgut glands in the cephalon of Sidneyia. Like Bruton (1981) in his description of the specimen, we consider it likely that the structures in question are indeed gut diverticula but there is no basis for identifying them more precisely as the reniform, lamellar structures coded under this character.

27. Exopod on first post-antennal / first post-frontal appendage segment: (0) absent; (1) present. This character relates to Cotton and Braddy’s (2004) character 3.

28. Division of exopod: (0) exopod an undivided flap; (1) small flap with radiating lamellae; (2) small flap with radiating lamellae; (3) pefidem exopod divided into ca 6 articles. Identification of the exopod in Xiphosura follows Suzuki and Bergström (2008). This character groups conditions of the exopod shaft coded as independent characters by Cotton and Braddy (2004), e.g., state 0 corresponds to their character 16 and state 1 to their character 13. Our coding permits transformation between any two states without an extra implicit step.

29. Exopod setae: (0) short spiniform setae; (1) long, flattened, tapering distally, with slight separation; (2) lamellar setae (flattened, imbricating); (3) short, fine setae. A distinction is made between lamellipedian setae, which are imbricated (state 2), and the pointed, more distinctly separated and variably spiniform exopod setae of leanchoiliids (state 1). This distinction is consistent with the identification of megacheirans as non-lamellipedians (e.g., Hou and Bergström 1997; Bergström and Hou 2005). Although Cotton and Braddy (2004: character 18) regarded the form of the setae in Yohoia to be uncertain, we regard specimens figured by Whittington (1974: pl. 3: 3) as conforming to the leanchoilioid state. Squamacula differs from other taxa in its shorter, spiniform setae (state 0) (Zhang et al. 2004: text-fig. 1A, B). Offacolus has longer spiniform projections on the distal articles of the exopod that have been variably identified as either spines or setae (Sutton et al. 2002: fig. 4b) but their homology with the setae that splay regularly along the margin of a flap-like exopod (e.g., states 0–3) is uncertain. This and the following character for exopod setae are left as “?” for Offacolus. A homology between the gill lamellae of Xiphosura and exopod setae of lamellipedians has a long history (see Cotton and Braddy 2004: character 18). We follow Suzuki and Bergström (2008) in identifying the xiphosuran gills as outgrowths of the basis rather than of the exopod; this perspective negates a homology with the exopod setae of Lamellipedia. The polymorphic coding for Emeraldeilla reflects the two separate states (1+2) displayed by the exopods in the trunk (see Bruton and Whittington 1983: pl. 8: 45, 47; Edgecombe and Ramsköld 1999: fig. 11).

30. Differentiation of setae along exopod: (0) uniform or gradationally variable setae along length of exopod; (1) lamellar setae confined to proximal lobe, with distal lobe bearing slender setae.

31. Endopod segmentation (distal to coxa): (0) six or seven podomers and terminal claw or telotarsal spurs; (1) eight or more podomers and terminal claw; (2) ca. 15 podomers. State 1 is formulated to describe the segmentation of the leanchoiliid leg (García-Bellido and Collins 2007: text-fig. 6; Liu et al. 2007: fig. 5), in contrast to the reduced number of podomers in other euarthropods (Boxshall 2004). State 2 characterises Fortiforceps. A partial uncertainty coding is employed for Yohoia in which the precise number of podomers is undetermined and could be either state 0 or 1 (Whittington 1974: pl. 7: 4) but the spacing of the preserved podomere boundaries negates the possibility of state 2.

32. Endopods on anterior post-cephalic segments: (0) well developed; (1) rudimentary or lacking. Following Cotton and Braddy (2004: character 11), the absence of trunk endopods in Yohoia (Whittington 1974) is coded as a putative homologue with the suppression of post-cephalic endopods in Chelicera.
dex of 0.77. The strict consensus of these trees with support values is shown in Fig. 8. Leanchoiliidae is unambiguously supported in all 14 cladograms by four apomorphic characters: two limb-bearing cephalic segments posterior to the frontal appendage (character 3, state 1), long spinose projections on the distal part of the terminal three podomeres of the frontal appendage that bear flagella (character 6, state 1), 11 trunk segments (character 15, state 1), and division of the exopods into two lobes (character 28, state 1). The arrangement of four or five eyes in a subtransverse band across the cephalic shield is unique to Leanchoiliidae (character 9, state 1) but is not an unambiguous autapomorphy of the group because the state is uncertain in close relatives, notably Haikoucaris. It is apomorph for Leanchoiliidae only under particular optimisations (Delayed Transformation).

The internal relationships of Leanchoiliidae are stable across all 14 shortest cladograms. Leanchoilia is united by the lanceolate telson (character 23, state 2), a unique unambiguous autapomorphy. Within Leanchoilia, a sister group relationship between L. superlata and L. illecebrosa is well supported, receiving a Bremer support of 3 and jackknife frequency of 86%. These two species share four synapomorphies: a medially pointed anterior cephalic margin (character 2, state 1), flagella of the great appendage extending the length of the body (character 7, state 1), serrate lateral margins on the trunk tergites (character 17, state 1), and paired tergal carinae (character 20, state 1). As such, a species from Chengjiang (L. illecebrosa) and the Burgess Shale (L. superlata) are more closely related to each other than are the two Burgess Shale congeners, a relationship that weakens the possibility that the often co-occurring L. superlata and L. persephone could be sexual dimorphs (García-Bellido and Collins 2007) rather than separate species. The union of Leanchoilia and Oestokerkus is unambiguously supported by the shared midgut gland structure of both genera (character 26, state 1).

All shortest cladograms resolve Haikoucaris, Yohoia, and Fortiforceps, in that order, as progressively less closely related to Leanchoiliidae. The union of these three taxa with Leanchoiliidae yields a clade that corresponds to Megacheira sensu Hou and Bergström (1997) apart from the ambiguous placement of Jianfengia. In half of the 14 shortest cladograms, Jianfengia is sister to the other megacheirans, yielding a monophyletic Megacheira s.s. In the remaining cladograms, Jianfengia is sister to Xenopoda sensu Hou and Bergström (1997), Aglaspis, and Chelicerata. Haikoucaris and Leanchoiliidae are united by a frontal appendage composed of two spine-bearing articles in addition to the movable finger (character 5, state 1). Yohoia groups with these taxa based on spines fringing the telson (character 24, state 1), and Fortiforceps is united with them at a broader level based on the flap-like telson shape (character 23, state 1). When Jianfengia is placed as sister to the other megacheirans, the entire clade is supported by the raptorial frontal appendage (character 4, state 1) and the lack of a large hypostomal shield (character 13, state 0). In this set of cladograms, these features are non-homologous between Megacheira and Chelicerata, whereas in some cladograms with the alternative resolution of Jianfengia as closer to chelicerates, character 4 is optimised as homologous in Megacheira and Chelicerata.

Reanalysis of the data with implied weights finds two optimal trees (Fig. 9). Relationships within Leanchoiliidae under equal weights are completely stable to reweighting, as is the resolution of Haikoucaris as sister to Leanchoiliidae. As such, the character optimisations described above for the leanchoiliids are depicted the same in Fig. 9. The main difference between equal and implied weights involves the placement of Chelicerata. Under equal weights (Fig. 8), chelicerates are allied to Xenopoda (here Emeraldeilla + Sidneyia + Cheilo- niellon: sensu clade L in Hou and Bergström 1997: fig. 88) and Aglaspidida. A clade composed of Aglaspidida, Xenopoda, and Chelicerata was similarly identified by Hou and Bergström (1997: fig. 88, their clade K). In our analysis, this group consistently finds support from one or more posterior trunk segments lacking appendages (character 19, state 1) and depending on alternative internal resolutions it is variably supported by dorsally-positioned sessile eyes (character 8, state 1) and the absence of exopods on the first post-antennal/post-cheliceral limb (character 27, state 1). Under implied weights, however, chelicerates are more closely allied to Megacheira than to aglaspidids or xenopodans (Fig. 9).

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The major groupings in Fig. 9 correspond closely to those identified by Cotton and Braddy (2004). Notably, the clade uniting *Aglaspis*, Xenopoda, *Offacolus*, Chelicera, Jianfengia, and other Megacheira corresponds to their “Clade 3” (Cotton and Braddy 2004: fig. 8), for which they proposed the name Cheliceramorpha. The clade uniting *Cheloniellon*, *Aglaspis*, *Sidneyia*, and *Emeraldella* in Fig. 9 corresponds to their “Clade 5”, and the clade that groups Megacheira and Chelicerata is equivalent to their “Clade 4”. Their analysis did not identify megacheirans as a monophyletic group; Chelicerata was nested within the group, and among taxa considered here *Yohoia* was resolved closer to chelicerates than to Leanchoiliidae. In contrast, *Yohoia* was regarded by Bergström and Hou (2005) as more closely allied to Leanchoiliidae than to chelicerates, a megacheiran grouping more compatible with our cladograms. The analysis of “great appendage arthropods” by Vannier et al. (2009) identified a monophyletic Leanchoiliidae but a polyphyletic Megacheira (to the exclusion of *Haikoucaris* and *Jianfengia*). However, their resolution of Fortiforceps and even more so *Yohoia* as the closest relatives of Leanchoiliidae is as in our trees (apart from the different position of *Haikoucaris*).

In summary, a major controversy in the systematics of the “short great appendage” arthropods remains whether the chelicerates are nested within the group or are instead more closely allied to taxa conventionally identified as lamellipeds, specifically Xenopoda and Aglaspida. We find that both of these results are compatible with the available data depending on character weighting protocols. Nonetheless, the broader megacheiran-chelicerate issue does not cloud the status of leanchoiliids as a clade or the identification of their closest relatives (i.e., *Haikoucaris* and *Yohoia*), and the internal relationships of Leanchoiliidae are stable and supported by compelling characters.
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