The morphology of *Opabinia regalis* and the reconstruction of the arthropod stem-group

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Opabinia regalis Walcott is an enigmatic fossil from the Middle Cambrian Burgess Shale of uncertain affinities. Recent suggestions place it in a clade with *Anomalocaris* Whiteaves from the Burgess Shale and *Kerygmachela* Budd from the Greenlandic Sirius Passet Fauna; these taxa have been interpreted as 'lobopods'. Consideration of available *Opabinia* specimens demonstrates that reflective extensions from the axial region, previously thought to be either gut diverticula or musculature, can be accommodated in neither the trunk nor the lateral lobes that arise from it. They must therefore be external structures independent of the lateral lobes. On the basis of their sub-triangular appearance, size and taphonomy, they are considered here to represent lobopod limbs. Some evidence for the existence of terminal claws is also presented. The question of whether *Kerygmachela*, *Opabinia* and *Anomalocaris* constitute a monophyletic or paraphyletic grouping is considered. While they share several characters, most of these are plesiomorphies. Further, *Opabinia* and *Anomalocaris* share several arthropod-like characters not possessed by *Kerygmachela*. It is concluded that these three taxa probably form a paraphyletic grouping at the base of the arthropods. Retention of lobopod-like characters within the group provides important documentation of the lobopod–arthropod transition. A proper understanding of *Opabinia* and its close relatives, which may include the tardigrades, opens the way for a reconstruction of the arthropod stem-group. This in turn allows the construction of a speculative but satisfying scenario for the evolution of major arthropod features, including the origin of the biramous limb, tergites and arthropod segmentation. 'Arthropodization' may thus be seen not to be a single event but a series of adaptive innovations. □*OPABINIA, ANOMALOCARIS, KERYGMACHELA, Burgess Shale, problematica, Lobopodia, Arthropoda.*

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The enigmatic and delightful *Opabinia regalis* Walcott from the Burgess Shale has perhaps attracted more attention than any other taxon from this famous *Lagerstätte* (e.g., Walcott 1912; Hutchinson 1930; Raymond 1935; Størmer 1944; Tiegs & Manton 1958; Sharov 1966; Simonetta 1970; Whittington 1975; Bergström 1986, 1987; Briggs & Whittington 1987; Gould 1989; Simonetta & Delle Cave 1991; Budd 1993; Chen *et al.* 1994). Its affinities have been and continue to be much debated: Walcott himself regarded *Opabinia* as a highly primitive arthropod which might be seen as a 'missing link' between arthropods and their then presumed relatives the annelids; Hutchinson (1930) produced a notorious reconstruction showing the animal swimming upside down as an anostracan; Sharov (1966) placed it in the 'Proboscifera', ancestral to modern arthropods; Simonetta (1970) reconstructed it as a conventional arthropod. It was the monographic treatment of Whittington (1975), however, that set the modern study of the taxon on a firm basis. Crucially, he demonstrated that the frontal appendage was not a fused arthropod-like structure but rather consisted of a flexible, probably fluid-filled tube (Whittington 1975, p. 33), at the end of which were spinose grasping devices. Furthermore, he could find no evidence for jointed appendages as would be expected if *Opabinia* was an arthropod.

Opabinia presents a challenge to modern concepts of 'body-plans' and 'phyla' because it does not fit comfortably into any easily defined extant group. The large, presumably compound eyes and the 'grasping' frontal appendage are essentially arthropodan features. However, the highly flexible main body of the frontal appendage does not seem to be compatible with an arthropod-like musculature working on a lever-system. Such features are more characteristic of the annelids and the onychophorans (Manton 1977). Other unusual characteris-
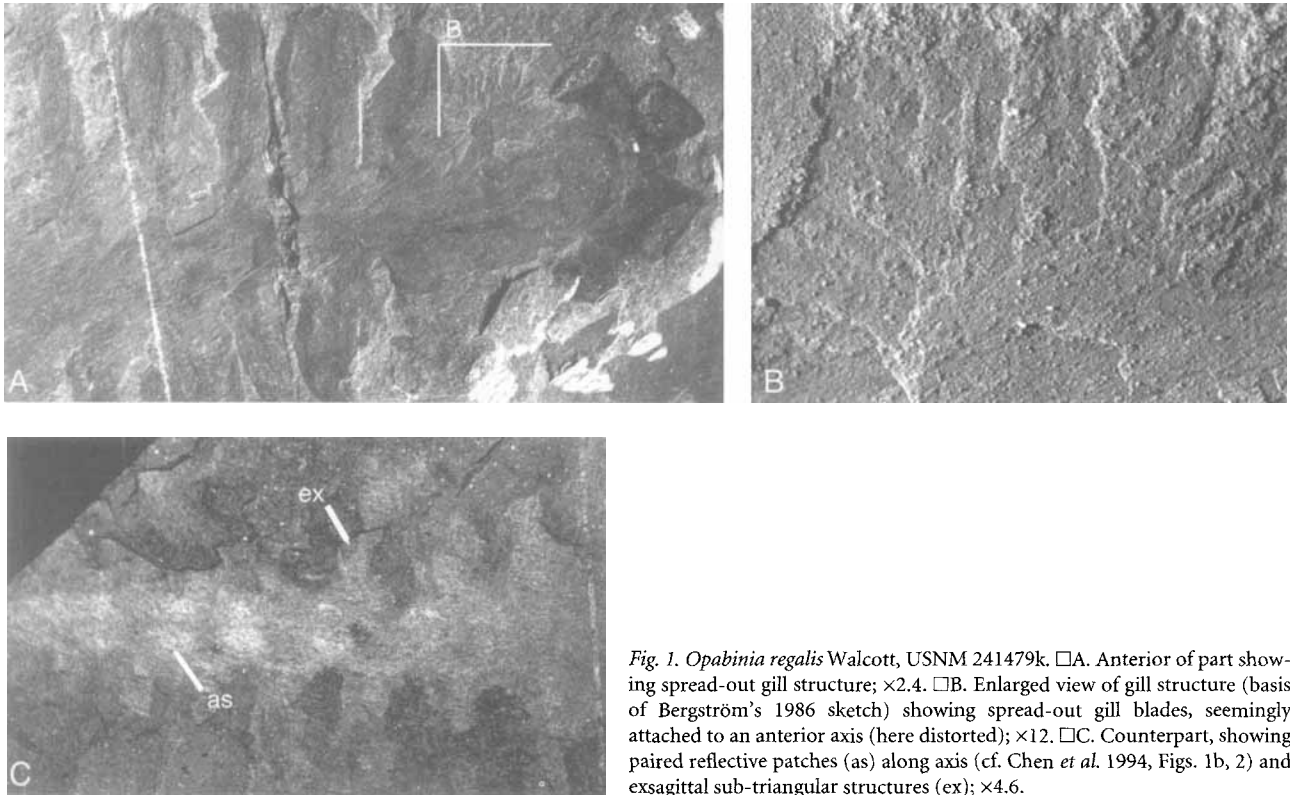
Fig. 1. Opabinia regalis Walcott, USNM 241479k. □A. Anterior of part showing spread-out gill structure; ×2.4. □B. Enlarged view of gill structure (basis of Bergström's 1986 sketch) showing spread-out gill blades, seemingly attached to an anterior axis (here distorted); ×12. □C. Counterpart, showing paired reflective patches (as) along axis (cf. Chen *et al.* 1994, Figs. 1b, 2) and exsagittal sub-triangular structures (ex); ×4.6.

tics include the flexible, lateral lobes and the lack of obvious walking appendages. Discussion of *Opabinia* in a cladistic context has only been attempted relatively informally (Budd 1993; Chen *et al.* 1994; Hou *et al.* 1995). Nevertheless, three broad scenarios are possible:

1   That *Opabinia* is a relatively derived organism, the non-arthropodan features of which are secondarily modified from originally arthropod-like character states (e.g., Chen *et al.* 1994).

2   That the non-arthropod character states are primitive, thereby placing *Opabinia* within the stem-group of the arthropods proper (e.g., Budd 1993).

3   That *Opabinia* cannot be placed sensibly in relation to the arthropods: it represents either an 'unknown body-plan' or is related to another group of organisms such as the aschelminths (e.g., Bergström 1991; Hou *et al.* 1995).

This range of options is complicated first by a certain lack of consensus on the morphology and possible homologies of *Opabinia* itself (e.g., Whittington 1975; Bergström 1986, 1987; Briggs & Whittington 1987) and secondly by the absence of any consensus on the systematic arrangement of the arthropods themselves. Both these points need to be addressed.

Morphology of Opabinia

Opabinia, as reconstructed by Whittington (1975), was an animal about 50 mm long. It possessed a cephalic region with five stalked eyes and with a long flexible appendage attached, the anterior end of which had a pair of grasping claw-like structures. The trunk was annulated with a series of lateral lobes, which had folded, gill-like structures above them. The last three segments were differentiated into a tail fan. However, Bergström (1986) restudied the key specimens and concluded that several aspects of Whittington's model needed revision; these criticisms will be considered below, together with some new observations based on previously unfigured specimens.

Bergström argued first that the so-called 'lateral lobes', regarded by Whittington as appendages, were simply extensions of the dorsal tergites and therefore were better regarded as pleurae, and secondly that the gill-like structures, interpreted by Whittington as imbricated sheets, were actually sets of individual lanceolate structures. These were interpreted as inserting not laterally into the body wall, as Whittington reconstructed his wrinkled sheets, but (by implication) along the anterior margins of the lateral lobes, and also (implied by comparison with *Anomalocaris*) continuing over the dorsum of the animal. Bergström (1986) included a 'slightly idealized sketch' of a previously unfigured specimen to illustrate his proposed
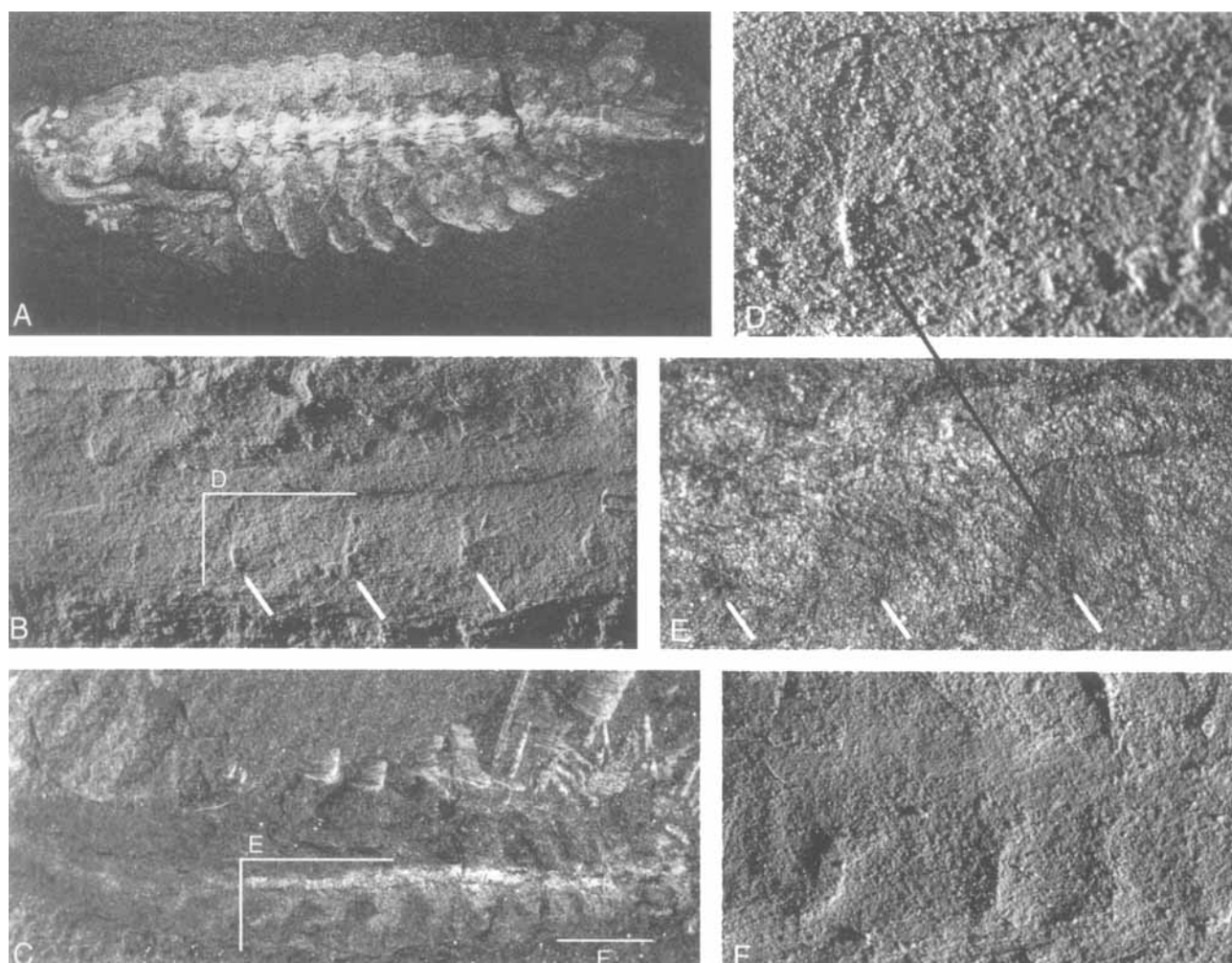
Fig. 2. Opabinia regalis Walcott. □A. USNM 155600. Lateral compression showing putative lobe channels; lobopod limbs and fading of lobe overlaps over the gut. See Fig. 3A for an interpretative drawing; ×2.4 (photograph kindly provided by H.B. Whittington). □B–F. USNM 274177, dorsolateral compression. □B. Coated specimen showing relief possessed by mineralized tips of limbs (see D for detail); ×3.0. □C. General view (uncoated) showing highly reflective gut with axial triangular extensions (see E, F for detail); ×3.4. □D. Close-up of one mineralized tip; ×8.0. □E. Axial region (compare Fig. 6) photographed under alcohol, showing gut and backward-pointing axial extensions with arrowed dark mineralized tips (putative limbs with claws). Equivalent structure in coated view (D) indicated by black arrow; ×4.5. □F. Close-up of anterior part of specimen (coated), showing relief possessed by limbs; ×5.8.

structure of the gills, as he was unable to obtain either *camera lucida* or photographic facilities while studying the specimens. This specimen is figured here for the first time (Fig. 1A, B). Although Bergström's portrayal rather exaggerates the degree of spread, the evidence from this specimen confirms his impression of the gills being sets of separate structures, attached along their anterior margin (presumably to the lateral lobes): there is some evidence of the presence of an axis to which the gill structures attach (Fig. 1B). If the lanceolate blades functioned as gills (a point denied by Bergström), then they would have required a connection to some internal body cavity or vascular system that extended into the lobes. The presence of such a body-cavity extension would not be consis-

tent with calling the lobes 'tergites'. Indeed, there is some evidence for the existence of such cavities. In USNM 155600 (Figs. 2A, 3A), the lateral lobes can be seen to have reflective strips along their anterior margins. Reflective patches in Burgess Shale fossils such as *Opabinia* and *Aysheaia* usually represent mineralization of internal body cavities. For example, a similar strip runs along the centre of the flexible trunk of the anterior appendage of *Opabinia* (Whittington 1975; Fig. 2A herein); it is interpreted as an originally fluid-filled channel. It is therefore reasonable to conclude that narrow cavities are present in the anterior margins of the lateral lobes in *Opabinia*.

Re-examination of the specimens has revealed no evidence for the gills continuing over the dorsum of the ani-
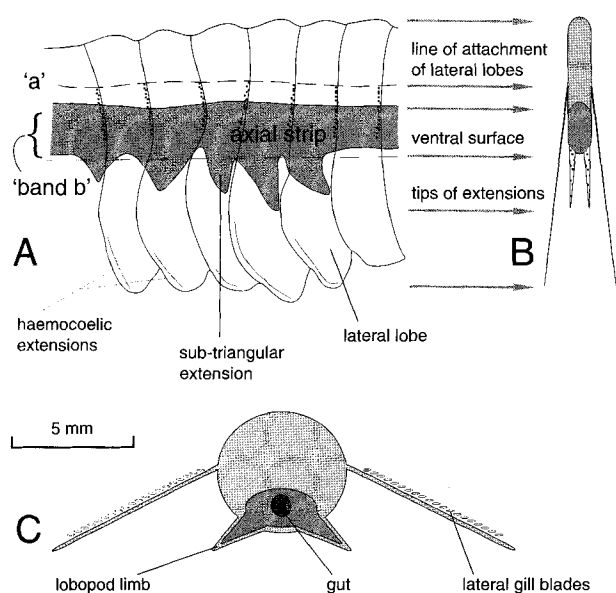
Fig 3. USNM 155600. □A. Interpretative drawing. Line of lateral lobe attachment fixed from beginning of overlap between lobes; ventral surface fixed by reference to mouth position and body diameter. See text for further details and discussion. □B. Reconstruction of end-on view of USNM 155600. □C. Revised reconstruction of cross-section of *Opabinia* (see also Fig. 7).
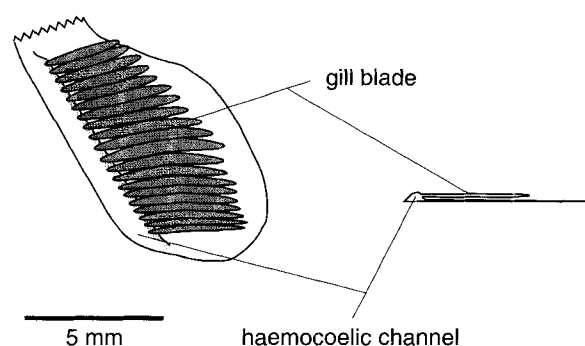

Fig. 4. Revised reconstruction of lateral lobes, showing gills attached to a slight bulge running along the anterior margin.

mal. Some dorsoventrally flattened specimens show longitudinal wrinkling along the body axis, but in USNM 131217 this continues almost to the anterior end of the cephalic region and thus is unlikely to represent gill-like structures. A revised reconstruction of the lateral lobes is presented in Fig. 4.

Bergström (1986) discussed some other characters of *Opabinia* that he felt should be revised. However, comparison with new material of the presumed relatives of *Opabinia* (see below), *Anomalocaris* and *Kerygmachela*, implies that, for example, the gills do indeed sit on top of rather than under the lateral lobes and that the tail fan of

Opabinia – similar to new material of *Anomalocaris* from the Burgess Shale (Collins 1992) and Chengjiang (Chen *et al.* 1994) – was reconstructed correctly by Whittington (1975).

As discussed below, the nature and point of attachment of the lateral lobes is critical to the possibility of *Opabinia* possessing limbs. Whittington's original description reconstructed the lobes as being attached laterally to the trunk. The evidence for this, however, is somewhat limited. One curious aspect of the lobes is the variability of their preserved appearance: Whittington regarded this variation as arising through foreshortening by compression. Because of this variability, there is no 'standard' length one can assume the lobes to be in any particular specimen, so that one cannot simply measure their length to determine their point of attachment. Moreover, the step between adjacent lobes tends to fade out adaxially/ dorsally (the 'band b' zone of Fig. 3A), so that the point at which they become separate structures from the trunk is uncertain. In lateral specimens, a clear overlap between the lobes may only be seen below the presumed ventral surface of the trunk (especially USNM 155600). Dorsal to this point, the lobe overlap is indistinct and appears to change direction to point in a more posterior direction. More dorsally (along a mid-lateral line), there is a more distinct overlap region, which leads into the boundaries between the segment-like annulations. The lobes might therefore actually be attached almost ventrally, rather than laterally. However, several lines of evidence point to Whittington's original reconstruction being essentially correct:

1   In the critical specimen USNM 155600, the prominent series of overlaps developed along the lateral midline (marked 'a' in Fig. 3A) are clearly differentiated from the segment boundaries just dorsal to them. Whittington dissected out the first few lobes of the opposite side of the specimen and demonstrated that the anterior half, at least, of this specimen was essentially a completely lateral compression. The 'series a' line of overlaps therefore cannot represent the bases of the lobes (attached in a more ventral position) pressed through from the other side in an oblique compression – they also imbricate in the wrong direction.

2   An overlap or boundary between either the lobes (if they attach laterally) or the 'segments' (if the lobes attach ventrally) must be present in the zone where they are only poorly preserved, and so the apparent absence of an overlap or boundary is not strictly relevant to the question of where the lobes attach.

3   If the length and (visible) width of the mid-trunk lobes are plotted against each other for each of Whittington's figured specimens, they may be seen to fall into a fairly well-constrained curve (Fig. 5). The lengths were measured either along a definite lobe overlap (usually
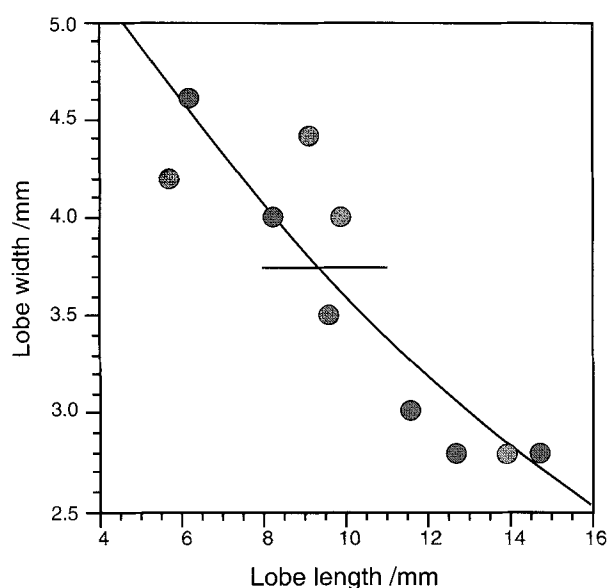
Fig. 5. Graph of exposed lobe width versus lobe length in previously figured specimens of *Opabinia*. Mid-trunk lobes were measured. There is a broad although not exact correspondence with position on graph and overall length of specimen (from Whittington 1975): average specimen length above horizontal line = 63 mm; below line = 52 mm.

in the dorsoventral compressions) or from a presumed mid-lateral attachment site (e.g., in USNM 155600). If in this specimen the lobe length is measured from a more ventral position, the relevant point plots well off the main trend. Consistency between specimens therefore supports a lateral attachment position.

As Whittington supposed, the differences in length between lobes of different specimens appear largely to be because of compressional variation. This is confirmed by a broad (although not exact) correspondence between total specimen length and aspect ratio of the lobes: the five specimens possessing the shortest, broadest lobes (all dorsal or oblique compressions) have an average specimen length of ca. 63 mm, while the other five specimens, possessing long, thin lobes (all lateral or oblique compressions) have an average specimen length of ca. 52 mm (average length of all ten specimens is ca. 58 mm). Much of the variation in specimen length (from 43 to 70 mm) may therefore be owing to compressional differences rather than primary size variation.

Consequently the lobes indeed seem to attach along a mid-lateral line, as in Whittington's original reconstruction (Whittington 1975, Figs. 82–84). The disappearance or fading of the lobe overlaps in the 'band b' region may be a taphonomic artifact. One explanation is that below this point the lateral lobes (in lateral compressions) are ventral to the trunk, whereas at this point and above they are supported by the trunk. It may have been easier for

sediment to infiltrate between the lobes where they were unsupported than where they were supported by the trunk (especially along the trace of the gut [Figs 2A, 3A], where early mineralization may have provided even more support). The difference in preservational regime between where the lobes were supported and where they were not may also explain why the direction of the lobe-overlaps changes over the gut trace (see also Bergström 1986 for a similar conclusion).

Opabinia as a lobopod

The concept of *Opabinia* as a lobopod, first mooted by Budd (1993) has had a mixed reception (Conway Morris 1994; Valentine 1994; Chen *et al.* 1994). It is clear that *Opabinia* does not easily conform to the conventional concept of a lobopod, as exemplified by the extant Onychophora. However, there is no reason to assume that all members of a particular clade must retain a certain number of cherished characters said to 'define' the clade, for to do so relies upon a typological rather than an evolutionary concept of a taxon.

The taxon *Kerygmachela kierkegaardi* was initially described as possessing a lobopod grade of organization (Budd 1993). If this proposal can be sustained, and if *Opabinia* can be shown to be related, then a similar grade of organization for *Opabinia* is established. The lobopod affinities of *Kerygmachela* have, however, been questioned (Chen *et al.* 1994). I do not regard this critique to be well-founded and will treat herein the lobopod-like characters of *Kerygmachela*, especially the nature of the axial wrinkles ('annuli' of Ramsköld 1992) and dorsal tubercles ('nodes' of Ramsköld 1992), as such (at least morphologically).

Opabinia specimens often possess a series of fairly well defined, sub-triangular reflective structures, arranged in a segmental fashion (Fig. 2A; Whittington 1975, Pls. II, VII, VIII, IX, XII, XIV, XV). These axial triangular structures have been suggested to represent oblique muscle blocks (Hutchinson 1930), gut diverticula or circulatory devices (Whittington 1975, p. 36). It has also been suggested that they represent lobopod limbs (Budd 1993). This suggestion is supported by three factors, apart from overall shape and size.

ANOMALOCARIS

The history of research on *Anomalocaris* is well known and need not be repeated here (see Gould 1989 and Collins 1996 for reviews). Bergström (1986) suggested that *Opabinia* and *Anomalocaris* are relatives, based on possession of dorsal gills and other constructional similarities. Although this idea was not intially favourably received

(Briggs & Whittington 1987), most workers seem subsequently to have accepted it (Collins 1996; Budd 1993; Chen *et al.* 1994; Briggs 1994; Wills *et al.* 1995).

Chen *et al.* (1994) compared the axial structures in *Opabinia* to adaxial rows of fibrous, oval structures preserved in specimens of *Anomalocaris* (Chen *et al.* 1994, Figs. 1b, 2). These structures are preserved ventrally and are clearly unlike limbs. However, the structures in *Anomalocaris* and *Opabinia* are demonstrably not directly comparable. The previously unfigured *Opabinia* specimen USNM 241479k shows both the sub-triangular structures and the paired adaxial spots, and they are clearly distinct from each other (Fig. 1C). The evidence from *Anomalocaris* does not refute the presence of limbs in *Opabinia*.

Position of the axial structures in OPABINIA

The triangular axial structures in *Opabinia* have been described either as being ventral or as being contained within the lateral lobes (Whittington 1975; Chen *et al.* 1994). A more careful consideration of the geometry of *Opabinia*, however, shows that neither of these alternatives is possible and that the triangular structures must be external and positioned beneath the main trunk.

Dorsoventral compressions of *Opabinia* such as USNM 205258 (Pl. IX of Whittington 1975) show the triangular axial structures to emerge from a central reflective strip and give the impression that they are contained within the body axis. However, the pair of triangular structures on segment 7 of this specimen take up a transverse width of ca. 8.5 mm. The average transverse width of the trunk of *Opabinia* is ca. 5 mm, and even allowing for the relatively large size of USNM 205258, the trunk could scarcely be wider than 6 mm. In dorsal view, therefore, there are some difficulties in finding the space to fit the axial structures into the trunk.

This problem is magnified by the evidence from the laterally preserved specimen USNM 155600 (Pls. VII, VIII of Whittington 1975; Figs. 2A, 3 herein), and the dorsolateral compression GSC 40251 (Pls. XIV–XVI of Whittington 1975). The former shows that the triangular structures pass well below the level of the mouth, which is presumed to lie just below the ventral surface of the animal. Whittington fixed the position of the ventral surface by reference to its position just posterior to the mouth, and at the posterior of the trunk, both places where the actual surface can be seen. In order to accommodate the triangular structures within the trunk, a large ventral bulge would have to be introduced into the midriff of the animal. Direct views of the ventral surface in the midsection of the trunk are not available, because the surface is hidden by the lateral lobes. However, the possibility of such a bulge being present is slight, because (a) the gut, which is very close to the ventral surface at the anterior
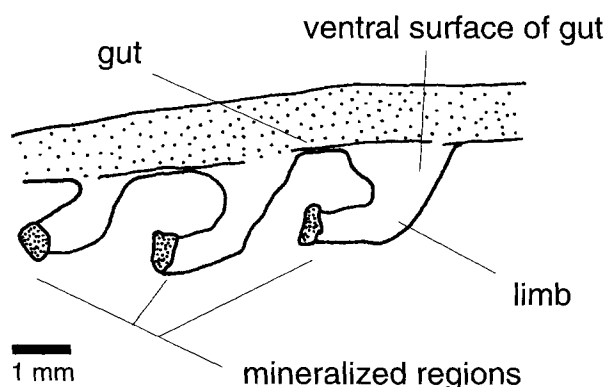

Fig. 6. Interpretative drawing of limb and claw structures in USNM 274177 (cf. Fig. 2E).

and posterior of the animal, stays straight all along the trunk, whereas it might be expected to be deflected downwards to follow the curve of the supposed bulge; (b) no sign of the start of a bulge is seen at either end of the animal; and (c) in the lectotype, USNM 57683, the lateral lobes of both sides of the animal have been compressed together, so that the lobes of either side are seen in an alternate series; no structure such as a distended midriff may be seen intervening between the lobes of each side.

It appears, then, that the axial triangular structures cannot be accommodated within the main body of the trunk. The lateral and dorsolateral preservations USNM 155600 and GSC 40251 also demonstrate that the structures cannot be associated with the lateral lobes either. USNM 155600 shows this most clearly. The axial strip to which the triangles are attached lies ventrally within the body, whereas the lobes are attached laterally, as discussed above. The triangles cannot therefore be internal to the lobes, but must project below the ventral surface of the body, as is clear from consideration of what an end-on view of this specimen must look like (Fig. 3). It must be stressed that although such evidence seems rather circumstantial, there is no other possibility for the position of the triangular structures, if indeed the lobes attach laterally, as discussed above.

Relief and claws of the limbs

Several specimens, including USNM 155600 and USNM 205258, show the putative limbs to possess some relief. This is particularly so in the anterior limbs of the previously unfigured specimen USNM 274177 (Fig. 2F). At the tips of the more posterior limbs in this specimen are small mineralized patches (Figs. 2B, D, E, 6) that have an elongate structure. They may represent sets of terminal claws, possession of which is a characteristic of many lobopod and arthropod limbs.
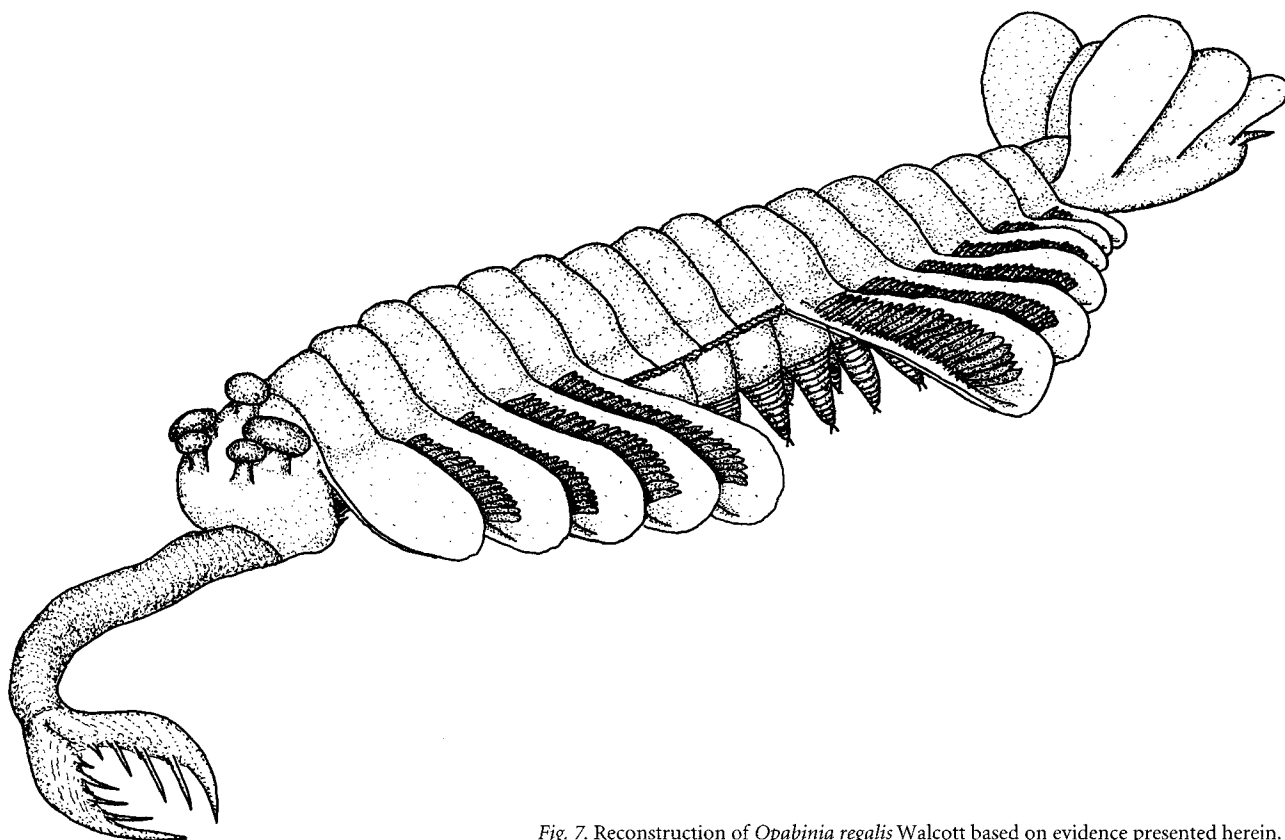
Fig. 7. Reconstruction of *Opabinia regalis* Walcott based on evidence presented herein.

Discussion

Restudy of figured and unfigured specimens of *Opabinia* has broadly confirmed Whittington's (1975) reconstruction. Some important differences have nevertheless emerged. The reconstruction of the gills by Bergström (1986) seems to be correct, in that they are lanceolate structures rather than wrinkled sheets. However, his other criticisms of the Whittington model are, in the light of new information now available, not upheld here. Bergström (1986, p. 246) also suggested that if *Opabinia* did possess limbs, they would be difficult to discover because of its overall morphology. The details of morphology presented above, when taken together, provide convincing evidence that *Opabinia* did in fact possess conical, probably lobopod-like limbs; a new reconstruction is presented in Fig. 7. The structures described above probably represent mineralization associated with the internal cavities of lobopod limbs. Similar patches of mineralization or coloration are clearly seen in lobopods such as *Paucipodia* (Chen *et al.* 1995a) and several others, including *Aysheaia* from the Burgess Shale (e.g., Whittington 1978; personal observation) and *Onychodictyon* (Ramsköld & Hou 1991, Fig. 6). In the cases known, the mineralization runs from that associated with the gut down to the claws (e.g., Chen *et al.* 1995a, Fig. 2E); precisely as it does in *Opabinia*. The

shape of the mineralized patch mirrors that of the limb itself.

This observation of limbs is central to the assessment of the systematic position of *Opabinia* and its probable relatives *Kerygmachela* and *Anomalocaris* (Budd 1993; Chen *et al.* 1994). This group of animals appears to contain representatives that are relatively 'arthropodized' (*Anomalocaris*), with arthropod-like frontal appendages, and also animals that are more 'lobopod'-like (*Kerygmachela*, *Opabinia*). Establishment of a revised morphological reconstruction allows further remarks to be made concerning the phylogenetic import of these taxa.

Arthropod systematics

The phylogeny of the arthropods has been a focus of heated debate for over a century, with views ranging from strict monophyly (Snodgrass 1938) through diphyly (Hessler & Newman 1975) to multiple polyphyly (Manton 1977). There is in fact hardly any consensus, apart from the probable relationship of the trilobites to the chelicerates (e.g., Briggs & Fortey 1989). In particular, the placement of the hexapods and crustaceans is problematic; some authors place the insects in a basal position,

separated from the crustaceans (in the extreme, this leads to a diphyletic view of the arthropods, such as that of Hessler & Newman 1975), whereas others place the two together in the Mandibulata (e.g., Ax 1987). Briggs & Fortey (1989) identified a large clade of arachnomorphs (trilobites + chelicerates + several Cambrian problematica) and placed the crustaceans as the sister group to these; the hexapods and myriapods were subsequently placed as the sister group to the entire crustacean + chelicerate + trilobite 'CCT' clade (Briggs *et al.* 1992; Wills *et al.* 1994). Molecular data (e.g., Field *et al.* 1988; Lake 1990; Ballard *et al.* 1992;) have tended to support a crustacean + hexapod clade but almost invariably place the myriapods in a basal position (see also Friedrich & Tautz 1995). However, this basal position may at least in part result from the myriapods being a 'long branch' taxon, i.e. their rRNA has accumulated changes at a faster-than-average rate for the rest of the arthropods, thus making them relatively dissimilar.

Character polarity within the arthropods is difficult to assess without an accepted high-level classification. In particular, does the 'uniramous' limb of the hexapods and myriapods or the 'biramous' limb of the CCT clade represent the ancestral character state for the arthropods? This polarity problem may be resolvable by reference to taxa (if they exist) that can be placed in the stem group of the arthropods as a whole.

The recognition of various lobopodous forms in the Cambrian, including *Hallucigenia*, *Microdictyon*, *Onychodictyon*, *Xenusion* (see Simonetta & Delle Cave 1991, Hou & Bergström 1995 for reviews) and *Kerygmachela* (Budd 1993) has greatly expanded the morphological scope of the lobopods. Although these new forms were originally thought to lie within the Onychophora, this now seems doubtful. Lobopods, as represented today by the onychophorans and the tardigrades, can be allied to the arthropods with a series of synapomorphies, including the possession of lateroventral limbs, non-septate haemocoel, ostiate dorsal vessel, centrolecithal cleavage of a yolky egg, deuterocerebral brain, and a moultable, chitino-proteinaceous exoskeleton (Boudreaux 1979; Brusca & Brusca 1990, p. 683; Budd 1993; Kinchin 1994). In addition, the extant Onychophora have a few autapomorphies of their own, including oblique body musculature and slime papillae: none of these obviously occur in any of the Cambrian lobopods. In this regard, it should be noted that taxa such as *Aysheaia* possess characters that appear to be more tardigradan than onychophoran, such as the lack of a trunk extension posterior to the last limb pair (Simonetta 1970; Whittington 1978). Although it has been customary to place *Aysheaia* within the Onychophora (Robison 1985; Gould 1989), Whittington's original suggestion that it represents a form ancestral to both onychophorans and the tardigrades might therefore be justified. The extant Tardigrada also possess several

autapomorphies associated with extreme miniaturization, including a pseudocoel, eutely of the cuticle and reduction in musculature (Dewel *et al.* 1993; Kinchin 1994).

The lobopods are usually treated either (by an eclectic taxonomist) as an 'annelids–arthropod intermediate' (e.g., Hou & Chen 1989), or (by a cladist) as the sister group to the 'Euarthropoda' (e.g., Ax 1987). Nevertheless, the suite of characters shared by arthropods, tardigrades and onychophorans is very close to those that define a lobopod, i.e. the onychophorans and tardigrades have retained a number of unmodified symplesiomorphies from the common arthropod–onychophoran–tardigrade ancestor. This suggests that the lobopod grade is paraphyletic.

The question of the actual relationships between the various lobopods and arthropods could be answered if some lobopods possessed synapomorphies with the arthropods that are not possessed by other lobopods. Such characters have been listed for at least the tardigrades (Brusca & Brusca 1990, p. 683), including possession of arthropod setae, non-serially arranged nephridia, striated, discrete bundles of musculature and true stepping gait in the limbs. It should be noted here that many modern authors do not regard the 'pseudocoelomate' characters of the tardigrades as phylogenetically significant (see Kinchin 1994 for review).

A 'lobopod' concept based even on the extant forms then, is likely to be paraphyletic. Other potential synapomorphies possessed by the Cambrian forms may include morphology of the limbs and degree of arthropodization.

Limbs

It has been suggested that the lateral, gill-bearing lobes of the anomalocaridids are homologous to the gill branches of the biramous arthropods (Simonetta & Delle Cave 1991; Budd 1993; Chen *et al.* 1994). If this were indeed the case, it would provide a valuable synapomorphy that united some of the arthropods with the anomalocaridids. Because relatives of the anomalocaridids (*Kerygmachela* and *Opabinia*) possess lobopod-like characters too, this would provide additional evidence of the paraphyletic nature of 'lobopods' and the pathway along which at least some of the arthropods emerged.

Such a homology is not entirely problem-free, especially as the limbs and the lateral lobes in *Kerygmachela* and *Opabinia* are not directly attached to each other, as they are in the biramous arthropods. Nevertheless, this hypothesis is probably the strongest contender for explaining the origin of the biramous limb. Little evidence has been hitherto available to support rival theories. Snodgrass (1938) thought that the biramous limb had arisen from structures on a lobopod-like limb; Emerson & Schram (1990) proposed the lateral marrying of pairs of
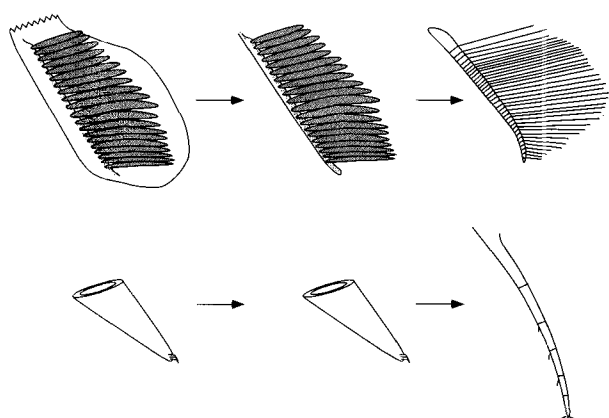
Fig. 8. Homologies and possible evolutionary transition between the lateral lobes, gills and limbs of *Opabinia* and equivalent structures in a basal biramous arthropod, *Marrella* (in part after Whittington 1971). Conversely, the gill components of the lateral lobes may have been lost in the tardigrades through miniaturization.

segments of a remipede-like crustacean, and Kukalova-Peck (1992) proposed that the original limb was polyramous, from which both uniramous and biramous limbs emerged. All of these theories have associated difficulties: the first is plausible but has little material evidence to support it; the second is weakened both by doubts about the primitive nature of the remipedes (Dzik 1993) and because seemingly even more basal arthropods such as *Marrella* (Whittington 1971; Briggs & Fortey 1989) and *Fuxianhuia* (Chen *et al.* 1995b) have an already well-established biramous limb; finally, the proposal of Kukalova-Peck (1992) suffers from some methodological weaknesses (by loading a hypothetical ancestral animal with all the morphologies possessed by its descendants, which are then shed appropriately in different lineages) and is undermined by the presence of an apparently stable biramous limb in the earliest arthropods.

It appears, then, that the anomalocaridid hypothesis for the origin of the biramous limb is at present the most plausible. It is supported by the probable identity in function of the lateral lobes in the anomalocaridids and the outer branches of the biramous arthropods, i.e. for supporting respiratory structures. The revised reconstruction of the lobe-gill structure in *Opabinia* presented herein provides further support for this homology. If the lateral lobes are to be regarded as possessing channels along their anterior margins, then they may be construed almost as a conventional lobopod-type limb, except with a broad flap-like extension attached: the gills are attached to the channels. Such a structure is clearly also rather like the outer branch of a biramous limb: the transformations required to convert it into such a structure include reduction of the flap and, of course, arthropodization (Fig. 8).

This proposed homology is complicated somewhat by the putative gill structures in *Anomalocaris*. As reconstructed by Whittington & Briggs (1985), these attach directly to the body wall and are contained within some sort of 'gill chamber'. However, it is fair to say that the gill structures and their attachment in *Anomalocaris* are poorly known, and the arrangement shown in the reconstruction is as yet hypothetical. Hou *et al.* (1995) have recently published some evidence in support of Bergström's (1986) view that the so-called gills in *Anomalocaris* are in actuality sets of lanceolate blades extending over the dorsum of the animal.

Arthropodization

Within the entire clade termed Lobopodia by Snodgrass (1938), which includes the Onychophora, Arthropoda and (although not specifically considered by Snodgrass) the Tardigrada, various degrees of 'arthropodization' are present. As well as the usual 'arthropods' (crustaceans, chelicerates, trilobites, hexapods, myriapods and other taxa of uncertain affinity), which fully sclerotize their cuticle, partial arthropodization is possessed by other taxa. The principal occurrences are:

1 Terminal claws of lobopods.
2 The jaws of extant onychophorans.
3 The cuticular plates of the echiniscid tardigrades (e.g., Greven 1984; Dewel *et al.* 1993; Kinchin 1994).
4 The various 'armourings' of the armoured lobopods of the Cambrian, such as *Hallucigenia, Microdictyon* and *Xenusion* (see Simonetta & Delle Cave 1991; Ramsköld 1992; Hou & Bergström 1995 for reviews). These are conceivably homologous with the dorsal armouring of the echiniscid tardigrades, although these latter seem to be derived.
5 The frontal appendages of *Anomalocaris*, perhaps the tail spines of *Kerygmachela* (which show signs of being composed of fused segments), and the dorsal compound eyes of *Anomalocaris* and *Opabinia*.

None of these occurrences represents a complete arthropodization as exhibited by conventional arthropods. However, it is clear that within the entire clade an *ability* to sclerotize the cuticle must be a highly symplesiomorphic character. Such an inherent ability might usefully be considered as an 'underlying synapomorphy' (Saether 1979). It is not at all clear that all of the occurrences of 'arthropodization' within the clade as a whole are homologous in the conventional sense. As Patterson (1978) presciently pointed out, though, such a conclusion need not support the extreme polyphyletic views of Manton (1977): all of the arthropods and lobopods *together* can be seen to form a monophyletic clade.

Reconstruction of the arthropod stem-group

Ramsköld (1992) and Hou & Bergström (1995) undertook thorough reviews of character distribution within the Cambrian lobopods (excluding the anomalocaridids and their relatives): these analyses are equally applicable to the stem-group of the arthropods. Apart from the position of the extant onychophorans (which Hou & Bergström 1995 ally with Onychodictyon on the basis of the presence of possible antennae and jaws in the latter) these analyses broadly agree. After analyzing the distribution and states of the characters, Ramsköld (1992) erected a morphocline, together with the comment that such an analysis at this level would probably be of more utility than simply putting characters through a phylogenetic analysis. I concur with this assessment and turn now to extending and modifying Ramsköld's scheme in the light of three hypotheses: (1) the lobopods are paraphyletic; (2) the anomalocaridid-like taxa share characters with both the lobopods and the arthropods, and (3) arthropods are derived from lobopods rather than vice versa. In particular, this last hypothesis has the effect of polarizing Ramsköld's morphocline in the direction he presents it (and indeed implies is the 'correct' direction), so that Aysheaia stands at a basal position. This polarization can be justified on the grounds that the Onychophora (which, as will be seen, stand at the basal end of the morphocline) possess 'primitive' characters such as cilia in the gonoducts and paired segmental nephridia. Compared to an outgroup such as the annelids or molluscs, these characters may be regarded as retained symplesiomorphies within the Lobopodia clade. Secondly, except for one study (Ballard et al. 1992), a derivation of onychophorans from arthropods has never seriously been considered, probably because of the much simpler organization of nervous system and musculature in the former. Ramsköld (1992) was not able to polarize the morphocline that he presented because he lacked the crucial evidence provided by Kerygmachela and the light thus shed on the phylogenetic position of Anomalocaris and Opabinia. This morphocline is in contrast to the scheme originally presented by Budd (1993), which placed Xenusion in a basal position on the basis of its lack of serial differentiation. However, I recognize that Ramsköld's original analysis provides a more secure basis for a phylogenetic reconstruction.

Several important features need to be considered:

1   '...unless secondarily lost, there are differentiated frontal appendages in all taxa under consideration' (Ramsköld 1992, p. 459). If the lobopods are paraphyletic, then one might expect some retention of this character within the anomalocaridid-like taxa and the arthropods. Although there are no clear homologies within the arthropods (though of course all arthropods do have some sort of modified anterior appendages), such characters are possessed by Kerygmachela, Opabinia and Anomalocaris. The clearest comparison is between the frontal appendages of Aysheaia and those of Kerygmachela. In these taxa, the frontal appendages are spinose along the inner margin, with a terminal group of longer spines, and the main body of the appendage is wrinkled. There is therefore a reasonable amount of detailed similarity between these structures. The frontal appendages of Opabinia are also similar but are placed on the end of a flexible trunk. Finally, in Anomalocaris, the frontal appendages have a similar arrangement of spines but appear to be be highly sclerotized and segmented. Such appendages may not be used to define a monophyletic group of anomalocaridid-like taxa because of their plesiomorphic distribution. However, taking Aysheaia as an outgroup, the character state in Kerygmachela seems the most primitive, with those of Opabinia and Anomalocaris being variously derived: these three taxa do not seem to present a straight-line morphocline in this character. The fleshy antennae of the extant onychophorans may be homologous with these features.

2   Annuli may be present in all of the taxa that Ramsköld studied, although in Hallucigenia no clear preservation of this feature can be seen in the Burgess Shale specimens (but they are preserved in H. fortis from the Chengjiang fauna; Hou & Bergström 1995). Again, Aysheaia represents one extreme of morphology, because the annuli are evenly spaced: in all other taxa except the recently described Paucipodia (Chen et al. 1995) the development of large tubercles above the limb pairs gives the taxa a 'heteronomous annulation' (Ramsköld 1992). The extant onychophorans possess annulations most similar to those of Aysheaia. However, annulations (in the sense employed by Ramsköld) are not present in the tardigrades, in Opabinia (apart from the flexible trunk to the frontal appendages), Anomalocaris, or any of the arthropods. The lack of annuli in Opabinia may represent the end-point of a line of evolution where the large annuli associated with each limb-pair have expanded to exclude the other annuli. Although the lack of external segmentation in extant onychophorans (which in this character appears to be morphologically similar to Aysheaia) has usually been regarded as secondary (especially if the onychophorans are seen as 'annelid–arthropod intermediates'), the phylogenetic reconstruction presented herein (and implicitly by Ramsköld 1992) suggests that this state is primitive within the clade. In turn, this suggests that the external (i.e. ectodermal) segmentation of the arthropods is derived independently from that of the annelids (cf. Conway Morris & Peel 1995; Eernisse et al. 1992; Valentine 1994).
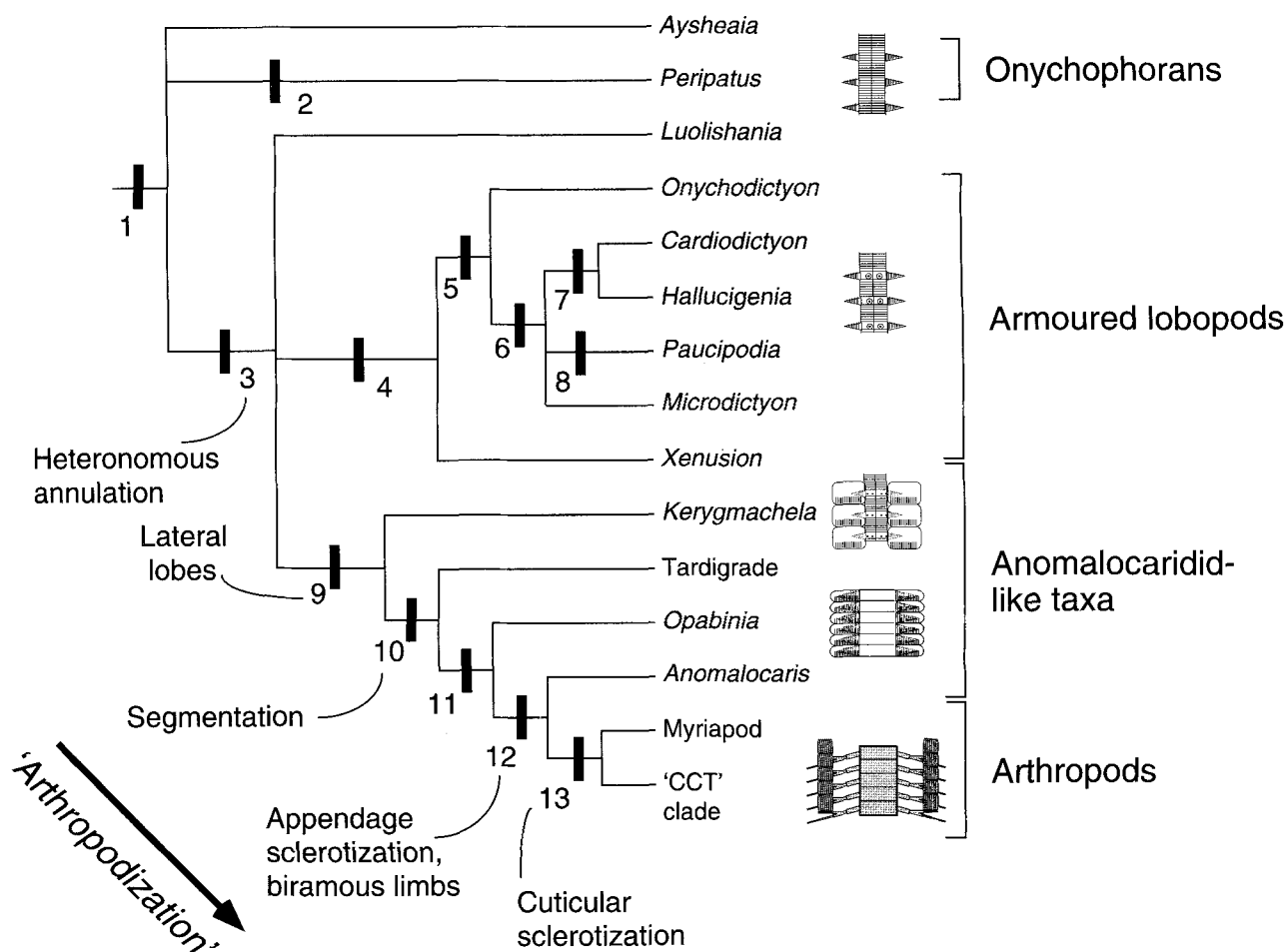
Fig. 9. A broad-scale reconstruction of the arthropod stem-group, mostly following Ramsköld's (1992) 'morphocline'. This has been converted into a phylogeny by the polarization discussed in the text. Based on data from Ramsköld (1992); Budd (1993); Wills et al. (1994); Hou & Bergström 1995; Chen et al. 1995a; Dewel & Dewel (1996) and herein. Important synapomorphies: 1. The plexus of arthropod characters of Budd (1993). 2. Onychophoran autapomorphies. 3. Heteronomous annulation, nodes. 4. Node enlargement. 5. 'Armoured' nodes. 6. Spine enlargement, effacement, limb spine loss, slender limbs. 7. ?Oval head shield. 8. Secondary loss of nodes. 9. Lateral lobes. 10. Arthropodan segmentation (= loss of small trunk annulations). 11. Large compound eyes, differentiation of trunk to form tail fan, gut diverticulae. 12. Sclerotization of appendages, fusion of lateral lobes and limbs to form biramous limb, gnathobases. 13. Sclerotization of tergites (CCT clade = crustaceans + chelicerates + trilobites: possibly + insects). Morphologies at various points and important lobopod–arthropod innovations are identified.

3 Plates, nodes, tubercles, etc. Ramsköld (1992) placed Aysheaia, with each annulus bearing a row of simple spine-bearing nodes, at one end of a morphocline, and taxa with well-developed spines (such as Cardiodictyon) at the other. This character also exists in a modified form in Kerygmachela, which possesses a row of four tubercles above each limb pair. However, there is no development of long spines, and in general the nodes are rather similar to those of Luolishania. The development of long and robust spines may therefore be a synapomorphy uniting the following taxa: Hallucigenia, Cardiodictyon, Onychodictyon and Microdictyon, with simple unelaborated nodes being present along the stem-group from Luolishania up to

Kerygmachela. If, as suggested by Dewel & Dewel (1996) the tardigrades should be considered as originating from the Kerygmachela–Opabinia–Anomalocaris grouping, none of which possess such plates, then the dorsal plates seen in the relatively derived echiniscid tardigrades may not be homologous with those possessed by the 'armoured lobopods'.

The above analysis, given the three hypotheses mentioned earlier, provides a basis for a broad-scale reconstruction of the arthropod stem-group (Fig. 9). As noted above, this phylogeny is based on the morphocline distinguished by Ramsköld (1992), polarized by reference to the direction of the lobopod–arthropod transition. However, it does not as such rely strictly on parsimony: the number and

nature of the available characters renders such an analysis less useful than usual. Nevertheless, it stands or falls on the implied homologies between various features.

The most basal taxon is probably the Onychophora, distinguished from the rest of the clade by their lack of enlarged tubercles or nodes. This is not a good character in that *Aysheaia* possesses a somewhat similar morphology. Following Ramsköld's morphocline, the possession of definite and few tubercles is a character defining all the other taxa, the basal members of which are *Luolishania* and *Xenusion*. The 'armoured lobopods' (*Hallucigenia, Cardiodictyon, Microdictyon, Onychodictyon* and, although having lost its nodes, *Paucipodia*) probably form a monophyletic grouping within this large clade. A further clade is defined by the possession of lateral lobes, shared by all the anomalocaridid-like taxa, probably including the most basal tardigrades (Kristensen 1984; Simonetta & Delle Cave 1991, Fig. 32 E, F; Kinchin 1994, Fig. 3.4; Dewel & Dewel, in press) and the arthropods. However, within this grouping, *Kerygmachela* is characterized by the retention of several plesiomorphic characters, including trunk annulation and dorsal tubercles (which appear to be most similar to those of *Luolishania*, so that those of *Xenusion* probably do not represent the stem-lineage morphology).

Although some characters can be adduced in support of a monophyletic anomalocaridid-like clade (Budd 1993; Chen *et al.* 1994), these are mostly weak (such as the possession of tail spines, which in any case are present in some tardigrades and also perhaps in arthropods as a telson). *Opabinia* and *Anomalocaris* may be united with the arthropods on the basis of the loss of annulations (i.e. development of external segmentation) and the presence of compound eyes. Further, the sclerotization and segmentation evident in the frontal appendages of *Anomalocaris* may also be a synapomorphy uniting it with the arthropods. The recent description of trunk limbs of an anomalocaridid, showing them to be biramous and gnathobasic (Hou *et al.* 1995), also adds considerable weight to the view that anomalocaridids are the sister group to the euarthropods. If this is correct, then the anomalocaridid-like taxa are paraphyletic, being arranged successively up the arthropod stem-group: *Kerygmachela, Opabinia* and *Anomalocaris*. If the tardigrades are to be placed within this grade, then they probably lie above the level of *Kerygmachela* (not possessing trunk annulation) and below that of *Anomalocaris* (not possessing sclerotized appendages). However, because of their miniaturization, it is difficult fully to assess their characters. Given that they do not possess large compound eyes or a serially differentiated trunk, one would place them between *Kerygmachela* and *Opabinia*, although these lacks may be secondary losses. Their style of trunk segmentation is, in this scheme, most similar to that of *Opabinia*, although in

some taxa it seems to be rather less well-organized (e.g., Dewel *et al.* 1993. fig. 5).

The lobopod–arthropod transition

The above analysis suggests that in the lobopod–arthropod transition, the first key feature was the development of lateral lobes, followed by external segmentation (via the development of heteronomous annulation), followed by sclerotization of the limbs and formation of the biramous limb, followed by sclerotization of the cuticle. Hence, the 'arthropodization' complex can be largely deconstructed into an orderly series of morphological innovations.

The relationships of the taxa above this point (i.e. the true arthropods), remains contentious. Herein, I shall consider the morphological transitions required by just one model of arthropod relationships, that of Briggs, Fortey and Wills. Cladograms produced by Briggs *et al.* (1992) and Wills *et al.* (1994) place the myriapods and hexapods at the base of a monophyletic arthropod tree, i.e. as the sister group to the 'Schizoramia' of Bergström (1976). This topology is far from enjoying a consensus, and, as briefly discussed before, the disagreement is compounded by three contributory factors: the splitting of the hexapods and myriapods by molecular data (implicitly supported by the study of homeotic gene distribution by Averof & Akam 1993); the dispute over the relationships between the various myriapodous groups (if indeed they form a monophyletic grouping), and the relatively late appearance in the fossil record of undoubted 'uniramous' arthropods (the earliest putative example, the Middle Cambrian *Cambropodus* (Robison 1990) is questionable). Uniramians appear to date from the Silurian (Jeram *et al.* 1990), and the question of the identity of their marine forbears seems legitimate. The basal position indicated for myriapods led to the suggestion that they may have acquired a fully sclerotized exoskeleton independently from the Schizoramia (Budd 1993), which might also explain their absence from the lower Palaeozoic fossil record. The alternative, if the anomalocaridids are correctly placed, would be that the uniramous limb of the myriapods is secondary. This has been questioned by several authors (e.g., Emerson & Schram 1990) if only because there is very little evidence that this is the case: the terrestrial isopod crustaceans are usually cited to show that *secondarily* uniramous limbs are always clearly so.

A strict cladistic assessment of the origin of full arthropodization is considerably complicated by the fact that arthropodization is a complex of interdependent events (Willmer 1990). Should 'arthropodized', even an 'unravelled' arthropodization as presented herein, be coded as a single character, or as many (e.g., possession of sclerotized exoskeleton, lever system of musculature, specialized osmoregulation and so on)? If the latter option is chosen,

then the 'arthropods' (Schizoramia + Hexapoda + Myriapoda) are effectively guaranteed to emerge as a monophyletic grouping. Conversely, reliance on particular 'synapomorphies' such as the uniramous limb is to a certain extent an arbitrary pre-supposition of the results one is seeking. In such cases, documentary evidence of novel character combinations as provided by the fossil record is crucial to the discovery of true clade topology.

The recognition of the position of the anomalocaridid-like animals at the top of the arthropod stem-group suggests a scheme of transitions that led up to full arthropodization (Fig. 9). Both elements of the biramous limb are present in *Opabinia* and *Kerygmachela*, but they are separate; Budd (1993) suggested that the linking of the two elements and arthropodization were effectively concurrent events. However, as *Anomalocaris* appears to possess biramous limbs, but not a sclerotized exoskeleton apart from the limbs, development of the biramous limb may be seen to have preceded complete sclerotization. Myriapods then, if basal, must be either independently sclerotized, or have secondarily lost the outer branch of a biramous limb. This remains a central problem in arthropod phylogeny which the present material does not address. However, the other alternative of the most basal arthropods being uniramous may now be ruled out by reference to *Anomalocaris*. It should also be noted that in this particular scheme, the apparently basal arthropod *Fuxianhuia* (Chen *et al.* 1995b) does not possess several characters that, by reference to an anomalocaridid outgroup, should be present at the base of the arthropod clade, including 'normal' limb segmentation and gnathobases.

Conclusions

Opabinia regalis appears to have possessed a series of claw-bearing lobopod limbs. However, characters possessed by it and its probable relatives *Anomalocaris* and *Kerygmachela* also indicate arthropodan affinities. Such a mix of characters is explicable if the lobopods are paraphyletic. The Cambrian lobopods, rather than falling into a monophyletic Onychophora, comprise the stem-group to the arthropods and in this sense provide similar information about the origins of the arthropods to that provided by the mammal-like reptiles about the origins of the mammals (Kemp 1982). The phylogenetic reconstruction presented here has the interesting implication that segmentation in arthropods has arisen independently from that of the annelids (cf. Eernisse *et al.* 1992).

'Arthropodization' may be a tendency throughout the clade and is represented in varying degrees by different member taxa, although it remains uncertain whether or not full arthropodization has been achieved more than once. In any case, a possible scenario for the stem-group

of the true arthropods is now available, from the most basal, onychophoran-like taxa, through the armoured lobopods, anomalocaridid-like taxa (including the extant tardigrades) to the most basal completely sclerotized taxa. The relationships within the true arthropods remain contentious, although taking a particular scenario (that of Wills *et al.* 1994) it is possible to speculate on the morphological transitions involved. This allows explicit hypotheses of homologies to be made, which are testable by reference both to extant taxa and to future fossil finds.

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