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Appendages of the arthropod *Kunmingella* from the early Cambrian of China: its bearing on the systematic position of the Bradoriida and the fossil record of the Ostracoda

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SUMMARY

The first discovery of the appendages belonging to the Bradoriida s.str. Arthropoda – generally supposed to have been ostracodes until now – is reported in *Kunmingella* from the early Cambrian soft-bodied 'Chengjiang' Lagerstätte of China. Although this evidence does not particularly clarify the affinities of *Kunmingella* within the Arthropoda, it does demonstrate that this genus, and by implication other taxonomically allied bradoriids in general, are neither ostracode, crustacean s.str. nor closely related to the Phosphatocopida (also conventionally classed as ostracodes). This has far-reaching implications for the stratigraphical distribution and evolution of the Class Ostracoda: that much (all?) of their Cambrian record is most likely spurious. The discovery also endorses the fact that arthropod radiation involved several different types of convergently bivalved groups.

1. INTRODUCTION

The Ostracoda is an important group of small bivalved Crustacea, represented by about 13000 described Recent species (Morin & Cohen 1991). Adults are typically 1–3 mm long. In numbers of individuals and species they are the most abundant fossil arthropods and have been extensively documented from throughout the Phanerozoic, spanning more than 500 Ma. Ostracodes were originally marine and probably benthic, but by the Silurian had expanded into reduced salinity and pelagic environments (Siveter 1984; Siveter *et al.* 1991). They have colonized virtually all types of marine, brackish and freshwater habitats and are widely used in biostratigraphy and in determining palaeoenvironments and palaeogeographies.

Traditionally, all small bivalved arthropods in the Cambrian have been referred to the Order Bradoriida Raymond (Raymond 1935), and the group is regarded as synonymous with the Cambrian record of the Ostracoda. The Bradoriida *sensu* Raymond encompasses more than 120 published, essentially Cambrian, genera (most descriptions are based on relatively few, often ill-preserved, specimens from the early Cambrian of China, and require reexamination). The earliest records (based on shell morphology) of representatives of ostracode taxa which occur in the Recent are of Podocopida from the Ordovician (e.g. see Whatley *et al.* 1993).

Two major groups of Bradoriida have been distinguished, the Bradoriina Raymond (Raymond 1935) and the Phosphatocopina Müller (Müller 1964); both are often treated at ordinal level, as in Müller (1982) and in this paper. Based on evidence from preserved soft-parts, some authors have recently hinted that the Phosphatocopida do not belong within the Ostracoda or even the Crustacea s.str. but rather are stem-group derivatives close to the level of the crown-group Crustacea (e.g. Walossek & Müller 1992; full analysis unpublished, but see below). Accepting that this affinity exists, knowledge of the hitherto unknown soft-part morphology of the Bradoriida s.str. is crucial not only in supporting or denying the assignment of that group to the Ostracoda, but also in serving as evidence of the existence of ostracodes in the Cambrian.

Based on new discoveries of specimens of the bradoriid *Kunmingella* with preserved appendages from the Cambrian of China, we present evidence that this genus is neither an ostracode nor closely related to the Phosphatocopida. By inference, other Kunmingellidae and the morphologically similar Cambriidae at the very least, and possibly the Bradoriida s.str. as a whole, are not ostracodes. This notion has the far-reaching

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implication that much, and possibly all, of the supposed Cambrian ostracode record is spurious.

2. GEOLOGICAL SETTING

Our finds of *Kunmingella* with appendages are from the exceptionally well-preserved 'Chengjiang' Lagerstätte, the world's oldest, major, Phanerozoic soft-bodied fauna, which was discovered in 1984 by H. X-G. (see Zhang & Hou 1985). The Chengjiang fauna is known from several localities in the early Cambrian Qiongzhusi Formation (ca. 50 m thick): near Kunming, east-central Yunnan Province; and in the southwestern part of the Yangtze Platform, southern China (figure 1; see Chen *et al.* 1989; Hou & Bergström 1991; Hou *et al.* 1991; and references therein). This assemblage, which first appears about 25 m above the earliest trilobites (*Abadiella*) and is known from more than 10 horizons, belongs to the lower part of the *Eoredlichia-Wutingaspis* trilobite Biozone (figure 2). By an indirect chain of correlation (e.g. Qian & Bengtson 1989; Bengtson *et al.* 1990; Palacios & Vidal 1992; Zang 1992) the 'Chengjiang fauna' is considered to be of probable late Atdabanian age.

Arthropods dominate the Chengjiang fauna, representing some 46% of more than 70 species recovered (Hou *et al.* 1991). A similar dominance also occurs in the three other spectacular Lagerstätten of Cambrian age, from the slightly younger early Cambrian Buen Formation at 'Sirius Passet' in North Greenland, the middle Cambrian Burgess Shale of British Columbia and the late Cambrian 'Orsten' of Sweden (e.g. Conway Morris 1986; Conway Morris *et al.* 1987; Conway Morris & Peel 1995; Müller & Walossek 1985, 1991).

The rocks of the Qiongzhusi Formation are predominantly finely laminated marine mudstones, probably deposited in an outer shelf setting (Chen *et al.* 1989); they show no signs of metamorphic alteration. Occasional intercalated sandstones possibly represent distal storm deposits.

Figure 1. Location of Chengjiang, Yunnan Province, southwest China

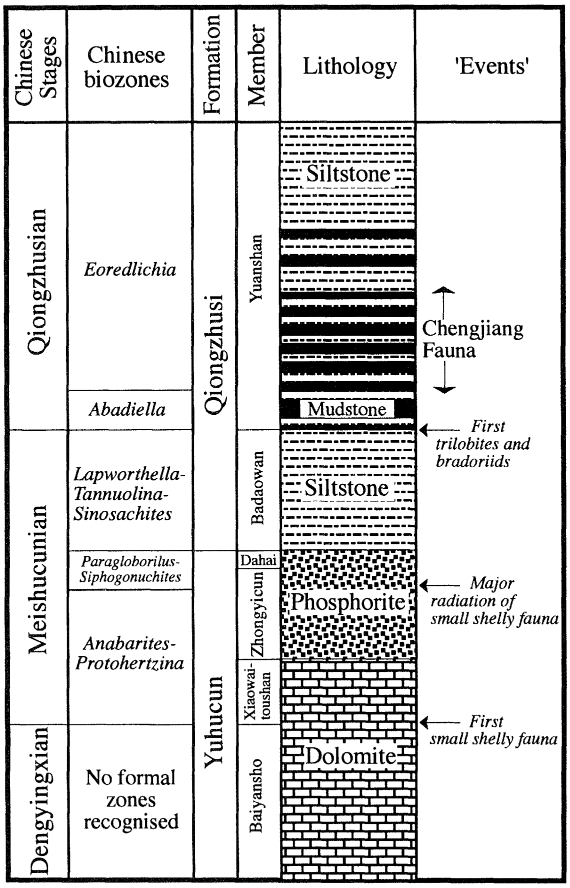

Figure 2. Stratigraphical position of the Chengjiang fauna, within the early Cambrian of Chengjiang County, Yunnan Province, southwest China (compiled from data in Chen *et al.* 1989 and Hou *et al.* 1991). The *Anabarites-Protohertzina* to *Sinosachites* small shelly fossil zones are as delimited in the nearby Meishucun section (Qian & Bengston 1989). The *Abadiella* and *Eoredlichia* zones are based on trilobites. The Cambrian-Precambrian boundary approximates to the base of the Meishucunian Stage.

3. CHENGJIANG BRADORIIDS WITH SOFT INTEGUMENT

(*a*) *Rarity*

Five bradoriid specimens displaying varying amounts of soft-part preservation have been recovered. They belong to the species *Kunmingella maotianshanensis* Huo & Shu (see Huo *et al.* 1983) and represent the only known evidence regarding appendage and body morphology of bradoriids s. str. The material is deposited in the Nanjing Institute of Geology and Palaeontology (NIGPAS), Academia Sinica, Nanjing, People's Republic of China.

Although these specimens are from a Lagerstätte in which soft tissue preservation is not uncommon, they nevertheless represent extremely rare finds. Bradoriids such as kunmingellids are the most common component of the Chengjiang fauna (thousands of valves,

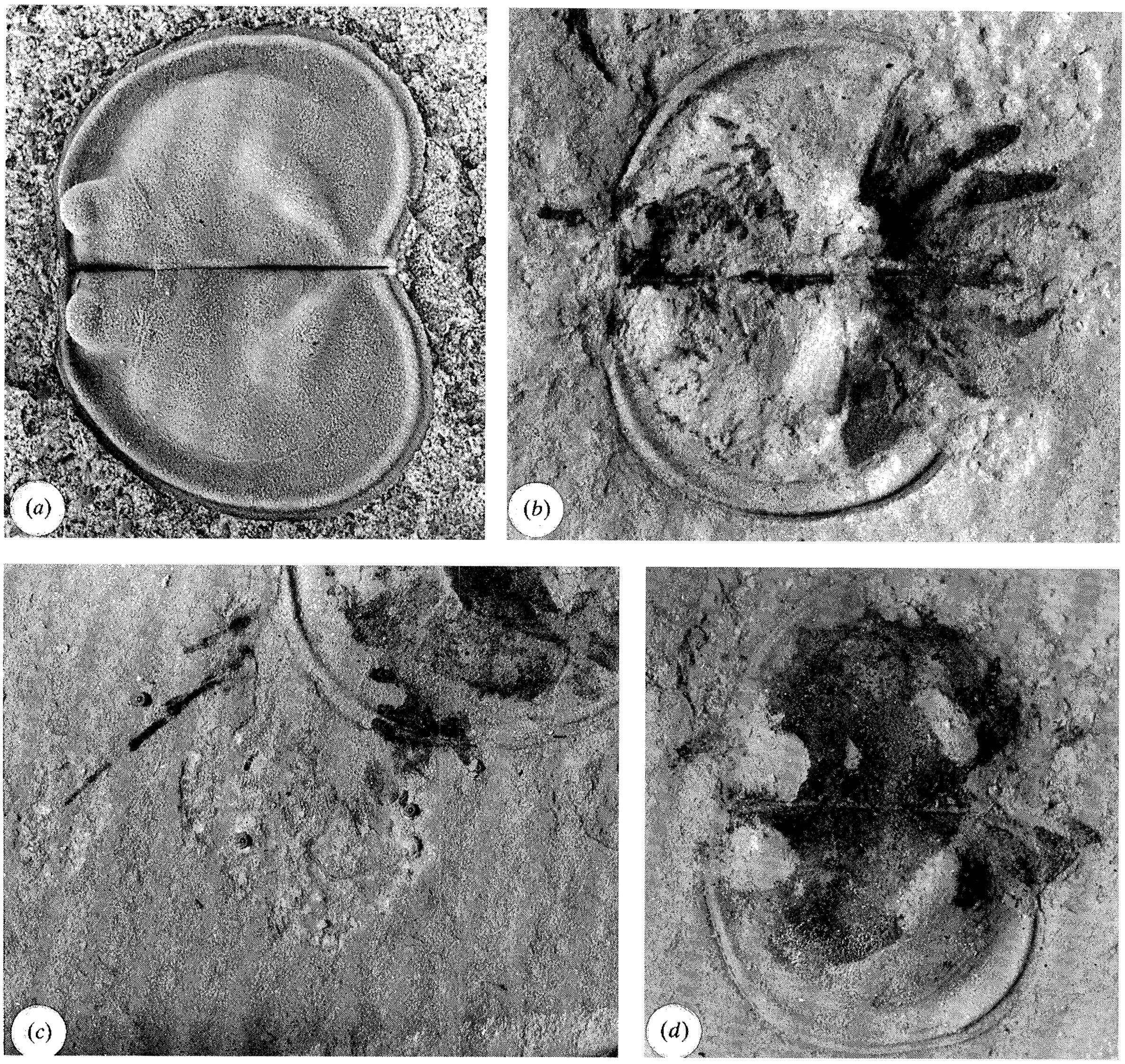

Figure 3. Light photographs of *Kunmingella maotianshanensis* Huo & Shu, 1983, Yuanshan Member, Qiongzhusi Formation, early Cambrian of Maotianshan, Chengjiang County, Yunnan Province, southwest China. (*a*) Dorsal view of complete, open carapace (left valve below), with valves conjoined; University of Oxford Museum, England, no. AY.33, x13.6. (*b*) Dorsal view of incomplete open carapace immersed under water (left valve below), showing conjoined valves and appendages (exposed by partly removing the shell); NIGPAS no. 78184, × 17. (*c*) right lateral view of ventral-posteroventral part of carapace immersed under water, showing traces of possible limbs inside and possible cerci-like caudal rami or endopodite of trunk appendage and adjacent hairs outside the carapace; NIGPAS no. 78185, × 17.9. (*d*) Dorsal view of incomplete open carapace immersed under water (left valve below), showing conjoined valves and appendages; NIGPAS no. 78186, x15.9.

representing 80 % of recovered individuals) and eight (six genera) of the 14 published species (ten genera) of bradoriids of the Qiongzhusi Formation are associated with soft-bodied fossils; and yet, no Chengjiang bradoriids have previously been discovered with soft-parts (cf. Hou & Bergström 1991). Bradoriid individuals are also common in the Burgess Shale (although represented by a single species; Siveter & Williams 1996) but again, no specimen is known with soft integument (cf. Conway Morris 1986). Undoubtedly, many bradoriid valves simply represent exuvia. Nevertheless, these data on Chengjiang and Burgess Shale material suggest possible poor soft-part preservation potential for the group, perhaps because of the composition and delicacy of their tissues (e.g. see Butterfield 1990).

(*b*) *Taphonomy*

The Chengjiang fauna has apparently undergone negligible *post mortem* transport (Hou *et al.* 1991). The fossils show no sign of disarticulation or abrasion and several species of the minor infaunal component, such as inarticulate brachiopods, show evidence of *in situ* preservation.

Our *K. maotianshanensis* specimens with soft-parts also show no evidence of transport. They are preserved, typically for Chengjiang bradoriids (see Hou & Bergström 1991), as articulated, partly flattened carapaces, parallel to lamination on slabs of mudstone. One of the five carapaces is closed; the others have their valves fully open, in 'butterfly' orientation (as is the case with many 'Orsten' phosphatocopid speci-

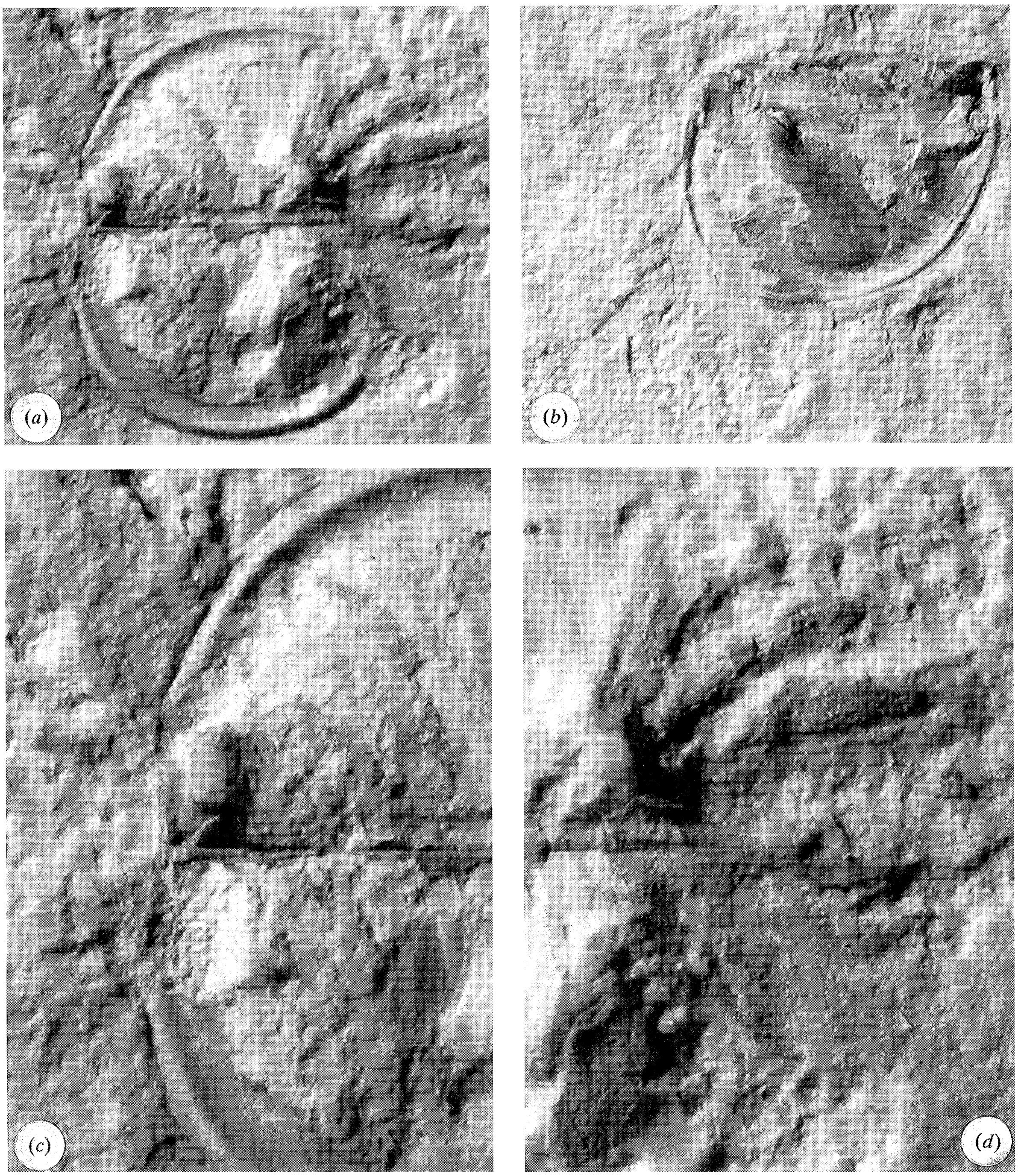

Figure 4. Light photographs of *Kunmingella maotianshanensis* Huo & Shu, 1983, Yuanshan Member, Qiongzhusi Formation, early Cambrian of Maotianshan, Chengjiang County, Yunnan Province, southwest China. (*a*, *c*, *d*) Dorsal view of uncoated, incomplete open carapace (left valve below), showing conjoined valves and appendages (exposed by partly removing the shell); NIGPAS no. 78184: (*a*) complete specimen, × 15.8. (*c*) anterior region, × 29. (*d*) posterior region, × 29. (*b*) right lateral view of uncoated carapace, showing traces of possible limbs inside and possible cerci-like caudal rami or endopodite of trunk appendage and adjacent hairs outside the carapace; NIGPAS no. 78185, × 14.5.

mens; D. W., personal observation), with the external surface exposed. The valves are 3.14–3.61 mm long, representing at most two possible moult stages. As sympatric conspecific valves are up to 4.4 mm long (H. X-G., unpublished data), it is possible that our specimens do not represent the final moult stage.

(*c*) ***Preservation and preparation***

Traces of the soft body and appendages of *K. maotianshanensis* are observed as essentially flattened features outlined by colour differences against the sediment background. No compositional analysis of the soft integument has been undertaken because of its scarcity and delicacy. The body and appendages of the best preserved and most complete specimen appear as

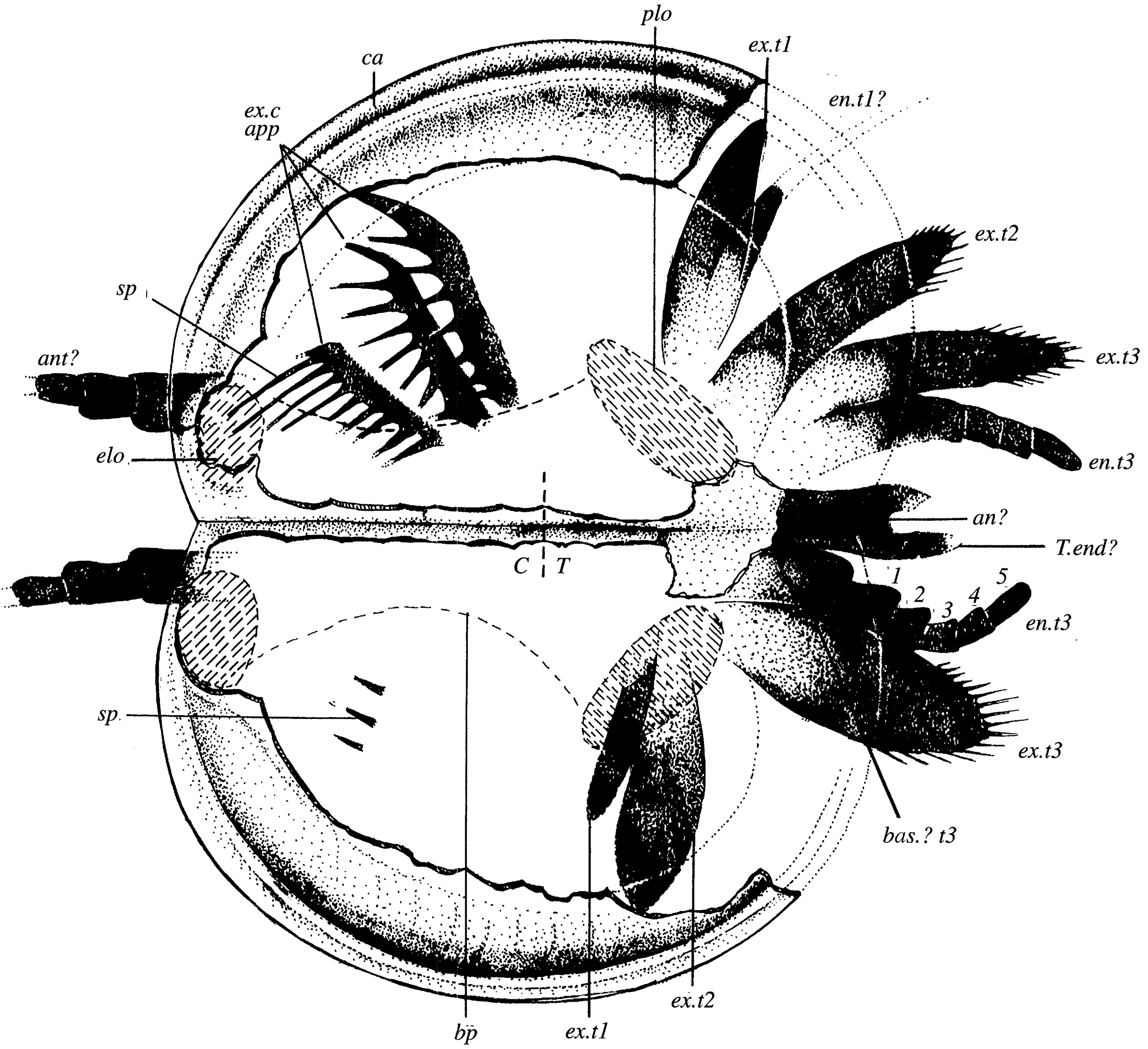

Figure 5. Interpretative reconstruction of features of NIGPAS no. 78184 of *Kunmingella maotianshanensis* Huo & Shu, 1983. Abbreviations: *an*?, anus; *ant*?, antennule; *app*, appendages; *bas*, basipodite (limb basis, carrying the rami); *bp*, supposed body proper; *C*(*c*), cephalic region (head); *ca*, 'carapace'; *elo*, so-called 'eye lobe'; *en*., endopodite; *ex*., exopodite; *plo*, posterior lobe; 1–5, podomeres 1–5 of endopodite; *sp*, spine; *T*(*t*), trunk region (trunk); *T. end*?, possible trunk end.

if pressed to the inner side of the valves (NIGPAS 78184; figures 3*b*, 4*a*,*c*,*d*), with the appendages and associated setae arranged radially from the central part of the animal. The appendages of this specimen were more completely exposed by mechanical exfoliation of the carapace (and parts of the body), from the outer side, using fine needles. Colour photography enhances the image of the preserved soft-parts against the surrounding matrix. In monochrome photography the soft-parts are seen most clearly when immersed in water.

(*d*) *Soft integument of* Kunmingella maotianshanensis

(i) *Orientation*

Our working hypothesis follows the convention of bradoriid specialists, that the small but prominent node near the dorsal margin of the shell of kunmingellid bradoriids is sited anterodorsally. In morphology and position this node is analagous to the so-called eye tubercle of podocope ostracodes, but we do not have the appropriate soft-parts preserved to verify its function in *K. maotianshanensis*. This orientation receives support from our favoured interpretation of the appendages present.

(ii) *Soft integument*

Specimen 1

(NIGPAS 78184; see figures 3*b*, 4*a*,*c*,*d*, 5): An open carapace (valves 3.18 mm long) containing most of the evidence of soft integument (viewed in dorsal aspect); has the remains of seven pairs of appendages and part of the supposed outline of the body. The latter is constricted at about mid-length, thus defining a narrow anterior and a wider posterior region (presumed head and trunk).

There is a pair of uniramous anterior appendages, possibly the antennules (1st antennae of some terminologies); the visible part of each, ca. 0.7 mm long, consists of at least three podomeres. In front of mid-length, right side, there are three, radially aligned, comb-like rami (length: 0.75–0.95 mm), each with

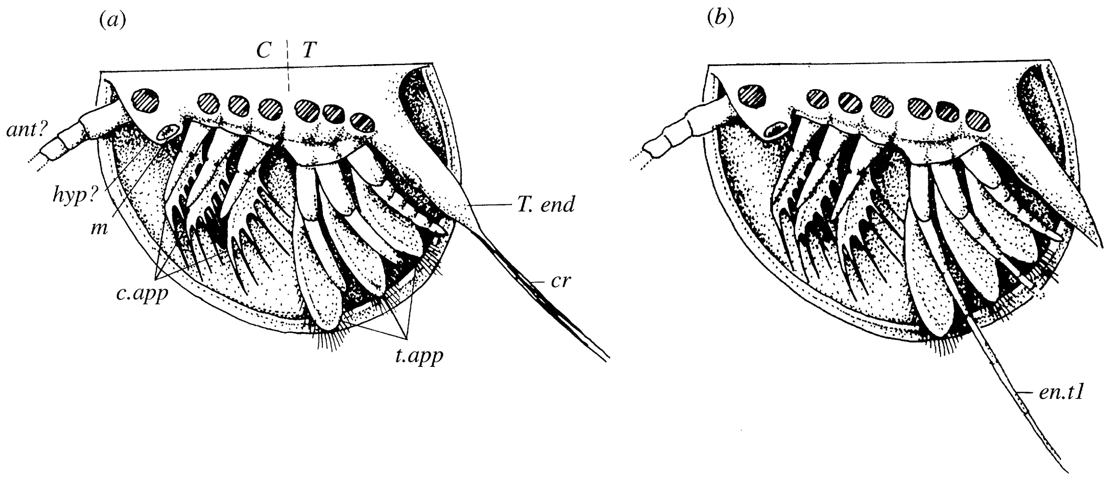

Figure 6. Tentative reconstructions of *Kunmingella maotianshanensis* Huo & Shu, 1983, in left lateral view with the left valve and left post-antennular appendages removed; the insertion areas of the limbs are indicated as lined areas. To emphasise the widening of the body in the region of the posterior lobe (= possible area of insertion of trunk limbs) the drawings are given as slightly oblique lateral views. The difference between the two reconstructions is that the slender, segmented structure outside the valve is interpreted either as cerci-like caudal rami (*a*) or as an endopodite of a trunk appendage (*b*). Abbreviatons: *ant*?, antennule; *C*, cephalic region; *c. app*, cephalic appendages; *cr*, possible cerci-like caudal rami; *en.t1*, endopodite of first trunk appendage; *hyp*?, hypostome; *m*, mouth; *t. app*, trunk appendages; *T. end*, trunk end; *T*, trunk region.

long, straight, slender spines somewhat regularly spaced along one margin. These three structures are possibly the exopodites of the cephalic appendages (the spines and setae of the grinding edge of an arthropod basipodite (not coxa; see Walossek 1993) are much shorter, more irregularly spaced and often arranged in pairs). This interpretation assumes a posterior tilting of these appendages on death; the overlapping nature of the marginal spines and the regular interspacing of the rami indicate that this may have occurred. The left side exopodites are not preserved except for the terminations of three marginal spines of one appendage.

Three pairs of assumed trunk limbs are visible on either side of the sagittal line; their area of insertion, and the widening of the body itself, corresponds generally to the site of the posterior lobe of the shell. The posteriormost pair of trunk limbs has both exopodites and endopodites visible. Of the two more anterior pairs of trunk limbs the right fifth limb shows a supposed exopodite and a slender, possible endopodite and the other limbs show only supposed exopodites. The exopodites are elongate, leaf-shaped, 1.3–1.45 mm long with, in some cases, a marginal fringe of fine setae. The most complete (left) endopodite, 1.32 mm long, consists of a minimum of five podomeres and a possible basipodite; the complete limb was possibly ca. 1.5 mm long. As seen, the corresponding right endopodite consists of at least four podomeres. A relatively short (ca. 0.8 mm long), elongate, sagittal structure projects and fades posteriorly from the region of the base of the posteriormost set of appendages and has a possible subterminal, central perforation (the latter might be an anus or an artifact); it is possibly the caudal end of the trunk.

Specimen 2

(NIGPAS 78185; see figures 3*c*, 4*b*): Closed valves as viewed in assumed right lateral aspect with a pair of long (2.29 mm), slender, segmented structures, perhaps representing cerci-like caudal rami or the endopodite of a trunk appendage, projecting posteroventrally from immediately adjacent to the posteroventral part of the valve (length: 3.61 mm). As these structures are not preserved for a short distance, at the critical point immediately outside the valve, there is the possibility that they are foreign to the animal in question, but this is considered unlikely.

Faint traces of three, slender, anteroventral-posterodorsally aligned, possible (head ?) limbs occur in the anteroventral part of the valve itself. The region between the possible caudal rami and the posteroventral part of the valve has many very faint, delicate, aligned hairs, similar in morphology to the marginal setae of the trunk limb exopodites of specimen 1, but no associated appendage(s) is discernible.

Specimen 3

(NIGPAS 78186; see figure 3*d*): An open carapace, 3.14 mm long, showing a pair of short, uniramous, poorly preserved anterior antennules similar to those of specimen 1; at least a single, left, posteriormost(?) trunk exopodite; and faint traces of possibly the left and right posteriormost trunk endopodites.

Specimens 4 *and* 5

(NIGPAS 78187, 78188; not figured): Both specimens show faint remains of body integument, but lack appendages.

(*e*) ***Reconstruction of* Kunmingella maotianshanensis**

The soft-part evidence, given above, is still too fragmentary to present a conclusive picture of this Cambrian fossil. For example, nothing is preserved of the inner lamella (the cuticle extending between the shell margin and the body proper), the details of the body itself, the mouth region and sternum or, with certainty, of the basipodites. Hence our tentative reconstruction (figure 6) is based mainly on the identifying drawing of specimen 1 (figure 5) and in part on knowledge of the soft-parts of other early arthropods, particularly those which have a relatively short body and a similar 'design' in that they are enclosed within a 'shell' (e.g. see *Agnostus pisiformis* [Linnaeus, 1758] in Müller & Walossek 1987). Accordingly, we have incorporated a hypostome with a mouth opening posteriorly, a characteristic of many Euarthropoda.

Some of the posterior limbs of *K. maotianshanensis* seem to be too large to be withdrawn completely under the carapace. Indeed, as seen, some of the posterior limbs and the supposed trunk end extend well beyond the margin of the shell (though this may be due in part to some posteriorly directed dislocation of the soft-parts). Hence, the trunk limbs are portrayed in part protruded, as is the trunk end. The slender, segmented structure outside the valve is interpreted either as a cercus-like caudal ramus (see figure 6*a*; cf. specimen 2) or as an endopodite of a trunk appendage (figure 6*b*; cf. specimen 1).

4. TAXONOMIC AFFINITY OF *KUNMINGELLA*

The valve morphology of *K. maotianshanensis* and other bradoriids is, in some respects, compatible with an ostracod affinity for the group. However, it is well established that a bivalved carapace is convergently developed, from different numbers of body segments (e.g. Dahl 1991), in quite different arthropods (e.g. Briggs 1978, 1983; Walossek 1993); for example, as in ostracodes, certain cirripede species and diplostracan branchiopods and several genera from the Burgess Shale (*Branchiocaris*, *Canadaspis*, *Odaraia*, *Perspicaris*, *Plenocaris*). Thus firm ideas on the affinities of such groups ultimately relies on evidence from appropriate soft-parts. The conventional notion (e.g. Sylvester-Bradley 1961; Müller 1964, 1979*a*, *b*, 1982; McKenzie & Jones 1979; Briggs 1983; Hinz 1993; Hinz-Schallreuter 1993*a*, *b*; Hinz-Schallreuter & Jones 1994) that bradoriids s. str. are ostracodes is challenged by the soft-part evidence from *K. maotianshanensis*.

(*a*) ***Ostracodes***

The Ostracoda are maxillopod entomostracans and, as such, are an in-group of the crown-group crustaceans, the Crustacea s.str. (for character sets see Walossek & Müller 1990, 1992, 1996). Typically, the outer lamella cuticle and peripheral part of the inner lamella cuticle of each valve of ostracodes are calcified (figure 7); such mineralization is weak or lacking in less than 5% of species (e.g. some myodocopes). An unmineralized, dorsal band of cuticle, the ligament, helps hinge the two valves of the carapace (a term here used in its traditional, descriptive sense – without evolutionary or phylogenetic implications – for the valve(s) forming a dorsal cephalic or cephalothoracic 'shield'; see Walossek 1993).

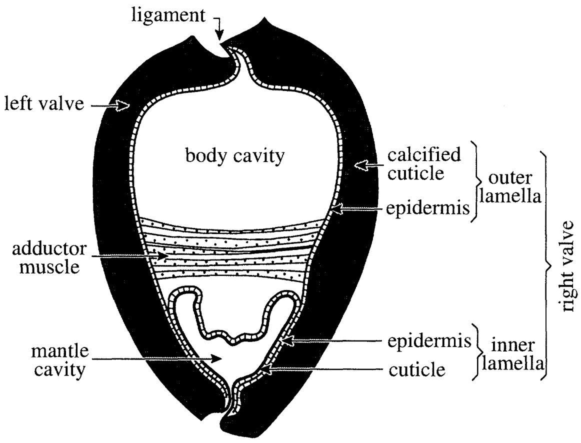

Figure 7. Relationship of the soft-parts and the shell in an ostracode, as exemplified in the Recent platycope *Cytherella abyssorum* G. O. Sars, 1866, from Norway; × 120 (adapted from Jaanusson 1985, fig 3A). Schematic transverse section at the position of the adductor muscle (viewed from the posterior); thickness of epidermis much exaggerated.

Ostracode valves have a true hinge; that is, a structure consisting of separate, dorsal, 'articulating' (opposing and interlocking) surfaces of the two valves. A feature typical of the ground-plan of Crustacea is that the carapace develops from a single, dorsal, naupliar 'head shield'. The Recent punciid *Manawa*, the ontogeny of which is unique in that it is the only ostracode known to have a single shield (in the nauplius and two other, metanaupliar larvae), provides a possible model of how the uni- to bivalved development of the carapace occurs (Swanson 1989*a*, *b*, 1990, 1991). This involves the bilateral extension of a single shield posteriorly as far as, and including, the maxillary segment, and the subsequent formation of a simple, dorsal, mid-line furrow of the shield to produce a hinge.

The segmentation of the body in ostracodes is normally betrayed only in the configuration of their appendages. The body, consisting of a head separated from a trunk region by a slight constriction, is suspended from its dorsal area of attachment to the carapace. In ostracodes the trunk region characteristically consists of only a thorax: abdominal constriction is extreme and an abdomen is known from only a few species (see Swanson (1989*b*) pp. 244 & 246, and (1990) pp. 12, 14 &15).

Attached, just in front of mid-length of the ostracode, to the inner lamella cuticle of each valve is an adductor muscle bundle contained within the isthmus, the lateral extension of the body (figure 7). Characteristically the site of attachment is marked on the valve by an adductor muscle scar field and/or an external node or sulcus.

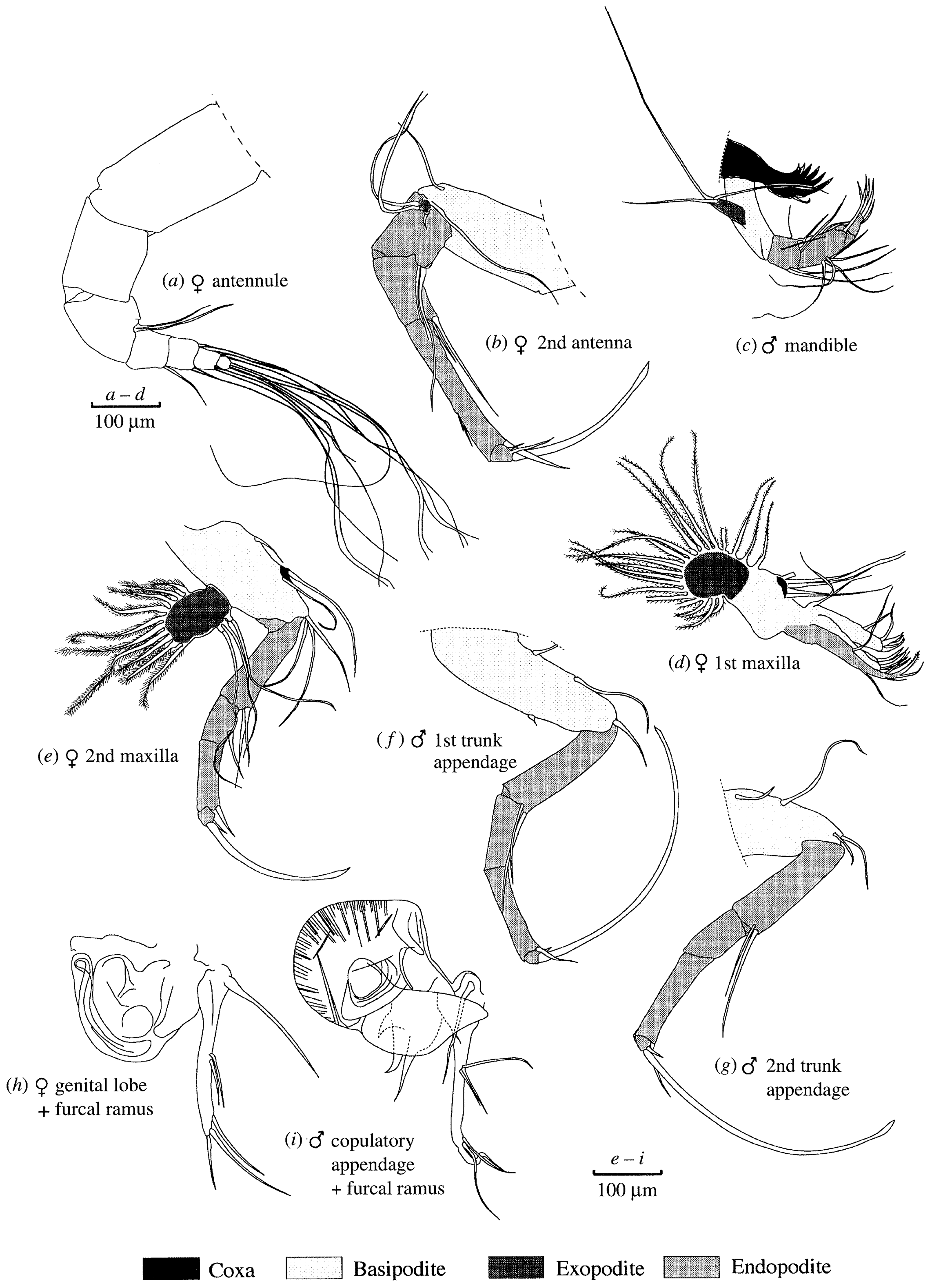

Figure 8. Morphology of the appendages of an ostracode, as exemplified in the Recent podocopid *Zabythocypris redunca* Athersuch & Gooday, 1979, from the northeast Atlantic (from Athersuch & Gooday 1979, text-figs 1, 2). Names for the various appendages are as given in Athersuch & Gooday, except for first thoracic leg (= second maxilla herein). Identification of basipodite, exopodite, endopodite and coxa (as shown in the key above) are made by the authors.

The appendages of major ostracode taxa differ from each other in detail, for example in the number of podomeres, rami and pairs. The typical pattern consists of a posteriormost pair of unsegmented, uniramous, claw- or seta-like furcal rami behind 7 (6 in Platycopina) pairs of appendages: uniramous antennules and biramous 2nd antennae, mandibles, 1st and 2nd maxillae and, on the trunk, 6th and 7th appendages (figure 8). The brush-shaped organ (present in some genera) and the copulatory organ are evidence of additional (8th and 9th), if less obvious, appendages. Moreover, the somite development in *Manawa* and in the platycopid Podocopida *Cytherella* reveals that the ostracode ground-plan originally included a trunk with a more definable segmentation, consisting of at least 10 somites (Hartmann 1963, 1964; Schulz 1976; Swanson 1989*a*, *b*, 1990, 1991; see also Walossek 1993; Walossek & Müller 1996). This implies that effacement of external segmentation and a reduction in the number of limbs has occurred within the ostracode lineage (apomorphy).

(*b*) *Evidence from soft-part morphology*

The head with a pair of antennules and three pairs of more or less similar biramous limbs with paddle-shaped exopodites, as found in *K. maotianshanensis*, is in fact a ground-plan feature of Euarthropoda and even of Crustacea s.l. (for the characterization of different levels of crustacean evolution see Walossek & Müller 1990, 1992, 1996; Müller & Walossek 1991; Walossek 1993). The body plan and appendage details of *K. maotianshanensis* indicate that it does not belong to the Ostracoda or to the Crustacea s.str.

The soft-parts of *K. maotianshanensis* depart from that of the Ostracoda in two important respects.

1. Number of trunk somites: at first sight both *K. maotianshanensis* and Recent ostracodes appear to have the same number of paired appendages and, therefore, by implication the same number of body somites. However, ostracodes differ in originally having at least 10 trunk somites and, accordingly, more paired limbs than they have at present (see above).

2. Post-antennular cephalic limbs: the form of the exopodites of the 3 post-antennular cephalic limbs of *K. maotianshanensis* indicates that these limbs have a similar morphology to each other. This scheme contrasts fundamentally with the morphologically well differentiated and functionally specialized equivalent appendages in ostracodes (second antennae, mandibles, first maxillae; figure 8). This criterion alone would exclude *K. maotianshanensis* from the Crustacea s.str. as defined in Walossek & Müller (1990) and Walossek (1993).

The soft-parts of *K. maotianshanensis* possibly differ from ostracodes in three other respects.

1. Isthmus and adductor muscle: none of the thousands of relatively thin, very well preserved valves of *K. maotianshanensis* show signs of a muscle scar, implying that it may have lacked an adductor muscle and associated isthmus system. Indeed, except possibly in the case of one specimen from the Burgess Shale (Siveter & Williams 1996), adductor muscle scars are not documented from any of the hundreds of known bradoriid species. We consider that the small, antero-dorsal depression of the shell of many bradoriids (see Hinz-Schallreuter & Jones 1994) is an unlikely alternative site of attachment from which any adductor-type muscles could function efficiently to effect the possible opening and closing of the two valves. Furthermore, to regard the broadly depressed ('sulcus'), central part of the valve of some bradoriids as the external expression of adductor muscle attachment is merely speculative.

2. Origin of the carapace: the carapace in kunmingellids may be of cephalothoracic origin, thereby contrasting with its exclusively cephalic origin in ostracodes and other crustaceans. In *K. maotianshanensis* it seems that the body may be attached to the carapace in a long, narrow band beneath the dorsal mid-line, from the antennulae to at least the posteriormost pair of limbs (such an arrangement exists in phosphatocopids; see below and figure 9). This, if verified, would therefore imply that the kunmingellid carapace would be neither like a euarthropodan head-shield (i.e. one that involves only cephalic segments and extends posteriorly to that somite carrying the third pair of biramous head appendages i.e. the first maxillae or maxillulae of crustacean terminology), nor a head shield as in the ground-plan of crown-group crustaceans (which, additionally, involves the second maxillae).

3. Posteriormost rami: Unlike in ostracodes, the possible, posteriormost (caudal) rami of *K. maotianshanensis* appear to be segmented.

The large, paddle-shaped exopodites of the 5–7th appendages of *K. maotianshanensis* also contrast markedly with the scheme in ostracodes. Only the 5th appendage i.e. the 2nd maxillae, of some ostracode groups have a discernible, much reduced, exopodite (figure 8). However, this cannot be regarded as a fundamental difference as a basically leaf-shaped exopodite characterizes the 2nd maxillae and trunk appendages of all crown-group Crustacea (e.g. Cephalocarida, Branchiopoda, Maxillopoda, Phyllopoda) and may therefore also have been the case in the ground-plan of Ostracoda. In general terms the morphology of the trunk exopodites of *K. maotianshanensis* recalls the lobate, setal-fringed exopodites of various ancient arthropods, such as those of the first 10 body segments of the Burgess Shale arthropod *Yohoia* Walcott, 1912 (see Whittington 1974). Most likely such an exopodite represents the plesiomorphic state of the euarthropodan post-antennular limb.

(*c*) *Evidence from valve morphology*:

1. The general design of the shell morphology of *K. maotianshanensis* (dorsally straight; lobate; postplete i.e. greatest height is posterior of mid-length), which is typical of many bradoriids, recalls that of the so-called 'straight-hinged' ostracodes such as the abundant Palaeocopida and Leperditicopida of the Palaeozoic. *Manawa* is also 'straight-hinged'.

2. Our preliminary, unpublished studies indicate that *K. maotianshanensis* has at least 6 moult stages. The few complete ontogenetic sequences known from bradoriids indicate that they are similar in their growth pattern to most ostracodes, there being ca. 8–9 moult stages with dimorphic adults in some species (e.g. see Zhang 1987; Hinz-Schallreuter 1993*a*; Zhang & Pratt 1993; Williams *et al.* 1994). Moreover, though very rare, a univalve to bivalve ontogenetic development is known from bradoriids (two species, including a *Kunmingella*; Zhang & Pratt 1993) and ostracodes (*Manawa*; Swanson 1989*a*).

3. *K. maotianshanensis* is typical of bradoriid valves (see Hinz 1993) in differing from ostracodes by lacking

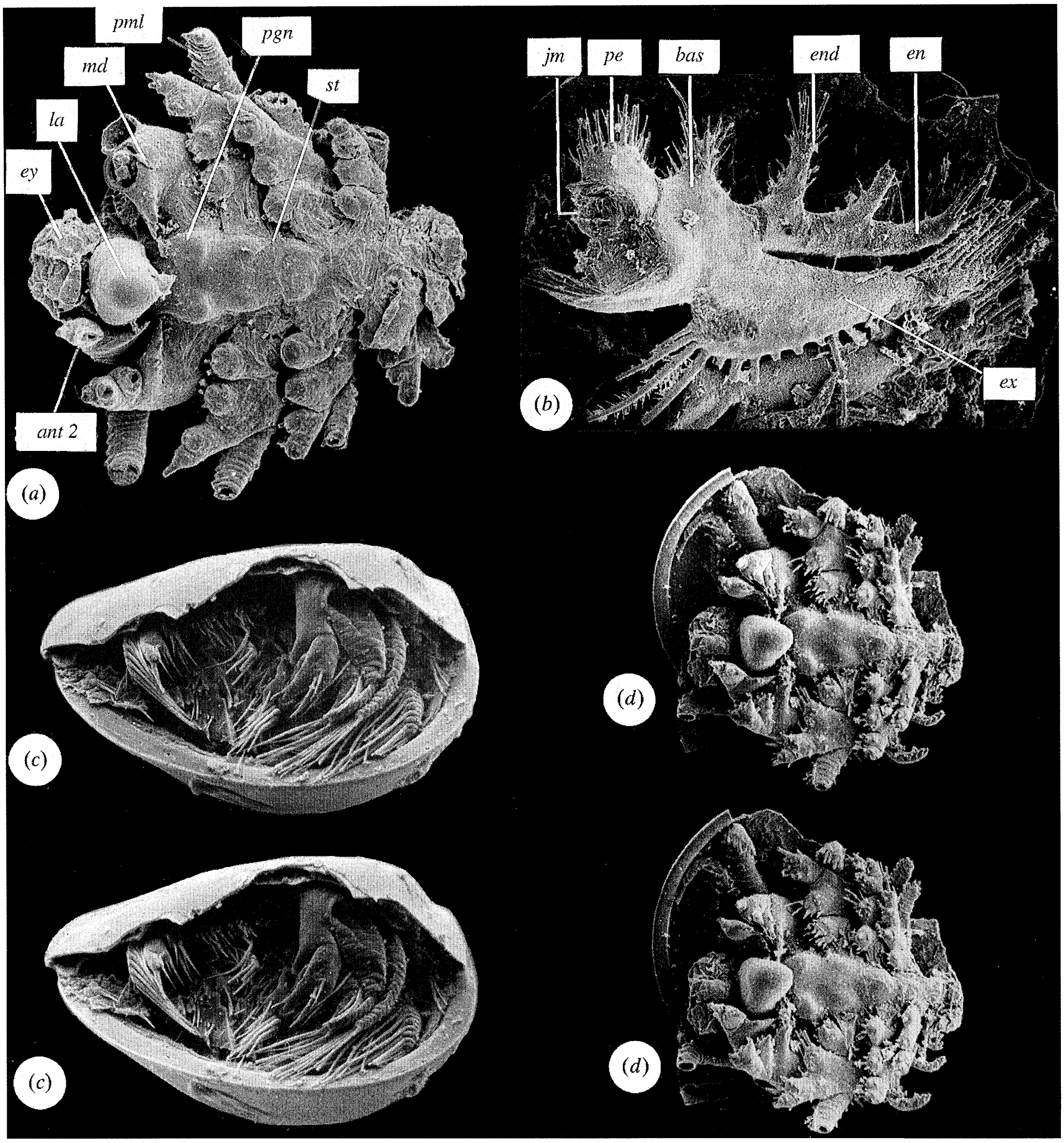

Figure 9. Scanning electron micrographs of hesslandonid phosphatocopids with soft-parts from the late Cambrian 'Orsten' of Gum, Västergötland, Sweden (micrographs courtesy of K. J. Müller). (*a*, *d*) *Hesslandona* sp. nov. (Müller unpublished). (*a*) Ventral view of larval specimen; University of Bonn no. UB1629, length ca. 625 μm. (*d*) Ventral view (stereo-pair) of larval specimen; University of Bonn no. UB 1627, length of shell ca. 625 μm. (*b*, *c*) *Hesslandona unisulcata* Müller, 1982. (*b*) Posterior view of detached post-mandibular limb, with many setae and subordinate bristles, of a late larval specimen; University of Bonn no. UB 1628, length (excluding setae) ca. 440 μm. (*c*) Oblique ventral view (stereo-pair), from right side, of carapace (most of right valve removed to show soft-parts) of larval specimen; University of Bonn no. UB 658, length of shell ca. 550 μm. Abbreviatons: *ant2*, second antenna; *bas*, basipodite (limb basis, carrying the rami); *en*, endopodite; *end*, endite; *ex*, exopodite; *ey*, eyes; *jm*, joint membrane; *la*, labrum; *md*, mandible; *pe*, proximal endite; *pgn*, paragnaths; *pml*, post-mandibular limb (all such limbs are of similar morphology); *st*, sternum.

a true hinge. The dorsal 'edges' of its valves appear to be unsculptured ('adont hinge' *sensu* Müller 1964).

4. The shell of *K. maotianshanensis* is thin and differs from the overwhelming majority of ostracodes in being only weakly mineralized. In fact, Bradoriida s. str. in general are, at best, only weakly mineralized (see Hinz 1993). Their shell composition is known from a few genera (*Anabarochilina* Abushik, 1960, *Beyrichona* Matthew, 1886, *Hipponicharion* Matthew, 1886, *Indiana* Matthew, 1902, *Liangshanella* Huo, 1956, *Petrianna* Siveter *et al.*, 1996) and is calcium phosphate (Siveter & Williams 1995, 1996; Siveter *et al.* 1996; Williams & Siveter 1996). We know of no bradoriid which has been demonstrated to be similar to ostracodes in unequivocally having a calcium carbonate composition for its shell. Copeland (1986) said that his svealutid bradoriid *Bullaluta*, from the late Cambrian of Canada, had a calcareous shell, but his three specimens appear

to be mostly internal moulds and the calcium carbonate might therefore be derived from the host sediment. Indeed, EDX (Energy Dispersive X-ray) analysis proves a calcium phosphate component for the carapace of other svealutids, such as Scandinavian material of *Anabarochilina* (Williams & Siveter 1996).

(*d*) *The taxonomic position of* Kunmingella

It is not possible, on present evidence, to resolve the affinities of *K. maotianshanensis* within the Arthropoda. Information about several key features is still lacking. For example, knowledge of the morphology of its mouth region in general and of the endopodites of its cephalic appendages are lacking and confirmation is needed on the configuration and attachment of the body area and on the occurrence and nature of the caudal rami and some of the trunk endopodites. The question of affinity is also difficult to resolve because of the sparsity of detailed knowledge about such features in many other early (Cambrian) arthropods. Nevertheless, we can say that *K. maotianshanensis* is not an ostracod or a crustacean s.str.

5. PHYLOGENETIC SIGNIFICANCE OF *KUNMINGELLA*

Granted that *Kunmingella* is representative of the Bradoriida s.str., this would imply the denials (*a*), (*b*) and endorsements (*c*) of ideas (see below), regarding the evolution and stratigraphic occurrence of ostracodes and arthropods in general.

(*a*) *Bradoriida s.str. are not ostracodes*

The conventional evolutionary opinion (references as in §4 above) which, with rare exceptions (e.g. Jones & Mckenzie 1980), treats bradoriids as a whole simply as ancestral ostracodes should now be regarded as false. Moreover, as bradoriids show closest morphological comparison in shell design to the palaeocopes and leperditicopes, it begs the question whether these groups, too, really are ostracodes (evidence of appendages in the palaeocopes and leperditicopes are currently limited to two, incompletely described palaeocope specimens: Müller 1979*b*).

(*b*) *The record of ostracodes in the Cambrian is refuted*

Denial of the conventional wisdom that ostracodes have a fossil record in the Cambrian stems from the notion that (not only bradoriids s.str. but) phosphatocopids, too, do not belong to the Ostracoda. That opinion, previously only briefly noted (Müller & Walossek (1991) p. 283, Walossek & Müller (1992) pp. 305, 309, Walossek & Müller (1996), Walossek *et al.* (1993) pp. 7, 11 and figure 3, Müller *et al.* (1995) p. 112), requires fuller justification herein.

(i) *Phosphatocopida with soft integument*

Phosphatocopid shells have a wide range of design, are typically preplete (greatest height anterior of mid-length), and are composed of supposedly primary, phosphatic material (Müller 1964, 1979*a*, 1982). Their hinge consists either of a single, simple line of junction between two valves or a double simple line demarcating the so-called interdorsum area (Müller 1979*a*, 1982); a true hinge is reported from only one 'phosphatocopid' species (see p. 8, figure 4K, Hinz 1993).

The soft integument of phosphatocopids is well known mostly from the late Cambrian of the Baltic (e.g. Müller 1979*a*, 1982), together with a few other specimens from the middle Cambrian of Australia (McKenzie & Jones 1979; Hinz-Schallreuter 1993*b*) and the early Cambrian of England (Hinz 1987) and a few isolated appendages of most likely phosphatocopid affinity also from the middle Cambrian of Australia (Walossek *et al.* 1993). It is uncertain from the published illustrations whether the supposed (poorly preserved) integument in the dabashanellid phosphatocopids from the early Cambrian of China (Jiang & Xiao 1985) represents soft-part preservation.

Phosphatocopids have a wide range of limb differentiation (Walossek unpublished data; and see for example figure 9 herein). As an extreme example, all post-antennular appendages (second antennae, mandibles, and post-mandibular legs) of some middle Cambrian phosphatocopids from Australia lack exopodites (Walossek *et al.* 1993), thus implying a benthic/crawling lifestyle for such forms.

(ii) *Phosphatocopida are stem-group Crustacea*

Evidence from Baltic 'Orsten' phosphatocopids with soft-parts helped in the characterization of various levels of crustacean evolution (Walossek & Müller 1990, 1992, 1996; Müller & Walossek 1991; Walossek & Szaniawski 1991; Walossek 1993). That scheme indicates, contrary to traditional opinion (e.g. Sylvester-Bradley 1961; Hinz 1993; Hinz-Schallreuter 1993*a*, *b*), that phosphatocopids are merely stem-group derivatives close to the crown-group Crustacea.

According to Walossek & Müller's scheme, phosphatocopids are recognized as Crustacea s.l. by the fact that they have:

1. Multiannulate exopodites in two special post-antennular appendages, the second antennae and mandibles.
2. Setation of the exopodites of the second antennae and mandibles oriented toward the endopodite.
3. Proximal endites on all post-mandibular limbs.

That phosphatocopids lie at an evolutionary level above other stem-group Crustacea (such as the late Cambrian *Martinssonia* Müller & Walossek, 1986, *Goticaris* Walossek & Müller, 1990, *Cambropachycope* Walossek & Müller, 1990 and *Henningsmoenicaris* Müller & Walossek, 1991), and close to the crown-group Crustacea is indicated by the presence of features such as: (i) a mouth in an atrium oris; (ii) a labrum covering (i.e. providing the ceiling to) the atrium oris and lying behind the site of the 'ancestral' hypostome; (iii) hairs on the sides of the labrum and on the sternum, to guide food particles towards the mouth; (iv) a well-sclerotized sternum with paragnaths; and (v) mandibles with a large coxal grinding plate (gnathobase).

Phosphatocopids can be separated readily from Crustacea s.str. by the particular fact that their earliest larva has four pairs of functional appendages ('head larva') rather than three ('short head larva', as in the nauplius of Crustacea s.str.; Walossek & Müller 1990); and by the homogeneous nature of their post-mandibular (feeding and locomotory) appendages. Accordingly, the first post-mandibular limb of phosphatocopids had not yet reached the level of development of a first maxilla, thus excluding them from any in-group taxon of the Crustacea s.str. and hence the Ostracoda. Furthermore, unlike Ordovician-Recent ostracodes (see §4*a* above), phosphatocopids apparently lack a true hinge, an isthmus and associated adductor muscle and segmentation of the trunk (segmentation fades out towards the anal region) and they have a long, narrow body attachment area (involving almost the complete trunk) and a supposedly primary, phosphatic shell.

Autapomorphic characters of phosphatocopids include: (i) minute first antennae (Müller 1979*a* (*in error*), 1982); (ii) three-segmented endopodites on all post-antennular limbs, each podomere of the post-mandibular limbs being drawn out into a seta-bearing protrusion; (iii) a peculiar morphogenesis of the mandible, in which the coxa fuses in part with the basipodite and therefore looks much like the typical coxa of Crustacea but, in fact, represents a 'syncoxa' into which the exopodite and endopodite are inserted (thus resembling the situation found in the euarthropod plan; cf. Walossek 1993, figure 54); and (iv) reduced trunk length and segmentation and its attachment, to the carapace, at least back to the 4th or 5th post-mandibular limb.

(*c*) *Arthropod radiation involved several bivalved groups*

The recognition that bradoriids are a group distinct from ostracodes further endorses the idea (e.g. see Briggs 1983) that Cambrian arthropod radiation involved many different types of convergently bivalved groups. They include small animals, as exemplified by the kunmingellid bradoriids, phosphatocopids, ostracodes, certain cirripede species, late larvae of ascothoracids and diplostracan Branchiopoda, as well as larger bivalved taxa such as *Branchiocaris*, *Plenocaris*, *Odaraia* and *Canadaspis*.

6. POSSIBLE LIFE HABITS OF *KUNMINGELLA*

The vast majority of ostracodes are benthic/nectobenthic crawlers and swimmers; the pelagic ostracode fauna consists essentially of weakly mineralized or unmineralized myodocope species (mostly Halocypridacea). Notions about life position and mode of life of *K. maotianshanensis* are necessarily speculative. If our interpretation of its orientation and soft-parts is valid, the species shows some interesting morphological similarities with limulids (Xiphosurida, Chelicerata) and notostracans (Branchiopoda, Crustacea) and may, therefore, have had similar life habits.

Both limulids and notostracans have a wide (though univalve) carapace covering much of the body and a tail carrying a spine or a pair of cerci-like caudal/furcal rami which function(s) as a stabiliser and lever during swimming or digging. Kunmingellids may have had a similar benthic lifestyle, stirring up the sediment and food with their post-antennular cephalic limbs and using their posteriorly directed trunk limbs mainly for locomotion. The posteroventrally oriented end of the trunk, with its possible long, segmented, articulated terminal rami, was perhaps fairly moveable, perhaps to aid stability or hovering in the water column.

These groups have other analogies, in antennal morphology (reduction) and in the development of the eyes (enlargement). Although the full length of the antennulae of *Kunmingella* is unknown, the morphology of those parts preserved suggest that these appendages may be relatively short and stout. Both the first and second antennae of notostracans are very small, their sensory function having shifted posteriorly to the first pair of trunk appendages. Limulids lack antennae: chelicerates lost such appendages early in their evolution. As a possible corollary to such reduction in size of the antennae, the eyes of notostracans are well developed, having originated ventrally and migrated to occupy a dorsally positioned bulge in the shell. Limulids have a pair of compound eyes situated in the middle of the opthalmic ridges on the anterodorsal part of the carapace. Such a reduction of sensory antennae in favour of the development of large eyes, may also apply in the case of kunmingellids, with their possible 'eye-lobe'. A similar situation can also be demonstrated in predatory arthropods such as the extant stomatopod malacostracan crustaceans and various Cambrian arthropods with large appendages such as *Jiangfengia* Hou, 1987, *Yohoia* Walcott, 1912 and probably also *Alalcomenaeus* Simonetta, 1970 (Walossek personal observation).

K. maotianshanensis is commonly found in 'butterfly' orientation of conjoined valves, a mode of preservation well known in late Cambrian phosphatocopids (Müller 1979*a*, 1982), early Palaeozoic myodocope ostracodes (see Siveter *et al.* 1991, figure 3) and bivalve molluscs. However, there is no clear evidence that the carapace of *K. maotianshanensis* was relatively widely gaped during life. *Post mortem* decay of its soft tissues may have facilitated the full opening of the valves.

7. SYSTEMATIC PALAEONTOLOGY

Order Bradoriida Raymond, 1935
(Archaeocopida Sylvester-Bradley, 1961; *partim*)
Family Kunmingellidae Huo & Shu, 1985

Genus *Kunmingella* Huo, 1956

Type-species. *Kunmingella maxima* Huo, 1956; original designation, p. 434. early Cambrian, Yunnan Province, southwest China.

Remarks: more than 25 species, all requiring modern study, have been referred to *Kunmingella*. The unrevised *Bradoria douvillei* Mansuy, 1912 is from the same locality and horizon as the type-species *Kunmingella maxima* and may be a senior synonym.

Occurrence: all species referred to *Kunmingella* are from the early Cambrian of China.

Kunmingella maotianshanensis Huo & Shu *in* Huo *et al.*, 1983
Figures 3*a–d*, 4*a–d*, 5, 6*a*,*b*.

1983 *Kunmingella* (*Validocostatella*) *maotianshanensis* subgen. et sp. nov.; Huo & Shu *in* Huo *et al.*, p. 59, plate 4, figures 7–15.

Diagnosis: smooth *Kunmingella* species with a complete, narrow lateroadmarginal ridge, anterodorsal node and tapering posterior lobe.

Lectotype: designated Huo *et al.* 1991; a carapace, Northwest University, Xian, no. D82011 (Huo & Shu *in* Huo *et al.* 1983, plate 4, figure 7).

Type locality: Yuanshan Member, Qiongzhusi Formation, early Cambrian of Maotianshan, Chengjiang County, Yunnan Province, southwest China

Dimensions: the valves we collected are up to 4.4 mm long.

Material: thousands of valves and carapaces. Our five specimens with soft-parts (NIGPAS 78184–78188) were collected from the upper part of the Qiongzhusi Formation, in the Maotianshan area, Chengjiang County, Yunnan Province.

Description: valve outline moderately postplete throughout ontogeny. Anterior cardinal corner less obtuse than posterior cardinal corner. Narrow, low lateroadmarginal ridge present, close to valve margin, between cardinal corners. Well developed node (so-called 'eye-lobe') anterodorsally; elongate, low, tapering lobe extends from just posterior of valve centre to terminate immediately in front of posterior cardinal corner. Valve surface is generally gently convex, lacks ornament. Valves apparently have a simple dorsal contact; no articulating hinge structures have been observed, either in single valves or conjoined, open carapaces. Soft-part morphology as given in §3(*d*) above.

Remarks: Huo & Shu designated *K. maotianshanensis* as type-species of *Kunmingella* (*Validocostatella*). However, until a revision is made of the genus we prefer not to assign the species to a subgenus. The species shows wide infraspecific variation. Indeed, our studies in progress indicate that it is probable that both the unrevised *Bradoria douvillei* Mansuy, 1912 and the designated type-species of the genus, *Kunmingella maxima* Huo, 1956, both of which are from the same locality and horizon as *K. maotianshanensis*, may be just two of the many synonyms of *K. maotianshanensis*.

Occurrence: Qiongzhusi Formation, early Cambrian, Chengjiang County, Yunnan Province, southwest China.

8. CONCLUSIONS

Clearly, more material is required to obtain a more conclusive picture of the soft-parts of *K. maotianshanensis* and the bradoriids in general. Nevertheless, the new evidence seems sufficient to demonstrate the following.

1. Kunmingellids and, by inference, bradoriids are not Crustacea s.str. and may not be even Crustacea s.l.; therefore, they cannot be ostracodes.
2. Kunmingellid bradoriids are not closely related to the Phosphatocopida, a stem-group crustacean taxon (and hence also not ostracodes).
3. Most (all?) of the Cambrian ostracode record is most likely spurious.

The new evidence also confirms the fact that arthropod radiation involved several different types of convergently bivalved groups, many of which are of small sized animals.

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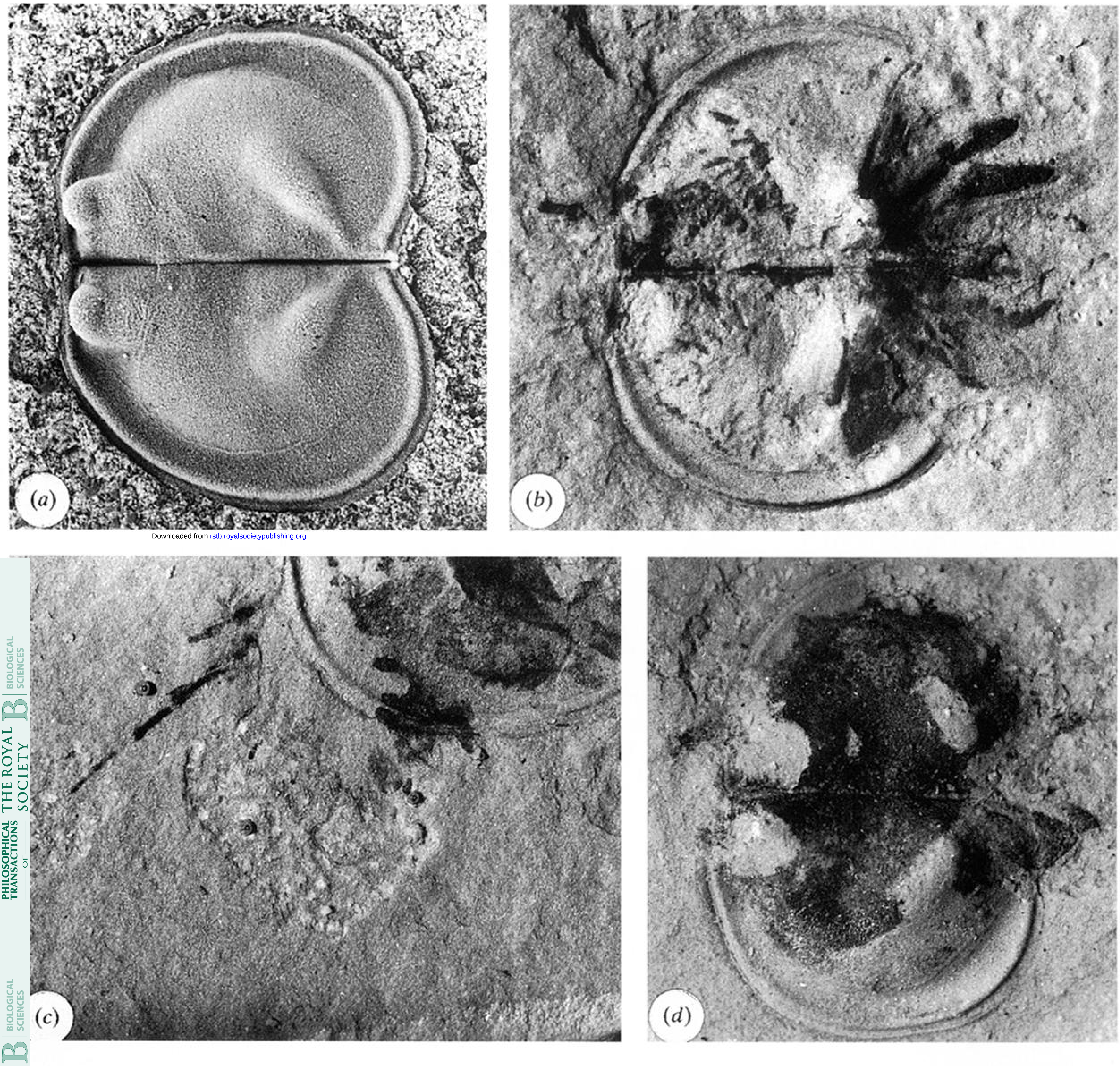
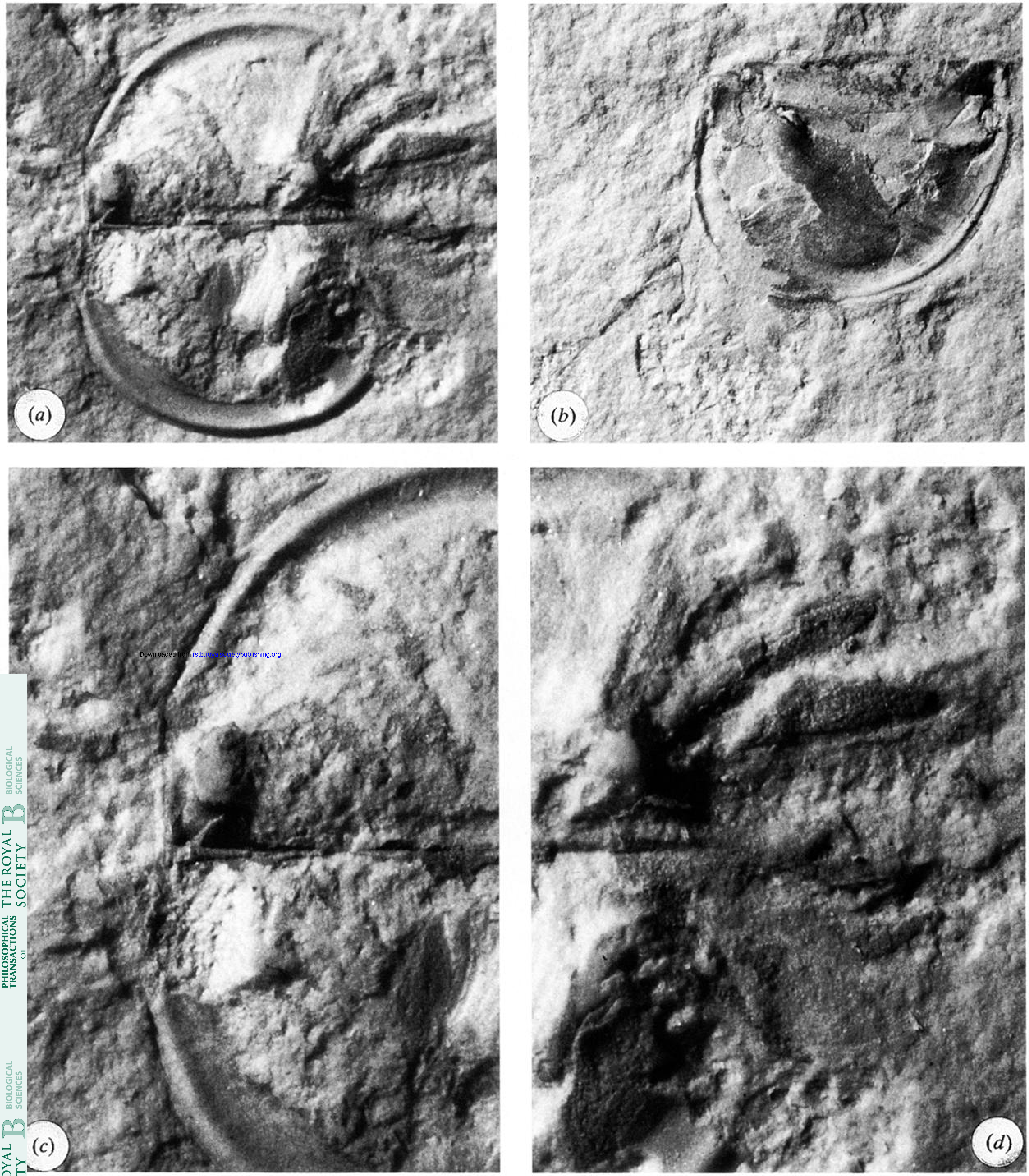
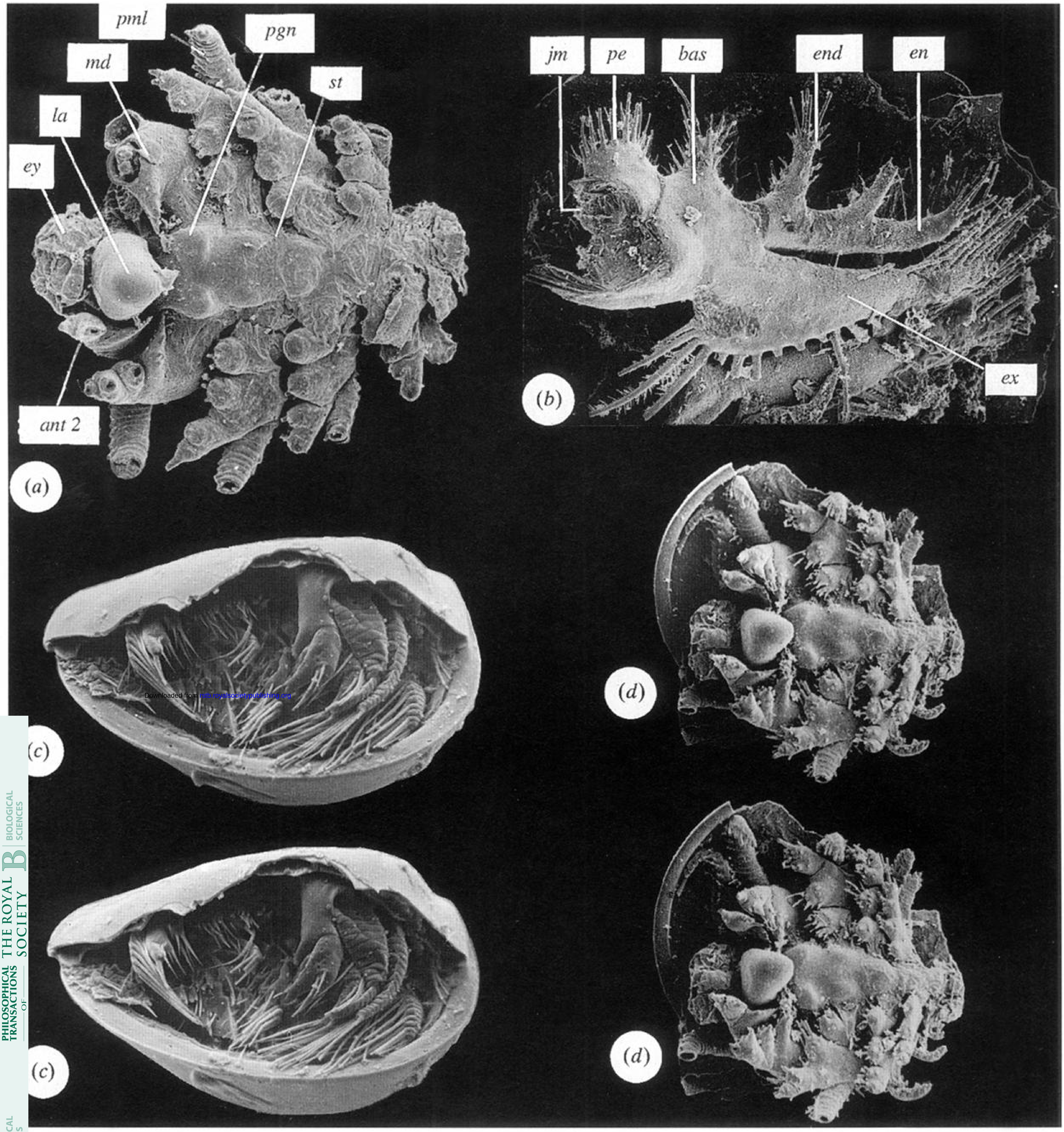


Figure 3. Light photographs of *Kunmingella maotianshanensis* Huo & Shu, 1983, Yuanshan Member, Qiongzhusi Formation, early Cambrian of Maotianshan, Chengjiang County, Yunnan Province, southwest China. (*a*) Dorsal view of complete, open carapace (left valve below), with valves conjoined; University of Oxford Museum, England, no. AY.33, x13.6. (*b*) Dorsal view of incomplete open carapace immersed under water (left valve below), showing conjoined valves and appendages (exposed by partly removing the shell); NIGPAS no. 78184, × 17. (*c*) right lateral view of ventral-posteroventral part of carapace immersed under water, showing traces of possible limbs inside and possible cerci-like caudal rami or endopodite of trunk appendage and adjacent hairs outside the carapace; NIGPAS no. 78185, × 17.9. (*d*) Dorsal view of incomplete open carapace immersed under water (left valve below), showing conjoined valves and appendages; NIGPAS no. 78186, x15.9.



igure 4. Light photographs of *Kunmingella maotianshanensis* Huo & Shu, 1983, Yuanshan Member, Qiongzhusi ormation, early Cambrian of Maotianshan, Chengjiang County, Yunnan Province, southwest China. (*a*, *c*, *d*) Dorsal ew of uncoated, incomplete open carapace (left valve below), showing conjoined valves and appendages (exposed y partly removing the shell); NIGPAS no. 78184: (*a*) complete specimen, × 15.8. (*c*) anterior region, × 29. (*d*) osterior region, × 29. (*b*) right lateral view of uncoated carapace, showing traces of possible limbs inside and possible erci-like caudal rami or endopodite of trunk appendage and adjacent hairs outside the carapace; NIGPAS no. 3185, × 14.5.



igure 9. Scanning electron micrographs of hesslandonid phosphatocopids with soft-parts from the late Cambrian
Orsten' of Gum, Västergötland, Sweden (micrographs courtesy of K. J. Müller). (*a*, *d*) *Hesslandona* sp. nov. (Müller
npublished). (*a*) Ventral view of larval specimen; University of Bonn no. UB1629, length ca. 625 μm. (*d*) Ventral
iew (stereo-pair) of larval specimen; University of Bonn no. UB 1627, length of shell ca. 625 μm. (*b*, *c*) *Hesslandona*
nisulcata Müller, 1982. (*b*) Posterior view of detached post-mandibular limb, with many setae and subordinate
ristles, of a late larval specimen; University of Bonn no. UB 1628, length (excluding setae) ca. 440 μm. (*c*) Oblique
entral view (stereo-pair), from right side, of carapace (most of right valve removed to show soft-parts) of larval
pecimen; University of Bonn no. UB 658, length of shell ca. 550 μm. Abbreviatons: *ant2*, second antenna; *bas*,
asipodite (limb basis, carrying the rami); *en*, endopodite; *end*, endite; *ex*, exopodite; *ey*, eyes; *jm*, joint membrane;
, labrum; *md*, mandible; *pe*, proximal endite; *pgn*, paragnaths; *pml*, post-mandibular limb (all such limbs are of
milar morphology); *st*, sternum.