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Morphological and Ecological Disparity in Naraoiids (Arthropoda) from the Early Cambrian Chengjiang Fauna, China

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ABSTRACT. *Misszhouia longicaudata* (Zhang & Hou) from the Chengjiang lagerstätte is separated from *Naraoia* Walcott by its antennular orientation, its smaller cephalic caeca and gut, lanceolate distal exopod lobe, and partial fusion of the exopod and first endopodal podomere. *Naraoia spinosa* Zhang & Hou (also from Chengjiang) shares derived characters with the type species, *N. compacta*. Deposit feeding is suggested for *Naraoia spinosa* by both morphology and preservational circumstances. New material shows previously unknown features in *Misszhouia longicaudata*, including frontal organs anterior to a sclerotised lobe of the hypostomal complex, the position of the mouth opening, details of antennule and biramous limb attachments, morphology of the sternites and limb rami, and the structure of the ventral cuticle in the cephalon and pleural areas.

The systematic status of *Naraoia* Walcott, 1912, and several allied non-mineralised arthropods has most recently been reviewed by Fortey & Theron (1994). These workers provided evidence that Naraoiidae Walcott, 1912, could be defined as a monophyletic group that unites the Lower-Middle Cambrian *Naraoia*, the Lower Cambrian *Liwia* Dzik & Lendzion, 1988, the Ordovician *Tariccoia* Hammann *et al.*, 1990, and the Upper Ordovician *Soomaspis* Fortey & Theron, 1994. Among a range of Early Palaeozoic Arachnata that are known from exceptionally-preserved faunas, naraoiids are of particular significance because they have been regarded as a possible sister or stem-group to trilobites (Fortey & Theron, 1994; Shu *et al.*, 1995).
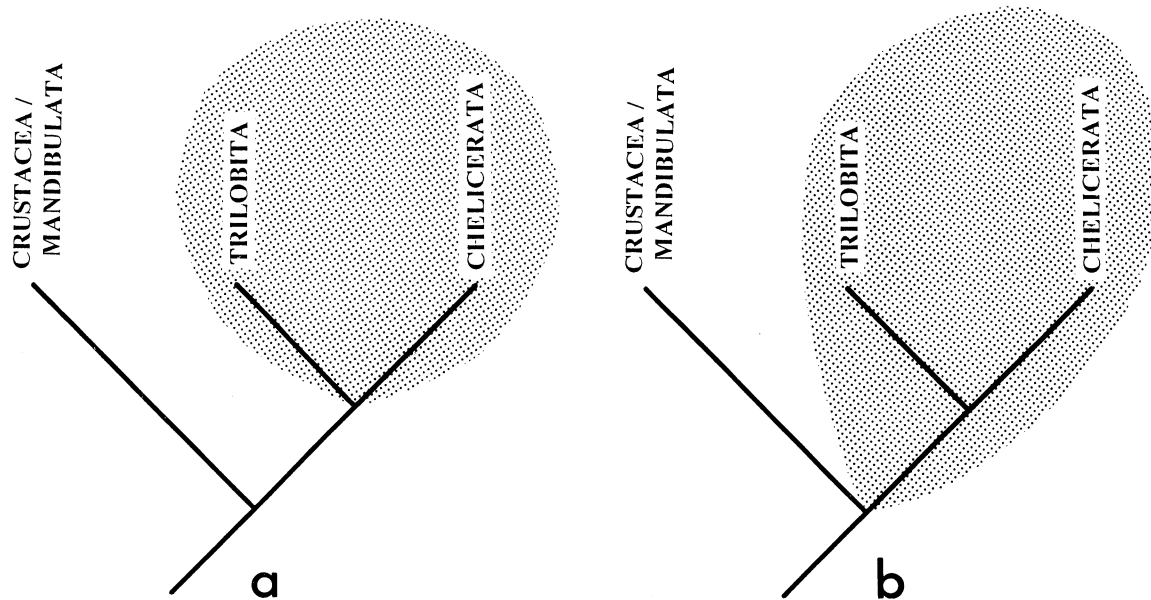
Fig. 1. Cladograms contrasting phylogenetic definitions of Arachnata. a, Node-based definition (Lauterbach, 1980). b, Stem-based definition (endorsed here).

A wealth of information on morphology and ecology of naraoiids is provided by abundant specimens from the Chengjiang fauna (Early Cambrian) of Yunnan Province, China. Zhang & Hou (1985) diagnosed the two Chengjiang naraoiids as species of *Naraoia*. The objectives of the present work are to demonstrate the breadth of anatomical and ecological variation in *Naraoia* as so defined, consider phylogenetic relationships between species, and revise the classification to reflect these relationships. We erect *Misszhouia* n.gen. for *N. longicaudata*.

Specimens illustrated in this work are housed in the Early Life Research Centre, Nanjing Institute of Geology and Palaeontology, Academia Sinica (prefixed ELRC). Material originates from the Yu'anshan Member of the Heilinpu (previously Qiongzhusi) Formation at Maotian Hill (Maotian'shan), the classic locality for the Chengjiang fauna. The *Eoredlichia/Wutingaspis* Zone, to which the Chengjiang fauna is assigned, has recently been assigned an early Botoman age (Landing, 1994; Zhuravlev, 1995), but biostratigraphic work by the senior author supports an earlier (late Atdabanian) dating. Quarries at Maotian Hill are numbered following the scheme used by Chen *et al.* (1995: 4–5).

Systematic Palaeontology

Arthropoda Siebold & Stannius, 1845

Arachnata Lauterbach, 1973

We employ the taxonomic name Arachnata with an explicit phylogenetic definition (see de Quieroz &

Gauthier, 1990, 1994, for elaboration of this concept). Arachnata is that monophyletic group composed of Chelicerata and all taxa more closely related to it than to Crustacea. Lauterbach's concept of Arachnata was "node-based" in the terminology of de Quieroz & Gauthier (i.e., a clade stemming from the most recent common ancestor of Trilobita and Chelicerata) (Fig. 1a). We have adopted a "stem-based" approach (Fig. 1b) in order to also accommodate extinct taxa branching from the stem lineage of Arachnata sensu Lauterbach (1973, 1980). With this definition, Arachnata will remain a stable, monophyletic entity regardless of new discoveries of stem group taxa.

Naraoiidae Walcott, 1912

Misszhouia n.gen.

Etymology. In honour of Miss Zhou Gui-qing, for her skilled preparation of Chengjiang fossils.

Type species. *Naraoia longicaudata* Zhang & Hou, 1985.

Diagnosis. A naraoiid with antennule directed anterolaterally, proximal part not strongly deflected outwards; four pairs of relatively small digestive caeca in cephalon, without ramifying anterior diverticula; trunk a single tergite, lacking articulations (shared with *Naraoia*); gut of relatively small diameter; exopod "fan" with large surface area composed of long lamellar setae; exopod attached along entire length of basis and at least proximal part of first podomere of endopod; exopod shaft

gently tapering distally; distal lobe of exopod lanceolate, not substantially expanded; endopod composed of seven podomeres including terminal claw.

Hypostome and frontal organs. Homologies between naraoiid and trilobite hypostomes appear complex, and some discussion is required in order to use a meaningful descriptive terminology for *Misszhouia*. The structure identified by Zhang & Hou (1985) as the hypostome of *M. longicaudata* is described here as the "ovate lobe of the hypostomal complex" (Figs 2c, 3a, 4). This ventrally convex lobe is a moderately large sternite (less than 30 percent the length of the cephalon). Its margins are not strongly defined, indicating weaker sclerotisation than that of the tergites. It is longitudinally ovate, with maximum width posterior to midlength.

Anterior to the ovate lobe of the hypostomal complex are three ventrally-bulging organs, here called frontal organs, of which the medial of the three is set forward of the other two (Figs 2c,d, 3, 4). The medial frontal organ is elongate and teardrop-shaped, the lateral pair more or less ovate. All three are preserved protruding strongly ventrally with an anteroventral slope making their anterior edge vertical or even slightly protruding in front of the cuticle at its base. The frontal organs are set upon a low relief, boomerang-shaped platform that appears to represent a weakly sclerotised sternite. Some specimens show the frontal organs and ovate lobe to be surrounded and joined by a thin sheet of tissue (arthrodial membrane or ventral cuticle) that extends out to the bases of the antennules (see below). The frontal organs and ovate lobe are thus conjoined as a structural complex that may include two lightly sclerotised sternites. If the attachment site of the antennules is to be regarded as a homologous landmark between naraoiids and trilobites, it is plausible to regard the hypostomal region of *Misszhouia* as including the whole complex—frontal organ sternite, the ovate lobe, and the intervening field of arthrodial membrane—and extending out to the antennular bases. This may, however, be a dubious assumption, given Müller & Walossek's (1987: 47) observations on the lability of antennular position within Crustacea. The lateral and posterior margins of the hypostomal complex are poorly defined (Fig. 2b–d); it is not certain that the shield-shaped impression seen in some specimens (Fig. 5b) is an accurate outline of the hypostomal complex.

Whittington (1977) noted that the hypostome of *Naraoia* was lightly sclerotised, and it was not identified with certainty. Fortey & Theron (1995: Table 2, character 6) coded the *Naraoia* hypostome as conterminant (attached) but that of *Misszhouia* is, in their terminology, natant. The hypostome does not have a sutural attachment to cephalic doublure, and no rostral plate is present; hypostomal attachment is by imbedding in soft tissue (see discussion of Ventral Cuticle below).

The presumed homology of the frontal organs in *Misszhouia* is with parts of the median eye complex in other arthropods. The lateral pair of frontal organs may represent the paired ventral frontal organs of Crustacea (Elofsson, 1965). Paulus (1979) speculated that the ventral eyes of xiphosurids may be the homologue of crustacean ventral frontal organs. As such, he hypothesised that a pair of ventral frontal organs—if present in chelicerates as well as crustaceans—were a general condition of the median eye complex in arthropods. Little evidence for frontal organs has been identified in Cambrian arachnates, although a correspondence with the paired reflective spots on the anterior "rostral" sclerite in *Helmetia* should be considered (see Briggs in Conway Morris *et al.*, 1982: pl. E). If so, the anterior sternite of helmetiids might be homologised with the boomerang-shaped, preantennular sternite in *Misszhouia*. A stringent test of homology with ventral frontal organs in extant arthropods is not possible without knowledge of their gangliar innervation (i.e., evidence for protocerebral innervation).

Comparison of the naraoiid frontal organs with the paired, pimple-like swellings in *Agnostus* described as frontal organs by Müller & Walossek (1987) is obvious. These organs similarly lie anterior to what has been described as the hypostome, leading us to speculate that the agnostid "hypostome" might correspond to the ovate lobe of *Misszhouia*, or only *part* of the trilobite hypostome. The view that the maculae of trilobites are ventral eyes (Lindström, 1901) has led to their proposed homology with the ventral eyes of xiphosurids (Størmer, 1934; Müller & Walossek, 1987: 46). It certainly appears unlikely that maculae would be homologous with the frontal organs of *Misszhouia*, given the more posterior position of the former on the main swelling (middle body) of the hypostome (Fig. 7).

Mouth. The anterior part of the digestive tract, the foregut, is rarely preserved in *Misszhouia longicaudata*, but details are well-displayed by specimen ELRC 11559 (Figs 2a, 3b). The mouth is situated at the rear edge of the ovate lobe of the hypostomal complex, and is directed posteriorly. The esophagus is narrow (Fig. 4a), extending only to the anterior edge of the ovate lobe. At this point the digestive tract expands to a much greater width (about three times that of the esophagus) and flexes upward and backward, forming a stomach overlying the esophagus. A pair of small, mud-filled, ovoid swellings are situated just outside the esophagus at a point about two-thirds of its length (from the rear). A mud-filled tube runs from each swelling posteriorly, converging towards and terminating at the mouth opening. We interpret the paired swellings as digestive glands, and the tubes as ducts leading to the mouth. Their homologue in extant arthropods is uncertain.

The configuration of the mouth and foregut in *Misszhouia* is that inferred for trilobite-allied arachnates in general (e.g., Cisne, 1975: fig. 8), but rarely directly observed in fossils. The second cephalic appendage pair is postoral in *Misszhouia* (versus paroral in *Agnostus* and stem lineage crustaceans; Müller & Walossek, 1987: 47); the antennules are the sole preoral appendage pair.
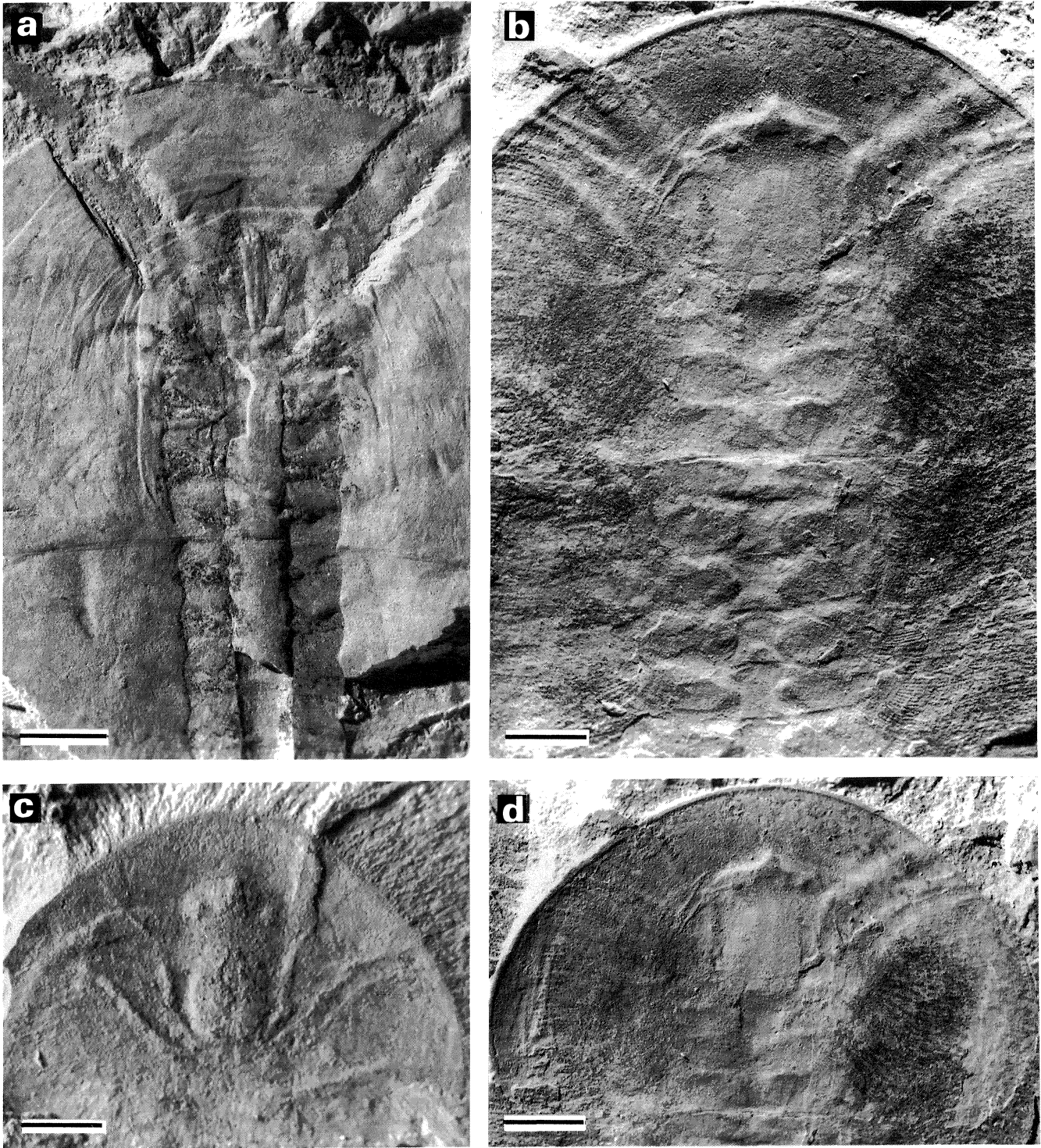
Fig. 2. *Misszhouia longicaudata* (Zhang & Hou, 1985). a, ELRC 11559, from locality MQA, detail of head shield and anterior part of trunk (see Fig. 3b for camera lucida drawing, Fig. 13c for complete specimen). Light from NW. Scale bar 2 mm; b, d, ELRC 11683a, from locality MN5. Ventral views, light from NNW (b), NW (d). Scale bars 2 mm (b) and 3 mm (d); c, ELRC 11558, from locality MQ1, ventral view of head shield (see Fig. 3a for camera lucida drawing). Light from W. Scale bar 1 mm.
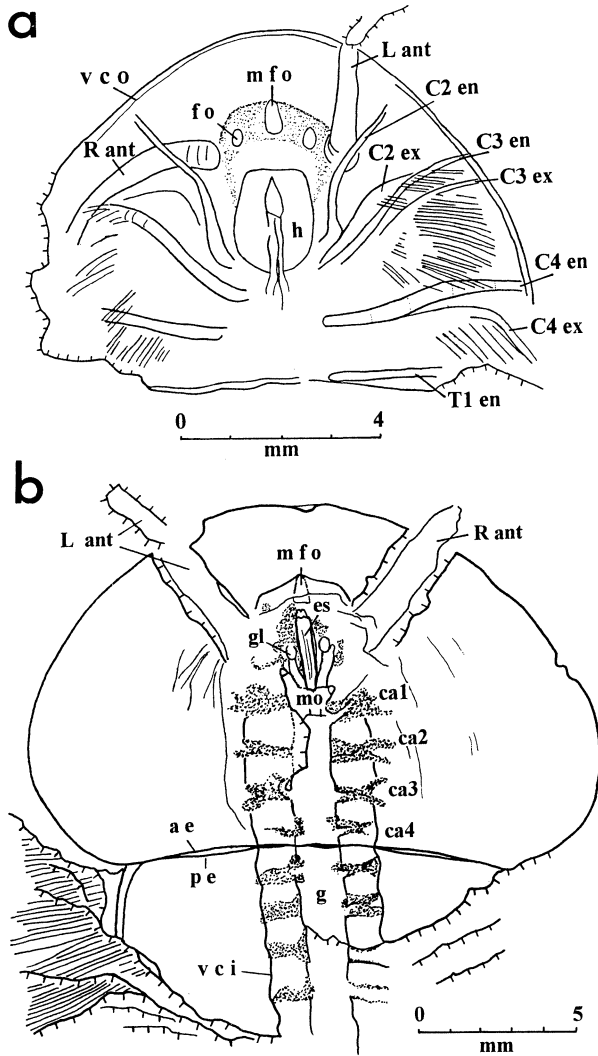
a

b

Fig. 3. *Misszhouia longicaudata* (Zhang & Hou, 1985). a, camera lucida drawing of ELRC 11558 (fig. 2c). b, camera lucida drawing of ELRC 11559 (Fig. 2a). See Appendix for abbreviations.

Antennular attachment. As noted above, the antennule is based at the anterolateral edge of the hypostomal complex (Fig. 2). There is considerable separation of the antennules and first post-antennular appendages (Figs 3a, 4). Some specimens show a few folds of arthrodial membrane at the base of the antennule (Figs 4, 8c), and arthrodial membrane or ventral cuticle is continuous from the antennular base to the ovate lobe and the frontal organs.

Whittington (1977) interpreted the antennule of *Naraoia compacta* as attaching anterior to the hypostome, and spaced far in front of the first pair of post-antennular appendages. The separation of the antennule and the first biramous appendage pair is confirmed for *Misszhouia*. There is less disagreement with Whittington's interpretation of the antennules attaching in front of the hypostome than would first appear to be the case because Whittington's "hypostome" (dotted outline in his fig. 96) corresponds to the ovate lobe only. The

relative position of the ovate lobe and antennular attachment shown by Whittington for *Naraoia compacta* is closely comparable to that of *Misszhouia*. The shape of antennomeres is also similar in *Naraoia compacta* and *Misszhouia* (Fig. 5b), these being wider than long proximally, and longer than wide distally.

Midgut caeca. Four pairs of lateral diverticula or gut caeca are present in the cephalon of *Misszhouia longicaudata* (Figs 2a, 3b). They are preserved as reddish-brown stains, extending laterally from the gut, and bifurcating distally. In specimens where the gut is mud-filled (Fig. 2a), the mud has also penetrated some distance into the caeca. The dark stain of the caeca is preserved both on the dorsolateral and ventrolateral sides of the gut, showing that the caeca had a complex set of small-scale ramifications of considerable dorsoventral extent. The cephalic caeca are equally-spaced relative to each other and of about equal size. The first caecum branches from the gut at the rear edge of the hypostome, i.e., directly dorsal to the mouth (Fig. 3b). Midgut caeca are comparably developed in the anterior part of the trunk, but become smaller and less defined behind the first five trunk segments.

This concentration of midgut caeca in the cephalon and anterior part of the trunk is a general character for a broader group including trilobites. Distantly related trilobites such as *Pterocephalia* (Chatterton *et al.*, 1994) and *Eoredlichia* (Shu *et al.*, 1995: fig. 15A,B) display a particular concentration of gut caeca in the cephalon and first few thoracic segments. The functional basis is evidently for chemical processing (enzyme production and absorption of nutrients) to occur well in front of the end of the gut.

Biramous limb attachment. The attachment sites of the post-antennular cephalic and trunk appendages are marked by a few strong, concentric, ovoid annulations (Figs 8a, 9a). The attachment site is larger in area than had been inferred to be the case for *Naraoia compacta* (Whittington, 1977) and for trilobites, but is smaller (relative to the size of limb base) than that observed in *Agnostus* (Müller & Walossek, 1987) and stem lineage crustaceans (Walossek & Müller, 1990). The annulations are regarded as a partially sclerotised, arthrodial membrane which connected the proximal podomere of the leg (the basis according to Walossek, 1993, 1995—not the "coxa", as has traditionally been inferred) to the body. This arthrodial membrane permitted considerable movement of the leg and proximal flexibility that has not been recognised in prior reconstructions of *Naraoia* or trilobites.

Walossek (1993, 1995) clarified homologies between the basis and limb rami (endopod and exopod) in Crustacea and early arachnates (Ramsköld & Edgecombe, 1996). The annulated arthrodial membrane to which the basis attaches in *Misszhouia* displays a resemblance to the attachment of the basis to the body in stem lineage crustaceans, such as *Martinssonia* (Walossek &
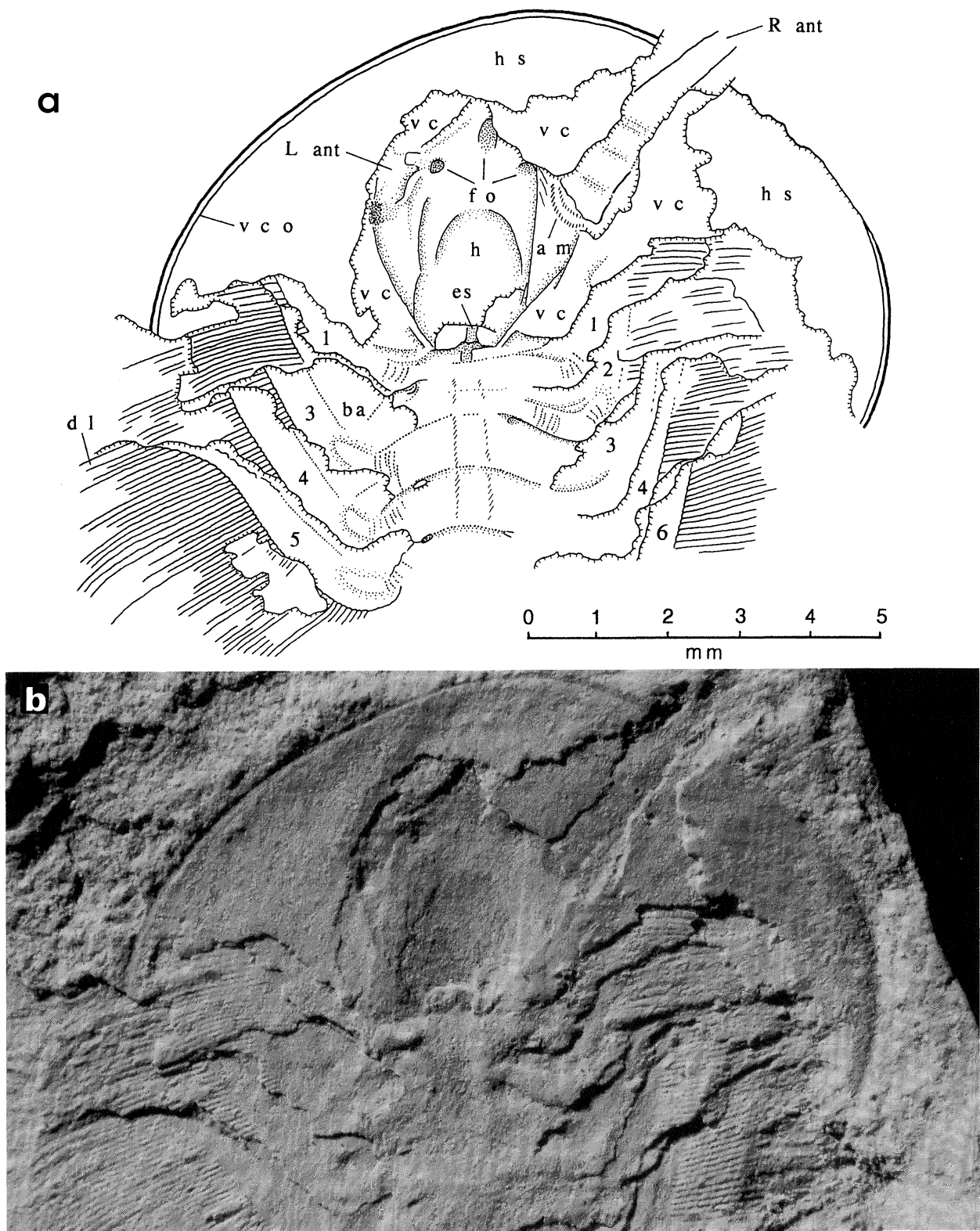
Fig. 4. *Misszhouia longicaudata* (Zhang & Hou, 1985). a, camera lucida drawing of head and anterior part of trunk of ELRC 11076a, from locality MQA. The specimen was embedded in the sediment tilted to the right side, so that ventral structures are displaced to the left. The biramous limbs are numbered 1 to 5 from anterior on the exopod shafts. See Appendix for abbreviations; b, ELRC 11076a. Light from NW (see Fig. 10b for trunk).

Szaniawski, 1991: fig. 7D). This suggests that the proximal articulation of the leg (proximal part of the basis) is homologous across the Crustacea and Arachnata. Disarticulated limbs of *Misszhouia longicaudata* (Figs 5d, 6, 11, 12) show that the proximal articulation is a sharply defined feature.

Tergite overlap. The overlap of the anterior edge of the trunk by the head shield is slight (Figs 2a, 3b), being clearly expressed on the pleural region, and no exoskeletal articulating structures are developed. Whittington (1977: fig. 96) reconstructed a much longer area of overlap between the tergites in *Naraoia compacta*.

Sternites. Between the attachment sites of all biramous appendages are hourglass-shaped sternites (Figs 8a, 10a, 13a). Three cephalic sternites are present behind the hypostome, these being progressively shorter (sag.) anteriorly and shorter than those along the trunk (Fig. 9a). There is little evidence for structural differentiation of the associated cephalic limbs, other than the generally more slender endopod and exopod shaft, notably on the first post-antennular limb (Figs 2c, 9c). The exopod fan on the first two pairs of biramous limbs is developed in a similar manner to that on the third, rearmost cephalic limb and the trunk limbs.

The presence of sternites associated with each of the post-antennular limbs in *Misszhouia* is similar to the presumed primitive chelicerate condition. In palpigrades, for example, sternites are associated with the chelicerae (I), pedipalps and third legs (II + III plate), and each of the remaining prosomal limbs (IV–VI) (Snodgrass, 1952: fig. 23B). Consequently we identify a complete set of post-antennular sternites as a general state for Arachnata. This provides another difference from *Agnostus*, which lacks an antennal (second cephalic) sternite (Müller & Walossek, 1987).

The region between the leg attachment sites in the trilobite *Placoparia* (Whittington, 1993: fig. 4) is very similar to that of *Misszhouia*, suggesting that trilobites could have had sclerotised but unmineralised sternites between the leg attachments. Trunk sternites of anomalocaridids (Hou *et al.*, 1995: figs 9, 10) are generally similar in outline to those of *Misszhouia*. Accordingly, we regard this sternal form as widespread throughout the Arthropoda.

Intersegmental tendons. Between the sternites and appendage attachment sites run narrow bands interpreted as transverse tendinous bars. These components of the general euarthropod intersegmental tendon system (Boudreaux, 1979) have also been identified in trilobites (Whittington, 1993). The tendinous bar between the third and fourth postoral sternite, i.e., at the position of the head/trunk juncture, is marked by a transverse fold (Ramsköld *et al.*, 1996: fig. 2B), indicating the point of flexure (Fig. 9a). Each of these sternites is associated with an appendage pair, and from this point of view, the cephalon has three postoral appendage pairs.

In dorso-ventral view, the fourth sternite extends across the articulation between the head and the trunk, about equally far in both directions or perhaps a bit further anteriorly. Functionally, however, the sternite would have been part of the trunk rather than the head. The boundary between the head and trunk, when traced through a cross-section of the animal, would thus not be vertical but an anteroventrally inclined plane.

Exopod. The exopod shaft of *Misszhouia longicaudata* is relatively narrow along its entire length. It is, however, notably widest proximally, and gently tapers distally (Figs 11, 12, 13a). Imbricating, flattened setae articulate to the rear edge of the exopod shaft along most of its length (i.e., in that extent homologous with the inner lobe of the exopod in trilobites such as *Olenoides* and *Eoredlichia*). The lamellar setae are usually more or less straight or slightly curved, indicating that they were fairly stiff, although some specimens demonstrate post-mortem deformation of the setae (Figs 5d, 6, 12b). A distal lobe is set off from the main shaft of the exopod by a transverse articulation (Fig. 13d). The lobe is lanceolate rather than markedly expanded as in *N. compacta*. The distal lobe typically bends backwards to parallel the course of the lamellar setae on the main shaft of the exopod (Figs 4a, 8b, 11), and bears many short, densely packed bristles along its outer edge (Fig. 8d).

The imbrication of the setae is clearly seen in several articulated specimens. In dorsal view, the scarp of each seta is directed outward, showing that the setae underlie each other outward (see lower right side in Fig. 11a). The proximal edge of the distal lobe is thus overlapped by a few setae in dorsal view, but is fully exposed in ventral view. This imbrication and difference in exposure of the distal lobe enables an unambiguous orientation also of isolated limbs. The specimen figured by Chen *et al.* (1991: fig. 6) shows the distal lobe partly overlapped by setae, and is thus seen in dorsal view (Fig. 12a). An isolated limb figured herein (Figs 11, 12b) shows the distal lobe fully exposed, and is a ventral view. The orientations are confirmed by the imbrication seen elsewhere in the exopod fan. An important difference between limbs seen in dorsal and ventral view is the shape of the proximal margin of the basis and the exopod shaft. In dorsal views this line forms a gentle embayment, whereas in ventral views the embayment is much deeper. This difference reflects the attachment of the articulating membrane and other tissues.

The exopod was attached along the entire length of the basis (Fig. 12), and this attachment extends onto at least the proximal part of the first podomere of the endopod. A strong attachment of the immense exopod "fan" by extending the length of its hinge along the basis is an obvious characteristic of *Misszhouia*. Ramsköld & Edgecombe (1996) proposed that such a hinge—the exopod connected with the entire length of the basis—is a more general character, shared with primitive Trilobita.
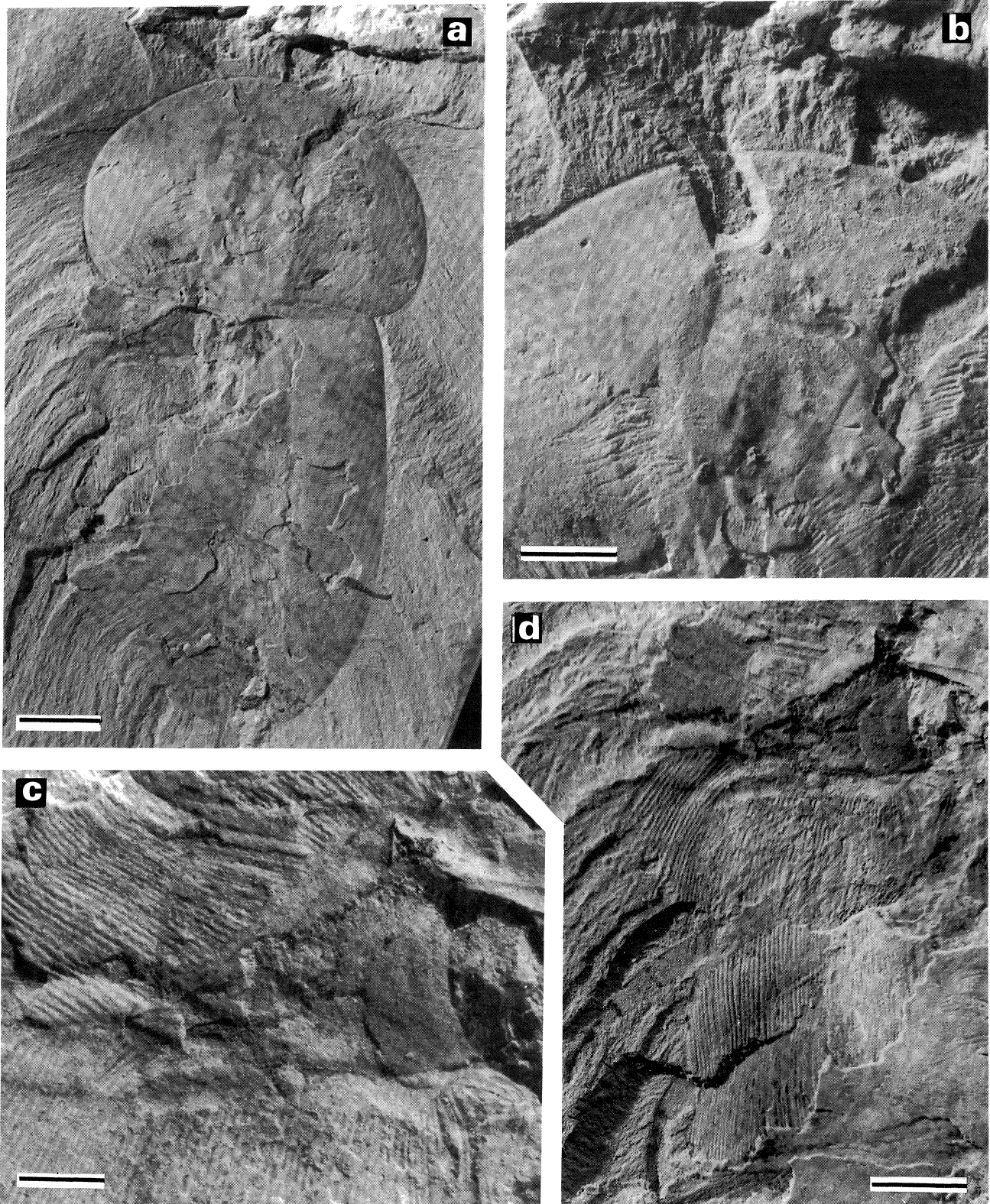
Fig. 5. *Misszhouia longicaudata* (Zhang & Hou, 1985). ELRC 11940, from locality MN4, all dorsal views. a, complete specimen, showing several disjointed, displaced, and overturned limbs. Light from WNW. Scale bar 4 mm; b, detail of cephalon, showing left antennule prepared beneath head shield. Light from NW. Scale bar 2 mm; c, appendages in anterior part of trunk on left side of specimen, showing basis and endopod in an approximately non-displaced position (appendage "X" in Fig. 6). Note sharply defined proximal edge of basis. Light from NNE. Scale bar 1 mm; d, anterior appendages on left side of trunk (see Fig. 6 for camera lucida drawing). Light from NNW. Scale bar 2 mm.
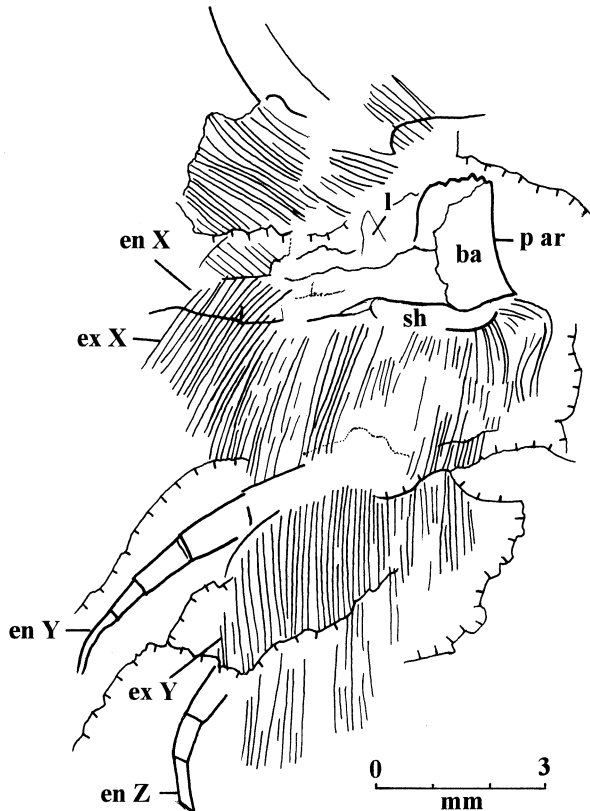
Fig. 6. *Misszhouia longicaudata* (Zhang & Hou, 1985). Camera lucida drawing of trunk appendages in specimen ELRC 11940 (Fig. 5d). See Appendix for abbreviations. "1" refers to endite on first podomere of endopod. Line separating basis and first podomere of endopod is a fracture rather than a joint. Three appendages labelled "X", "Y" and "Z".

Endopod. The basis and the first podomere of the endopod appear to have a non-functional joint, because a well-developed articulation has not been detected (Figs 11, 13b, 14). The first podomere is shortened, being about 60 percent the length of the second podomere, and is unique in its development of a strong, angular endite. Podomeres 2–4 are each of about equal length, whereas podomeres 5 and 6 are 70 percent the length of these. The terminal (seventh) podomere is a stout claw.

The discovery of seven podomeres in the endopod of this naraoiid (Fig. 12), versus six in *Naraoia compacta* (Whittington, 1977) allows the possibility of precise homologies between all podomeres in the endopod of *Misszhouia* and that of trilobites (Müller & Walossek, 1987: fig. 27).

Ventral cuticle. The term ventral cuticle is here used for the lightly sclerotised integument protecting the internal tissues on the ventral side of the animal. This delicate structure is virtually never preserved in fossilised arthropods, the only major exception being phosphatised material such as the Upper Cambrian Orsten fauna (e.g., "inner lamella" of Müller & Walossek, 1987). Some specimens of *M. longicaudata* may be the first to show significant portions of it in non-phosphatised fossil arthropods, due to the split of the rock which has passed, is smaller or larger areas, along the ventral cuticle.

In the distal areas, the surface of the ventral cuticle is smooth and featureless (Fig. 4). Some small folds (which are presumably preservational) are seen both perpendicular to the margin in the trunk (Fig. 9b), and parallel to the margin of the head shield (Fig. 9c; see section on Doublure). Embedded in the ventral cuticle, without clearly defined margins, are structures such as the components of the hypostomal complex. Where
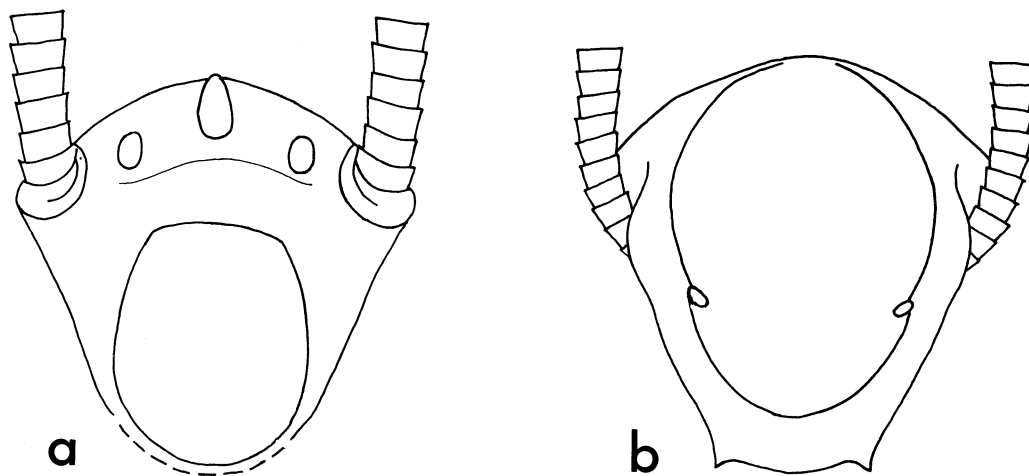

Fig. 7. Comparison of naraoiid and trilobite hypostomes, showing antennular attachments. a, *Misszhouia longicaudata*; b, *Ceraurinella*. Morphology and orientation of antennules based on *Triarthrus* (Whittington and Almond, 1987).
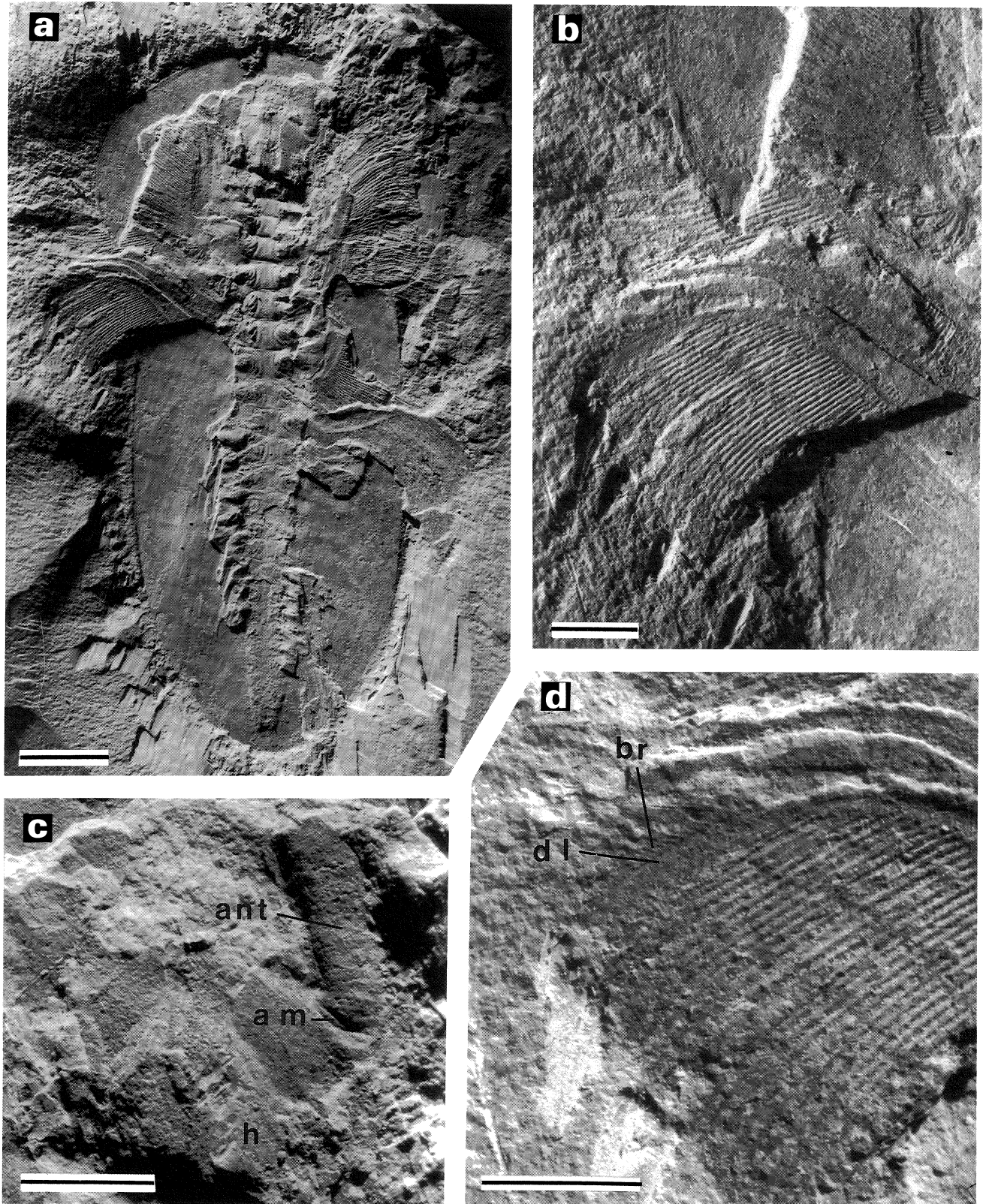
Fig. 8. *Misszhouia longicaudata* (Zhang & Hou, 1985). ELRC 11590b, all ventral views (see Ramsköld *et al.*, 1996: fig. 2 for counterpart). a, complete specimen. Light from NNW. Scale bar 5 mm; b, detail of left side, showing appendages in anterior part of trunk. Light from WNW. Scale bar 2 mm; c, detail of hypostomal complex, showing attachment of antennule (ant), arthrodial membrane (a m) and ovate lobe of hypostomal complex (h). Light from N. Scale bar 2 mm; d, detail of distal part of appendage in Fig. b. Bristles (br) on outer edge of distal lobe of exopod (d l) are indicated. Light from NNE. Scale bar 2 mm.
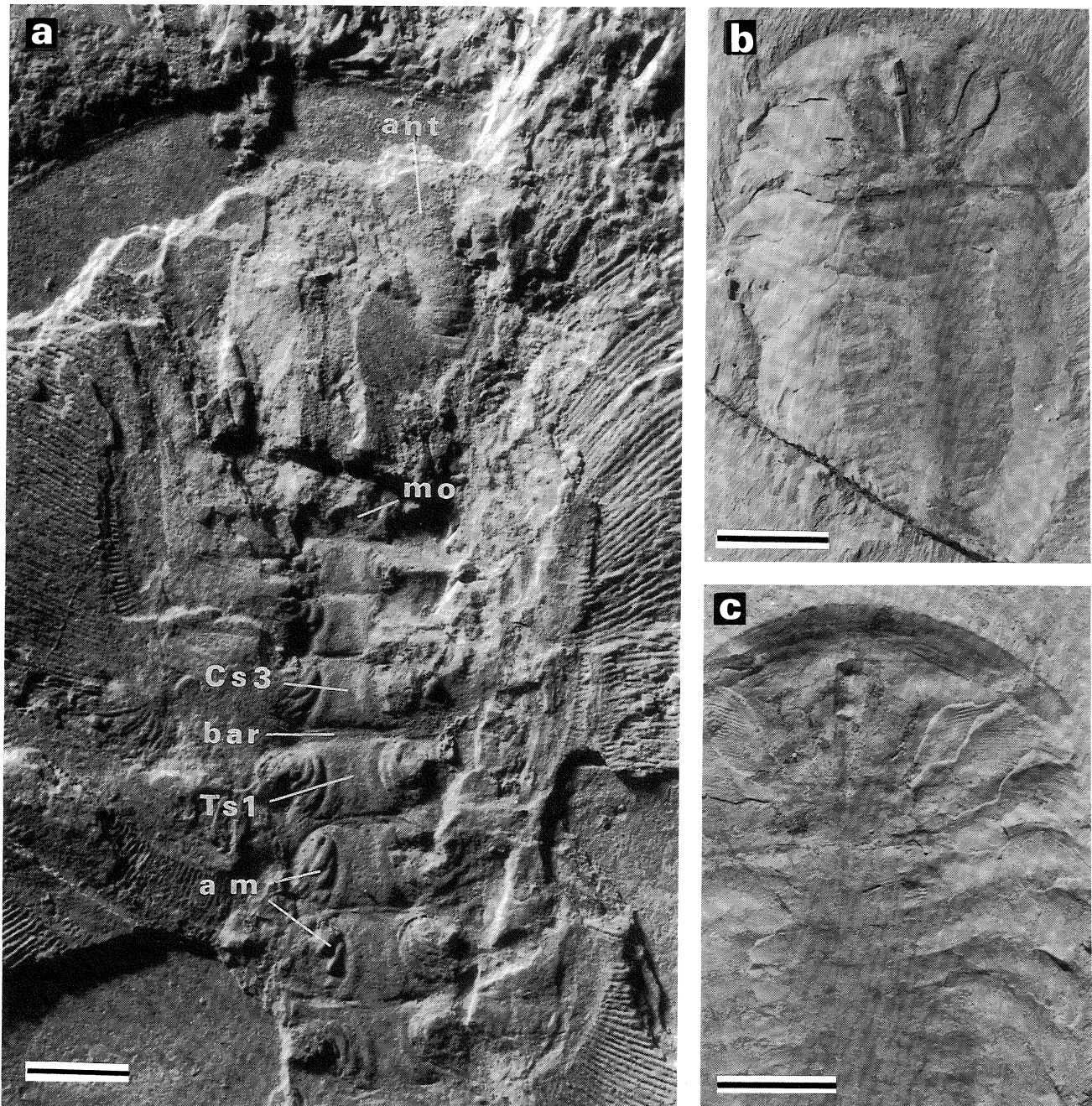
Fig. 9. *Misszhouia longicaudata* (Zhang & Hou, 1985). a, ELRC 11590b, detail of cephalon and anterior part of trunk (see Fig. 8 for additional views) in ventral view. See appendix for abbreviations. "bar" is tendinous bar at juncture between third cephalic sternite (Cs3) and first trunk sternite (Ts1). Position of mouth (mo) approximate. Light from NW. Scale bar 2 mm; b, c, ELRC 11684, from locality MQ1. b, ELRC 11684a, dorsal view, specimen exposing ventral cuticle in much of the cephalon and on right side of trunk. Mud-filled esophagus appears to extend too far posteriorly to accurately show position of mouth at its posterior end, and part of the digestive tract shown in relief may belong to the midgut. Light from NNW. Scale bar 4 mm; c, ELRC 11684b, ventral view, detail showing ventral cuticle in the cephalon. Note the position of the relatively small exopods of the first post-antennular cephalic appendage pair (left one complete). Light from NW. Scale bar 3 mm.
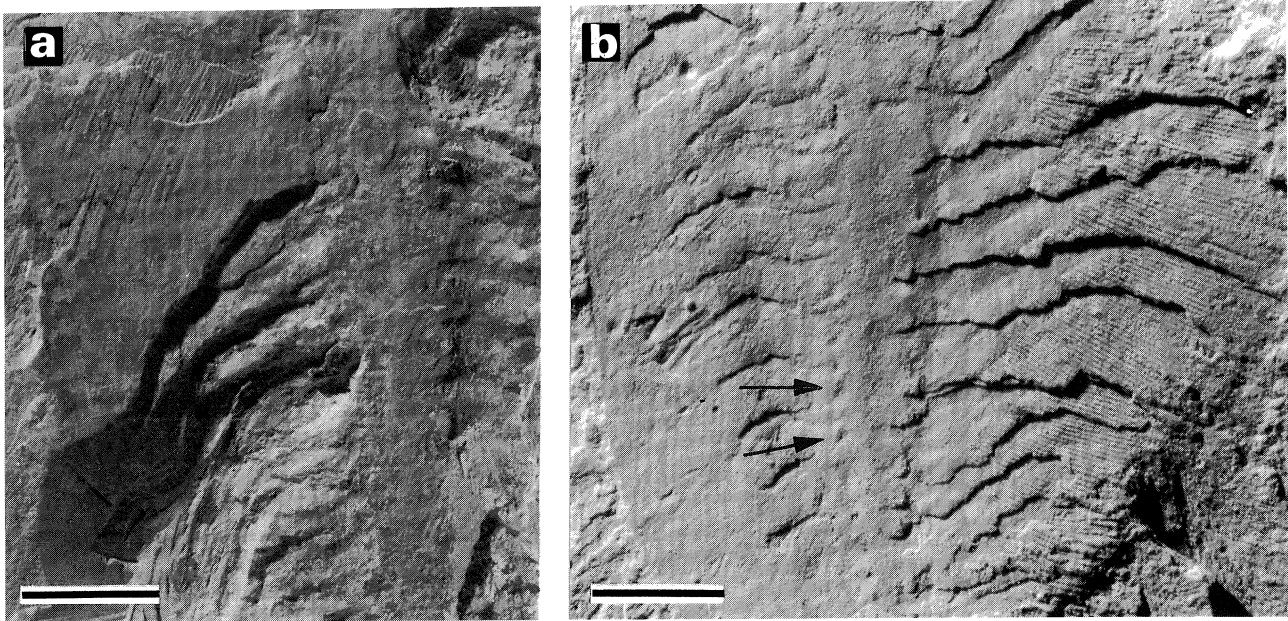
Fig. 10. *Misszhouia longicaudata* (Zhang & Hou, 1985). a, ELRC 11590a, posterior part of trunk in dorsal view (detail of Ramsköld *et al.*, 1996: fig. 2a, after preparation of trunk limbs. See Fig. 8a for counterpart). The split has passed along the ventral surface of the trunk stem. Light from NNW. Scale bar 3 mm; b, ELRC 11076a, from locality MQA, trunk in dorsal view (see Fig. 4 for head and anteriormost part of trunk). The split has passed through the body at a plane immediately below the dorsal exoskeleton. Arrows point to paired axial impressions where dorsoventral musculature attached to the ventral side of the exoskeleton. Light from NW. Scale bar 2 mm.

movable structures, such as the antennules, are based in the ventral cuticle, the cuticle forms a series of concentric annuli around their base (Figs 3a, 4, 8c). These annuli show that the cuticle was not sufficiently elastic in itself to permit major deformation, but that flexibility had to be achieved by folding rather than through stretching and contraction.

In the lateral two-thirds, the ventral cuticle roughly followed the convexity on the dorsal shields (Figs 9b, 10b). Adaxially, in the limb-bearing part of the animal the cuticle flexed abruptly ventrally to surround the limb bases that extend laterally from the axial trunk stem. The adaxial limit of the ventral cuticle, that is, the adaxialmost extent of mud penetration between the cuticle and the exopods, is commonly sharply outlined in the specimens, seen as a gently undulating, exsagittal line (Figs 2a, 3b). The cuticular covering on the ventral side of the axial trunk stem consists of sternites with annulated ventral cuticle between the the limb bases and the sternites.

Doublure. The ventral cuticle attaches laterally on the ventral side just inside the margin of the head and trunk shields. Mud has penetrated inside the tissues up to the line of attachment, which can be seen in many specimens as a line parallel to the margin of the tergites (Figs 2b,d, 4), effectively leaving only the thickness of the dorsal shield outside the line. In *Naraoia compacta*, this line has previously been interpreted as the margin of a very narrow doublure

(Whittington, 1977: 421–422). There is no evidence in either *Naraoia* or *Misszhouia* of a doublure in the sense of the margin of the tergite being flexed or rolled under to form a continuation of the sclerotised shield on the ventral side.

Other lines seen parallel to the margin of the shields in the fossils can also be rejected as candidates for a doublure margin. In the head shield, a line about 15 percent of the shield diameter is sometimes seen in both *N. compacta* (Whittington 1977: pl. 3, figs 16–20) and *M. longicaudata* (Fig. 9b,c). In *N. compacta* the line coincides with the distal extent of the diverticula, but since *M. longicaudata* lacks such diverticula, the line may represent the inner limit of a somewhat strengthed portion of the ventral cuticle. This is not, however, closely comparable to a doublure as defined above. Another line, or scarp, is seen even further adaxially in some specimens of *N. compacta* (Whittington 1977: pl. 2, figs 9–12). This line is clearly situated on the dorsal shield rather than on the ventral side and is a postdepositional artifact caused by compaction which exaggerated the limits of the axial region.

Relationships

With the above morphological considerations, several characters are identified that separate *Misszhouia longicaudata* as sister to a clade including *Naraoia compacta* and *N. spinosa*. We

infer that *N. spinifer* Walcott, 1931, belongs to this latter clade, based on the pervasive similarity of its exoskeletal features to those of *N. spinosa*. Given the inadequate state of knowledge of its soft anatomy, however, the systematic position of *N. spinifer* is not further explored here.

Implicit in this consideration of relationships is the monophyly of Naraoiidae sensu Fortey & Theron (1994). We endorse several characters identified as naraoiid synapomorphies by Fortey & Theron (1994: 842)—the transversely oval or semicircular head shield, lack of dorsal eyes, and the pygidial tergite exceeding the length of the head shield. To this list of synapomorphies uniting *Liwia, Naraoia, Misszhouia, Tariccoia*, and *Soomaspis*, we add a unique aspect of tagmosis, the distinctive narrowing of the anterior part of the trunk relative to the head shield and posterior part of the trunk. This condition is observed in naraoiids regardless of the presence or absence of trunk articulations. The hypothesis that Naraoiidae is a monophyletic group (Fig. 15) means that notions of a paraphyletic "nectaspid" grade as ancestral "soft-bodied trilobites" (Shu *et al.*, 1995: fig. 20B) should now be abandoned. Phylogenetic analyses will be better served by considering the internal components of "Nectaspida" (e.g., Naraoiidae, Tegopeltidae) as separate terminal taxa.

Within this context of a naraoiid clade, synapomorphies of *Naraoia* (*compacta + spinosa*) that exclude *Misszhouia longicaudata* are:

1. large, ramifying anterior pair of digestive diverticula in the cephalon. These are well known for *N. compacta* as well as *N. spinosa* (Figs 16a,c, 17, 18b, 19), in which they are typically mud-filled in relief, and occupy most of the genal region. In *Misszhouia longicaudata*, four pairs of relatively small caeca are present in the cephalon (Figs 2a, 3b) all of which bifurcate distally. The anterior pair of caeca are not differentiated in size, a situation in striking contrast to *Naraoia*;

2. bloated, mud-filled gut. The width of the gut of *Naraoia compacta* (Whittington, 1977: figs 54, 64) and *N. spinosa* (Figs 18b, 19) exceeds that of *Misszhouia longicaudata* (Fig. 18a) by a considerable degree, indeed to an extent not matched by other Chengjiang arthropods (see discussion in "Ecological disparity" below). The bloated, mud-filled gut of *Naraoia* is thus regarded as a shared derived state;

3. laterally deflected antennules. The antennule of *Misszhouia* runs anterolaterally from the hypostome (Figs 2–4, 8c), lacking the strong lateral deflection present proximally in *N. compacta* (Whittington, 1977, figs 5, 49, 51, 60) and *N. spinosa* (Figs 16a,b, 17, 22a, 23). The antennules in *Misszhouia* were evidently capable of rotation at their attachment, allowing a somewhat lateral orientation (compare

Figs 2b and 8c for range of variation), whereas in *N. spinosa* the antennules were forced to flex anteriorly far distal to their attachment in order to reach an exsagittal direction (Fig. 16b), but the proximal part consistently runs transversely from the hypostome. Relevant outgroup taxa such as Trilobita (Whittington & Almond, 1987; Shu *et al.*, 1995), Tegopeltidae (Whittington, 1985: figs 2, 3), and Helmetiida (Hou, 1987: pl. 3, fig. 2) also lack a strong proximal deflection of the antennule. The apomorphic state in *Naraoia* is also shared by *Liwia* which, contrary to its reconstruction (Dzik & Lendzion, 1988: fig. 5A), has strongly deflected antennules (Dzik & Lendzion, 1988: fig. 4A,B).

Based on these synapomorphies, characters shared by *Misszhouia longicaudata* and *Naraoia compacta* (e.g., a massive ventral projection on the first podomere of the endopod, a state unknown for *N. spinosa*) are interpreted as plesiomorphies for a broader clade uniting the two genera. This prediction is supported by the presence of such an endite in outgroup taxa, such as the primitive trilobite *Eoredlichia* (Ramsköld & Edgecombe, 1996).

The exopod of *Naraoia spinosa* is observed to have a paddle-like distal lobe in at least some appendages, e.g., those in the anterior part of the trunk (Figs 16d,e, 17). An expanded distal lobe in *N. compacta* and *N. spinosa* is regarded as a symplesiomorphy, given that basal trilobites (*Eoredlichia* and *Olenoides*) likewise possess a distal lobe (Ramsköld & Edgecombe, 1996) fringed with bristles. As such, the lanceolate distal lobe of *Misszhouia* is regarded as the derived condition, modified from the large, flattened lobe possessed by the common ancestor of trilobites and naraoiids.

The prior classification implies that *Misszhouia* and *Naraoia* are closest relatives within the Naraoiidae sensu Fortey & Theron (1994). The lack of free thoracic segments provides the most obvious synapomorphy to distinguish this clade from *Liwia, Tariccoia*, and *Soomaspis* (character 4 in Fig. 15a). The monophyly of a grouping of these latter three genera ("Liwiinae" sensu Fortey & Theron, 1994) is, however, dubious, being based exclusively on the primitive retention of trunk articulations. Notably, *Liwia* shares lateral deflection of the antennules with *Naraoia*. This putative synapomorphy (character 5 in Fig. 15b) is in conflict with the grouping of *Naraoia* and *Misszhouia* on the basis of trunk fusion. Additional characters from poorly-known taxa (such as *Liwia*) will be required to resolve the incongruence. In contrast to the alternative phylogenies suggested by Fortey & Theron (1994: text-fig. 2), which relied on a single character (number of trunk articulations), we suggest that the Ordovician naraoiids *Tariccoia* and *Soomaspis* are each others' closest relative. Synapomorphic for this group are an extreme widening of the doublure (Hammann *et al.*, 1990: text-fig. 4b; Fortey & Theron, 1994: text-fig. 1A) that is not observed in the other naraoiids (cf. *Misszhouia longicaudata*; Fig. 2b,d), and the development of a median keel on the pygidium.
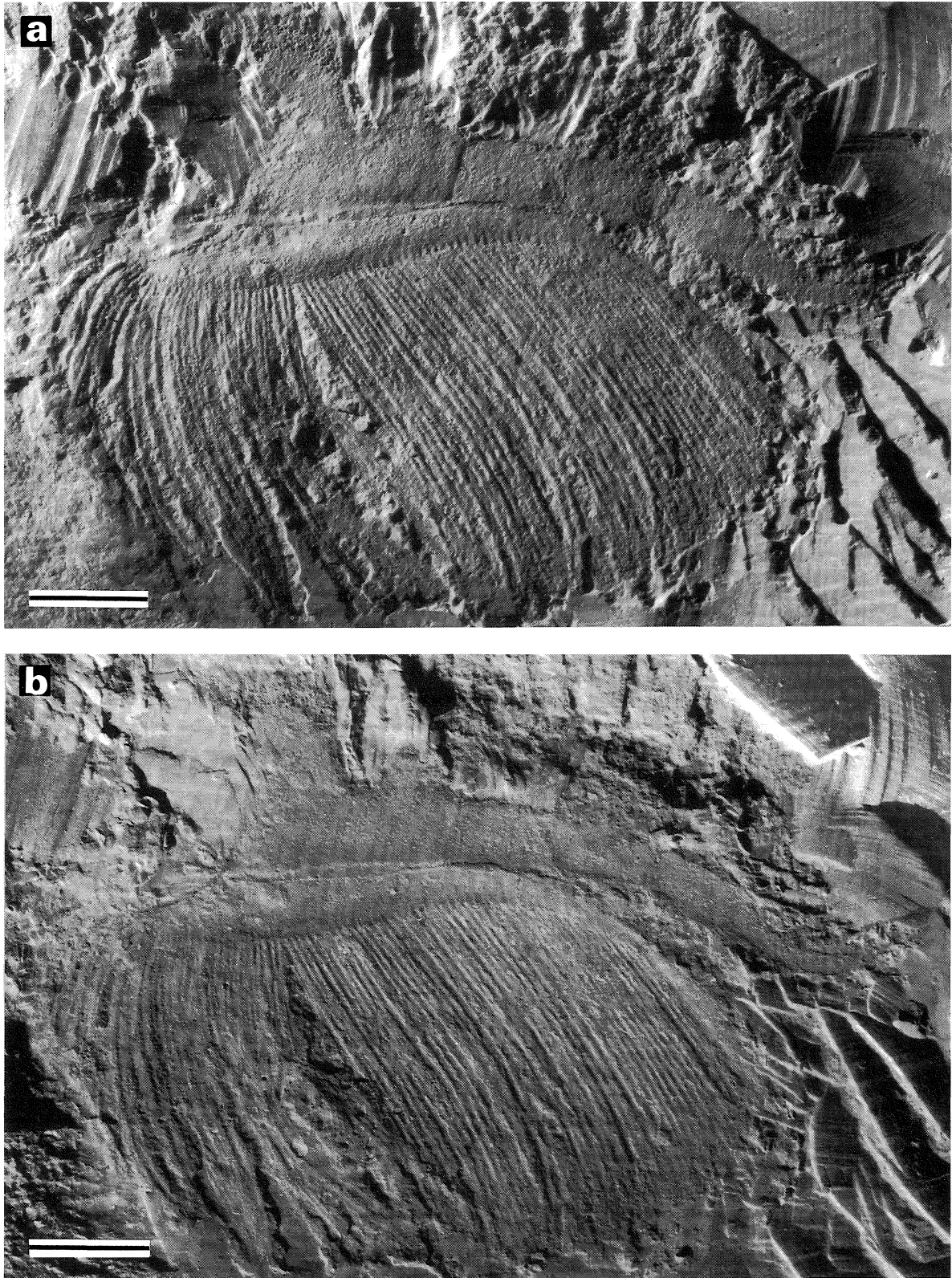
Fig. 11. *Misszhouia longicaudata* (Zhang & Hou, 1985). ELRC 1300a, from locality MW2, ventral view (see Fig. 12b for camera lucida drawing). Scale bars 2 mm. a, very low light from WNW, emphasising podomere joints in endopod; b, low light from ENE, emphasising proximal edge of basis and exopod shaft, joint between exopod shaft and distal lobe, and tip of endopod.
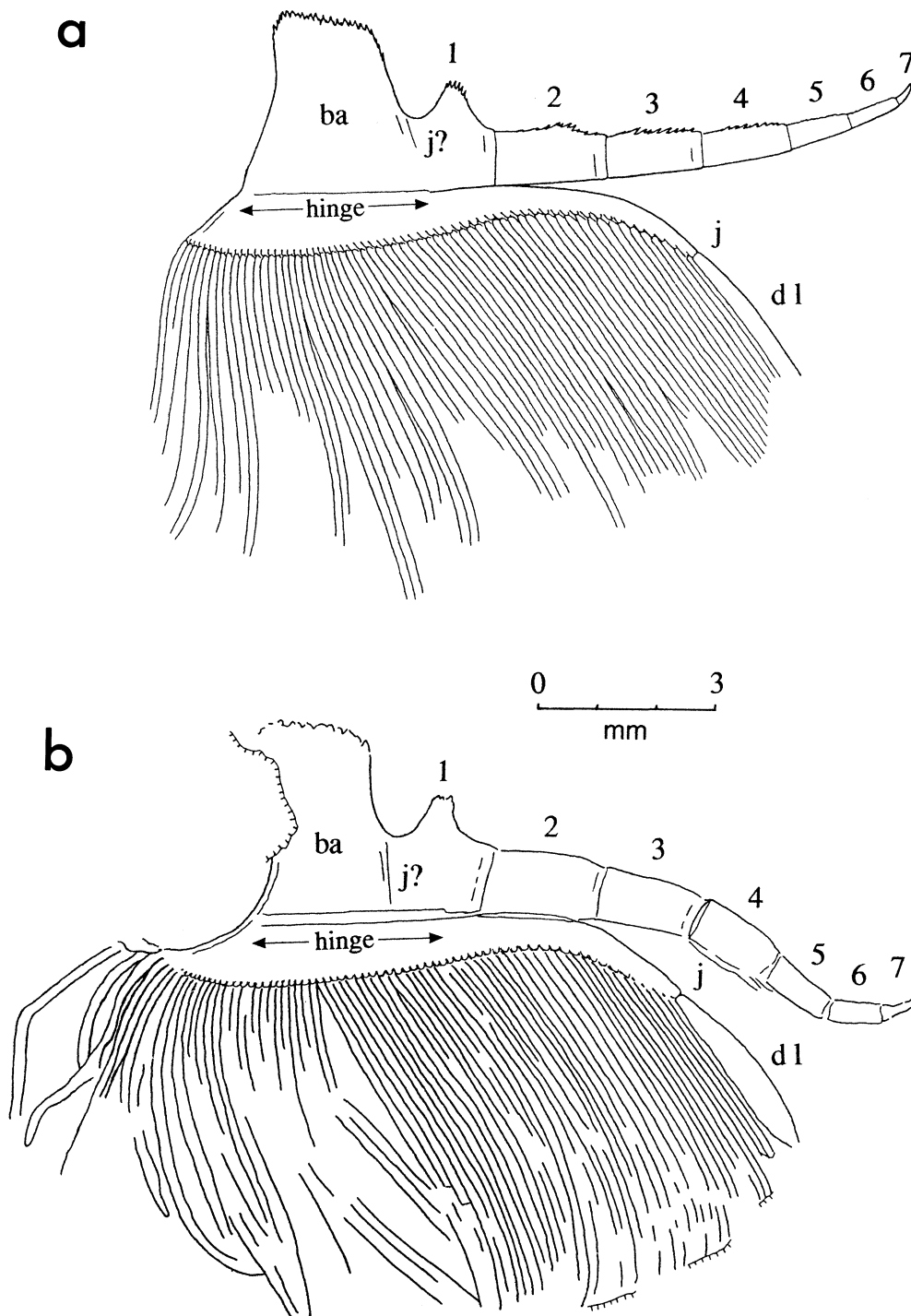
Fig. 12. *Misszhouia longicaudata* (Zhang & Hou, 1985). Interpretive line drawings of limbs preserved disarticulated from the body. Endopod podomeres are numbered 1 to 7. a, specimen figured by Chen *et al.* (1991: fig. 6), dorsal view; b, ELRC 1300a (Fig. 11), ventral view. See Appendix for abbreviations. "j" indicates joint between exopod shaft and distal lobe, "j?" is linear depressions possibly indicating a fused joint between the basis and the first podomere of the endopod.
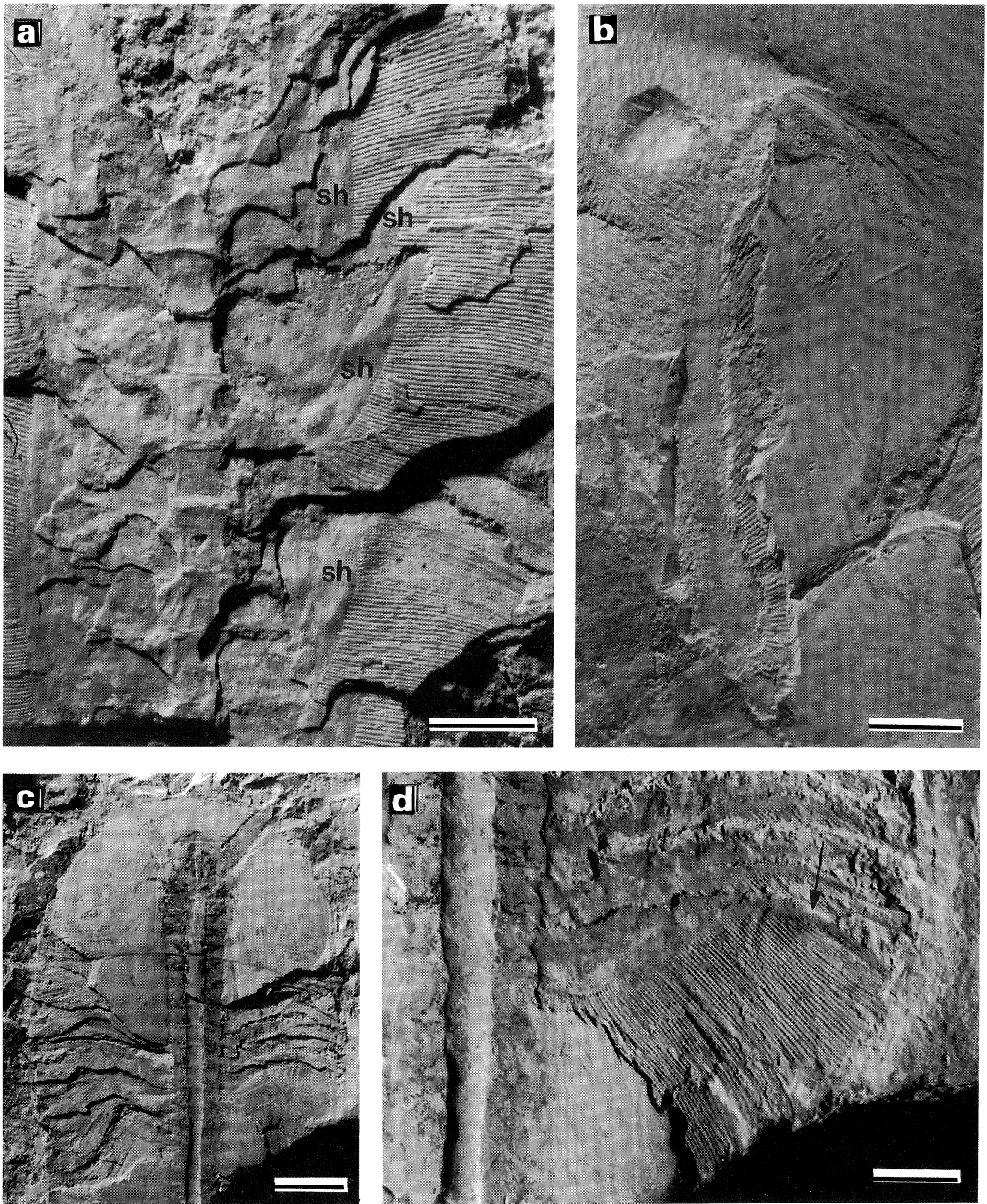
Fig. 13. *Misszhouia longicaudata* (Zhang & Hou, 1985). a, ELRC 11555, from locality MW2, dorsal view of specimen with exoskeleton removed. "sh" indicates exopod shafts. Light from N. Scale bar 2mm; b, ELRC 11561a (see Fig. 14 for camera lucida drawing; see Ramsköld *et al.*, 1996: fig. 1A for counterpart), dorsal view. Exposed endopod is that of first trunk limb. Light from NW. Scale bar 2 mm; c, d, ELRC 11559, from locality MQA. c, view of entire specimen. Light from NW. Scale bar 5 mm; d, detail of trunk, showing mud-fill removed from gut. Arrow indicates articulation of distal lobe of exopod. Light from W. Scale bar 2 mm.
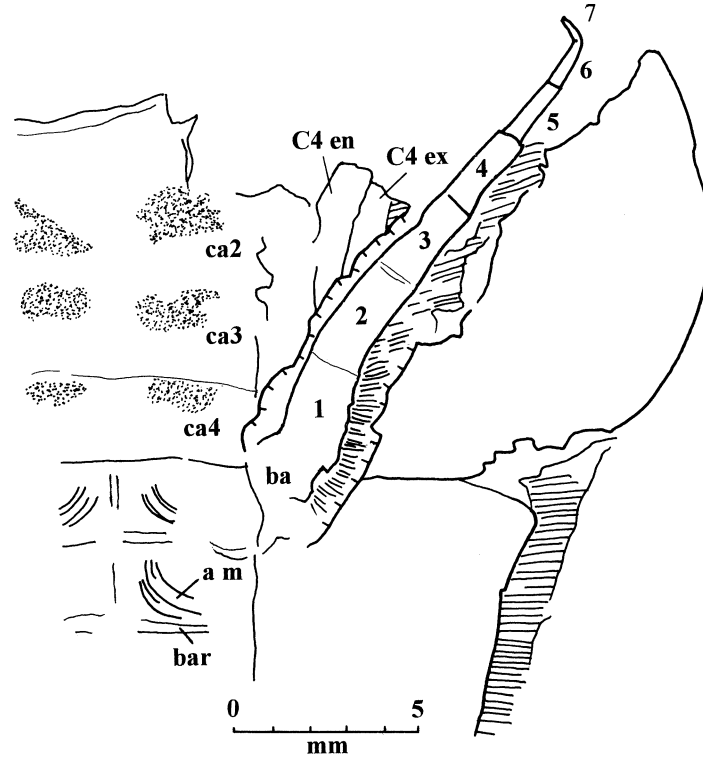
Fig. 14. *Misszhouia longicaudata* (Zhang & Hou, 1985). Camera lucida drawing of ELRC 11561a (see Fig. 13b). Labelled endopod is that of first trunk limb; the exopod "fan" along its posterior edge belongs to the last cephalic limb ("C4 ex"). See Appendix for abbreviations. Endopod podomeres are numbered 1–7.
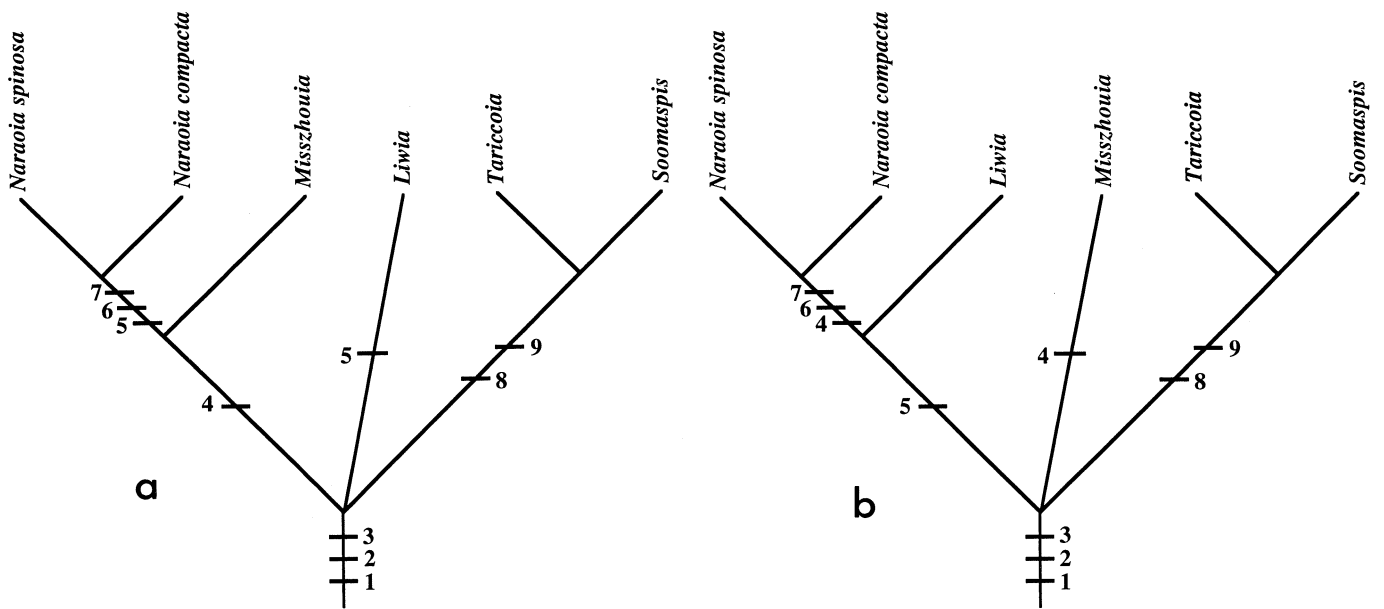

Fig. 15. Alternative cladograms of relationships within Naraoiidae, showing either *Misszhouia* (a) or *Liwia* (b) as sister taxon to *Naraoia*. Numbers refer to derived characters as follow: 1. trunk narrowed anteriorly relative to head shield, widest posteriorly; 2. lack of dorsal eyes; 3. pygidium longer than head shield; 4. trunk fused as single tergite; 5. laterally deflected antennules; 6. large, ramifying anterior pair of gut diverticula; 7. bloated, mud-filled gut; 8. very wide doublure; 9. median keel on pygidium.
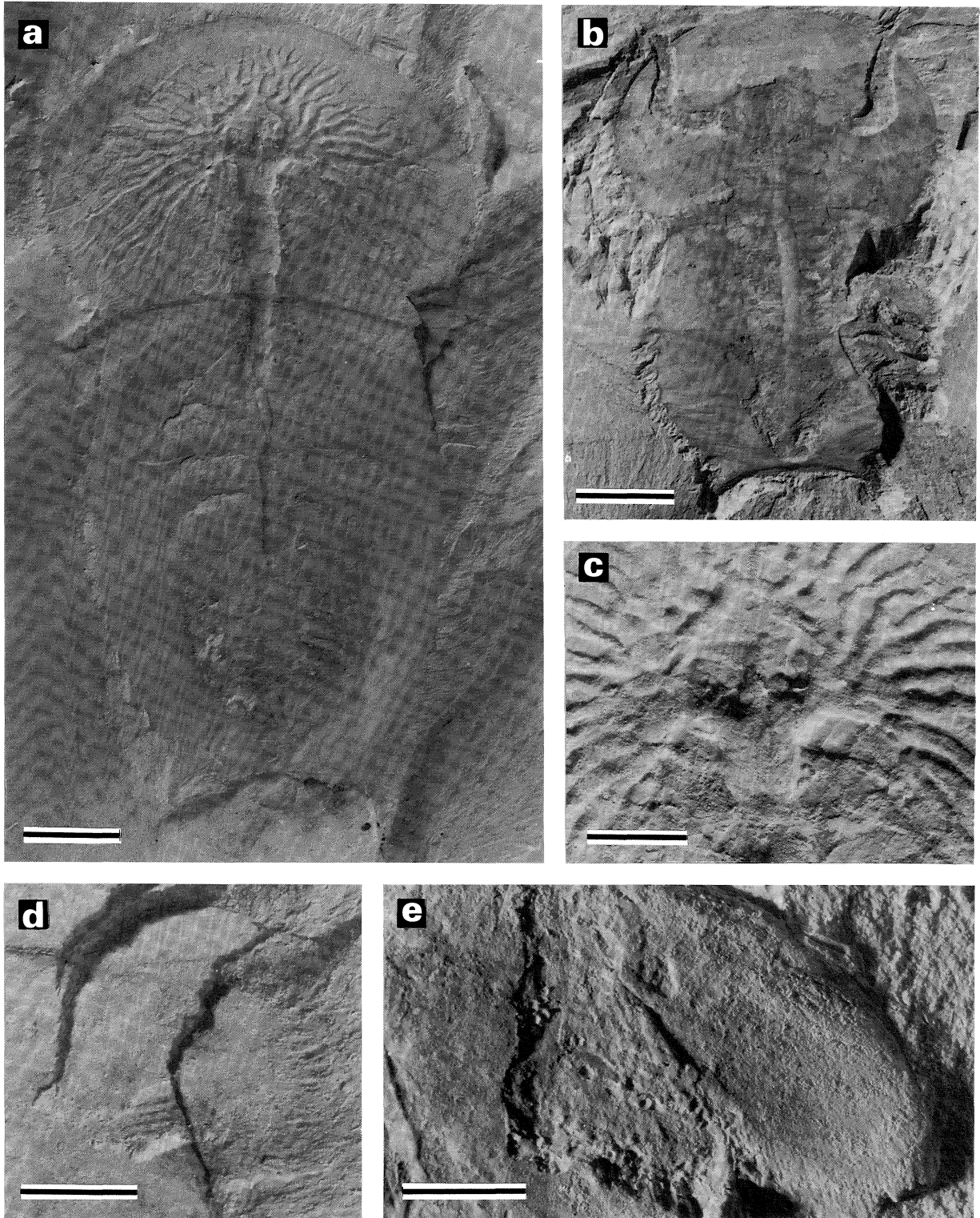
Fig. 16. *Naraoia spinosa* Zhang & Hou, 1985. a, c, d, ELRC 16182b, from locality MQA (see Fig. 17 for camera lucida drawing). a, dorsal view of large individual. Note that right antennule is recurved anteriorly distal to the head shield, but is oriented laterally from its attachment point. Light from NW. Scale bar 4 mm; c, detail of cephalon, showing foregut and proximal parts of anterior diverticula. Light from NW. Scale bar 2 mm; d, detail of distal parts of anterior two trunk exopods. Light from NW. Scale bar 2 mm. b, ELRC 16074a, from locality MW2, dorsal view of complete specimen with head shield excavated to expose antennules. Light from NW. Scale bar 5 mm; e, ELRC 16070, dorsal view of distal lobe of trunk exopod. Light from W. Scale bar 2 mm.
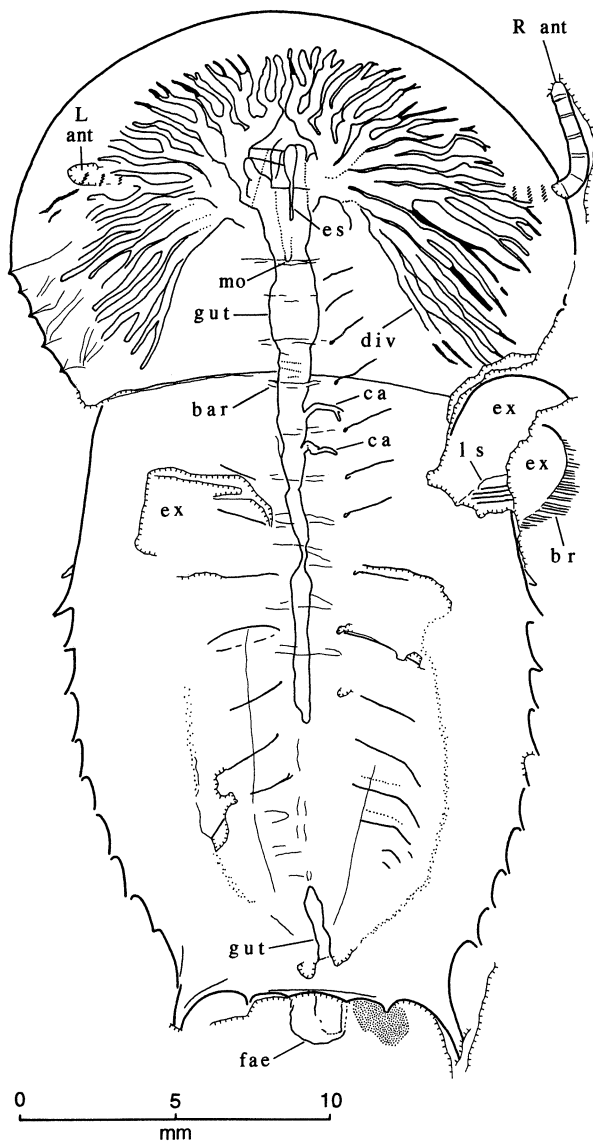
Fig. 17. *Naraoia spinosa* Zhang & Hou, 1985. Camera lucida drawing of ELRC 16182b (see Fig. 16a,c,d). See Appendix for abbreviations.

New information on the ontogeny of naraoiid appendages is available from *Naraoia spinosa* (Figs 22, 23). This may provide another source of data for evaluating relationships within Naraoiidae and between naraoiids and other groups. Post-antennular appendages of juveniles have short, non-imbricate setae splaying from the slender shaft of the exopod, as well as splaying distally from the tip of the exopod. The typical arachnate imbrication of the lamellar setae is attained later in ontogeny, and we accordingly regard the state shown by juveniles of *N. spinosa* as a plesiomorphy. Juvenile naraoiid morphology shows a closer approximation to exopod structure in *Agnostus pisiformis* than has been detected in other taxa at more advanced stages of

ontogeny. In some instances, these similarities are detailed. For example, the first post-antennular cephalic limb of *Agnostus* (Müller & Walossek, 1987: fig. 6B) and the antennule of *Naraoia spinosa* (Fig. 22a) possess very similar configurations of setae. The comparable region is situated distally on the second appendage in *Agnostus* but may extend farther proximally on the antennule of *Naraoia*. In both taxa, a short seta is developed on the posteromedial edge of each podomere on its anterior margin, whereas a pair of long setae is present on the posterior edge of the podomeres. Given the lack of evidence for an especially close relationship between agnostids and naraoiids, this arrangement in juvenile morphology is evidently a deeply nested character. The antennule of *Agnostus* appears to be serially homologous with the sole ramus of the following limb, i.e., the antennal exopod (both bearing stiffened setae on similarly shaped podomeres). Cisne (1981: 130) made essentially the same conjecture, that the trilobite antennule is the serial homologue of the post-antennular exopod shaft. The inferred serial homology of the antennule and the antennal exopod in *Agnostus* provides an explanation for the similarity of the the antennule of *Naraoia spinosa* to the antenna of *Agnostus*. It is thus not surprising that the antennule of juvenile *Naraoia* bears setae similar to those on all post-antennular exopods. Müller & Walossek (1987: 35) observed that the structure of the setose exopod of the antenna of *Agnostus* resembles the swimming limbs of crustacean larvae. Accordingly a locomotory function might be ascribed to the setose antennule of juvenile *Naraoia*, which assumes a predominantly sensorial function later in ontogeny.

Ecological disparity

Inferences about life habits can be made from the anatomical differences between *Naraoia* and *Misszhouia*. This morphological disparity is consistent with differences in the manner of preservation of the two taxa. On both counts (morphology and preservational style), *Naraoia spinosa* may be identified as a deposit feeder.

The two naraoiids in the Chengjiang fauna possess markedly different digestive systems. *Misszhouia longicaudata* shows a relatively simple gut, with small, segmentally set caeca that ramify close to the gut. The gut is narrow, not wider than the sternites (Figs 2a, 13c, 18a), about 7–8% of the exoskeletal width. In contrast, the gut in *Naraoia spinosa* is equipped with a complex system of ramifying diverticula that fills much of the cephalon, leaving only a narrow margin free of the diverticula. The gut itself is 14–18% of the exoskeletal width, twice as wide as in *M. longicaudata*. The thickness of the mudfill indicates that prior to compaction, the gut in both species was circular in section. The gut in *N. spinosa*, when filled, thus held a volume four to five times that of *M. longicaudata*, and even more when the caeca are included.

A very large, complex system of gut diverticula and a gut with great holding capacity indicate that the diet
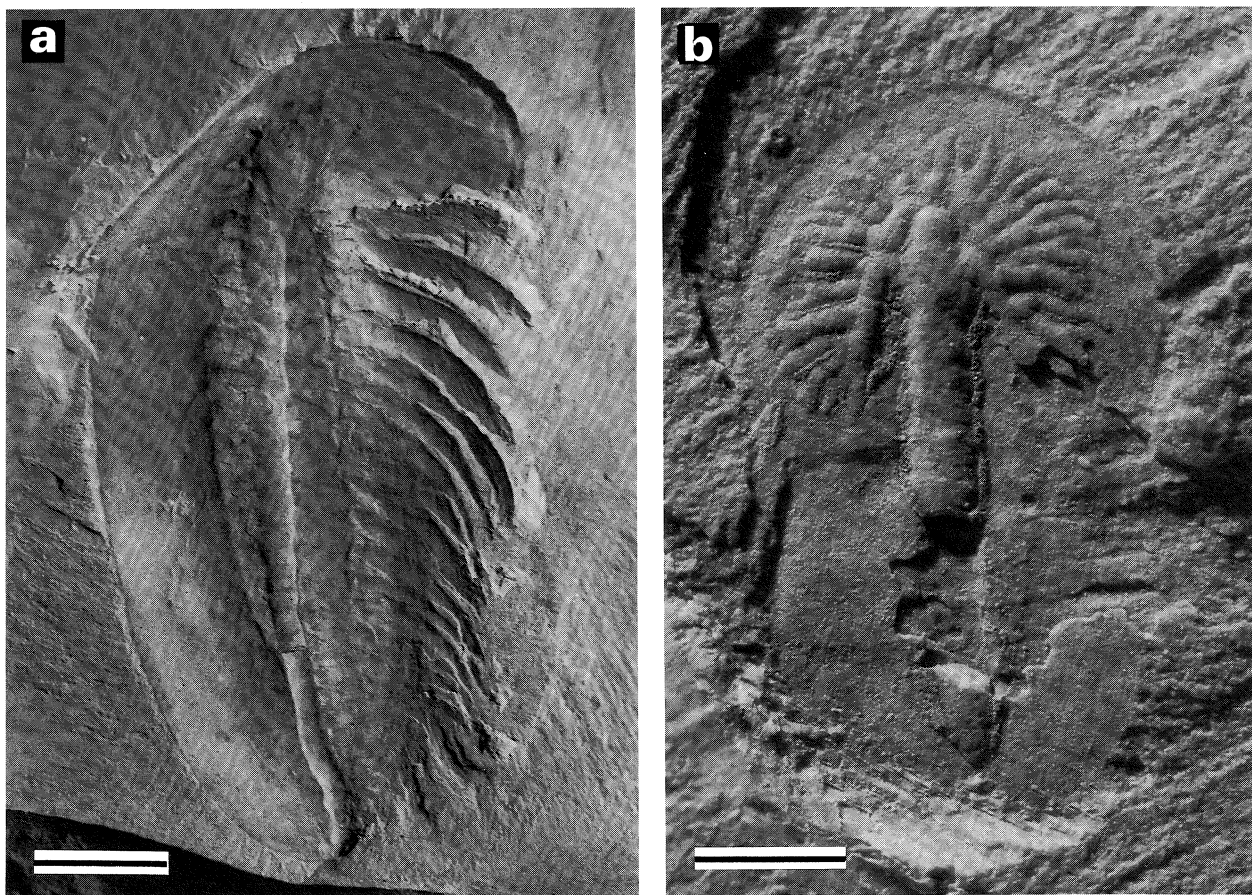
Fig. 18. a, *Misszhouia longicaudata* (Zhang & Hou, 1985). ELRC 11686a, specimen in dorsolateral view. Light from W. Scale bar 5 mm; b, *Naraoia spinosa* Zhang & Hou, 1985. ELRC 12131a, from locality MN4 (see Fig. 19 for camera lucida drawing). Small individual showing mud-filled gut and diverticula. Scale bar 1 mm.

of *Naraoia spinosa* was low in nutrition. The majority of *N. spinosa* specimens are preserved with the digestive system filled with sediment indistinguishable from the surrounding matrix. The frequency of mudfill of the gut and mud-packed diverticula in the cephalon provide strong evidence that sediment ingestion was the typical feeding mode of *N. spinosa*, and we conclude that it was a deposit feeder.

A deposit feeding mode of life for *Naraoia spinosa* agrees well with other aspects of its morphology. Its antennules are directed laterally, not anteriorly where they would both hinder the cephalon ploughing or digging into the mud, and risk damage during such activity. Another feature apparently adapted for this life style is the shape of the exopods. These do not have slender distal lobes and huge fans of setae comparable to those in *Misszhouia longicaudata*. Instead, at least the anterior trunk limbs have exopods with large, paddle-shaped distal lobes and short lamellar setae on the shaft (Figs 16d,e, 17), a morphology well suited for digging into soft sediment.

The mode of life outlined here for *Naraoia spinosa* is also suggested by the attitudes in which the specimens

are preserved. The cephalon is usually preserved at an angle to the bedding plane, and is quite commonly directed nearly vertical into the sediment (Fig. 20a). Also the trunk is usully preserved at an angle to the plane of bedding (Fig. 20b), and the angle between the head and trunk has a mode between 80 and 100 degrees, with some specimens folded through 120–130 degrees (Fig. 21). It is not known whether these attitudes are the result of struggle during entombment or if individuals are preserved *in situ*.

Misszhouia longicaudata lacks the features indicating deposit feeding in *Naraoia spinosa*. The anteriorly directed antennules would have hindered ploughing in the sediment, and the delicate exopods would be unsuitable for digging. The large, imbricating exopod fans could conceivably be difficult to free from mud, and whatever their function (respiration, swimming, or other), that function would hardly have benefitted from a mud cover. In *M. longicaudata*, the gut is only rarely mud-filled, and we interpret these instances as the result of mud ingestion during death struggle, parallelled in many other animals in the Chengjiang fauna. Specimens of *M. longicaudata* display less declination of the head and
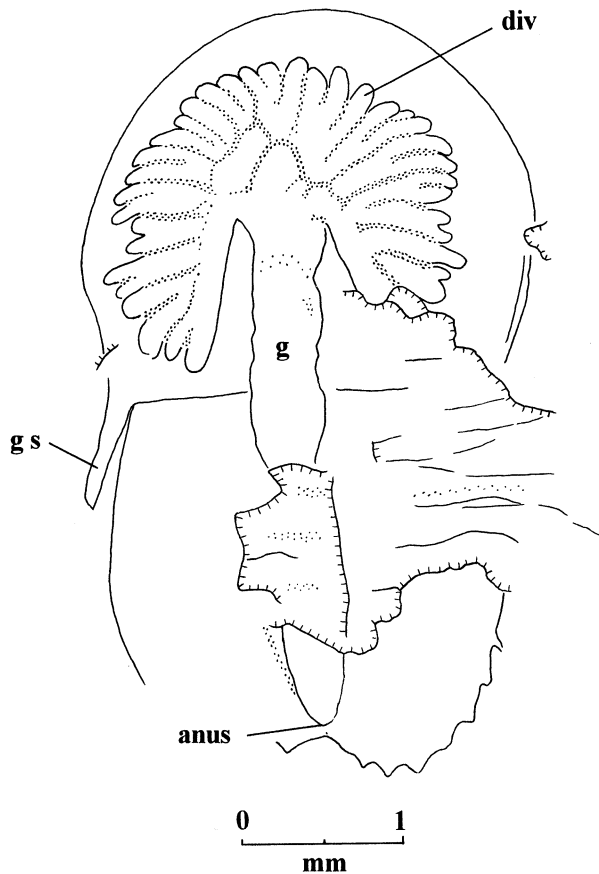
Fig. 19. *Naraoia spinosa* Zhang & Hou, 1985. Camera lucida drawing of ELRC 12131a (see Fig. 18b). See Appendix for abbreviations.

trunk shields into the sediment than is the case for *Naraoia spinosa* (Figs 20, 21).

The large, spinose endite on the basis in *Misszhouia* resembles the condition in trilobites and other arthropods that have been interpreted as predators and/or scavengers, and we regard these habits as probable for *M. longicaudata*. Whittington (1977) interpreted *Naraoia compacta* as a predator and scavenger based primarily on the size of the gnathobase on the basis and the spinose endite on the first podomere of the endopod. He disputed the possibility that deposit feeding was a major part of its habits (1977: 438). As discussed above, we cannot uphold this claim with respect to the closely allied *N. spinosa*.

Naraoia compacta and *N. spinosa* share most features interpreted here to indicate deposit feeding. Such features present in both species are the extensive gut diverticula in the cephalon, the high holding capacity of the gut, and the laterally directed antennules. As in *N. spinosa*, the gut in *N. compacta* is often preserved filled with mud. Whittington (1977: figs 66, 67) documented specimens of *Naraoia compacta* with the head and trunk shield flexed at right angles. As detailed above, flexure
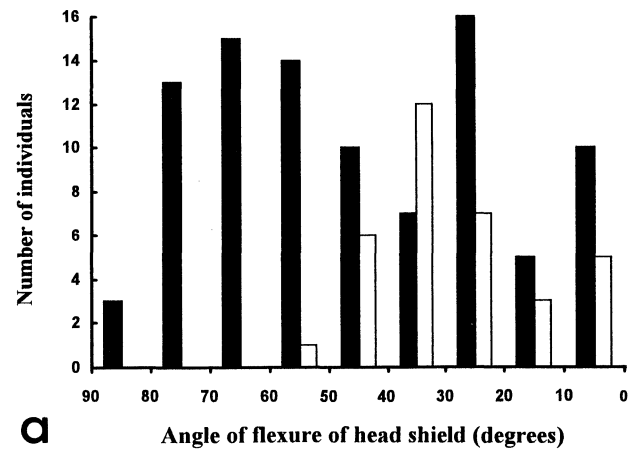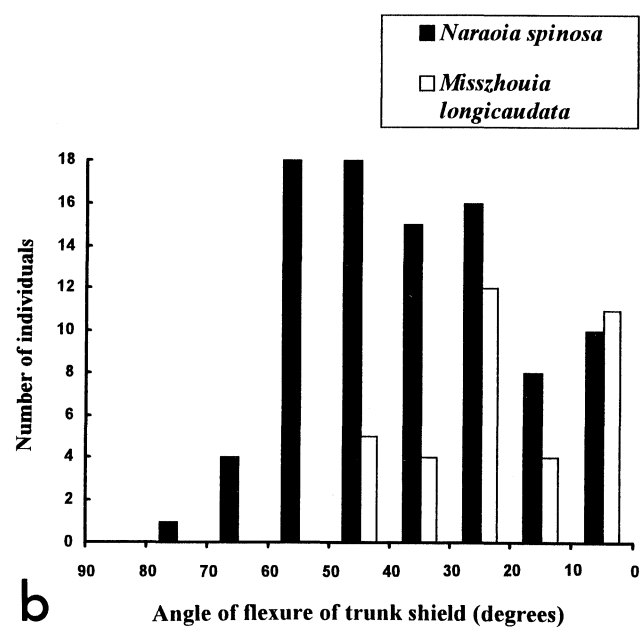
Fig. 20. Histogram depicting angle of flexure of head shield (a) and trunk shield (b), measured from horizontal bed surface, for *Naraoia spinosa* (N=93 and 90 for Figs a and b, respectively) and *Misszhouia longicaudata* (N=34 and 36 for Figs a and b, respectively) from the Chengjiang fauna.
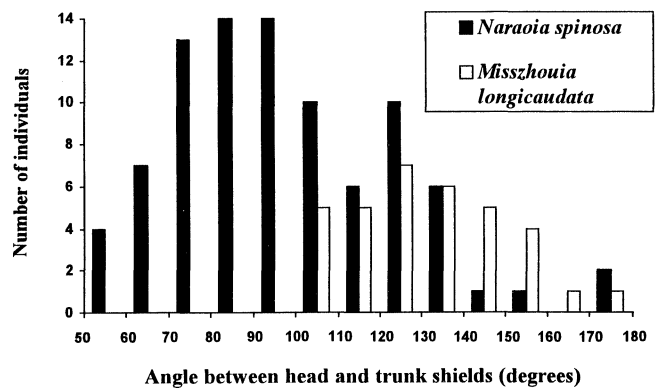

Fig. 21. Histogram depicting angle between head and trunk shields for *Naraoia spinosa* (N=88) and *Misszhouia longicaudata* (N=34).
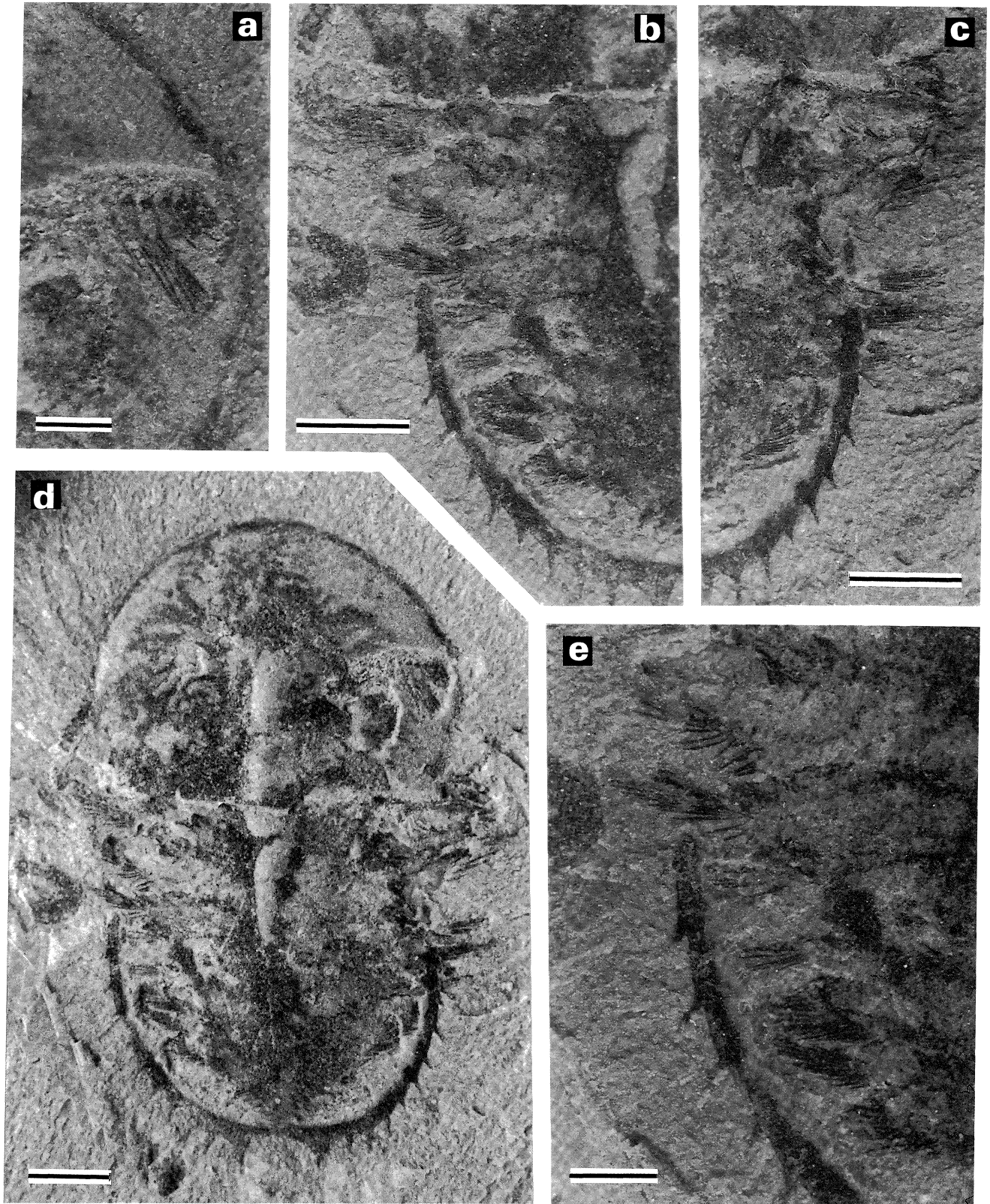
Fig. 22. *Naraoia spinosa* Zhang & Hou, 1985. Juvenile specimen ELRC 10983, from locality MN5 (see Fig. 23 for camera lucida drawing). All dorsal views, high light from S except Fig. d, high light from W. a, detail of right antennule. Note short setae on anterior edge of antennomeres, long paired setae on posterior edge of antennomeres. Scale bar 0.5 mm; b, left side of specimen. Scale bar 1 mm; c, right side of specimen. Scale bar 1 mm; d, complete specimen. Scale bar 2 mm; e, detail of left side of trunk. Scale bar 0.5 mm.

at the head/trunk juncture is also the common preservational mode for *N. spinosa*. The only significant anatomical difference between the two species of *Naraoia* appears to be the limb structure in *N. compacta*, characterised by more slender distal lobes of the exopods (but stouter than in *Misszhouia longicaudata*). However, it should be noted that the limbs in *N. spinosa* are still largely unstudied, and that the complete shape of the exopod fan and the presence of endites in that species are unknown. The failure of specimens of *N. spinosa* to part along a large exopodal surface (as is the case for *Misszhouia*) indicates that the exopod fan of *N. spinosa* is of smaller area than in *N. compacta*.

Whittington's (1977) interpretation of feeding habits of *Naraoia compacta* is based mainly on the large gnathobases. The large, undivided posterior shield was regarded as another adaptation for capturing soft prey (by providing an expansive area for muscle attachments), but this feature may be typical for a broader group of naraoiids (Fig. 15a). We consider that several features indicate deposit feeding for *N. compacta*, and that the only feature possibly indicating predation—the spinose

endites—is unknown in *N. spinosa*. We might, however, infer its presence also in that species, given the broader distribution of this state in basal trilobites (Ramsköld & Edgecombe, 1996). A detailed investigation of feeding habits of naraoiids is beyond the scope of this contribution, but the discussion presented here at least indicates that the mode of life of naraoiids is more varied than previously thought.

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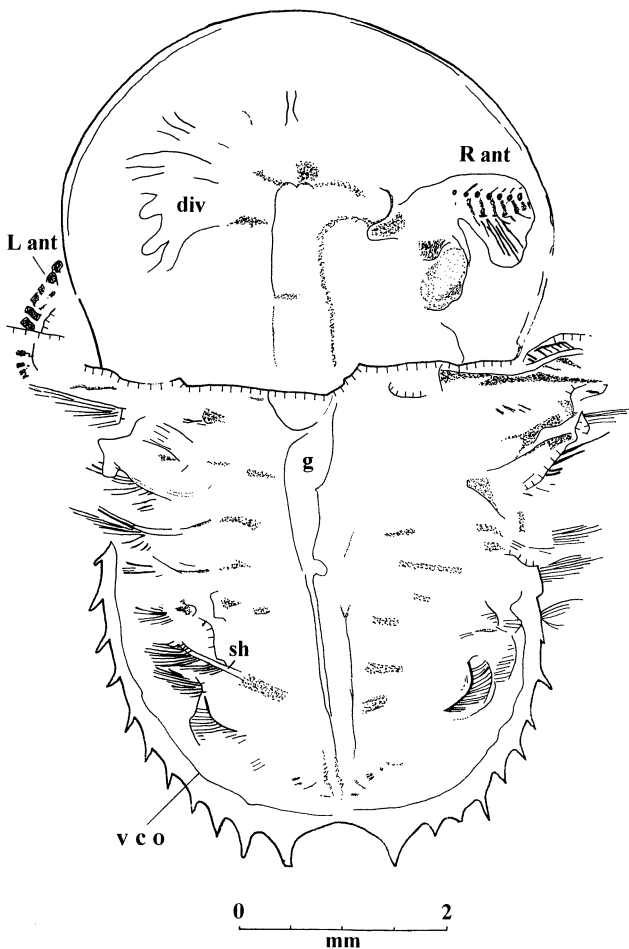
Fig. 23. *Naraoia spinosa* Zhang & Hou, 1985. Camera lucida drawing of ELRC 10983 (see Fig. 22). See Appendix for abbreviations.

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Appendix 1

Abbreviations used in Figures

a e	anterior edge of trunk shield
a m	arthrodial membrane
ant	antennule
ba	basis
bar	transverse tendinous bar
br	bristles on distal lobe of exopod
C2–C4	cephalic limbs 2–4
ca	caecum
div	anterior gut diverticulum
d l	distal lobe of exopod
es	esophagus
en	endopod
ex	exopod
fae	faeces outside gut
f o	frontal organ
g	gut
gl	digestive gland
g s	genal spine
h	ovate lobe of hypostomal complex
h s	head shield
L	left
l s	lamellar setae of exopod
m f o	median frontal organ
mo	mouth
p ar	proximal articulation of basis
p e	posterior edge of head shield
R	right
sh	shaft of exopod
T1	first (anteriormost) trunk limb
v c	ventral cuticle
v c i	inner margin of ventral cuticle
v c o	outer margin of ventral cuticle