

RESTUDY OF SOME BURGESS SHALE FOSSILS

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INTRODUCTION

The following notes deal with certain of the very remarkable fossils discovered by the late C. D. Walcott in the Middle Cambrian Burgess Shale. The material examined was all collected by Walcott at the now celebrated locality "on the west slope of the ridge between Mount Field and Wapta Peak, 1 mile [1.6 km.] northeast of Burgess Pass, above Field, British Columbia." The present contribution is submitted in the belief that the forms discussed are of considerable interest to students of living invertebrate animals though they are likely to be somewhat neglected by palaeontologists on account of their isolated occurrence as fossils. The diverse systematic positions of the two forms discussed makes it desirable to present the material in two parts; it is, however, convenient to assemble all the photographs on a single plate at the end of the second contribution.

My very best thanks are due to the authorities of the United States National Museum, and in particular to Dr. Charles E. Resser, who most generously provided every facility for the study and description of the material in their charge. To Doctor Resser I am particularly grateful for the photographs which constitute Plate 1.

I am also much indebted to Prof. Alexander Petrunkevitch, of Yale University, who has freely given me access to his immense store of knowledge and to his beautiful preparations of Arthropoda; to Dr. L. A. Borradaile, of Selwyn College, Cambridge, England, who some years ago allowed me to transcribe certain parts of his valuable notebooks relating to the Arthropoda, which have been of great value in the present work; and to Miss L. Krause, artist to the Osborn Zoological Laboratory, for the trouble she has taken over the reconstruction of the animals under discussion.

I. ON OPABINIA AND RELATED PALAEOZOIC ANOSTRACA

Branchiopod Crustacea of the Burgess Shale.—Walcott (1912) described eight new genera of Branchiopoda in his collections from the Burgess Shale. Four of these genera were placed in a new

Anostracan family Opabinidae, the remaining four were distributed among as many families of the Notostraca. These fossils have subsequently been considered by Raymond (1920), Fedotov (1924), and Henriksen (1928). The three authors have come to different conclusions on some of the forms. On the whole Henriksen's contribution is of the most value because he has been able to study new material of certain species, collected by Walcott after the publication of his original paper. Of the Notostraca only one form, *Burgessia bella*, is considered as properly placed by either Fedotov or Henriksen. Henriksen allows three of Walcott's genera of Anostraca to remain in that group, very properly removing *Leancoilia* to the Merostomata. He considers that *Yohioia* should form the type of a new Anostracan family and that the problematic *Bidentia* is perhaps allied with *Opabinia*. Fedotov is very doubtful about *Yohioia* and *Bidentia* but all authors are unanimous that *Opabinia* is rightly placed as an Anostracan.

The present distribution of the Branchiopoda.—The Branchiopoda rival the Rotifera as the most characteristic invertebrate animals of inland waters. Very few species inhabit the sea, while the group is spread through a very wide range of fresh-water habitats. The three groups of large forms, the Anostraca, Notostraca, and Conchostraca are to-day essentially crustaceans of temporary seasonal waters, flourishing best in semidesert and steppe environments. The Cladocera, now so widespread in both seasonal and perennial waters, are probably derived from the larger "phylopod." A very few species of Cladocera inhabit the sea, and these are for the most part neritic. It is clear that chemical conditions have played little part in restricting the Branchiopoda to inland waters. *Artemia salina* Linnaeus can tolerate a far higher salinity than that of the sea; moreover recent unpublished experiments strongly suggest that certain supposed cases of the limitation of Cladocera by chemical conditions are fallacious. The occurrence of an undoubted Anostracan in an ancient marine deposit is therefore of considerable interest to the fresh-water ecologist. Since none of the authors referred to has given entirely satisfactory descriptions of *Opabinia* it seemed desirable to reexamine the material in order to gain additional information on its structure in the hope that it would throw light on the disappearance of the Branchiopoda from the sea.

Material examined.—Walcott separated his *Opabinia* into two species, the typical *Opabinia regalis* and a doubtful species, *O.?* *media*. The latter, distinguished by its smaller size and lesser number of segments, is based on very poor material in which a segmental count must necessarily be very uncertain. Since no very small specimens are included in the material of *regalis* it is very probable that

the younger stages are represented by *media* which may for the present be treated as the young of the former species. Of *regalis* Walcott had four specimens of supposed males and two "females." The latter, as indicated below, are probably not rightly referred to *Opabinia*. I have examined eight specimens of *O. regalis* in which the head is sufficiently preserved to show the frontal process, two in which it is well preserved but apparently lacks the process, and numerous fragments.

OPABINIA REGALIS Walcott

Opabinia regalis WALCOTT, 1912, Smiths. Misc. Coll., vol. 57, p. 167.

Opabinia ? media WALCOTT, 1912, Smiths. Misc. Coll., vol. 57, p. 170.

Head.—The most complete indication of the structure of the head is given by the two specimens U.S.N.M. 57683 and 57684, figured by Walcott, by a dorso-ventrally compressed specimen figured here from a retouched photograph left by Walcott (pl. 1, fig. 4), and by a dorso-ventrally compressed specimen very similar to specimen 57683. All the specimens are represented by both sides of the split pieces of shale in which they are fossilized. The most conspicuous feature of the head is the large frontal process which is visible in all these specimens and in four other much less perfect ones. It consists of an elongate cylindrical process, inserted on the extreme front of the head, in the unfigured laterally compressed specimen it is bent round at the side of the head covering the ventral part of the latter; in specimen 57683 it is flexed upwards, while in the two dorso-ventrally compressed specimens it is shown squeezed out straight forward. In none of these positions is there any sign of breakage so that the process was certainly flexible. In the specimen figured from Walcott's photograph in Plate 1, Figure 4, traces of an internal cavity can be made out so that it was probably erectile, being filled with fluid as is the process of *Thamnocephalus* (Evans, 1915). In the laterally compressed specimen 57683 the process, though hard to measure on account of its flexure, is clearly less erected than in either dorso-ventrally compressed specimens. Anteriorly the process is dilated in the two latter specimens and is distinctly cleft apically. The extreme tip bears a number of large spinous projections. The whole surface of the process is somewhat wrinkled and the apical part apparently bears some very small spines arranged in irregular rings. Well preserved compound eyes are found on the dorso-ventrally compressed specimens. In the individual figured on Plate 1, Figure 4 the large dark ommatidial part is particularly clear. The ocular peduncle appears to have been very similar to that of modern Anostraca. In the laterally compressed specimen 57683 the eyes, though much broken, can also be made out, the stalks on which they are set being directly dorsally. No appendages could be found on the head by Walcott.

In specimen 57683 there is a small crack in the exo-skeleton just above the insertion of the frontal process. This crack was probably formed by the flattening of some projecting structure; traces of a small protuberance can be made out in the same position in the unfigured laterally compressed specimen. It is possible that these remains represent the point of insertion of small antennules. Alternatively these appendages may have been attached to a papilla situated behind the crack just mentioned and below the eye on specimen 57863. It is, however, quite possible that the antennules, always small in the Anostraca, have become entirely obsolete. The whole

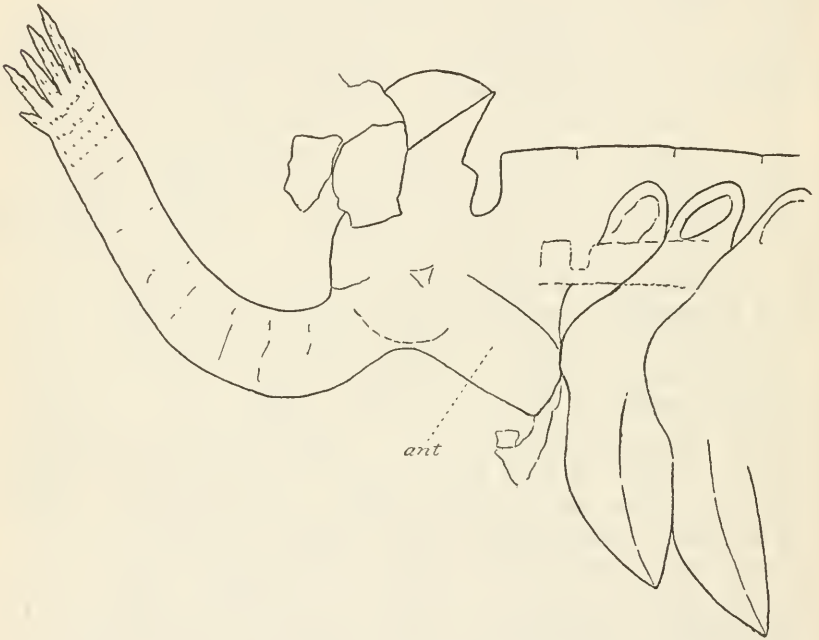


FIGURE 1.—OPABINIA REGALIS WALCOTT. ANTERIOR END OF COTYPE (U.S.N.M. 57683);
ant., ANTENNA. (ABOUT $\times 2.5$)

of the ventral posterior part of the head in specimen 57683 is probably the antenna. (Fig. 1.) This region bears a very close resemblance to the folded antenna of the female of any recent species of Anostraca, and is separated from the dorsal part of the head by a faint but definite groove. The frontal process, if homologous with that of living forms, was developed from fused internal branches of the antennae, but the latter show no other indication of having been modified as extensive secondary sexual organs. No ventral views of the head exist so the mouth parts remain unknown.

Trunk.—According to Walcott the trunk consists of 16 somites bearing foliaceous appendages. The sutures in his photograph of

specimen 57683 are much retouched. After considerable study of all the material I was unable to detect more than 15 appendage-bearing somites and believe that the first segment figured by Walcott is really part of the head and does not bear a leg.

Abdomen.—The abdomen consisting of a broad spatulate lobe is apparently divided into two parts. The larger anterior part has a concave posterior edge produced at the side into a pair of spines, between which the much smaller posterior division lies. The anus opens on the posterior part of the latter. The structure of this region is well shown in specimen 56784. (Walcott 1912, pl. 28, fig. 1.) The large anterior part is clearly a true segment; the status of the posterior part must remain doubtful.

Appendages.—Considerable diversity in appearance is exhibited by the trunk appendages of different specimens. This is probably due to the position of fossilization rather than to any actual differences implying a mixture of species. The lateral aspect of the trunk appendages can best be studied in specimen 57683. In this specimen the first 14 are flat leaflike lobes hanging down at the side of the body. (Fig. 1.) Each appendage apparently lies somewhat in advance of the segment bearing it, so that the upper anterior margin slopes obliquely upward and backward to the insertion which is marked by the remains of musculature. Walcott said that the appendages were jointed, but I can find no trace of joints, nor would such be expected in a foliaceous appendage. Attached to the outer surface he also describes "gills" and a "strongly setiferous lobe" on the distal part of the appendage. The supposed gills in Walcott's figure are marks made by irregular splitting of the shale and no trace of them is to be found either in the well-preserved anterior appendages in specimen 57683 or in other relatively perfect specimens. The anterior part of the limb is, however, somewhat dilated in the former specimen, but the convexity is not separated by any suture or joint from the limb itself. The "strongly setiferous lobe" presumably refers to the whole posterior part of the distal end of the appendage. This area in 56783 is clearly demarcated from the rest of the appendage and may represent a flabellum. It is, however, not certainly detectable in other specimens. The setae are probably illusionary; I can detect no certain setae on the external surface of any limb.

The internal edge of the foliaceous appendage carried a series of very strong thick setae. (Fig. 2*b*.) These are visible in both well-preserved dorso-ventrally compressed specimens and in various fragments. In all cases they are exposed by the breaking away of the outside flat surface of the appendage. The latter was presumably considerably curved in frontal section, the concavity being directed

backwards. When compressed the outer surface of the appendage would then cover the inner edge as is actually found in the specimens. In no case can the insertion of the setae on the inner edge of the appendage be unequivocally made out, but it is probable that there was no very unequal development of certain endites for the setae are very evenly developed throughout the whole length of the appendage.

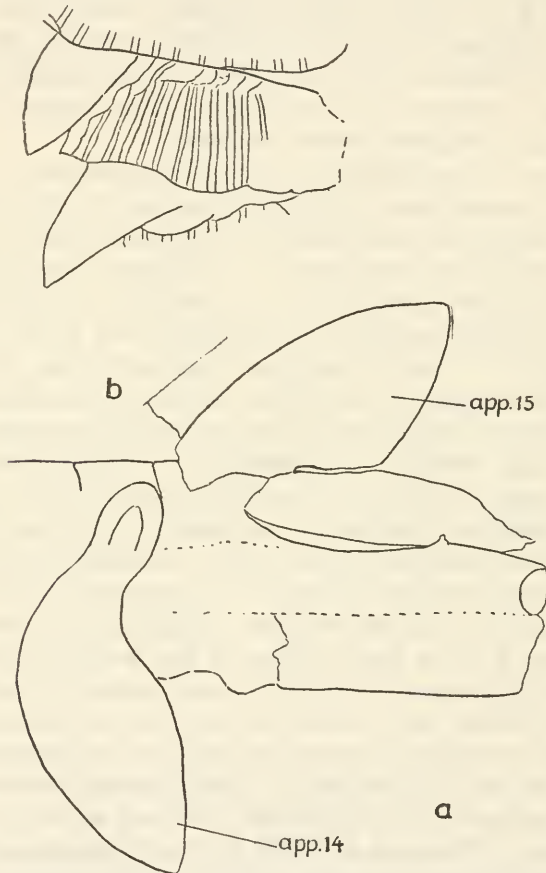


FIGURE 2.—*OPABINIA REGALIS* WALCOTT. *a*, POSTERIOR END OF COTYPE (U.S.N.M. 57683); *app. 14*, LEFT APPENDAGE OF FOURTEENTH TRUNK SOMITE; *app. 15*, RIGHT APPENDAGE OF FIFTEENTH TRUNK SOMITE ($\times 5$). *b*, LEFT APPENDAGE OF SEVENTH TRUNK SOMITE OF COTYPE (U.S. N.M. 57684) ($\times 5$)

The last pair of appendages, on the fifteenth segment, was clearly not directed ventrally in life but more laterally than those at the anterior end of the body. In specimen 56783 it consists of a flat platelike structure, the edges of which are imperfectly preserved. (Fig. 2.) The plate lies at a lower level than the rest of the

specimen, while in the very similar unfigured laterally compressed individual a comparable plate is visible lying above the specimen. In the dorso-ventrally compressed specimen 56784 no such structure can be made out; it has probably not been exposed in the splitting of the shale. The best interpretation to be placed on this appendage is that it formed, with the abdomen, a sort of tail fan. In the individual discussed below and figured on Plate 1, Figure 3, the last appendage is shown clearly on the left-hand side, lying in such a position against the abdomen. The condition of the posterior appendages, here shown as broad simple plates, indicates that there was no essential difference between the fifteenth and the other appendages. Unfortunately the condition of the anterior part of this specimen is not sufficiently good to allow the number and structure of the anterior appendages to be made out.

Internal structure.—Walcott mentions a "very beautiful specimen showing some details of the interior." This is presumably the individual figured from his photograph in Plate 1, Figure 4. The only certainly determinable structures are the alimentary canal and the obliquely arranged segmental musculature.

Supposed female of Opabinia.—Walcott described two specimens of the same general appearance as *O. regalis*, but with a reduced frontal process and with filiform caudal cerci. These specimens he believed to be the females of *Opabinia*. It is very improbable that the presence of a caudal cercus would characterize the female sex in this group so that in all probability these two specimens, which are very poorly preserved, represent an entirely different animal. It has previously been indicated that remains of eight individuals bearing a frontal process exist in the collection. In addition to these are two specimens which, though quite well preserved, are without any such organ. The better specimen of these is figured in Plate 1, Figure 3. The head ends anteriorly as a truncate lobe in front of the stalked eyes. It is possible that the process lies at a different level in the shale or has been broken, the general appearance of the specimen however is against such a supposition, and I am inclined to think that the two individuals without frontal processes represent the true female of *Opabinia regalis*.

Comparison with living Anostraca.—In discussing the relationship of *Opabinia* with modern Anostraca the following resemblances may first be noted:

1. Absence of a carapace.

This characterizes two groups of Branchiopoda, the Anostraca and the Lipostraca. From the solitary representative of the latter

group, *Lepidocaris* (Scourfield 1926), *Opabinia* differs in numerous characters as mentioned below.

2. General form and size.

The general appearance of *Opabinia* as shown particularly in the laterally compressed specimens and indicated in the conjectural restoration (fig. 3a) must have been very close to that of modern Anostraca. In size it was larger than the majority of modern species, but female specimens of *Branchinecta ferox* (Milne Edwards) may reach 70 mm. in length (Daday 1910), which size is almost identical with that of the best preserved female *Opabinia regalis*. The large size of all the Anostraca is in striking contrast to that of the minute Lipostracan *Lepidocaris*.

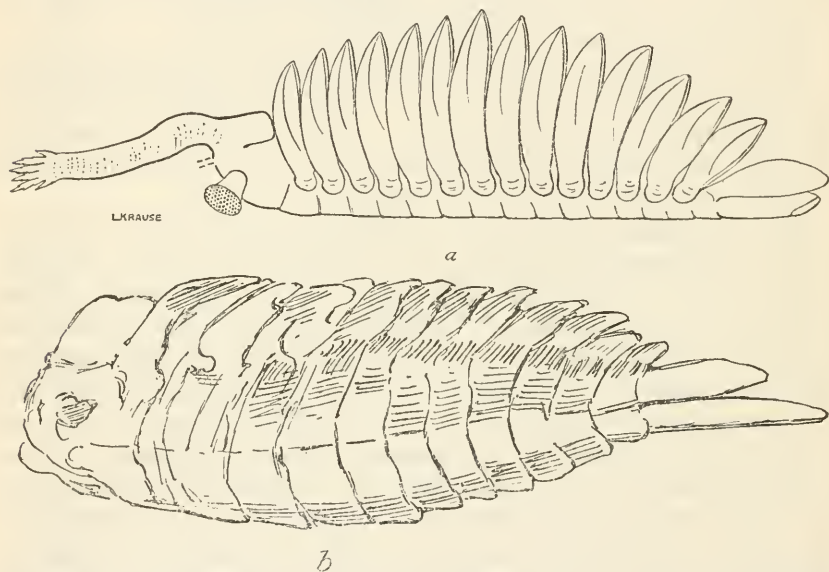


FIGURE 3.—PALAEANOSTRACA. *a*, *OPABINIA REGALIS* WALCOTT, CONJECTURAL RESTORATION. (ABOUT $\times 1\frac{1}{4}$.) *b*, *ROCHDALIA PARKERI* H. WOODWARD $\times 4$ (AFTER WOODWARD, BY COURTESY OF THE EDITOR OF THE GEOLOGICAL MAGAZINE.)

3. The presence of pedunculate eyes.

This is the most diagnostic character of the Anostraca among the orders of Branchiopoda and is amply fulfilled by *Opabinia*. No eyes are known in *Lepidocaris*, while the other orders all have sessile eyes.

4. The position of the antenna and the probable reduction of the antennule.

If these structures have been rightly interpreted *Opabinia* more closely resembles the Anostraca than any other group.

5. The nearly uniform series of foliaceous trunk limbs.

This condition is characteristic of most of the "phyllopod" Branchiopoda.

6. The presence of a frontal process which was probably confined to the male.

The frontal process is developed from the fused internal or frontal appendages of the antennae in the males of various living Anostracans (*Branchinella*, *Dendrocephalus*, *Thamnocephalus*). The structure in *Opabinia* though differing in detail from that found in these recent forms is quite comparable in position and general structure.

These characters, most of which have been discussed very briefly by previous authors, clearly indicate that *Opabinia* is rightly placed in the Anostraca. Considerable differences are, however, apparent when a more detailed comparison is made.

1. The number of body segments in *Opabinia*, at most 17, is less than that found in any of the living Anostraca, which always have at least 19.

2. The number of appendage bearing segments, 15 in all, is on the other hand greater than that found in any living forms save the Polyartemiidae, and the number of postpedigerous segments, one or two, is strikingly less than the 8 or 9 of all modern forms. Calman (1909) argues that the condition of the Polyartemiidae is secondary because there is a postgenital abdomen of 8 segments comparable to that of the other families in the group. The number of pedigerous segments in this family is in fact variable, being 17 in *Polyartemiella* and 19 in *Polyartemia* so that it is not at all unlikely that addition of segments has occurred here, as it certainly has in the Notostraca. If we assume that the primitive number of segments in the Anostraca is that retained by the majority of modern species, the ancestral form presumably had 19 or 20 pedigerous segments. This number accords well with what is known of the primitive numbers in other groups of Crustacea, moreover, *Lepidocaris*, which is in some respects the most archaic known crustacean, had 18, of which the posterior one was probably compounded of two or three somites. It would appear, therefore, very probable that *Opabinia* has a slightly reduced number of body segments. The condition of the postpedigerous portion suggests that, as in *Lepidocaris*, reduction was occurring from behind.

3. The detailed structure of the foliaceous appendage was apparently different to what is found in living Anostraca. If branchiae were really absent as seems almost certain, the appendages of *Opabinia* show some resemblance to the anterior members of the series of *Lepidocaris* which also lack these structures. The modification of the posterior appendage to form part of an incipient tail fan is unique among the Anostraca.

4. The absence of a caudal furca in *Opabinia* may perhaps be correlated with the lateral position of the posterior appendages. It is not impossible, as has been indicated above, that the whole post

pedigerous part of the body is reduced in *Opabinia*. In living Anostraca the furca is absent only in the extreme form of *Artemia salina* var *köppeniana* (S. Fischer) and in the very specialized genus *Thamnocephalus*.

5. The form of the frontal process, though comparable in general with that of certain modern genera has a much longer unpaired proximal region and a correspondingly shorter distal paired portion.

All of these differences with the doubtful exception of the number and nature of the foliaceous appendages point to *Opabinia* being considerably less generalised than the modern Anostraca.

Other fossil Anostraca.—Fossil Anostraca are exceedingly rare. Apart from the Burgess Shale forms only three species appear to be recorded. The Eocene *Artemia vectensis* (H. Woodward)¹ shows us a species essentially like modern forms at the beginning of the Tertiary. Apart from this form no member of the group is known between Palaeozoic and modern times. Two species are recorded from the Coal Measures of Europe. *Branchipusites anthracinus* Goldenberg (1875) from Saarbrücken is so fragmentary, being based on the middle portion of a body with supposed foliaceous appendages, that its Anostracan nature is open to doubt. *Rochdalia parkeri* H. Woodward (1913) based on a whole individual from the Middle Coal Measures of Sparth Bottoms, Rochdale, Lancashire, is fairly well preserved and of great interest in the present discussion. The specimen was fossilised in a small clay iron stone nodule. It is 28 mm. long and consists of a head, 11 pedigerous segments that are clearly defined, and a "telson" with a "lateral plate." The head apparently bears a pedunculate eye; on its ventral surface lies a structure which Woodward terms the "proboscis" and which presumably represents an unmodified antenna. In Woodward's figure very definite indications of a segment bearing an appendage lies between the head and the first of his segments, so it is possible that there are really 12 pedigerous segments. The appendages are figured as of the simplest foliaceous type, traces of the attachment of branchiae are said to exist. The misnamed "telson" probably represents the last pedigerous segment bearing a laterally placed appendage which Woodward terms the "lateral plate"; possibly one or more post-pedigerous segments have become fused into this segment. The general appearance suggests strongly that considerable reduction has occurred in the segmentation. In so far as *Rochdalia* can be elucidated it is clearly closer to *Opabinia* than to any living

¹ This species was described by Woodward (1879) as *Branchipodites vectensis*. Daday (1910) has with good reason referred it to *Artemia*, but it seems highly improbable that the modern species *salina* is identical with the Eocene representative of the genus so that Woodward's specific name should stand until the two species are conclusively proved to be identical.

Anostracan. If *Opabinia* is derived from a primitive Anostracan with a few postpedigerous segments, most of which have been lost posteriorly, *Rochdalia* seems to have carried the reduction still further.

Of the remaining Burgess Shale species considered as Anostraca by Henriksen, namely *Yohobia tenuis* and *Bidentia difficilis*, both are clearly much more remote from the living Anostraca than is *Opabinia*. Both genera have but 12 post-cephalic segments, so exceeding the latter in their reduction of the body segmentation. *Bidentia* is very inadequately known from Walcott's account, and *Yohobia* is almost equally in need of further study. The pedunculate eyes of the latter probably indicate its anostracan affinities, though as Henriksen points out the genus differs from all known Anostraca in the peculiar pleural expansions of its first eight segments. It is worth pointing out, however, that the Lipostracan *Lepidocaris* has very distinct jointed pleura. Henriksen places *Yohobia* in a new family, the Yohoidae; if *Bidentia* is ever better known the same course will probably be necessary. For the present we may conclude that these forms represented highly specialized and aberrant marine Anostraca.

Ecological Considerations.—As has been pointed out the modern Branchiopoda are essentially organisms of seasonal waters or have clearly been derived from such. The marine Anostraca of the early Paleozoic represent a more specialized series of morphological types than the living representatives of the order. *Opabinia* with its fan-like arrangement of the posterior appendages must have presented a more caridoid appearance than a modern Anostracan though was probably sufficiently like the latter in form to have swum dorsal side downward. Moreover, if *Yohobia* is rightly referred to the group there is definite evidence from the position in which the latter animal is fossilized (Walcott, 1912, pl. 29, figs. 7, 8, and 12) that the characteristic flexure of the body of the higher Crustacea had developed in the Anostraca. It is clear, therefore, that at a remote period a development of the Anostraca occurred in the sea giving forms which were ecologically comparable to various types of higher Crustacea that have replaced them. This group of marine Anostraca characterized by a reduction in the segmentation probably invaded inland waters, for *Rochdalia* was presumably a fresh-water form. The morphologically primitive modern Anostraca have become specialized in their life history for existence in dry regions and have suffered no competition from similar developments by more advanced Crustacea of other groups that have replaced the marine branch of the order. It is highly probable that other living orders of Branchiopoda shared in the marine development of the group in early

Paleozoic times. *Burgessia bella* Walcott (1912) is referred by both Walcott and Henriksen to the Notostraca; my own reexamination of the material adds nothing to their account. This form is of particular interest as its internal organs can be seen in great detail. If a modern Notostracan were similarly fossilised the most prominent internal organs visible would undoubtedly be the large maxillary glands in the carapace of which no trace can be seen in *Burgessia*. Their absence in a marine form is in accordance with what is found in other Crustacea, where "excretory" organs are better developed in fresh-water forms than in marine, and function as regulators of water content and osmotic pressure (Schlieper, 1929).

Systematic Position.—In order to express the considerable differences existing between modern species of Anostraca and *Opabinia* and its ally *Rochdalia*, the order may be conveniently divided into two suborders in the following way:

Suborder 1. EUANOSTRACA

Anostraca with 19 or more segments of which at least 11 are pedigerous, followed by a postpedigerous, postgenital, region of at least 8 segments. Trunk appendages with branchiæ and flabellum. Caudal furca present (except in *Thamnocephalus*) median frontal process, if developed, strongly bifurcate.

Family² 1, Polyartemidae Simon, Recent, Circumarctic.

Family 2, Artemidae Grochowski, Recent and Eocene, Cosmopolitan.

Family 3, Branchipodidae Daday, Recent, Old World.

Family 4, Chirocephalidae Daday, Recent, Old World and North America.

Family 5, Streptocephalidae Daday, Recent, Old World and North America.

Suborder 2. PALAEANOSTRACA

Anostraca with not more than 17 segments, of which 11–15 are pedigerous followed by a very reduced postpedigerous region. Trunk appendages apparently deficient in exites. Caudal furca absent in known forms.

Family 1, Opabinidae Walcott.

Fifteen pedigerous segments followed by a postpedigerous portion divided into two parts, of which at least the anterior one is presumably segmental. Frontal process bifurcated only at the apex.

Type *Opabinia* Walcott with one certain species, *O. regalis* Walcott, Middle Cambrian, British Columbia.

²Daday (1910) and Barnard (1929).

Family 2, *Rochdaliidae*, new family.

Twelve pedigerous segments with no separate postpedigerous region distinguishable.

Type *Rochdalia* H. Woodward with one species *R. parkeri* H. Woodward, Coal Measures, England.

Incertae sedis.

Family *Yohoidae* Henriksen.

Type *Yohoa* Walcott, with a single certain species *Yohoa tenuis* Walcott, Middle Cambrian, British Columbia.

Family?

Bidentia difficilis Walcott, Middle Cambrian, British Columbia.

Family?

Branchipusites anthracinus Goldenberg. Coal Measures, South Germany.

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2. ON THE ONYCHOPHORAN *AYSHEAIA PEDUNCULATA* WALCOTT

In his contribution dealing with the extraordinary annelid fauna of the Burgess Shale, Walcott (1911) described among other new forms a unique specimen which he named *Aysheaia pedunculata*, placing it as a polychaet in a new family the Aysheidae. The remarkable resemblance of this fossil, as illustrated by Walcott, to the living Onychophora could not fail to impress itself on anyone familiar with the recent members of the group. *Aysheaia* has therefore been placed in or near the Onychophora by various authors since it was first made known (Brues 1923, Handlirsch, 1925, 1926, Walton, 1927), but no further details of its structure have hitherto been published.

While examining the specimens of *Opabinia* described above, it seemed probable that a reinvestigation of *Aysheaia* would be profitable in the hope that any relationship it bears to the living Onychophora might be more certainly determined.

Type specimen.—The type of *Aysheaia pedunculata* consists of a very distinct worm-like fossil, 31 mm. long, lying on a piece of shale near a well preserved example of the problematic worm *Ottoia prolifica* Walcott. On the same slab are fragmentary remains of *Marrella* and other animals. A reverse specimen of that part of the slab bearing the type of *Aysheaia* also exists in the collection. The left side of the worm is probably perfect and shows at least 10 pairs of appendages. The posterior region on this side is rather confused, but it is highly probable that an eleventh appendage is lying close up against the tenth which is otherwise unaccountably thick. Most of the right margin behind the fifth appendage is missing. Walcott describes the anterior end of the animal as forming a head which is said to consist of "a central narrow longitudinal section—a rounded lobe on each side of its posterior half that suggests large eyes; the anterior end appears to have short slender tentacles projecting forward." On examining the type I was surprised to find that this head is very ill defined, and composed of a material of different texture to that of the rest of the fossil. The boundaries of the parts are very obscure, and seeing that there is absolutely no trace of such a structure in any of the undescribed material, much of which is in very perfect condition, it is probably either a piece of prolapsed alimentary canal, or a decayed fragment of one of the very numerous organisms associated with *Aysheaia* in the same slab of shale. It is unnecessary to describe the other features of this specimen here as their true nature will become apparent when viewed in the light of the better preserved additional material.

*Additional specimens of *Aysheaia pedunculata*.*—The collections made by Walcott subsequent to the publication of his preliminary

paper contain eight other specimens of *Aysheaia* from the same horizon, which may be enumerated as follows:

(a) Length 25 mm., dorso-ventrally compressed, most of right side missing; 11 appendages clear on right, posterior appendage of

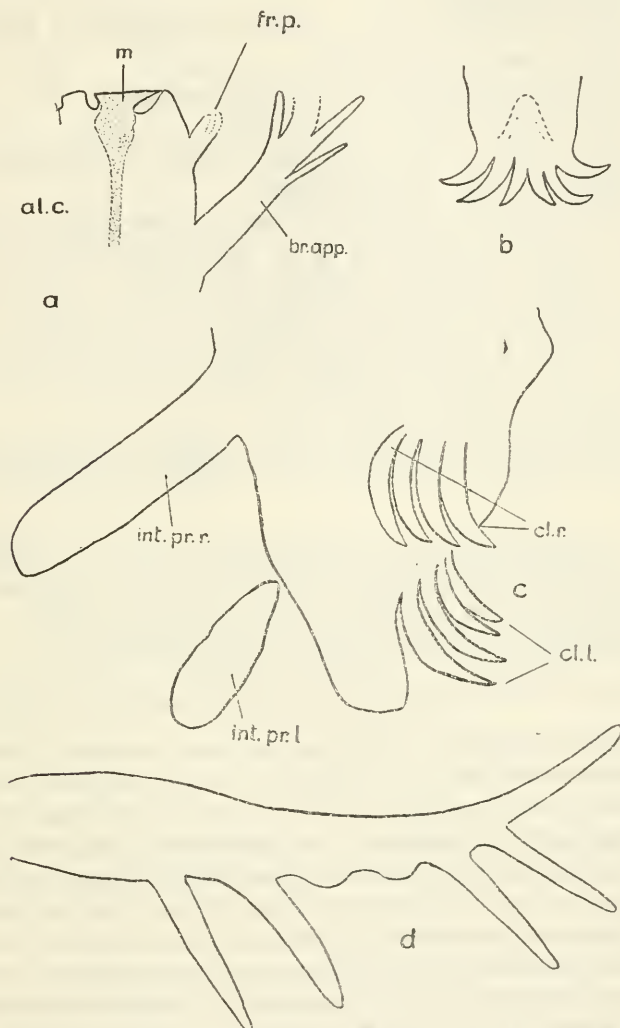


FIGURE 4.—*AYSHEAIA PEDUNCULATA* WALCOTT. *a*, ANTERIOR END OF SPECIMEN *a*; *m*., MOUTH; *al. c.*, ALIMENTARY CANAL; *fr. p.*, FRONTAL PAPILLA; *br. app.*, BRANCHED APPENDAGE ($\times 10$). *b*, FOURTH RIGHT LEG OF SPECIMEN *a* SHOWING SIX CLAWS AND SUB-APICAL TRIANGULAR AREA ($\times 50$). *c*, SUPERIMPOSED POSTERIOR LEGS OF SPECIMEN *a*; *cl. r.*, CLAWS OF RIGHT LEG; *cl. l.*, CLAWS OF LEFT LEG; *int. pr. r.*, INTERNAL PROCESS OF RIGHT LEG; *int. pr. l.*, SUPPOSED INTERNAL PROCESS OF LEFT LEG ($\times 50$). *d*, BRANCHED APPENDAGE OF SPECIMEN *b* ($\times 25$)

left apparently lying close under its fellow, and visible on the right-hand side. (Fig. 4, *a-c*.)

(b) Length 45 mm., laterally compressed, portions missing from the mid posterior region. Eleven appendages on right, indications

of the left posterior appendage by the side of the right. (pl. 1, fig. 2 and fig. 4d.)

(c) Length about 50 mm., very imperfect and curled up, 8 appendages clearly defined.

(d) Length about 12 mm., a small curled specimen poorly preserved with at least 9 appendages.

(e) Posterior fragment, 24 mm., 8 appendages. (Pl. 1, fig. 1.)

(f) Length 28 mm., 10 or 11 appendages.

(g) Length about 25 mm., curled; at least 9 appendages.

(h) Length 14.5 mm., 11 appendages.

Size and number of segments.—From the above list it is clear that *Aysheaia* reached a size of about 50 mm., that the best preserved specimens show 11 segments bearing conspicuous appendages, and that this number is the same in both small (14.5 mm.) and large (45 mm.) animals. The detailed structure of the animal is best indicated in the two specimens designated as (a) and (b), the latter being illustrated in Plate 1, Figure 2.

Body wall.—The dorsal edge of (b) shows a row of papillae compressed sideways, representing the most dorsal papillae of a

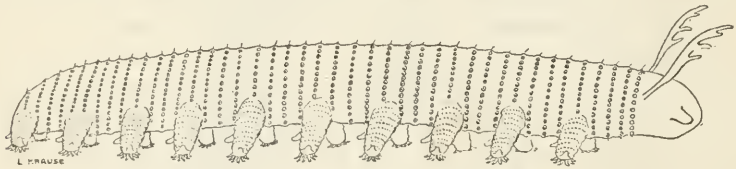


FIGURE 5.—*AYSHEAIA PEDUNCULATA* WALCOTT, CONJECTURAL RESTORATION

series of transverse rows which can be made out in all the specimens. Except on the dorsal margin of (b) the papillae are chiefly represented by small apical pits which probably each bore a minute seta as in modern *Onychophora*. At least 4 papillae are found dorsal to the gut on the right side of (b), so that the upper half of each ring had at least 8. Walcott made out 13 in a row on the type, probably the complete annulus consisted of 14 or more. Four annuli appear to correspond to each appendage in the trunk region, and so to each segment; there are, moreover, 4 annuli of papillae on the anterior end of (b), which clearly correspond to the segment of the branched appendage.

Legs.—The legs appear in all the specimens as the flattened remains of slightly tapering truncate cylinders. They are annulated, as are those of recent *Onychophora*, the best preserved show at least 8 annulations. Each leg ended in a group of claws; on the fourth right leg of (a) 6 claws can be distinguished, 3 turned forward and 3 backward. (Fig. 4b.) On the other legs only 3, 4, or 5 claws can be found. In (b) the claws are all turned backwards; it is probable

that in life they were directed posteriorly, 3 a little inward and 3 a little outward, and that the apex of the leg figured is somewhat twisted. The apices of the legs of (*b*) show traces of a central structure represented by a minute dark longitudinal elongate spot, a similar more triangular area can be seen (fig. 4*b*) in the fourth right leg of (*a*). These areas of dark material are very indefinite, but probably represent a similarly placed triangular region free from large papillae, situated above the foot in modern Onychophora, as *Peripatopsis capensis* (Grube). From the side of some legs, notably the third left of the type (Walcott, 1911, pl. 23, fig. 9), and the posterior pair (fig. 4*c*) of (*a*) a spurlike elongation can be seen lying as if it was projecting from the internal surface of the leg, pointing forward in the former specimen, backward in the latter. These structures are presumably the straight setae of Walcott, the claws being his hooked setae. They are, however, not composed of the whitish material into which the claws have been transformed, but are fossilized exactly like the rest of the body and therefore were probably soft walled. Since they are found on both third and last legs they presumably occurred on all the legs but were hidden during fossilization. The 10 posterior appendages of *Aysheaia pedunculata* therefore consisted of wide slightly tapering annulated limbs bearing six apical claws and possibly other terminal structures, and a ventral or internal organ to which the name "internal process" may be conveniently applied. The bases of the unexposed legs on the left side of (*b*) are presumably represented by the swellings in the middle of the body above each leg.

Branched appendage.—The segment immediately in front of the first pair of legs carries a pair of appendages which in the dorso-ventrally compressed specimens lie in an exactly comparable position to the legs. In specimen (*b*), however, these appendages seen from the side, are apparently directed forward and downward on the right, backward and upward on the left. The head is probably twisted, but there can be little doubt that the appendages in question were inserted at a somewhat higher level on the body wall than were the following 10 pairs of legs. The position of fossilization in (*b*), moreover, strongly suggests that they were very mobile and could take up a variety of positions. This pair of appendages differs radically from the legs in not possessing claws and in being furnished with a number of branches or processes. In the left-hand branched appendage of (*b*) two apical and two basal processes are distinguishable (fig. 4*d*), and there are indications of two papillae in the middle region. In the left-hand appendage of (*a*) and in that of the type three processes at least are present. In (*b*) all lie on the anterior side of the appendage, in (*a*) two

are posterior. In all probability they did not arise directly one above the other; the axis of the appendage is doubtless somewhat twisted in some of the specimens.

Head and associated structures.—None of the hitherto undescribed specimens show any of the head structures described by Walcott. Since (*a*) and (*b*) are very perfect it seems best, for reasons already given, to disregard to problematic "head." The actual head—that is, that part of the animal in front of the branched appendages—seems to have had an irregularly truncated margin which probably bore papillae. On the right-hand side of the head in (*a*) a short appendage or frontal papilla of uncertain structure can be made out. (Fig. 4 (*a*) *fr. p.*) No horny jaws can be detected, though the fine preservation of the claws in this specimen makes it almost certain that they would have been detectable had they existed. The mouth seems to have been terminal, and a slightly dilated buccal cavity is indicated.

Internal organs.—The unbranched alimentary canal containing dark material can be seen almost throughout the whole length of the body in several specimens. The position of the anus can not be determined.

Habitat.—There can be no doubt that the deposit in which *Aysheaia* was fossilised is of marine origin. The evidence afforded by the whole of the associated fauna points in this direction. Moreover, the presence of no less than nine specimens in the collection indicates that the organism was not a casual straggler washed in from the land, but a true member of the marine association with which it is found. Two morphological points are of interest in this connection.

1. The characteristic Onychophoran form of the body was apparently as strikingly developed in the Middle Cambrian marine form under consideration as in the terrestrial Peripatidae and Peripatopsidae of to-day. Many zoologists have objected to the division of the living Onychophora into two families with many genera on the grounds that the whole assemblage is a very uniform one in spite of considerable differences in detail. In *Aysheaia* we have a form living under entirely different ecological conditions from those of the modern species, and at a very remote time, yet having an external appearance, which in life must have been extraordinarily similar to that of the living representatives of the group. The considerable structural differences which do occur are only manifest when a minute examination is made. Presumably the internal structure of the body of *Aysheaia* presented differences of great importance; tracheae are hardly likely to have been present in a form that we may reasonably assume was primitively marine.

2. The position of the mouth deserves a passing mention. In the modern Onychophora the mouth lies in a ventrally situated oral cup. The ventral position of the mouth is clearly of considerable value in feeding on solid material, particularly in a terrestrial animal. Terminal mouths may persist or be developed in burrowing forms, but outside the polychaet annelids are uncommon among the higher invertebrates. It is, therefore, of interest that *Aysheaia* had apparently acquired ambulatory limbs while still retaining a terminal mouth.

Relationship to modern Onychophora.—The strongest evidence in favor of placing *Aysheaia* in the Onychophora is that afforded by the nature and appearance of the body wall and form and disposition of the appendages. From the modern Onychophora *Aysheaia* differs in the following ways.

1. The smaller number of segments in *Aysheaia*.

No modern Onychophoran has less than 14 segments bearing clawed legs. This corresponds to a total of 17 segments. In *Aysheaia* there are 10 segments bearing clawed legs and probably two more, making a total of 12.

2. The small number of annuli to each segment.

Aysheaia has 4 annuli of papillae, the modern species all have more than 12.

3. The large number of claws on the walking legs.

All modern Onychophora have two claws on each trunk appendage, supported by a complex foot. In *Aysheaia* there are six claws and the foot was presumably much less elaborate. In the embryo of *Peripatus corradoi* Camerano, Bouvier (1907, p. 38, fig. 43) figures each claw as covered with a cuticular layer, afterwards shed, bearing a number of large denticles. It is highly probable that the claws in adult Onychophora are compound, each representing one of the two groups of three in *Aysheaia*.

4. The internal process of the trunk appendages.

This structure may possibly be homologous with the eversible coxal vesicles of many modern Onychophora, but would seem to lie more distally. The proximal portion is very probably covered by the base of the leg in all the specimens in which the process is shown. The internal process may well have been respiratory; the possession of a soft lobe or spur on the leg would seem more in accordance with an aquatic than a terrestrial habitat, whatever its function.

5. The terminal mouth.

This difference has already been discussed.

6. The structure and arrangement of the anterior appendages.

The interpretation of the head of *Aysheaia* is somewhat speculative and is treated at length below.

The first two differences are difficult to evaluate. Various species of Peripatopsidae approach nearer to *Aysheaia* in these respects more than do the Peripatidae, but there is no evidence that the Peripatopsidae are primitive in this. From a general point of view it is more reasonable to suppose that the small number of segments, if not that of the annuli, is a specialized reduction rather than a primitive character in *Aysheaia*. The greater number of claws may be reasonably regarded as primitive and so may the internal appendage on the legs, particularly if it is correlated with a marine habitat or is homologous with the coxal vesicles which are found only in primitive Onychophora and tend to undergo a progressive reduction. If the interpretation of the head given below be regarded as correct *Aysheaia* is much more primitive in this respect than any living Onychophoran.

Head of Aysheaia.—In the recent Onychophora there are three appendages anterior to the legs which, being considerably modified, may be considered as defining the head in the adult. These three appendages, the antennae, the jaws, and the slime papillae, are usually regarded, following the classical work of Sedgwick (1885–8) as belonging to the first three mesoblastic somites, it being supposed that no reduction in the segmentation has occurred at the anterior end of the animal. The somites from which these appendages develop are originally all postoral, the first later moves forward to form the preoral lobes from which the antennae arise. The second and third appendages, which are postoral throughout development, show certain characters which make it reasonably probable that they are derived from legs of the same type as the trunk legs of the adult. Thus the jaws are comparable to legs in which the main axis is very reduced and the claws hypertrophied, while the slime papillae may be regarded as footless legs with greatly hypertrophied crural glands. The antennae differ from the succeeding appendages in exhibiting no trace of an origin from legs and in originating more dorsally than any of the rest of the series. Holmgren (1916) in his great work on the Arthropod brain, homologises with great certainty the antennae of the Onychophora with the palps of the Polychaets. Lying in front of the palps in the Polychaets are prostomial “antennae” or “tentacles,” which are variously developed and may be median or paired. These tentacles are innervated by a nerve which has the same relations to the brain as the *nervus tegumentarius* in the Onychophora. In the embryos of some Peripatidae, as *Peripatus edwardsi* Blanchard, described by Kennel (1885) and *Eoperipatus weldoni* Evans investigated by Evans (1901), indications are found of frontal organs which presumably represent the annelid tentacles, lost

in all adult living Onychophora. The anterodorsal region of the brain of the Polychaets, bearing eyes, tentacles, nuchal organ, etc., is of multiple origin, though strictly comparable with the same region in the Onychophora. It is still a matter of debate whether its various components are to be regarded as somites or as presegmental; still less can we determine whether the frontal organs of the embryos of Peripatidae are serially homologous with succeeding appendages. A discussion of the apparent segmentation of this region is outside the scope of the present paper for which purpose it seems best to consider only the appendages, no other indications of segmentation being preserved in the fossils under consideration.³ If we are to give any weight whatever to a phylogenetic interpretation of embryology, we may conclude that at some stage in their ancestry the modern Onychophora passed through a stage in which the head bore a pair of postoral antennae, and that these were preceded by some sort of tentacle or frontal organ and succeeded by a series of uniform trunk legs bearing claws and crural glands as in the modern forms.

The following speculative interpretation of the head of *Aysheara* fits well into the scheme derived from the embryological findings. It has already been indicated that the branched appendage, as shown in the laterally compressed specimen (*b*), lies at a rather higher level than the succeeding members of the series of appendages. This fact alone tends to indicate that it is homologous with the antenna of the modern Onychophora in spite of its less anterior and clearly postoral position. Like the antennae, moreover, it is structurally dissimilar to the succeeding appendages and lacks claws. It is, therefore, within the limits of justifiable speculation to equate the two organs. Posterior to the branched appendage of *Aysheara* lies a uniform series of legs. It has, however, been pointed out that such evidence as is available strongly suggests that the two appendages succeeding the antenna of modern Onychophora were at some stage similar to the other legs. In front of the branched appendages in specimen (*a*) lies a small papilliform projection which was probably tactile or trophic. If the above speculation is sound we can regard this as homologous with the frontal organ of the embryo of the Peripatidae. It is to be noted that there is every probability in favour of an Onychophoran with a terminal mouth having a very uncephalized anterior end; moreover, the segments are relatively long throughout *Aysheara*, so that every opportunity is

³Through the kindness of Prof. Alexander Petrunkevitch I have been able to examine his very fine collection of serial sections of the heads of West Indian species of *Peripatus*. The brain in these forms seems to be substantially like that of *Peripatopsis capensis* (Grube) described by Holmgren, and I can add nothing of importance to the conclusions of the latter worker.

given for a diagrammatic representation of the fundamental structure in the adult animal. The conditions may be presented schematically in the following way:

Peripatus:

Frontal organ (embryonic).
Antenna.
Jaw.
Slime papilla.
1st trunk leg.

Aysheaia:

Frontal papilla.
Branched appendage.
1st trunk leg.
2nd trunk leg.
3rd trunk leg.

Relationships to other forms.—*Aysheaia* does not indicate any relationship between the Arthropoda and Onychophora; it merely indicates what was the general structure of the oldest members of the latter group and emphasizes its isolation. The six setalike claws alone serve to bring the Onychophora nearer to the existing polychaets, and if the Onychophora had a polychaet origin it must have been in the very remote past from some extremely generalized ancestor. It is clear that the general form of the group is not correlated with terrestrial life. The recent discovery of *Xenusion auerswaldae* Pompeckj in supposedly Algonkian rocks suggests that segmented animals with annulated uniramous appendages at one time played a large part in the earth's fauna. Heymons (1928), indeed, in discussing *Xenusion*, suggests that the modern Onychophora, Tardigrada, and Pentastomida represent merely the relics of an important palaeozoic assemblage of animals. *Aysheaia* gives us some idea of the marine ancestors of one of the few surviving members of that fauna.

Systematic position.—It is becoming clear to most investigators of the Arthropoda that the Onychophora, in spite of their tracheal respiration and their reduced coelom and its corollaries, are misplaced in the Arthropoda. In Kükenthal and Krumbach's Handbuch, the most authoritative survey of the Animal Kingdom yet published, the Onychophora and Arthropoda are separated, and it is probable that such a course will be adopted generally in the future. The most rational course seems to be to follow Lankester in the classification used in his Treatise (1900) and include the arthropods and annelids in one phylum Appendiculata, or to revive the old Cuvierian group Articulata as has been done by various authors.

The Arthropoda, Onychophora, and Annelida may then be considered as subphyla. Possibly this rank also should be given to some of the "Stelenchopodous" groups and to *Xenusion*. For the present purpose the following scheme may be adopted.

Phylum ARTICULATA

Triploblastic metamericly segmented animals, with more than three segments, skeleton primarily ectodermal, mouth and anus both may be derived from blastopore.

(a) Subphylum ANNELIDA

(b) Subphylum and class ONYCHOPHORA

Articulates with cylindrical leglike walking appendages arranged segmentally and armed with terminal claws; body wall soft, muscular, indistinctly segmented and annulated with rings of papillae; in recent forms coelome reduced, heart ostiate, cilia confined to generative ducts.

Order 1. PROTONYCHOPHORA

Extinct marine Onychophora with a terminal mouth, a frontal papilla and clawless branched appendage followed by a series of legs bearing six claws.

Family Aysheidae Walcott. Middle Cambrian. British Columbia.

Order 2. EUONYCHOPHORA

Terrestrial Onychophora with a tracheal respiratory system. First three somites bearing preoral antennae and two postoral modified legs which form jaws and slime papillae, frontal organs vestigial in embryo. Trunk legs with a complex foot and two claws.

Family Peripatopsidae Bouvier; recent; temperate southern hemisphere.

Family Peripatidae Evans; recent circumtropical.

(c) Subphylum ARTHROPODA

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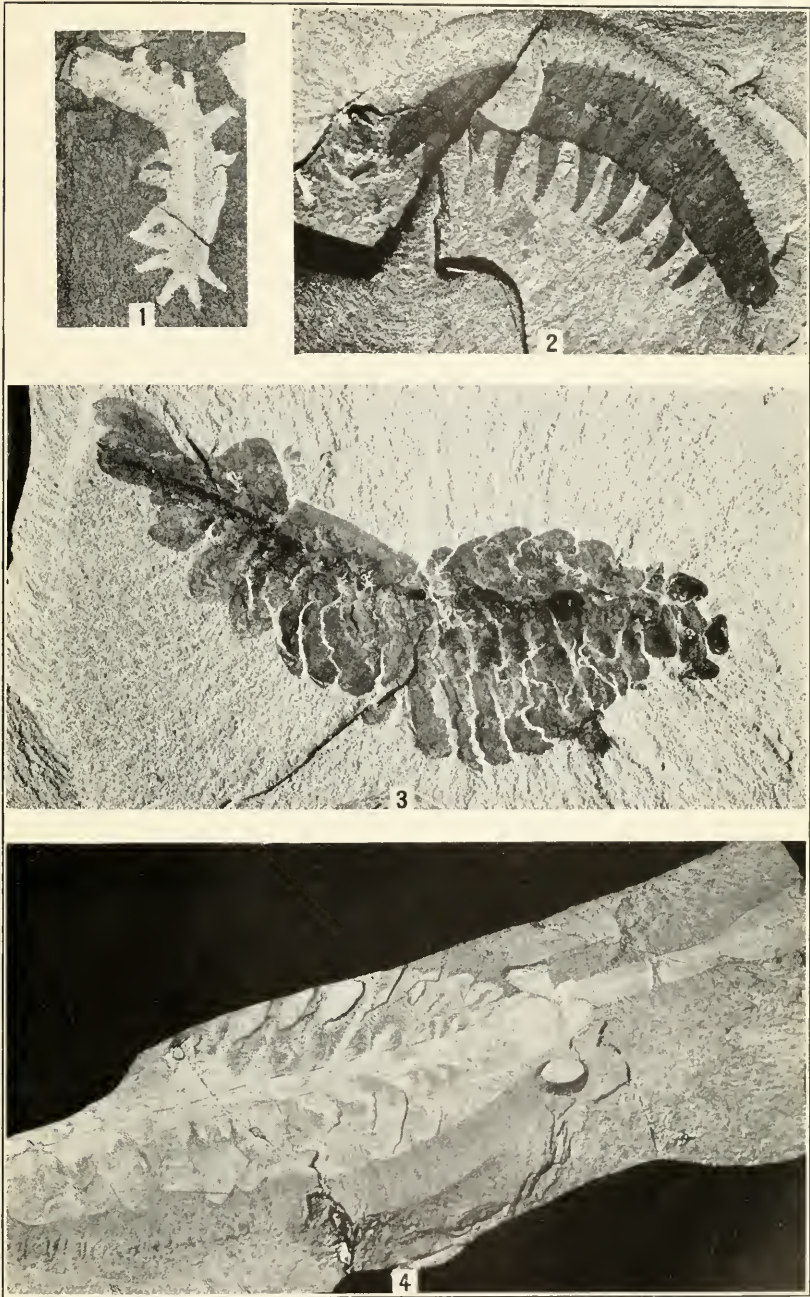
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DESCRIPTION OF PLATE

- FIGURE 1. *Aysheaia pedunculata* Walcott, specimen *c.* ($\times 1\frac{1}{2}$).
2. *Aysheaia pedunculata* Walcott, specimen *b.* ($\times 1\frac{1}{2}$).
3. *Opabinia regalis* Walcott, supposed female ($\times 1\frac{1}{2}$).
4. *Opabinia regalis* Walcott, supposed male ($\times 1\frac{1}{2}$).

Figures 1 and 4 are from retouched photographs left unpublished by the late Dr. C. D. Walcott; Figures 2 and 3 from unretouched photographs prepared under the direction of Dr. C. E. Resser.



AYSHEAIA PEDUNCULATA AND OPABINIA REGALIS
FOR EXPLANATION OF PLATE SEE PAGE 24