# *Cindarella* and the arachnate clade Xandarellida (Arthropoda, Early Cambrian) from China

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ABSTRACT: *Cindarella eucalla* Chen *et al.* from the Early Cambrian Chengjiang fauna is the closest relative of *Xandarella spectaculum* Hou *et al.* *Cindarella* and *Xandarella* are united as Xandarellida, a further component of Cambrian arachnate diversity. Diagnostic of Xandarellida are ventral eyes, a posterior extension of the head shield that covers anterior trunk segments, and multiple somites per tergite in the rear part of the trunk. Somites and tergites are decoupled throughout the trunk in *Cindarella*. The bilobate structure of the exopod in xandarellids is widespread throughout the Arachnata.

KEY WORDS: Arachnata; Early Cambrian; Xandarellida; Chengjiang fauna.
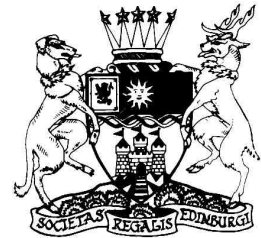
A characteristic feature of Cambrian arthropod assemblages is the diversity of Arachnata (see discussion below for a phylogenetic definition). Species richness within this clade (Arachnomorpha of Størmer 1944; Bergström 1992; Wills *et al.* 1995) is dominated by Trilobita and Chelicerata, the latter including all post-Palaeozoic arachnates. But Early Palaeozoic faunas, notably Cambrian Lagerstätten, reveal additional extinct taxa that extend the morphological and taxonomic range of Arachnata. These include a variety of taxa grouped as trilobitomorphs (Størmer 1959; Bergström 1992). The objective of much current research is the placement of these taxa—such as helmetiids, trilobites, tegopeltids, naraoiids, aglaspidids, cheloniellids, limulavids, and emeraldellids—on the stem lineage of Chelicerata.

We here describe a species from the Early Cambrian Chengjiang fauna which has revealed an additional component of early arachnate diversity, the clade Xandarellida (Chen *et al.*, 1996)*. Both known members, *Xandarella* Hou *et al.*, 1991 and *Cindarella* Chen, Ramsköld, Edgecombe & Zhou *in* Chen *et al.*, 1996, have been found at the Maotian Hill (Maotian'shan) locality in Chengjiang county, Yunnan Province, China. The Chengjiang fauna occurs in the Yu'anshan Member of the Heilinpu (previously Qiongzhusi) Formation (Luo *et al.* 1994), of the *Eoredlichia/Wutingaspis* Zone. Recent correlations have shifted the position of this zone from the upper Atdabanian to the slightly younger lower Botoman (Landing 1994; Zhuravlev 1995). One of the authors (Chen J.-y.) regards this revision as inadequately substantiated, a majority of evidence favouring an Atdabanian age assignment.

Since the discovery of the Chengjiang fauna in 1984 (Zhang & Hou 1985), it has become known as the most species-rich and best preserved Early Cambrian Lagerstätte (Hou *et al.* 1991). It therefore has a unique importance for the understanding of life during the latter phases of the Early Cambrian explosive radiation of metazoans. At present close to one hundred species are known from the fauna, virtually all of

them having their unmineralised tissues preserved. Selected major discoveries include the *Microdictyon* animal (Chen *et al.* 1989), the recognition of the lobopod clade (Ramsköld & Hou 1991), the identification of anomalocaridids as an arthropod clade (Chen *et al.* 1994), and the earliest chordates (Chen *et al.* 1995a; Shu *et al.* 1996).

For details of the localities see Chen *et al.* (1995c). Detailed maps for the Maotian'shan sites are found in Sun & Zhan (1991). All specimens illustrated in this work are housed in the Early Life Research Centre, Nanjing Institute of Geology and Palaeontology, Academia Sinica (prefixed ELRC).

Descriptions in this paper apply the term *antennule* to the flagelliform first appendage of many fossil arachnates (including xandarellids). This recognises its homology with the first antenna (antennule or antennula) of Crustacea (Müller & Walossek 1986). The proximal section of post-antennular limbs is described as the *basis*, to recognise homology with crustaceans (Walossek 1995; Ramsköld & Edgecombe 1996).

1. Systematic palaeontology

Arthropoda Siebold & Stannius, 1845

Arachnata Lauterbach, 1973

Discussion. Following Chen *et al.* (1997), we use the taxonomic name Arachnata with an explicit phylogenetic definition (de Quieroz & Gauthier 1990, 1994). We define Arachnata as the most inclusive clade including Chelicerata but not Crustacea. Arachnata as proposed by Lauterbach was a node-based taxon in the terminology of de Quieroz & Gauthier (i.e. a clade stemming from the most recent common ancestor of Trilobita and Chelicerata). In contrast, we adopt a stem-based approach in order to also accommodate extinct taxa branching from the stem lineage of Arachnata *sensu* Lauterbach (1980). With this definition, Arachnata will remain a stable, monophyletic taxon regardless of new discoveries of stem group taxa.

Xandarellida Chen, Ramsköld, Edgecombe & Zhou *in* Chen *et al.*, 1996

Diagnosis. Arachnates with lateral eye originating ventrally; cephalon bearing flagelliform antennule and four or more pairs of biramous appendages of same structure as trunk appendages; head shield extended posteriorly to cover anterior
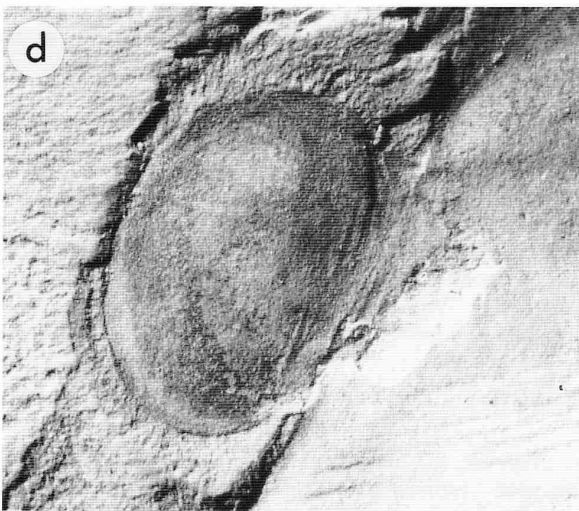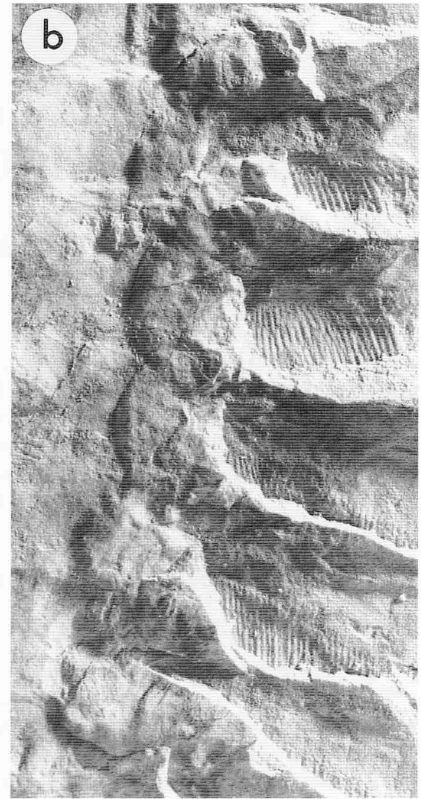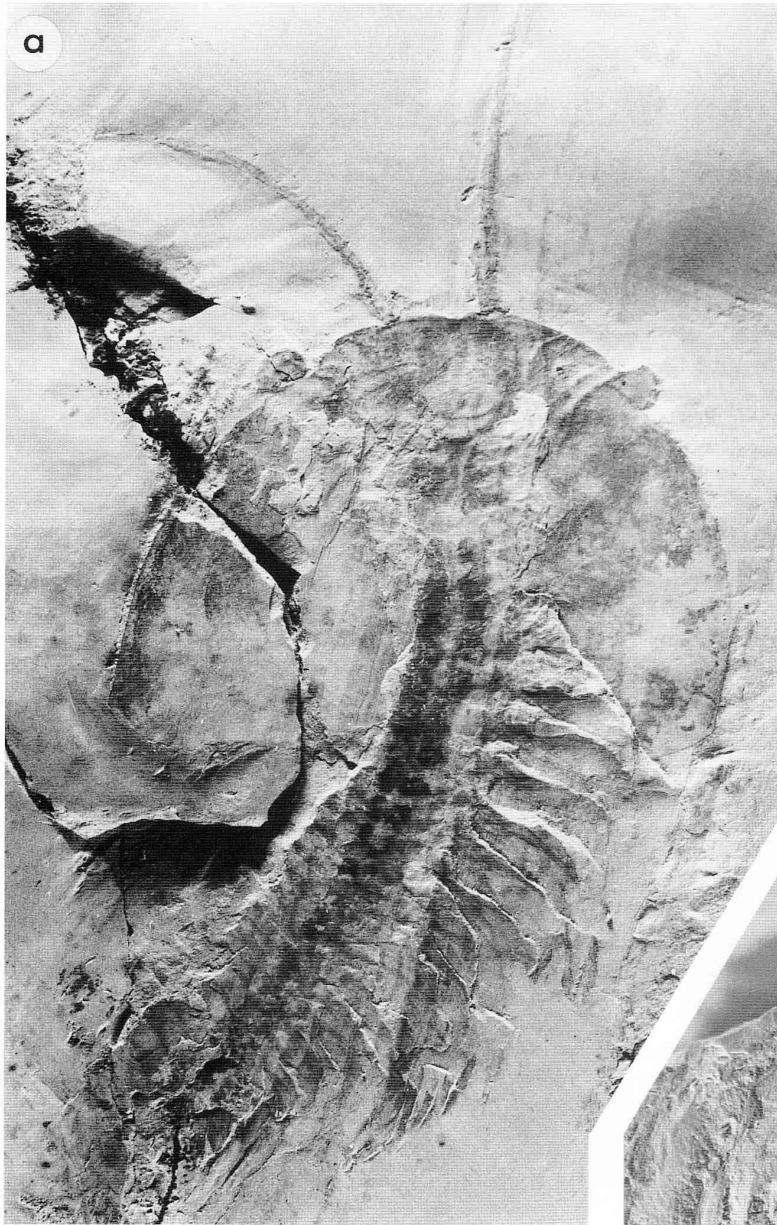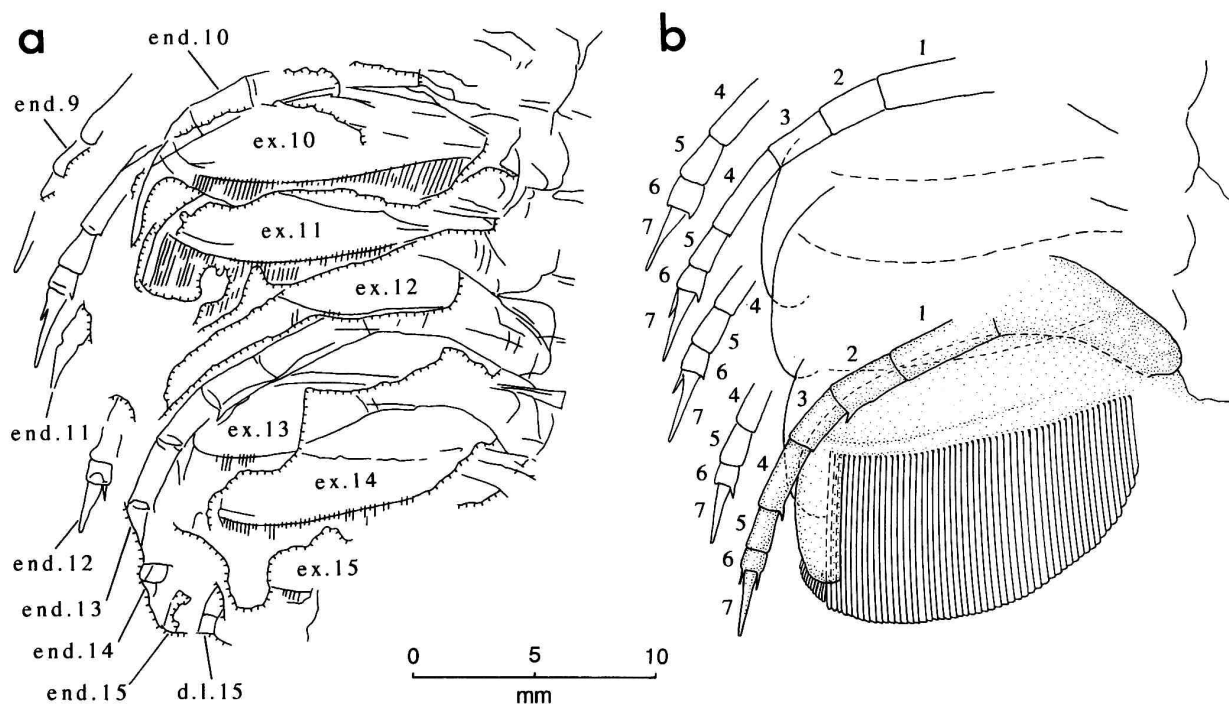
Figure 2 *Cindarella eucalla* Chen *et al.* Holotype ELRC 1850lb from MN5. (a) Camera lucida drawing of part of left side, dorsal view (see Fig. 1c). The area corresponds to the central part of that shown in Figure 4. Proximal lobe of exopod (ex.), endopod (en.), and distal lobe of exopod (d.l.) indicated. (b) Composite drawing of area shown in (a) but in ventral view, combining preserved limb parts from part and counterpart. Missing portions of some podomeres and outlines of distal lobes reconstructed. Fringe of setae on limb 13 largely reconstructed. Length of setae is minimum length, based on preserved length in exopod 11 (see Fig. 4). Limb 13 shown with some relief, presence of weak tubercles on basis probable but not certain. Dashed line indicates known minimum posterior extent of basis, i.e., portion behind this line is overlapped by the succeeding basis. Dashed outline of most distal setae indicate that they are dorsally overlapping the distal lobe. Length of setae on distal lobe is minimum length, based on limbs 12 and 13.

trunk somites, with small median area of attachment; hypostome shield-shaped, natant, situated well behind anterior margin of cephalon; trunk with anterior tergites covering one appendage pair, at least posterior four covering an increasing number of appendage pairs; posterior trunk tergite(s) bearing median spine; terminal tergite composed of one pleural lappet fused to posteromedian element.

Discussion. Many of the distinctive diagnostic characters of *Xandarella* Hou *et al.*, 1991 are observed in *Cindarella* Chen, Ramsköld, Edgecombe & Zhou *in* Chen *et al.*, 1996, and the two are accordingly grouped as a clade, Xandarellida. We use an apomorphy-based definition (de Quieroz & Gauthier 1990) of Xandarellida. When the sister group of Xandarellida is identified, the taxon can be defined using a stem-based definition.

Because appendage structure has not been described for *Xandarella* (except for the antennules), the systematic significance of the many distinctive states of the appendages of *Cindarella* are uncertain. We have thus not employed aspects of endopod, exopod, and limb base structure in the diagnoses of Xandarellida or *Cindarella*. It is, however, probable that many, if not most, aspects of limb design are shared between the two genera. In addition to the synapomorphies listed above, potential synapomorphies of Xandarellida (presently confirmed for *Cindarella*) include the following: a long, slender

terminal podomere on the post-antennular head limbs and trunk limbs, with a pointed tip; endopods slender, most podomeres lack endites, and their spinosity is limited to a short ventral spine at the distal margin; and, a leaf-shaped inner lobe of the exopod.

Structure of the exopod of *Cindarella* demonstrates membership of the Xandarellida in Arachnata. A basal synapomorphy of the clade (Bergström 1992), the exopod 'fan' composed of imbricating lamellar setae that articulate to the shaft or proximal lobe of the exopod, is developed in *Cindarella* similarly to trilobites and other taxa traditionally grouped as Trilobitomorpha. On the basis of exoskeletal similarities, Hou *et al.* (1991) particularly compared *Xandarella* to aglaspidids and to 'merostome' chelicerates (xiphosurids and eurypterids), although no precise phylogenetic hypotheses were indicated. The development of proximal and distal lobes of the exopod is a conspicuous similarity with a group including trilobites, naraoiids (see Ramsköld & Edgecombe 1996), and *Emeraldella* Walcott, 1912 (see Bruton & Whittington 1983, figs 45 & 47, for exopod lobes very similar to those of *Cindarella*). Homologues of the proximal and distal lobes cannot be identified with a reasonable measure of confidence in chelicerates (e.g. in the opisthosomal limbs of xiphosurids). It would appear, however, that the bilobate exopod defines a very inclusive group of arachnates because it is observed in

Figure 1 *Cindarella eucalla* Chen *et al.* (a)–(c) Holotype ELRC 18501 from MN5. (a) ELRC 18501a, ventral view, × 1·7, light from NNW. (b) ELRC 18501a, ventral view, detail of proximal parts of trunk limbs, × 5·2, light from ENE. (c) ELRC 1850lb, limbs on left side of trunk, dorsal view, × 4·9, light from WSW. Note that relief appears reversed with this lighting (see Fig. 2a for a camera lucida drawing). (d) Paratype ELRC 18502 from MQ1, dorsal view of left eye, × 9·2, light from NNW (see Fig. 8 for complete specimen).
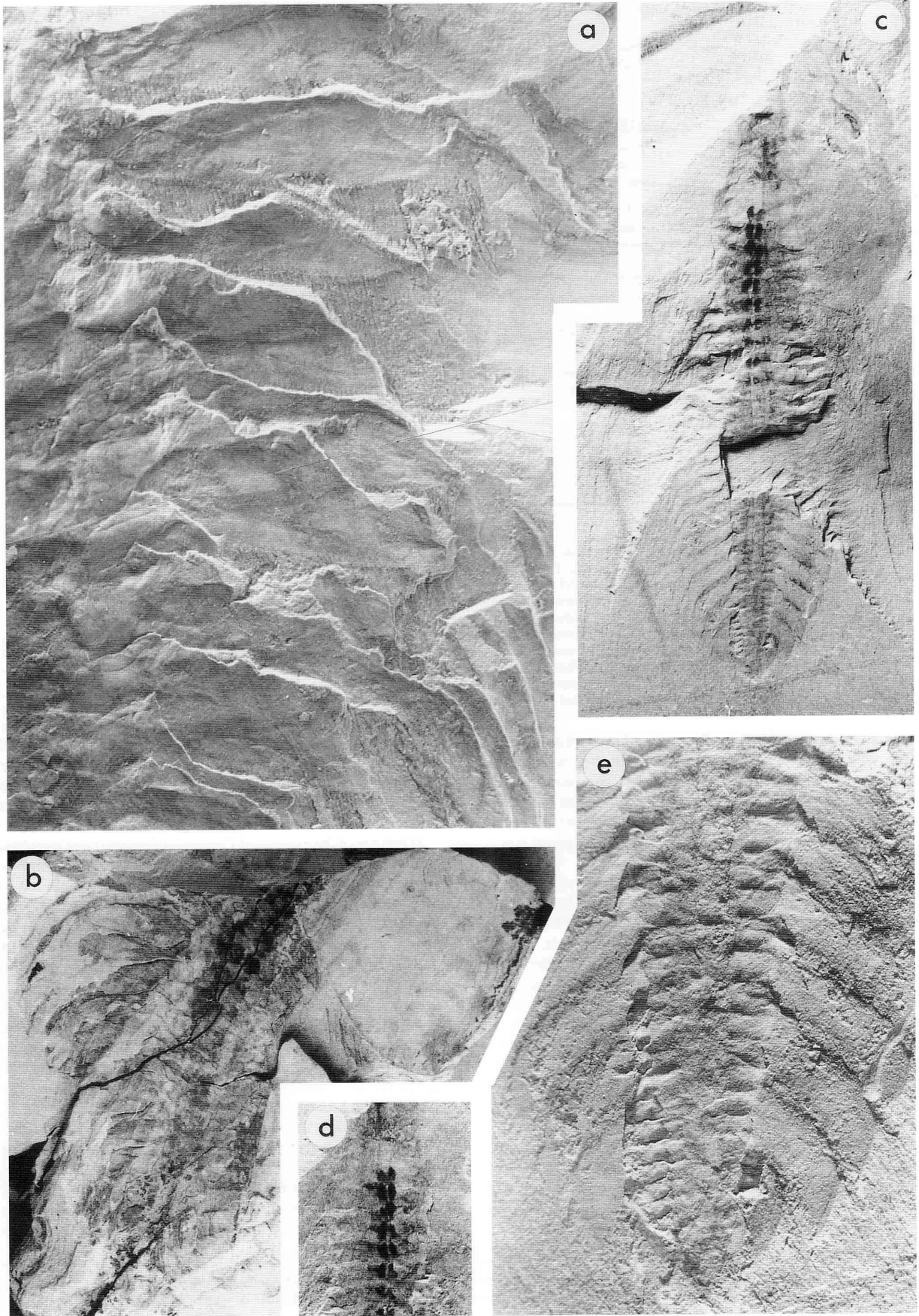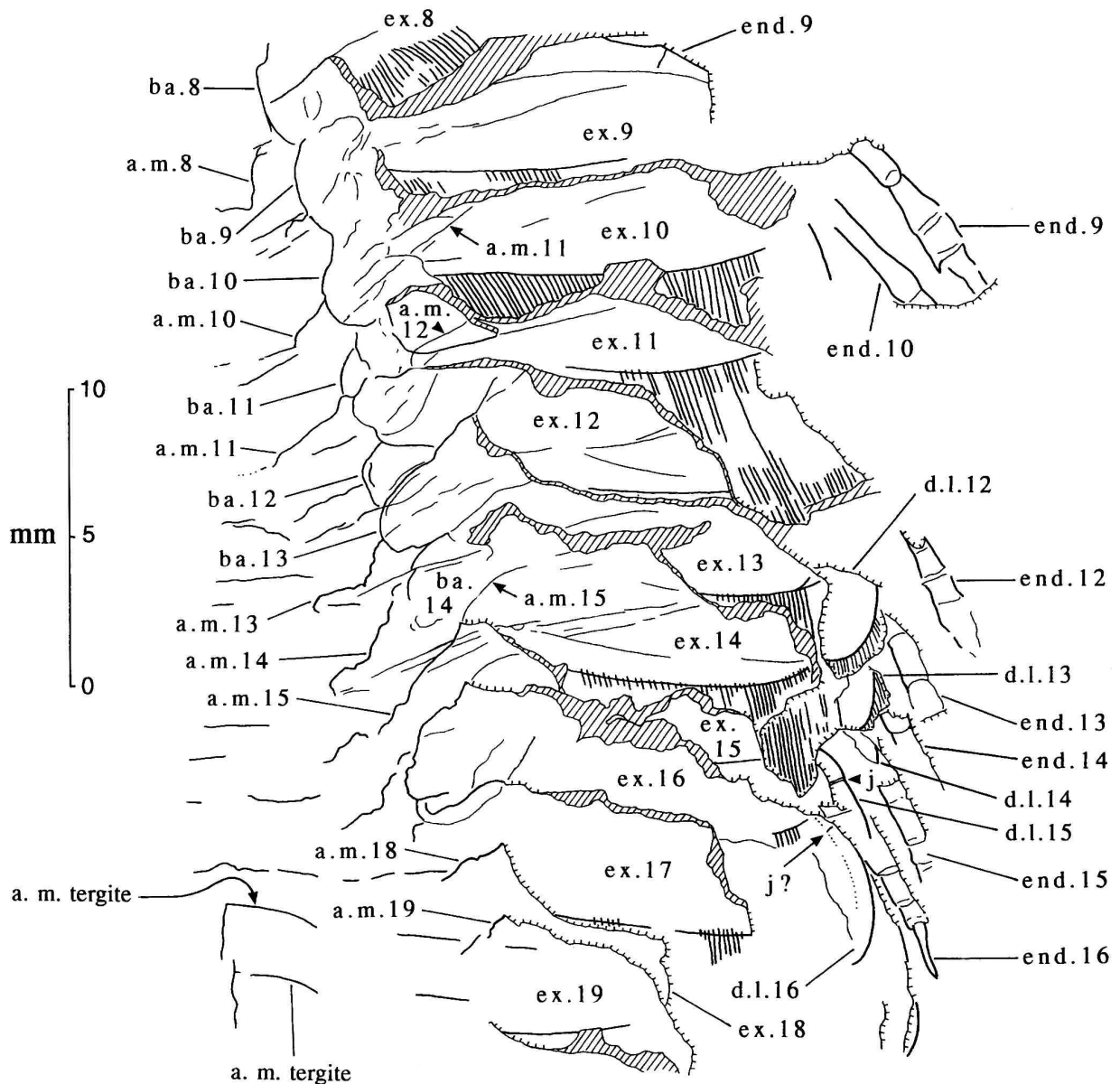
Figure 4 *Cindarella eucalla* Chen *et al.* Holotype ELRC 18501a from MN5. Camera lucida drawing of part of right side, ventral view (see Fig. 3a). Basis (ba.), joint between proximal lobe and distal lobe of exopod (j), anterior margin (a.m.) of limbs and possible tergites indicated; other labels as in Figure 2. Each line that is labelled anterior margin (a.m.) adaxial to the basis is the anterior margin of the articulating membrane attaching to the basis. The irregular course of this margin may be a preservational artefact, or may at least partly indicate presence of weak annulation. The undulating line connecting the adaxial edge of the limb bases is mainly composed of overlapping bases, but may anteriorly also include portions of the sediment scarp formed at the inner edge of sediment penetration between the limbs and the pleural membrane above. The joint between the exopod shaft and the distal lobe in limb 15 is clear in both part and counterpart and appears to be a real feature. The tergite margins on the lower left side are situated across the sagittal line relative to the limb-bearing area shown.

Sanctacaris, a taxon that does not appear to be particularly closely related to Trilobita or Xandarellida. The distal lobe of the trunk expods is identified in *Sanctacaris* as a broad, posterolaterally extended flap bearing a fringe of bristles (Briggs & Collins 1988, pl. 72, fig. 2). It is clearly differentiated from the main (proximal) lobe of the exopod that bears the lamellar setae along its posterior edge (Briggs & Collins 1988, pl. 73, figs 3, 4). The differentiation of the setae and bristles

Figure 3 *Cindarella eucalla* Chen *et al.* (a)–(b) Holotype ELRC 18501 from MN5. (a) ELRC 18501a, ventral view of appendages on left side of trunk, × 5·2, light from NNW (see Fig. 4 for a camera lucida drawing). (b) ELRC 18501b, dorsal view, × 1·7, high light (see Fig. 1c for detail). (c)–(e) ELRC 18505 from MQ1, a nearly complete individual. (c) 18505a, dorsal view, × 1·8, light from N (see Fig. 5a for camera lucida drawing of head and exposed anterior part of trunk). (d) 18505b, gut caeca in anterior part of trunk, × 1·9. (e) 18505a, detail of posterior part of trunk, dorsal view, × 5·7, low light from N (see Fig. 5b for a camera lucida drawing).
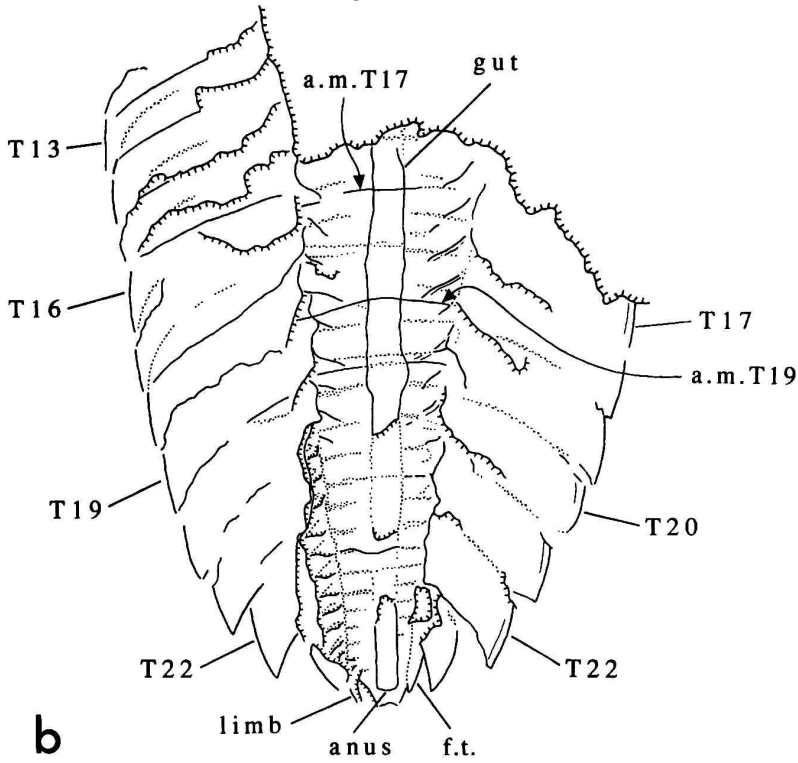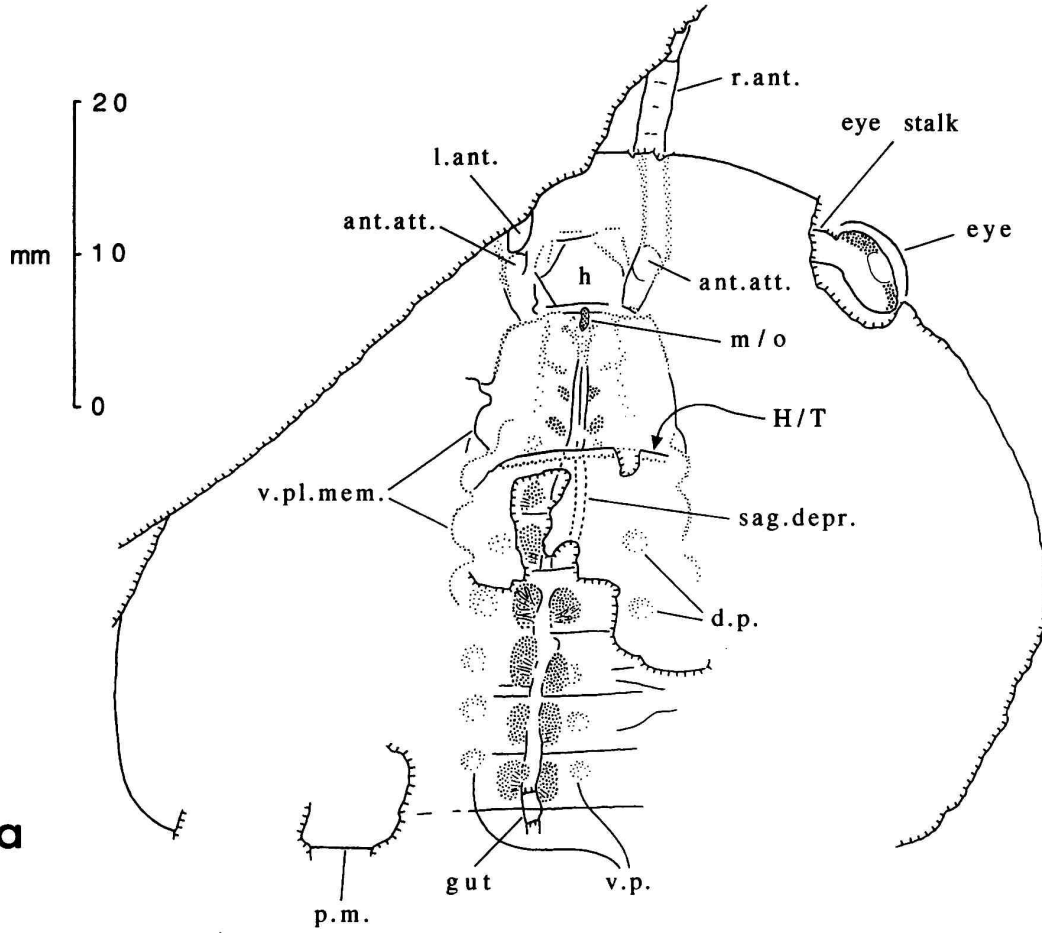
Tergite number	Number of segments covered by tergite	Segments
16	1.5	
17	1.55	
18	1.7	
19	1.8	
20	2.0	
21	2.3	
22	2.65	
23	3.1	

and relative configurations of the proximal and distal lobes permit homology with the bilobate exopod of other Palaeozoic arachnates. The implication of this for the placement of Xandarellida is that the bilobate exopod may only be informative for recognising the group as arachnatan, rather than uniquely allying it with any particular subgroup.

The ventral eye position in Xandarellida has consequences for Bergström's (1992) theory that eyes borne on the dorsal surface of the exoskeleton are an arachnate ('arachnomorph' *sensu* Bergström) synapomorphy. Bergström contrasted the arachnate state with an anteroventral or frontal eye position deemed diagnostic of a broad crustacean group. Assuming that this character is cladistically reliable, the presence of anteroventral eyes in an arachnate taxon (Xandarellida) would imply that this condition is not a shared derived character of crustaceans but, rather, is a general state for Schizoramia or Euarthropoda, as had been speculated by Lauterbach (1988). Further it would imply that the xandarellid clade diverged from other arachnates (including trilobites and chelicerates) before the incorporation of the eyes into the dorsal exoskeleton. It might be thought less plausible that the trilobite–chelicerate state (eyes incorporated into the dorsal cuticular surface) would undergo a reversal to stalked anteroventral eyes in *Cindarella*. The test for these alternative hypotheses concerning eye position will be congruence with a broader range of morphological characters. There is evidence that eye position exhibits homoplasy within Arachnata (e.g. ventral eyes in helmetiids and tegopeltids versus dorsal eyes in the closely allied Trilobita), and the character may not be reliable for diagnosing fundamental arthropod taxa.

The ventral eye of *Cindarella* provokes a new interpretation of the eye in *Xandarella*. The globular eye of *X. spectaculum* is situated in a circular hole in the exoskeleton that extends to the lateral margin of the head shield as a narrow slit. Although the eye of *Xandarella* was capable of dorsal vision it differs fundamentally from the dorsal eyes of trilobites, and was evidently produced by development of the hole to accommodate an eye that originated ventrally (as in *Cindarella*).

It is important to distinguish between two different types of multisegmental posterior tagma in Arachnata. We stress that the term *pygidium* is inappropriately applied to xandarellids. The thorax/pygidium boundary corresponds to an important shift in development. In trilobites, naraoiids (e.g. *Liwia*, *Soomaspis* and *Tariccoia*), and helmetiids the thoracic tergites each correspond to a single somite, whereas the pygidium marks the point at which tergites cease being released anteriorly (from the transitory pygidium) in ontogeny. We regard this style of thoracic/pygidial tagmosis as a synapomorphy for Naraoiidae, Helmetiidae, Tegopeltidae and Trilobita. Use of the term 'pygidium' should be restricted to this type of tagma. The second type of a posterior multisegmented tagma

occurs in taxa showing a decoupling of tergite divisions from the underlying segmentation. Such decoupling is described below for xandarellids, and may be more widespread. In these forms, the segmentation, as expressed by limbs and tendinous bars, describes a progressive decrease in segment lengths posteriorly, whereas the tergites are either all equally long (as in *Cindarella*) or increase in length posterorly (as in *Xandarella*). The result is that several posterior tergites each cover more than one segment, with a lack of correspondence between tergite boundaries and segment boundaries. Although the posteriormost tergite in taxa such as *Xandarella* is superficially similar to a pygidium, the developmental mode is fundamentally different. As well, trunk tergites show considerable overlap, rather than articulating edge-to-edge as in trilobites. Xandarellids more closely resemble *Emeraldella* (Bruton & Whittington 1983, figs 23, 55) and *Sidneyia* (Bruton 1981, figs 24, 73) than trilobites in this respect, although the similarity is probably plesiomorphic. A more precise positioning of the Xandarellida within the Arachnata is premature, pending a detailed phylogenetic analysis by the authors.

Cindarella Chen, Ramsköld, Edgecombe & Zhou *in* Chen *et al.*, 1996

Etymology. For its phonetic similarity to *Xandarella*.

Type species. *Cindarella eucalla* Chen, Ramsköld, Edgecombe & Zhou *in* Chen *et al.*, 1996

Diagnosis. As for *Cindarella eucalla*. *Cindarella* is the most inclusive clade including *Cindarella eucalla* but not *Xandarella spectaculum*.

Discussion. *Cindarella* is distinguished from *Xandarella* by the following criteria: a longer cephalic shield, with overlap of the anterior six trunk tergites by its posterior, carapace-like extension; a rounded (versus spinose) genal angle; the eye situated anteroventrally, rather than within a round hole that perforates the dorsal exoskeleton; there are at least fifteen (versus four), posterior multisegmental trunk tergites, and they are not lengthened (exsag.) relative to the anterior tergites; and, median spines extend from the posterior margins of the last three trunk tergites (versus a median spine on the terminal tergite alone in *Xandarella*).

Cindarella eucalla Chen, Ramsköld, Edgecombe & Zhou *in* Chen *et al.*, 1996
(Figs 1–15)
Naraoia sp.—Chen *et al.* 1992, p. 281.
Naraoia-like specimen—Gore, 1993, p. 132–33.
Cindarella eucalla Chen, Ramsköld, Edgecombe & Zhou gen. et. sp. nov.—Chen *et al.*, 1996.

Etymology. Latin *eucalla*, beautiful.

Holotype. Complete specimen, part and counterpart, ELRC 18501a–b (Figs 1a–c, 2, 3a, b, 4), from locality MN5, north slope of Maotian'shan, Chengjiang.

Figure 5 *Cindarella eucalla* Chen *et al.* (a)–(c) ELRC 18505 from MQ1, a nearly complete individual, dorsal view. (a) Camera lucida drawing of the head region. The trunk begins at the H/T-line; the anterior six trunk segments are indicated by paired gut caeca. Scale bar applies to (a)–(c). (b) Camera lucida drawing of the posterior region (see Fig. 3e). Tergites are exposed in the pleural areas; the sagittal trunk portion exposes more ventral structures including tendinous bars and proximal limb parts. (c) Diagrammatic representation of the relationship between tergites and segments (as indicated by limbs and tendinous bars) in the posterior region, same scale as (a) and (b). The posterior edge of each tergite is shown as a transverse line. Tergites are shown with similar length (sag.) throughout, based on evidence from this and other specimens. Tergite/segment relationships posterior to tergite 23 are not clear. Features indicated in (a) and (b) are the right eye and eye stalk, gut and anus, a posterior limb, right and left antennules (r.ant., l.ant), antennule attachments (ant.att.), hypostome area (h), mouth and/or esophagus (m/o), head/trunk junction (H/T), the adaxial limit of the ventral pleural membrane (v.pl.mem.), a sagittal depression (sag.depr.) indicating a structure overlying the gut, paired dorsal depressions (d.p.) of unknown significance, paired ventrally situated depressions (v.p.) related to limb attachments (possibly attachment site of dorsoventral muscles), posterior margin of head shield (p.m.), tergites 13 to 22 (T13–T22), the anterior margin of T17 (a.m. T17) and T19 (a.m. T19), and a fused anterior pleural rib (f.t.) on the bicomposite terminal tergite (T24).
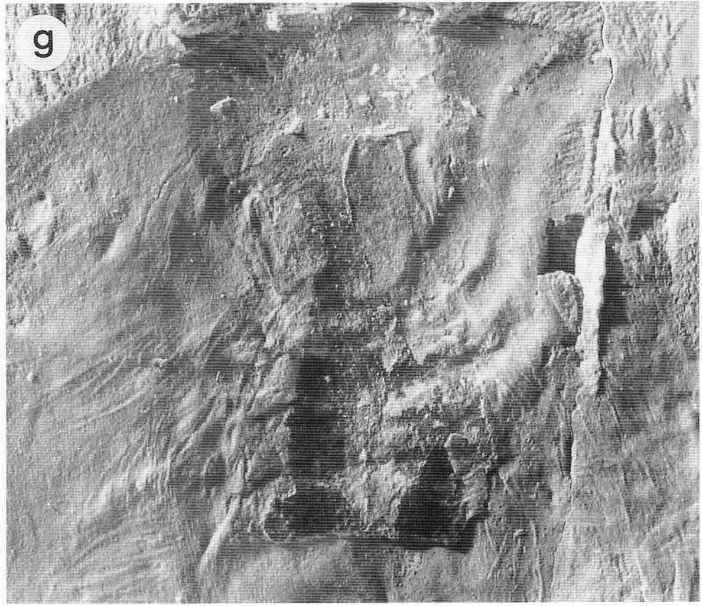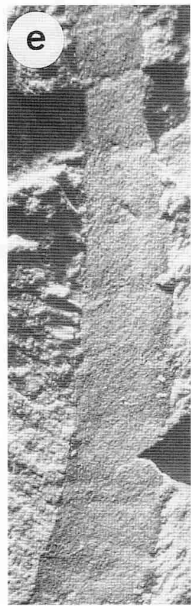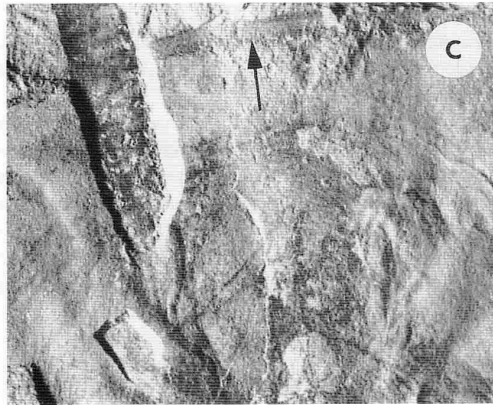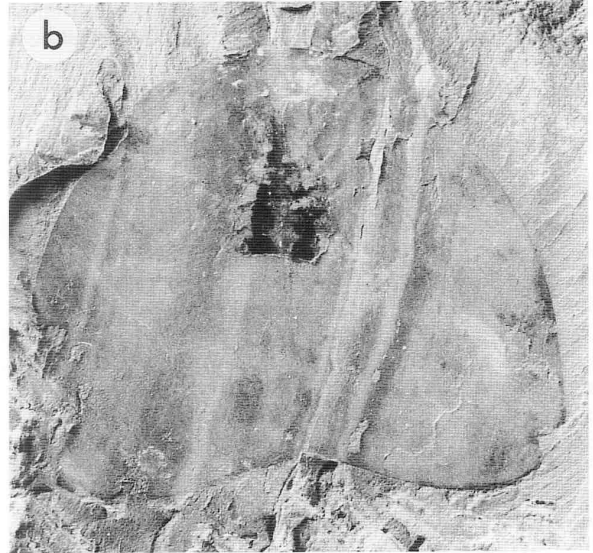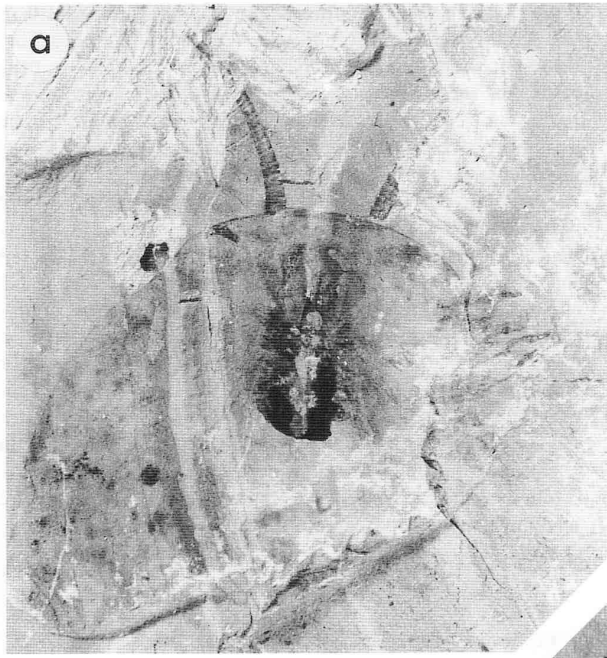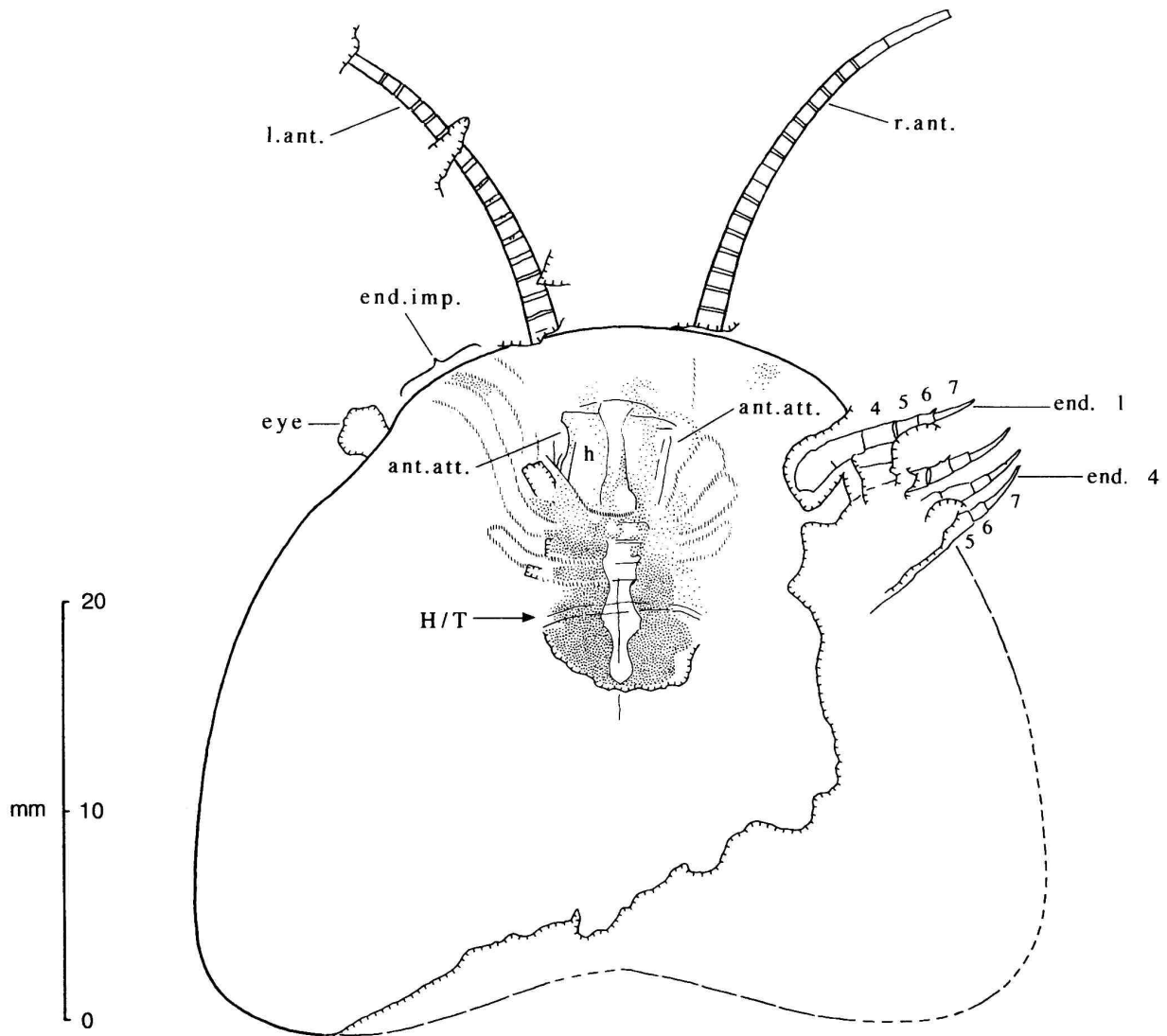
Figure 7 *Cindarella eucalla* Chen *et al.* Camera lucida drawing of ELRC 18507a from MQ1, a dissociated head, dorsal view (see Fig. 6a, d). The posterior and right lateral margins have been added from the counterpart (Fig. 6b), with long dashes indicating preserved parts and short dashes indicating inferred parts. Features indicated are the left eye (incompletely exposed), left and right antennules (l.ant., r.ant.), antennule attachment sites (ant.att.), hypostome (h), head/trunk junction (H/T), impressions of endopods on the left side (end.imp.), and endopods 1 and 4 on the right side (end. 1, end. 4), with the distal podomeres numbered on the assumption of seven endopod podomeres as is observed in the trunk.

Paratype. ELRC 18502a–b from locality MQ1, west slope of Maotianshan.

Other material. ELRC 18503a, 18505a–b, 18507 (from locality MQ1), 18504a–b (from locality MN6, north slope of Maotianshan), 18506a–b (from locality MN5).

Diagnosis. Xandarellid with cephalic shield overlapping anterior six trunk segments; four pairs of post-antennular cephalic appendages; genal angle rounded; stalked eye originating beneath anterolateral part of cephalon; trunk composed of 21–23 tergites, bearing approximately 37 appendage pairs; number of appendages per tergite increases progressively from

one to about four posteriorly; posterior tergites not lengthened relative to anterior ones; median ridge extending into terminal spine on posterior three trunk tergites.

Description. Length (sag.) of cephalic shield about 75% of width (in ELRC 18507, sagittal length 30·5 mm, maximum length 34·5 mm, width 41 mm), 35–38% of total exoskeletal length (in ELRC 18502, length of head shield 43·2 mm, length of exoskeleton including median spines 115 mm); posteromedian margin of cephalon gently convex forward; lateral margin of head shield weakly concave where eye protrudes, otherwise evenly rounded; shallow sagittal depression in head shield

Figure 6 *Cindarella eucalla* Chen *et al.* (a)–(e), (g) ELRC 18507 from MQ1, head shield (see Fig. 7 for a camera lucida drawing). (a) 18507a, dorsal view, × 1·8, high light from NW. (b) Counterpart ELRC 18507b, ventral view, × 1·8, light from NW. (c) 18507a, dorsal view, left antennule exposed under head shield, × 5·7, light from W. Arrow points to inferred outer margin of ventral cuticle (see also Fig. 1a). (d) ELRC 18507a, endopods of four cephalic limbs, × 7·5, light from W. (e) ELRC 18507a, detail of left antennule, × 10·4, light from NW. (g) ELRC 18507b, × 4·6, low light from NW emphasising relief. (f) ELRC 18505 from MQ1. Detail of midgut caeca in anterior part of trunk, × 11, light from N.
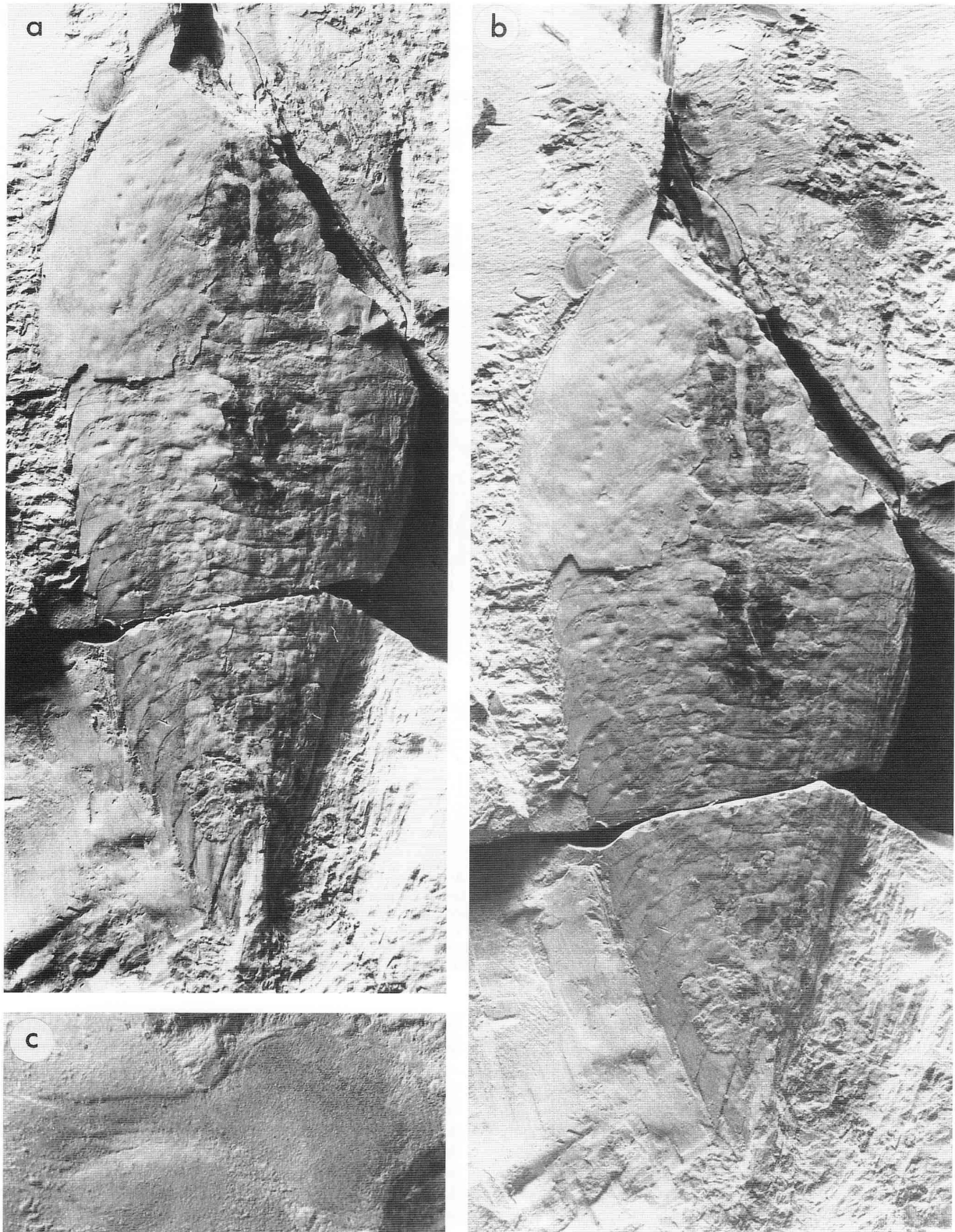
Figure 8 *Cindarella eucalla* Chen *et al.* (a)–(b) Paratype ELRC 18502 from MQ1, a nearly complete individual (see Fig. 9 for a camera lucida drawing). (a) Dorsal view, × 1·5, low light from NW to emphasise relief. (b) Dorsal view after preparation of right eye, × 1·6, high light from N. (c) ELRC 18506a from MN5, detail of right eye showing stalk beneath head shield, × 8·0, light from NW (see Fig. 10a for view of complete head shield).

anterior to hypostome in a few specimens; eye globular, ovoid in outline, attached by moderately long, slender stalk, positioned at anterolateral margin of head shield, usually partly beneath head shield but entire visual surface capable of rotation outside head shield; possible visual surface indicated by consistent darker colouration of outer region of eye;

doublure lacking; hypostome shield-shaped, slightly wider than long, with narrow (tr.) anterior wing; antennule long, flagelliform, attaching against side of hypostome and running approximately straight forward under head shield, widely diverging anterior to cephalic shield; antennomeres short, disc-like proximally, becoming longer than wide distally; first post-antennular cephalic appendage originates against posterolateral corner of hypostome, closely spaced to succeeding two appendage pairs; fully extended cephalic endopods project outside head shield; all four post-antennular cephalic appendages of equal size; boundary between head and trunk somites at 41·5–44% length (sag.) of head shield.

Esophagus narrow tube above hypostome, gut loops back at anterior edge of hypostome; gut narrow, without constrictions between segments; midgut caeca immediately lateral to the midline along ventrolateral edge of gut in the cephalon and anterior trunk segments; cephalic caeca ovate or digitate, extending anterolaterally; trunk caeca preserved as paired reniform stains or larger, more irregular smears; each caecum has an internal system of approximately transverse or slightly splayed tubules; gut slightly narrowed far posteriorly; anus set close to posterior margin of terminal tergite.

Gnathobase not observed on limb base, but spines possibly represented by ventrally directed tubercles in dorsoventrally-compressed specimen; trunk endopods apparently composed of seven podomeres; proximal four podomeres long, tubular, some bearing a small distal spine on ventral margin but otherwise lacking spines or endites where best known in anterior and middle part of trunk; distal parts of four cephalic endopods similar to more completely-known trunk endopods; distal podomere long, slender, terminating as a single point; second-last podomere short, bearing subsidiary spine on trunk appendages; third-last podomere longer than second, widening distally, flask-shaped on trunk legs; trunk exopods with flattened, leaf-shaped proximal lobe bearing abundant long, narrow lamellar setae of typical 'trilobitomorph' aspect, underlying each other outwards; distal lobe of exopod narrow flap, directed posteriorly, set off from proximal lobe by an articulation; several lamellar setae overlap the inner dorsal part of distal lobe of exopod; distal lobe bearing short setae along its posterior edge, these setae of comparable thickness to those along the proximal lobe; cephalic exopods poorly known, apparently present on all post-antennular limbs and similar in structure to anterior trunk exopods; pleural membrane (ventral cuticle) extends inwards to attachment sites of appendages, preserved as an undulating scarp marking limit of sediment penetration, extends outwards to just inside cephalic margin, preserved as a concentric rim around head shield.

Trunk composed of 21–23 tergites, anterior six beneath head shield corresponding to single somites; possibly without significant sclerotisation, posterior part of seventh trunk tergite (T7) protrudes behind head shield; trilobation not clearly defined by relief of tergites, axial furrow lacking; anterior trunk tergites of moderate convexity (tr.), increasing significantly posteriorly, with pleural region steeply sloping; posterior edge of anterior trunk tergites approximately transverse; anterior edge gently scalloped backwards in axial region; tergites progressively flexed posteriorly towards back of trunk; tergites imbricate anteriorly with 50% overlap, such that most of trunk has a double covering; posterolateral corner of tergites angular, more acutely so posteriorly; possible articulating structures in pleural region present but not well known, small boss on anterior edge of tergite, situated at about 30% of trunk width; pleural furrows absent; tergites of equal length in axial region throughout trunk, including portion overlapped by head shield; two slender but moderately broad-based

median spines originating at junctures of last three trunk tergites as continuation of median ridge; terminal tergite apparently composed of a ridge- or spine-bearing segment fused to the posteromedian element, with pleural lappet of anterior segment distinct, bearing about four pairs of appendages.
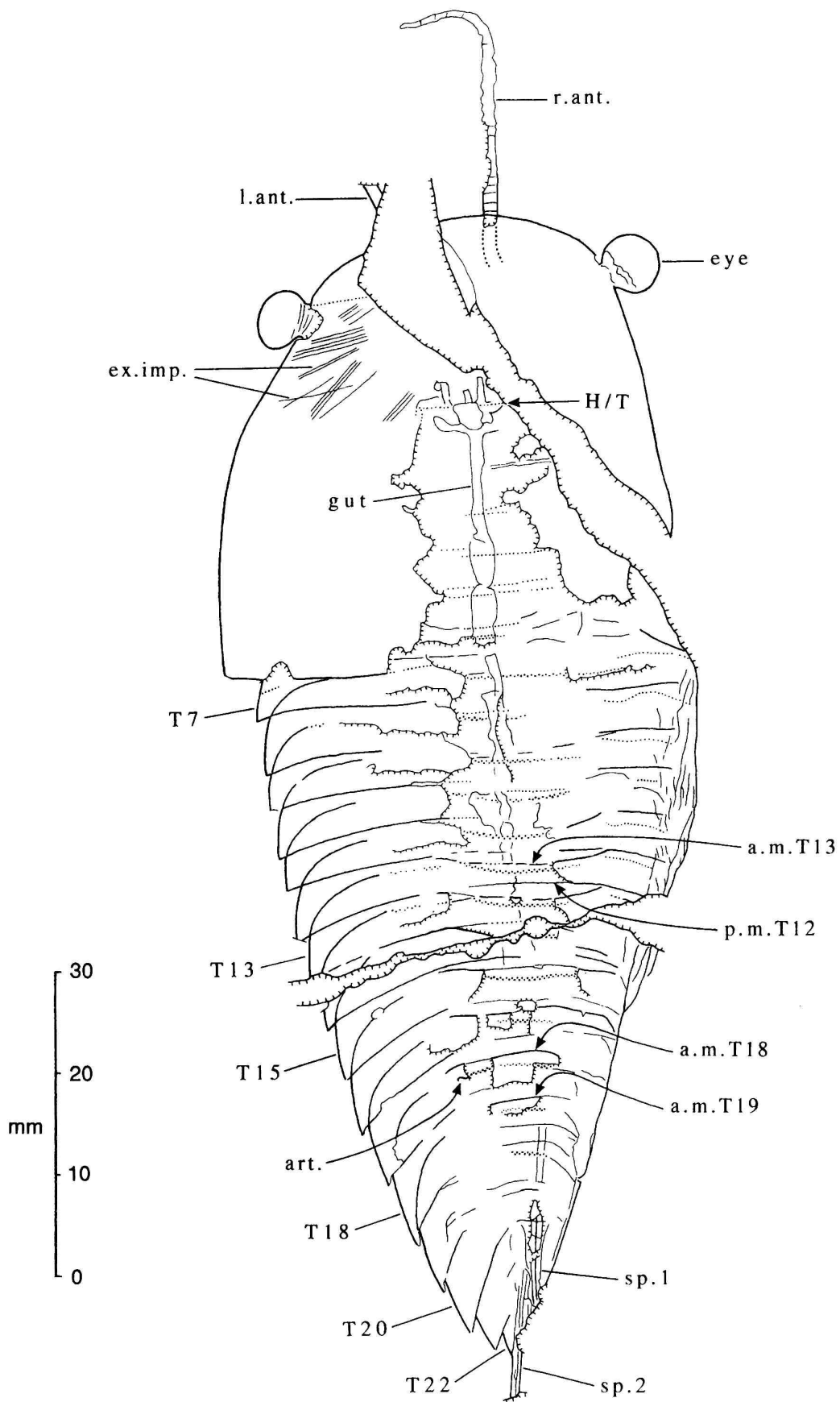
1.1. Discussion

The brief species description above is supplemented with the following remarks, which discuss the evidence for our morphological interpretations with reference to individual specimens of *Cindarella eucalla*.

1.1.1. Boundary between cephalon and thorax. ELRC 18505 (Figs 3c, d, 5a) illustrates the relationship between the head shield and trunk segments in *Cindarella*. A sharp transverse line marks the limit of matrix penetration behind four post-antennular cephalic segments indicated by the spacing of paired gut caeca. Six segments with strong caeca lie under the head shield posterior to this line. The matrix line corresponds to the juncture of the head and trunk, the latter inferred to include six articulated segments beneath the head shield. The matrix limit is lost in ELRC 18507b (Fig. 6b, g) due to a fracture a short distance anterior to this line. In the preserved part there are three pairs of caeca plus a possible, small fourth anterior pair. Running laterally and anteriorly from the anterior three of these are leg-shaped ridges. These ridges are seen as depressions in the counterpart ELRC 18507a, where excavation revealed the legs running close to the matrix surface of the depressions (Figs 6a, c, 7). The number of post-antennular limbs in ELRC 18507a is clearly shown to be four. The endopods of these four legs extend relatively far lateral to the margin (Figs 6d, 7). In ELRC 18501 five segments with strong caeca are rotated relative to the axis of the head shield, following the curve of rotation of the free part of the trunk (Fig. 1a). This independent rotation indicates that these segments are part of the trunk, rather than the cephalon.

The head shield can be compared with a crustacean carapace in that it covers the anterior part of the trunk as well as the cephalic segments (see Section 1.1.3). In ELRC 18505 (Fig. 5a) the junction between the head and trunk (H/T) is seen as the sharply defined, anterior limit of sediment penetration between the head shield and the underlying trunk tergites. This limit forms an anteriorly weakly convex line (actually a sediment scarp), shown by preparation to coincide with the anterior margin of the first trunk segment. The H/T is situated at 42·6% (from anterior) of the sagittal length (L = 44·5 mm) of the head shield. In the similarly sized specimen ELRC 18502 (Figs 8a, b, 9), the H/T is in the same position, at 41·5% of the length of the head shield (L = 43·2 mm). Both specimens show six trunk segments completely overlapped by the head shield, while the posterior half of the seventh tergite protrudes behind the shield. In ELRC 18506 (Figs 10a, 11a), the H/T is situated at 44% the length of the head shield (L = 40 mm). In the trunk part covered by the head shield there are five pairs of caeca, with space for a sixth pair posteriorly. In ELRC 18507 (Fig. 7), in which only the anteriormost part of the trunk is preserved, the H/T is at 42·8% the length of the head shield (L = 30·5 mm). Thus, in the available material of differently sized adult specimens, the relative sizes of the cephalic portion of the head shield and its posterior extension remain constant.

The juncture between the head and trunk also appears to be marked by a change in the form of gut caeca. These are small and ovate (Fig. 5a) or digitate (Fig. 11a) anterior to H/T as defined above. Posterior to H/T, the caeca are enlarged, typically reniform, and have an internal network of tubules (Figs 5a, 6f, 12a, 13). We note that the concentration of gut

r.ant.

l.ant.

eye

ex.imp.

H/T

gut

T 7

a.m.T13

p.m.T12

T 13

30

a.m.T18

20

T 15

a.m.T19

mm

art.

10

T 18

sp.1

T 20

0

T 22

sp.2

caeca in the head and anterior part of the trunk in *Cindarella* is a more general state, shared by trilobites (Chatterton *et al.* 1994; Shu *et al.* 1995), tegopeltids (Ramsköld *et al.* 1996, fig. 1A), and naraoiids (Chen *et al.* 1997). Given that chelicerates have caeca arising along the length of the midgut (Clarke 1979), it may well prove that the condition shared by trilobites and xandarellids is basic for Arachnata.

1.1.2. **Appendage structure and preservation.** The appendages, in particular those centrally in the trunk, are known in some detail, allowing reconstruction in different views. The most proximal part of the appendage is where it attaches to the ventral side of the trunk a short distance from the sagittal line (Figs 3e, 5b). Arthrodial membrane rises from the trunk stem to attach to the inner edge of the basis. No annulations or folds are preserved in this membrane, and since annulations are well preserved when present in other Chengjiang arachnates such as the naraoiid *Misszhouia* (Chen *et al.* 1997), the tegopeltid *Saperion*, and the helmetiid *Kuamaia*, we assume that they were originally weak or lacking. The basis is incompletely known. In the key specimen ELRC 18501 the limb bases are flattened more or less dorsoventrally (Figs 1–4). There are therefore no endite lobe or endite spines visible, but the limb base appears to possess ventrally directed tubercles that may indicate the presence of a gnathobase (see basis of limb 13 in Figs 3a, 4). There is no evidence for medially-directed endites. In this view, the basis appears to run from the trunk as a tubular structure of even width. We assume that the limb base was directed nearly vertically adjacent to its junction with the trunk, and then curved ventrolaterally to a more horizontal position. When the individual was entombed in the sediment, the basis would rotate posteriorly to rest against the basis in front of it. The undulating edge or scarp running the length of the trunk (Figs 1b, 4) is mainly composed of overlapping limb bases but may to some extent be a composite of the proximal margins of limb bases and the inner limit of the sediment-filled space between the ventral cuticle and the limbs.

The exopod attached to the dorsal or posterodorsal aspect of the basis. The actual line of attachment is not preserved with certainty in any leg, although in ELRC 18501 there are several candidate lines in appropriate position (Fig. 4, limbs 10–12, 14). These lines are all straight, and we interpret the joint as a hinge joint by analogy with other arachnates where we have been able to analyse the joint between the exopod and the basis (Ramsköld & Edgecombe 1996). The posterior margin of podomere 1 is overlapped by the exopod shaft in limbs 10 and 13, showing that podomere 1 was not joined to the exopod shaft.

In life, the endopod would have been oriented in a vertical plane, horizontal proximally and curving ventrally to a vertical orientation distally. The exopod would come off the posterodorsal surface of the basis, so that the anterior edge of the exopod shaft overlapped the endopod to some extent. The exopod would have sloped posterodorsally, so that a series of imbricating exopods overlay the series of endopods. Each exopod (including the fan of lamellar setae) is up to three times the length between two neighbouring exopods (Fig. 2b),

so that in vertical cross section, in any one place there would be two or three exopods overlapping each other (Fig. 14b).

Endopod morphology is revealed by ELRC 18507a (four cephalic endopods; Figs 6d, 7) and 18501 (several endopods from the central part of the trunk; Figs 2, 4). Podomere boundaries vary from distinct to exceedingly weak or non-preserved, and there are occasional additional lines simulating podomere boundaries in obviously impossible places. Due to the small number of preserved endopods, our interpretation of number of podomeres in the proximal half of the endopod is less well supported than for the distal half. For certain, however, the specimens demonstrate that the distal part of the endopod is very similar in each of the post-antennular head limbs and in trunk limbs. Two consecutive limbs from the trunk in ELRC 18501 show that the long, pointed podomere is preceded by a short, tubular podomere bearing a short distal spine, and this preceded by a considerably longer podomere that significantly widens distally. These three distal podomeres are differentiated from all those more proximally on the endopod, which are elongate and tubular. ELRC 18507a demonstrates that the three distal podomeres are similarly differentiated on the cephalic endopods. The distal podomere in all four post-antennular cephalic legs is a long, slender spine, preceded by two podomeres that are significantly shorter than those more proximally. In the cephalic as well as the trunk endopods, the second last podomere is shorter than the third last.

The scant available evidence indicates the presence of seven podomeres in the trunk endopods. Proximal to the third last podomere is invariably a long and slender podomere, numbered 4 in Figure 2b. This podomere is completely preserved in two legs only, numbers 10 and 13, in ELRC 18501 (Fig. 2a). The podomere is significantly longer in limb 10 than in limb 14. In the cephalic limbs in ELRC 18507a (Fig. 7) the equivalent podomere is even shorter, but still longer than the two following podomeres (5 and 6). The joint between podomeres 4 and 3 is preserved in limb 13 only, but is there unambiguous. Podomere 3 is preserved in limbs 10 and 13, and in both limbs its position is below the most distal part of the exopod shaft. Its length is twice its width. The joint to podomere 2 is unambiguous in limbs 10 and 13, whereas the joint between podomeres 2 and 1 is only preserved in limb 13. Podomere 2 has a spine distally at its ventral or posteroventral edge. Podomere 1 is fairly completely preserved in limb 13, but its anterior or anteroventral part is not visible proximally, so any presence of an endite is unknown. The joint to the basis is reasonably clearly preserved, and is unlikely to be a preservational artifact.

The presence of additional joints should not be excluded, although the presently available material lends no support for such interpretation. The very long podomere 4 is unusual among comparable arachnates, but the material shows it as a single podomere. The presence of joints in the section called podomere 1 herein cannot be ruled out completely, as well as the presence of an additional podomere proximal to this section. Nothing in the material does, however, indicate such presence. The finding of seven podomeres in the endopod is

Figure 9 *Cindarella eucalla* Chen *et al.* Camera lucida drawing of paratype ELRC 18502 from MQ1, an almost complete individual in nearly dorsal view with a slight tilt to the right (see Fig. 8a, b). The right side is flexed vertically down into the matrix, progressively more so posteriorly. The head shield and tergites are exposed in the pleural areas, whereas the sagittal trunk portion (including that underlying the head shield) exposes structures between the gut and the underside of the tergites. Features indicated are the right eye and gut, right and left antennules (r.ant., l.ant.), impressions of exopod setae (ex.imp.), head/trunk junction (H/T), tergites 7 to 22 (T7-T22), the anterior margin (a.m.) of T13, T18, T19, the posterior margin (p.m.) of T12, an articulating device (art.), and the first (sp. 1) and second (sp. 2) axial spines. A third, posteriormost spine is likely concealed in the matrix.
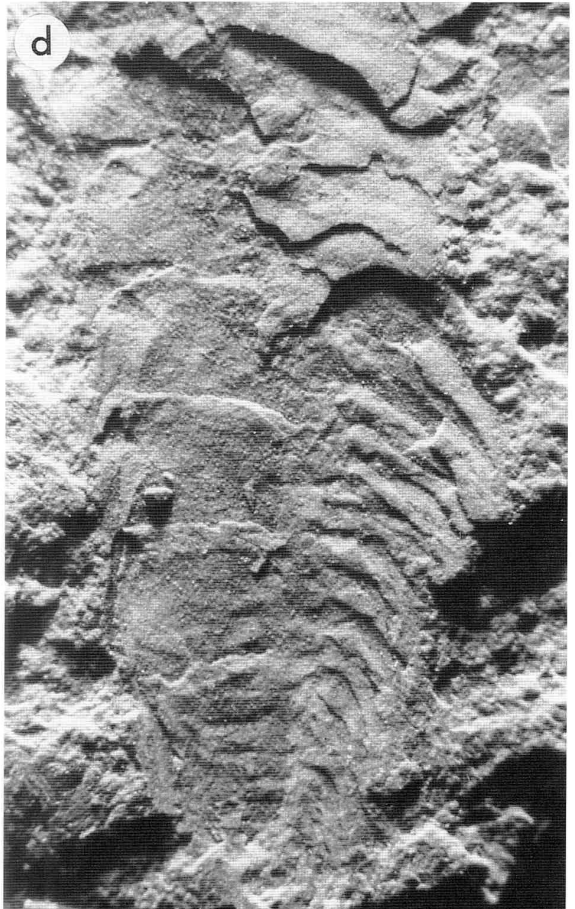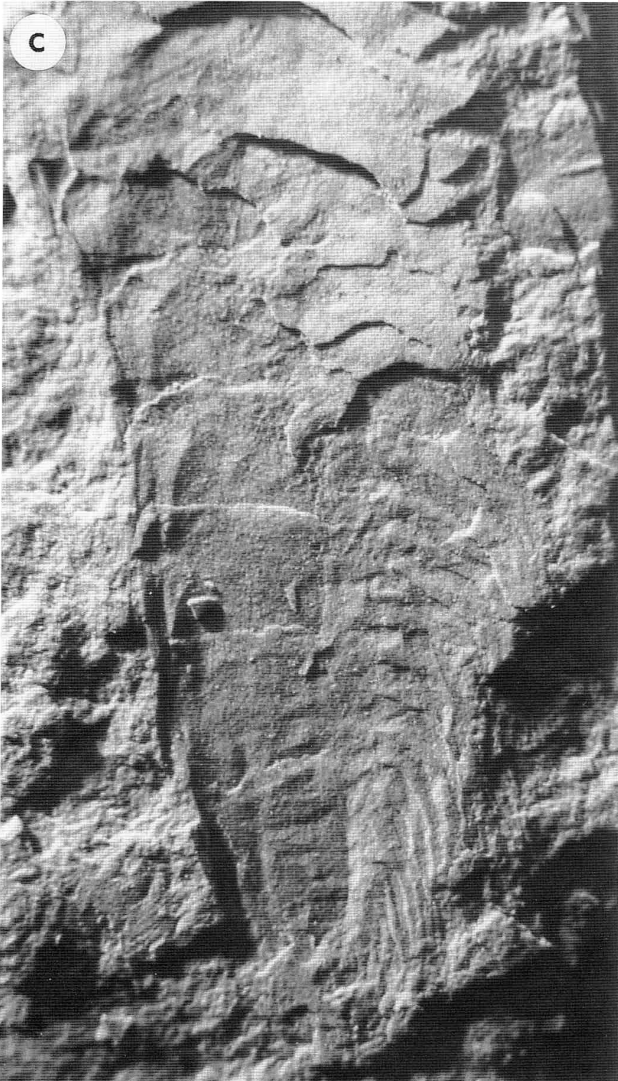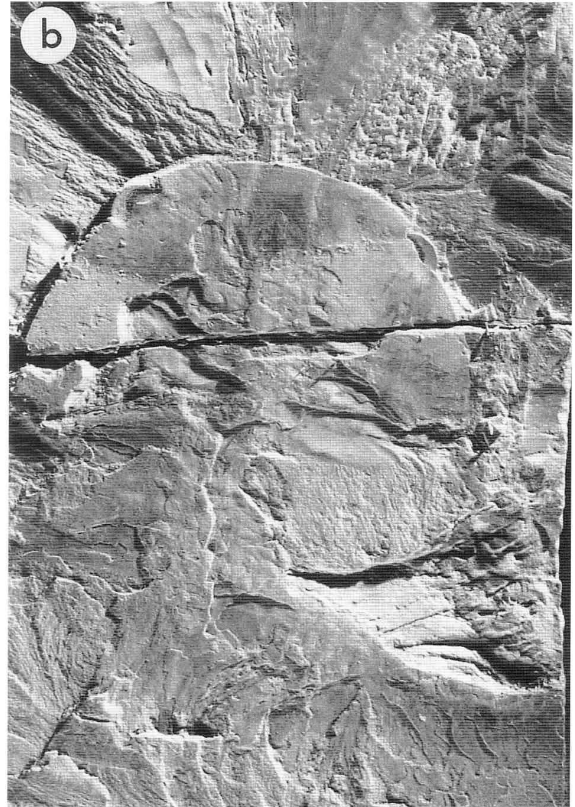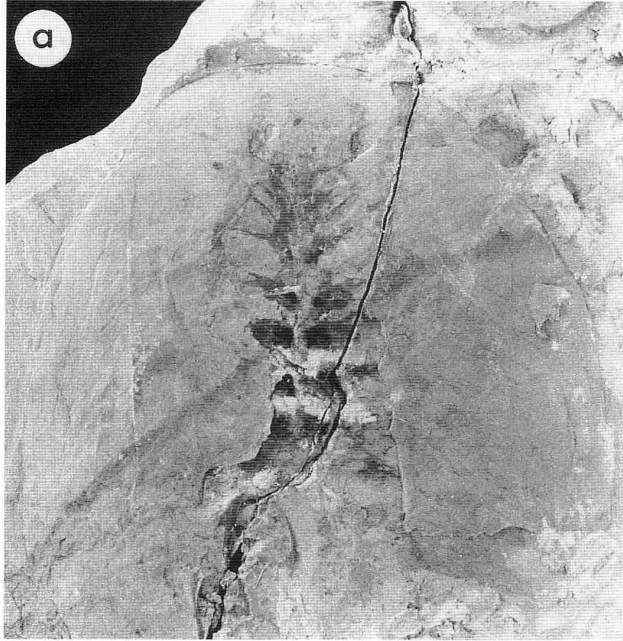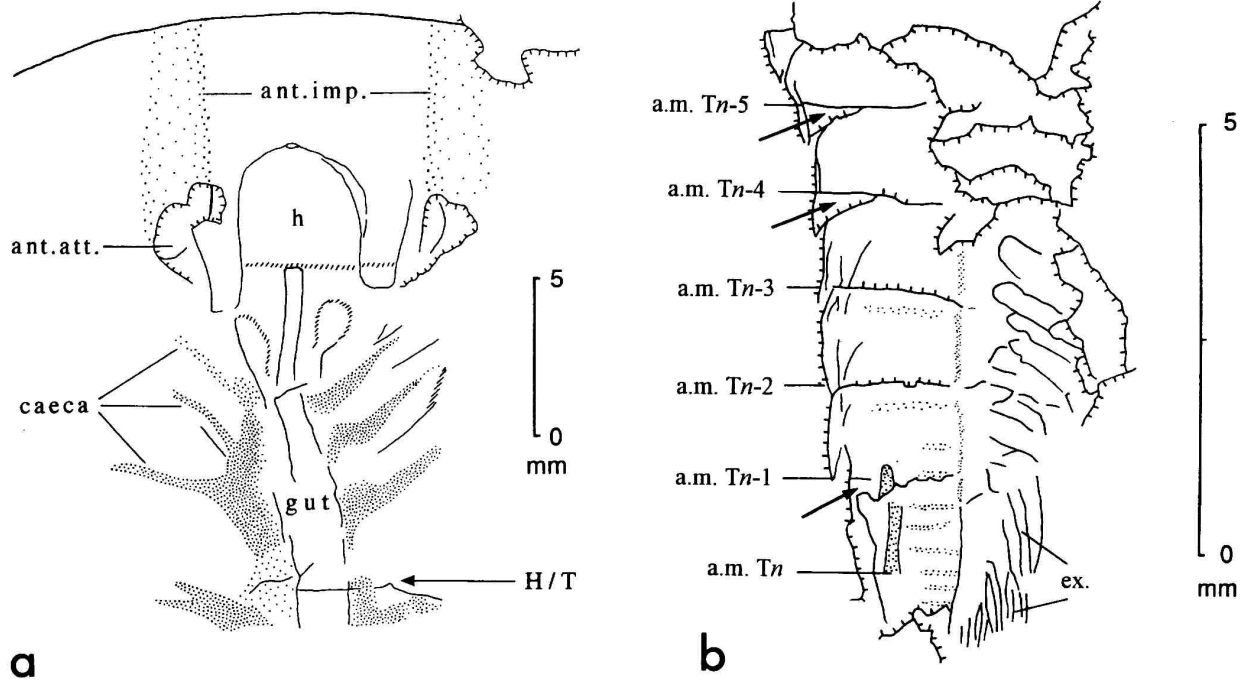
Figure 11 *Cindarella eucalla* Chen *et al.* (a) Camera lucida drawing of ELRC 18506a from MN5, dorsal view (see Fig. 10 for photograph of entire cephalon). Three pairs of posteromedially directed caeca join the gut anterior to the head/trunk junction. Labels as in Figure 5a. (b) Camera lucida drawing of ELRC 18504 from MN6 (Fig. 10c, d). Anterior margin (a.m.) of tergites indicated. Tergites numbered with reference to posterior one (T n). Arrows point to overlap of adjacent tergites.

consistent with many other Cambrian arachnates, including trilobites, *Emeraldella*, *Sidneyia*, and naraoiids.

The imbrication of the lamellar setae is not well exposed in any exopod, but in a few places in ELRC 18504a (Fig. 10b) it is clearly seen that the setae underlie each other outward. Also in ELRC 18501, the setae can be seen to imbricate in the same way (in limbs 10 and 14, see Figs 3a, 4). This orientation is confirmed by the overlap of setae on the proximal part of the distal lobe of exopod 11. This arrangement has been adopted in the reconstructed exopod fan of limb 13 in Figure 2b. The arrangement is similar to that in the naraoiid *Misszhouia* (Chen *et al.* 1997). The shared arrangement of setal imbrication leads us to postulate here that this is a configuration primitive for a broad group of arachnates. Long lamellar setae are maintained far posteriorly in the trunk of *Cindarella eucalla* (Fig. 12b).

Cephalic exopods are partly exposed in ELRC 18504a (Fig. 10b). In at least the second post-antennular limb, the inner lobe of the exopod has a leaf-shaped outline and a fringe of lamellar setae similar to those on the trunk exopods (including those of segments overlapped by the head shield). Impressions of long lamellar setae are also evident in the cephalic region of ELRC 18502 (Fig. 9). Taken together with the similarity of cephalic and trunk endopods, the post-antennular limbs of *Cindarella* show no evidence for tagmosis. This lack of post-antennular tagmosis in limb design aligns xandarellids with trilobites and their allies (including helmetiids, tegopeltids, and naraoiids), although, being a plesiomorphic character for Arachnata and even Euarthropoda, it does not provide evidence for a unique line of descent.

In our reconstruction of *Cindarella eucalla* (Fig. 14), the limbs are shown fully extended laterally, without an indication of gait. Following seminal work by Manton (1952 and many other papers) on living arthropods, it has been a convention to analyse gait patterns in exceptionally-preserved fossil arthropods (Whittington 1975, 1977; Bruton 1981). Manton's concept of gait refers to the relative duration of the forward to the backward stroke of the leg and the phase difference between successive legs. Gait analysis for fossils rests on a number of arbitrary decisions, and is at best speculative (Bruton 1981, p. 645). The stance of the legs in our reconstruction permits maximal exposure of limbs, and is not necessarily one possible in life.

1.1.3. Decoupling of tergites and somites. Specimen ELRC 18505a (Figs 3e, 5b) is informative in showing both the tergites and the proximal parts of the limbs. This is because in the axial region, the split has gone down level from the tergites to the limb bases. The specimen enables a reconstruction of the relationship between tergites and limbs, i.e. segments. Plotting the lengths of tergites 16–23 in a graph (Fig. 5c) shows that their length in the axial region does not vary within error of measurement. Further, the length of each tergite in this posterior trunk region is nearly identical to the length seen in the trunk region overlapped by the head shield. We therefore assume their lengths to be identical throughout the trunk.

The limb bases are well exposed on both sides throughout the posterior trunk portion. Each limb base is separated from the neighbouring ones by a deep, transverse furrow. The limbs become progressively smaller posteriorly, each separating furrow being set progressively closer to the preceding one. On

Figure 10 *Cindarella eucalla* Chen *et al.* (a) 18506 from MN5, dorsal view of head shield, × 1·7, high light from N (see Fig. 11a for a camera lucida drawing). (b)–(d) ELRC 18504 from MN6, nearly complete individual. (b) Dorsal view, × 2·4, light from NNE. (c) Detail of posterior part of trunk, × 12·4, low light from NNW. (d) Detail of posterior part of trunk, × 12·4, low light from N (see Fig. 11b for a camera lucida drawing).
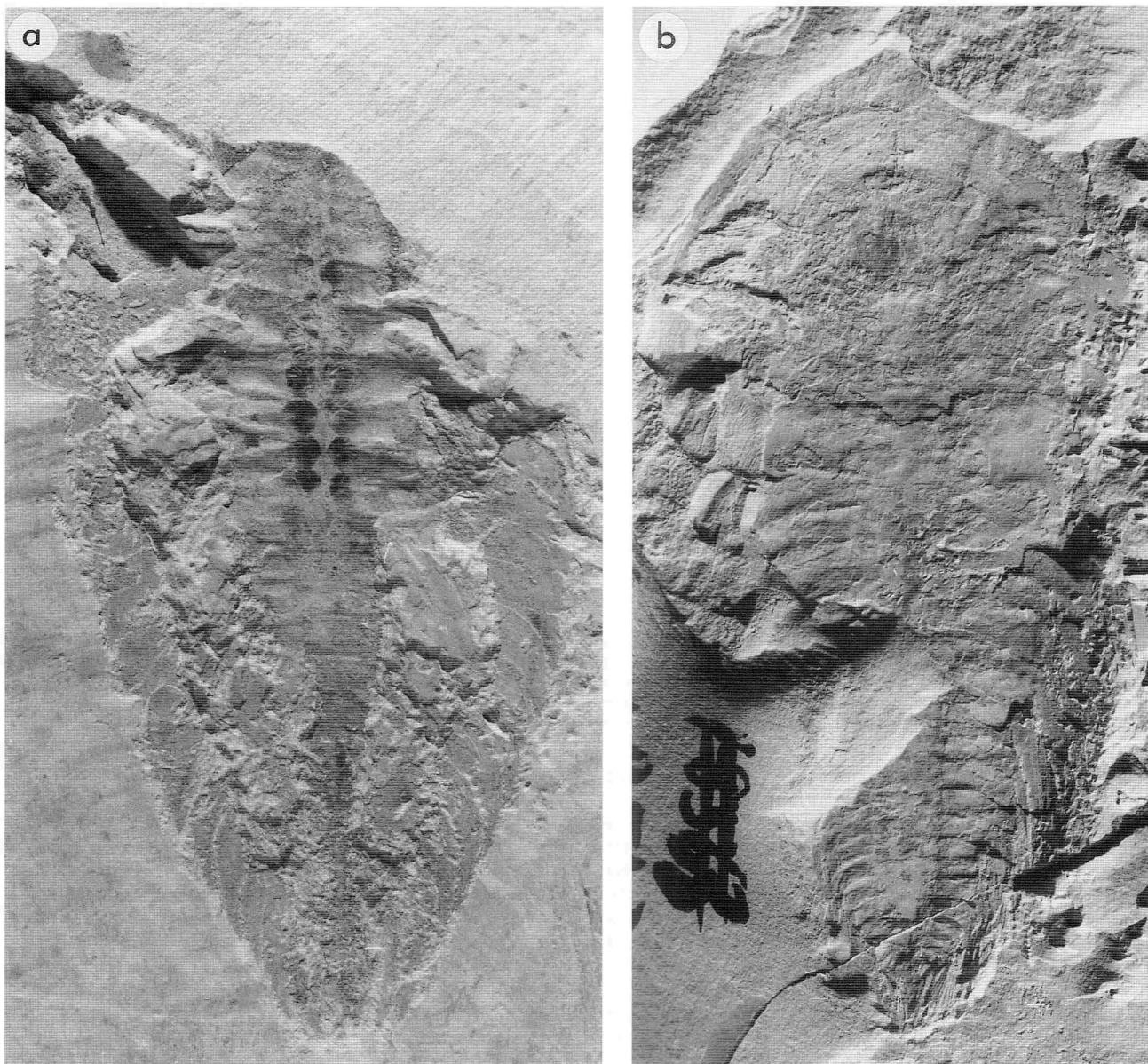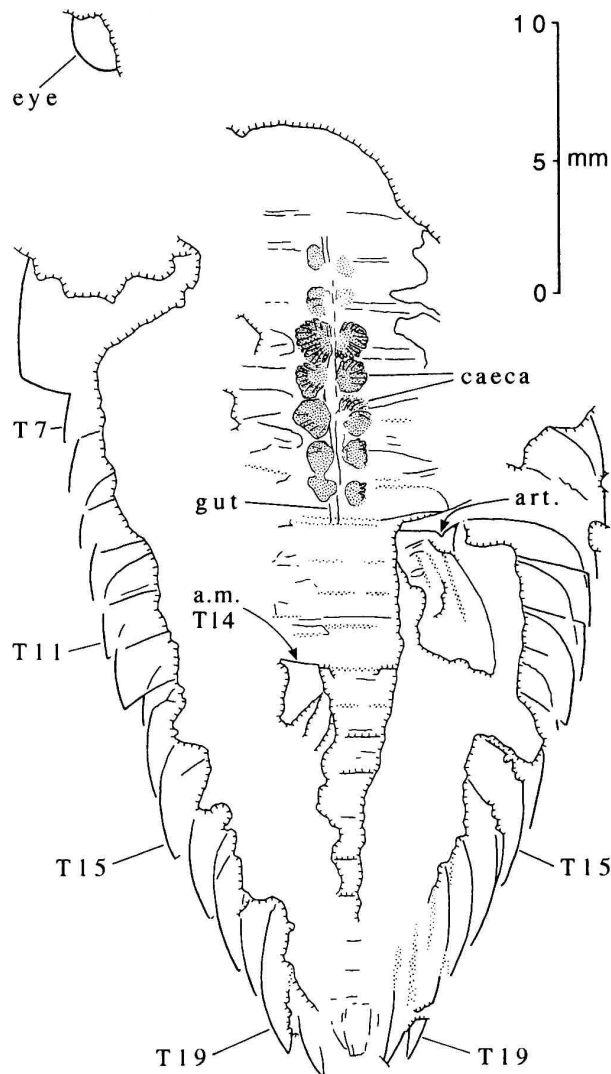
Figure 12 *Cindarella eucalla* Chen *et al.* (a) ELRC 18514 from MQ1, a small individual lacking much of the head shield, ventral view, ×4·6, high light from N (see Fig. 13 for a camera lucida drawing). (b) ELRC 18512 from MQ1, a poorly preserved specimen, dorsal view, ×1·9, low light from NW. Note sagittal depression in head shield anterior to hypostome.

the limb base itself, two sets of oblique furrows are seen (Figs 3e, 5b). The more proximal furrow (best seen in the anterior part of the posterior trunk portion) is anterolaterally directed, and is situated on the dorsal surface of the limb. Outside the exsagittal line delimiting the trunk stem (best seen on the lower left side), the proximal limb parts show a posterolaterally directed scarp, with its edge anteriorly. This scarp probably shows the overlap of the exopod shaft on the basis.

With the limb bases thus identified, they can be plotted and correlated with the tergites. The result (Fig. 5c) is somewhat surprising. There is no correlation at all between the tergites and the internal segments, as evidenced by the limbs. Tergite lengths remain constant, but under each tergite, an increasing number of segments are crowded. It should be noted that each tergite does not cover a particular number of segments, but just a portion of the row of segments. The segments thus show complete decoupling from the tergites. The relation between

tergites and segments in the trunk portion covered by the head shield seems to be close to one-to-one, as is evidenced by the presence of one pair of caeca between each transverse line taken to indicate a tergite margin. At the first tergite preserved in the posterior trunk portion, the sixteenth, there are 1·5 segments, and the number increases to 3·1 under tergite 23 (see Fig. 5). The measured segment lengths almost perfectly ($R^2 = 0.9998$) fit a curve of the equation $y = 1/(1 + cx^2)$, where x is tergite number, y is number of segments covered by tergite x, and c is a constant (-0.00127). This equation predicts a near one-to-one relationship between tergites and segments in the trunk portion covered by the head shield, and that, e.g. T8 will cover 1·1 segments and T12 1·25 segments. This condition of posteriorly increasingly smaller and more closely spaced segments under equally sized trunk divisions is not unique, and is seen, e.g. in the notostracan branchiopod *Triops*. As in *Cindarella*, in *Triops* the anterior part of the

Figure 13 *Cindarella eucalla* Chen *et al.* Camera lucida drawing of ELRC 18514 from MQ1, ventral view (see Fig. 12a). Features indicated are the right eye, some midgut caeca, the gut, tergites 7 to 19 (T7-T19), the anterior margin of T14 (a.m. T14), and an articulating device (art.) apparently connecting the anterior edge of T10 with T9.

trunk is covered by a head shield, the carapace, and the dorsal surface of the trunk is divided into roughly equally sized divisions. In *Cindarella* these divisions are the tergites, whereas in *Triops* the trunk cuticle is divided by transverse furrows into annulations. The relationship between the annulations and the segments, as expressed by limbs, is decoupled, and each of these annulations cover a posteriorly increasing number of limb pairs. These similarities between *Cindarella* and *Triops* do not indicate close affinity, a hypothesis rejected by a larger body of evidence, but are thought to reflect development freed from the usual constraints of tergite/ segment interdependence.

The total number of limb-bearing segments in the trunk can be calculated using the information above. Tergites 16–23 in the preserved posterior section illustrated in Figure 5b–c cover 16·6 segments. Assuming a continued decrease in segment size posteriorly, there would be approximately three and one half segments covered by the posterior tergite (which appears to be composed of two fused components, an anterior pleural rib and a posteromedian element). An extrapolation of the calculated change in segment lengths anteriorly in the trunk, from tergites 1 through 15, indicates that there would

be 17 segments in this area. The 24 trunk tergites would thus cover a total of 37 segments, plus or minus one or a few.

The posterior end of ELRC 18504b confirms and complements the interpretation presented here for the posterior part of ELRC 18505. In 18504, the animal's right side (to the left in Figs 10c, d, 11b) was strongly flexed ventrally along the margin of the axial area (the area covering the trunk stem). In the specimen, the left side and most of the axial area is therefore preserved parallel to the plane of bedding whereas the right side is exsagittally folded and the pleural area is lost. The tergite margins are well exposed in the axial region. On the left side of tergites six and seven from posterior (T n-5 and T n-6), the overlap between tergites is exposed at the edge of the axial area. The sagittal lengths of the seven tergites anterior to the terminal one can be accurately measured, and they show no variation in length (1·45–1·5 mm). The anterior edges of T n-2 and T n-3 are largely intact, whereas the anterior edge of T n-1 is partly broken off, revealing the base of a dorsally protruding sagittal structure, a median ridge or spine. On T n-1 a similar ridge runs the entire length of that part of the tergite not underlying T n-2. The visible portion of the ridge is interrupted at the anterior margin of T n. The latter tergite
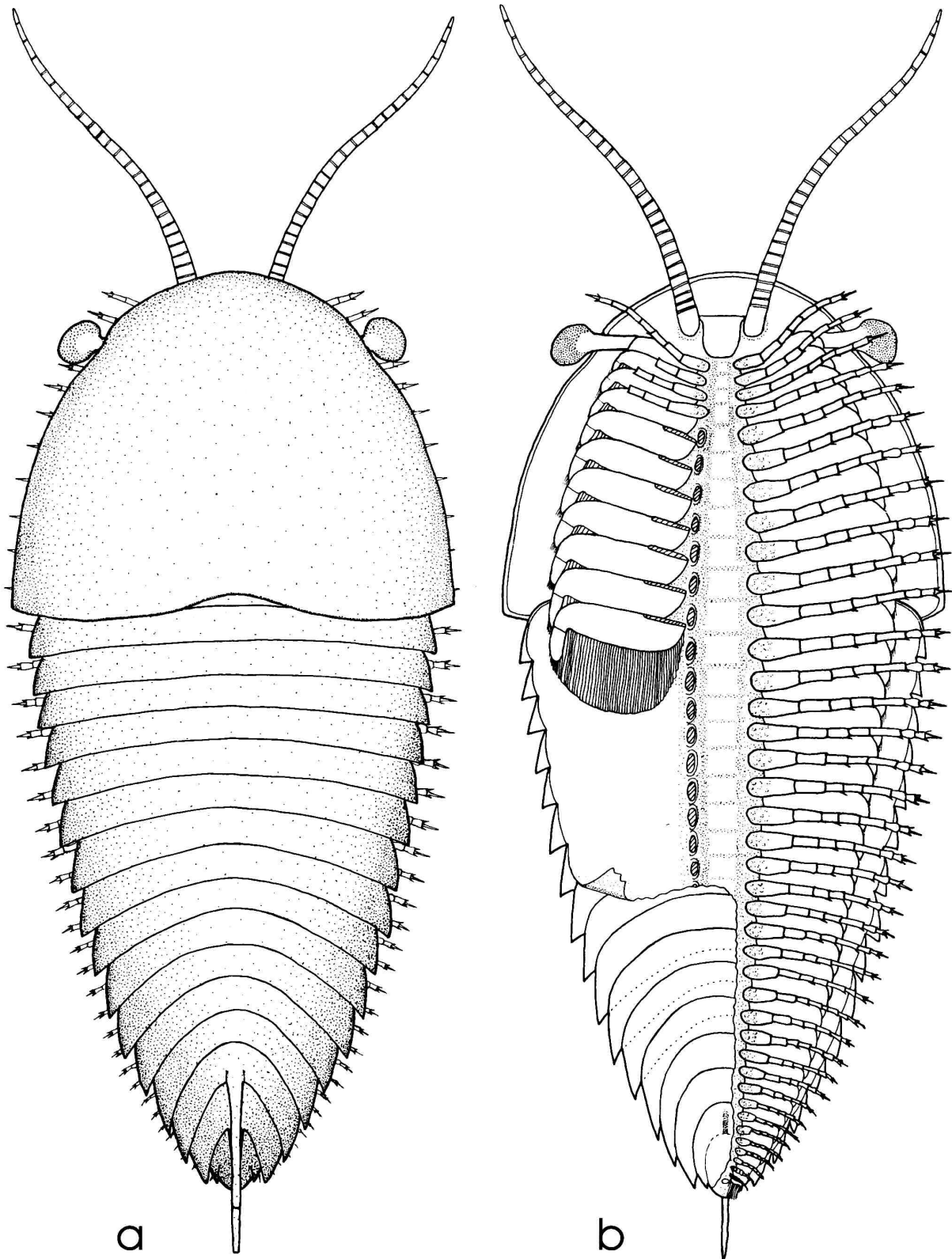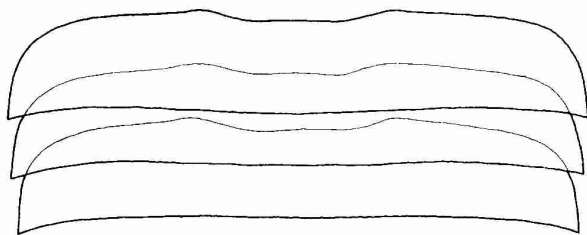
Figure 14 Reconstruction of *Cindarella eucalla* based on all material. Limbs are drawn in a fully extended state rather than in the stepping posture of a metachronal wave: (a) dorsal view, (b) ventral view. The left side shows successive removal of the endopods, exopods, and ventral cuticle from front to back to expose, first, the exopods, then the smooth ventral cuticle, and lastly the ventral surface of the exoskeleton. The posterior margins of three tergites are indicated by dotted lines. The outer limit of ventral cuticle in the trunk is based on information from the helmetiid *Kuamaia lata* which has similarly shaped tergite edges and in which the attachment line can be observed. Length of proximal antennomere(s) is conjectural. Morphology of the sternum is based on *Misszhouia* (Chen *et al.* 1997). Attachment sites of appendages, indicated by oblique hatching, are positioned on the inclined sides of the trunk stem. Base of median spine on terminal tergite is visible whereas bases of spines on T20 and T21 were likely concealed by tergite behind.

is not separated from the exoskeletal area behind by a scarp, and it thus appears to be fused to it. If so, Tn and Tn-1 together form the terminal tergite.

In the posterior three tergites in ELRC 18504b, impressions of paired appendages are seen on both sides of the sagittal line. Tergite Tn is not fully exposed, but three segments can be seen in the exposed portion. Tn-1 shows four segments, and there are three in Tn-2. On the animal's left side, a series of imbricating limb structures are exposed. Most or all of these are exopod shafts. Correlation between the tergites and exopods is ambiguous, but it is clear that the same pattern of posterior decrease in size is present as in ELRC 18505. An approximate count of somites per tergite anterior to Tn gives the following figures: 4, 3, 2–3, 2–3. Correlation of these figures with those of ELRC 18505 (Fig. 5c) indicates that Tn and Tn-1 correspond to the bicomposite terminal tergite, Tn-2 corresponds to T23 and so on. This correlation yields the same result as that based on the spine-bases and fusion of tergites discussed above. One consequence of this is that a comparison with ELRC 18502 (Fig. 9) indicates that the latter specimen shows spines of the second and third last tergites, and that the spine (or ridge) on the terminal tergite is not exposed. Another consequence is that in 18504, the spine-base on Tn-2 is concealed by the overlap with Tn-1, a circumstance supported by the fact that the spine-base of Tn-1 is exposed only due to the anterior margin of Tn being broken off. We conclude that the second and third last tergites carried posteriorly based median spines, and the anterior part of the terminal tergite carried a median ridge or possibly spine.

The amount of overlap between succeeding tergites in the anterior and posterior parts of the trunk are shown in the Figures 14b and 15. Both the shape of the tergites and the amount of overlap are reminiscent of the situation in *Fuxianhuia* (compare Fig. 15 with Chen *et al.* 1995b, fig. 4D). The pronounced tergite overlap in both of these taxa, in the trunk as well as the extension of the head shield to cover anterior trunk tergites, may be structurally/functionally correlated with the decoupling of tergites and appendages in each. That is, 'double covering' of the tergum might loosen the normal constraints on tergite/somite correlation. Most evidence (notably from appendage structure) would indicate that the decoupling of trunk segmentation is convergent between *Cindarella* and *Fuxianhuia* (see Wills 1996 and Edgecombe & Ramsköld 1996 for a debate). Another problematic group that displays a degree of decoupling of tergites and somites is the Euthycarcinoidea (Schram & Rolfe 1982). The tergites in euthycarcinoids cover a variable number of sternites, although this is effected by variation in the length of the tergites. There was, however, evidently an enhanced degree of mobility of the sternum relative to the tergum. There is no compelling evidence that the euthycarcinoid condition is any more than analogous to the tergal/sternal decoupling in xandarellids. Euthycarcinoids possess sternal and endoskeletal modifications

that are lacking in xandarellids, such as wide, strongly sclerotised sternites, and strong, segmental apodemes that extend posterodorsally and medially from the limb base into the body. The functional basis for segment decoupling in the two groups is unlikely to have been the same.

2. Acknowledgements

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