

Appendages of early Cambrian *Eoredlichia* (Trilobita) from the Chengjiang biota, Yunnan, China

Xianguang Hou¹, Euan N. K. Clarkson², Jie Yang¹, Xiguang Zhang¹, Guangqing Wu¹ and Zibo Yuan¹

¹ Yunnan Key Laboratory for Paleobiology, Yunnan University, Kunming, 650091, China

² School of Geosciences, University of Edinburgh, West Mains Road, Edinburgh EH9 3JW, Scotland, UK

ABSTRACT: The early Cambrian Chengjiang biota in Yunnan, southern China has yielded many articulated exoskeletons of the spiny redlichiid trilobite *Eoredlichia intermedia*, of which some have their appendages exceptionally well preserved. Both of the paired uniramous antennae of a medium-sized holaspis consist of 46–50 short segments (articles), each of which bears a fine spine near its inner edge. Behind the antennae there are twenty-one pairs of biramous limbs: three pairs are situated underneath the cephalon, one pair underneath each of the fifteen thoracic segments, and probably three pairs underneath the small pygidium. The endopod consists of a broad basis and seven podomeres, of which the last is divided into three terminal spines. The exopod is blade-like, and according to one interpretation, is dorsally hinged to the basis of the endopod; an alternative suggestion being that both the endopod and exopod are split from the basis, the latter being independent and not forming part of the endopod. The exopod has a prominent anterior rim, and possesses about forty long filaments along the posterior margin, and short setae along the rounded distal lobe. The basic appendage features of the redlichiid trilobites, and likewise the gut, are comparable to those of other known Cambrian polymerid trilobites that belong to more distantly related clades.



KEY WORDS: guts, Lower Cambrian, southern China, trilobites

Trilobites constitute a highly successful group of arthropods which flourished during the Palaeozoic. More than 20,000 species have been described, of which, however, only about twenty species have been reported with appendages still surviving (Hughes 2007). Such exceptional preservation has revealed some basic information about the soft parts of some trilobite clades, but cannot yet provide a thorough understanding of the anatomy of this highly diversified arthropod group.

Within the Redlichian Province, redlichiid trilobites represent a remarkable group of pioneer arthropods. They appear suddenly, and are widely distributed in the Lower Cambrian of the Yangtze Platform (Zhou & Yuan 1982), where *Eoredlichia*, one of the zonal index fossils, defines the second trilobite biozone (*Eoredlichia*–*Wutingaspis* zone) of the Qiongzhusian (=Chiungchussian) Stage in which the Chengjiang biota occurs (Hou & Bergström 1997; Hou *et al.* 2004). Many articulated redlichiid exoskeletons have been described from southern China, and some of them have been assigned to different growth stages (Lu 1940; Zhang 1962, 1986).

The Chengjiang biota has become well known since it was discovered in 1984 because of the high diversity of the Early Cambrian metazoans showing extraordinarily well preserved soft parts (Hou *et al.* 2004). As has often been pointed out, based on alpha diversity or relative abundance, trilobites do not constitute a dominant portion of the arthropod fossils in the Chengjiang Lagerstätte. Four trilobite genera have been described from the Chengjiang deposit: *Eoredlichia*, *Yunnanocephalus*, *Kuanyangia* and *Wutingaspis*. In total, trilobite specimens account for less than 2% of all individuals within the Chengjiang biota. This present study is focused on the soft

body anatomy of the redlichiid trilobite *Eoredlichia intermedia* (Lu 1940). These trilobites are notably characterised by articulated dorsal exoskeletons, of which some have their long, slender genal, pleural and axial spines preserved. A few specimens with appendages, including uniramous antennae and biramous limbs, have been preserved and have attracted attention (Shu *et al.* 1995; Ramsköld & Edgecombe 1996; Hou & Bergström 1997). Some of the interpretations of appendage structure given by Shu *et al.* (1995) were found to be erroneous by Ramsköld and Edgecombe (1996) and Hou and Bergström (1997), and were modified. Whereas the present conclusions largely accord with those of these latter authors, a good number of well-preserved new specimens has accumulated in recent years, allowing a substantially fuller description than has previously been possible.

1. Material and methods

About 1100 trilobite specimens have been collected from the Chengjiang Lagerstätte that occurs at the lower-middle portion of the *Eoredlichia*–*Wutingaspis* zone of the Lower Cambrian Qiongzhusian Stage, most of them having been discovered at the Ercaicun and Mafang sections near Haikou town in Kunming and a few at Ma'anshan and Maotianshan sections in Chengjiang County, Yunnan Province (Fig. 1). Of these, about 600 specimens have been referred to *Eoredlichia intermedia*, of which most are articulated dorsal exoskeletons ranging in overall length from 2.0 mm to 86.0 mm. Their ontogeny will be described in a later work. There are only 25 specimens that have appendages preserved.



Figure 1 Geographical map showing the Lower Cambrian fossil sites in the Kunming–Chengjiang area, Yunnan, southern China.

All appendage-bearing specimens of *E. intermedia* are dorso-ventrally compressed and the biramous legs are located underneath the hard exoskeleton. The legs were revealed by careful preparation with a needle under a Nikon SMZ-10A microscope. This work was done mainly by the two junior authors, Wu and Yuan, from 2003 to 2007. The specimens were photographed with the light from about 45° from NW direction. A professional FinePix S2 Pro digital camera was used for the larger specimens and another Olympus E-20P digital camera linked to a Nikon SMZ1000 microscope was used for smaller specimens and for parts of the large specimens. The camera-lucida drawings were made using the Nikon SMZ-10A microscope.

All specimens used for this present study are housed in the Yunnan Key Laboratory for Paleobiology at Yunnan University in Kunming, Yunnan Province, China (YKLP).

2. Preservation

The processes that led to the exceptional preservation of the Chengjiang biota have been discussed previously (Hou *et al.* 2004), as have the associated sedimentology and taphonomy (Zhu *et al.* 2001; Gabbott *et al.* 2004; Zhang & Hou 2007). Moreover, several authors have discussed taphonomic processes in other soft-bodied faunas (Burgess Shale, Sirius Passet, Kaili, Emu Bay) (Babcock & Peel 2007; Bergström *et al.* 2007; Caron & Jackson 2006; Lin 2006, 2007; Paterson *et al.* 2008), and a consensus view that all these deposits share a common mode of fossilisation is now emerging (Gaines *et al.* 2008; Page *et al.* 2008). However, the paleoenvironment in which the Chengjiang organisms were once living and subsequently buried remains obscure.

In appendage-bearing trilobites from the Burgess Shale, the appendages are never preserved in a symmetrical arrangement about the axis of the exoskeleton, but are inevitably displaced. The preserved arrangements of the appendages related to the exoskeleton have been greatly modified by processes operating

during burial and compaction (Whittington 1975). Likewise, some of the appendage-bearing trilobites from the Chengjiang biota have been affected in a similar way to those of the Burgess Shale, as the limbs and the exoskeleton appear to have been shifted laterally (Figs 2D, 5). Such a distortion of the soft parts may have arisen during post-mortem transportation or during final diagenesis, since most Chengjiang organisms were presumed to have been transported or only gently transported before being buried (Hou *et al.* 1991, 2004; Zhu *et al.* 2001; Zhang & Hou 2007), and are apparently flattened to some extent within the host mudstone. Nonetheless, some specimens have their hypostomes ventrally preserved underneath the anterior part of the cephalon with little or no displacement (Shu *et al.* 1995; Figs 2A, 3), since the hypostome is tightly attached to the rostral plate which forms part of the ventral doublure of the trilobite.

The articulated dorsal exoskeletons of *E. intermedia* present in the Chengjiang biota, including those with appendages attached, lie mostly parallel to the bedding surface, except for a few that have been dorso-laterally compressed (Figs 7C, F, 9, 10). The mechanism behind the burial style has been attributed to gravitational constraint (Zhang & Hou 2007). Moreover, the condition of preservation of the soft-parts may vary greatly in appendages located on different parts of an individual, or from specimen to specimen. For instance, the limbs located underneath the thorax may display distinctly articulated podomeres, but in the same individual none of the corresponding exopods have survived (Figs 2E, 6). Even the paired antennae of the same specimen may be preserved in different ways, as an example, the segments of the antenna on the right side of one specimen (Fig. 2C) are better defined than these on the left. Following the method of Whittington (1975) the limbs of each specimen are described and illustrated first and more general conclusions are presented later.

Terms used to describe the exoskeletons and appendages of this redlichiid trilobite mainly follow Whittington (1975) and Ramsköld & Edgecombe (1996).

3. Summary of observations

The appendages of *Eoredlichia intermedia*, like those of other trilobites, consist of a single pair of uniramous antennae, three pairs of biramous appendages in the cephalon, (some trilobites have four) and one pair for each thoracic segment. It is probable that there were three pairs in the very small pygidium (Figs 2D, 5). No anal cerci have been detected. The observations recorded here largely confirm the basic structure of the appendages as defined by Ramsköld & Edgecombe (1996) and Hou & Bergström (1997), but substantially extend current knowledge on account of the numerous specimens described and illustrated. A new reconstruction of the biramous limb is presented. In addition, the structure of the gut is described for the first time.

Antennae. The bases of the antennae are slightly swollen, with rounded proximal terminations. They are set quite deeply inside the cephalon, as far back as the anterior edges of the ocular ridges (Figs 2A, 3, 7D, E). They converge anteriorly on either side of the neck of the hypostome, to diverge outwards again where they cross the cephalic border. The proximal section of each antenna has eight to ten broad, short articles, each ornamented with a sharp, inwardly directed spine, pointing towards the midline (Fig. 2C). Distal to these the antenna is narrower, the articles becoming cylindrical and about twice as long as they are broad (Figs 7B, H, 11). The antennae consist of up to 45 articles, and are usually straight, as if held rigidly in life. However, in one small specimen (YKLP10983,

Figs 7B, 13), however, they are directed almost forwards. The angle of divergence of the antennae varies from specimen to specimen, rarely they point almost forwards, but more normally they diverge between about 30 and 50 degrees from the midline. Each antenna is about the length of the cephalon, and tapers slightly towards the tip. Fine spines or setae on the antennae have been reported in some later trilobites (Whittington 1975, 1997). It seems likely that antennal segments bearing fine spines may represent an essential feature evolved by many, if not all trilobite lineages.

Biramous appendages. The biramous appendages, like those of all other described trilobites (Whittington 1997), consist of an endopod or walking leg, and an exopod, which is generally interpreted to function as a gill. The most proximal part of the leg is the stout, swollen basis, which is almost as wide as the thoracic segment that bears the biramous limbs. This may be variously interpreted as part of the endopod, or the joint from which both endopod and exopod arise (see earlier discussion and summary below). Even after ventral compression, the bases underneath two adjacent thoracic segments have never been found overlapping, extending towards the midline as a rounded gnathobase with about 12 short spinose endites. The ventral edge of the basis bears sparsely-placed long spines (Figs 7F, 10).

The endopod is composed a chain of seven podomeres, the final one of which terminates in three short claws, though these are not often preserved. The three cephalic and the anterior thoracic endopods, up to about the middle of the thorax, are relatively slender, and although they bear short spines, these are not often well-preserved. Towards the rear of the trilobite, however, the endopods become shorter, stouter, and more spinose; each podomere revealed as having a downwardly directed endite on its lip, or outer extremity. Many of the joints between the podomeres display a curious double structure, represented by a pair of parallel lines rather than a single one. This may have originally been a strengthening annulus or ring round the extremity of each podomere, which when flattened has the appearance of a short strap.

The exopod consists of a main lobe, being a flat blade some four times as broad (tr.) as it is long (sag.). It is more-or-less parallel-sided, though the anterior edge tapers somewhat towards the basis. The rear edge has a slight indentation some 4/5ths of the distance to its outer extremity, defining a rounded distal lobe. This lobe is not separated by any furrow or other structure from the main lobe, and does not seem to be detached or separate from it. In several specimens the distal lobe is traversed by an oblique crescentic ridge, tapering outwards (Figs 2A, 3, 2B, 4, 7A, 8). This may be an original structure, but is more likely to be the impression of the underside of the overlying thoracic pleural spine. In some specimens the main lobe bears an oblique line, a ridge or furrow, running obliquely and inwardly from the outer extremity of the hinge between the basis and the exopod; this line reaches to about half way across the main exopod lobe. Whether this is a real structure or a preservational artefact is uncertain; the present authors consider it to be the rear edge of the basis showing through. To the rear edge of the main lobe is attached a fringe of some 40 parallel filaments, extending as far backwards as the length of two thoracic pleurae, or twice the length of the main lobe (sag.); they are far longer than previously supposed. The distal lobe bears a shorter fringe of radial filaments.

The junction between the endopod and the exopod has been investigated by Ramsköld & Edgecombe (1996). They interpreted the proximal part of the exopod as connected to the basis by a straight hinge, which would have enabled the endopod to operate independently of the exopod. This straight

hinge is exhibited by several of the specimens available to the present authors (Figs 2A, 3, 2B, 4, 2D, 5, 7A, 8, 7C, 9), who concur with this interpretation. This hinge would enable the endopods, acting as walking legs and propelling the animal forwards by metachronal rhythm, to act more-or-less independently of the exopods when moving. The exopods, lying in a horizontal plane and overlapping one another rearwards, between endopod and ventral membrane were probably capable of some rhythmic up-and-down movement as the trilobite walked, thereby ventilating the gills. The function of the blade-like main and distal lobes is uncertain; they may have functioned only as strong supports for the gill filaments. Since the filaments of the main lobe are of such great length, it is hard to see how the exopods could have swung downwards far enough to enable the lobes to have functioned effectively as swimming paddles.

A new reconstruction of the biramous leg for *Eoredilichia intermedia* (Lu) is made here (Fig. 14) based on the present study. In the reconstruction of Ramsköld & Edgecombe (1996, figs 1C, D), the basis is shown extending ventrally as in *Naraoia*, with the gnathobasal endites below. From the limited evidence available, although in other respects in agreement with Ramsköld & Edgecombe, a lateral position for the gnathobase is preferred, as a direct continuation of the endopod and basis, and in the same plane.

It is well known that *Olenoides* shows a progressive reduction in the size of appendages posteriorly, as is the case in many other trilobites (Whittington 1975), and is certainly the case for *Eoredilichia*. Likewise, the appendages in the anterior thoracic region are larger, and the endopods more slender than those towards the rear.

As has been pointed out by Edgecombe & Ramsköld (1999) and other authors, the appendages of *Eoredilichia* are very similar to those of Middle Cambrian *Olenoides* and Early and Middle Cambrian *Naraoia*, and it is likely that this kind of organisation formed the ground-plan for Cambrian polymerid trilobites. *Eoredilichia*, like *Naraoia* and *Olenoides*, seems to have been a versatile, though comparatively unspecialised trilobite, possibly capable of feebly swimming, though without using the exopods, which lie in a plane above the endopods.

Gut morphology. The shape of the gut is known from three specimens, YKLP 10967 (Figs 2E, 6), YKLP 10968 (Fig. 7A) and YKLP 10982 (Fig. 7E). The best preserved of these, YKLP 10967, described in detail below (section 4.4), shows the straight, tubular alimentary canal and nine paired diverticulae as far as ta 4, with a possible gut trace through ta 5 and ta 6. YKLP 10968 shows that the gut is of similar form, again with nine paired diverticulae. In this case a narrow axial trace continues backwards from ta 4 to the rear of the trilobite; exactly where it terminates is unclear because of breakage. YKLP 10982, less well preserved, has again nine pairs of diverticulae. From these specimens it may be inferred that the gut is basically a straight tube, not greatly expanded below the glabella, with four pairs of diverticulae below the glabella and five pairs in the anterior part of the thorax, extending to the rear margin of ta 4. Behind this the gut is narrower and has no diverticulae.

Much interest attaches at the present time to feeding habits in trilobites and the evolution of predator-prey systems (Babcock 2003). Whittington (1997, p. 139) envisages *Olenoides* as a scavenger/predator, and that the ventrally spinose endopods could seize prey or decayed material by inward flexure. The food would then be conveyed to the median groove, with the spinose coxae on either side, where it would be shredded during its forward passage to the mouth. Lin (2007) on the basis of the preserved gastrointestinal system in *Olenoides* from the Kaili Biota of Guizhou, supports this

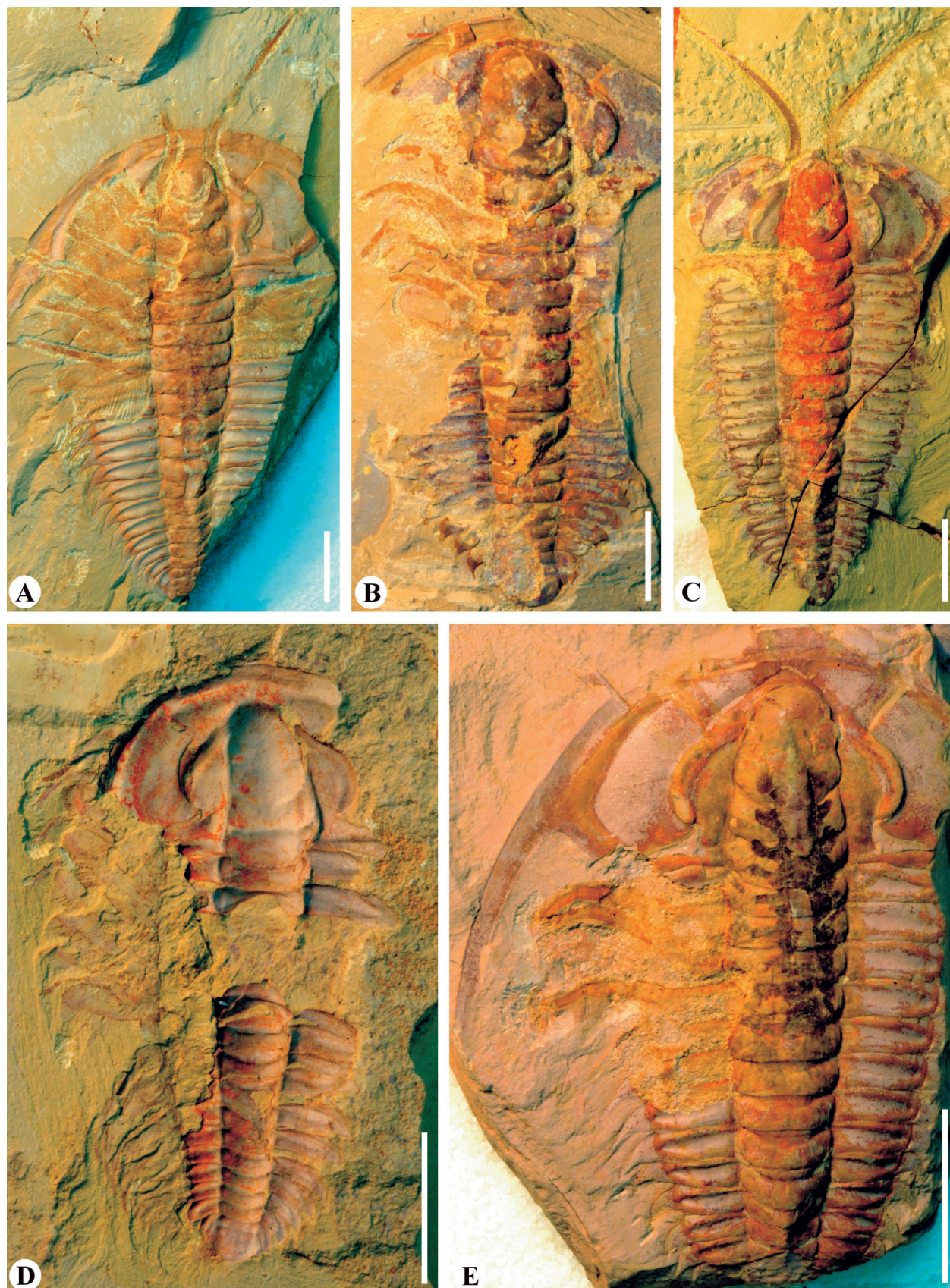


Figure 2 Appendage-bearing specimens of *Eoredlichia intermedia* (Lu) from the *Eoredlichia–Wutingaspis* zone of the Lower Cambrian Qiongzhusian Stage. (A, C, D) Mafang section, Haikou, Kunming; (B) Ercaicun section, Haikou, Kunming; (E) Maotianshan section, Chengjiang. Scale bars=1 cm. (A) YKLP10964, paired antennae as far back as the anterior edge of the ocular ridges; (B) YKLP 10965, large specimen 62 mm in length, the second thoracic segment with a fairly distinct endopod preserved along its length and terminating in three spines; (C) YKLP 10973, a pair of well-preserved antennae with five short, broad articles bearing short spines, directed inwards towards the median plane; (D) YKLP 10966, several exopods with a slight indentation in their posterior margin, defining the distal lobe, the two very small lobes with filaments extending beyond the posterior margin of pygidium; (E) YKLP 10967, anteriorly the symmetrically placed lobes of the gut diverticulae attached to the alimentary canal.

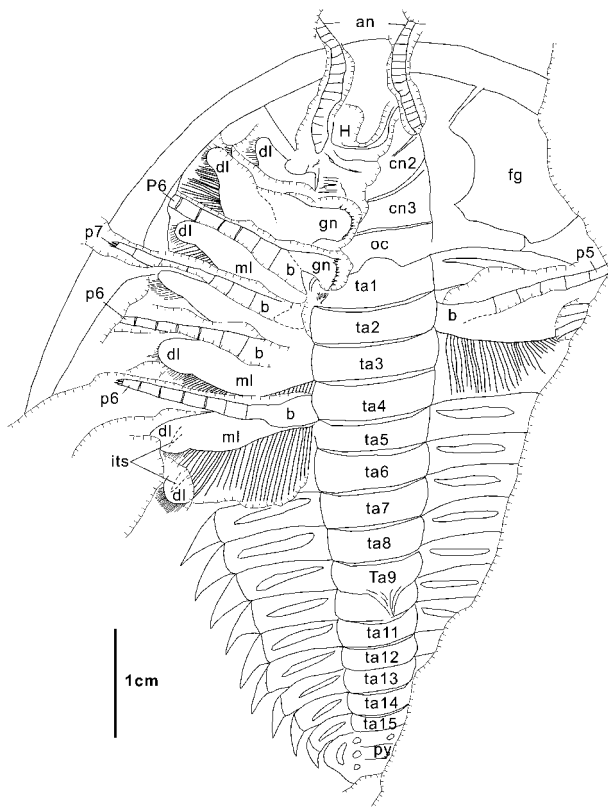


Figure 3 Drawing of YKLP 10964 (Fig. 2A). Abbreviations for all drawings: (ac) alimentary canal; (an) antennae; (b) basis; (cn) cephalon; (dl) distal lobe; (el) eye lobe; (en) endopod; (ex) exopod; (fg) free gena; (gd) gut diverticulae; (gn) gnathobase; (H) hypostome; (its) impression of overlying thoracic spine; (ml) main lobe; (oc) occipital ring; (p) podomere; (pl) pleural lobe; (py) pygidium; (ta) thorax.

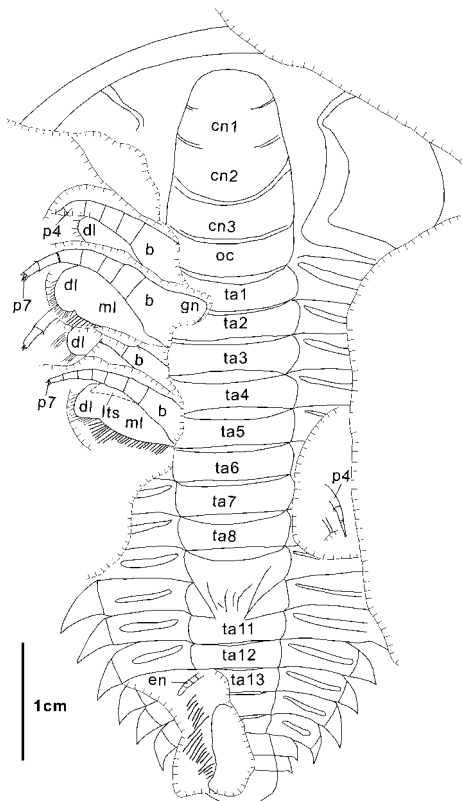


Figure 4 Drawing of YKLP 10965 (Fig. 2B). Abbreviations: see caption to Figure 3.

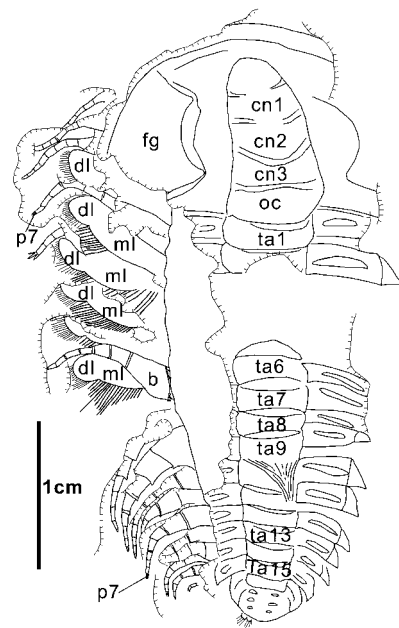


Figure 5 Drawing of YKLP 10966 (Fig. 2D). Abbreviations: see caption to Figure 3.

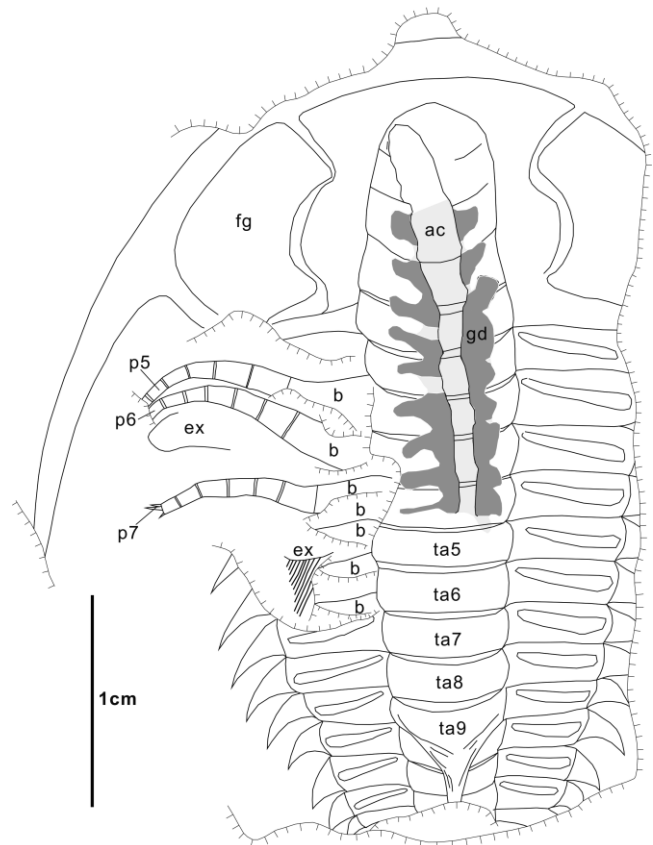
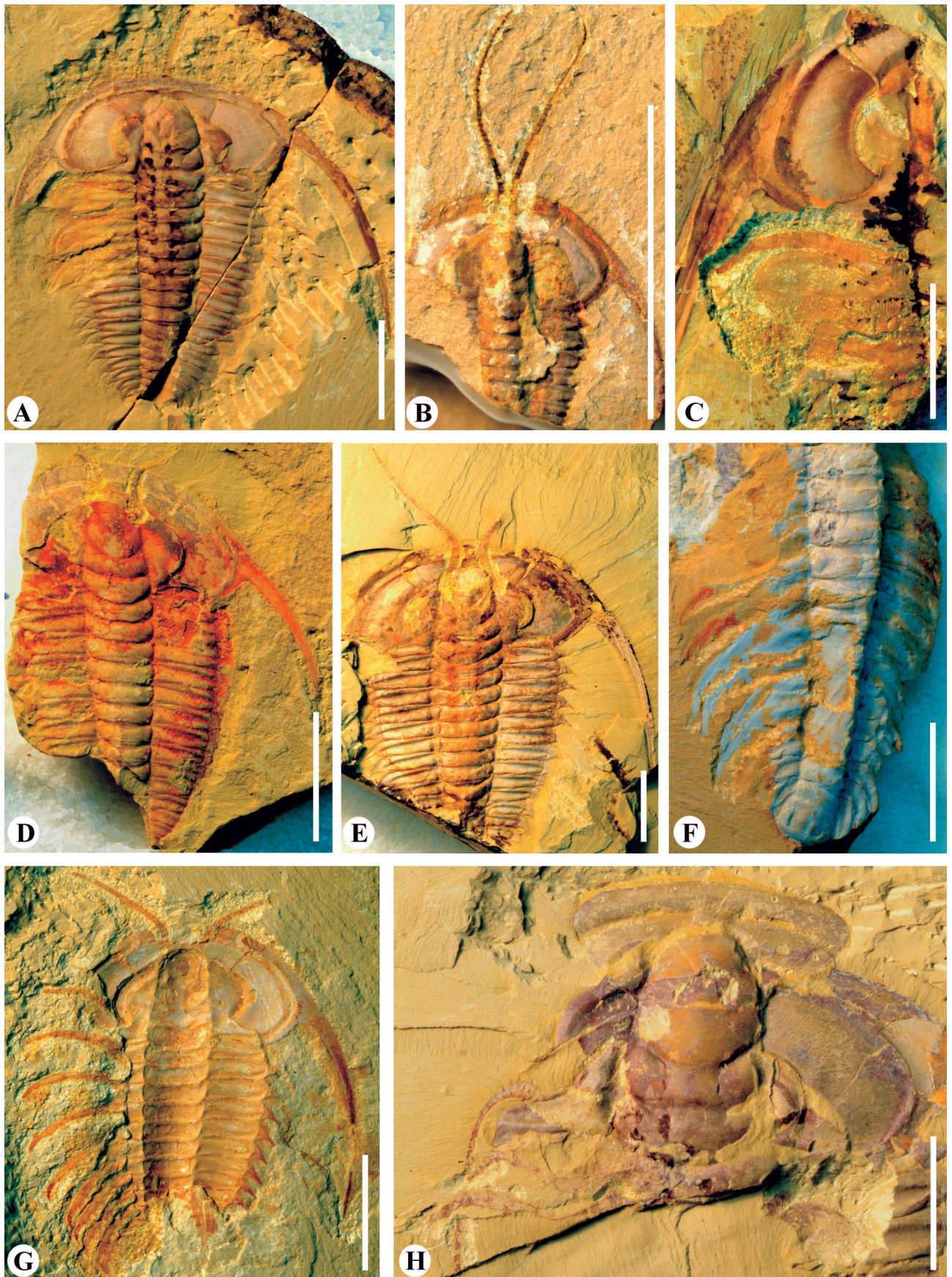


Figure 6 Drawing of YKLP 10967 (Fig. 2E). Abbreviations: see caption to Figure 3.

model. He interprets *Olenoides* as a heterotroph, able to feed upon organic remains or small soft-bodied invertebrates, depending on what was available. Chatterton *et al.* (1994) described the digestive system of *Pterocephalia* from the Upper Cambrian of British Columbia. This bears a striking resemblance to that of *Eoredlichia* in the presence of (?eight) paired diverticulae confined to the anterior part of the gut, extending some way into the thorax. These authors suggest that this condition is plesiomorphic for Cambrian trilobites and their



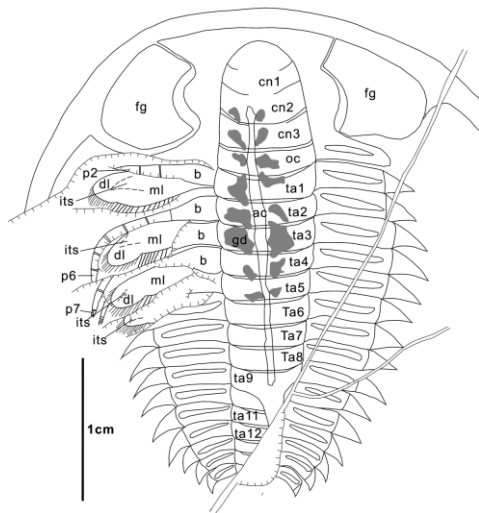


Figure 8 Drawing of YKLP 10968 (Fig. 7A). Abbreviations: see caption to Figure 3.

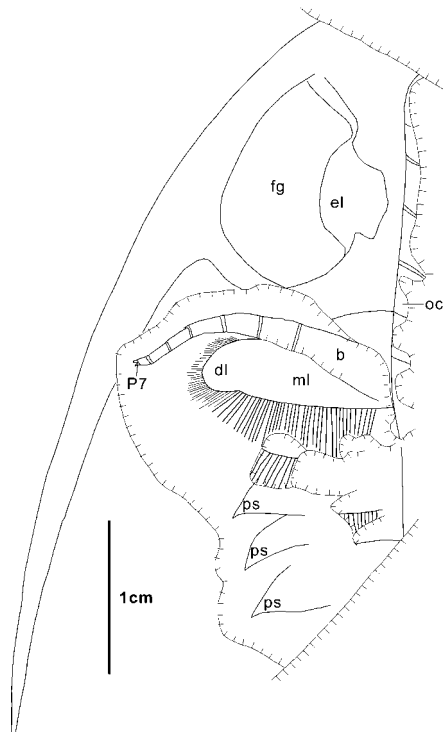


Figure 9 Drawing of YKLP 10969 (Fig. 7C). ps=pleural spine. For other abbreviations, see caption to Figure 3.

probable sister group Nectaspida (including *Naraoia*). The presence of detrital minerals in the gut suggested to Chatterton *et al.* that *Pterocephalia* was a deposit feeder, though since the

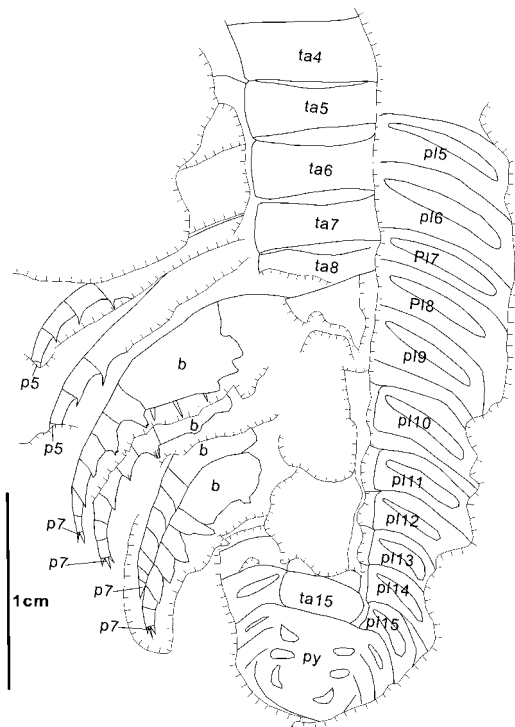


Figure 10 Drawing of YKLP 10970 (Fig. 7F). Abbreviations: see caption to Figure 3.

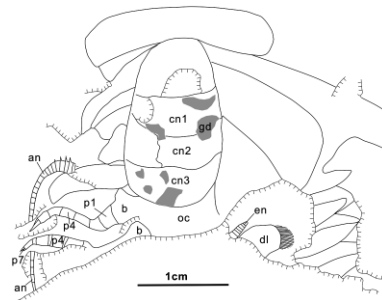


Figure 11 Drawing of YKLP 10971 (Fig. 7H). Abbreviations: see caption to Figure 3.

appendages remain unknown, it is not possible to tell whether they were also adapted for predation. Although the anterior-most part of the gut in *Eoredlichia* is relatively narrow and not distended as a stomach in the one specimen in which it is preserved, it is otherwise like that of other Cambrian trilobites in which the digestive system is known. For the moment the scavenger/predator model for *Eoredlichia* is as good as any.

Figure 7 Appendage-bearing specimens of *Eoredlichia intermedia* (Lu) from the *Eoredlichia*–*Wutingaspis* zone of the Lower Cambrian Qiongzhusian Stage. (A–G) Mafang section, Haikou, Kunming; (H) Ercaicun section, Haikou, Kunming. Scale bars=1 cm. (A) YKLP 10968, gut diverticulae with symmetrical black crescentic markings, attached to the alimentary canal; (B) YKLP 10983, a small incomplete specimen with the right antenna with 45 articles although its base not exposed; (C) YKLP 10969, the exopod almost complete, the main lobe attached by a distinct straight hinge joint to the basis, the full main lobe with 37 filaments. (D) YKLP 10984, the bases of the antennae deeply recessed within the cephalon on either side of the hypostome; (E) YKLP 10982, excavated anteriorly to show the bases of the antennae; (F) YKLP 10970, the swollen basis in ninth thoracic segment, which has a nearly straight rear edge bearing three long spines, about equal to the three proximal podomeres in width (tr.), the proximal podomeres showing an endite with three or four small spines; (G) YKLP 10972, in the endopods of thoracic segments ta 5–10, the outer five or six podomeres distinguished, each with an endite, ventrally directed, emerging from its outer edge where it joins with the next podomere; (H) YKLP 10971, on the right side, an endopod and a distal lobe of exopod with filaments which are thin and plate-shaped like the filaments of the main lobe, rather than needle-shaped.

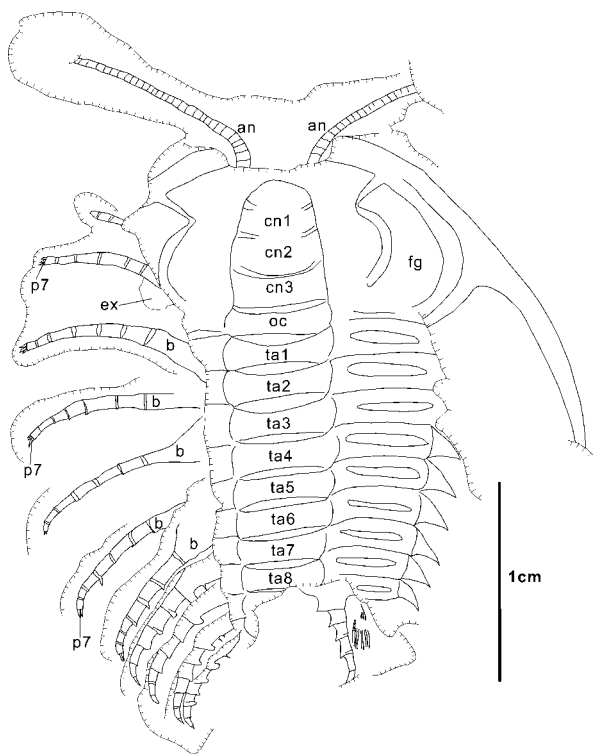


Figure 12 Drawing of YKLP 10972 (Fig. 7G). Abbreviations: see caption to Figure 3.

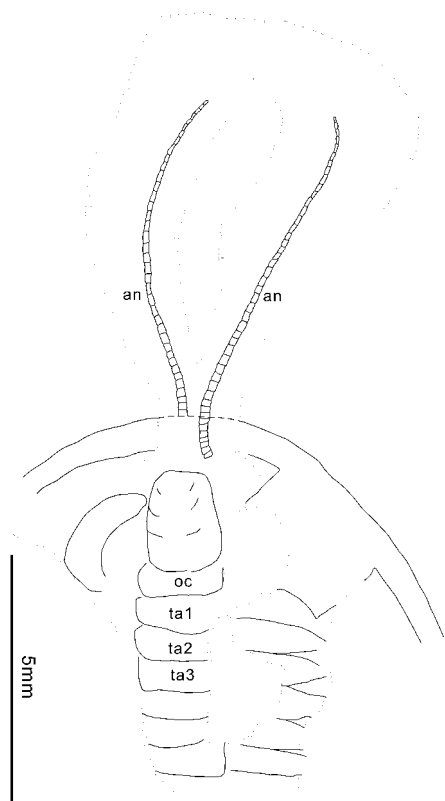


Figure 13 Drawing of YKLP 10983 (Fig. 7B). Abbreviations: see caption to Figure 3.

4. Description of the specimens of *Eoredlichia intermedia* (Lu 1940)

4.1. YKLP 10964 (Figs 2A, 3)

This large specimen, 66 mm in length, is probably the most informative amongst the present material. It is almost

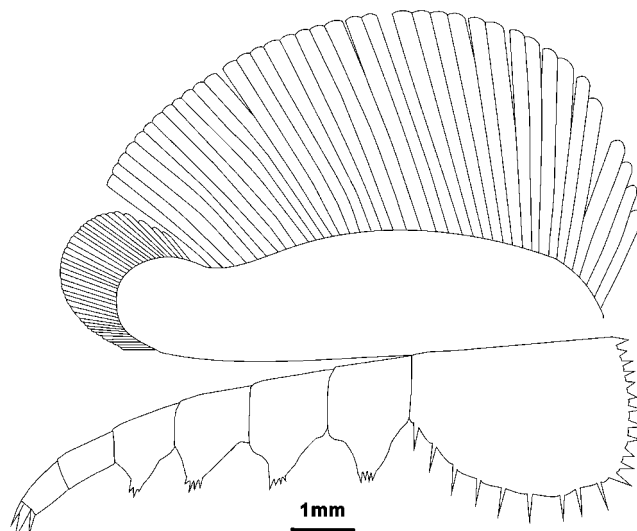


Figure 14 Reconstruction of a biramous (particularly a thoracic) appendage of *Eoredlichia intermedia* (Lu), shown as preserved in a compacted state rather than in its original life position.

complete, and is preserved in dorsal view, though obliquely broken on the right side. The left side is intact and only the tip of the pygidium is missing. The specimen is pale red in colour, with only the axis being darker; contrasting with the pale buff-coloured matrix. The whole left side of the body has been excavated as far back as the sixth thoracic segment, and on the right side appendages 2–4 are now exposed by preparation.

The bases of the antennae are slightly swollen and are set deep within the body, as far back as the anterior edge of the ocular ridges. Anteriorly the antennae converge forwards, following the contour of the hypostomal neck, and at the anterior border of the cephalon, curve outwards again to run straight, diverging from the sagittal plane at about 30 degrees. Most of the right antenna is preserved; in both antennae the individual articles are visible, though poorly defined.

Seven biramous appendages are present on the left side, three belonging to the cephalon and four to the thorax. Of the first two cephalic appendages (cn 1 and cn 2), only part of the exopod is present, with visible, though imperfect filaments. It is smaller than the more posterior exopods, and confined within the cephalic rim. To the left of the antennal base, however, is a well-preserved fan of filaments, presumably belonging to the same exopod. The posterior appendages (cn 3 and ta 1) bear both endopods and exopods. Although the junctions between these two components are obscure, cn 3 and ta 1 have both been excavated to expose the gnathobases (gn), which form prolongations of the basis, or basal joint of the appendage. These gnathobases extend inwards across the axial furrow towards the mid-line. They appear parallel-sided, and have rounded ends with about 12 tiny spines. The following two thoracic appendages (ta 2 and 3) are preserved in a similar way to cn 3, though they are larger and the endopods extend out beyond the body. The fourth thoracic appendage (ta 4) is well preserved and shows the structure of the whole biramous limb very clearly. The basis is swollen, and the straight endopod is clearly defined; it is slender, with seven podomeres, the distal one being composed of three well-preserved spines. The exopod has a broad, flat, blade-like main lobe, about four times as long as it is wide (exsag.). Though subparallel sided, it is somewhat more slender where it joins the basis, and distally there is an indentation in the rear margin, defining a small distal lobe. The latter does not seem to be a separate structure, due to a lack of clear division from the main lobe. A slightly curving oblique ridge, tapering outwards, traverses the distal

lobe. Although this feature occurs in many other specimens, it is regarded as no more than an impression of the overlying thoracic spine. From the rear margin of the main lobe, more than 30 parallel filaments extend as far as the rear edge of the sixth thoracic pleura; this filamentary array is typically long (sag.). The distal lobe is fringed with a radial fan of short filaments. Two interpretations are possible for the relationship between the basis and the rest of the limb. One is that the exopod is dorsally hinged to the basis, and that the basis is thus part of the exopod. The other is that both the endopod and the exopod split from the basis, and thus that the latter is not part of the endopod. In the present material the junction between the basis and the exopod, where visible, forms a straight line, which appears to confirm the interpretation of Ramsköld & Edgcombe (1996) that it is a hinge joint. The exopod, as in other trilobites, lies above the endopod, and such a joint would allow the exopod to remain undisturbed and independent, even if there was considerable leg movement of the endopod. If so then the basis and the exopod are parts of the same structure.

On the right side is the well-exposed second thoracic segment (ta 2). The endopod is straight, and lies parallel with the leading edge of the exopod, and at least a basis and five other podomeres are visible. Much of the filament array is present, though broken at the right side.

A pattern of pale red and yellow concentric and wavy lines covering the surfaces of most of the preserved appendages is probably diagenetic in origin.

4.2. YKLP 10965 (Figs 2B, 4)

A very large specimen, 62 mm in length, in dorsal view, with a preserved medium-brown cuticle. Antennae are not preserved, but appendages are otherwise exposed in three areas, in the left anterior region of the thorax, the left posterior area, and the middle part of the thorax on the right side. In the left anterior region are present the appendages of the first five thoracic segments (ta 1–5). Ta 1 shows a poorly preserved endopod and exopod with little defined structure. Ta 2 displays a fairly distinct endopod preserved along its length, terminating in three spines. The straight hinge-joint is faintly distinguishable between the endopod and the exopod. The latter is of typical form, with a broad main lobe and a rounded distal lobe retaining some of its short filaments. The appendage is prolonged inwardly into a gnathobase, though no endites can be distinguished. In ta 3, part of the exopod is retained, as is part of the endopod with its distal lobe, though displaced from its true position. The appendage of the fourth thoracic segment (ta 4) is present, with its endopod having its distal joint broken off, and its exopod with a distinct main lobe and distal lobe, both with a fringe of filaments. The endopod/exopod junction is obscure.

The left posterior part of the thorax displays some oblique, tapering rods and, anteriorly, a chain of podomeres of a small endopod. The oblique rods presumably represent exopod filaments; they are shorter and stouter than those of the anterior regions. On the right side in the centre are a few indifferently preserved endopods, with three or four podomere spines remaining.

4.3. YKLP 10966 (Figs 2D, 5)

This inverted specimen, originally 39 mm long, is pale pink in colour, with reddish patches. Antennae are lacking, but appendages are preserved in the thorax along most of the left side. The anterior group consists of both endopods and exopods, slightly displaced from their original position, and radiating out fanwise from the centre. At least six of these are present, but it is uncertain to which segments they belong. The

distal podomeres of the endopods are preserved, the second displaying short, sharp spines. Several exopod lobes are present, crushed down one upon another; the whole area has many preparation-scarps and only the most posterior exopod lobe is seen in its entirety. Several sets of exopod filaments are visible, though none are complete; exopods show a slight indentation in their posterior margin, defining the distal lobe. Distal lobes, each with a fringe of filaments are visible for exopods of the thoracic segments ta 1–6. The endopod of ta 6 shows the swollen basis, and part of the gnathobase, which curls distally round the anterior margin of the exopod, though the anterior edge is broken. The straight hinge joint between the basis and the exopod is clearly distinct. This appendage also shows the characteristic shape of the main exopod lobe, and the well-defined distal lobe. Some filaments remain attached to the main exopod lobe and these terminate at the junction with the gnathobase.

A posterior set of appendages consists entirely of endopods, of which nine or ten are present; they are closely spaced, with their distal podomeres subparallel with the sagittal plane. A series of repeated preservation-scarps in the enclosing sediment has broken the anterior edges of most of these endopods, and only the posterior parts are fully visible. Several of these endopods are otherwise complete along their length, and some of the podomeres retain their sharp spines. One or two terminal spines are present on some of the endopods.

The two very small lobes with filaments extend beyond the posterior margin of pygidium, representing two appendages in the pygidium.

4.4. YKLP 10967 (Figs 2E, 6)

An individual, preserved dorsal side up, originally 39 mm long, retaining anteriorly the symmetrically placed lobes of the gut diverticulae, attached to the alimentary canal, four pairs in the cephalon and four or five in the thorax. The left side has been prepared to show three endopods of ta 2, 3 and 4. These extend outside the body, each having a swollen basis and seven podomeres. Preservation is better towards the outer extremities, and the fourth endopod clearly shows three short terminal spines. The exopods are only present as fragments. The anterior edge of the basis is present in ta 5, 6, and 7, and overlying ta 6 is a tiny fragment showing exopod filaments.

This specimen shows a very clear trace of the gut, or at least part of it, slightly displaced, and lying obliquely towards the right hand side. It consists of a central, parallel-sided tube, faintly yellowish-green in colour, extending from the front of the glabella to ta 4. From this tube arise nine pairs of curving, relatively narrow lobes, each reaching about half way to the axial furrow, and preserved as a dark brown mineral. There are four lobes in the glabella (including the occipital ring) directed obliquely forwards, and the fourth pair are connected by the brown mineral, which has been removed elsewhere. The five pairs of lobes in the thorax, one for each segment, are laterally directed. A faint median trace in ta 5 and ta 6 may represent a further continuation of the gut. The shapes of the gut and its diverticulae have clearly been picked out by the gut contents, but give no real indication as to what these contents originally were. A similar intestinal system is present in YKLP 10968 (Fig. 7A) and YKLP 10982 (Fig. 7E)

4.5. YKLP 10968 (Figs 7A, 8)

An individual preserved dorsal side up, originally 34 mm long, excluding the dorsal spine, which lies at a higher level. This specimen is pale brown in colour, and preserves the alimentary canal as a darker brown axial streak. Gut diverticulae are represented by symmetrical black crescentic markings,

attached to the alimentary canal, for three cephalic and the first five thoracic segments, and are closely comparable with those of other specimens (cf. Figs 2E, 7E). Antennae are not present in this specimen. The left side has been prepared to show several thoracic appendages.

The appendage of the first thoracic segment (ta 1) shows an endopod, lacking structure, and partially obscured by the overlying exopod, of which the anterior edge is broken. The distal lobe is distinct, with filament bases present, and the bases of longer filaments attach along the posterior margin of the exopod. Ta 2 has a well-preserved endopod curling round the anterior margin of the exopod. The basis is swollen and six podomeres are preserved, the seventh being broken off. Each of the joints displays a kind of annulus, or ring, with parallel edges, when flattened appearing strip like. This is shown by several other specimens, including YKLP10966 (Fig. 2D), 10967 (Fig. 2E), 10969 (Fig. 7C) and 10972 (Fig. 7G). The main exopod lobe is joined to the basis by an unmistakable straight hinge. An array of filaments, truncated during preparation, attaches to the rear edge of the main exopod lobe. This fringe largely obscures the endopod of ta 3, behind which is the broad exopod, with a well-preserved distal lobe with its fan of short filaments. The terminations of the endopods of ta 3 and ta 4, however, are present, each showing at least two terminal spines. The exopod of ta 4 is partially present. The distal lobes of ta 1–4 bear a crescentic ridge, as seen in some other specimens.

4.6. YKLP 10969 (Figs 7C, 9)

This specimen consists of a detached librigena, dorsal side up, originally belonging to a large cephalon approximately 20 mm in length. Just posterior to the librigena the appendage of the first thoracic segment (ta 1) is exposed, picked out in pale red. This is the best-preserved appendage in the material available to us. The basis is swollen and seven podomeres of the endopod taper distally; though the outer termination is slightly obscure, two terminal spines appear to be present. The exopod is almost complete, the main lobe attached by a distinct straight hinge joint to the basis. The full array of exopod filaments is well-preserved from the rear edge of the main lobe, though truncated posteriorly. 37 filaments are preserved on the rear edge of the main lobe, and there may be about 40 filaments, because a space representing some three filaments is present on the proximal portion of the rear edge. A rounded distal lobe preserves a radial fringe of short filaments. Fragments of a second and third exopod underlie ta 1 posteriorly.

4.7. YKLP 10970 (Figs 7F, 10)

Both part and counterpart of this specimen have been prepared for study; the individual originally being 53 mm long, the cephalon is separated from the body. The exoskeleton has been replaced by a white mineral. Stout endopods have been preserved in the central and posterior parts of the body. Of the first two (ta 7 and 8) only the distal three podomeres are present, picked out as a red film, each showing a characteristic spine at the joint. The terminal parts are broken off. The remaining endopods are preserved in the same white mineral as the exoskeleton, and are stoutly built, spinose, and closely spaced together. Ta 9 shows the swollen basis that has a little straight rear edge which bears three long spines. The basis is about equal to the three proximal podomeres in width (tr.). The proximal four out of seven podomeres show an endite with three or four small spines. Ta 10–12 show similar structures, the endites on the proximal podomeres being especially well developed. Some parts of the exopods are present on the counterpart, along with some poorly preserved exopod filaments, but reveal no further structural details.

4.8. YKLP 10971a (Figs 7H, 11)

This specimen consists of the part and counterpart of the cranidium of a very large individual, together with the right librigena, with its long spine. The cephalon, 23 mm in length, is greyish-brown in colour and has not been greatly flattened. Paired black lobate markings on both part and counterpart represent gut diverticulae.

This important specimen, dorsal side up, shows details of a detached antenna, displaced from its original position and strongly curving like a hook, with the more distal part lying subparallel with the sagittal plane. It seems to lack the basal portion, which would have inserted below the anterior border, but otherwise retains 17 articles. The proximal five of these are appreciably broader and shorter than the distal set, and each is provided with a thin, sharp spine at the junction with the next article. In life, these spines faced inwards, toward the mid-line of the trilobite, as shown by specimen YKLP10973 (Fig. 2C). Distal to this set, the antenna curves sharply and becomes narrower, the articles becoming longer as well as more slender, each being a short, spineless cylinder, with its length about twice its width. The last five preserved articles are detached but lie in a chain continuous with the others.

Overlying the antenna are two endopods, the anterior one with a swollen basis, and altogether seven podomeres in moderately good preservation. The second endopod appears broader, probably due to crushing, and has five preserved podomeres. The joints, as in specimen YKLP 10969 (Figs 7A, 8) and others, show an annular ring, with parallel edges, appearing strap-like when crushed. On the right side of this specimen an endopod and a distal lobe of exopod with filaments are present. The filaments of the distal lobe are thin and plate-shaped like the filaments of the main lobe, rather than being needle-shaped (Fig. 13).

4.9. YKLP 10972 (Figs 7G, 12)

An inverted specimen, of which the rear part is damaged. The original length would have been 28–30 mm, excluding appendages. It is brownish-red in colour, the underside of the cephalon being pale grey. The left side has been prepared to show a range of endopods; the exopods are generally represented by imperfectly preserved, greyish flat lobes. No exopod filaments are present, except in a small patch on the right side towards the rear.

The antennae diverge more strongly than in most specimens; their bases are not seen. Nothing remains of cn 1; cn 2 is represented only by a fragment of an endopod, and that of cn 3 by a slender curving rod in which separate podomeres are faintly discernible. Ta 1–4 are of similar form, and appear to preserve their full length. The swollen basis is generally apparent and podomeres 1–7 can be seen in some cases; the tips of the endopods are curved and tapering, and several of these bear up to three terminal spines. A faint exopodal lobe can be distinguished for cn 3.

Whereas these anterior appendages are slender, and are spread out like a fan, the endopods of thoracic segments ta 5–10 inclusive are shorter, stouter and more spiny; they are closely spaced and subparallel. In most cases, the outer five or six podomeres can be distinguished, each with an endite, originally ventrally directed, emerging from its outer edge where it joins with the next podomere. The tip of each endopod ends in a sharp point; it is not clear whether or not there were terminal spines or claws. Appendages posterior to those of the tenth thoracic segment are not present.

On the right side, a single displaced set of appendages, lying subparallel with the sagittal plane, exposes at least the outer five podomeres of the endopod, the distal one sharply curved, together with a fragment of exopod with filaments lying

adjacent. This appendage probably belongs to the seventh or eighth thoracic segment.

4.10. YKLP10973 (Fig. 2C)

This specimen, 54 mm long, is completely preserved in dorsal view. It is preserved in a brownish mineral, with the axis picked out in orange red, the rest of the exoskeleton is somewhat abraded. A pair of well-preserved antennae is present, the individual articles being present on the right side, and to a lesser extent on the left. On the right side, four or five of the articles are short and broad and bear short spines, directed inwards towards the median plane (cf. specimen YKLP 10971). A single endopod belonging to cn 3 displays the swollen basis, and tapers markedly distally. The podomeres are well defined, though no spines are visible, and the terminal joint is lacking.

4.11. YKLP10982 (Fig. 7E)

This large, almost complete individual, 46 mm long, is preserved dorsal side up. It has been excavated anteriorly to show the bases of the antennae deeply recessed within the cephalon, on either side of the hypostome. The character is also proved by specimen YKLP10984 (Fig. 7D). It also shows paired red patches in the cephalon and anterior part of the thorax, interpreted as diverticulae of the gut.

4.12. YKLP10983 (Figs 7B, 13)

This small incomplete specimen, originally 12 mm long, bears a pair of antennae, which are usually directed forwards and are curving rather than diverging and straight. The right antenna shows about 45 articles, although its base is not exposed. Although there has evidently been some displacement, it is possible that the antennae of smaller protaspides were more flexible.

5. Acknowledgements

The study was supported by the National Natural Foundation of China (40730211, 40672003), 973 Program of China (2006CB806400) and Department of Science and Technology of Yunnan Province (2005D0002Z), which enabled a month-long visit to Yunnan by ENKC in March 2007. We are most grateful to our referees, Greg Edgecombe and Jih Pai-Lin, whose comments have greatly improved the quality of the final manuscript.

6. References

- Babcock, L. E. 2003. Trilobites in Paleozoic predator-prey systems and their role in reorganization of Early Paleozoic ecosystems. In Kelley, P. H., Kowalewski, M. & Hansen, T. A. (eds) *Predator-prey interactions in the fossil record*, 55–92. New York: Kluwer Academic/Plenum Publishers.
- Babcock, L. E. & Peel, J. S. 2007. Palaeobiology, taphonomy and stratigraphic significance of the trilobite *Buenellus* from the Sirius Passet Biota, Cambrian of North Greenland. *Memoirs of the Association of Australasian Palaeontologists* **34**, 331–48.
- Bergström, J., Hou, X.-G. & Hålenius, U. 2007. Gut contents and feeding in the Cambrian arthropod *Naraoia*. *GFF* **129**, 71–6.
- Caron, J.-B. & Jackson, D. A. 2006. Taphonomy of the Greater Phyllopod Bed community, Burgess Shale. *Palaios* **21**, 451–65.
- Chatterton, B. D. E., Johanson, Z. & Sutherland, G. 1994. Form of the trilobite digestive system; alimentary structures in *Pteroecephalia*. *Journal of Paleontology* **68**, 294–305.
- Edgecombe, G. D. & Ramsköld, L. 1999. Relationships of Cambrian Arachnata and the systematic position of Trilobita. *Journal of Paleontology* **73**, 263–87.
- Gaines, R. R., Briggs, D. E. G. & Zhao, Y.-L. 2008. Cambrian Burgess Shale type deposits share a common mode of fossilization. *Geology* **36**, 755–8.
- Gabbott, S. E., Hou, X.-G., Norry, M. J. & Siveter, D. J. 2004. Preservation of Early Cambrian animals of the Chengjiang biota. *Geology* **32**, 901–4.
- Hou, X.-G., Ramsköld, L. & Bergström, J. 1991. Composition and preservation of the Chengjiang fauna – a Lower Cambrian soft-bodied biota. *Zoologica Scripta* **20**, 395–411.
- Hou, X.-G., Aldridge, R. J., Bergström, J., Siveter, D. J., Siveter, D. J. & Feng, X.-H. 2004. *The Cambrian fossils of Chengjiang, China: the flowering of early animal life*. Oxford: Blackwell Publishing, 233 pp.
- Hou, X.-G. & Bergström, J. 1997. Arthropods from the Lower Cambrian Chengjiang fauna, southwest China. *Fossils and Strata* **45**, 1–116.
- Hughes, N. C. 2003. Trilobite tagmosis and body patterning from morphological and developmental perspectives. *Integrative and Comparative Biology* **43**, 185–206.
- Hughes, N. C. 2007. The evolution of trilobite body patterning. *Annual Review of Earth and Planetary Sciences* **35**, 401–34.
- Lin, J.-P. 2006. Taphonomy of naraoids (Arthropoda) from the Middle Cambrian Kaili Biota, Guizhou Province, South China. *Palaios* **21**, 15–25.
- Lin, J.-P. 2007. Preservation of the gastrointestinal system in *Olenoides* (Trilobita) from the Kaili Biota (Cambrian) of Guizhou, China. *Memoirs of the Association of Australasian Palaeontologists* **33**, 179–89.
- Lu, Y.-H. 1940. On the ontogeny and phylogeny of *Redlichia intermedia* Lu (sp. nov.). *Bulletin of Geological Society of China* **XX** (3–4), 333–42. [In Chinese.]
- Page, A., Gabbott, D. S. E., Wilby, P. R. & Zalasevic, J. A. 2008. Ubiquitous Burgess Shale-style ‘clay-templates’ in low-grade metamorphic mudrocks. *Geology* **36**, 855–8.
- Paterson, J. R., Jago, J. B., Gehling, J. G., Garcia-Bellido, D. C., Edgecombe, G. D. & Lee, M. S. Y. 2008. Early Cambrian arthropods from the Emu Bay Shale Lagerstätte, South Australia. In Rabano, I., Gozalo, R. & Garcia-Bellido, D. (eds) *Advances in Trilobite Research*, 319–25. Madrid: Instituto Geológico y Minero de España.
- Ramsköld, L. & Edgecombe, G. D. 1996. Trilobite appendage structure: *Eoredlichia intermedia* reconsidered. *Alcheringa* **20**, 269–76.
- Shu, D.-G., Geyer, G., Chen L. & Zhang, X.-L. 1995. Redlichian trilobites with preserved soft-parts from the Lower Cambrian Chengjiang fauna (South China). *Beringeria, Special Issue 2*, 203–41.
- Whittington, H. B. 1975. Trilobites with appendages from the Middle Cambrian, Burgess Shale, British Columbia. *Fossils and Strata* **4**, 97–136.
- Whittington, H. B. 1997. The trilobite body. In Whittington, H. B., Chatterton, B. D. E., Speyer, S. E., Fortey, R. A., Owens, R. M., Chang, W. T., Dean, W. T., Jell, P. A., Laurie, J. R., Palmer, A. R., Repina, L. N., Rushton, A. W. A., Shergold, J. H., Clarkson, E. N. K., Wilmot, N. V. & Kelly, S. R. A. (eds) *Treatise on Invertebrate Paleontology Part O, Trilobita, Revised. Volume 1: Introduction, Order Agnostida, Order Redlichiida*, 87–114. Boulder, Colorado, and Lawrence, Kansas: Geological Society of America and University of Kansas Press, 530 pp.
- Zhang, W.-T. 1962. On the genus *Eoredlichia*. *Acta Palaeontologica Sinica* **10** (1), 36–44. [In Chinese with English summary.]
- Zhang, W.-T. 1986. Correlation of the Cambrian of China. *Palaeontologia Cathayana* **3**, 267–85.
- Zhang, X.-G. & Hou, X.-G. 2007. Gravitational constraints on the burial of the Chengjiang fossils. *Palaios* **22**, 448–53.
- Zhou, Z.-Y. & Yuan, J.-L. 1982. A tentative correlation of the Cambrian System in China with those in selected regions overseas. *Bulletin of the Nanjing Institute of Geology and Palaeontology, Academia Sinica* **5**, 289–306. [In Chinese with English abstract.]
- Zhu, M.-Y., Zhang, J.-M. & Li, G.-X. 2001. Sedimentary environments of the early Cambrian Chengjiang biota: sedimentology of the Yu'anshan Formation in Chengjiang County, eastern Yunnan. In Zhu, M.-Y., Van Iten, H., Peng, S.-C. & Li, G.-X. (eds) *The Cambrian of South China. Acta Palaeontologica Sinica* **40** (supplement), 80–105.