

# *Opabinia* and *Anomalocaris*, unique Cambrian 'arthropods'

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The Cambrian *Opabinia* and *Anomalocaris* are odd animals known mainly from the Middle Cambrian Burgess Shale. *Opabinia* has usually been regarded as an arthropod, e.g. as a branchiopod crustacean. Parts of *Anomalocaris* have been referred to three or four different phyla. Recent redescrptions have clarified much of their morphology and resulted in their removal from the arthropods. Additional observations and considerations indicate that the two genera have important similarities, including scale-like structures arranged segmentally in transverse dorsal sets, which are separated by transverse tergal plates. Although external views are rare, traces of segmented appendages are identified in *Anomalocaris*. The animals are therefore again considered as arthropods, although they do not seem to be related to any of the other arthropod phyla. □ *Burgess Shale fossils, Cambrian, Arthropoda, Opabinia, Anomalocaris.*

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The famous Burgess Shale fauna from the Middle Cambrian of British Columbia was originally described by Charles D. Walcott early in this century. Debate on the morphology and systematic position of the Burgess Shale fossils has continued until now. There are primarily three reasons for this. First, the fossils are strongly flattened, which makes separation of structures difficult. Second, the fossils are often split open so that various internal surfaces are exposed. The viewer therefore often looks out from the inside, which means difficulty observing the external morphology. Third, many fossils are unique representatives of groups otherwise unknown to science.

Even though many of the Burgess Shale fossils have recently been thoroughly restudied, it is no surprise that there still remain uncertainties and possible alternative interpretations. This is demonstrated below for *Opabinia* and *Anomalocaris*, where reconsideration of some features results in reconstructions quite different from those recently proposed. *Opabinia* is of ordinary size, while *Anomalocaris* is a giant competing in size with the largest Cambrian paradoxid trilobites.

## *Opabinia*

The genus is represented by a single species, *O. regalis* Walcott 1912, known only from the Middle Cambrian Burgess Shale. This remarkable animal had been regarded as an anostracan bran-

chiopod, but Størmer (e.g. 1959) recognized the 'filaments' and regarded it as a trilobitomorphic. The animal was thoroughly redescribed by Whittington (1975), who made several new interpretations. The following is based partly on his description and partly on a study of specimens made during a visit to the U.S. National Museum in 1979.

Whittington showed that there is a comparatively small head carrying five large stalked eyes on the dorsal side (Fig. 1A). On the anteroventral side there is a long annulated frontal process or proboscis ending in a number of spines, apparently forming a grasping organ. The mouth opening is behind the proboscis and faces backwards. Behind the head there is a series of 15 plate-like tergites, each overlapping its neighbour behind. Between each two tergites there is a transverse series of lamellae. Whittington (1975; figure references below refer to that publication) thought that each set of lamellae formed a lamellated plate situated on top of the corresponding tergite (Fig. 1B, C). However, in specimen USNM 241479 (Fig. 1F), not illustrated or discussed by Whittington, the most anterior set of lamellae is nicely spread out like a fan demonstrating that the individual elements are lanceolate blades or scales (Fig. 1D, E). These are attached to an axis in their anterior end. The blades are fairly well exposed also on the left side of specimen USNM 205258 (Figs. 44, 49). Each blade set is probably covered by a corresponding tergite rather than

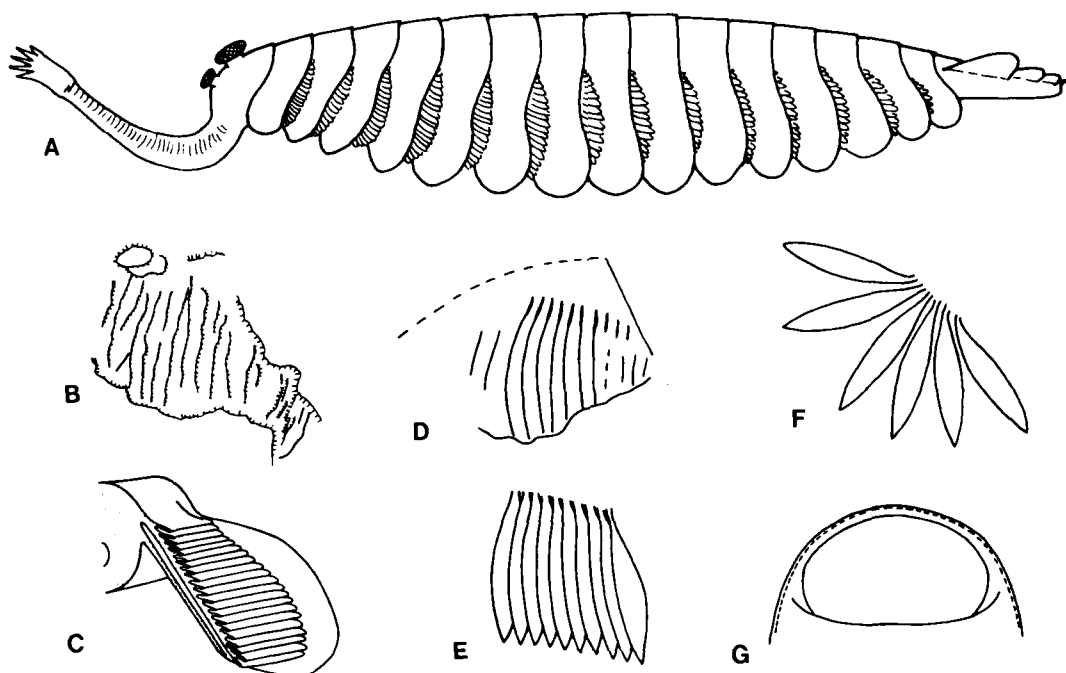


Fig. 1. *Opabinia regalis* Walcott 1912. □ A. New reconstruction,  $\times 2$ . □ B and C. Whittington's drawing of appendage g9 in specimen USNM 57648 (mirror image) and his reconstruction (Whittington 1975, Figs. 13–16 and 84). □ D and E. New drawing of same appendage in counterpart and reconstruction showing imbricated lancets. □ F. Slightly idealized sketch drawing of spread out lancets in first appendage ('g2') of specimen USNM 241479. □ G. Suggested cross section through one segment. The body is covered by one large tergite and, beneath it, a series of lancets shown as short dashes. Drawn on the ventral side is a sclerite known only from the tail of the body but presumably present on each segment.

underlain by one (Fig. 1G); in Whittington's figures this means that blade set g. 2 (there is no g. 1) goes with tergite 1.1, and so on.

Behind the fifteenth tergite there are three pairs of plates apparently directed laterodorsally, while the plates in front no doubt point latero-ventrally (Fig. 1A). There is no sign of blade sets. Whittington's reconstruction (Fig. 82) shows a still more surprising detail: each plate underlies rather than overlies its neighbour behind. This raises the question whether these plates are ventral in position rather than dorsal. Figs. 44, 45 and 51 show a similar reversal of imbrication in lobes 11–15. Whittington (p. 23) noted this reversal without comments, but the implications are very interesting. Apparently lobes 11–15 are not dorsal but ventral plates. Such a conclusion is in agreement with the absence of blades in this region. The existence of ventral plates probably also explains the appearance of Whittington's Fig. 4. The double plates seen here probably are not left and right side tergites, as suggested by

Whittington, but dorsal and ventral plates of the same side. Thus, the body is probably covered by 15 dorsal plates alternating with blade rows and with 18 ventral plates. The first 15 of the latter meet the dorsal plates laterally, while the last three extend freely in dorsolateral direction.

Segmentally arranged paired patches of reflective material were regarded by Whittington (1975:36) to represent internal organs, such as gut diverticula or circulatory organs. Similar patches in *Anomalocaris* were supposed by Whittington & Briggs (1985) to represent gills (see below).

The symmetrical arrangement of the proboscis spines indicates that the two spine sets form left and right halves of the grasping organ. This is also suggested by illustrations such as Figs. 4, 12, 44, 64, 73 and 74. It is concluded below that the proboscis probably represents a fused pair of appendages. If this is correct, a left and right arrangement is also logical.

## *Anomalocaris*

For a long time these animals were known only from disrupted parts. The body was thought to represent a holothurian echinoderm (*Laggania cambria* Walcott 1911) while the mouth was identified as a medusoid coelenterate (*Peytoia nathorsti* Walcott 1911) and the segmented limbs as crustacean bodies (*Anomalocaris canadensis* Whiteaves 1892). Briggs (1979) and Bergström (1979, 1981) both concluded that *Anomalocaris* more probably represented the limbs of a large animal than the entire body. Recent studies have shown that the different structures belong together in animals of unique construction (Briggs 1979; Briggs & Mount 1982; Briggs & Robison 1984; Whittington & Briggs 1982, 1985). The description by Whittington & Briggs (1985) covers the material very well, and there is usually not much to be added. However, as pointed out by the authors themselves, the difficulty to interpret the flattened remains means that the reconstruction given is only one of several possible solutions. I will present an alternative, which is basically in accord with their description and in fact includes details which they omitted from the reconstruction because of the problems in fitting all data into a single model. Some few but possibly important observations are also added.

Two species are known at present, viz. *Anomalocaris canadensis* Whiteaves 1892 and *A. nathorsti* (Walcott 1911). There is only a single reasonably complete individual of the former, so the reconstruction will be based on the latter. Illustrations referred to below are those of Whittington & Briggs (1985) – there is no need to republish any of those here.

The head is covered by a head shield with a marginal ventral doublure (Fig. 2). The ventral side has a square mouth opening surrounded by a ring of plates, with inwards directed teeth. Just in front of the mouth there is a pair of stout, arthropod-like limbs with well developed segmentation. The limbs are spiny, and in *A. nathorsti* each podomere carries a long spiny blade. Behind the mouth there are three pairs of ventral flaps and three dorsal sets of transverse scaly structures; these features are similar to those of the successive body segments but smaller. On the dorsal side the head is thought to carry a pair of eyes.

Whittington & Briggs (1985) convincingly demonstrated a series of fin-like flaps extending laterally, apparently from the ventral side of the

body. These are in series with the three pairs of ventral flaps in the head (Fig. 2). They are segmentally arranged but very long, so that there is a wide overlap between successive flaps, each extending outside (i.e. ventral to) its neighbour behind. The flaps appear to have strengthening rays. The authors also demonstrated the presence of similarly imbricated dorsal flaps. However, the dorsal flaps are of two kinds, one with thin, blade-like scales or lamellae like those in the head, the other plate-like, without scales. From their specimen descriptions it is clear that these two dorsal flap types alternate in an imbricated series, in which each flap extends outside (i.e. dorsal to) its neighbour behind (Fig. 84: tergite 2/gill or lamellar area c/t3/gd/t4/ge/t5). The authors state (p. 592) that they did not use this information in their reconstruction, which instead shows an entire dorsal body shield behind the head.

One of the specimens exhibits segmentally arranged transverse rods (?), which are annulated, mineralized with carbonate-apatite (probably at least this structure is meant), and extends over the midline of the animal (Figs. 31–34). The authors demonstrated how lanceolate, round-tipped thin blades or scales (Figs. 76 and 99, gu) form long transverse imbricated series (e.g. more than 33 blades in Fig. 86, gc). Similar series are not shown in the reconstructions (Figs. 101, 102, 104). Now, Fig. 34 shows how these blades are associated with the annulated rods and also present over the middle of the back. The rod annuli and the blades show the same spacing, and it is difficult to avoid the conclusion that the annuli constitute the points of origination for the blades; the authors hinted in this direction by stating that the rods are situated in the proximal portions of the lamellar areas (p. 592). If each presumed tergite forms a cover for one row of blades ('lamellar area'), as shown in Fig. 84, it is easy to understand why the tergites are not represented in these internal splits. In conclusion, the arrangement means that the annulated rods are no internal structures but extend across the dorsal surface, where they give rise to the numerous lanceolate blades (Fig. 2). As the entire dorsal surface is thus covered by such blades, there is no possibility that an entire dorsal body shield can be attached to the body behind the head, and segmental tergites remain the only possibility.

The authors meant that the segmented transverse structures seen in Figs. 31–34 (Fig. 3B herein) are identical to those in Figs. 56–59 (Fig.

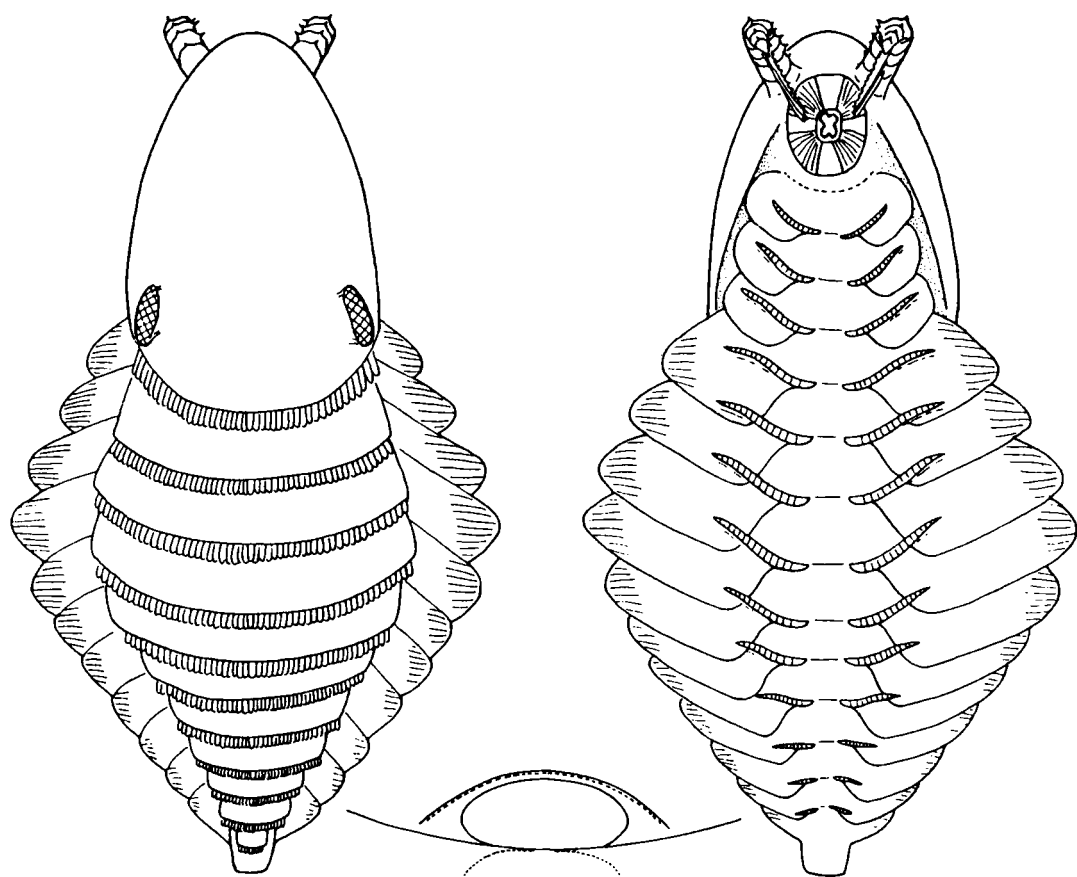


Fig. 2. *Anomalocaris nathorsti* (Walcott 1911), in dorsal and ventral views and cross section of one segment (cf. Fig. 1G), new reconstructions.  $\times 0.3$ .

3A herein). However, this must be a mistake. In the former figures the structures are above the ventral plates, and leave concave imprints on the upper side of these plates when removed, while in the latter figures the structures are seen below the ventral plates, and concave imprints are seen on the under side. Moreover, in the former figures the structures form continuous, single rods, while in the latter they are not really continuous over the midline (although drawn as if they were in Fig. 59) and in some cases are seen to bifurcate towards the ends. Apparently, therefore, the figures represent two quite different structures, one of which is dorsal, the other ventral in position. The ventral structures seem to be entirely free from the ventral plates except where attached, and the only easy explanation for them is that they are ventral appendages, probably multisegmented and apparently divided into at least two

branches. It is possible that a scrutiny of other specimens may reveal additional appendages, e.g. in the specimen in Figs. 51–55, in which there are some structures that look like segmented distal parts of legs. A single appendage seems to be preserved under ventral plate no. 4 in Figs. 44, 45, 50.

As pointed out by Whittington & Briggs, the dorsal repetition of 'lamellar areas', plates and rods corresponds to the ventral repetition of plates (and appendages), which is a good indication of true segmentation (Fig. 2). Also the paired reflective spots seen in e.g. Figs. 47 and 50 fit into the segmental pattern. These spots were supposed by Whittington & Briggs (p. 593; Figs. 101, 102, 104) to represent lamellate gills situated between the dorsal and ventral plates. Although this is possible, specimens like those in Figs. 13–16 and 31–34 may indicate that the spots are

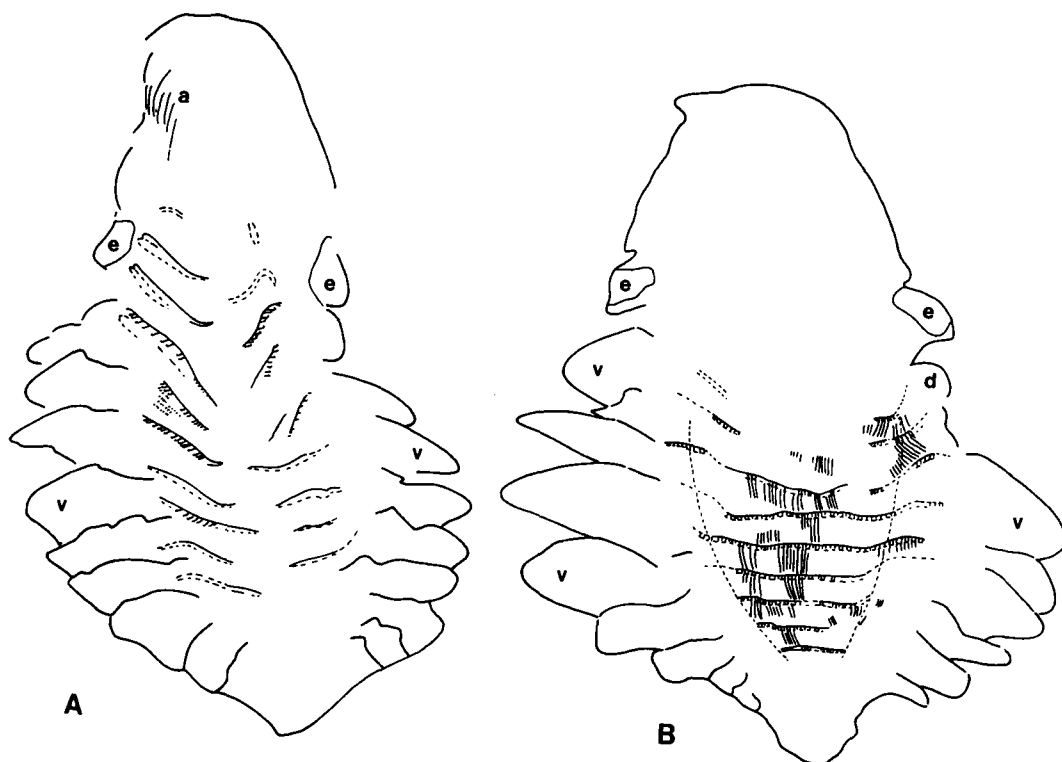


Fig. 3. *Anomalocaris nathorsti* (Walcott 1911), drawings of small specimens, measuring 126 and 96 mm, respectively. □ A. Specimen USNM 274146 in ventral view, showing poorly preserved segmental appendages. □ B. Specimen USNM 274142 in dorsal view, with segmental rods apparently giving rise to lancets (lamellae). Note that these lamellae are distributed over the middle of the back, not only laterally as the 'gills' in the reconstruction of Whittington & Briggs (1985, Figs. 101, 102, 104). a, anterior appendage; d, dorsal sclerite; e, eye; v, ventral sclerite.

within the borders of the compact body, and I would not be surprised if they instead represent internal organs such as muscles or digestive diverticula. Also the margin of the head is notably reflective, as are the supposed stalked eyes, which are much farther back on the head than the supposed eyes in *A. canadensis*.

### Comparison between *Opabinia* and *Anomalocaris*

Judging from previously published descriptions, the two genera appear to be utterly dissimilar, and Whittington & Briggs (1985:604) did not even mention *Opabinia* in their discussion on the affinities of *Anomalocaris*. However, a comparison based on the above reconsiderations and new reconstructions reveals a number of similarities. Both are segmented (Figs. 1A, 2). Both have a dorsal body cover of imbricated plates alternat-

ing with sets of lanceolate blades and a ventral body cover of imbricated plates (Figs. 1A, G, 2). Both appear to have large stalked eyes. Both have a segmented or annulated food manipulating organ in front of the mouth. Admittedly this organ is a single median limb or proboscis in *Opabinia* (Fig. 1A), while it forms a pair of limbs in *Anomalocaris* (Fig. 2), but fusions of paired limbs are of common occurrence among arthropods and should present no problem in this case. This list of similarities includes some completely unique characters found nowhere else in the animal kingdom, particularly the combination of single ventral and double dorsal plates of unique morphology, and there is reason to believe that *Opabinia* and *Anomalocaris* can be fairly closely interrelated, provided of course that the interpretations are reasonably correct.

A possible problem is that there appear to be segmented limbs in *Anomalocaris*, whereas no limbs have been recognized in *Opabinia*. This

seeming difference should not be exaggerated. *Opabinia* appears to have been more highly vaulted than *Anomalocaris* and is typically pressed flat from its sides rather than dorso-ventrally. This meant that even the large ventral plates were unknown until now, and possible limbs should be even more difficult to find than in *Anomalocaris*, where they were also previously unknown.

## Relationships

After all, *Anomalocaris* appears to have segmented appendages. By definition it therefore should be called an arthropod. By inference this could also be the case with *Opabinia*. I have previously suggested (Bergström 1979, 1981) that *Anomalocaris* represents some myriapod-like uniramian group, but the new evidence hardly favours such an idea. New information for instance on the structure of the appendages is important for any serious discussion on the relationships of these animals. Recent arthropods fall into at least three different phyla, the Schizoramia (crustaceans etc.), Uniramia (insects and myriapods) and ?Aschelminthes (tardigrades) according to Bergström (1986). *Anomalocaris* and its possible relative *Opabinia* may represent still another phylum with arthropodization tendencies.

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