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A New Leanchoiliid Megacheiran Arthropod from the Lower Cambrian Emu Bay Shale, South Australia

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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 (Megacheira) 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 Megacheira corresponds to a clade in most analyses.

Key words: Arthropoda, Megacheira, Leanchoiliidae, *Oestokerkus*, *Leanchoilia*, *Alalcomenaeus*, midgut glands, phylogeny, Cambrian, South 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 Megacheira 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 Leanchoiliida, 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 polytomy 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 spinose 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). *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, *Leanchoilia* has also been reported from the Spence Shale of Utah (*Leanchoilia superlata*? [Briggs et al. 2008]); *Leanchoilia*? *hanceyi* Briggs and Robison, 1984], and the Kaili Formation, Guizhou, China (*Leanchoilia* sp. of Zhao et al. 2005).

Herein we add new diversity and biogeographic data for 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 shoreline 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) *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).

Institutional abbreviation.—SAM P, South Australian Museum, Adelaide, Australia, palaeontological collections.

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.

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 fibre 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 ×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 imple-
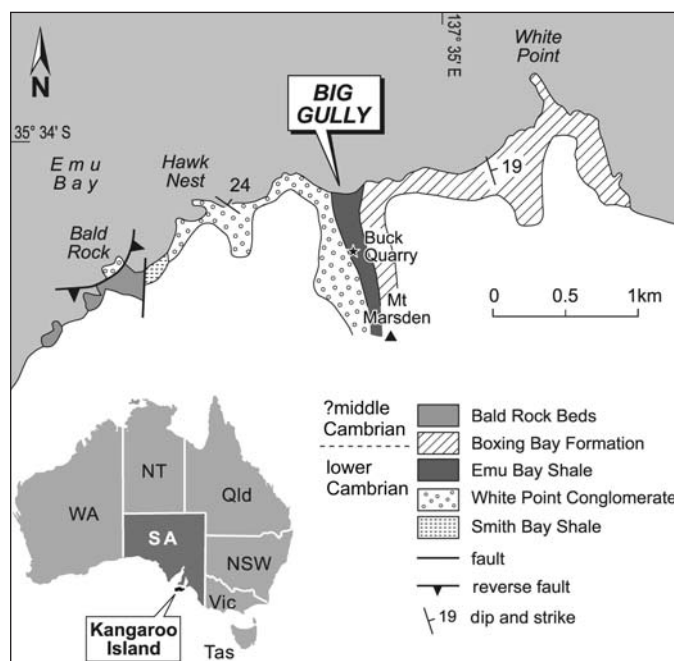

Fig. 1. Geology of the area near Buck Quarry, north east coast of Kangaroo Island, South Australia (modified from García-Bellido et al. 2009).

mented 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.

Systematic palaeontology

Phylum Arthropoda Siebold and Stannius, 1845

Class Megacheira Hou and Bergström, 1997

Order Leanchoiliida Størmer, 1944

Family Leanchoiliidae Raymond, 1935

Genus *Oestokerkus* nov.

Type species: *Oestokerkus megacholix* sp. nov., see below.

Etymology: From Greek *oïstos*, arrow and *kerkus*, tail; with reference to the forked shape of the telson.

Diagnosis.—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, $3A_2$, 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.
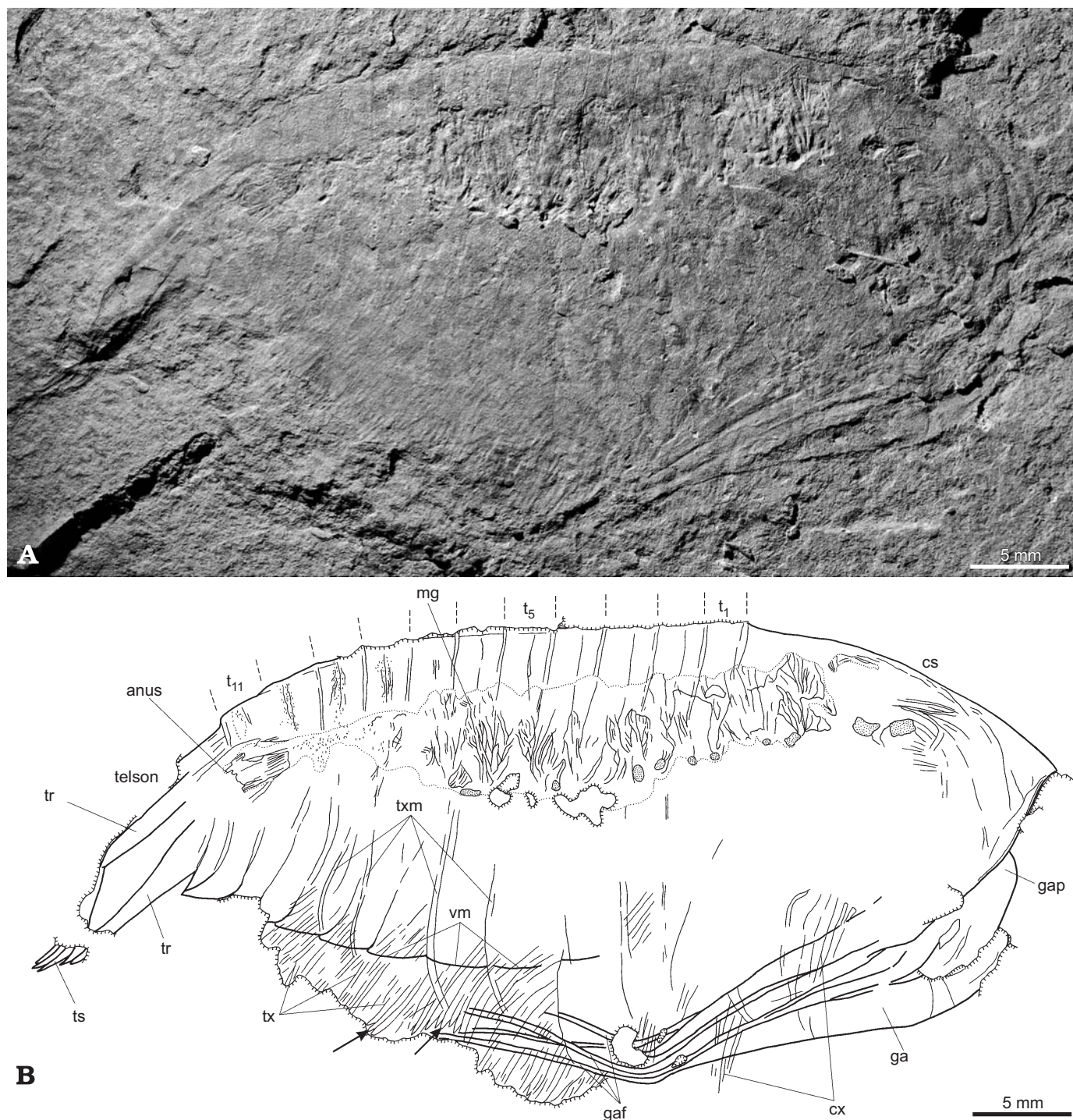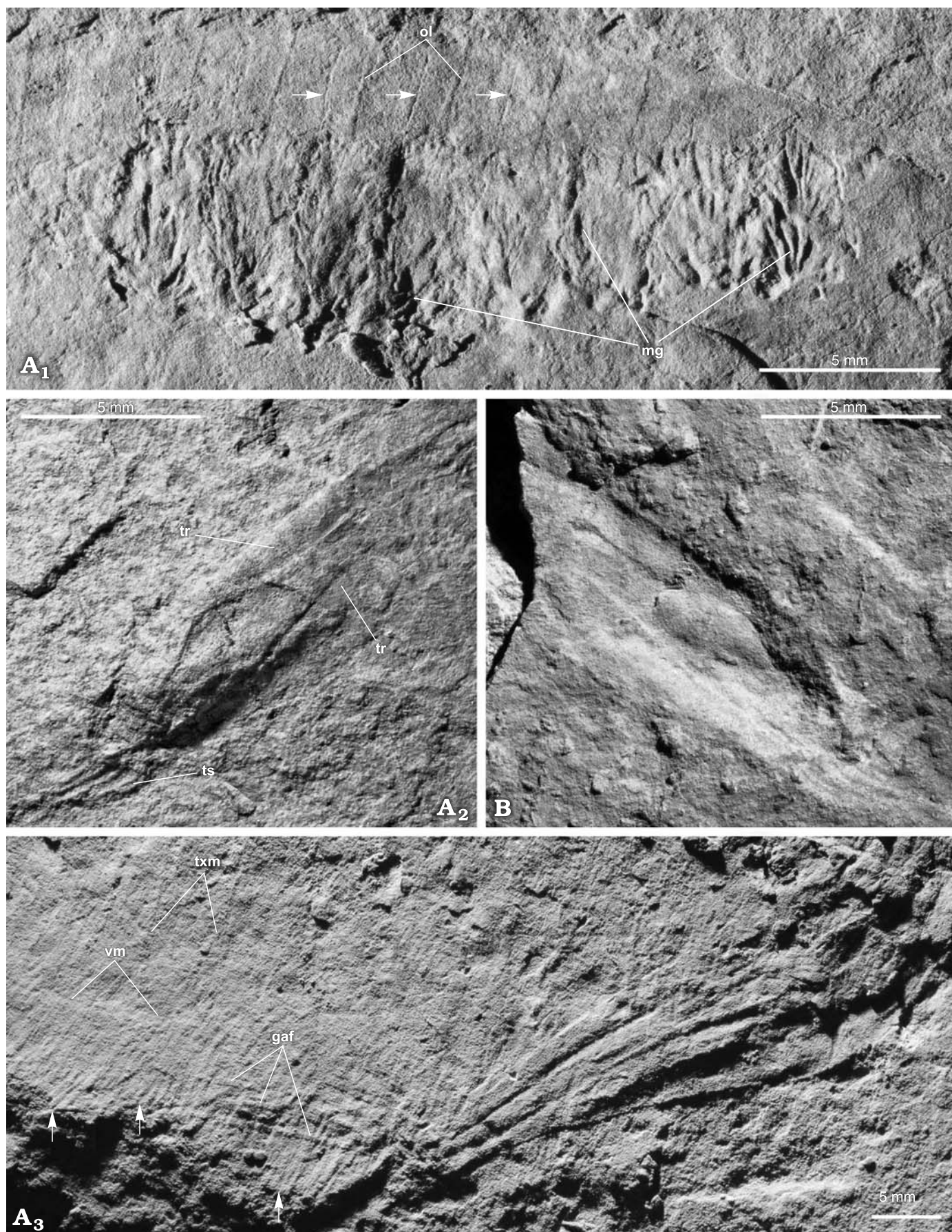
Fig. 2. Leanchoiliid megacheiran arthropod *Oestokerkus megacholix* gen. et sp. nov. Holotype SAM P43631a. **A**. Photograph. **B**. Interpretative camera lucida drawing. Arrows indicate tips of trunk exopod setae. Abbreviations: cs, cephalic shield; cx, cephalic exopods; ga, great appendage; gaf, great 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. A$_1$. Midgut glands and tergite →
boundaries in dorsal part of trunk. Arrows indicate furrows that may represent position of dorsal transverse tendons. A$_2$. Telson, light from NE. A$_3$. 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.
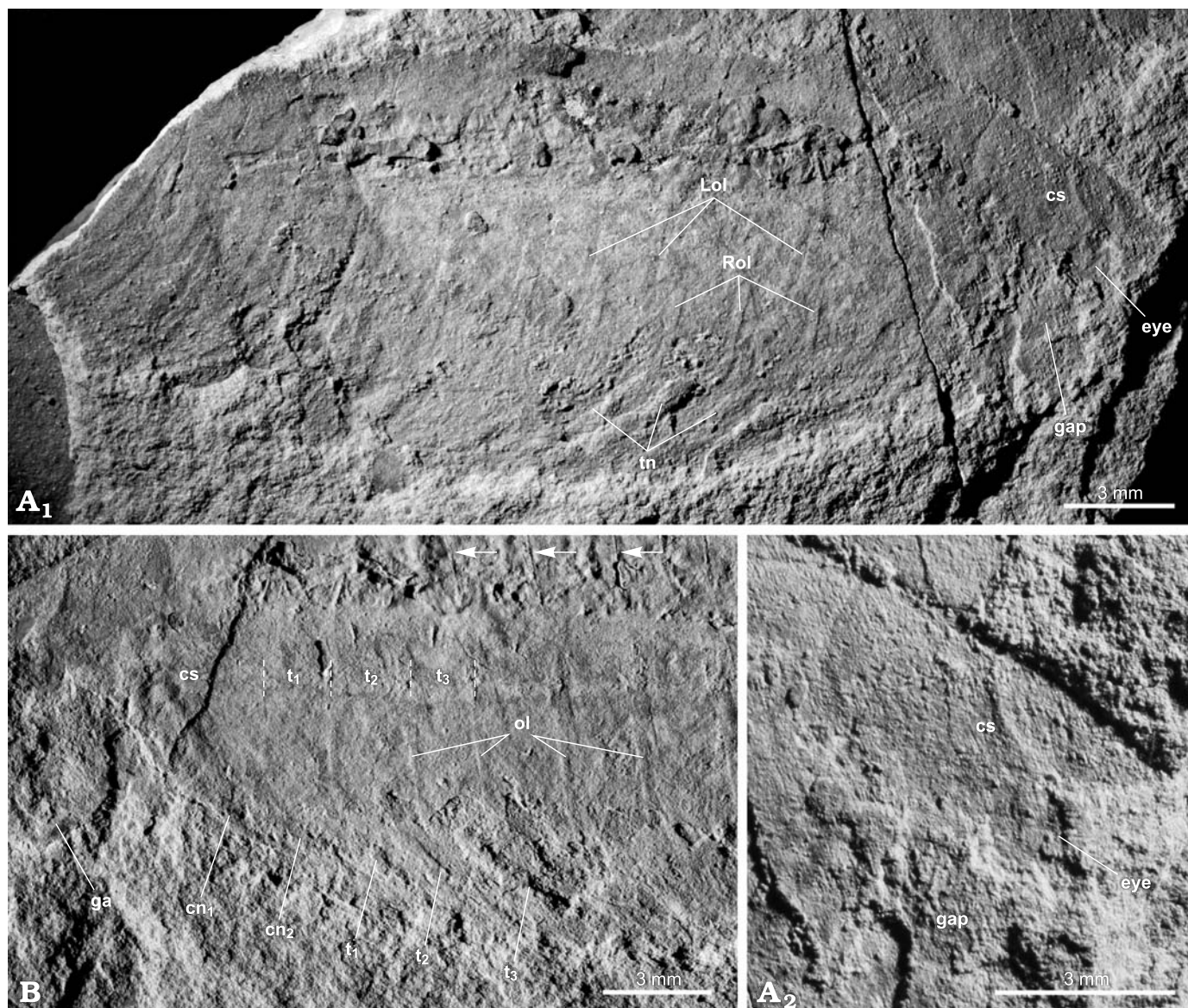
Fig. 4. Leanchoiliid megacheiran arthropod *Oestokerkus megacholix* gen. et sp. nov. SAM P45167. **A**. P45167a. A₁, cephalic shield and most of trunk; A₂, detail of cephalic shield. **B**. P45167b. A₂ and B light from NE. Overlap between adjacent tergites offset on left (Lol) and right (Rol) sides of body. Boundaries between cephalic shield and anterior trunk tergites delimited in B by dashed lines. Arrows mark positions of inferred dorsal transverse tendons. Abbreviations: cn1–2, cephalic endopods; cs, cephalic shield; gap, peduncle of great appendage; ol, overlap between adjacent trunk tergites; t1–t3, tergites of trunk segments 1–3; tn, trunk endopods.

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).

Fig. 5. Leanchoiliid megacheiran arthropod *Oestokerkus megacholix* gen. →
et sp. nov. **A**. SAM P 15531. **B**. SAM P43630b. Light from NE. Abbreviations: cs, cephalic shield; ga, great appendage; gap, peduncle of great appendage; mg, midgut glands; ol, overlap between adjacent trunk tergites; tx, trunk exopods.
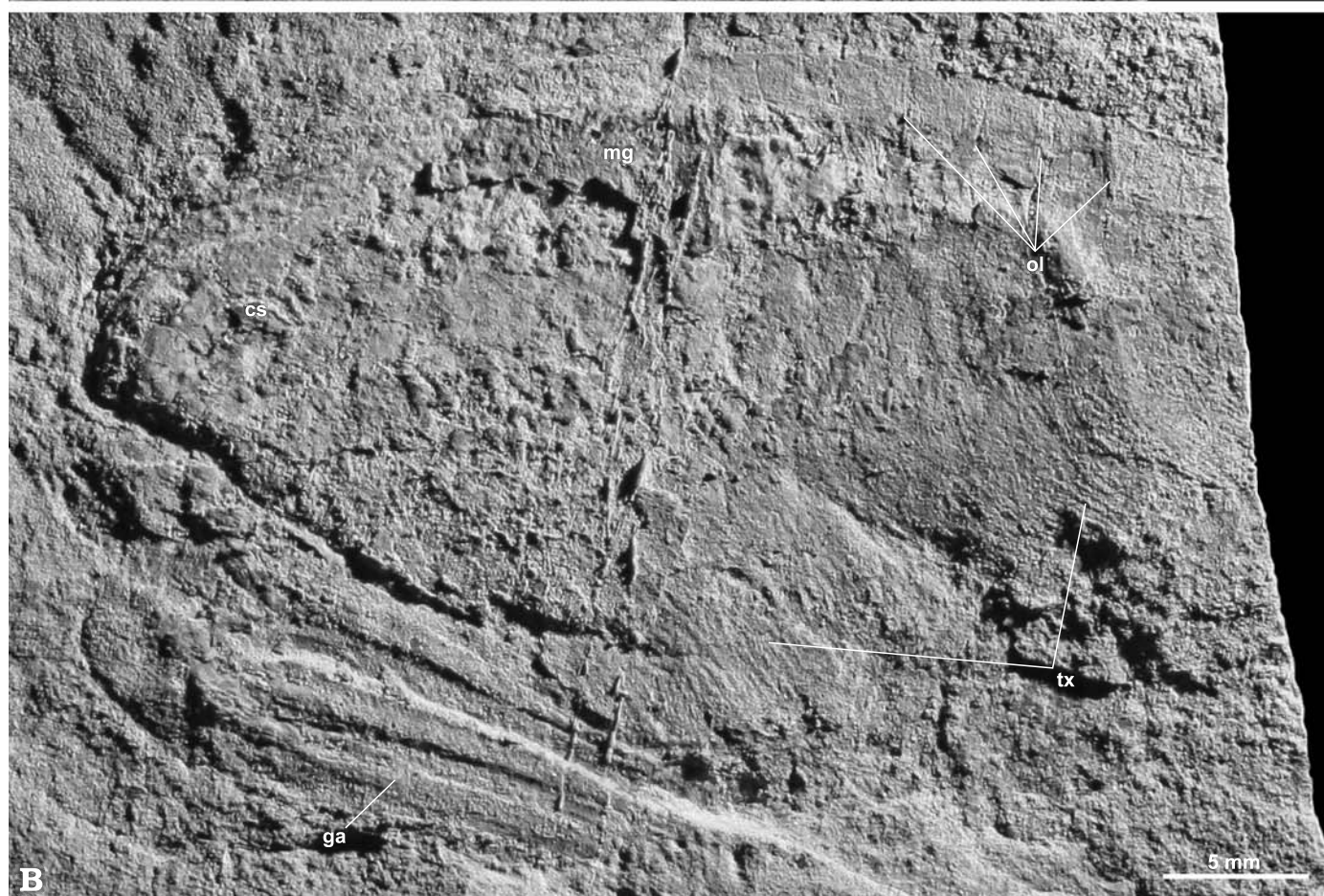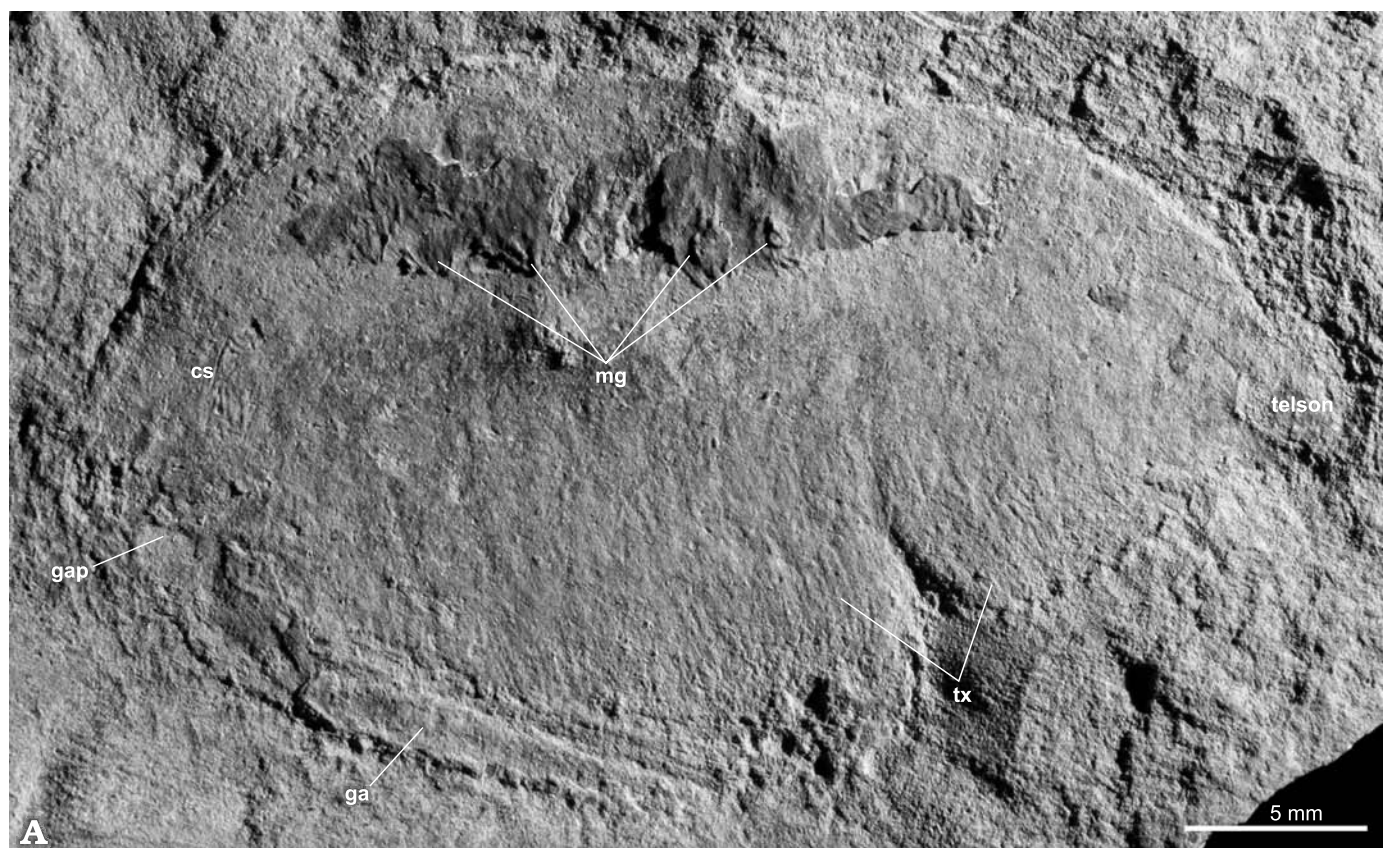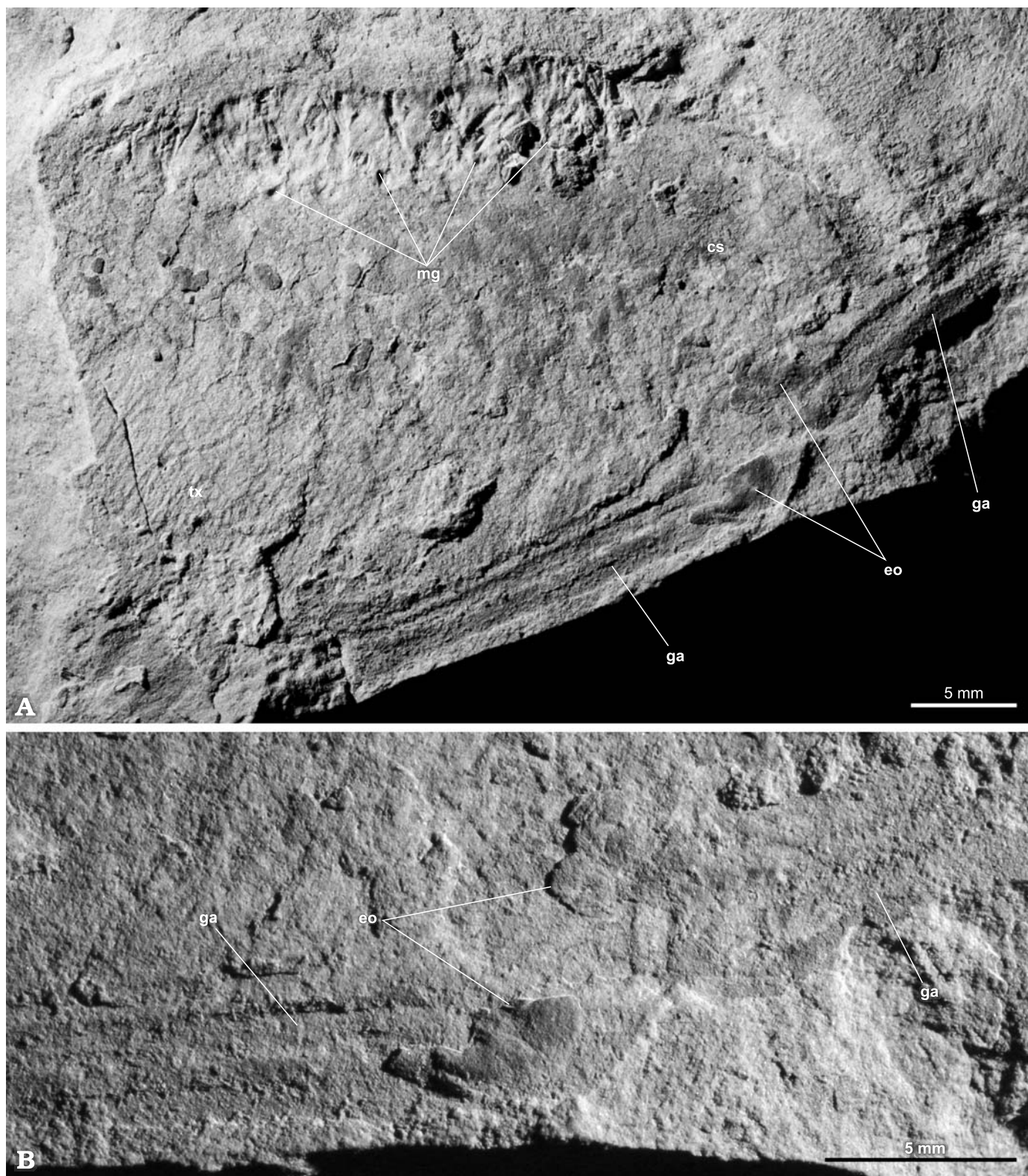
Fig. 6. Leanchoiliid megacheiran arthropod *Oestokerkus megacholix* gen. et sp. nov. SAM P45168. **A**. head and anterior part of trunk. **B**. Detail of spinose projections of great appendages and excretory organs (sensu Bruton and Whittington 1983). Abbreviations: cs, cephalic shield; eo, excretory organ; ga, great appendage; mg, midgut glands; tx, trunk exopods.

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. 7. Reconstruction of *Oestokerkus megacholix* gen. et sp. nov. in lateral view. Total length and annulations on the flagella and positions of podomere boundaries of the frontal appendage are based on *Leanchoilia superlata* (Bruton and Whittington 1983).

margins straight for much of their length or slightly curved terminally; distal spinose 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 P45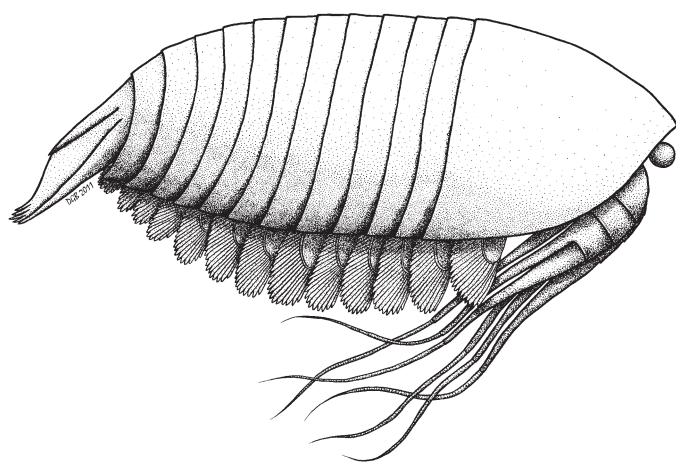908, corresponding to excretory organ of Bruton and Whittington (1983). Long flagella extending from each of the three spinose projections, seen only in SAM P43631 (Figs. 2, 3A$_3$), of similar, narrow width along its preserved extent; annulations indistinguishable.

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, 3A$_1$, 4A$_1$, 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. 3A$_1$, 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, 3A$_3$, 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 dorsoventral 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. 3A$_1$, 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, 3A$_2$, 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 chelicerates, a number of taxa representing groups that have been proposed as possible chelicerate relatives (e.g., *Sidneyia*, *Aglaspis*, *Cheloniellon*) 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., trilobite-allied lamellipedians. Because artiopodan inter-relationships 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 *Alalcomenaeus* and *Leanchoilia* at the species level. Within Chelicerata, Cotton 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 leanchoiliids. 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 non-euarthropod outgroups, an exercise beyond the scope of this study.

Characters

1. Mineralised cuticle: (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).

2. Curvature of anterior margin of cephalic shield: (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 *Offacolus*; the median spine of a series that fringes the cephalic margin is not convincingly homologised with the median projection in leanchoiliids.

3. Number of cephalic somites/appendages: (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 *Aglaspis* is as discussed by Paterson et al. (2010: character 2). Coding for *Alalcomenaeus cambricus* (state 1) follows Briggs and Collins (1999), *Leanchoilia illecebrosa* (state 2) follows Liu et al. (2007), and *Leanchoilia persephone* and *Leanchoilia superlata* (state 1) follows García-Bellido and Collins (2007).

4. Form of first cephalic appendage: (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 Chelicerata, 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 Chelicerata.

5. Number of spine-bearing articles on frontal appendage: (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 *Yohoia* (Whittington 1974: pl. 6: 1–3, pl. 7: 3–6, pl. 9: 4–6) and *Fortiforceps* (Hou and Bergström 1997: figs. 31C, D, 32A, 33B, C, E) to two in *Haikoucaris* (Chen et al. 2004: fig. 2A, B) and Leanchoiliidae, or only one, the last being a chelicera.

6. Long spinose projections on distal part of terminal three podomeres of frontal appendage bearing a flagellum: (0) absent; (1) present. The morphology of the great appendage in Leanchoiliidae 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 podomere series) and character 8, state 1 (presence of an annulated flagellum) are thus grouped as a single trait here.

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

Taxon							
Squamacula	0000-	- -2-0	0110?	00000	10- -0	?1000	?0
Cindarella	0030-	- -000	0010?	00000	10- -0	11121	00
Kuamaia	00?0-	- -001	0011?	10000	10- -0	11121	00
Kwanyinaspis	00???	??001	00112	100?0	?1000	?1121	00
Olenoides	1020-	- -100	0011?	00000	10- -0	01121	00
Retifacies	0020-	- -000	0010?	00000	11000	?1020	00
Aglaspis	10(2/3)0-	- -100	00101	00010	01001	?0???	00
Sidneyia	0000-	- -000	01102	00110	01101	00020	00
Emeraldella	0040-	- -2- 0	00103	00110	01001	001(1+2)1	00
A. cambricus	00111	10010	00001	00000	01110	01110	10
L. illecebrosa	01211	11010	00001	01001	01210	11110	10
L. persephone	00111	10010	00001	00000	01210	11110	10
L. superlata	01111	11010	00001	01001	01210	11110	10
L. hanceyi	00???	??0?0	00?01	000?0	01210	?????	??
O. megacholix	00?11	1?0?0	00001	00000	01110	11?10	?0
Jianfengia	0021?	0-000	00005	00000	01000	010(1/2)0	?0
Fortiforceps	00210	0-0?0	00004	00000	01100	01230	20
Yohoia	00210	0-000	00003	00011	01110	00010	(0/1)1
Haikoucaris	00211	0-0?0	00003	00000	01(1/2)?0	?1010	?0
Cheloniellon	0040-	- -100	00100	10010	01300	?0030	00
Offacolus	02412	0-200	0000?	00010	01000	?13- -	01
Xiphosura	00412	0-100	10000	00?10	01000	000- -	01
Eurypterida	00412	0-100	10002	00010	01000	00- - -	01

7. Length of flagellate great appendage: (0) flagella terminating at midlength of trunk; (1) flagella extending to end of body. Coding is applicable to Leanchoiliidae only, distinguishing some *Leanchoilia* species that resemble *Alalcomenaeus* in having relative short great appendages (state 0) versus the longer appendages in *L. superlata* and *L. illecebrosa*.

8. Position of lateral facetted 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 Leanchoiliidae. The distinction between three median eyes in *Alalcomenaeus cambricus* (Briggs and Collins 1999) and two in *Leanchoilia illecebrosa* (Liu et al. 2007) and both *Leanchoilia 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 admittedly 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. *Kwanyinaspis* has a large hypostome similar to that found in aglaspidids (photograph of the holotype of *Kwanyinaspis maotianshanensis* 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 *Leanchoilia illecebrosa*, a featured shared by *Leanchoilia 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 *Leanchoilia illecebrosa*, 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 *Haikoucaris 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.

24. Telson fringed with spines: (0) spines absent; (1) spines present. Presence of telson spines was introduced as a character by Hendricks 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 cerci 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 cerci 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 metameric 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$_1$, 6A). The gut of *Alalcomenaeus cambricus* 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) exopod differentiated into proximal and distal lobes; (2) small flap with radiating lamellae; (3) pediform 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 leanchoiliid 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 *Emeraldella* 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 podomeres and terminal claw or telotarsal spurs; (1) eight or more podomeres and terminal claw; (2) ca. 15 podomeres. 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 podomeres in other euarthropods (Boxshall 2004). State 2 characterises *Fortiforceps*. A partial uncertainty coding is employed for *Yohoia* in which the precise number of podomeres 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 Chelicerata.

Results

As a convention for depicting the trees, networks are rooted on *Squamacula*, which separates artiopodan Lamellipedia (sensu Hou and Bergström 1997) from a group that includes Megacheira, Chelicerata, and Xenopoda, all members of which possess a telson.

Under equal weights, 14 shortest cladograms have a length of 77 steps, with a Consistency Index of 0.64 and Retention In-

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 apomorphic 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 Mega-
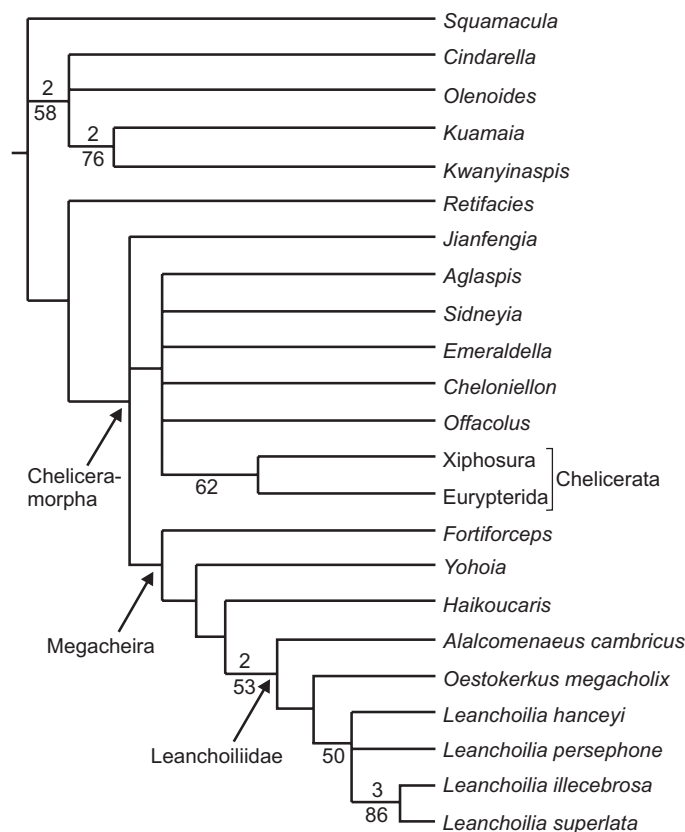

Fig. 8. Strict consensus of 14 shortest cladograms (77 steps) based on character data in Table 1. Numbers above nodes are Bremer support; those below nodes are jackknife frequencies >50%. Cheliceramorpha corresponds to a clade with the same composition in Cotton and Braddy (2004).

cheira 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 *Emeraldella* + *Sidneyia* + *Cheloniellon*: 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).
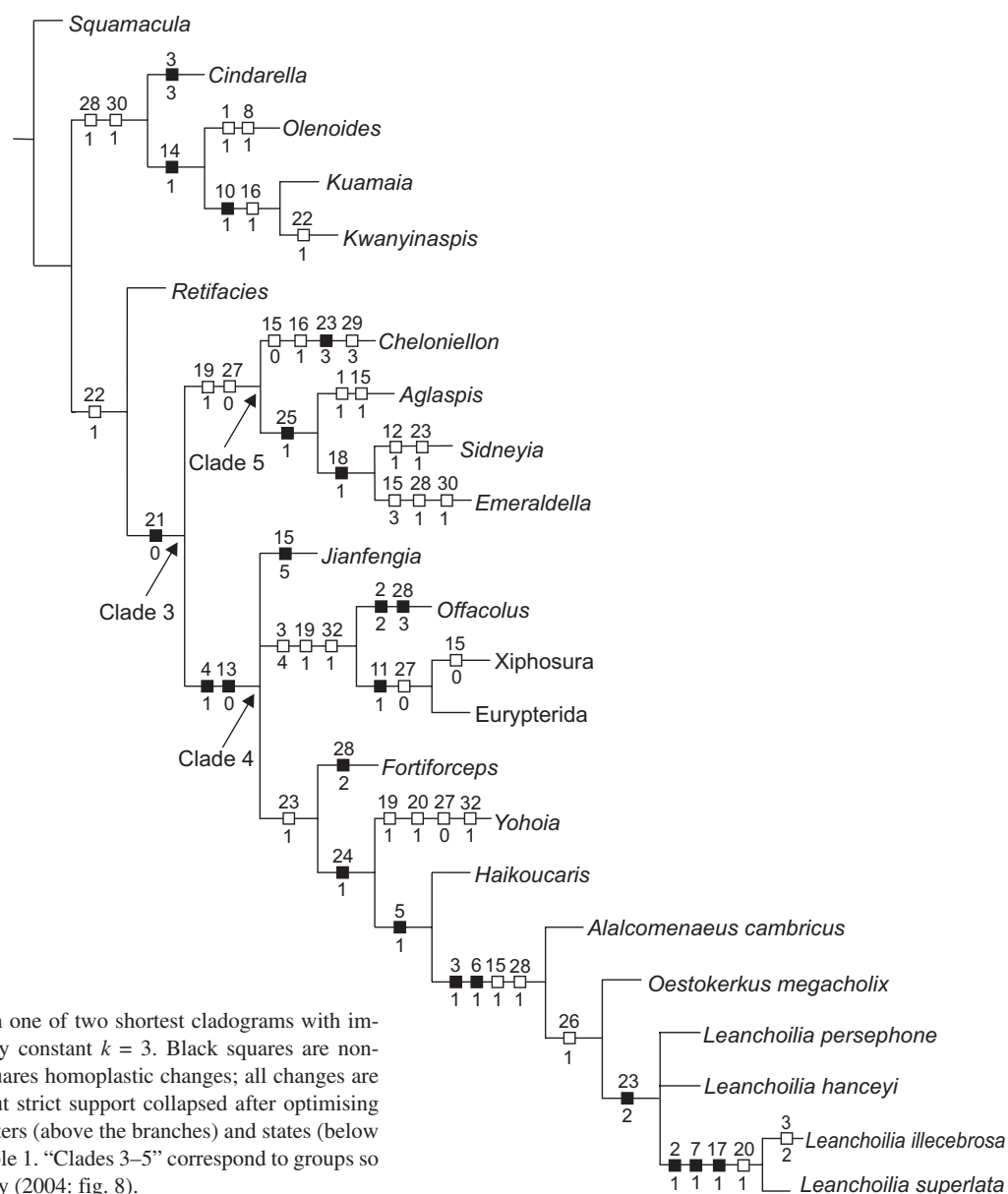
Fig. 9. Characters optimised on one of two shortest cladograms with implied weights using a concavity constant $k = 3$. Black squares are non-homoplastic changes, white squares homoplastic changes; all changes are unambiguous. Branches without strict support collapsed after optimising characters. Numbers for characters (above the branches) and states (below the branches) correspond to Table 1. "Clades 3–5" correspond to groups so numbered by Cotton and Braddy (2004: fig. 8).

The major groupings in Fig. 9 correspond closely to those identified by Cotton and Braddy (2004). Notably, the clade uniting *Aglaspis*, Xenopoda, *Offacolus*, Chelicerata, *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 lamellipedians, specifically Xenopoda and Aglaspidida. 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.

Acknowledgements

References

Bergström, J. and Hou, X.-G. 2005. Early Palaeozoic lamellipedian arthropods. *In*: S. Koenemann and R.A. Jenner (eds.), Crustacea and Arthropod Relationships. *Crustacean Issues* 16: 73–93.

Bitsch, J. and Bitsch, C. 2007. The segmental organization of the head region in Chelicerata: a critical review of recent studies and hypotheses. *Acta Zoologica* 88: 317–335.

Bousfeld, E.L. 1995. A contribution to the natural classification of Lower and Middle Cambrian arthropods: food gathering and feeding mechanisms. *Amphipacifica* 2: 3–34.

Boxshall, G.A. 2004. The evolution of arthropod limbs. *Biological Reviews* 79: 253–300.

Bremer, K. 1994. Branch support and tree stability. *Cladistics* 10: 295–304.

Briggs, D.E.G. and Collins, D. 1999. The arthropod *Alalcomenaeus cambricus* Simonetta, from the Middle Cambrian Burgess Shale of British Columbia. *Palaeontology* 42: 953–977.

Briggs, D.E.G. and Robison, R.A. 1984. Exceptionally preserved nontrilobite arthropods and anomalocaridids from the Middle Cambrian of Utah. *University of Kansas Paleontological Contributions* 111: 1–23.

Briggs, D.E.G., Lieberman, B.S., Hendricks, J.R., Halgedahl, S.L., and Jerrard, R.D. 2008. Middle Cambrian arthropods from Utah. *Journal of Paleontology* 82: 238–254.

Bruton, D.L. 1981. The arthropod *Sidneyia inexpectans*, Middle Cambrian, Burgess Shale, British Columbia. *Philosophical Transactions of the Royal Society of London, Series B* 295: 619–656.

Bruton, D.L. and Whittington, H.B. 1983. *Emeraldella* and *Leanchoilia*, two arthropods from the Burgess Shale, Middle Cambrian, British Columbia. *Philosophical Transactions of the Royal Society of London, Series B* 300: 553–582.

Budd, G.E. 2002. A palaeontological solution to the arthropod head problem. *Nature* 417: 271–275.

Butterfield, N.J. 2002. *Leanchoilia* guts and the interpretation of three-dimensional structures in Burgess Shale-type fossils. *Paleobiology* 28: 155–171.

Chen, J.-Y. 2004. *The Dawn of Animal World* [in Chinese]. 366 pp. Jiang Science and Technology Press, Nanjing.

Chen, J.-Y., Waloszek, D., and Maas, A. 2004. A new "great-appendage" arthropod from the Lower Cambrian of China and homology of chelicerate chelicerae and raptorial antero-ventral appendages. *Lethaia* 37: 3–20.

Cotton, T.J. and Braddy, S.J. 2004. The phylogeny of arachnomorph arthropods and the origin of the Chelicerata. *Transactions of the Royal Society of Edinburgh: Earth Sciences* 94: 169–193.

Daley, A.C., Budd, G.E., Caron, J.-B., Edgecombe, G.D., and Collins, D. 2009. The Burgess Shale anomalocaridid *Hurdia* and its significance for early euarthropod evolution. *Science* 323: 1597–1600.

Dunlop, J.A. 2006. New ideas about the euchelicerate stem-lineage. *In*: C. Deltshev and P. Stoev (eds.), European Arachnology 2005. *Acta Zoologica Bulgarica* (Supplement 1): 9–27.

Dunlop, J.A. and Selden, P.A. 1997. The early history and phylogeny of the chelicerates. *In*: R.A. Fortey and R.H. Thomas (eds.), Arthropod Relationships. *Systematics Association Special Volume* 55: 221–235.

Edgecombe, G.D. and Ramsköld, L. 1999. Relationships of Cambrian Arachnata and the systematic position of Trilobita. *Journal of Paleontology* 73: 263–287.

Farris, J.S., Albert, V.A., Källersjö, M., Lipcomb, D., and Kluge, A.G. 1996. Parsimony jackknifing outperforms neighbor-joining. *Cladistics* 12: 99–124.

García-Bellido, D.C. and Collins, D. 2007. Reassessment of the genus *Leanchoilia* (Arthropoda, Arachnomorpha) from the Middle Cambrian Burgess Shale, British Columbia, Canada. *Palaeontology* 50: 693–709.

García-Bellido, D.C., Paterson, J.R., Edgecombe, G.D., Jago, J.B., Gehling, J.G., and Lee, M.S.Y. 2009. The bivalved arthropods *Isoxys* and *Tuzoia* with soft-part preservation from the lower Cambrian Emu Bay Shale Lagerstätte (Kangaroo Island, Australia). *Palaeontology* 52: 1221–1241.

Goloboff, P.A. 1993. Estimating character weights during tree search. *Cladistics* 9: 83–91.

Goloboff, P.A., Farris, J.S., and Nixon, K.C. 2008. TNT, a free program for phylogenetic analysis. *Cladistics* 24: 774–786.

Harzsch, S. and Hafner, G. 2006. Evolution of eye development in arthropods: phylogenetic aspects. *Arthropod Structure & Development* 35: 319–340.

Hendricks, J.R. and Lieberman, B.S. 2008. New phylogenetic insights into the Cambrian radiation of arachnomorph arthropods. *Journal of Paleontology* 82: 585–594.

Hou, X.-G. and Bergström, J. 1997. Arthropods of the Lower Cambrian Chengjiang fauna, southwest China. *Fossils and Strata* 45: 1–116.

Jago, J.B., Zang, W., Sun, X., Brock, G.A., Paterson, J.R., and Skovsted, C.B. 2006. A review of the Cambrian biostratigraphy of South Australia. *Palaeoworld* 15: 406–423.

Liu, Y., Hou X.-G., and Bergström, J. 2007. Chengjiang arthropod *Leanchoilia illecebrosa* (Hou, 1987) reconsidered. *GFF* 129: 263–272.

Luo, H., Hu, S., Chen, L., Zhang, S., and Tao, Y. 1999. *Early Cambrian Chengjiang fauna from Kunming region, China* [in Chinese]. 129 pp. Yunnan Science and Technology Press, Kunming.

Luo, H., Hu, S., Zhang, S., and Tao, Y. 1997. New occurrence of the Early Cambrian Chengjiang fauna in Haikou, Kunming, Yunnan Province, and study on Trilobitoidea. *Acta Geologica Sinica* 71: 122–132.

Nixon, K.C. 2002. *WINCLADA. Version 1.99.08.* Cornell University, Ithaca, NY.

Orr, P.J., Siveter, D.J., Briggs, D.E.G., Siveter, D.J., and Sutton, M.D. 2000. A new arthropod from the Silurian Konservat-Lagerstätte of Herefordshire. *Proceedings of the Royal Society, Series B: Biological Sciences* 267: 1497–1504.

Paterson, J.R. and Brock, G.A. 2007. Early Cambrian trilobites from Angorichina, Flinders Ranges, South Australia, with a new assemblage from the *Pararaia bunyerooensis* Zone. *Journal of Paleontology* 81: 116–142.

Paterson, J.R. and Jago, J.B. 2006. New trilobites from the Lower Cambrian Emu Bay Shale Lagerstätte at Big Gully, Kangaroo Island, South Australia. *Memoirs of the Association of Australasian Palaeontologists* 32: 43–57.

Paterson, J.R., Edgecombe, G.D., García-Bellido, D.C., Jago, J.B., and Gehling, J.G. 2010. Nektaspid arthropods from the lower Cambrian Emu Bay Shale Lagerstätte, South Australia, with a reassessment of lamellipedian relationships. *Palaeontology* 53: 377–402.

Paterson, J.R., Jago, J.B., Gehling, J.G., García-Bellido, D.C., Edgecombe,

G.D., and Lee, M.S.Y. 2008. Early Cambrian arthropods from the Emu Bay Shale Lagerstätte, South Australia. 319–325. *In*: I. Rábano, R. Gozalo, and D. García-Bellido (eds.), Advances in Trilobite Research. *Cuadernos del Museo Geominero* 9: 319–325.

Shultz, J.W. 2007. A phylogenetic analysis of the arachnid orders based on morphological characters. *Zoological Journal of the Linnean Society* 150: 221–265.

Stein, M. 2010. A new arthropod from the Early Cambrian of North Greenland, with a "great appendage"-like antennula. *Zoological Journal of the Linnean Society* 158: 477–500.

Stürmer, W. and Bergström, J. 1978. The arthropod *Cheloniellon* from the Devonian Hunsrück Shale. *Paläontologische Zeitschrift* 52: 57–81.

Sutton, M.D., Briggs, D.E.G., Siveter, D.J., Siveter, D.J., and Orr, P.D. 2002. The arthropod *Offacolus kingi* (Chelicerata) from the Silurian of Herefordshire, England: computer based morphological reconstructions and phylogenetic affinity. *Proceedings of the Royal Society, B: Biological Sciences* 269: 1195–1203.

Suzuki, Y. and Bergström, J. 2008. Respiration in trilobites: a reevaluation. *GFF* 130: 211–229.

Vannier, J., García-Bellido, D.C., Hu, X.-X., and Chen, A.-L. 2009. Arthropod visual predators in the early pelagic ecosystem: evidence from the Burgess Shale and Chengjiang biotas. *Proceedings of the Royal Society, B: Biological Sciences* 276: 2567–2574.

Whittington, H.B. 1974. *Yohoia* Walcott and *Plenocaris* n. gen., arthropods from the Burgess Shale, Middle Cambrian, British Columbia. *Geological Survey of Canada, Bulletin* 231: 1–21.

Wills, M.A., Briggs, D.E.G., Fortey, R.A., Wilkinson, M., and Sneath, P.H.A. 1998. An arthropod phylogeny based on fossil and recent taxa. *In*: G.D. Edgecombe (ed.), *Arthropod Fossils and Phylogeny*, 33–105. Columbia University Press, New York.

Wilson, L.A. 2006. *Food for thought: a morphological and taphonomic study of fossilised digestive systems from Early to Middle Cambrian taxa.* 275 pp. Unpublished Ph.D. thesis, University of Cambridge, Cambridge.

Zhang, X.-G. and Hou, X. 2007. Gravitational constraints on the burial of Chengjiang fossils. *Palaios* 22: 448–453.

Zhang, X.-L., Han, J., Zhang, Z., Liu, H., and Shu, D. 2004. Redescription of the Chengjiang arthropod *Squamacula clypeata* Hou and Bergström, from the Lower Cambrian, South-west China. *Palaeontology* 47: 605–617.

Zhao, Y., Zhu, M., Babcock, L.E., Yuan, L., Parsley, R.L., Peng, J., Yang, X., and Wang, Y. 2005. Kaili Biota: a taphonomic window on diversification of metazoans from the basal Middle Cambrian: Guizhou, China. *Acta Geologica Sinica* 79: 751–765.