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FOSSIL PRIAPULID WORMS

BY

SIMON CONWAY MORRIS

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With 30 plates, 99 text-figures, and 4 tables

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ABSTRACT. The morphological details of some fossil worms from the Middle Cambrian Burgess Shale of southern British Columbia are described with the aid of reconstructions and plates with accompanying explanatory camera-lucida drawings. The species described are: *Ottoia prolifica* Walcott, *Selkirkia columbia* sp. nov., *Louisella pedunculata* Walcott, *Ancalagon minor* (Walcott) gen. nov., *Fieldia lanceolata* Walcott, *Scolecofurca rara* gen. et sp. nov., and *Lecythioscopa simplex* (Walcott) gen. nov. The preservation of these fossils is unusually fine. External details include a number of cuticular specializations on the probosces such as spines, teeth, hooks, and papillae. Most of the worms have trunk spines or hooks, whilst *L. pedunculata* is also characterized by two rows of trunk papillae. Features of internal anatomy that have been recognized in *O. prolifica* include the gut, retractor muscles, and a nerve cord. Internal organs of the other worms are generally less well defined. *O. prolifica* fed on hyolithids, occasional brachiopods, and even members of its own species. *S. columbia*, *L. pedunculata*, and *A. minor* were also apparently predators, whereas *F. lanceolata* was probably a deposit feeder. The feeding habits of *S. rara* and *L. simplex* are uncertain. All the worms are burrowers: *O. prolifica* and *L. pedunculata* in particular show marked adaptations for this way of life. The influence of decay and rotting prior to fossilization of the specimens is recognized and discussed.

With the possible exception of *S. rara* and *L. simplex*, these Burgess Shale worms can be accommodated within the Priapulida, which today forms a small phylum of marine infaunal worms. This taxonomic assignment is determined by the structural homology that exists between the armed probosces of these worms and modern priapulids. The Pennsylvanian priapulid *Priapulites konecniorum* Schram from the Mazon Creek area of Illinois is also redescribed. Information on Cambrian and Pennsylvanian priapulids permits a tentative phylogeny to be proposed. It is evident that the Priapulida was a far more diverse group in the past than it is at present. The possible affinity of the priapulids with the endoparasitic phylum of Acanthocephala is re-examined in the light of the similarity between the Burgess Shale priapulids, especially *A. minor*, and a hypothetical proto-acanthocephala.

Nomenclatural changes amongst the Burgess Shale priapulids include the establishment of two new genera (*Ancalagon*, *Lecythioscopa*) and one new species (*Selkirkia columbia*) for worms previously described by Walcott. Several cases of synonymy are noted. They include *Miskoia preciosa* Walcott and *M. placida* Walcott which are junior synonyms of *L. pedunculata* and *O. prolifica* respectively.

A number of other fossils that have been placed in *Ottoia* and *Selkirkia* by Walcott and other authors are reappraised. One specimen from the Cambrian Kinzer Shale formerly placed in *Ottoia* appears to belong within the Palaeoscolecidae (Annelida), which is represented by *Protoscolex* and *Palaeoscolex*. Aspects of this family, which ranges from the Cambrian to the Silurian, are reviewed.

CONTENTS

INTRODUCTION

THE soft-bodied invertebrate fossils from the celebrated Burgess Shale (Middle Cambrian) arguably show some of the most exquisite preservation known. The general character of the fauna has long been known, but it is only now that a reassessment of the entire biota is being undertaken (Conway Morris 1976*a*, *b*, 1977; Hughes 1975; Whittington 1971*b*, 1974, 1975*a*, *b*).

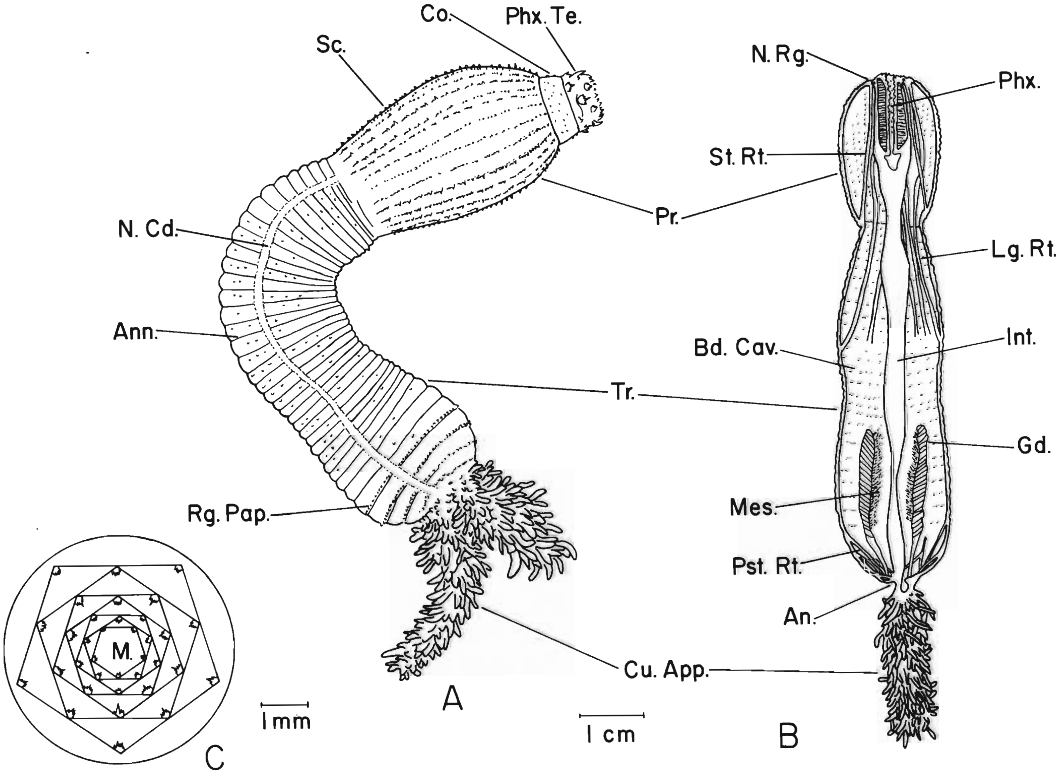
The Burgess Shale was discovered by Charles Doolittle Walcott, Secretary of the Smithsonian Institution, in 1910 on the west side of the ridge connecting Mount Field and Wapta Mountain, British Columbia, following the discovery the previous year of a detached block containing soft-bodied fossils (Walcott 1911*a*). Exploitation by quarrying during the years 1910–1913 and 1917 of a stratum near the base of the shale, the Phyllopod bed, as well as another unit 19·8 m (65 ft) higher which is now known as Raymond's quarry, yielded over 50 000 specimens. This collection is now in the National Museum of Natural History, formerly the United States National Museum (USNM), Washington, D.C.

In 1966 (Aitken *et al.* 1967) and 1967 (Aitken and Fritz 1968) a Geological Survey of Canada (GSC) team led by Dr. J. D. Aitken reopened the two quarries with the co-operation of the authorities of the Yoho National Park and Parks Canada, Department of Indian and Northern Affairs, Ottawa, as part of the larger geological survey called Operation Bow-Athabasca (Price 1967). The specimens collected by this team are at present in Cambridge. Those relevant to this study were studied in conjunction with specimens from other institutions, in particular the USNM, where the Walcott Collection comprising the type specimens and a large amount of additional material are housed.

C. D. Walcott included in his 1911*c* publication preliminary descriptions of the Burgess Shale (Middle Cambrian) worms *Ottoia prolifica*, *O. minor* (= *Ancalagon minor* gen. nov.), *Selkirkia major* (= *S. columbia* sp. nov.), and *Miskoia preciosa* (= *Louisella pedunculata*), whilst in 1912*a* and 1931 he included accounts of *Fieldia lanceolata* and *Canadia simplex* (= *Lecythioscopa simplex* gen. nov.). These worms, together with *Scolecofurca rara* gen. et sp. nov., are described herein. *O. prolifica* has long been recognized as being priapulid-like, but the other published species have received very little attention. It is the purpose of this paper to show that these worms, with the possible exceptions of *S. rara* and *L. simplex*, can be placed in the phylum Priapulida. For convenience, the Burgess Shale priapulids are referred to here collectively under the informal name archaeopriapulids. In addition, the Carboniferous priapulid *Priapulites konecniorum* Schram, 1973 is redescribed. A number of fossils that have been placed in the archaeopriapulid genera *Ottoia* and *Selkirkia* are briefly reappraised.

The priapulids are a small phylum of burrowing marine worms with a characteristic retractable spiny proboscis and an annulated trunk, often with one or two caudal appendages (text-fig. 1A, B). The proboscis bears twenty-five rows of scalids, which are separated from pentagonally arranged, circum-oral multidentate teeth by an unarmed collar or buccal ring (text-fig. 1C). The teeth extend into and line the muscular pharynx, although their pattern changes from pentagonal to quincunxial. The gut is straight with terminal openings, and it lies in a large undivided body cavity. The paired urino-genital organs are of a type peculiar to priapulids. They consist of intimately associated excretory and reproductive tissue that discharge their contents into common ducts that open either side of the anus. The nervous system is superficial and simple. It consists of a circum-pharyngeal ring located in the proboscis collar and an unganglionated nerve cord. Further details of priapulid anatomy, especially in comparison with archaeopriapulids, will be found below.

The most comprehensive work on the modern priapulids is by Land (1970). He recognized two families: the Priapulidae, comprising the genera *Priapulus* (two species, *P. caudatus* and *P. tuberculatospinosus*), *Priapulopsis* (two definite species, *Pr. bicaudatus* and *Pr. australis* and possibly *Pr.* (?) *cnidephorus* Salvini-Plawen, 1973), *Acanthopriapulus* (one species, *A. horridus*) and *Halicryptus* (one species, *H. spinulosus*); and the Tubiluchidae, comprising the monospecific genus *Tubiluchus corallicola*. In addition, a third family, the Maccabeidae, consisting of one genus *Maccabeus* (one species, *M. tentaculatus*) has since been described (Por 1972; Por and Bromley 1974). The priapulid described by Salvini-Plawen (1974) as *Chaetostephanus praeposteriens* is synonymous with *M. tentaculatus* Por, 1972 (Calloway pers. comm.). *Priapulopsis* has



TEXT-FIG. 1. Modern priapulid worms. A, external view of *Priapulopsis bicaudatus* (from Théel 1906, pl. 1, fig. 3 and pl. 2, fig. 10). B, longitudinal section of *Priapulus caudatus* (from Hammond 1970*b*, fig. 1). C, anterior view showing the pentagons of circum-oral teeth in *P. caudatus* (from Murina and Starobogatov 1961, fig. 3*a*). The cm scale refers to A and B, the mm scale to C.

two caudal appendages, *Priapulus*, *Acanthopriapulus*, and *Tubiluchus* have a single appendage, whilst *Halicryptus* and *Maccabeus* lack an appendage. Other distinguishing features between these genera include the type and distribution of proboscis scalids and circum-oral teeth, as well as the nature of the trunk ornamentation.

Salvini-Plawen (1974) placed the Priapulidae and Tubiluchidae in the Order Priapulimorpha, and the Maccabeidae in the Order Seticoronaria. As noted below, study of the archaeopriapulids does not support the validity of these orders.

Explanation of abbreviations used in the text-figures

An.	Anus
Ann.	Annulations
An. Set.	Anal setae
At.	Anterior
At. Rt.	Anterior retractor muscle
At. Set.	Anterior setae
At. Tr.	Anterior trunk
Bd. Cav.	Body cavity
Bd. Wl.	Body wall
Bur.	Bursa
C. Tr.	Central trunk
Ca.	Canals feeding trunk papillae from body cavity
Cir. Ms.	Circular muscles
Co.	Collar or peribuccal ring
Ct. Vis.	Cutaneo-visceral muscles
Cu. App.	Caudal appendage
Cut.	Cuticle
d — d	Line of demarcation between two body regions
Dt.	Duct
Dec.	Area of decay
Fd.	Folding over of the body
Fl. Fe.	Flowage feature
Fn. S.	Fine spines
Fo. Bd.	Foreign body
Ga.	Ganglia
Ga. Cl.	Ganglion cells
Gd.	Urinogenital system
Giz.	Gizzard
Gl.	Gland
Gut	Gut
Gut C.	Gut contents
Hd. S.	Head spines
Hyp.	Hypodermis
In. F.	Internal furrows of gut wall
Int.	Intestine
Lg. Ms.	Longitudinal muscles
Lg. Pr. S.	Long proboscis spines
Lg. Rt.	Long retractor muscle
Lg. Tr. S.	Long trunk spines
M.	Mouth
Mes.	Mesentery
Ms.	Muscle
N. Cd.	Nerve cord
N. Rg.	Nerve ring
Nk. Rt.	'Neck' retractor muscle
Oes.	Oesophagus
Or. Hk.	Oral hook
Or. S.	Oral spines
Pen. Anc.	Penetration anchor
Phx.	Pharynx
Phx. Te.	Pharynx teeth
Pn.	Protonephridia
Pr.	Proboscis
Pr. Hk.	Proboscis hook
Pr. Pap.	Proboscis papillae
Pr. S.	Proboscis spines
Pr. Tt.	Proboscis tentacle
Pr. Wl.	Proboscis wall
Pst. Hk.	Posterior hook
Pst. In.	Posterior invagination
Pst. Rt.	Posterior retractor muscle
Pst. Tr.	Posterior trunk
R. Ar.	Reflective area, of uncertain origin
Rg. Pap.	Ring papillae
Rt. Ms.	Retractor muscle
S.	Spine
Sc.	Scalid
Sed.	Sediment
Sn. Pap.	Sensory papilla
So. Cl.	Solitary clump of trunk papillae
Sp.	Spinule
St. Pst. Rt.	Short posterior retractor muscle
St. Rt.	Short retractor muscle
Tb.	Tube
Ter. Anc.	Terminal anchor
Ter. Co.	Terminal cone
Tr.	Trunk
Tr. Pap.	Trunk papillae
Tr. S.	Trunk spines
Tr. Set.	Trunk setae

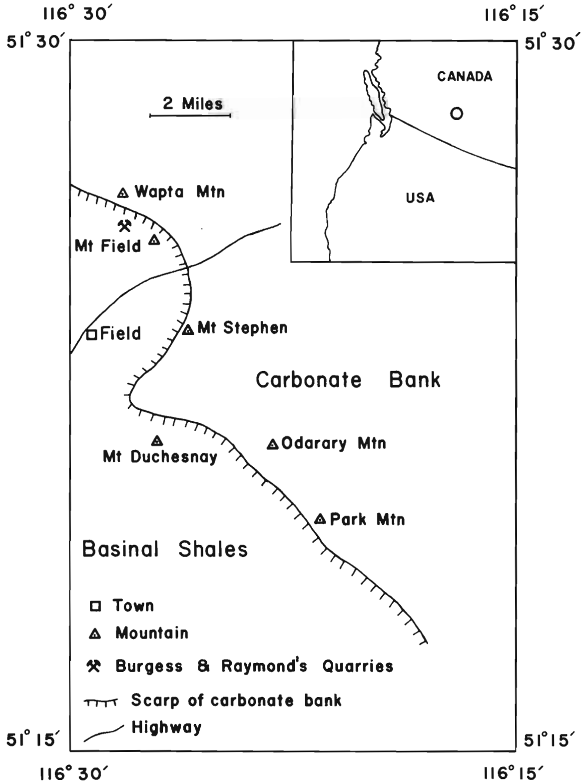
Abbreviations for depositories of specimens:

USNM	United States National Museum, Washington D.C. (now the National Museum of Natural History).
GSC	Geological Survey of Canada, Ottawa.
PE	Field Museum, Chicago.
ROM	Royal Ontario Museum, Toronto.

STRATIGRAPHY

THE stratigraphic position of the Burgess Shale was clarified by Fritz (1971). The Burgess Shale forms a predominantly shale lenticle in the otherwise impure limestone and shale sequence of the Stephen Formation (Middle Cambrian). The shale lies within the *Pagetia bootes* faunule of the *Bathyuriscus–Elrathina* Zone. The Stephen Formation is a basinal succession and was deposited to the south-west of a carbonate bank which had prominent and steep relief (text-fig. 2). The Burgess Shale was deposited within an embayment of the carbonate bank (McIlreath 1974) in water several hundred metres deep (Fritz 1971).

Two horizons within the Burgess Shale have yielded soft-bodied fossils. The lower of these is the Phyllopod bed (7 ft 7 in, 2·31 m) which is within the lowermost division (h.) of the Burgess Shale (Walcott 1912*b*) and is exposed in the Burgess quarry (USNM locality 35k). About 19·8 m (65 ft) above the Burgess quarry the other soft-bodied fossil horizon is present in Raymond's quarry (USNM locality 35k/10) (Walcott 1912*a*; Raymond 1935). The biota of the Phyllopod bed is more diverse, of somewhat different character, and better preserved than that recovered from Raymond's quarry. The two



TEXT-FIG. 2. Map of the area around Field, British Columbia (redrawn from McIlreath 1974, fig. 2), with inset map showing location of area with respect to western North America.

quarries are situated on a ridge connecting Wapta Mountain to Mount Field at an elevation of about 2286 m (7500 ft) (long. 116° 28′ 30″, lat. 51° 26′ 50″), 4·8 km (3 miles) north of Field, southern British Columbia (text-fig. 2).

All the archaeopriapulids, with the exception of *Scolecofurca rara*, are found in the Phyllopod bed. The strata exposed in Raymond's quarry are generally poorer in archaeopriapulids and have yielded only *O. prolifica*, *Selkirkia columbia*, and the only known specimen of *Scolecofurca rara.* Details of the vertical distribution of each species within the quarries are given below.

The stratigraphic horizon of *Priapulites konecniorum* is given with its systematic account.

Preservation

The archaeopriapulids are preserved in the same manner as the trilobitoid *Marrella splendens* Walcott (Whittington 1971*a*), and the great majority of other Burgess Shale fossils. The fossils consist of films that are darker than the surrounding matrix. Parts of the fossil, in particular the hooks, spines, gut, and muscles are, however, distinguishable in high-angle light as reflective areas. Preliminary analyses by Mr. R. A. Chappell (National Physical Laboratory, Teddington) using Auger Spectroscopy, indicate that the film that forms the body wall of *O. prolifica* is composed of calcium aluminosilicates (in atomic %: Ca 3·8 ± 0·4, Al 10 ± 5, Si 21·2 ± 5, O 60 ± 10, C 5), although the reflectively preserved gut also contains magnesium (Ca 4·4 ± 0·4, Mg 4 ± 2, Al 10 ± 5, Si 16·6 ± 7, O 60 ± 10, C 5). The composition of the rock is fairly close to that of the fossil although calcium is depleted (Ca 1·9 ± 0·2, Al 15 ± 5, Si 18 ± 5, O 60 ± 10, C 5). Fossilization must have been rapid to give the soft-bodied preservation, but how the silicate film formed and at what stage in diagenesis is still unknown. The concentration of carbon in the fossil film is low, and the earlier view that the fossils are preserved as carbonaceous films is incorrect. The film is often dimpled with minute pyritic spherules, which occasionally reach larger sizes. Whittington (1974) interpreted them as an integral part of the film, but they may have been embedded into the film during compaction. Examination of thin sections of the Burgess Shale confirms that pyrite spherules, often in lensoid masses, exist unassociated with the fossil films. Very occasionally some of the proboscis armature of *Selkirkia columbia* has been preserved in framboidal pyrite.

The observation of Whittington (1971*a*, *b*) that the appendages of *M. splendens* are separated by thin layers of sediment led him to suggest that this species, at least, was buried in a moving sediment cloud. The variable orientation of the specimens supported this conclusion and demonstrated that Walcott's (1919) hypothesis of the animals dropping to the sea-floor from the overlying water is untenable. Further research is indicating that all the benthonic species were buried in the same manner as *M. splendens* (Whittington 1974, 1975*a*, *b*; Hughes 1975). As is discussed below study of external features in *O. prolifica*, *S. columbia*, and *L. pedunculata* show that they have a variable orientation within the sediment. The other archaeopriapulids lack distinctive external features that indicate the orientation of specimens. It is reasonable to assume that the archaeopriapulids, which were all infaunal, suffered the same preservational history and were transported and buried by mudflows. Unlike *M. splendens* and the other arthropods the archaeopriapulids lacked appendages so that the specimens generally lie on a single bedding plane. Thus, Whittington's (1975*a*, fig. 3) demonstration of how slight variation in the level of step-like splitting through fossils affects the exposure of the appendages is not directly applicable to these apodous worms.

The fossils consist of part and counterpart. Definition of the part is normally based on the relative prominence of organs such as the gut and muscles as compared to the counterpart. In a few cases distinction between part and counterpart is arbitrary, but in general the counterpart is a thinner, more residual film. Some of the fossil films have suffered varying degrees of disruption that presumably occurred during compaction. The films are sometimes interrupted by sediment wedges, and the tube of *S. columbia* is often crinkled or otherwise distorted. Further discussion of these features will be found below.

The preservation of the Mazon Creek fossils, which include *P. konecniorum*, has been discussed by Richardson and Johnson (1971). The soft-bodied fossils are restricted to ironstone nodules. They are usually preserved as impressions distinguishable from the rest of the nodule by their generally lighter colour. It is apparent that the mechanism that led to the soft-bodied preservation in the Burgess Shale must have differed from that operating in the Mazon Creek nodules.

THE ARCHAEOPRIAPULIDS

SYSTEMATIC PALAEONTOLOGY

Phylum PRIAPULIDA
Family OTTOIIDAE Walcott, 1911
Genus OTTOIA Walcott, 1911

Type and only known species. Ottoia prolifica Walcott, 1911.

Diagnosis. Cylindrical and extensible body bilaterally symmetrical, but with pronounced anterior external radial symmetry. Divisible into anterior proboscis and annulated trunk. Proboscis invaginable into trunk, armed from posterior to anterior in everted proboscis with hooks, spines, and spinules, anterior end extensible. Trunk has about a hundred annulations, posterior end armed with dorsal and lateral hooks, posterior eversible as unannulated bursa. Mouth at end of proboscis, leading to pharynx, gizzard (?), and thence to straight or irregularly looped intestine with folded internal walls. Anus at posterior end of the trunk or bursa if everted. Undivided spacious body cavity. Musculature consists of body-wall muscles, four sets of anterior retractor muscles, and one or two sets of posterior retractor muscles. Mesenteries and gut suspensor muscles support internal organs. Ventral (?) nerve cord, possibly ganglionated.

Ottoia prolifica Walcott, 1911

Plates 1-14; text-figs. 36-67

1911 *Sidneyia inexpectans* Walcott, pl. 3, fig. 1.
1911 *Ottoia prolifica* Walcott, p. 58, pl. 8, fig. 1.
1911 *Ottoia prolifica* Walcott, pp. 117, 128-131, 142, 144, pl. 19, figs. 1-5.
1911 *Ottoia minor* Walcott, pl. 22, fig. 6 (non pl. 22, fig. 5).

1912 *Ottoia prolifica* Walcott, p. 153.
1912 *Ottoia prolifica* Walcott, p. 188, 190.
1925 *Ottoia prolifica* Ruedemann, p. 85.
1931 *Ottoia prolifica* Roy and Croneis, p. 241.
1931 *Miskoia placida* Walcott, p. 4, pl. 2, fig. 1.
1931 *Ottoia minor* Walcott, pl. 9, figs. 2, 4 (non pl. 9, figs. 1, 3, 5–7).
1933 *Ottoia prolifica* Meyer, pp. 524–527, figs. 380–381 (cop. Walcott 1911, pl. 19, figs. 1–2).
1939 *Sidneyia inexpectans* Størmer, p. 234, fig. 30.g (cop. Walcott 1911, part of pl. 3, fig. 1).
1944 *Sidneyia inexpectans* Størmer, p. 90, fig. 17.12 (cop. Walcott 1911, part of pl. 3, fig. 1).
1944 *Ottoia prolifica* Størmer, p. 140.
1953 *Ottoia prolifica* Lang, pp. 338–339, figs. 6–7 (cop. Walcott 1911, pl. 19, figs. 1–2).
1958 *Ottoia prolifica* Golvan, pp. 580, 585, fig. 11.
1959 *Sidneyia inexpectans* Størmer, fig. 16.4 (cop. Walcott 1911, part of pl. 3, fig. 1).
1962 *Ottoia prolifica* Howell, p. W169, fig. 107(1) (cop. Walcott 1911, pl. 19, fig. 5).
1962 *Ottoia prolifica* Gekker and Ushakov, p. 828.
1963 *Sidneya* [sic] *inexpectans* Simonetta, p. 105.
1966 *Sidneyia inexpectans* Sharov, p. 34, fig. 19c (cop. Walcott 1911, part of pl. 3, fig. 1).
1968 *Ottoia prolifica* Land, p. 249.
1974 *Ottoia prolifica* Por and Bromley, p. 195.
1975 *Ottoia prolifica* Crompton, p. 494–495, fig. 2, pl. 3*a–c* (*a*, *b*, cop. Walcott 1911, pl. 19, figs. 1–2).
1976 *Ottoia prolifica* Conway Morris, p. 200, 201.
1976 *Ottoia prolifica* Banta and Rice, pp. 79–89, figs. 1–30 (5–7, cop. Walcott 1911, pl. 19, fig. 1).

This and other synonymy lists presented herein omit nearly all the numerous references in textbooks and other sources where only passing mention is made. Such information is available in Conway Morris 1976*b*.

Diagnosis. As for the genus.

Lectotype. USNM 57619, Walcott 1911*c*, pl. 19, fig. 1. Designated by Banta and Rice (1976).

Paralectotypes. USNM 57620–57623. Walcott 1911*c*, pl. 19, figs. 2–5.

Other material. USNM 57486 (counterpart is 196377), 57647, 83928, 83939b, d, 172976–172989, 172990 (counterpart is 172992). Banta and Rice (1976) figs. 1–4, 8–29. USNM 188593–188601, 188603–188620, 188628, 188634–188639, 193695, 196106, 196204, 196531 (counterpart is 199413), 198565–198583, 198585–198595, 198818, 198922, 199096 (counterpart is 199106), 199101, 202470. There are about 1000 additional USNM specimens. GSC 8311, 8311a, b, 11351 (three specimens), 11537 (four specimens), 15407, 40972, 45322–45326. The GSC collections of 1966 and 1967 total 139 specimens. ROM 1229, 25880, 32238 (two specimens) and many unnumbered specimens. Stuttgart 14703. British Museum (Natural History) A2624, A9795 (three specimens). Sedgwick Museum A1695. Bristol University Geol. Mus. 13387. Oslo Univ. Pal. Mus. A19468. Peabody, Yale 3467, 5828 (sixteen specimens). Princeton Geol. Dept. unnumbered specimen. Harvard (MCZ) unnumbered specimens.

History of research

In his systematic description of *O. prolifica* Walcott (1911*c*) illustrated five specimens (Pl. 1, figs. 1–5; Pl. 2, fig. 6; text-figs. 36, 37). Two other specimens were, however, illustrated in earlier papers by Walcott. In his first paper on the Burgess Shale fauna (Walcott 1911*a*) the arthropod *Sidneyia inexpectans* was described. One of the specimens (USNM 57486) was interpreted as 'A portion of a branchial leaf or lamella showing something of the structure' (Walcott 1911*a*, p. 32, pl. 3, fig. 1). Walcott's figure was retouched, but examination of the specimen itself showed that there are three (one poorly preserved) terminal hooks (Pl. 1, fig. 6) exactly comparable to the posterior hooks of *O. prolifica* (see e.g. Pl. 1, fig. 1; Pl. 8, figs. 6, 7). The counterpart (USNM 196377) of this specimen, located by Dr. D. E. G. Briggs, shows the same feature. Although Størmer (1939, 1944, 1959) and Sharov (1966) followed Walcott's interpretation neither Simonetta (1963) nor Dr. D. L. Bruton (pers. comm.) were able to interpret USNM 57486 as *S. inexpectans* in their studies. This specimen is interpreted here as a decayed specimen of *O. prolifica*. Another specimen of *O. prolifica*, correctly identified, was included in a photograph of the medusoid *Peytoia nathorsti* (Walcott 1911*b*, pl. 8, fig. 1).

Since the original description (Walcott 1911*c*) all later statements and conclusions, with the exception of Banta and Rice (1976), have relied on this publication. *O. prolifica* has been mentioned and illustrated in many textbooks, e.g. Howell (1962) and Gekker and Ushakov (1962), compared wth other fossil worms without success, e.g. Ruedemann (1925*a*) and Roy and Croneis (1931), and allied with some of the extant aschelminth worms, e.g. Meyer (1933), Størmer (1944), Lang (1953), Golvan (1958), Land (1968), Crompton (1975), and Banta and Rice (1976).

In addition to the supposed specimen of *S. inexpectans* discussed above, in the opinion of the author, Walcott (1911*c*, pl. 22, fig. 6; 1931, pl. 9, figs. 2, 4) also misidentified certain specimens of *O. prolifica* as *O. minor*. *O. minor* is herein renamed *Ancalagon minor* (Walcott) gen. nov. A second species of *Miskoia* Walcott, 1911, *M. placida*, that Walcott erected on the basis of a single specimen (Walcott 1931, pl. 2, fig. 1) is also regarded here as a synonym for *O. prolifica*. Further discussion of these synonymous specimens will be found below.

Vertical and horizontal distribution

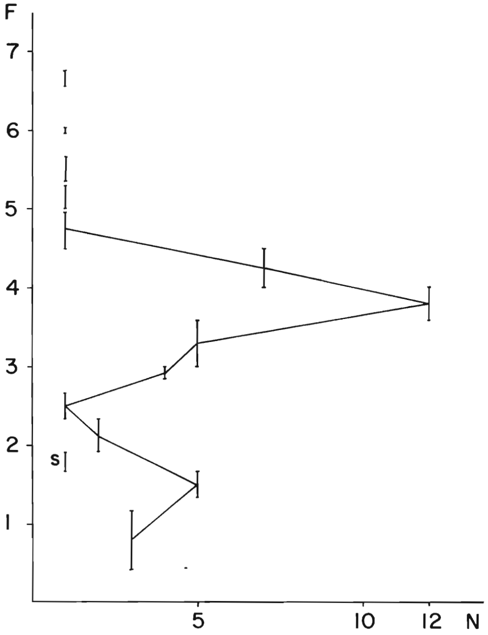
Nearly all the specimens collected by Walcott are labelled 35k, and so are presumably from the Phyllopod bed exposed within the Burgess quarry. Walcott (1912*a*) noted *O. prolifica* from layer no. 10 (7·6–48·3 cm (0 ft 3 in–1 ft 7 in) above the base of the Burgess quarry) and also from above layer no. 5 (from 116·8 cm (3 ft 10 in) upwards). No more details of the vertical distribution are available from his collections.

The distribution of the GSC specimens through the Burgess quarry is shown in text-fig. 3. Although the small sample (forty-five specimens) precludes definite conclusions, there appear to be maxima at 40·6–50·8 cm (1 ft 4 in–1 ft 8 in) and 109·2–121·9 cm (3 ft 7 in–4 ft 0 in). The largest of the three maxima of *M. splendens* (Whittington 1971*b*, fig. 1) is a few centimetres above the latter maximum. Such coincidence may be fortuitous as other species have maxima at other levels. Only one specimen was found from the south end of the quarry where Fritz (1971) noted that the number and quality of specimens decreased as compared with the rest of the Burgess quarry.

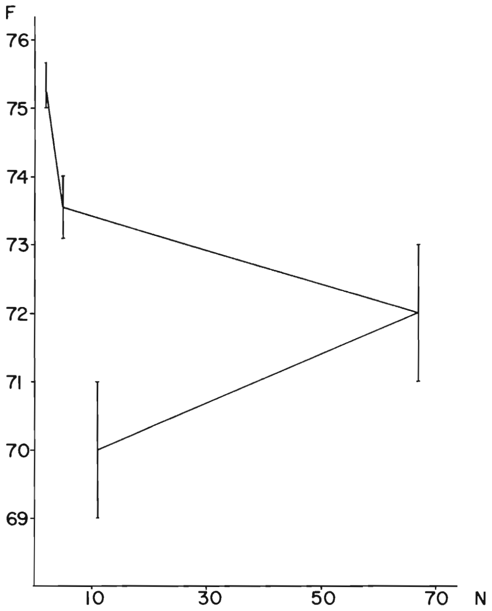
Text-fig. 4 illustrates the distribution of the GSC specimens from Raymond's quarry. A maximum exists at 21·6–22·3 m (71 ft–73 ft) above the base of the lower Burgess quarry. The total range of the GSC specimens of *O. prolifica* within the Burgess Shale is 22·93 m (75 ft 3 in) 0·13–23·06 m (0 ft 5 in–75 ft 8 in).

Introduction to morphology

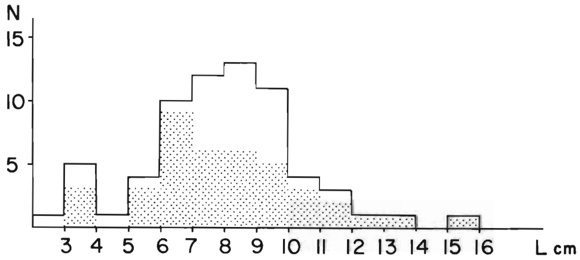
Text-fig. 5 shows the variation in length amongst sixty-seven complete GSC specimens from the Burgess and Raymond's quarries. Curved specimens were measured along the arc to an accuracy of about 5%. There does not appear to be any marked difference



TEXT-FIG. 3. Vertical distribution of forty-five GSC specimens of *Ottoia prolifica* from the Burgess quarry. Four specimens were omitted from consideration. In this text-fig. and figs. 4 and 18 the thickness of rock from which each sample came is shown by the vertical bar. The base of the quarry, taken here at 0 ft 0 in, is equivalent to the level 5 ft 0 in. in Whittington (1971*a*, figs. 3, 5; 1971*b*, fig. 1; 1974, fig. 1) and Hughes (1975, fig. 1). F, height in feet above base of quarry; N, number of specimens; S, single specimen from south end of quarry.



TEXT-FIG. 4. Vertical distribution of eighty-five GSC specimens of *Ottoia prolifica* from Raymond's quarry. Four specimens were omitted from consideration. F, height in feet above base of Burgess quarry; N, number of specimens.



TEXT-FIG. 5. Size-frequency histogram of length (posterior tip to proboscis spines) of sixty-seven GSC specimens of *Ottoia prolifica* from the Burgess and Raymond's quarries. Stippled area refers to sample from Raymond's quarry. N, number of specimens; L cm, length in cm.

between length frequency in the samples from each quarry. In the archaeopriapulids short specimens are often wider than elongate ones (Walcott 1911*c*), suggesting that they could contract substantially. Thus the length frequency graphs of archaeopriapulids (text-figs. 5, 31) can give only an indication of the variation in size. The average length of *O. prolifica* is about 8 cm. Values fall away fairly evenly to 3 and 15 cm. The low number of specimens in the 4–5 cm range, giving a bimodal effect to the histogram, is presumably of no significance. This effect is a product of a small sample and no discrete gap would be expected in this soft-bodied species.

Banta and Rice (1976) gave the length of the shortest specimens as 'about 3 cm', but smaller specimens have been noted, e.g. USNM 202470 1·0 cm, USNM 198565 1·6 cm (Pl. 2, fig. 3), USNM 188616 2·5 cm (Pl. 2, fig. 7), and USNM 188617 2·7 cm (Pl. 2, fig. 4). Comparison of these juvenile specimens, which are morphologically identical to the adults, with those illustrated by Walcott (1931) (Pl. 2, figs. 2, 5; text-fig. 39) as *O. minor* (= herein *Ancalagon minor* (Walcott)) demonstrates that the latter specimens (USNM 83939b, d) are also juvenile examples of *O. prolifica.* Another specimen (USNM 57647) identified by Walcott (1911*c*) as *A. minor* is also taken to be a young specimen of *O. prolifica* with both ends turned upwards (Pl. 2, fig. 1; text-fig. 38). The longest specimen is about 15 cm long.

No significant differences have been found within *O. prolifica* to justify division into subspecies. The suggestion by Lang (1953) that USNM 57619 and 57620 (Pl. 1, figs. 1, 2; text-fig. 36) might represent two different species cannot be confirmed. Although specimens can show different features, this is ascribed to the vagaries of preservation rather than original specific variation.

The internal and external anatomy is shown in the form of a hypothetical dissection and cross-sections (text-figs. 6, 7). The body can be divided into an anterior proboscis that could invert into the trunk. The 'collar' that Banta and Rice (1976) designated as the region separating the proboscis from the trunk is included here in the proboscis. The proboscis carried the gut and did not have a receptacle to house it. All the armature is visible in the completely everted proboscis. Proximally there were at least twenty-eight rows of posteriorly directed hooks with smaller spines between each row. They were succeeded by a single circle of anteriorly directed spines. There then followed an unarmed area, while more distally there were multispinose teeth or spinules. The spinules gave way to an unarmed area that terminated in an extensible sac. The trunk possessed between seventy and a hundred annulations. The most anterior annulation is taken to delimit the trunk and proboscis. Near the posterior end of the trunk there were eight (dorsal?) hooks arranged concentrically. Posterior to these hooks an unannulated bursa, which carried the hind gut, could evert.

The openings of the gut were terminal. The gut lay in a large body cavity. Possible body-wall musculature has been identified, and more certainly several sets of retractor muscles. No vessels or other circulatory organs have been noted. A longitudinal nerve cord, presumably ventral and apparently ganglionated, was present.

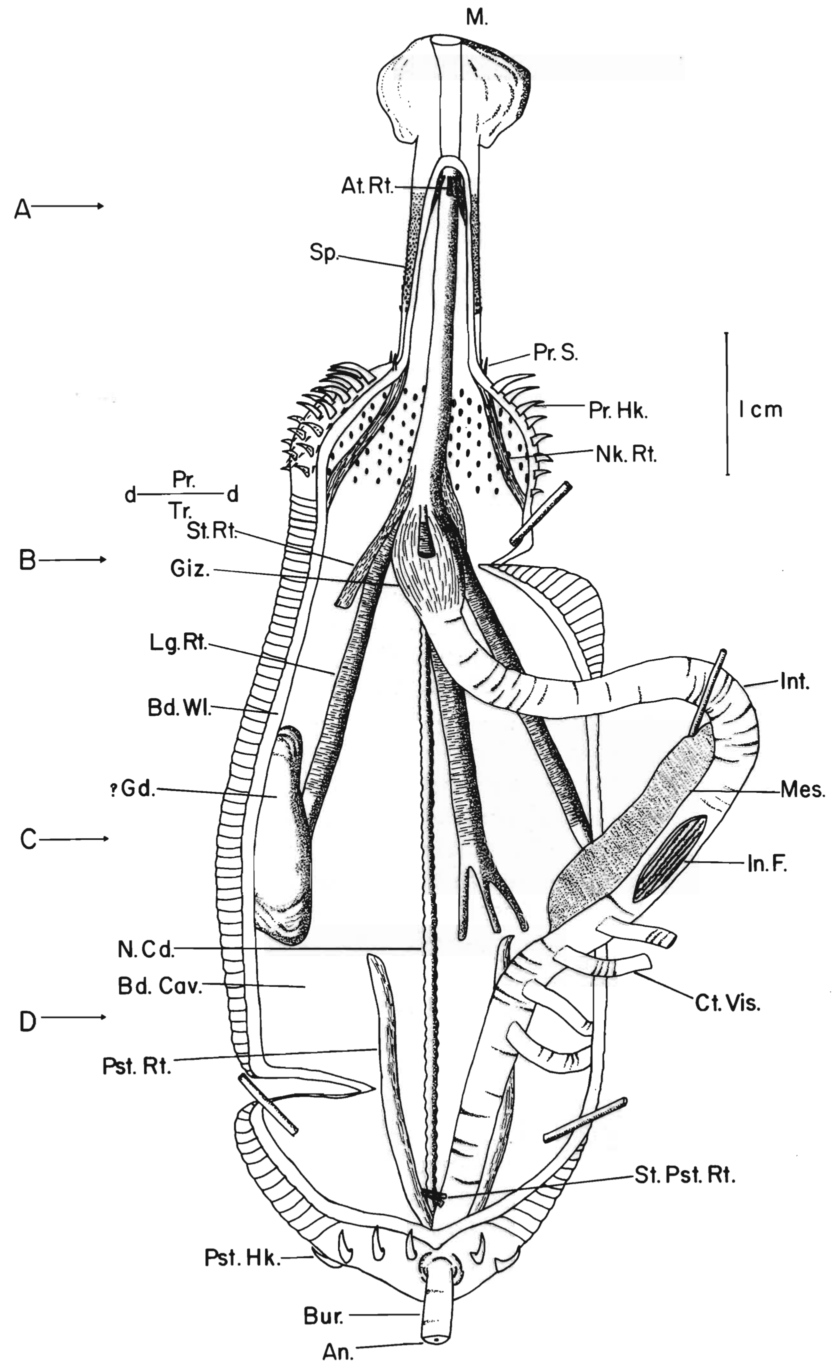
The only external bilaterally symmetrical feature was the posterior hooks which appear to have been arranged in two groups of four hooks. Internally the longitudinal nerve cord defined this symmetry. The dominant radial symmetry, especially prominent at the anterior, was superimposed and presumably reflects the burrowing mode of life.

Banta and Rice (1976) noted that nearly all the specimens are laterally flattened. They went on to state that 'The consistent occurrence of the posterior hooks on the inside of the body curve . . . indicates that compression usually occurred in a plane very near the plane of bilateral symmetry'. The eight posterior hooks occupied about 250° of the posterior circumference of the trunk. Hence, a specimen could have been flattened through this angle of 250° and one or two posterior hooks would always be visible in silhouette against the rock matrix. The varying degree of exposure of the posterior hooks demonstrates, therefore, that within a longitudinal axis *O. prolifica* shows as much variation in orientation as was noted by Whittington (1971*a*) for *M. splendens.* Banta and Rice's (1976) conclusion that flattening was usually along the plane of bilateral symmetry is considered here to be incorrect. Whittington (1971*a*) noted that even the abundant and small *M. splendens* (average length about 10 mm) is rarely orientated with its longitudinal axis vertical to the bedding plane. It is not surprising that the large elongate specimens of *O. prolifica* and the other archaeopriapulids almost invariably came to lie horizontally, rather than steeply or vertically inclined, to the bedding plane.

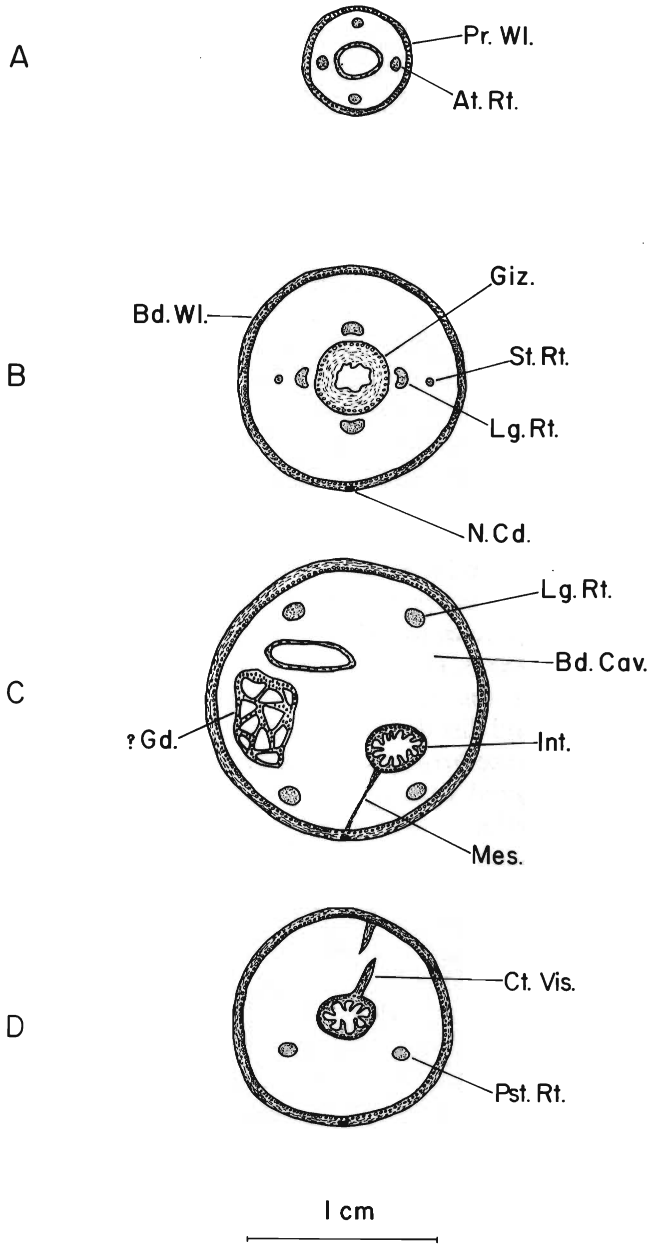
Morphological details

The cuticle and its specializations. The modern priapulids, in common with other worms, possess a cuticle that restricts size changes to certain limits, as well as protecting the animal (Hammond 1970*a*). In a number of specimens (Pl. 3, figs. 1, 4; Pl. 4, fig. 1; Pl. 10, fig. 1; Pl. 13, fig. 7; text-figs. 40, 42, 44, 56) some of the body wall, preserved as a reflective film, has contracted and left a less- or non-reflective area, interpreted as the cuticle, that maintains the original outline of the animal. In another specimen (USNM 198592) the anterior end has been withdrawn leaving a dark area (Pl. 3, fig. 2; text-fig. 41). It is probable that sudden contraction (in USNM 198592) or decay (other specimens) sufficiently loosened the cuticle from the rest of the body wall. As discussed below, during decay of modern priapulids the body wall almost always contracts and folds away from the cuticle within a few days of death. The detachment of the cuticle suggests that moulting was a normal activity in life. USNM 198592 may have been on the threshold of moulting when its introduction into the hostile environment of the Phyllopod bed resulted in sudden muscular contraction and detachment of the cuticle. Recent priapulids moult at fairly frequent intervals (Shapeero 1962*a*, *b*).

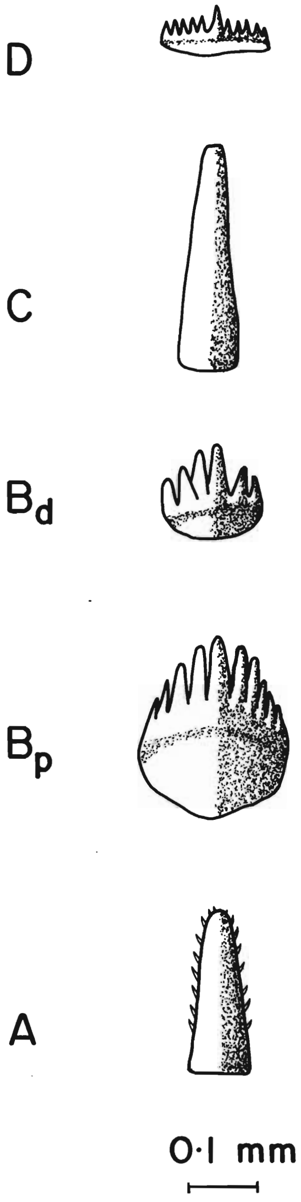
The trunk was annulated (Walcott 1911*c*) and the annulations are usually preserved as reflective lines (Pl. 9, fig. 8; Pl. 12, figs. 4, 8; Pl. 13, fig. 7; text-figs. 55, 62, 64). They consisted of ridges which in contracted specimens were between 1 and 2 mm high (Pl. 3, fig. 3; text-fig. 41). The most anterior annulation is arbitrarily taken to delimit the trunk. With the exception of the eversible bursa, the entire trunk was annulated. They were most prominent at the anterior (Meyer 1933) and posterior ends of the trunk (Pl. 2, fig. 6). Their spacing varies according to the degree of curvature and contraction. Typical values are 0·4–0·8 mm for the anterior (Walcott 1911*c* quoted 0·7 mm), 1 mm for the central length, and 0·5–1·0 mm for the posterior (Walcott 1911*c* quoted 1·4 mm). No specimen has every annulation preserved, but estimates give a total in the adult of about a hundred. There is no conclusive evidence that the annulations of those archaeopriapulids that possessed them were more than superficial.



TEXT-FIG. 6. Hypothetical dissection of *Ottoia prolifica*. Body cut open along the dorsal mid-line and the body wall pinned back to reveal internal organs. The gut has been pulled out of the body cavity by cutting through the mesentery and two of the cutaneo-visceral muscles. The intestine has been opened to show internal furrows. The proboscis and bursa are both fully everted. A, B, C, and D refer to the positions of the hypothetical transverse sections (text-fig. 7).



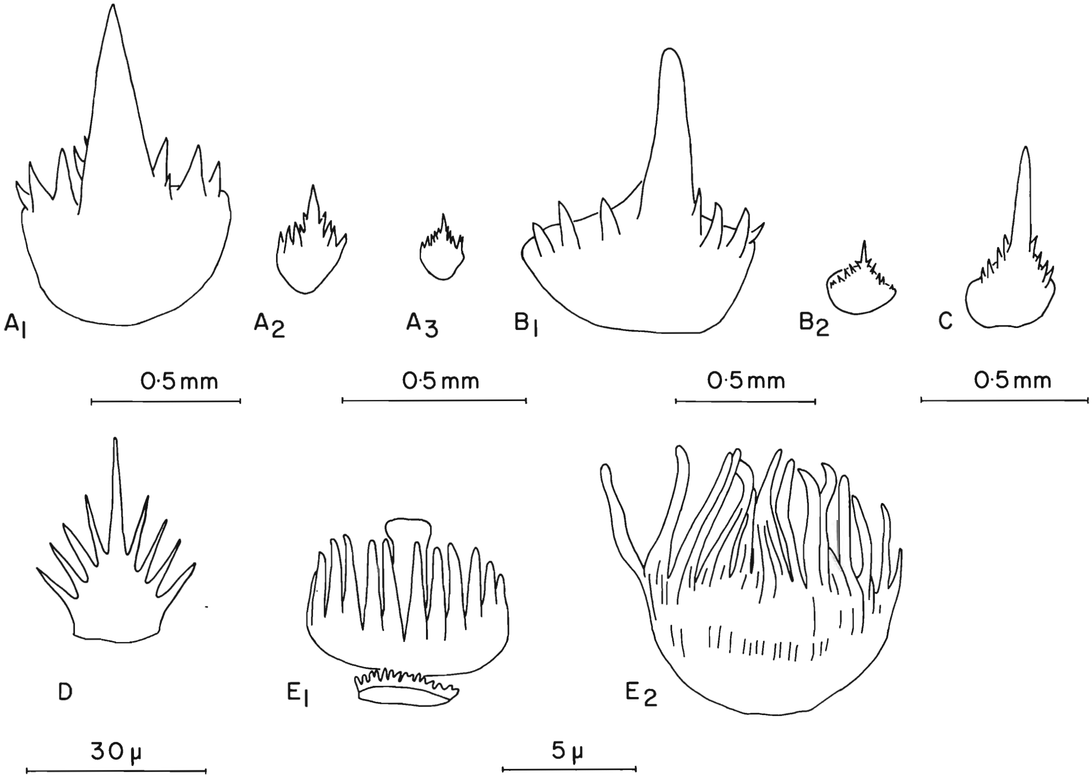
TEXT-FIG. 7. Hypothetical transverse sections (A–D) of *Ottoia prolifica*. The position of the sections with respect to the entire animal is given in text-fig. 6.



TEXT-FIG. 8. The four types (A–D) of proboscis spinule in *Ottoia prolifica*. Their distribution on the everted proboscis is shown in text-fig. 12. Note change in size within type B spinule from proximal (B_p) to distal (B_d) positions.

The cuticle carried specializations on the proboscis and posterior end of the trunk. Three variations of cuticular ornamentation existed on the proboscis. In the fully everted proboscis they were from the distal end: multispinose teeth or spinules, proboscis spines and proboscis hooks (text-fig. 6).

Banta and Rice (1976) adopted the term ‘spinule’ in preference to Walcott's (1911*c*) less descriptive term ‘papillae’. They stated that the most proximal spinules had four to seven ‘claw-like points’ while ‘At the edge [which the author assumes to mean the distal end] of the proboscis, the spinules appear to have a less complex structure’. Re-examination suggests that there were, in fact, four types of spinule (text-fig. 8) which are similar to the teeth of modern priapulids (text-fig. 9). In the completely everted proboscis the most proximal, type A, consisted of a central cone (0·3 mm long), with a fringe of about fifteen minute spines (about 0·05 mm long) (Pl. 3, figs. 5, 6; Pl. 4, fig. 6; Pl. 6, fig. 4; text-figs. 43, 46, 51). These spinules formed a single circle around the base of the spinule field, and in an obliquely compressed proboscis (Pl. 4, figs. 1, 2; text-fig. 44) the type A spinules form a fringe around the anterior edge of the proboscis. Hypothetical removal of this distortion would result in the spinules forming a circle. Immediately adjacent and distal to the former spinules was the type B variety. They were arranged in longitudinal rows, each row being staggered with respect to its neighbours so that about twenty oblique rows were formed (Pl. 5, figs. 1, 2, 4; text-fig. 47). Such a disposition is termed quincunxial and each spinule is surrounded at an equal distance by four others. These spinules presumably correspond to the ‘proximal spinules’ identified by Banta and Rice (1976). Each spinule consisted of a wide base that supported broad spines. The central spine was longer than the flanking spines not only on the distal part of the type B spinule field (Banta and Rice 1976), but also on the proximal spinules. Well-preserved spinules are seen to carry eight to nine spines although usually five or less spines are visible (Pl. 4, fig. 6; Pl. 6, fig. 4; Pl. 14, fig. 3; text-figs. 46, 51, 67). The variability in the number of spines is probably in part original, and the proximal type B spinules may have carried more spines than the distal ones. No evidence of the spines being ‘claw-like’, i.e. recurved (Banta and Rice 1976) has been noted by the author. These spinules decreased in size distally from about 0·3 mm long, 0·25 mm high to 0·1 mm long, 0·15 mm high.



TEXT-FIG. 9. Teeth of modern priapulids. A_1, A_2, and A_3, teeth of *Priapulus caudatus* from rows 4, 8, and 12 respectively (from Land 1970, figs. 2 and 3). B_1 and B_2, teeth of *Priapulopsis bicaudatus* from rows 2 and 11 (from Land 1970, fig. 24). C, tooth of *Halicryptus spinulosus* (from Land 1970, fig. 38). D, tooth of *Maccabeus tentaculatus* (from Salvini-Plawen 1974, fig. 8b). E_1 and E_2, pectinate tooth (with manubrium) and fimbrilla of *Tubiluchus corallicola* (from Kirsteuer and Rutzler 1973, figs. 6.22 and 6.25).

The type B spinules were succeeded by about five rows of smooth spines, the type C spinules (0·4 mm long). They were apparently arranged quincunxially (Pl. 5, figs. 1–3; text-figs. 47, 48). In most specimens these spinules are visible only at the edge of the proboscis where they are reflectively contrasted against the matrix (Pl. 5, fig. 5; Pl. 6, fig. 3; text-fig. 50). In common with the other spinules they pointed forwards in the fully everted proboscis. The reversal of pointing direction in the proboscis of USNM 198578 (Pl. 5, figs. 1, 2; text-fig. 47) is attributed here to the folding over of this decayed proboscis along the narrow strip carrying the type C spinules. The possibility that they faced in this anomalous direction in life cannot, however, be dismissed. This is because occasionally parts of a row or rows of pharyngeal teeth of modern priapulids, homologous to the spinules, are reversed (Théel 1911, pl. 1, fig. 6).

The fourth and most distal variety of spinule, type D (0·3 mm long, 0·1 mm high) had a similar morphology to the type B spinules (Pl. 5, figs. 1–3; Pl. 6, fig. 5; text-figs. 47, 48).

Posterior to the spinules, and separated from them by an unarmed area, was a circle of about forty to fifty spines (0·5 mm long) termed the proboscis spines (text-fig. 6).

Banta and Rice (1976) suggested that the proboscis spines formed two circles. Re-examination by the author suggests that an apparent double row of spines could result either by the superposition of the spines of the front and back of certain specimens, or by several proboscis spines preserved in silhouette on the edge of the proboscis (Pl. 12, fig. 9; text-fig. 64). The proboscis spines were, with the exception of USNM 196106 (Pl. 5, fig. 6), invariably directed anteriorly in the everted proboscis (Banta and Rice 1976) (Pl. 4, figs. 5, 6; Pl. 6, fig. 3; Pl. 14, fig. 3; text-figs. 46, 50, 67). In some specimens with an inverted proboscis the spines are visible through the body wall (Pl. 7, fig. 2; text-fig. 52).

The most proximal cuticular elements of the proboscis were the proboscis hooks (Walcott 1911*c*). Although they were arranged quincunxially (Pl. 4, fig. 5; text-fig. 46) their spacing is such that longitudinal rows are easily recognizable (Pl. 5, fig. 5; Pl. 11, fig. 1). Small spines were located between the longitudinal rows. Banta and Rice (1976) estimated that there were between twenty-four and twenty-eight rows of hooks. They arrived at this figure by virtue of the fact that between thirteen and fifteen rows, including the two rows in silhouette against the rock on either side of the proboscis, are visible in the specimens, i.e. $13+13+2 = 28$. As at least two rows of hooks can be superimposed at the edges of the proboscis owing to the high degree of curvature, this method of calculating the number of rows is inaccurate. Banta and Rice (1976) went on to state that 'The central 11 to 13 rows almost certainly represent the rows on only one side of the animal, because the rows in counterpart compressions do not match exactly'. This implies that the fossils split down the middle upon breaking open the rock. Whittington (1974) considered that this may have happened in some specimens of the arthropod *Yohoia tenuis* Walcott, 1912*a*, while Whittard (1953) noted such splitting in *Palaeoscolex piscatorum* (Annelida). In the fossil worms from the Burgess Shale, including *O. prolifica*, counterparts can be matched. The counterpart is frequently fainter than the part of the fossil, suggesting that it is a residuum. Nevertheless, it is possible to estimate roughly the number of rows regardless of whether all the rows are visible, as Banta and Rice (1976) suggested, or half of them are hidden beneath the fossilized film. One specimen (Pl. 7, fig. 3) has its proboscis bent almost perpendicular to the body, so revealing all the rows. In this small specimen (4 cm long) they total twenty-eight although in mature specimens the total may have been slightly greater.

The morphology of the proboscis hooks varies along the length of each row (Banta and Rice 1976) from anterior slender hooks (1 mm long) with small bases to posterior short recurved hooks (0·4 mm long) with prominent bases. The longitudinal variation in hook length partially compensates for the curvature of this section of the proboscis (Pl. 6, fig. 2; Pl. 14, fig. 3; text-fig. 67), so that all the hooks can hold the sediment during burrowing. Banta and Rice (1976) termed them 'spine-hooks' stating that the more anterior elements were spines. Although the proximal ends of the spines are often obscured, a number of specimens have 'spines' with distinct bases and so are considered here as hooks (Pl. 6, fig. 6; Pl. 7, fig. 5). There were about eight hooks in each row. The proximal hooks possessed, apparently on one side only, about six lateral spines (0·2 mm long) that extended along most of the length of the hook (Pl. 4, fig. 4; text-fig. 45). They are believed to be lateral because they are only visible in specimens that have suffered oblique crushing.

Between the longitudinal rows of proboscis hooks there were rows of smaller narrow spines that decreased in size posteriorly from 0·4 mm to 0·2 mm long (Pl. 4, fig. 5; Pl. 6, figs. 2, 6; text-fig. 46). They may represent reduced proboscis hooks.

USNM 172986 (Pl. 8, fig. 1) was described by Banta and Rice (1976, figs. 22, 23) as having more than twenty longitudinal lines of a 'finely beaded appearance' on the anterior trunk. They interpreted them as possibly representing cuticular ornamentation and incorporated them into their reconstruction of the animal (1976, fig. 30). This specimen was re-examined by the author in the USNM and the lines noted. However, upon gentle washing with distilled water, a standard practice with dirty USNM specimens many of which have remained unexamined for years, the dark lines disappeared permanently (Pl. 8, fig. 2). It is concluded that the lines were dust-markings for the following reasons: the most delicate fossilized features remain intact however vigorous the washing; the area of USNM 172986 that was washed was noticeably cleaner than the surrounding region; and such markings are not present on the counterpart of USNM 172986 which was located by the author, or on any other specimen however well preserved. The trunk lacked spines or other cuticular hairs.

The end of the trunk bore hooks (Walcott 1911*c*). Although they probably totalled eight, it is very unusual for a specimen to show more than six hooks. The posterior hooks were all the same size and shape. Their height was slightly greater than their length, and differences of 0·1–0·2 mm are usual. Their length varied from 0·7 to 1·3 mm (0·35–0·6 mm in juvenile specimens), whilst their height was 0·9–1·6 mm (0·45–0·9 mm in juveniles).

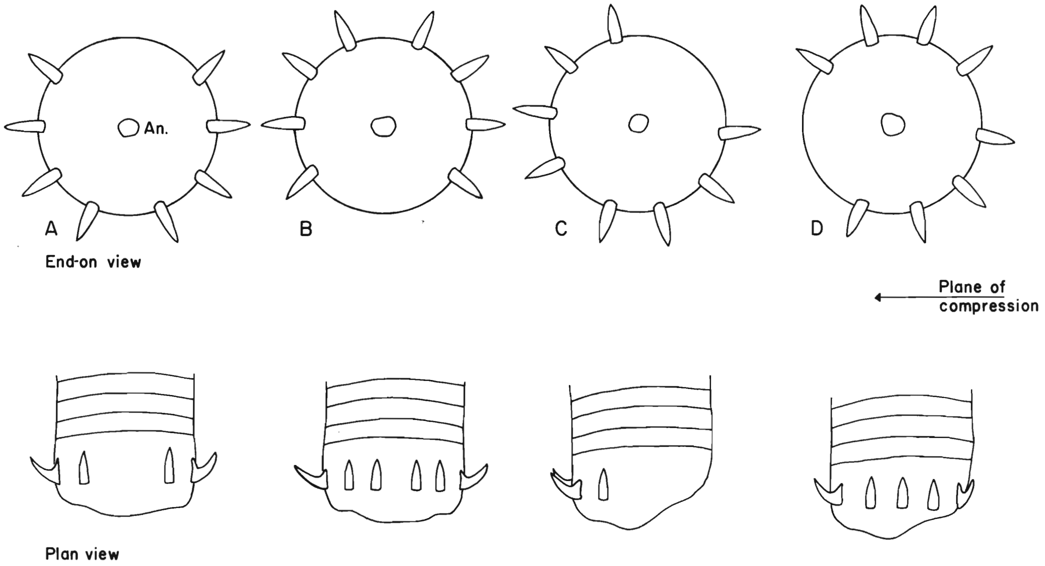
The base of the concave side of each hook was shown by Banta and Rice (1976, fig. 30) to be excavated. The position of the hook at differing angles to the bedding plane determines whether the cavity, preserved as a dark area in the otherwise reflective hook, is visible. In hooks preserved parallel to the bedding plane the cavity is invisible (Pl. 2, fig. 7; Pl. 14, fig. 2; text-fig. 67). The cavity is partially exposed when the hook is obliquely inclined to the bedding plane (Pl. 4, fig. 3; Pl. 8, figs. 4, 6; text-fig. 44) and it becomes wholly clear in hooks that lie at right angles to the bedding plane (Pl. 7, fig. 7; Pl. 8, fig. 9).

The posterior hooks are always located on the concave side of curved specimens (Banta and Rice 1976). These authors suggested that there 'were from two to eight hooks, usually arranged bilaterally, sometimes in a circlet'. Their reconstruction shows four hooks arranged bilaterally (1976, fig. 30). The author's studies indicate that eight hooks were disposed in an arc of about 250° (text-fig. 10). In specimens where the posterior hooks extend across the entire trunk they usually total six, the two median hooks being separated by a slightly greater amount than the more lateral ones (Pl. 1, fig. 5; Pl. 7, fig. 6; Pl. 8, fig. 10; text-fig. 37). In other specimens, however, four hooks are separated by a wide unarmed gap (Pl. 6, fig. 1; Pl. 8, fig. 11; text-fig. 49). Assuming that the hook on each edge of the trunk is common to both aspects the total was eight hooks, being bilaterally symmetrically arranged in two groups of four. The flattened surface of the trunk is taken to represent 180° of the original circumference. As only six of the eight hooks are exposed each hook can be 'allocated' 36° so that all the hooks must have occupied about 250° of the circumference. The majority of specimens have one or two posterior hooks visible with the remaining posterior hooks either hidden beneath the fossil film (Pl. 3, fig. 4; Pl. 8, fig. 5; text-fig. 42), or pressed down on to the exposed surface (Pl. 2, fig. 7; Pl. 9, figs. 1, 9). The degree of visibility of the hooks depends upon the exact orientation of the animal upon burial (text-fig. 10). Banta and Rice's idea that the hooks enclosed a gonopore is impossible to confirm as neither they nor the author has been able to identify unequivocal gonads. It should be noted that Banta and Rice's (1976, fig. 26) claim that USNM 172988 (Pl. 9, fig. 9) has two hooks preserved is apparently incorrect. The author has identified five: three in silhouette and two pressed on to the trunk. The slightly above average height (1·6 mm) is not considered here to be indicative of polymorphism, contrary to the tentative suggestion by Banta and Rice (1976).

The posterior hooks could be inverted into the posterior trunk, so reversing their facing direction (text-fig. 14). Inversion did not proceed much beyond the retraction of the posterior hooks. Occasionally the hooks are preserved on the point of eversion (Pl. 9, fig. 2), while the great majority of specimens have the hooks fully everted. Eversion of the posterior trunk beyond the hooks produced a narrow extension called the bursa.

Resser (*in* Walcott 1931) confused, in the opinion of the author, the posterior and anterior of the supposed new species *Miskoia placida* Walcott, 1931. The only specimen (USNM 83928, Pl. 9, figs. 3, 4) bears no significant resemblance to the type species of *Miskoia*, *M. preciosa* Walcott, 1911*c*, which, as noted below, is synonymous with *Louisella pedunculata* Walcott, 1911*b*. The six 'teeth' (Pl. 9, fig. 5) are comparable to the posterior hooks of *O. prolifica* in shape, size, and arrangement. The blunt shape of the anterior end is due to complete inversion of the proboscis. This specimen is unusual in its straightness and lack of internal detail. *M. placida* must, nevertheless, be considered as a junior synonym of *O. prolifica*.

Musculature. Body-wall muscles. Almost all modern worms with a well-defined body cavity such as priapulids, annelids, and sipunculids have the body-wall muscles arranged in an outer layer of circular and an inner layer of longitudinal muscles. *O. prolifica*



TEXT-FIG. 10. Explanation of variable appearance (plan view) of posterior hooks noted in specimens of *Ottoia prolifica*, according to their orientation with respect to the bedding plane (plane of compression).

possessed a spacious body cavity and in this and the other archaeopriapulids the body-wall muscles were probably arranged in the same manner as its modern relatives (text-fig. 7). The broad contracted and narrow elongate specimens presumably owe their shape to the action of these muscles. In a few specimens the body wall is preserved as a reflective film which rarely extends to the edge of the animal (Pl. 14, fig. 2; text-fig. 67), and is more often detached from the overlying cuticle due to decay (Pl. 3, figs. 1, 4; Pl. 4, fig. 1; text-figs. 40, 42, 44). The muscles of the body wall were evenly distributed and were not grouped into bundles. The narrow reflective strands running parallel to the long axis of the animal (Pl. 10, fig. 2; Pl. 12, fig. 7; text-fig. 57) could represent remnants of the longitudinal muscles. Walcott (1911*c*) also noted possible longitudinal muscles in the lectotype (Pl. 1, fig. 1; text-fig. 36), but the prominent longitudinal strand is considered here as an anterior retractor muscle. In the majority of specimens the body-wall muscles appear to have decayed completely, leaving the non-reflectively preserved cuticle which was more resistant to decay.

Walcott (1911*c*) suggested that the annulations reflected circular musculature. The annulations were most distinct at the anterior and posterior of the trunk. These regions carried the eversible proboscis and bursa which were protruded by body fluid pressure most probably derived from contraction of well-developed circular muscles. The occasional narrowness of the anterior and posterior is due to contraction of these muscles (Pl. 2, fig. 6; Pl. 13, fig. 4).

Retractor muscles. Withdrawal of the proboscis almost certainly entailed the use of anterior retractor muscles, as in modern priapulids and sipunculids. Some specimens have reflective strips that are close to, or touching, the gut at the anterior, but become separated posteriorly. They are interpreted as the remains of retractor muscles on account of their similarity to the positioning and appearance of the same muscles in modern worms. Four sets of anterior retractors have been identified, as well as two posterior sets that may have been used for retraction of the bursa and posteriormost trunk.

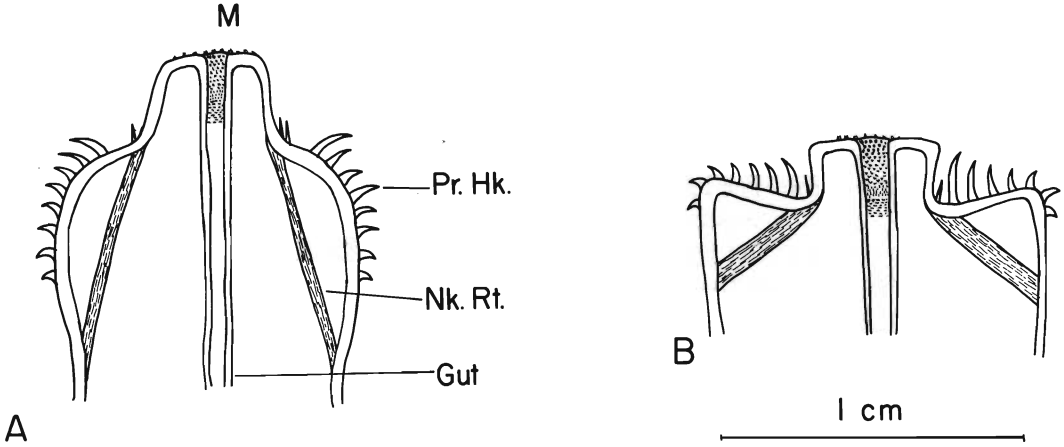
Three to four reflective strands, interpreted as muscles, are occasionally preserved within the distal part of the everted proboscis (Pl. 6, fig. 3; Pl. 9, fig. 7; text-figs. 50, 54). It is suggested that their distal insertion, which appears to have been bifurcate, was on to the gut, whilst proximally they were inserted on to the inside of the proboscis wall. They are termed the anterior proboscis retractors and would have been used in the first stage of proboscis inversion. The length of these muscles is so short in comparison with the proboscis that upon inversion the position of the insertion points would have been reversed. They would then have acted as protractors and helped to evert the terminal proboscis. Differential contraction of these muscles would have bent the distal end of the proboscis (Pl. 5, fig. 5).

More posteriorly there are reflective strands interpreted as short and long anterior retractors. The short retractors were a set of at least two thin muscles which were slightly anterior to a thicker and longer set (Pl. 3, fig. 1; text-fig. 40). Typically, however, only the latter set is recognizable, presumably because it was more resistant to decay (Pl. 6, fig. 2; Pl. 10, fig. 1; text-fig. 56). Usually two muscles are visible, sometimes three (Pl. 10, fig. 4; text-fig. 58), and it is likely that the total was four. In some species of sipunculid worms the total varies from specimen to specimen (Gibbs 1973), and it is possible that the long retractors showed a similar variation. The proximity of the retractor muscles at the anterior to the gut suggests that they were attached to it. Each muscle was inserted separately. The posterior insertion of these retractors on to the body wall was via three strands (Pl. 14, fig. 1; text-fig. 66). Similar splitting of the posterior end of retractor muscles is seen in some sipunculids (Shipley 1890) and priapulids. Occasionally thin strands parallel the main retractor muscles (Pl. 10, fig. 1; text-fig. 56). These strands may have been subsidiary retractors as in some sipunculids (Gibbs 1973). Alternatively decay of the muscles may have resulted in longitudinal splitting. The faint, closely spaced transverse striations preserved on the left-hand retractor muscle in USNM 188620 (Pl. 9, fig. 8; text-fig. 55) may be original.

The anterior trunk could also invert and in such cases the short anterior retractors could act as protractors. The distance between the insertion points of the long anterior retractors was, however, too great for them to act as protractors. Although protractor muscles would have aided eversion of the proboscis, the principal mechanism of eversion was almost certainly pressure derived from the fluid of the body cavity.

The presence of a fourth set of anterior muscles, the 'neck' retractors, can be deduced from the unusual configuration of the proboscis in USNM 198586 (Pl. 6, fig. 4; text-fig. 51). The proboscis hooks are preserved at the point of inversion, although the unarmed area enclosing the inverted spinules remains protruded. Normally this unarmed area inverts prior to the inversion of the proboscis hooks (text-fig. 12). This configuration is explicable by postulating the existence of a set of muscles with both insertion points on the inside of the anterior body wall (text-fig. 11). Such muscles are known in the parasitic acanthocephala where they are termed neck retractors (Hammond 1966, text-fig. 3; Pl. 1, fig. 4).

The bursa and trunk bearing the posterior hooks were probably withdrawn with the aid of retractor muscles. Posterior reflective strands are interpreted as long (Pl. 2, fig. 1; text-fig. 38) and possibly short (Pl. 4, fig. 3; text-fig. 44) posterior retractor muscles.



TEXT-FIG. 11. Hypothetical longitudinal sections of the proboscis of *Ottoia prolifica* to illustrate the effect of contraction of the postulated 'neck' retractor muscles. A, shape of proboscis as normally preserved. B, abnormal shape in USNM 198586 with 'neck' retractor muscles contracted, see Plate 6, fig. 4; text-fig. 51.

Gut muscles. A swelling of the anterior gut in USNM 188599 (Pl. 10, figs. 5, 6) has numerous longitudinal dark lines preserved upon it. These lines may represent a concentration of muscles of the gut wall. This part of the gut is termed the gizzard on the assumption that it could macerate soft-bodied prey.

Cutaneo-visceral muscles and suspensory fibres. Reflective bands that run radially from the intestine towards the concave edge of the animal (Pl. 11, fig. 7) probably represent cutaneo-visceral muscles which suspended the gut from the body wall. Cutaneo-visceral muscles have also been recorded from polychaetes (Clark and Clark 1960; Dales 1963), sipunculids (Wesenberg-Lund 1957; Hyman 1959), and echiuroids (Bock 1942; Wesenberg-Lund, 1955).

A few specimens have fine lines that traverse parts of the trunk. They are interpreted as sheets of fibrous or muscular mesentery. In GSC 45324 the fibres proceed from the gut towards the convex side of the animal, perhaps as a single sheet (Pl. 13, fig. 5). They appear to be unrelated to the cutaneo-visceral muscles because they were attached to the opposite side of the body wall. They are quite distinct from the annulations and probably helped to support the gut within the body cavity. In other specimens some of the fibres cross the gut, so that they presumably had another function (Pl. 12, fig. 6; text-fig. 63). They cannot be circular muscles of the body wall because they are preserved at a distinct angle to the annulations. Land (1970) noted that mesenteries support the urinogenital organs and retractor muscles in modern priapulids.

Body cavity. Banta and Rice (1976) stated that 'The body cavity was clearly spacious' and referred to USNM 172976, 172979, and 57619 (1976, figs. 1, 4, 5). The author has been unable to find any unequivocal evidence in USNM 172976 (Pl. 11, fig. 2) and 57619 (Pl. 1, fig. 1; text-fig. 36) for a body cavity. USNM 172979 (Pl. 11, fig. 1) has a trunk with a broad central area contrasted against flanking strips. This feature could be interpreted as a central cavity bordered by the body walls. Banta and Rice (1976) preferred to regard it as possible evidence for a membranous tube sheathing the gut. The interpretation adopted here is that the lateral areas represent cuticle which has maintained the shape of the body while the body wall, represented by the central area, has shrunk during decay.

There is, however, definite evidence for a body cavity. The gut is preserved in looped (Pl. 10, fig. 1; Pl. 12, fig. 6; text-figs. 56, 63) and kinked positions (Pl. 3, fig. 1; text-fig. 40), whilst in the other archaeopriapulids the gut is sometimes displaced across the trunk (Pl. 18, fig. 3; Pl. 25, fig. 6). This demonstrates that a space existed to accommodate these contortions. The proboscis and bursa in *O. prolifica* and the other archaeopriapulids were almost certainly everted by fluid pressure. The most likely reservoir of such fluid would have been the body cavity which was undivided by septa.

Proboscis, gut, and bursa. The most prominent internal feature to be preserved is a reflective, or otherwise contrasting, band running from the tip of the proboscis to the posterior extremity of the trunk. The band must represent the gut. It was noted by Walcott (1911*c*), although he considered that the mouth lay at the base of the narrower distal part of the proboscis. Meyer (1933), Lang (1953), and Banta and Rice (1976) stated that the gut ascended the proboscis so that its opening was terminal.

The proboscis and bursa carried the gut and were presumably themselves extensions of the body wall. It is, however, more convenient to group them with the gut proper because they were so intimately associated with it. The animal probably fed with only part of its proboscis everted. The anterior length, which was exposed in the fully everted proboscis, remained retracted as the pharynx and in direct continuation with the gut proper.

Walcott (1911*c*, figs. 1, 4, 5) and Banta and Rice (1976), figs. 1, 2, 9, 15, 16) illustrated some of the stages of proboscis protrusion, and all stages of eversion are shown in text-fig. 12. It is convenient to divide the eversion into six stages, although in *O. prolifica* and other archaeopriapulids it presumably could be a continuous process in life.

Stage 1: the entire proboscis was inverted and the anterior trunk could also be withdrawn (Pl. 12, fig. 1; text-fig. 60). The positioning of the base of the proboscis at the anteriormost annulation is, therefore, arbitrary. The sole specimen of the synonymous species *Miskoia placida* Walcott, 1931 (Pl. 9, figs. 3, 4) owes its unusual shape to the inversion of the anterior trunk. Initial eversion brought the proboscis hooks close to eversion (Pl. 7, figs. 1, 2; text-fig. 52). The part carrying the proboscis hooks could invert so making its distinction from the rest of the proboscis by Banta and Rice (1976) as a 'collar zone' unnecessary. Furthermore, the term 'collar' is inappropriate because, as is noted below, it incorrectly implies a comparison with the collar of the modern priapulids.

Stage 2: further eversion revealed the proboscis hooks (Pl. 8, fig. 3), followed by the proboscis spines (Pl. 12, fig. 9; text-fig. 64).

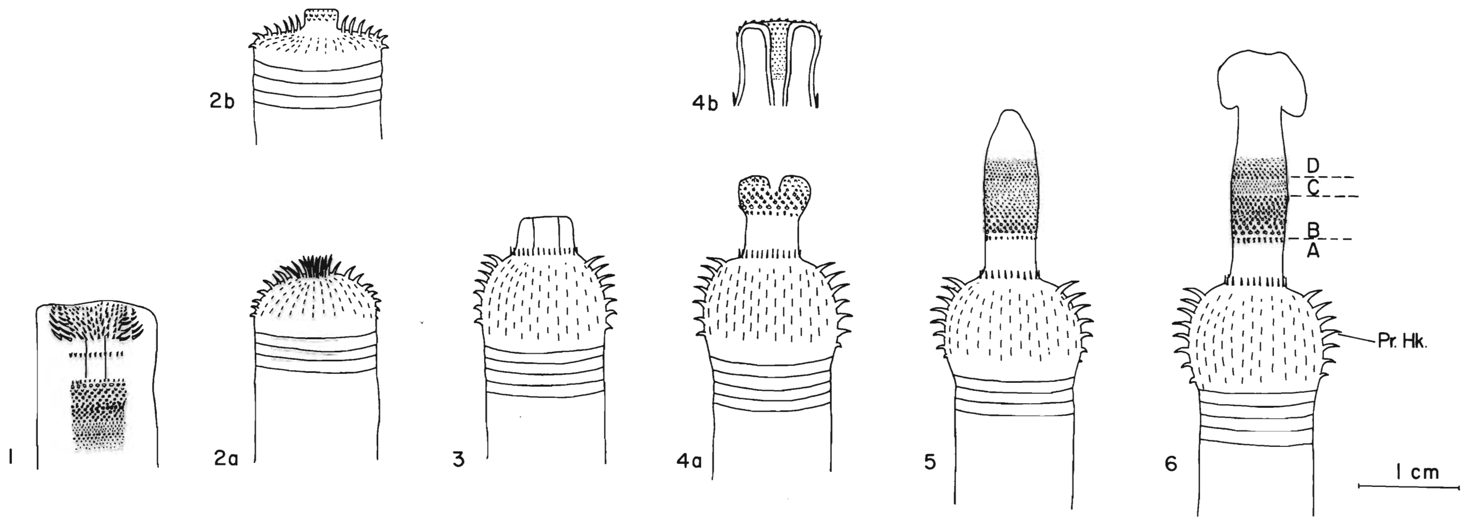
Stage 3: the unarmed area of the proboscis was the next section to evert (Pl. 6, fig. 2). Within this unarmed area the inverted spinules can often be discerned (Banta and Rice 1976).

Stage 4: continued eversion exposed the spinules. Walcott (1911*c*) considered that the end of the proboscis of USNM 57620 (Pl. 1, figs. 2, 3) had been broken off. In fact, the tip of the proboscis which bears spinules lies on a different level to the rest of the specimen due to differential compaction of the sediment. None of the archaeopriapulids have their probosces detached. Whittington (1975*a*) suggested that several specimens of *Opabinia regalis* Walcott had their probosces broken off before burial, perhaps during turbulent transport in the mudflows. The type A spinules were the first to appear (Pl. 3, fig. 5; text-fig. 43), then type B (Pl. 4, fig. 5; Pl. 5, fig. 4; Pl. 14, figs. 1, 2; text-figs. 46, 66, 67), and finally types C and D (Pl. 6, figs. 1, 5).

The position within stage 4 where the type A and larger more proximal type B spinules were everted, whereas the smaller distal type B and types C and D remained inverted, would have been ideal for feeding. The larger spinules probably grasped the prey and the smaller spinules that lined the first part of the lumen that led to the gut proper would have prevented the escape of the food by virtue of their posteriorly directed spines (text-fig. 12). The modern priapulids use their pharyngeal teeth for feeding in exactly this manner.

Stage 5: eversion beyond the spinules revealed a length of unarmed proboscis (Pl. 1, fig. 4; Pl. 2, fig. 3; Pl. 10, fig. 5; Pl. 11, fig. 2).

Stage 6: this, the final state of eversion, exposed the most distal unarmed length (Pl. 5, fig. 5; Pl. 9, fig. 7; text-fig. 54). The end section was apparently thin walled and usually swollen, presumably with body-cavity fluid, into an irregularly shaped balloon-like

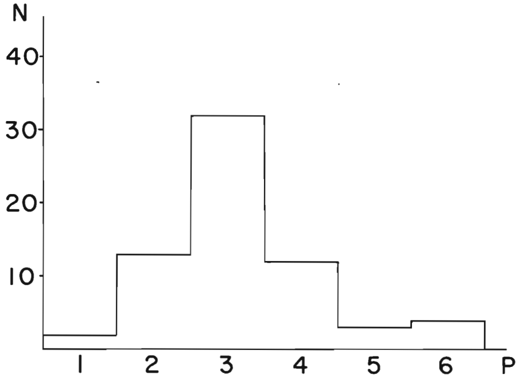


TEXT-FIG. 12. Eversion of proboscis of *Ottoia prolifica* divided into six stages. Fig. 2*b* shows the proboscis shape adopted when the 'neck' retractor muscles contract. Fig. 4*b* is a hypothetical longitudinal section of the anterior of fig. 4*a*. A, B, C, and D illustrate the distribution of each spinule type, see text-fig. 8.

structure (Pl. 7, fig. 4). Despite Banta and Rice (1976, figs. 2, 21) illustrating the swollen terminal end they stated that beyond the spinules 'there is little structure . . . because of . . . poor preservation'.

Inversion of the proboscis would have been the reverse of its eversion. It is, however, possible that on reaching stage 2 the proximal part of the proboscis bearing the hooks infolded while the unarmed length that contained the inverted spinules remained protruded (Pl. 6, fig. 4; text-fig. 51). Such a configuration arises during the retraction of the acanthocephalan proboscis (Hammond 1966).

The frequency of each stage of proboscis eversion is shown in text-fig. 13. The majority of specimens have their proboscces preserved in stage 3. This stage may, therefore, represent the proboscis position adopted by most of the dying animals. Banta and Rice (1976) raised the point that eversion of the proboscis may have been a pathological reaction to an unfavourable environment. Moreover, in the modern priapulids *Tubiluchus corallicola* (Kirsteuer and Land 1970, figs. 4, 9, p. 236), *Halicryptus spinulosus* (Zengera 1870, Pl. 10, fig. 4), and the possibly related kinorhynchs the proboscis can be artificially everted further than happens in life so as to reveal the pharynx which is equivalent to the narrower distal half of the proboscis of *Ottoia prolifica* (text-fig. 33). Rathke (1806) referred to a membranous tube which was sometimes extruded from the mouth of *Priapulus* when it was taken out of the water. Although Lang (1948*a*) declared that he had not seen this phenomenon in animals dying *under* water, the author believes that Rathke observed the eversion of the pharynx resulting from extreme muscular contraction. During the decay of *P. caudatus* the pharynx can completely evert but, unlike *O. prolifica*, the distal end never forms a swollen sac. The probable use of the swollen end of the proboscis in burrowing, together with the presence of the anterior proboscis retractor muscles, suggests that the extent of eversion observed in *O. prolifica* was normal. Furthermore, if pronounced eversion was a death reaction it is difficult to see why the fully everted probosces (stages 5 and 6) form only 10% of the total sample (text-fig. 13). Johnson and Richardson (1969, p. 134) noted that 'Modern marine animals possessing probosces . . . usually withdraw them at death'. This supports the suggestion made above that stage 3 represents the death position.

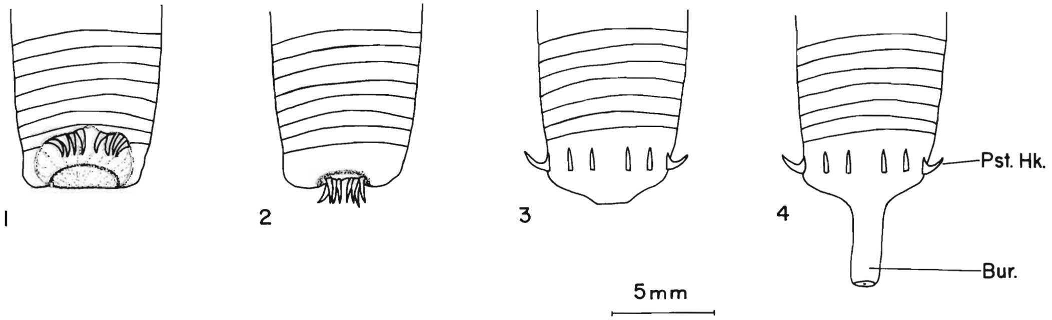


TEXT-FIG. 13. Histogram illustrating relative frequency of the six stages of proboscis eversion (P) in *Ottoia prolifica* against number of specimens (N). Sample consisted of sixty-six GSC specimens.

When the mouth formed in stage 4 the true gut was preceded by a tube formed by the inverted remainder of the proboscis. Immediately posterior to the mouth this tube was lined by the distal posteriorly directed spinules and so formed the pharynx. An unarmed length of tube, the oesophagus, separated the pharynx from the rest of the gut that never everted. The initial length of the gut was a simple tube, succeeded by a muscular sac or gizzard (Pl. 10, figs. 5, 6). Posterior to the gizzard the intestine had a constant width for the rest of its length (Pl. 10, fig. 1; text-fig. 56). The intestine was sometimes straight (Walcott 1911*c*; Banta and Rice 1976), but it was often bent or looped. The finely divided gut contents within the intestine of USNM 188593 (Pl. 10, fig. 7) have six shallow longitudinal troughs impressed into them. The troughs probably represent infolding of the internal wall of the gut, but it is unlikely that they were produced by longitudinal muscles. The gut-wall muscles in modern priapulids consist of an outer layer of longitudinal muscles and an inner layer of circular muscles. If muscles were impressed on to the gut contents transverse and not longitudinal impressions would be expected. The intestine of recent priapulids has internally transverse folding (Wesenberg-Lund 1929) as a device to increase the surface area available for digestion. It is assumed that the longitudinal folds in *O. prolifica* had this function. Longitudinal folds for the same purpose have also been reported from the fossilized intestines of bivalves (Cox 1960) and gastropods (Casey 1960). The transverse striations on the gut of the Burgess Shale arthropod *Leanchoilia superlata* Walcott were, however, interpreted by Raymond (1935) as circular muscles.

Banta and Rice (1976) noted that in some specimens (about 1% of the GSC collections) the trunk has a narrow posterior extension or bursa. The bursa was an eversible part of the posterior trunk (Pl. 3, fig. 4; Pl. 8, fig. 5; text-figs. 6, 14, 42). The wall of the bursa was probably thin, because like the distal end of the proboscis it is sometimes swollen (Pl. 8, figs. 6, 7). Eversion of the bursa is believed by the author to have been a normal activity of the animal and not a pathological reaction like the protrusion of the hind gut in modern *Priapulus* (Lang 1948*a*), or a product of post-mortem crushing (Banta and Rice 1976). The length of the bursa ranged from 0·1 cm to 1·3 cm, the majority being 0·4–0·5 cm long. GSC 45325 (Pl. 13, fig. 6) is exceptional in having a bursa 3·5 cm long.

The bursa carried the gut and gut contents are sometimes present (Pl. 9, fig. 1). Although these contents are very close to the anus as in recent *Priapulus* there is no



TEXT-FIG. 14. Eversion of posteriormost trunk and bursa of *Ottoia prolifica* divided into four stages.

tendency for them to be formed into faecal pellets (Lang 1948*a*, pl. 2, fig. 1). The anus was situated at the posterior extremity of the trunk (Pl. 8, fig. 10; Pl. 9, fig. 10; Pl. 11, fig. 3) or the bursa when it was everted (Pl. 9, fig. 1). The author has found no positive evidence for Banta and Rice's (1976) suggestion that the bursa had a genital function.

The majority of specimens lack gut contents. Banta and Rice (1976) commented upon 'conspicuous deposits' of pyrite, although the author has noted only occasional grains. They also mentioned 'dense material . . . resembling the matrix of the surrounding rock'. Such contents are presumably the unrecognizable black shreds and granules present in some specimens which cannot be said to resemble the matrix. They have a macerated appearance and are almost always confined to a short length of the posterior intestine, suggesting that they represent a digested residue (Pl. 3, fig. 1; Pl. 9, fig. 1; Pl. 12, fig. 6; Pl. 14, fig. 1; text-figs. 40, 63, 66). USNM 198587 (Pl. 11, fig. 8) is exceptional in having two-thirds of the length of the intestine occupied. Very few specimens (Pl. 11, fig. 9) have gut contents that appear to contain sediment. One specimen (USNM 193695) has within its gut a nodule (0·5 × 0·2 cm) composed of interlocking quartz crystals rimmed with minute pyrite cubes. Similarly USNM 199096 has three such nodules, the largest being 1·0 × 0·5 cm as well as a nodule of calcite. The quartz may have been ingested while the pyrite could represent a diagenetic reaction rim.

TABLE 1. Number of hyolithids in gut of *Ottoia prolifica*

Number of hyolithids in gut of specimen	1	2	3	4	5	6
Number of specimens of *Ottoia prolifica*	20	8	2	0	0	1

Thirty-one specimens have the hyolithid *Hyolithes carinatus* Matthew (see Walcott 1911*c*, pl. 19, fig. 7; Yochelson 1961) in the gut (Pl. 11, figs. 3, 6). Table 1 shows the number noted per specimen. The majority of specimens (65%) possess one hyolithid, but the greatest observed number is six. Of the eleven specimens with more than one hyolithid, only one specimen has one orientated opposite to the other two. In the other ten specimens all the hyolithids point in the same direction. Hyolithids with apices anteriorward in the gut predominate (forty-one specimens) against the reverse (seven specimens). At least half the hyolithids have opercula, which normally detached on death. This suggests that they were eaten alive for food rather than ingested by chance; whilst the preferred orientation indicates that *O. prolifica* chose the method of ingestion, i.e. the hyolithids were hunted. The modern priapulid *P. caudatus* also shows a preference for the direction in which it grasps and eats other members of its own species (Lang 1948*a*). Three specimens have a single brachiopod in the gut (Pl. 11, fig. 6). The shells of the hyolithids and brachiopods are entire, and it is concluded that the proboscis spinules were not powerful enough to break them.

In USNM 198922 (Pl. 11, fig. 5; text-fig. 59) a proboscis of *O. prolifica* is preserved within the gut. Although the anterior of USNM 198922 is missing, the specimen can be orientated by the posterior hooks. The proboscis is disposed in the opposite sense to what it would be if inverted (compare Pl. 7, figs. 1, 2; text-fig. 52). It is concluded that the proboscis belongs to another specimen. *O. prolifica*, like modern *Priapulus* (Lang 1948*a*), was cannibalistic.

Very rarely specimens are associated with clumped masses of hyolithids with occasional brachiopods and other unrecognizable remains which are informally termed 'hyolithid patches'. These patches apparently fall into the same class as the specimens of *Planolites* which Walcott (1911*c*, p. 142, pl. 22, fig. 1) claimed were 'associated with *Ottoia prolifica*'. The composition of the hyolithid patches does not closely resemble the gut contents of *O. prolifica* and their association is by chance.

Banta and Rice (1976) suggested that a 'thin-walled sac' enclosed the gut, and cited USNM 57619 (Pl. 1, fig. 1; text-fig. 36) and USNM 172979 (Pl. 11, fig. 1). It is desirable to determine whether it really existed because the presence of such a sac could have important phylogenetic implications. The evidence against this interpretation in these, or any other specimens, has been discussed above in the section on the body cavity.

Nervous system. Two specimens show two thin parallel, reflective lines running at right angles to the annulations (Pl. 12, figs. 2–5; text-figs. 61, 62). These lines are interpreted as the remains of a longitudinal nerve cord (0·3 mm wide) on the strength of their resemblance to the nerve cord of modern worms. The two lines probably represent the margins of a single cord rather than two separate cords. The distance between the two strands increases at each annulation and the swellings may, therefore, represent regular ganglia. No lateral nerves have been observed although it is possible that they are obscured by the reflectively preserved annulations. In modern priapulids, however, lateral nerves appear to be either wanting (Scharff 1885) or very fine (Apel 1885).

In common with practically all other invertebrates the nerve cord in *O. prolifica* was probably ventral. The two specimens are incomplete and there is little evidence as to whether the concave side of the animal, which bore the posterior hooks, was dorsal or ventral. In the part of USNM 188636 the nerve cord overlies the gut (Pl. 12, fig. 2; text-fig. 61). In the counterpart the nerve cord is preserved only as a residual trace, whereas the posterior hooks are clearly impressed on to the gut. This suggests that the nerve cord and posterior hooks were on opposite sides of the body, the latter being dorsal. Assuming that the curvature of this worm was invariable it is possible that the convex side was ventral. This is opposite to the opinion expressed, without supporting evidence, by Banta and Rice (1976).

As is noted below, the proboscis scalids of the Kinorhyncha may be homologous with the proboscis hooks of *O. prolifica.* In addition to their use in burrowing the kinorhynch scalids have a sensory function (Moritz and Storch 1972). It is conceivable that the proboscis hooks, especially the proximal ones with their lateral spines, were also sensory.

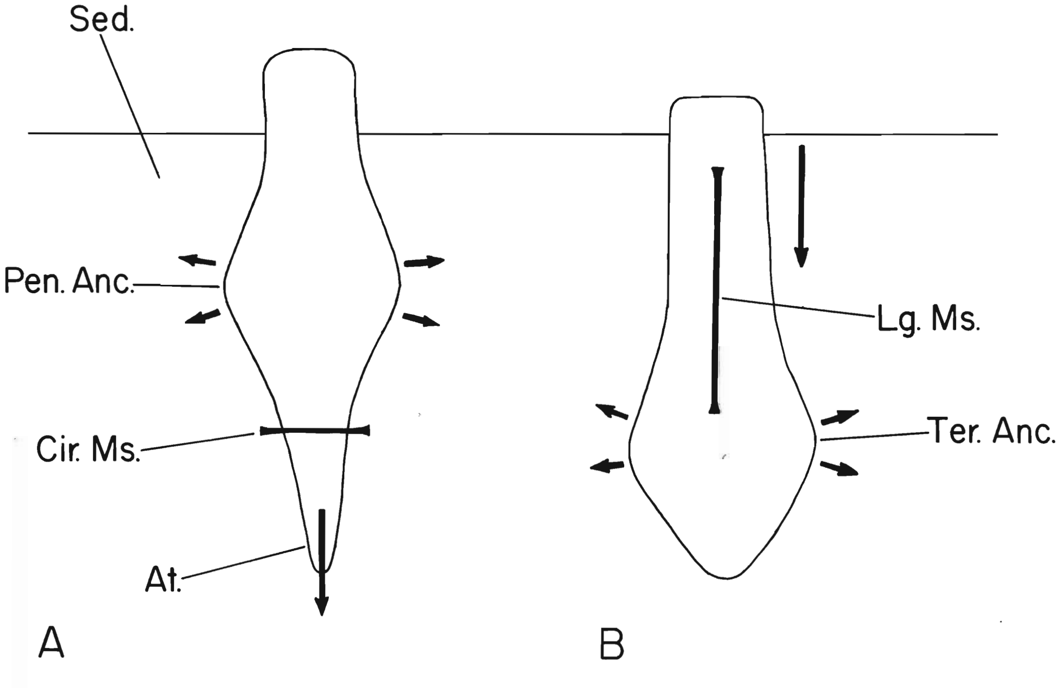
Urinary and reproductive systems. Lang (1953) suggested that a diffuse reflective area in the posterior of the lectotype (Pl. 1, fig. 1; text-fig. 36) might represent the remains of a urinogenital system, although Banta and Rice (1976) commented that such a feature is of rare occurrence. Moreover, this reflective area has no coherent form that permits definite comparison with any organ. Some specimens possess reflective, or otherwise contrasting areas (Pl. 2, fig. 4; Pl. 3, fig. 1; Pl. 10, figs. 2, 3; Pl. 13, fig. 1; text-figs. 40, 57, 58, 65) which may represent parts of a urino-genital system. As *O. prolifica* is closely related to the recent priapulids it is to be expected that their urinogenital organs were similar.

USNM 198588 (Pl. 13, fig. 7) possesses a regular row of individual reflective blocks that could be interpreted as a segmentally repeated organ. They are regarded, however, as a retractor muscle that has been subdivided into blocks by the annulations.

Mode of life. The use of the proboscis in feeding and the nature of the food have been discussed previously. In the modern carnivorous and cannibalistic priapulids (Lang 1948*a*) the gut is usually empty or has only a little sediment and plant material (Fischer 1925; Land 1970). Both the mouth armature and the general absence of gut contents indicate that *O. prolifica* was also carnivorous. The macerated remains in the posterior intestine represent the digested residue of various animals.

Whatever the orientation of the animal, as determined by reference to the posterior hooks (text-fig. 10), the proboscis has the same aspect showing that it was externally radially symmetrical. This suggests that the worm burrowed, i.e. moved through an environment uniform on all sides (Meyer 1933). Banta and Rice's (1976) statement that the worms did not burrow in the Phyllopod bed itself is borne out by the total absence of bioturbation of the finely laminated sediment (Piper 1972).

Burrowing animals such as sipunculids (Zuckerkandl 1950; Trueman and Foster-Smith 1976), echiuroids (Fisher and MacGinitie 1928*b*), annelids (Trueman 1966*a*, 1966*b*), scaphopods (Trueman 1968*a*), and bivalves (Trueman 1967, 1968*b*) all have the same fundamental mode of burrowing (Trueman 1968*c*, 1975) (text-fig. 15). It is likely



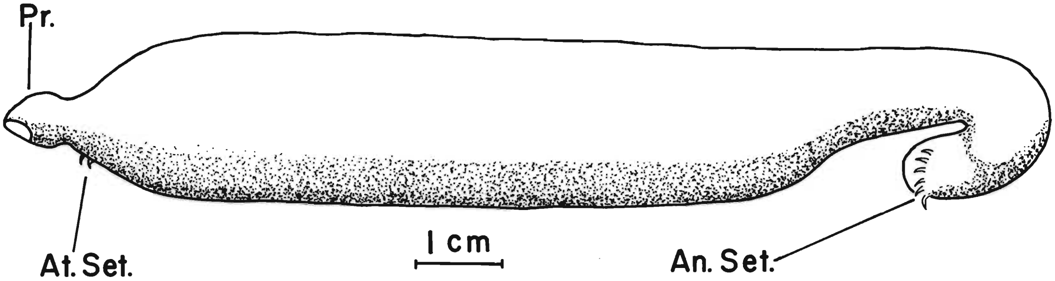
TEXT-FIG. 15. Explanation of the two main stages in the burrowing of a soft-bodied animal. A, penetration anchor forms as the anterior probes forward by contraction of the circular muscles. B, the anterior swells forming the terminal anchor so that contraction of the longitudinal muscles pulls the animal forward. The short arrows refer to the action of the anchors, and the long arrows to the part of the body in movement. From Trueman 1975, fig. 3.1.

that *O. prolifica* burrowed in the same manner. The following burrowing cycle, more complex than that proposed by Banta and Rice (1976), is postulated:

1. Body contracted within the sediment. Proboscis at stages 1 to 2, and posterior hooks also inverted.
2. Circular body-wall muscles contracted and elongated the body, especially the anterior trunk (Pl. 13, fig. 4). This contraction increased the pressure of the body-cavity fluid so that the proboscis started to evert (stages 3 to 4). The everted proboscis hooks, and probably the posterior hooks, gripped the sediment and prevented the animal from being pushed backwards as the proboscis everted. According to Trueman's (1968*c*) terminology, they acted as the 'penetration anchor'. The habitual curvature of *O. prolifica* would have also helped anchor the animal by increasing the frictional resistance, as in *Priapulus* (Hammond 1970*b*).
3. The proboscis completely everted (stages 4 to 5).
4. The end of the proboscis dilated (stage 6) and so acted as the 'terminal anchor' in Trueman's terminology (1968*c*). A similar feature is seen in *Sipunculus* where the end of the proboscis dilates as a holdfast in the burrowing cycle (Andrews 1890; Peebles and Fox 1933; Zuckerkandl 1950; Trueman and Foster-Smith 1976).
5. The proboscis hooks relaxed their hold on the sediment and the posterior hooks reinverted. The longitudinal body-wall muscles contracted and dragged the animal forwards, whilst the 'terminal anchor' ensured that the animal did not slip backwards.
6. The anterior retractor muscles reinverted the proboscis.

This burrowing cycle differs somewhat from that of *Priapulus* (Friedrich and Langeloh 1936; Hammond 1970*b*), perhaps because of the greater eversibility of the proboscis.

There is circumstantial evidence that *O. prolifica* sometimes lived in a burrow, but it was so well adapted to burrowing that it is unlikely that any burrow was permanent. Although the curvature of the body may have been an aid in burrowing, it may also reflect its habitual posture in a burrow. The extensible bursa carried the most posterior intestine and it may have protruded out of the burrow for defecation. The bursa could also have extended into the overlying water as a respiratory organ. The posterior hooks have a similar arrangement to the incomplete circle of setae in the echiuroid *Urechis*. In *U. caupo* the retractable setae are separated by a mid-ventral unarmed gap (Fisher and MacGinitie 1928*a*) which corresponds to the unarmed arc of 110° separating the posterior hooks in *O. prolifica*. *U. caupo* can bend the posterior end backwards over the trunk so that the setae can be brought against the burrow walls for excavation. The absence of mid-ventral setae is to avoid damage to the dorsal surface when the animal is excavating (Fisher and MacGinitie 1928*b*) (text-fig. 16). *O. prolifica*, however, never has its posterior trunk contorted in this way. Reports on the mode of life of the most closely related of the recent priapulids to *O. prolifica*, the Priapulidae, are conflicting. Wesenberg-Lund (1929) claimed that *Priapulus* sometimes inhabited a burrow which can be U-shaped, whilst Lang (1948*a*) stated the reverse with the animal at rest living vertically with its mouth on the level of the sediment surface. Lang (1948*a*) and R. Hammond (1970*b*; pers. comm.) did not, however, observe any burrows or tubes and considered them to be free-living.



TEXT-FIG. 16. The echiuroid worm *Urechis caupo* in the position used for excavating its burrow (from Fisher and MacGinitie 1928*b*, fig. 2).

Banta and Rice (1976) observed that its shape suggests that *O. prolifica* did not swim. They mentioned the pelagic poeobiids (aberrant polychaetes) as having a body shape not dissimilar to that of *O. prolifica*. However, unlike *O. prolifica* the poeobiids have a gelatinous body that renders them well suited for a pelagic way of life (Robbins 1965). Some sipunculids (Zuckerkandl 1950; Fisher 1954) and echiuroids (Gislén 1940) which have body shapes and compositions like *O. prolifica* can swim. It is unlikely, however, that such large numbers of *O. prolifica* could have been trapped by the benthonic mudflows unless they were also benthic. There is some evidence to suggest that the muds in which the worms lived were anaerobic and the modern priapulids are often found in black muds smelling of H_2S (Wesenberg-Lund 1929; Fänge and Åkesson 1952; Land 1970).

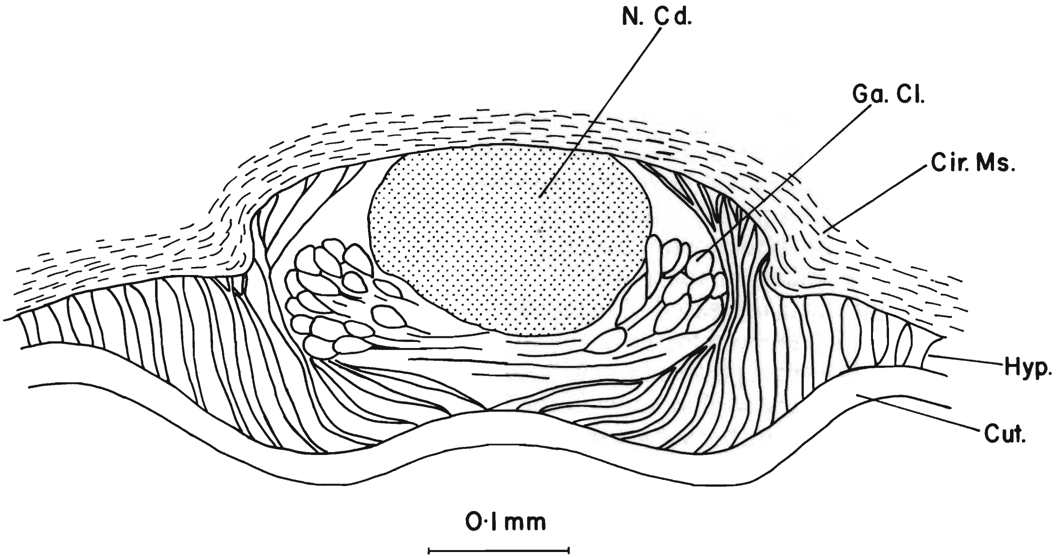
No specific respiratory organ has been identified, although the bursa may have had this function. Some modern priapulids have one or two caudal appendages, but they are not directly comparable to the bursa because they do not carry the gut. The appendages of *Priapulus* and *Priapulopsis* (text-fig. 1A, B) are not essential for respiration (Lang 1948*a*), but are probably useful (Fänge and Mattisson 1961) especially at low oxygen tensions (Nyholm and Bornö 1969). The observations by Fischer (1925) and Wesenberg-Lund (1929) that the appendage projected above the sediment, as the bursa of *O. prolifica* may have done, were denied by Lang (1948*a*). Gases probably diffused through the body wall into the body cavity where they were circulated to all parts of the body.

Tightly coiled and very contracted specimens may be in defensive attitudes. The defence positions of *Sipunculus nudus* are similar (Zuckerkandl 1950).

Preservation and decay. Evidence for the decay of Burgess Shale specimens is more widespread than was noted by Whittington (1971*a*). In *O. prolifica* an entire spectrum of decay is recognizable. Specimens that were unaffected by decay, presumably because fossilization was too rapid, have the body wall preserved as a reflective film that obscures the details of internal anatomy (Pl. 14, fig. 2; text-fig. 67). In slightly more decayed specimens the reflectively preserved body wall has pulled away from the overlying cuticle and the internal organs become clearer (Pl. 3, fig. 1; Pl. 4, fig. 1; text-figs. 40, 44). Further decay resulted in preservation of only remnants of the body wall (Pl. 10, fig. 2; text-fig. 57). The above specimens are uncommon and decay usually advanced so that the gut, retractor muscles, and other internal organs became visible

(Pl. 6, fig. 2; Pl. 10, fig. 1; text-fig. 56). The most resistant part of the animal was the cuticle. Certain specimens (Pl. 6, fig. 1; Pl. 7, fig. 1; Pl. 12, fig. 8; text-figs. 49, 52, 64) sometimes have the gut but lack most other internal organs and the collapsed body evidently consisted almost entirely of cuticle. Typically such specimens are bent at unusually sharp angles or are even twisted over. They are similar in appearance to the moulted cuticle of modern *Priapulus* (Lang 1948*a*, pl. 2, fig. 4). The traces of the internal organs show, however, that the fossils are decayed remnants and not moults. The specimen (USNM 57486) interpreted by Walcott (1911*a*, pl. 3, fig. 1) as part of the branchial appendage of *Sidneyia inexpectans* was shown above to belong to *O. prolifica*. This specimen is very decayed and consists almost entirely of annulated cuticle that has been folded over (Pl. 1, fig. 6). Similar cases of folding over were noted by Johnson and Richardson (1969, fig. 65) in the enigmatic animal *Tullimonstrum* from the Pennsylvanian of Illinois. In very decayed specimens the shape of the body is disorganized (Pl. 13, fig. 2). A few specimens consist of the anterior proboscis only (Pl. 5, figs. 1–3; text-figs. 47, 48). Lang (1948*a*, pl. 2, fig. 4) illustrated the moulted cuticle of a specimen of *Priapulus* with the cuticle of the pharynx (= anterior proboscis) everted and almost completely detached from the rest of the specimen. The fossil specimens may represent such examples after detachment of the anterior proboscis. Alternatively, the thick armoured cuticle of the proboscis may have made it more resistant to decay.

Curiously both the specimens with nerve cords preserved (Pl. 12, figs. 2–5; text-figs. 61, 62) are incomplete and composed mostly of fossilized cuticle, although the gut is preserved in USNM 188636. It is surprising, therefore, that the delicate nerve cord has been preserved. One explanation is that, as in modern priapulids (Scharff 1885), the nerve cord lay within the hypodermis and very close to the cuticle (text-fig. 17). In these specimens nearly all the body wall, along with most or all the internal organs, rotted



TEXT-FIG. 17. Transverse section of nerve cord and surrounding tissue in the trunk of *Priapulus caudatus* (from Scharff 1885, pl. 14, fig. 6). Note the proximity of the nerve cord to the surface of the animal.

away so laying bare the nerve cord which had until then been protected by the body wall. The disorganized appearance of these specimens with a discontinuous length of nerve cord suggests that during decay the area of body wall protecting the nerve cord now preserved did not decay as rapidly as the remainder. The time of fossilization was therefore critical in order to stop decay destroying the nerve cord as well.

In USNM 198581 (Pl. 9, fig. 6; text-fig. 53) only the posterior end of the trunk is preserved and anteriorly the specimen fades into the matrix. A possible reason for this differential preservation is that the anterior of the animal lay above the sediment where decay was probably faster.

Varying degrees of decay, therefore, reveal different features of the animal, as Johnson and Richardson (1969) noted with the enigmatic *Tullimonstrum*. This fact also indicates why so many specimens have to be studied in order to gain an understanding of the anatomy.

Studies on the decay of modern priapulids under varying conditions have confirmed the above observations. Within a few days of death the body wall detaches itself from the overlying cuticle as it folds and shrinks (R. Hammond, S. Norris, pers. comm.). Further decay results in the internal organs, especially the gut and some of the retractor muscles, becoming very clear. The cuticle maintains the general shape of the body. As was noted above, the pharynx sometimes completely everts so that the proboscis is equivalent to stage 6 in the sequence of proboscis eversion. The last stage in decay of recent priapulids results in the cuticle rupturing and its disappearance.

Very few specimens have a dark non-reflective stain associated with them (Pl. 11, fig. 2). This stain is almost invariably found with *M. splendens* (Whittington 1971*a*, *b*) and less commonly with other Burgess Shale species. Conway Morris (1976*b*, 1977) concluded that the stain was a product of decay and Whittington's (1971*a*, *b*) interpretation of it as body contents squeezed out by sediment compaction was considered less likely.

Although the majority of specimens have suffered slight decay, it was rarely severe and the preservation can be regarded as exquisite. Some factor must have removed the animals from the decay system: one possibility is that the soft tissues were impregnated by a mineral solution that influxed from beyond the Phyllopod bed. Although the process of fossilization must have begun shortly after deposition, it is unlikely that it finished within a brief period and prolonged diagenesis was probably responsible for the calcium aluminosilicate film that is now present. Subsequent to at least partial fossilization, the sediment must have started to compact as the thickness of the superincumbent strata increased. Zangerl (1971) has commented at some length on the fact that very well-preserved fossils have the appearance of having been 'squashed flat'. He was able to show that physical squashing does not take place and other factors must be invoked. It is suggested that some of the flattening of the Burgess Shale fossils was caused by decay reducing the substance of the animal and partially collapsing the body.

Many specimens are crossed by grooves that are, of course, ridges on the counterpart (Pl. 1, figs. 1, 2; Pl. 3, fig. 2; Pl. 14, fig. 2; text-figs. 36, 41, 67). These presumably formed during compaction. The fossilized film can sometimes be traced across the groove, but more often rock intervenes. In cases where the film does not fail across the groove it is assumed that the fossils were fairly soft and pliable at the time of production of the grooves and had not attained final rigidity by this stage. In one specimen of *Louisella* *pedunculata* (Pl. 24, figs. 1, 3; text-fig. 86) the fossil film has evidently flowed slightly with the surrounding rock. Flowage presumably occurred during compaction. Other specimens were evidently more brittle and rigid, because the fossil film cannot be traced across the groove and occasionally the adjacent film is cracked (Pl. 11, fig. 4).

USNM 188619 (Pl. 13, fig. 3) is surrounded by a zone of rock planes that lie at an angle to the fossil film. Such structures exist in their incipient stage around other specimens. This feature is rare and it probably represents a response to the rock failing around a flat area of discontinuity, i.e. the fossil film. Analagous structures (the B planes) form on the edge of joint planes (Price 1968, fig. 47).

Family SELKIRKIIDAE fam. nov.

Genus SELKIRKIA Walcott, 1911

Type and only known species. Selkirkia columbia sp. nov.

Diagnosis. Tubicolous priapulid. Body divisible into anterior armed proboscis and trunk. Proboscis partially invertable, armed from anterior to posterior with spinules and spines of varying length, terminal area anterior to spinules smooth and conical. Trunk located within tube, armed with anterior rows of papillae. Gut straight with terminal openings, externally unregionated, mouth surrounded by proboscis spinules. Undivided body cavity. Finely annulated tube, open at both ends, with oval cross-section.

Selkirkia columbia sp. nov.

Plate 15, figs. 2–10; Plates 16–18, 19, figs. 1–3; text-figs. 68–78

1911	*Selkirkia major* Walcott, pp. 120–122, pl. 19, fig. 6.
1912	*Selkirkia major* Walcott, p. 153.
1912	*Selkirkia major* Walcott, p. 190.
1913	*Selkerkia* [sic] *major* Walcott, p. 337.
1928	*Selkerkia* [sic] *major* Walcott, p. 361.
1931	*Selkirkia major* Walcott, pp. 7, 40, pl. 10, figs. 1, 2.
?1938	*Selkirkia pennsylvanica* Resser and Howell, pp. 205, 215, pl. 4, fig. 10 (non Pl. 5, fig. 8).
1944	*Selkirkia major* Størmer, p. 140.
1961	*Selkirkia major* Yochelson, p. 152.
1962	*Selkirkia major* Howell, p. W167, fig. 106 (5) (cop. Walcott 1911, pl. 19, fig. 6).
1969	*Selkirkia major* Robison, pp. 1170, 1173.

Derivation of name. The trivial name refers to the geographical location of this fossil.

Diagnosis. As for the genus.

Holotype. USNM 57624 Walcott 1911*c*, pl. 19, fig. 6.

Paratypes. USNM 83941a, b.

Other material. USNM 66521, 193892, 198617–198635, 198641–198642, 202769. There are many additional specimens, chiefly preserved without soft parts, in the USNM. GSC 8317 (two specimens), 8317b, 45321, 45327–45330. The GSC collections of 1966 and 1967 total 159 specimens. Oslo Univ. Pal. Mus. A5139. Peabody, Yale 9153. Rom 1228, 25873, and un-numbered specimens.

History of research. This species was first illustrated as *Orthotheca major* from a single specimen (USNM 96542) by Walcott (1908, pl. 1, fig. 11) (Pl. 15, fig. 1) from the *Ogygopsis* Shale (the 'fossil beds' on Mount Stephen; USNM locality number (14s)) which stratigraphically is a little below the Burgess Shale (Fritz 1971). The discovery of new specimens from the Burgess Shale which showed soft parts led Walcott (1911*c*, pl. 19, fig. 6) (Pl. 15, fig. 10; text-fig. 70) to remove the species *major* from *Orthotheca* Novak, 1886 (which is now confined to a genus of Hyolitha) to form the type species of the new genus *Selkirkia* Walcott, 1911*c*. In the same paper Walcott attributed two other new species to *Selkirkia*: *S. gracilis* and *S. fragilis* (Walcott 1911*c*, pl. 19, figs. 8, 9). These two species are not priapulids, and their generic position is briefly discussed at the end of this paper. The holotype of *S. major* (USNM 96542) is, however, comparable to *S. gracilis* Walcott, 1911. The rate of tapering of the tube of USNM 96542 is much less than the most extreme narrow aspect tube noted in *S. major* (text-fig. 21), but is the same as other specimens of *S. gracilis*. It differs from nearly all other specimens of *S. gracilis*, however, in having the posterior tip missing, but it is impossible to determine whether this is due to fossilization processes. The degree of curvature in the tubes of *S. gracilis* varies and the straightness of USNM 96542 is not unique.

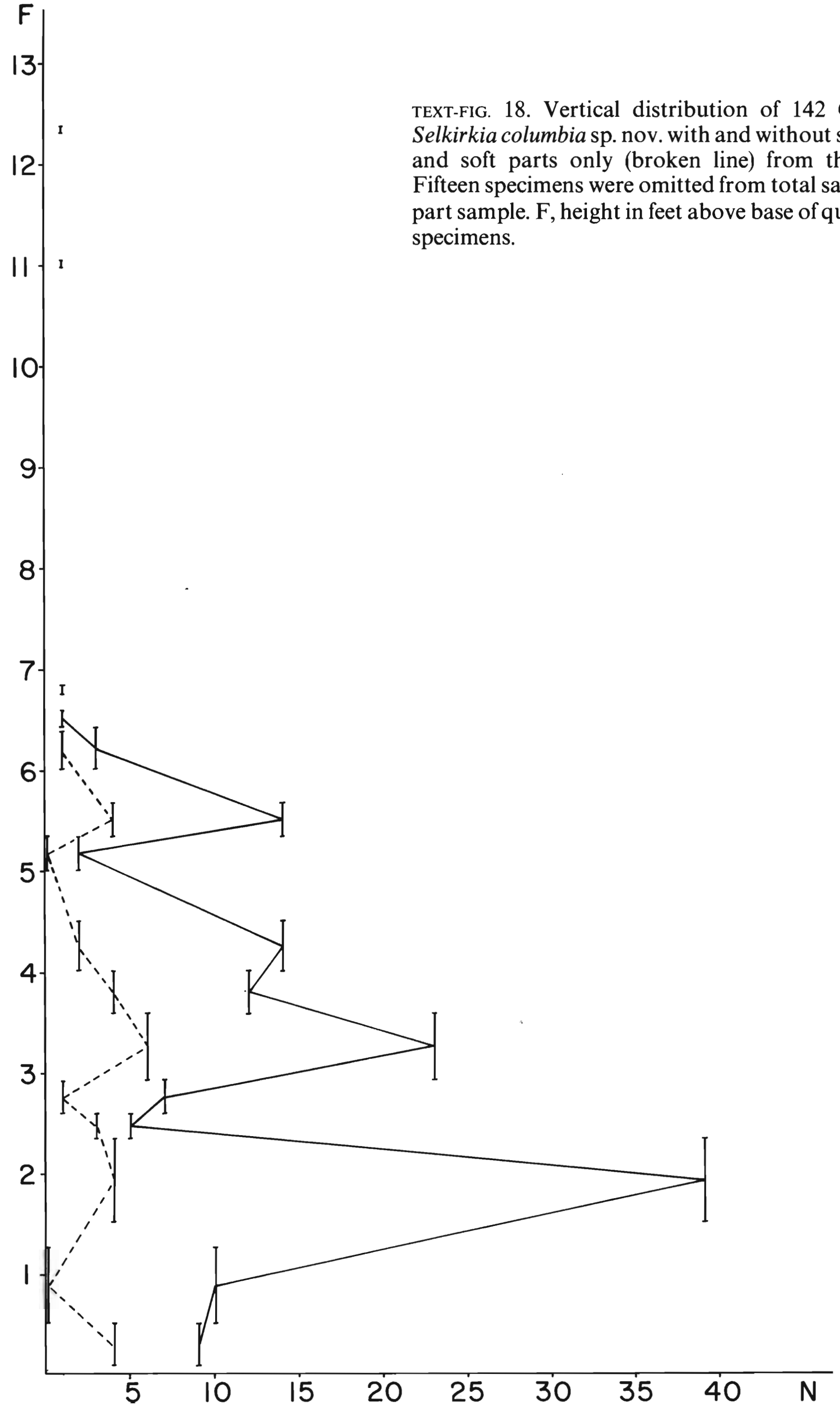
S. gracilis Walcott, 1911*c* is, therefore, taken to be a junior synonym of '*Selkirkia*' *major* Walcott, 1908. Walcott erected *Selkirkia* 1911*c* with *S. major* as the type species, and cited USNM 96542 in the synonymy list of this species. His diagnosis for *Selkirkia* is, however, clearly based on the soft parts of the specimens from the Burgess Shale which he attributed to *S. major* in his 1911*c* description, and the genus has subsequently been so understood. In this sense *Selkirkia* is a priapulid and is far more widely known in the literature than *S. gracilis* and *S. fragilis*. In the interest of stability it would surely be best to maintain *Selkirkia* based on the specimens illustrated and mentioned by Walcott in 1911 and give them a new specific name. Accordingly the author has made a request to the International Commission on Zoological Nomenclature to designate *S. columbia* as the type species of that genus by exercising its plenary powers.

Later Walcott (1931, pl. 10, figs. 1, 2) illustrated two more specimens (Pl. 15, figs. 2–4, 7–9; text-figs. 68, 69). Other than his very brief description in 1911 this worm has received only passing attention, e.g. Howell (1962), although Størmer (1944) briefly dwelt on possible relationships with other worms.

Discussion on other species attributed to *Selkirkia* will be found below.

Stratigraphic horizon and vertical distribution. All, save two, of the GSC specimens are from the Burgess quarry which exposes the Phyllopod bed. The vast majority of the USNM specimens are labelled 35k and so are also from this locality (Walcott 1912*a*). The remaining two GSC specimens are from Raymond's quarry.

Walcott (1912*a*) noted that within the Phyllopod bed *S. columbia* occurred in the highly fossiliferous layer no. 10 (7·6–48·3 cm (0 ft 3 in–1 ft 7 in) above the base of the quarry) but he gave no further details. The vertical distribution of 142 GSC specimens, both with and without soft parts, within the Burgess quarry is given in text-fig. 18. The total range is 373·2 cm (12 ft 3 in), specimens being recovered from between 2·5 and 375·7 cm (0 ft 1 in and 12 ft 4 in). There are two pronounced maxima at 45·7–71·1 cm (1 ft 6 in–2 ft 4 in) and 88·9–109·2 cm (2 ft 11 in–3 ft 7 in). The former coincides in part with the lesser of the two maxima of *O. prolifica* (text-fig. 3). The distribution of specimens with their soft parts preserved is also shown in text-fig. 18. Their distribution follows rather closely that of the total sample and no stratum seems to be disproportionately enriched with specimens possessing soft parts. The two GSC specimens from



TEXT-FIG. 18. Vertical distribution of 142 GSC specimens of *Selkirkia columbia* sp. nov. with and without soft parts (solid line) and soft parts only (broken line) from the Burgess quarry. Fifteen specimens were omitted from total sample, two from soft part sample. F, height in feet above base of quarry; N, number of specimens.

Raymond's quarry are from 21·3–21·6 cm (70 ft–71 ft) and 21·9 m (72 ft) above the base of the Burgess quarry. The total range of *S. columbia* within the Burgess Shale is thus almost 21·9 m (72 ft).

Specimens have also been collected from the *Ogygopsis* Shale (USNM locality 14s) which is a highly fossiliferous shale lenticle within the Stephen Formation (Walcott 1908) and from the middle Cambrian Titkana Limestone (USNM locality 61v, Walcott 1913, 1928). These limestones are probably equivalent to the Eldon Formation although the fauna was compared to that of the Stephen Formation (Walcott 1913). The limestones are 322 km (200 miles) north of the Burgess Shale.

Introduction to morphology. The great majority of the specimens (126 out of a total of 159 GSC specimens) are empty tubes and lack the soft parts. The reasons for this discrepancy are discussed below.

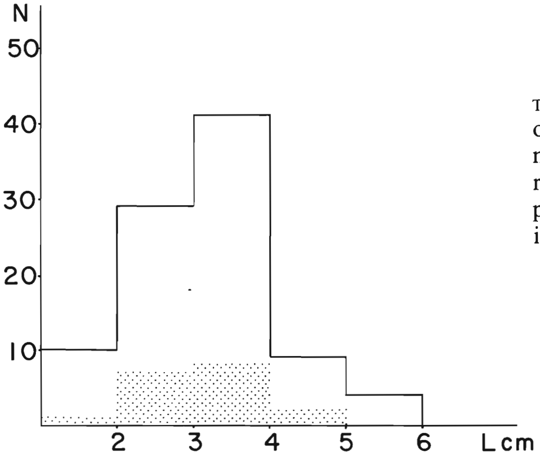
The tube was open at either end, had an oval cross-section, and tapered posteriorly. The proboscis protruded beyond the tube. The anterior of the proboscis was externally radially symmetrical and could invert. It was armed from anterior to posterior with: multispinose teeth or spinules, several concentric rows of fine long spines, shorter spines, and finally an area of spines that decreases in size posteriorly. The trunk occupied the tube and relatively little detail can be discerned through the tube. The anterior of the trunk was armed with rows of papillae, but the remainder appears to have been smooth. The gut was straight with terminal openings, the mouth being surrounded by the spinules. There were at least two sets of anterior proboscis retractor muscles. All the specimens lie with their longitudinal axes parallel to the bedding plane.

Morphological details. The tube. S. columbia is the only tubicolous priapulid from the Burgess Shale. The rigid tube was annulated and was open at both ends. The wider anterior aperture lacked an operculum (Walcott 1911*c*). The author has been unable to find any evidence in support of the statement by Walcott (1911*c*, p. 120) that 'The apical end is broken off on all the specimens'. This is because the delicate pointed end of another tube fossil, *S. gracilis* (now interpreted as a junior synonym of '*Selkirkia*' *major*) is almost invariably preserved. It is difficult to understand how the latter species nearly always retained the apex of the tube, whereas that of *S. columbia* was always detached. The author prefers to regard the blunt end of the tube of *S. columbia* as original.

The tube had fine annulations (Walcott 1911*c*) (Pl. 17, fig. 5). Measured values are a rather constant 4 per 0·1 mm, so that a 4 cm long tube has about 1600 annulations. Each annulation consisted of a very fine, non-bifurcating ridge that was apparently separate from its neighbours. It is assumed that they were secreted by an anterior zone of the trunk, thus the tube can be regarded as a specialized division of the cuticle. The rate of accretion is unknown, but the regularity of the spacing indicates a quiet undisturbed environment.

Walcott (1911*c*, p. 121) speculated briefly on the composition of the tube. Considering a calcareous composition less likely, he suggested that it was 'probably chitinous or parchment-like'. The crumpling and distortion of some tubes, together with the absence of such disturbance in originally calcareous brachiopod shells, militates against the tube being calcareous. Furthermore, a calcareous tube would be expected to have maintained greater relief during compaction of the shale than the flattened tubes actually do. The cuticle of modern priapulids contains chitin, although in newly moulted priapulids the cuticle consists of tanned proteins only (Carlisle 1959; Shapeero 1962*a*). The absence of chitin in the lorica of the larva (Lang 1948*b*) which, like the tube of *S. columbia* is a direct extension of the cuticle, suggests that the tube may not have been chitinous. Walcott (1911*c*) suggested that the anterior end of the tube was slightly thickened. However, this end is sometimes crumpled (Pl. 18, fig. 5; text-fig. 76) suggesting that it was thinner and more liable to distortion.

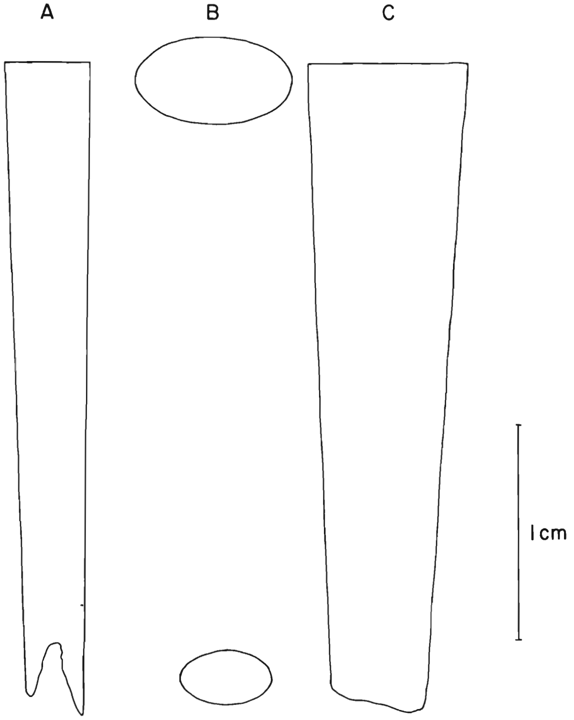
Text-fig. 19 shows the variation in the length of ninety-three tubes from the GSC collection. The average length is about 3 cm. The longest tube measured is 7·5 cm (USNM 202769), and this is 0·7 cm greater than the longest noted by Walcott (1911*c*).



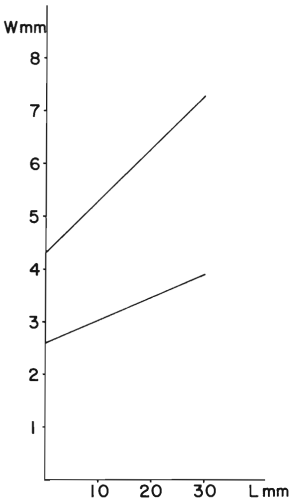
TEXT-FIG. 19. Size-frequency histogram of total length of ninety-three GSC tubes of *Selkirkia columbia* sp. nov. (with and without soft parts). The stippled area refers to eighteen GSC tubes with associated soft parts. N, number of specimens; L cm, length of tube in cm.

The shortest specimens that can be attributed to *S. columbia* are about 0·3 cm long (Pl. 15, fig. 5). Only about half the specimens (eighteen out of thirty-three) with soft parts have complete tubes. Nevertheless, they have nearly the same distribution of lengths as those lacking the soft parts. The tubes, therefore, behaved in the same way during transport irrespective of whether they were occupied, and neither group is deficient in any size fraction.

The degree of parallelism of the edges of the tube varies. In some specimens the tube is narrow and the sides are sub-parallel—the narrow-aspect tubes (Pl. 15, fig. 8; text-fig. 69), whereas in others the tube is broad and the sides taper posteriorly—the broad aspect tubes (Pl. 15, figs. 2, 3; Pl. 16, fig. 6; text-fig. 68). Yet others are intermediate between these two aspects. The broad and narrow aspects are interpreted as the extremes of a tube with an oval cross-section (text-fig. 20). Thus, the width of the narrow-aspect tube defined the minor axis (L_1), that of the broad-aspect tube the intermediate axis (L_2), and the length of the tube the major axis (L_3) of a truncated cone. Text-fig. 21 shows the increase of width with length for the known extreme aspects. It is assumed that the cross-sectional shape of the tube was constant for the species and has not materially altered with compaction. In a tube 3 cm long L_1 varied from 0·26 (posterior) to 0·39 cm (anterior) whilst L_2 varied from 0·43 to 0·73 cm. The ratio $L_1 : L_2$ varied from 1:1·7 (posterior) to 1:1·9 (anterior) so that the anterior of the tube was slightly more flattened. The volume of a 3 cm long tube can thus be calculated to be about 0·45 cm^3.



TEXT-FIG. 20. Tube of *Selkirkia columbia* sp. nov. The annulations are omitted. A, narrow-aspect tube with subparallel sides. B, transverse sections of tube at anterior and posterior showing the oval cross-section. C, broad-aspect tube with tapering sides. Note that the two posterior flaps are visible in A but lie on top of each other in C.



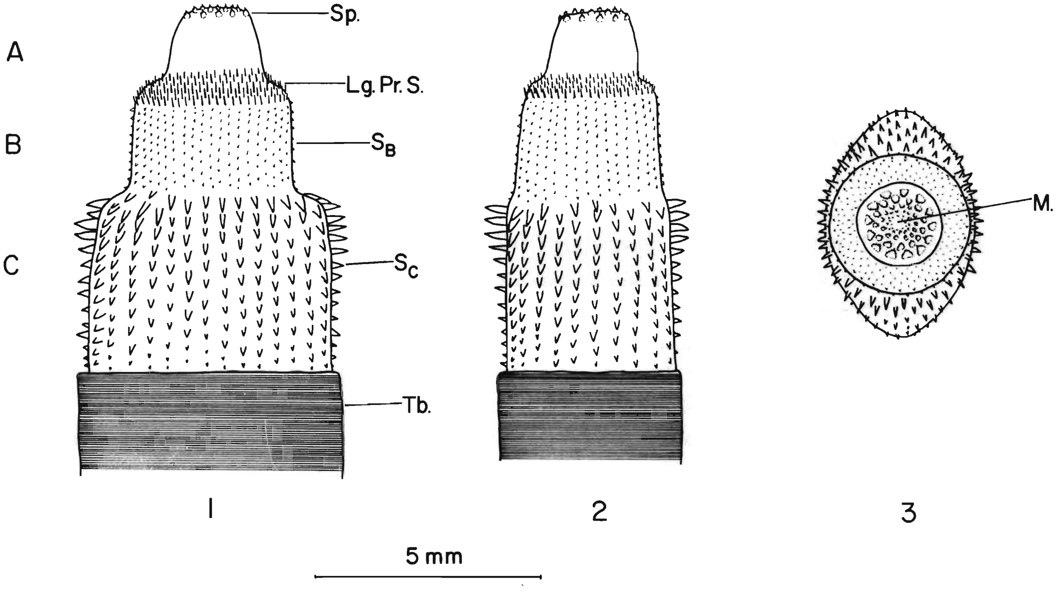
TEXT-FIG. 21. Graph to show the variation in width (W in mm) and length (L in mm) of the extreme narrow- (lower line) and broad-aspect tubes (upper line) of *Selkirkia columbia* sp. nov. that have been observed.

The tube was continuous without sutures or joints except that the posterior end of the tube consisted of two flaps, one slightly longer than the other (Pl. 15, fig. 6). The flaps are only readily visible in narrow-aspect tubes. In broad-aspect tubes the flaps are superimposed, although they are often separated by sediment that flowed into the gap formed by these flaps (Pl. 16, fig. 3).

Five tubes are known to carry epizoa. USNM 198623 (Pl. 17, fig. 2) has a brachiopod (*Nisusia burgessensis*) attached, GSC 45327 (Pl. 16, fig. 8), USNM 66521 (Pl. 16, fig. 5), and Peabody 9153 each carry a sponge (*Eiffelia globosa* Walcott, 1920), whilst GSC 45327 also has an undetermined tubular organism. USNM 66521 is one of the syntypes of *E. globosa* (Walcott 1920, pl. 86, fig. 1). The tube is obscure in Walcott's figure and he presumably thought their juxtaposition was by chance. GSC 45321 (Pl. 16, fig. 4) has another sponge species (*Pirania muricata* Walcott, 1920) fastened to it. All these tubes are empty and lack the soft part. This suggests that *S. columbia* belonged to the vagrant benthos and no epizoa could settle on the tube until after the death of the animal. The sponges and brachiopod species are usually found unattached and the tubes were not regularly used as a substrate. Indeed, *N. burgessensis* could act as a substrate itself for the sponge *Hazelia nodulifera* (Walcott 1920, pl. 71, fig. 3). The sponge *P. muricata* can provide a substrate for the brachiopod *Dictyonina*. The frequency and specificity of this latter association suggests, however, a definite relationship with the brachiopod gaining by placing itself in the water currents produced by the sponge. The sponge presumably neither gained nor lost any material benefits. *Dictyonina* is also occasionally found attached to the tube of *Tubulella flagellum* (Matthew). The primitive crinoid *Echmatocrinus brachiatus* is, however, always found attached. In one case it is the tube of *S. fragilis* and in another a hyolithid (Sprinkle 1973, text-fig. 44; Pl. 42, figs. 1–3; Pl. 43, figs. 1, 2, 6). Attachment of the epizoa cannot have taken place within the area of deposition of the Phyllopod bed because the environment there was inimical to metazoan life. Settling must have occurred in the pre-slide environment. Growth to their present size took some time, perhaps several months or even years judging by the probable life span of some brachiopods (Rudwick 1965). It is surprising that these semi-permanent immobile tubes were not used more frequently as a substrate for sessile organisms. *S. columbia* was a burrower and upon death it may have lain too deep in the sediment to be available as substrate.

The cuticle and its specializations

The proboscis carried a variety of spines and multispinose teeth or spinules. The clarity of some spines may have resulted from the decay of the underlying body wall leaving the more resistant cuticle (Pl. 15, fig. 9; text-fig. 69). For convenience the everted proboscis is divided into three divisions: A (anterior) to C (text-fig. 22). These divisions



TEXT-FIG. 22. Reconstruction of the proboscis of *Selkirkia columbia* sp. nov. The proboscis is everted as far as the proximal spinules (stage 3 in text-fig. 25). 1, proboscis in broad aspect with three divisions (A–C) clearly demarcated from one another. 2, proboscis in narrow aspect with divisions B and C scarcely demarcated from one another. 3, anterior view of proboscis looking into mouth. Divisions A and B are circular, whilst C is elliptical and follows the oval section of the tube. See text for full explanation.

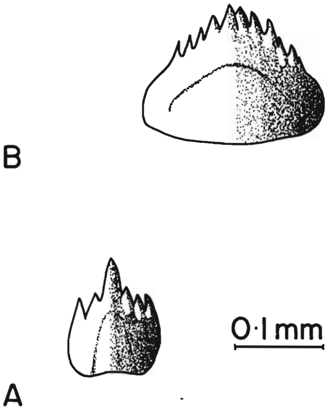
are not directly related to the zonation of the archaeopriapulid proboscis discussed below (text-fig. 33). Walcott (1911*c*, p. 121) mentioned, but did not figure, a specimen (almost certainly USNM 198617, Pl. 16, fig. 1; text-fig. 71) with 'a conical terminal section with several small-jointed appendages about its posterior end. My present impression is that . . . the appendages are a circle of gills.' These appendages are the spinules and were used for feeding rather than respiration. The leading edge of the spinule was dentate (Pl. 15, fig. 7), the teeth being directed anteriorly in the everted proboscis (Pl. 18, fig. 6; text-fig. 76). It appears that the most proximal spinules carried about seven spines and were slightly smaller (0·15 mm long and high) than the immediately distal spinules (0·3 mm long, 0·25 mm high) which possessed about ten spines (text-fig. 23). Over all the spinules decreased in size distally to approximately 0·05 mm across. They were arranged quincunxially in about ten oblique rows (Pl. 16, fig. 7). The spinules are very similar in shape and arrangement to those of *O. prolifica*.

Posterior to the spinules the proboscis was unarmed (Pl. 15, figs. 4, 9; Pl. 16, fig. 1; Pl. 17, fig. 1; Pl. 18, fig. 6; text-figs. 68, 69, 71, 72, 76). Beyond this unarmed area the proboscis increased in diameter into division B. The most anterior armature of division B was about five rows of very thin and long (about 0·4 mm) anteriorly directed spines, termed here the proboscis long spines (Pl. 15, fig. 4; Pl. 17, fig. 1; text-figs. 68, 72). They were probably disposed quincunxially. This is difficult to determine as they are usually only visible on the sides of the proboscis or the end of it where division A has been inverted (Pl. 17, fig. 3; text-fig. 73). Posterior to the long spines there were shorter ones (0·1–0·2 mm long) (Pl. 15, figs. 4, 9; Pl. 17, fig. 1; Pl. 18, fig. 6; text-figs. 68, 69, 72, 76) which were arranged quincunxially (Pl. 15, fig. 3; Pl. 17, fig. 8; text-fig. 68).

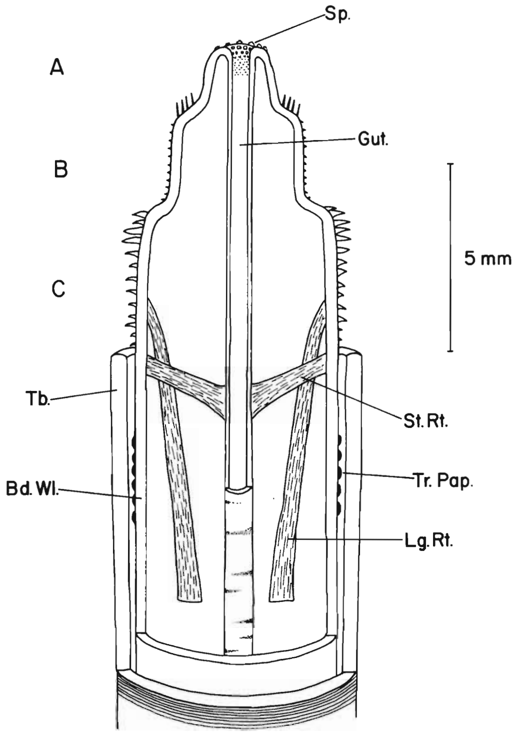
The proximal division C also carried spines possibly arranged in irregular quincunxes. They decreased in size (0·8–0·2 mm) in an irregular manner to the posterior. The distal spines are especially prominent (Pl. 15, figs. 4, 9; Pl. 16, figs. 1, 2; Pl. 17, fig. 1; Pl. 18, fig. 6; text-figs. 68, 69, 71, 76).

The anterior trunk rarely projected beyond the opening of the tube. The trunk immediately behind the proboscis spines (division C) was unannulated (Pl. 18, fig. 7; text-fig. 77). Slightly more posteriorly, however, the trunk was armed. The armature consisted of at least twenty-six longitudinal rows of papillae, thirteen being visible on one side of one specimen. Each row was made up of six to eight papillae (0·1 mm diameter) (Pl. 17, fig. 4). The rest of the trunk was apparently smooth. The most probable function of the papillae was to act as graspers for holding the animal to the tube. Similar organs, the girdles and adhesive plaques, exist in the tube-dwelling Pogonophora (Ivanov 1963).

Musculature. Two probable sets of anterior retractor muscles have been identified (text-fig. 24). In USNM 198632 (Pl. 18, fig. 7; text-fig. 77) a reflective strip runs sub-parallel to the gut. It is interpreted as the remains of a retractor muscle that was inserted anteriorly on to division C of the proboscis and posteriorly on to the trunk wall. Its contraction would have helped withdraw the proboscis. Only one muscle has been preserved but it is likely that at least two existed. Differential contraction by one muscle would have bent the proboscis sideways (Pl. 15, figs. 2–4; text-fig. 68). In other specimens (Pl. 17,



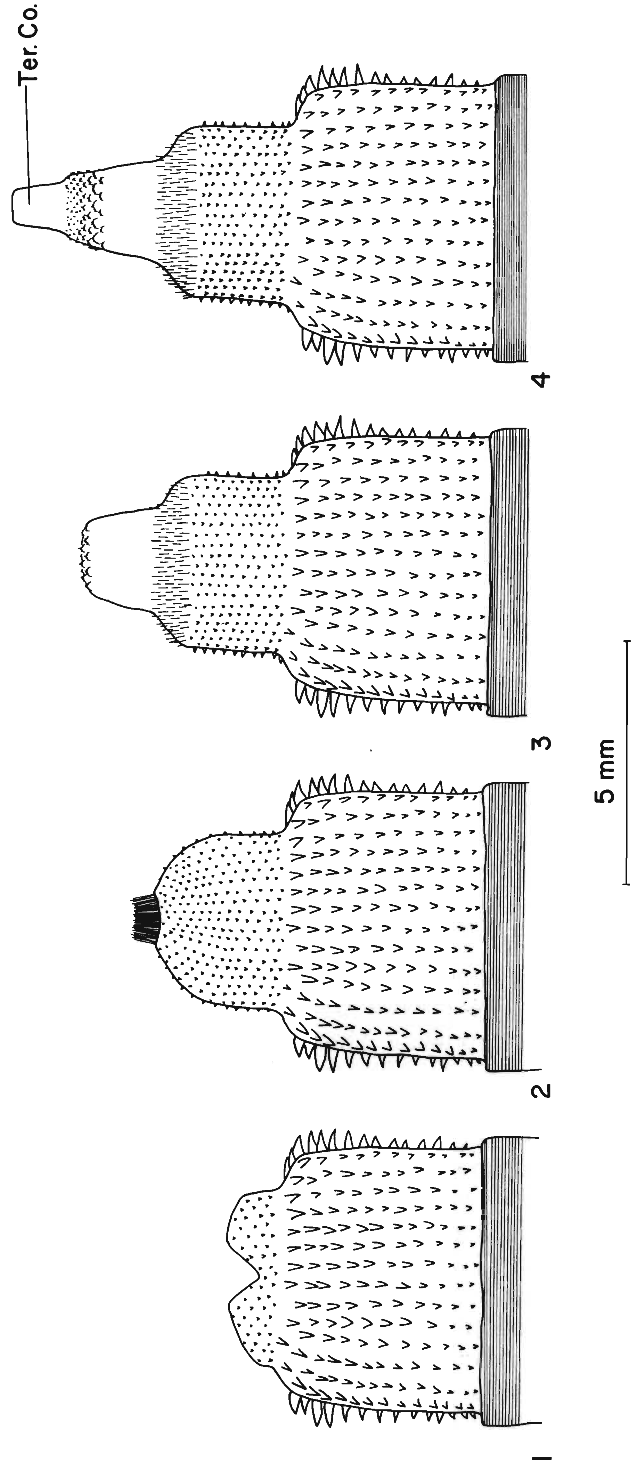
TEXT-FIG. 23. Two types of proboscis spinule in *Selkirkia columbia* sp. nov. Type A was probably slightly proximal to type B in the everted proboscis. Note the similarity to the spinules of *Ottoia prolifica* (text-fig. 8) and teeth of modern priapulids (text-fig. 9).



TEXT-FIG. 24. Hypothetical longitudinal section of the anterior of *Selkirkia columbia* sp. nov. to demonstrate the gut and retractor muscles. A, B, and C refer to the divisions of the proboscis.

figs. 5, 7; text-fig. 74) a reflective band either side of the gut runs forwards and outwards towards the edge of the trunk. These bands are interpreted as short retractors inserted on to the gut and the base of the proboscis. Their contraction would also have helped to withdraw the proboscis.

Proboscis and gut. In broad-aspect specimens the three divisions of the proboscis are clearly demarcated from each other by increasing width, division C being the widest (Pl. 15, figs. 2–4; Pl. 18, figs. 5, 6; text-figs. 68, 76). In narrow-aspect specimens, however, although the three divisions are still distinguishable by their different armature, the widths of divisions B and C are almost the same, whereas division A is again markedly narrower (Pl. 15, figs. 8, 9; Pl. 17, fig. 1; text-figs. 69, 72). This suggests that division A was completely delimited from division B by a concentric constriction. The width of division C as compared with division B was, however, greater only parallel to the intermediate axis (L_2) of the tube. Thus the constriction between divisions B and C did not extend all around the proboscis. Divisions A and B were circular in cross-section, whereas division C was elliptical (text-fig. 22).



TEXT-FIG. 25. Eversion of proboscis of *Selkirkia columbia* sp. nov. divided into four stages.

The proboscis could partially invert. This process can be divided into four stages (text-fig. 25):

Stage 1: it is uncertain whether all of division B could invert. USNM 198627 (Pl. 17, fig. 6) apparently has this division inverted but preservation is too poor to be certain.

Stage 2: the anterior part of division B could, however, certainly invert, because the distal long spines of this division are sometimes partially inverted (Pl. 18, figs. 2, 3). Further eversion completely exposed the long spines (Pl. 17, fig. 3; text-fig. 73).

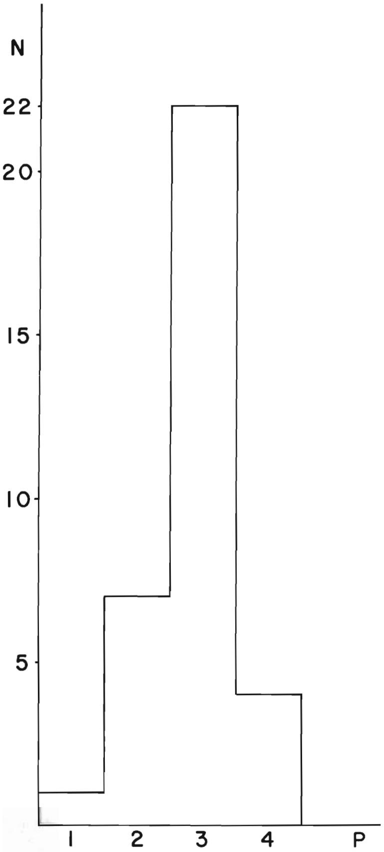
Stage 3: continued eversion revealed division A. The proximal spinules (Pl. 18, fig. 6; text-fig. 76) were followed by the smaller distal spinules (Pl. 16, fig. 7).

Stage 4: an unarmed terminal cone that tapered to a blunt point was the final section to evert (Pl. 16, fig. 1; Pl. 18, fig. 4; text-fig. 71).

The frequency of each stage is illustrated in text-fig. 26. Thirty-four specimens from the GSC and USNM collections were sufficiently well preserved, but another thirty-two specimens were too poorly preserved to be of use. Stage 3 is the most abundant and comprises 65% of the total sample. This stage could represent the proboscis position adopted by the dying animal.

The proboscis could also be withdrawn into the tube *in toto*. One specimen (Pl. 18, fig. 1; text-fig. 75) has only the most anterior spines of division C projecting beyond the tube, while another specimen (Pl. 17, fig. 3; text-fig. 73) apparently has the whole of division C withdrawn into the tube. The elliptical cross-section of division C presumably allowed it to conform with the oval cross-section of the tube. Most of the proboscis of GSC 45328 (Pl. 19, fig. 3) appears to lie within the tube, whilst that of USNM 198634 (Pl. 18, fig. 8), although very poorly preserved, seems to be withdrawn even further.

The reflective band extending from the anterior of the proboscis into the trunk is interpreted as the gut (Pl. 15, figs. 2, 3; Pl. 16, fig. 6; Pl. 18, figs. 3, 5; text-figs 68, 76). *S. columbia* probably fed in the same manner as *O. prolifica* with the proboscis in stage 3 of eversion so that the terminal cone and the area bearing the distal spinules were inverted and formed a lumen leading to the gut proper. The larger proximal spinules grasped the prey, whilst the smaller inverted ones with their posteriorly directed spines prevented its escape. The gut extended through the proboscis (Pl. 15, fig. 9; Pl. 16, fig. 6; text-fig. 69) and thence to near the end of the tube. The gut was externally unregionated and unlike



TEXT-FIG. 26. Histogram illustrating relative frequency of the four stages of proboscis eversion (P) in *Selkirkia columbia* sp. nov. against number of specimens (N). Sample consisted of thirty-four GSC and USNM specimens.

O. prolifica was never looped. Such a lack of contortion is presumably because of the restricting size of the body cavity. The very rare gut contents are similar in composition to those of *L. pedunculata* and *Ancalagon minor*, and consist of unrecognizable matter dotted with minute spherules. The general absence of food suggests that this worm was carnivorous.

Unrecognizable features. One specimen (Pl. 19, figs. 1, 2; text-fig. 78) has a reflective area that consists of a swollen anterior sac and a kinked posterior strand. One interpretation of this feature is that it represents a reproductive or excretory organ composed of a gland leading into a duct. More posteriorly in the same specimen there is another reflective area that remains unidentifiable.

Mode of life. The external radial symmetry of the anterior of the proboscis suggests that *S. columbia* was a burrower. It is difficult to imagine this worm either swimming or floating. The following burrowing cycle is postulated:

1. Proboscis inverted at stage 1.
2. Contraction of the body-wall circular muscles increased the pressure of the body-cavity fluid so completely everting the proboscis. To prevent the animal being pushed backwards as the proboscis probed forwards into the sediment the tube offered frictional resistance as in modern burrowing scaphopods (Trueman 1968*a*). The tube, therefore, acted as the 'penetration anchor' (Trueman 1968*c*).
3. The proboscis dilated and its spines gripped the sediment and acted as the 'terminal anchor' (Trueman 1968*c*). The tube was dragged forwards over the proboscis by the contraction of longitudinal muscles. The trunk papillae gripped the tube to prevent it remaining behind.
4. The proboscis completely inverted with the aid of retractor muscles.

No specific respiratory organ has been identified. The two posterior flaps of the tube probably delimited a hollow space which may have been lined with tissue so providing a respiratory surface. If this was the case, the posterior may have protruded into the overlying water for the purpose of respiration.

Preservation and decay. Only about 20% of the specimens have their soft parts preserved; the remainder are empty tubes. Although decay of organisms within the Burgess Shale was more widespread than previously realized (Whittington 1971*a*), such decay was slight in comparison with most environments. It rarely advanced far and fossils of completely soft-bodied forms are almost invariably entire. Complete decay of the soft parts of *S. columbia*, therefore, cannot have taken place within the area of deposition of the Phyllopod bed, i.e. post-slide environment. Such decay which left the empty and more resistant tube presumably took place prior to transport and burial. This is supported by the observation that tubes that bear epizoa are always empty (Pl. 16, figs. 4, 5, 8; Pl. 17, fig. 2). The epizoa could have existed only outside the inimical environment of the Phyllopod bed which was hostile to all, or nearly all, metazoan life as may be witnessed by the absence of bioturbation. Practically no cases of soft-bodied preservation within the Stephen Formation have been recorded outside the Burgess and Raymond quarries although some of the more resistant components of soft-bodied species have been found in the *Ogygopsis* Shale, e.g. tubes of *S. columbia*, individual scales of *Wiwaxia corrugata*, and head shields of *M. splendens* (Whittington 1971*b*). The soft parts of any organism that died outside the favoured locality where the Phyllopod bed was being deposited disappeared due to decay and predation. Decay of the harder parts, such as the tubes of *S. columbia*, outside the Phyllopod bed was slow and fossilization preserved them. Decay of the soft parts was probably fairly rapid. It is, therefore, very likely that those specimens with their soft parts preserved were swept in alive. Only the peculiar post-slide environment protected the soft parts from destruction. Although there are about three times as many GSC specimens of *S. columbia* as *Ottoia prolifica* from the Burgess quarry (157 to 49), at the time of burial living specimens of *S. columbia* were slightly less common than living *O. prolifica* (33 specimens of *S. columbia* with soft parts to 49 of *O. prolifica*). There is, therefore, a fossil population bias in favour of *S. columbia* because of the greater resistance of the tube to rotting and decay.

Evidence for decay of the soft parts themselves is slight although some parallels to *O. prolifica* can be noted. In very well-preserved specimens the body wall of the proboscis forms a reflective mat (Pl. 15, fig. 4; text-fig. 68), whereas it is more usual for the reflective proboscis spines to be set against a dark background suggesting that the body wall has rotted away leaving the more resistant cuticle. In these latter specimens the gut and sometimes the retractor muscles become more obvious. Those specimens which are indifferently preserved may owe much of their indistinctness to decay (Pl. 17, figs. 4, 6).

Family MISKOIIDAE Walcott, 1911

Genus LOUISELLA Walcott, 1911 (non MISKOIA Walcott, 1911)

Type and only known species. *Louisella pedunculata* Walcott, 1911 (non *Miskoia preciosa* Walcott, 1911).

Diagnosis. Compressed body bilaterally symmetrical but with pronounced anterior external radial symmetry, divisible into anterior proboscis and trunk. Proboscis partially invaginable, armed from anterior to posterior with short spines, oral spines, long spines, and papillae. Trunk divisible into four regions: A (anterior) to D. Trunk A ornamented with concentric zones of short spines and two longitudinal rows of long spines. Trunk B carries concentric zones of spines and two longitudinal rows of papillae. Trunk C is armed with spines and is partially invertible, and trunk D is unarmed and invertible. Straight gut with terminal openings, mouth leads to pharynx, oesophagus, gizzard, and intestine.

Louisella pedunculata Walcott, 1911

Plate 19, figs. 4–8; Plates 20–23; Plate 24, figs. 1–6; text-figs. 79–86

1911 *Louisella pedunculata* Walcott, pp. 45, 53, pl. 13, fig. 4.
1911 *Miskoia preciosa* Walcott, pp. 114–116, 131, pl. 18, figs. 1–5.
1912 *Miskoia preciosa* Walcott, p. 152.
1912 *Louisella pedunculata* Walcott, p. 153.
1912 *Miskoia preciosa* Walcott, p. 190.
1912 *Louisella pedunculata* Walcott, p. 190.
1912 *Louisella pedunculata* Clark, pp. 276–278.
1913 *Louisella pedunculata* Clark, pp. 488, 501, 505–506.
1928 *Louisella pedunculata* Fedotov, p. 89.

1932 *Louisella pedunculata* Croneis and McCormack, pp. 126, 127.
1943 *Louisella pedunculata* Sieverts-Doreck, p. 58.
1955 *Louisella pedunculata* Frizzell and Exline, p. 34.
1957 *Louisella pedunculata* Madsen, p. 281.
1958 *Lonisella* [sic] *pedunculata* Lehmann, p. 84.
1961 *Louisella pedunculata* Seilacher, p. 69.
1962 *Miskoia preciosa* Howell, p. W165, fig. 106.7*a–b* (cop. Walcott 1911, pl. 18, figs. 1, 5).
1962 *Louisella pedunculata* Howell, p. W170, fig. 107.7 (cop. Walcott 1911, pl. 13, fig. 4).
1964 *Louisella pedunculata* Baranova and Gekker, p. 193.
1971 *Louisella pedunculata* Durham, pp. 1106–1107.
1974 *Louisella pedunculata* Durham, pp. 752, 755.

Diagnosis. As for the genus.

Holotype. USNM 57588. Walcott 1911*b*, pl. 13, fig. 4.

Paratypes. USNM 57616–57618. Walcott 1911*c*, pl. 18, figs. 1–5.

Other material. USNM 198643–198656, 200596. There are about thirty additional USNM specimens. GSC 8231, 8319, 8319a, b.

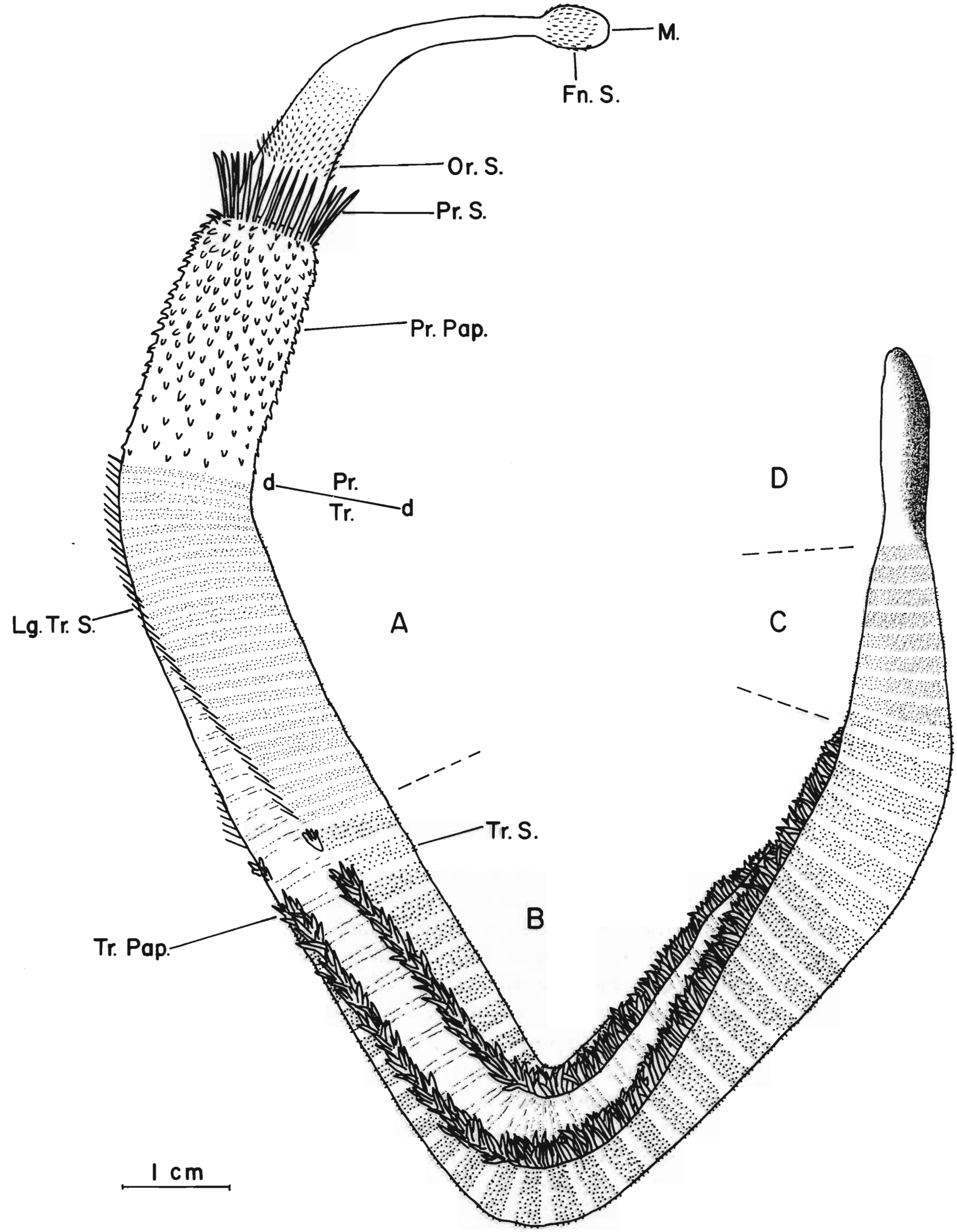
History of research. In his second paper on the Burgess Shale fauna Walcott (1911*b*, pl. 13, fig. 4) described a new genus and species, based on a single specimen (USNM 57588), as *Louisella pedunculata* (Pl. 19, figs. 5–7; text-fig. 79). He considered it to be a holothurian (Echinodermata) drawing attention to the flattened body (the ‘sole’) with its two longitudinal rows of papillae (the ‘podia’) and bunches of ‘tentacles’ at either end. His description was not inconsistent with that of a holothurian and the poorly reproduced figure is not dissimilar to how a fossilized holothurian might appear. In his next paper (Walcott 1911*c*, pl. 18, figs. 1–5) (Pl. 19, figs. 4, 8; Pl. 20, figs. 1–5; Pl. 21, fig. 5) another new genus and species, *Miskoia preciosa*, was described. Amongst other features, this possessed two longitudinal rows of trunk papillae, the ‘parapodia’ of Walcott (1911*c*). When the holotype of *L. pedunculata* was examined in the USNM the author came to the conclusion that the ‘podia’ are, in fact, the same as the trunk papillae of *M. preciosa*. In the holotype the body has been folded under itself at both ends so that the two rows of trunk papillae project outwards like clusters of tentacles. Furthermore, the body of the holotype is spinose (Pl. 19, fig. 6; text-fig. 79), as is the trunk of definitive specimens of *M. preciosa*. *L. pedunculata* must be taken as the senior synonym of *M. preciosa* on the grounds of priority of publication.

The history of research has thus been confused by the false separation of these two species. Following Walcott’s (1911*b*) publication of *L. pedunculata*, its proposed position within the Holothuroidea was vigorously attacked by H. L. Clark (1912) and equally strenuously supported by A. H. Clark (1913); the latter author, in fairness, pointing out that despite H. L. Clark removing it from the holothurians he had not offered a valid alternative. Croneis and McCormack (1932, p. 127) apparently accepted Walcott’s (1911*b*) suggestion although they commented that ‘further information is needed’. Fedotov (1928) and Frizzell and Exline (1955) did not consider *L. pedunculata* to be a holothurian but they offered no other suggestions. Madsen (1957) believed it to be a sedentary polychaete, possibly a terebellid. Howell (1962) placed it within the Sipunculida but gave no explanation for such a placement. *M. preciosa*, on the other hand, has received only passing mention and no critical attention.

Stratigraphic horizon and vertical distribution. Walcott (1912*a*) noted this worm from layer no. 12 (0·0–3·8 cm (0 ft 0 in–0 ft 1·5 in) above the base of the Burgess quarry, as *M. preciosa*), and from layer no. 10 (7·6–48·3 cm (0 ft 3 in–1 ft 7 in)), as *L. pedunculata*). The total known range is 48·3 cm (1 ft 7 in).

Mode of preservation. The specimens occur in a variety of positions. Some are straight (Pl. 20, figs. 1–3), others curved (Pl. 22, fig. 1; text-fig. 82) while yet others have part of their body bent at an acute angle (Pl. 21, fig. 1; text-fig. 81). Of particular interest are specimens that, by tracing the longitudinal rows of trunk papillae, can be seen to be rotated (Pl. 21, fig. 1; Pl. 23, figs. 1, 2; text-figs. 81, 84), or even completely twisted over (Pl. 21, fig. 6). Only very decayed and collapsed specimens of *O. prolifica* are thus distorted and such a feature has not been recorded in *A. minor* and *F. lanceolata.* The twisting in *L. pedunculata* is due to a compressed body. The bilaterally symmetrically arranged trunk papillae lie on the broad flat part of the trunk, so that the original compression of the trunk must have been dorso-ventral rather than lateral. The twisting is not infrequent and is not confined to decayed specimens. The absence of such distortion in the other archaeopriapulids indicates that their bodies were more cylindrical. The torsion cannot be solely due to currents turning the animals over on the sea-floor, because in twisted specimens the two parts are sometimes separated by a layer of sediment (Pl. 21, fig. 6). Turbulent transport in mudflows probably contorted the bodies and upon deposition sediment separated the parts of the animal as occurs in other Burgess Shale species (Piper 1972; Whittington 1971*a*). The thickness of this sediment parting is between 1 mm (Pl. 21, fig. 6) and 2 mm (Pl. 23, fig. 5; text-fig. 85). It might be assumed that sediment of the Phyllopod bed, in common with similar sediments, compacted by about ten times its original thickness. Thus, the original separation would have been up to 2 cm which appears to have been impossibly large. It is concluded that the degree of compaction probably was not as great and the separation may not have been much more than it is at present. One peculiarity of some organic-rich muds is that they appear to harden easily (Love 1962). Such strengthening would lead to a greater resistance to compaction produced by superincumbent strata.

Introduction to morphology. L. pedunculata was the longest of the archaeopriapulids, and adult specimens were between 15 and 20 cm long. The animal can be divided into two parts: an anterior partially invertible proboscis and a trunk (text-fig. 27). When the proboscis was fully everted the distal spinose portion was swollen (Walcott 1911*c*). Posteriorly an extensible unarmed length was succeeded by a field of spines arranged quincunxially. Behind these spines the proboscis increased in width and at this point there was a ring of long flattened spines. The proximal proboscis was papillate. The trunk may be divided into four parts, A (anterior) to D, on the basis of the varying surface ornamentation. The proportions in length between divisions A, B, C, and D were about 2:5:1:1. Trunk division A had numerous concentric zones of short spines separated by unarmed rings. There were also two longitudinal rows of long spines. Division B had similar but wider armed and unarmed zones. The long spines were replaced by two rows of papillae. Division C was also spinose and may have had unarmed concentric zones as well. The posterior division D lacked spinulation and could be inverted into division C. The most prominent internal organ was a straight gut with terminal openings.



TEXT-FIG. 27. Reconstruction of *Louisella pedunculata*. The animal is twisted about its long axis so as to show the nature and arrangement of the trunk ornamentation. Proboscis fully everted. The trunk divisions (A–D) are demarcated by dashed lines.

Externally the bilateral symmetry was defined by the two longitudinal rows of division B papillae. It is unknown whether the trunk papillae were dorsal or ventral but the orientation of the specimens can be determined by reference to these papillae (text-fig. 28). Whatever the orientation, the proboscis has the same aspect and must, therefore, have been radially symmetrical.

Morphological details. The cuticle and its specializations. The reflectively preserved body wall has sometimes pulled away from the spinose cuticle (Pl. 21, fig. 1; Pl. 22, figs. 6, 7; Pl. 23, fig. 1; text-figs. 81, 83, 84). This feature is attributed to the processes of decay. The clarity of the trunk spines results from the displacement of the underlying body wall.

The cuticle carried several specializations on both the trunk and the proboscis. The fully everted proboscis revealed four types of armature: anterior spines, oral spines, long spines, and papillae (text-fig. 27).

Walcott (1911*c*) termed the most distal armature 'fine papillae', but the more precise term of anterior spines (2 mm long) is adopted here. These anteriorly directed spines occupied the posterior two-thirds of the swollen distal end of the proboscis and were arranged quincunxially in about twenty-five oblique rows (Pl. 19, fig. 8). An unarmed length separated the quincunxially disposed, anteriorly directed oral spines from the anterior spines (Pl. 20, figs. 1–3; Pl. 21, fig. 3; text-fig. 81). The oral spines formed about twenty-five oblique rows. The proximal oral spines (1 mm long) were smooth and slightly curved (Pl. 20, fig. 4; Pl. 21, fig. 4). The more distal spines were smaller (0·1 mm long), but probably similar in shape (Pl. 20, fig. 4; Pl. 21, fig. 3). The anterior and oral spines can be discerned through the body wall in the partially inverted proboscis (Pl. 20, fig. 6; text-fig. 80).

Behind the oral spines the proboscis was inflated and at this point there was a prominent group of anteriorly directed spines (3·5–4·0 mm long). Walcott (1911*c*) termed them 'setae', but the less committal term of long spines is used here. They probably formed a single circle and not several rows as Walcott (1911*c*) suggested (Pl. 20, figs. 4, 6, 7; Pl. 21, fig. 3; text-figs. 80, 81). In specimens with probosces largely retracted the long spines point directly forward, but where the proboscis is everted they are inclined obliquely to the body. Occasionally the end of the proboscis is directed downwards into the sediment so that the long spines radiate across the bedding plane (Pl. 19, fig. 4; Pl. 24, figs. 1, 2; text-fig. 86). The long spines were flattened and consisted of a thickened leading edge, preserved as a darker strip with definite relief, and a trailing blade (Pl. 21, fig. 2). In specimens where the long spines are very thin, they are presumably preserved edge-on (Pl. 20, fig. 6; text-fig. 80). The leading edge is curved at the distal end (Pl. 21, figs. 2, 7). Typically about twenty long spines are visible so that they probably totalled forty to fifty.

The posteriorly directed, rather conical papillae (Walcott 1911*c*) arose immediately behind the proboscis long spines (Pl. 20, figs. 6, 7; Pl. 21, fig. 3; Pl. 22, fig. 2; text-figs. 80–82). The anteriormost papillae (0·7 mm long) were slightly longer and more slender than the remainder (0·4–0·5 mm long) (Pl. 21, fig. 7; Pl. 24, fig. 2; text-fig. 86). The papillae appear to have been arranged in irregular quincunxes. There were approximately twenty oblique rows. They decreased in number but not in size posteriorly. The anterior margin of the trunk is arbitrarily taken to begin behind the last papillae.

The varying cuticular ornamentation of the trunk allows the recognition of four divisions: A (anterior) to D. Division A had long spines (1·5 mm long) directed obliquely forwards. They ran from the proboscis papillae to near to the trunk papillae of division B. The spines numbered about twelve per cm in uncontracted specimens. Only one row has been noted (Pl. 21, fig. 1; Pl. 22, figs. 1, 3; Pl. 24, fig. 5; text-figs. 81, 82), but as it was in continuation with one of the two rows of trunk papillae it is concluded that the long spines were similarly disposed. The rest of the surface of division A had concentric spinose zones (1 mm broad) separated by smooth zones (0·5 mm broad) (Pl. 19, fig. 4; Pl. 23, fig. 4; text-fig. 84). The latter zones tend to be obliterated in contracted specimens (Pl. 24, fig. 5). Some of the concentrically arranged spines may have been larger than others (Pl. 22, fig. 1; text-fig. 82).

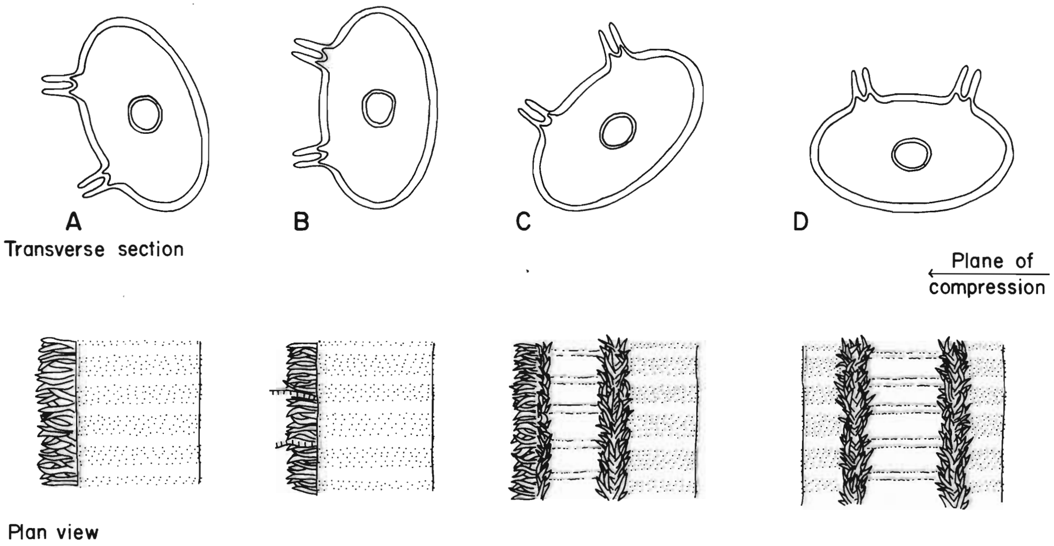
Walcott (1911*c*) drew attention to structures on division B that he termed 'parapodia', on the mistaken assumption that this worm (as *M. preciosa*) was a polychaete. The 'parapodia' are termed here trunk papillae. Unlike parapodia they were continuous along the length of division B, and the two rows were not on opposite sides of the trunk. No other feature is consistent with their interpretation as parapodia. The trunk papillae (2 mm long) were arranged in two longitudinal rows (Pl. 22, figs. 5, 6; Pl. 23, figs. 1, 2; text-figs. 83, 84) and in such specimens (broad-aspect) the width of the trunk is greater than in specimens where one row of trunk papillae runs down the side of the animal (narrow-aspect specimens) (Pl. 21, fig. 1; text-fig. 81). Sometimes in the latter specimens the underlying row is visible, being separated from the upper row by a wedge of sediment (Pl. 24, figs. 1, 4; text-fig. 86). This suggests that the trunk was compressed and had an oval cross-section. The observed twisting of the body also supports this interpretation. The compression was dorso-ventral with the trunk papillae situated on either the broad dorsal or ventral surface of the trunk. The specimens are preserved in different orientations with respect to the bedding plane, as may be determined from the position of the rows of trunk papillae (text-fig. 28). The width of the trunk in broad-aspect is the intermediate axis (L_2), the width in narrow aspect the short axis (L_1), and the length of the trunk the long axis (L_3) of the flattened cylinder that defined the shape of the trunk. Values of L_1 and L_2 cannot be as accurately determined as those for the rigid tube of *S. columbia* because this worm was soft-bodied. Nevertheless, the measured values indicate the ellipticity. The average for L_1 and L_2, derived from six specimens (three each) which were not markedly contracted or expanded, is 1·2 cm and 1·8 cm respectively. It is very probable that the degree of ellipticity was variable. In specimens that are twisted L_1 must have been reduced. By assuming that 180° of the circumference of the trunk of a broad-aspect specimen is exposed upon flattening of the fossil, the two rows of trunk papillae must have been separated by an arc of about 50°.

Each trunk papilla was attached individually to the trunk (Pl. 23, fig. 3). Walcott's (1911*c*) assertion that they branched has not been confirmed, although the papillae usually overlap giving a tangled appearance. The two rows of papillae were continuous, except for a solitary clump that preceded each row (Pl. 21, fig. 1; Pl. 23, fig. 1; text-figs. 81, 84). As noted above the 'podia' described by Walcott (1911*b*) in the holotype are trunk papillae. The papillae are arranged in a chevron pattern (Pl. 22, fig. 4) and each row probably consisted of two lines of papillae. In very contracted specimens the trunk immediately adjacent to the papillae is thrown into oval-shaped depressions with slightly shorter intervening rises (Pl. 23, fig. 6; text-fig. 85). It is believed that contraction has accentuated an otherwise invisible feature. The raised areas might represent canals that fed the papillae with fluid from the body cavity. Such a function is plausible because the papillae probably acted as gills.

Division B was also armed with concentric zones of spines with intervening unarmed zones (Pl. 22, figs. 6, 7; Pl. 23, fig. 1; text-figs. 83, 84). They are comparable to those of division A, except that the zones are wider. Each spinose zone was five times wider than the unarmed zone, typical values being 2·0 mm and 0·4 mm respectively. In contracted specimens the unarmed zones practically disappear and the spinose zones are almost continuous. Each armed zone carried about five roughly concentric rows of spines consisting of simple cones (0·2 mm long). These alternating zones occupied the greater part of the circumference of division B. There is, however, little trace of them between the rows of trunk papillae and they were either absent or very reduced (Pl. 22, fig. 6; Pl. 23, figs. 1, 2; text-figs. 83, 84).

The spinose division C began behind the last trunk papillae (Pl. 21, fig. 1; Pl. 23, fig. 5; text-figs. 81, 85). The spines were similar in size and shape to those of division B and they may have alternated with unarmed zones (Pl. 21, fig. 8). Where division C is inverted the spines on the posterior tip change their pointing direction and it seems likely that at least part of division C could invert.

The most posterior division D was unarmed and unannulated. It was separated from division C by a slight constriction (Pl. 21, fig. 8). Its absence in the majority of specimens, together with the evidence for the partial inversion of division C, shows that it was usually withdrawn. It was probably equivalent to the unannulated bursa of *O. prolifica*.



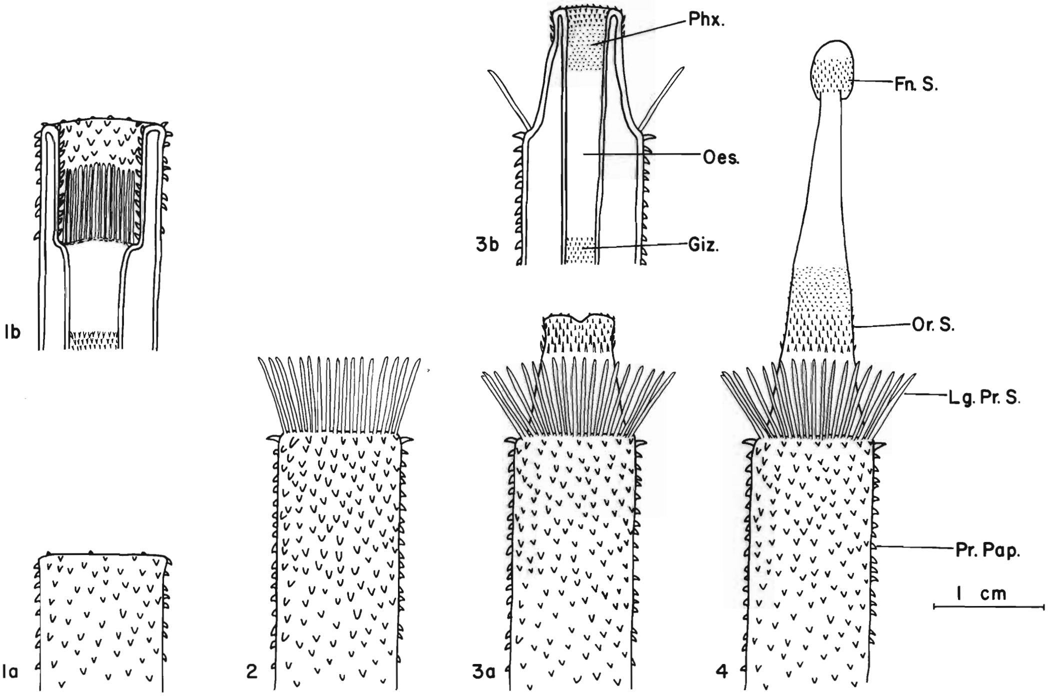
TEXT-FIG. 28. Explanation of variable appearance (plan view) of trunk division B which carries trunk papillae in *Louisella pedunculata*, according to the orientation with respect to the bedding plane (plane of compression). In B the lower series of trunk papillae are separated from the upper series by a layer of sediment and are, therefore, shown between the two hachured lines.

Musculature. The existence of very long thin specimens (Pl. 20, figs. 1–3) and short broad ones (Pl. 23, fig. 5; text-fig. 85) is presumably due to action of body-wall muscles. The variation in width is not in the case of these two illustrated specimens due to the original dorso-ventral compression of the trunk, because they both have the same orientation with the trunk papillae running along one side of the trunk (text-fig. 28). The body wall is preserved as a homogeneous reflective mat (Pl. 20, fig. 7) which sometimes has pulled away from the cuticle. The concentric spinose zones of the trunk could reflect underlying circular muscles.

It is likely that the proboscis was inverted by retractor muscles, although no actual remains have been noted. The configuration of the proboscis in USNM 198643 (Pl. 21, fig. 7), with the proboscis long spines at a lower angle to the body than is usual for this stage of proboscis eversion, is explicable by postulating the existence of 'neck' retractors similar to those of *O. prolifica* (text-fig. 11).

Proboscis and gut. The eversion of the proboscis can be divided into four stages (text-fig. 29).

Stage 1: at least half of the papillate length of proboscis could invert (Pl. 24, fig. 6) and the proboscis may have been able to retract completely. The long spines were, of course, withdrawn. Their length is such that on inversion they probably did not rotate their free ends to point posteriorly. They presumably remained anteriorly directed, as occurs today with the long proboscis stylets in the larva of the gordioid worms.

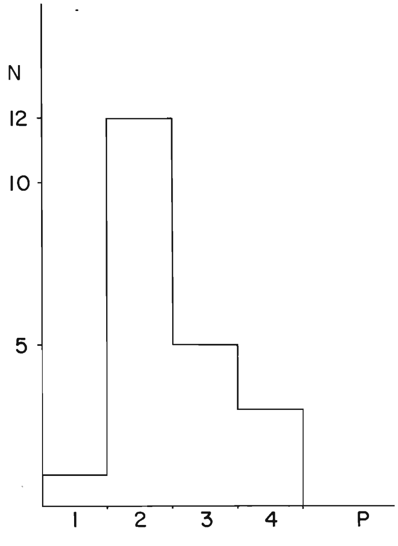


TEXT-FIG. 29. Eversion of proboscis of *Louisella pedunculata* divided into four stages. Figs. 1*b* and 3*b* show hypothetical longitudinal sections of figs. 1*a* and 3*a* respectively.

Stage 2: protrusion of the proboscis revealed the anterior papillae and then the long spines (Pl. 22, fig. 2; text-fig. 82) which when fully everted were parallel to the body (Pl. 20, fig. 7). The remainder of the inverted proboscis is sometimes visible through the body wall (Pl. 20, fig. 6; text-fig. 80).

Stage 3: continued eversion exposed the oral spines (Pl. 21, fig. 7). The long spines rotated so as to lie at an oblique angle to the body. At one point within stage 3 the larger oral spines were everted, whilst the more anterior ones remained inverted. As with *O. prolifica*, such an arrangement would have been suitable for feeding. The larger spines could have grasped the prey and the finer ones, with their posteriorly directed points, prevented its escape. Thus, the mouth formed in this stage and the first length of the gut consisted of the inverted remainder of the proboscis.

Stage 4: further eversion revealed an unarmed length which although contracted in the inverted proboscis (1 cm long in USNM 198644; Pl. 20, fig. 6; text-fig. 80) was capable of considerable extension upon eversion (2·6 cm in USNM 57616; Pl. 20, figs. 1–3). The last part of the proboscis to evert was the spinose section (1 cm long). This section had the same width as the unarmed length in the inverted proboscis (Pl. 20, fig. 6; text-fig. 80), but upon eversion and elongation of the unarmed length it maintained its width, so appearing bulbous (Pl. 19, fig. 8).



TEXT-FIG. 30. Histogram illustrating relative frequency of the four stages of proboscis eversion (P) in *Louisella pedunculata* against number of specimens (N). Sample consisted of twenty-one specimens.

The frequency of each state of eversion is shown in text-fig. 30, the most numerous of which is stage 2. All stages are believed to have been a normal part of the activity of the animal.

The inverted proboscis formed the first part of the gut when the worm fed. Immediately behind the mouth the tube leading to the gut proper was lined with backward-pointing oral spines, so that it can be considered as a pharynx. The pharynx was succeeded by a short unarmed tube that is called the oesophagus. Upon complete eversion of the proboscis the oesophagus formed, of course, the extensible unarmed length that separated the oral spines from the anterior spines. The anterior spines may have been effective in grinding food so that this region is termed the gizzard. It is unrelated to the proposed gizzard of *O. prolifica* which never everted.

The true gut commenced after the gizzard as an undifferentiated straight intestine that extended posteriorly to the terminal anus (Pl. 20, figs. 1–3; Pl. 23, fig. 1; text-fig. 84). The location of the anus would have depended on the degree of eversion of trunk divisions C and D. In some specimens part of the anterior intestine has marked relief, often in the shape of an elongate drop (*c.* 1·5 cm long) (Pl. 21, figs. 5, 6; Pl. 23, figs. 1, 2, 4; text-fig. 84). Walcott (1911*c*, p. 115) noted this feature as 'an expansion at about the anterior third' of the gut, but despite prominent relief the intestine does not expand. It may not be a persistent feature of the anatomy. This is because it is absent in some well-preserved specimens (Pl. 21, fig. 1; Pl. 22, fig. 1; text-figs. 81, 82) and its position varies, so that it may be adjacent to the gizzard (Pl. 24, fig. 5) or further back (Pl. 20, figs. 1, 2). Exceptionally most of the intestine has prominent relief. This peculiarity of the intestine might conceivably represent ingested food. Its composition is indeterminate, but there seems to be a high proportion of sediment. The posterior intestine also occasionally carries unidentifiable masses, similar in appearance to those of *O. prolifica*, that must represent digested residues (Pl. 21, fig. 1; Pl. 23, fig. 5; text-figs. 81, 85).

Mode of life. The proboscis possessed external radial symmetry. Such anteriorly positioned symmetry is typical of burrowing worms. A possible cycle of burrowing is:

1. Animal contracted and proboscis inverted.
2. The circular muscles contracted so increasing the fluid pressure and everting the proboscis. As the narrower length of the proboscis everted the proboscis long spines rotated to lie at about 60° to the body to act as a 'penetration anchor' (Trueman 1968*c*) which prevented the rest of the body from being pushed backwards as the proboscis probed into the sediment. The trunk spines provided additional frictional resistance. The paucity or absence of spines between the two rows of trunk papillae is probably because this area was not in close contact with the sediment.
3. The proboscis completely everted. Its spiny end gripped the sediment as the 'terminal anchor' (Trueman 1968*c*) to prevent backsliding as the animal dragged itself forwards by contraction of the longitudinal muscles.
4. The proboscis reinverted.

The surface area of the animal would have been increased enormously by the trunk papillae so that they may well have functioned as gills. They were probably filled with body-cavity fluid which served to distribute oxygen. *L. pedunculata* is the only archaeopriapulid to have possessed a recognizable respiratory organ and it is presumably not coincidental that it is also the largest. It is likely that when the animal was not burrowing it lay with the trunk papillae in contact with the overlying water.

Preservation and decay. In some specimens the body wall has become detached from the overlying cuticle because of decay. A few specimens (Pl. 22, fig. 1; text-fig. 82) show partial disintegration of the body and an associated dark stain presumably caused by more advanced decay. Patches of pyritic spherules found on a few specimens may represent fossilized bacterial floras that lived on the corpses.

Family ANCALAGONIDAE fam. nov.
Genus ANCALAGON gen. nov.

Type and only known species. Ancalagon minor (Walcott, 1911) gen. nov.

Derivation of name. The generic name is derived from Ancalagon the Black who was a legendary dragon or worm.

Diagnosis. Cylindrical body with pronounced external radial symmetry, divisible into anterior armed proboscis and finely annulated trunk. Short anterior proboscis armed with hooks and probably invaginable into posterior proboscis which bears backwardly directed, slightly curved spinose hooks. Trunk has thin setae, possibly in transverse rows. Gut with terminal openings, unregionated along length.

Ancalagon minor (Walcott, 1911) gen. nov.

Plate 24, figs. 7–9; Plate 25; Plate 26, figs. 1–6; text-figs. 87–91

1911	*Ottoia minor* Walcott, p. 129, pl. 22, fig. 5 (non fig. 6).
1912	*Ottoia minor* Walcott, p. 153.
1912	*Ottoia minor* Walcott, p. 190.
1928	*Ottoia minor* Dacqué, fig. 27*c* (cop. Walcott 1911, pl. 22, fig. 5).
1931	*Ottoia minor* Walcott, pp. 6–7, pl. 9, figs. 5–7 (non figs. 1–4).

Diagnosis. As for the genus.

Holotype. USNM 57646. Walcott 1911*c*, pl. 22, fig. 5.

Paratypes. USNM 83939e, f. Walcott 1931, pl. 9, figs. 5–7.

Other material. USNM 188621–188622, 193506, 196357, 198606–198610, 200592, 202229 (counterpart numbered 202228), 202707 (counterpart numbered 203034), 203016. GSC two unnumbered specimens.

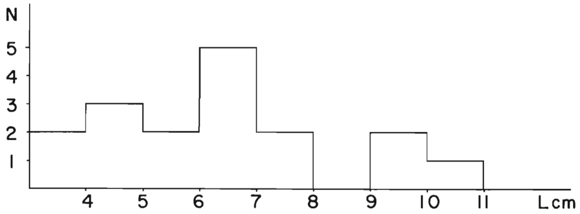
History of research. Walcott (1911*c*) (Pl. 24, fig. 7) first illustrated this species together with a short description in which differences with *O. prolifica* were noted. Despite these differences Walcott included this worm within the genus *Ottoia.* The author considers that the variation with *Ottoia* warrants the establishment of a new genus: *Ancalagon.* The reasons for separating *A. minor* from the genus *Ottoia* are discussed more fully below. In the years after publication, *A. minor* was mentioned in passing (Walcott 1912*a*, *b*; Dacqué 1928) and new material was illustrated by Walcott in 1931 (Pl. 9, figs. 5–7) (Pl. 24, fig. 8; Pl. 25, figs. 1–3; text-figs. 87, 88).

In the opinion of the author several specimens illustrated by Walcott as *A. minor* must be referred to other species. Those illustrated in his plate 22, fig. 6 (Walcott 1911*c*) (Pl. 2, fig. 1; text-fig. 38) and his plate 9, figs. 2 and 4 (Walcott 1931) (Pl. 2, figs. 2, 5; text-fig. 39) are identified as *O. prolifica.* Resser (*in* Walcott 1931, p. 7) noted that 'it is very doubtful whether the forms ... shown on Pl. 9, figs. 2 and 4 belong to this species'. The specimen illustrated in his plate 9, fig. 1 (Walcott 1931) probably belongs to *O. tenuis* (Walcott 1911*c*), although it is too poorly preserved for definite identification. *O. tenuis* is, in fact, unrelated to *Ottoia* or any other archaeopriapulid and will be described elsewhere. The specimen shown in his plate 9, fig. 3 (Walcott 1931) is a specimen of the archaeopriapulid *Fieldia lanceolata* Walcott (Pl. 26, fig. 7).

Less than twenty specimens of *A. minor* are known, few of which are well preserved. *A. minor* is over fifty times rarer than *O. prolifica.*

Vertical distribution. Walcott (1912*a*) noted *A. minor* from the richly fossiliferous layer no. 10 (7·6–48·3 cm (0 ft 3 in–1 ft 7 in) above the base of the Burgess quarry), but he gave no further details. The two GSC specimens are from 71·1–81·3 cm (2 ft 4 in–2 ft 8 in) and 121·9–137·2 cm (4 ft 0 in–4 ft 6 in) above the base of the quarry. The total range is, therefore, 129·5 cm (4 ft 3 in).

Introduction to morphology. Most specimens are preserved straight (Walcott 1911*c*) (Pl. 24, fig. 9; Pl. 25, fig. 6; Pl. 26, fig. 3; text-fig. 91), but some are gently curved (Pl. 24, fig. 7; Pl. 25, fig. 1; text-fig. 88). Greater degrees of curvature are rare (Pl. 24, fig. 8; Pl. 26, fig. 4; text-fig. 87). Occasionally one or both ends are bent with respect to the central trunk (Pl. 25, fig. 5; text-fig. 89) sometimes to the extent of coming to lie underneath the rest of the body (Pl. 25, fig. 4).



TEXT-FIG. 31. Size-frequency histogram of total length of seventeen specimens of *Ancalagon minor* gen. nov. One markedly contracted specimen omitted. N, number of specimens; L cm, length in cm.

Text-fig. 31 illustrates the variation in length of seventeen specimens, the average being 6 cm. The low number in the interval 5–6 cm and absence at 8–9 cm is presumably a result of the low sample. One short (4 cm long) specimen (Pl. 26, figs. 1, 2; text-fig. 90) is also very broad, suggesting that it is a contracted adult; whereas another short (3·1 cm) specimen (Pl. 24, fig. 8; text-fig. 87) is not swollen and must represent a juvenile specimen.

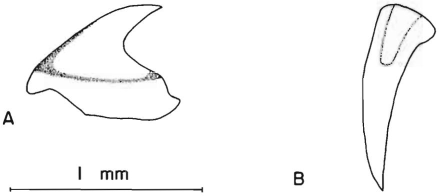
The proboscis was armed with hooks and spines. Although the proboscis could apparently invert only slightly, it has the same groundplan as the invertible probosces of other archaeopriapulids. The proboscis occupied between a seventh and a tenth of the total length of the animal. The specimens all show the same aspect and it is concluded that the animal was externally radially symmetrical.

The most anterior armature of the proboscis were prominent hooks arranged circumorally. Behind the proboscis hooks there was an unarmed zone which was succeeded by posteriorly directed, slightly curved spinose hooks that became more sparsely distributed and finally disappeared posteriorly. The point of disappearance is taken as the anterior limit of the trunk. The entire trunk was finely annulated and in addition bore fine hair-like setae.

Few details of internal anatomy have been preserved. The gut was straight, had terminal openings, and lay in a relatively narrow body cavity.

Morphological details. The cuticle and its specializations. The clarity of the trunk setae in USNM 198608 (Pl. 26, fig. 1; text-fig. 90) may be due to the rotting away of the underlying body wall leaving the more resistant cuticle. In other specimens the body wall, preserved as a reflective mat, has pulled away from the overlying non-reflectively preserved cuticle during decay (Pl. 25, figs. 4, 5; Pl. 26, fig. 3; text-figs. 89, 91). The cuticle of the trunk was annulated (Pl. 26, fig. 6; text-fig. 91). Their spacing was 0·2–0·25 mm, and a specimen with a trunk 4 cm long would have had about two hundred annulations. They were finer and had less relief than those of *O. prolifica* and consequently are not as well preserved.

The most anterior armature of the proboscis was a group of about ten equally sized hooks with prominent bases (0·6 mm high, 0·5 mm wide) (Pl. 25, figs. 2, 3; text-figs. 32, 88). They are termed oral hooks because they were apparently disposed circum-orally. The proximity of the proboscis spines to the anterior, together with the apparent absence of the oral hooks, in some specimens, suggests that the distal proboscis could invert (Pl. 26, figs. 1, 2; text-fig. 90). Separated from the oral hooks by an unarmed area were numerous posteriorly directed spinose hooks termed proboscis hooks (Pl. 24, fig. 7; Pl. 25, figs. 2, 3; Pl. 26, figs. 1–3; text-figs. 88, 90, 91). Walcott (1931, pl. 9, fig. 7) depicted spines on the intermediate zone, but examination of the illustrated specimen failed to reveal any such spines (Pl. 25, figs. 2, 3; text-fig. 88). Their presence must be due to retouching of the photograph. The proboscis hooks appear to have been disposed in steep oblique rows, possibly quincunxially. They were slightly curved and had a small expanded base (text-fig. 32). The hooks decreased in size from 1·0 mm (anterior) to 0·2 mm (posterior) and they also became more sparsely distributed posteriorly. Some of the hooks preserved on the edge of the proboscis of USNM 83939f have a core of minute pyritic spherules. It is possible that this core represents an original cavity. No specimen has been recognized with its proboscis hooks inverted into the trunk.



TEXT-FIG. 32. Oral hook (A) and spinose hook (B) from the proboscis of *Ancalagon minor* gen. nov. Spinose hook may have a basal cavity.

The trunk carried fine spines or setae (0·5–1·5 mm), possibly sensory, which are most prominent in contracted specimens (Pl. 26, figs. 1, 2; text-fig. 90). They may have formed concentric rows.

Musculature. The swollen nature of some short specimens was probably caused by the action of body-wall muscles. Although remains of the body wall have been identified, no muscles can be seen within. The annulations might reflect circular body-wall muscles. The apparent absence of retractor muscles may be correlated to the inability of the proboscis to invert appreciably.

Body cavity. The displacement of the gut across the body is evidence for a body cavity (Pl. 25, fig. 6). However, as the gut occupied up to half of the interior of the animal (Pl. 25, fig. 1; text-fig. 88) the body cavity cannot have been spacious. Swollen reflective areas surround the gut at the ends of the gut (Pl. 24, figs. 8, 9; Pl. 25, figs. 4, 5; Pl. 26, fig. 3; text-figs. 87, 89, 91). These reflective areas presumably represent the body wall. The body wall may have tended to contract along the mid-length of the trunk due to decay. It is possible, however, that the body cavity was restricted along the mid-length, but more spacious at the ends of the animal.

Proboscis and gut. Unlike the other archaeopriapulids, there is no evidence that *A. minor* could invert more than the oral hooks of the proboscis. The prominent oral hooks appear to have been suited to grapple with sizeable prey, suggesting that this worm was a predator.

The straight reflective strip that ran from the anterior to the posterior tips is interpreted as the gut (Pl. 24, fig. 8; Pl. 25, figs. 1, 5, 6; Pl. 26, fig. 3; text-figs. 87–89, 91). The gut shows no external regionation. The anus was terminal. Gut contents have been noted only in one specimen (Pl. 24, fig. 7) where a small unrecognizable mass occupies part of the hind gut. The general absence of gut contents also suggests a carnivorous diet.

Mode of life. The prominent external radial symmetry suggests that this worm was a burrower. The inability of the proboscis to invert substantially means that the postulated burrowing cycle must have differed from the other archaeopriapulids. *Halicryptus* has a shorter proboscis than the other Priapulidae and peristaltic movements of the trunk are important in burrowing (Friedrich and Langeloh 1936). *A. minor* may have burrowed in a similar manner to *Halicryptus.* A possible cycle is:

1. Body contracted.
2. Circular muscles contracted elongating the anterior body. The slight curvature of the body and the trunk setae would have acted as the 'penetration anchor' (Trueman 1968*c*) preventing the animal being pushed backwards as the anterior, possibly aided by slight proboscis eversion, probed into the sediment.
3. The anterior proboscis dilated slightly and the proboscis spines gripped the sediment as the 'terminal anchor' (Trueman 1968*c*). Longitudinal muscles dragged the rest of the animal forwards.
4. Body contracted.

No specific respiratory organs have been recognized. Presumably gases diffused through the body wall.

Preservation, decay, and predation. Examples of detachment of the body wall from the cuticle were noted beforehand. The same feature is found in other archaeopriapulids and there is good evidence that it is due to decay. The body wall of USNM 198606 (Pl. 25, fig. 6) appears to have ruptured, while in USNM 188621 (Pl. 26, fig. 4) decay has proceeded further and parts of the trunk are missing. Only one specimen of *A. minor* (Pl. 24, fig. 7) has the dark stain associated with it.

An ostracod is superimposed on the anterior end of one specimen (Pl. 26, fig. 5). A very small proportion (less than 0·1%) of *M. splendens* have the same species of ostracod associated with them (Whittington 1971*b*, p. 20; Pl. 1, figs. 1–3). Whittington noted that this association may be chance superposition, or that alternatively, the ostracod was feeding on *M. splendens* or vice versa. Whittington preferred the former suggestion. It may be significant that in *M. splendens* they are always situated on the ventral side of the cephalic shield between the lateral and median cephalic spines. This constancy in position is unlikely to be fortuitous and may be because the ostracods were parasitic, although parasitic ostracods are unknown today. The author suggests that the ostracods were feeding on the dead animals. Green (1959) reported that ostracods could live in water smelling of H_2S, and there is evidence that the water above the Phyllopod bed was similarly poisoned. The majority of Burgess Shale ostracods are unattached. Their rarity in association with other species is probably because the majority of specimens were buried and unavailable to surface scavengers.

Systematic position. From the above description it is clear that Walcott's (1911*c*) placement of *A. minor* within the genus *Ottoia* cannot be upheld. The more slender and straighter shape, the finer (Walcott 1911*c*) and more numerous annulations, the shorter average length, the absence of posterior hooks and the different proboscis armature of *A. minor*, as compared with the type species *O. prolifica*, combine to show that the former worm cannot be accommodated in the genus *Ottoia*. The new generic name *Ancalagon* is proposed. The derivation of the name is given above.

Family FIELDIIDAE

Genus FIELDIA Walcott, 1912

Type and only known species. Fieldia lanceolata Walcott, 1912.

Diagnosis. Cylindrical body with pronounced external radial symmetry, divisible into anterior proboscis and trunk. Proboscis capable of partial inversion, armed with anterior spines and hooks. Trunk divisible into anterior, central, and posterior regions. Anterior trunk armed with concentric rows of spines, central trunk spinose, and carries the swollen sediment-filled mid-gut, posterior trunk spinose. Gut straight with terminal openings.

Fieldia lanceolata Walcott, 1912

Plate 26, figs. 7-8; 27; Plate 28, figs. 1-4; text-figs. 92-96

1912 *Fieldia lanceolata* Walcott, pp. 153, 154, 188, 189, pl. 32, fig. 8.
1931 *Ottoia minor* Walcott, pl. 9, fig. 3.

Diagnosis. As for the genus.

Holotype. USNM 57717, Walcott, 1912*a*, pl. 32, fig. a.

Other material. USNM 83939c, 188633, 198598-198605, 198615, RoM 32572.

History of research. Walcott (1912*a*, pl. 32, fig. 8) mistook the holotype (USNM 57717) for a crustacean carapace. He regarded the spines, which in fact flank both sides, as appendages. In his posthumous paper Walcott (1931, pl. 9, fig. 3) (Pl. 27, fig. 7) misidentified another specimen (USNM 83939c) for *A. minor*. Resser (*in* Walcott 1931, p. 40) considered it to be 'the anterior end of a poorly preserved' specimen of *A. minor*. Comparison with better-preserved specimens found during a search through the extensive collections of Burgess Shale fossils in the USNM, Washington D.C., in March 1973, demonstrates that USNM 57717 and 83939c are examples of the central trunk region of *F. lanceolata*.

This worm is a rare component of the fauna and all but two of the specimens are incomplete.

Vertical distribution. Walcott (1912*a*) noted that the holotype came from level 10 (7·6–48·3 cm (0 ft 3 in–1 ft 7 in) above the base of the Burgess quarry). All the other specimens are labelled 35k and are, therefore, also from the Phyllopod bed but no details of their distribution within the bed are available.

Introduction to morphology. Specimens are preserved in both straight (Pl. 27, fig. 1; text-fig. 92) and curved positions (Pl. 27, fig. 6; text-fig. 95).

The body can be divided into an anterior proboscis and trunk. Spines formed the most anterior proboscis armature, whilst more posteriorly there were small hooks. The trunk may be divided into three regions: anterior, central, and posterior. The ratio of length between these regions is about 1:1:1·5. All these regions were spinose and the central trunk contained an expanded length of the gut that was usually filled with sediment. The posterior trunk may have been expanded in its middle. The animal was externally radially symmetrical having the same aspect in all specimens. The lengths of the two complete specimens are 4·6 and 5·3 cm.

Morphological details. The cuticle and its specializations. The proboscis carried two, or possibly three, varieties of armature. In the fully everted proboscis there was a group of about thirty circum-oral proboscis spines (0·15 mm long) (Pl. 27, fig. 2; text-fig. 92). The spines were succeeded by an unarmed zone. The base of this zone may have been encircled by spinose elements, but as the evidence is circumstantial (Pl. 27, figs. 2, 7; text-figs. 92, 95) they have been omitted from text-fig. 33c. Immediately to the posterior there were proboscis hooks (0·3 mm high) (Pl. 27, fig. 2; text-fig. 92). Their arrangement and total number is unknown. The trailing edge of each hook was apparently serrated. The posteriormost proboscis hooks are taken to delimit the proboscis.

All three sections of the trunk were spinose but there were no annulations. The spines of the anterior trunk (0·2–0·4 mm long) were arranged in at least ten concentric rows (Pl. 27, fig. 1; text-fig. 92), although in contracted specimens this pattern disappears (Pl. 27, figs. 6, 7; text-fig. 95). The spines of the central trunk (0·3–0·5 mm long) are only visible along the edges of the trunk where they are silhouetted against the rock (Pl. 26, fig. 7; Pl. 27, figs. 1, 3–6; Pl. 28, fig. 2; text-figs. 92–95). As the expanded gut within this region is reflective, the similarly reflective spines become invisible. However, in specimens where the gut does not underlie the wall of the central trunk the spines can be seen to have covered the surface (Pl. 28, figs. 1, 3; text-fig. 96). The spines of the posterior trunk (0·4 mm long) appear to be more sparsely distributed than those of the rest of the trunk (Pl. 27, figs. 1, 6; text-figs. 92, 95).

Musculature. Specimens have been preserved in contracted (Pl. 27, fig. 7; text-fig. 95), extended (Pl. 27, fig. 1; text-fig. 92), and flexed (Pl. 28, fig. 4) postures. It is likely that these shapes were produced by the action of body-wall muscles.

Proboscis and gut. Only two specimens have the proboscis preserved. Both probosces appear to be at the same stage of eversion (Pl. 27, figs. 2, 7; text-figs. 92, 95). It is unknown whether the proboscis was capable of further eversion or retraction.

Along the length of the animal there runs a poorly defined reflective band interpreted as the gut. The mouth was probably formed in the everted proboscis, with food being ingested by the circum-oral spines. The area immediately behind the mouth is preserved as an ovoid reflective mass (Pl. 27, figs. 1, 2, 7; text-figs. 92, 95) that may represent a muscular pharynx.

The central trunk is very reflective and, unusually for these soft-bodied fossils, nearly always has prominent relief (Pl. 27, figs. 3–6; Pl. 28, figs. 1–4; text-figs. 93–96). In USNM 198615 (Pl. 26, fig. 8) the central trunk has been broken open and the relief can be seen to be due to sediment infilling. The reflective nature of this area is not caused by the sediment, because in USNM 198597 (Pl. 27, fig. 1; text-fig. 92) this region is flat but still reflective. The reflective area generally occupies all the central trunk, but occasionally the body wall extends beyond the reflective mass, thus demonstrating that it was internal (Pl. 28, figs. 1, 3; text-fig. 96). The reflective area is interpreted as an expanded length of the gut that occupied most of the central trunk and was habitually filled with sediment. The central gut is covered by an open reticulate network of less reflective lines (Pl. 26, figs. 7, 8) and this suggests that the gut wall differed structurally from the anterior and posterior gut. None of the other archaeopriapulids have such a conspicuous accumulation of sediment, so it cannot have seeped into the animal after death. Presumably this part of the gut was used for storing the sediment whilst the organic constituents were digested.

The gut within the anterior and posterior trunk regions was not specialized and was narrower than the central section (Pl. 27, figs. 3–5; Pl. 28, figs. 1, 3; text-figs. 93, 94, 96). The anus was terminal.

Mode of life. The external radial symmetry suggests that this worm was a burrower. The burrowing cycle was probably similar to that of *A. minor*:

1. Body contracted.
2. Circular muscles contracted so elongating the animal with the anterior, perhaps aided by eversion of proboscis, probing forward. The posterior trunk spines acted as the 'penetration anchor' (Trueman 1968*c*).
3. The anterior trunk swelled (Pl. 27, fig. 7) and the spines and proboscis hooks gripped the sediment to act as the 'terminal anchor' (Trueman 1968*c*). The 'penetration anchor' relaxed and contraction of longitudinal muscles dragged the animal forwards.

The accumulation of sediment within the central gut suggests that this species was a sediment eater. The relative insignificance of the proboscis armature, in comparison with other archaeopriapulids, also indicates that it was not a predator.

Preservation and decay. The majority of specimens have only the central trunk well preserved, and the anterior and posterior sections of the trunk either cannot be distinguished from one another or are absent (Pl. 26, fig. 8; Pl. 27, figs. 3, 4; Pl. 28, fig. 2; text-fig. 93). It appears that the anterior and posterior were less resistant to decay. The infilling of sediment and the possibly thicker wall of the central gut may have been factors in the preferential preservation of the central trunk.

TWO PROBABLE ARCHAEOPRIAPULIDS

Genus SCOLECOFURCA gen. nov.

Type and only known species. Scolecofurca rara sp. nov.

Derivation of name. The generic name is derived from the Latin and means forked worm, a reference to the two anterior tentacles.

Diagnosis. Body divided into proboscis and trunk. Probably papillate proboscis bearing two anterior tentacles. Trunk annulated, posterior end unknown. Gut straight, anterior length including a possibly eversible spinose zone.

Scolecofurca rara sp. nov.

Plate 29, figs. 1–3; text-fig. 99

Derivation of name. The trivial name refers to its rarity.

Diagnosis. As for the genus.

Holotype and sole specimen. GSC 45331.

The preservation of the only known specimen is only moderately good. The proboscis has extraneous organic debris scattered over it which obscures details. The trunk is disrupted by compression furrows.

This worm differs from the other archaeopriapulids in a number of respects and is recognized as a new genus and species. The new name *Scolecofurca rara* is proposed.

Stratigraphic horizon. The specimen was collected by the GSC team from Raymond's quarry 20·4–21·0 m (67 ft–69 ft) above the base of the Phyllopod bed.

Morphology. The part of the only specimen lacks the posterior end, whilst the counterpart is also without the anterior tip (Pl. 29, figs. 1, 2). This is due to rock breakages. The specimen is 6·5 cm long but the original length may have been about 9 cm.

The body can be divided into an anterior proboscis and a trunk (Pl. 29, fig. 1; text-fig. 99). The proboscis was 1·4 cm long and of more or less constant width. The lateral margins of the proboscis are irregular and this suggests that it bore papillae or some other surface ornamentation (Pl. 29, fig. 3; text-fig. 99). The anterior end was blunt and carried two short tentacles (3 mm long) (Pl. 29, figs. 1, 3; text-fig. 99).

The trunk was annulated. The separation of the annuli was about 7 mm. The trunk increased in width behind the proboscis to a maximum value of 2 cm and then tapered posteriorly to a width of 1·1 cm.

Within the specimen there is a longitudinal band interpreted as the gut. The most anterior length to be preserved consisted of a simple tube. More posteriorly the gut was dilated. This dilatation was armed with quincunxially arranged papillae or spines (Pl. 29, figs. 1–3; text-fig. 99). Behind this dilatation the gut continued as a simple tube. Except for some reflective strands that may represent muscles, no other features of the internal anatomy are preserved.

Mode of life. In common with the other archaeopriapulids this worm is assumed to have burrowed with the aid of the proboscis. The proboscis tentacles may have been sensory, rather than employed in obtaining food. The nature of the food is unknown.

Systematic position. The anterior of the specimen has a considerable resemblance to the partially inverted proboscis of *L. pedunculata*. The apparently papillate proboscis is probably equivalent to the proximal papillate part of the proboscis of *L. pedunculata*. The anterior length of the gut of *S. rara* would, if everted, closely resemble the distal half of the proboscis of *L. pedunculata* (text-fig. 29). There is, however, no equivalent to the oral teeth of *L. pedunculata*, but the papillae located on the dilatation of the gut have a counterpart with the anterior spines of *L. pedunculata* (Pl. 20, fig. 6; text-fig. 80).

The presence of the two tentacles and the absence of the long proboscis spines and oral spines demonstrates that *S. rara* cannot be included within *L. pedunculata*. Furthermore, the trunk appears to have lacked both spines and papillae. *S. rara* does not approach any of the other archaeopriapulids more closely than *L. pedunculata*, so that the erection of a new genus and species is justified.

Genus LECYTHIOSCOPA gen. nov.

Type and only known species. Lecythioscopa simplex (Walcott, 1931) gen. nov.

Derivation of name. Lecythioscopa is derived from lecythus (Latin—bottle) scopa (Latin—brush). Dr. K. J. McNamara (University of Queensland) kindly pointed out the resemblance of this worm to a bottle brush.

Diagnosis. Body, probably radially symmetrical, divided into an anterior head consisting of a short anterior length and a swollen area bearing at least ten spines, and a long trunk of constant width. Posterior extremity unknown. Gut straight, probably with terminal openings.

Lecythioscopa simplex (Walcott, 1931) gen. nov.

Plate 28, figs. 5–7; text-figs. 97–98

1931 *Canadia simplex* Walcott, p. 6, pl. 9, fig. 9.

Diagnosis. As for the genus.

Holotype. USNM 83937. Walcott 1931, pl. 9, fig. 9.

Other material. USNM 198714.

History of research. Apart from the holotype that was illustrated by Walcott (1931, pl. 9, fig. 9), only one other specimen which is associated with a polychaete worm has been located in the USNM collections. The author believes that some nomenclatural confusion exists around this worm. One of the species of polychaete worms that Walcott (1911*c*, p. 119) included in the genus *Canadia* Walcott was *C. dubia*. He noted that it was 'a small chaetiferous annelid not over 10 mm in length. One specimen shows a bundle of very fine setae on each side near the head.' This is an accurate description of *L. simplex* (formerly *C. simplex*) as illustrated by Walcott 1931. The trivial name *dubia* suggests, furthermore, that Walcott was uncertain about placing the species in *Canadia*. Moreover, his description of another polychaete *C. irregularis* Walcott, 1911*c* (p. 120) as 'A small slender species not over 20 mm in length. The setae are irregular in size and appearance and suggest partially worn macerated specimens of the slender forms of *C. setigera*', clearly does not match the specimens illustrated as *C. irregularis* by Walcott in 1931 (pl. 6, figs. 4–6; pl. 7, fig. 3) and these particular specimens can be referred to the type species of *Canadia*, *C. spinosa* (Conway Morris, 1976*b*). This description does, however, correspond closely to the specimens of *C. dubia* that were illustrated by Walcott in 1931. It is, therefore, likely that the illustrations of *C. dubia* (Walcott, 1931) should apply to the description of *C. irregularis* (Walcott, 1911*c*), and the illustration of *C. simplex* (Walcott, 1931) to the description of *C. dubia* (Walcott, 1911*c*), but final proof is lacking. The only description that definitely refers to *L. simplex* is by Resser (*in* Walcott 1931, p. 6) where he noted 'A tiny organism that appears as a slender tube with a termination surrounded by a ring of setae'. As is discussed below this species cannot be accommodated in the genus *Canadia*, and *Lecythioscopa* gen. nov. is proposed.

Stratigraphic horizon. Both the specimens are labelled 35k and so are from the Phyllopod bed of the Burgess quarry (Walcott 1912*a*). No details of the vertical distribution of this worm in the Phyllopod bed are available.

Morphology. The body can be divided into an anterior head composed of two sections, and a posterior trunk (Pl. 28, figs. 5–7; text-figs. 97, 98). Both the specimens (USNM 83937 and 198714) lack the posterior end of the trunk owing either to rock breakage or poor preparation by an earlier worker. It is likely that the body terminated as a simple tube. The lengths of USNM 83937 and 198714 are 7·3 and 4·2 mm respectively.

The anterior section of the head was a simple unarmed tube which was 0·5 mm long and 0·14 mm wide in USNM 83937, and 0·3 mm long and 0·18 mm wide in USNM 198714. The posterior section of the head was slightly swollen in USNM 198714 with respect to the anterior tube and trunk. It was 0·2–0·3 mm long, about 0·3 mm wide, and bore slender, straight spines which were between 0·2 and 0·3 mm long (Pl. 28, figs. 5–7; text-figs. 97, 98). They apparently arose in one or two circlets from this section. About twelve spines are visible, but they may have totalled over twenty in life.

The length of trunk preserved in USNM 83937 and 198714 is 6·5 and 3·7 mm respectively. It was smooth and increased in width slightly to about 0·3 mm. In both specimens the posterior half is curved (Pl. 28, figs. 5–7; text-figs. 97, 98).

The anterior section of the head in USNM 83937 has a median channel interpreted as the gut (Pl. 28, figs. 5, 6; text-fig. 97). This suggests that the mouth was terminal. The trunk of USNM 198714 contains a strip, interpreted as the gut, that extends along its entire length (Pl. 28, fig. 7; text-fig. 98). The finely granulated contents of the gut are unidentifiable. The row of five 'nodules' in the posterior trunk of USNM 83937 may also represent gut contents (Pl. 28, figs. 5, 6; text-fig. 97). No other internal organs are preserved.

Mode of life. L. simplex was apparently externally radially symmetrical and was, therefore, probably a burrower. Its scarcity is probably due to two factors: it is very small and easily overlooked especially if poorly preserved, and it probably was not originally common.

Systematic position. In comparing this species with the type species of *Canadia*, *C. spinosa* Walcott, 1911*c* (Polychaeta), it differs in so many respects that it cannot be referred to this genus. *C. spinosa* is characterized by broad notosetae that extend across the dorsum, thinner fan-shaped bundles of neurosetae, and a pair of prominent anterior tentacles (Conway Morris 1976*b*). *L. simplex* shows none of these features. There is, indeed, little evidence that this worm was a polychaete. The trunk is smooth and lacks parapodia. The anterior spines did not arise from parapodia but apparently in circles.

L. simplex does not resemble any known living or fossil genus. It does, however, have some similarity to the other archaeopriapulids. Despite superficial differences between the archaeopriapulids the basic structure of the proboscis is constant and can be divided into three zones (text-fig. 33). The head of *L. simplex* may be equivalent to the archaeopriapulid proboscis. The swollen spinose section could belong to zone I, which bears the proboscis hooks in *O. prolifica*, whilst the anterior section may be equivalent to zones II and III, which in *O. prolifica* bear the proboscis spines and spinules respectively. This comparison may be incorrect because zone III is armed in all archaeopriapulids, but appears to be smooth and unarmed in *L. simplex*. The minute size of the anterior section, however, makes this observation uncertain. It is unknown whether the head could invert.

OTHER FOSSIL PRIAPULIDS

Family PRIAPULIDAE Gosse, 1855?
Genus PRIAPULITES Schram, 1973

Type and only known species. Priapulites konecniorum Schram, 1973.

Diagnosis, modified from Schram 1973. Cylindrical and extensible body, divisible into anterior proboscis, annulated trunk, and monocaudal smooth (?) caudal appendage. Proboscis armed with simple scalids arranged in about five series per row. Rows total about twenty. Pharyngeal armature unknown. Trunk with about thirty to forty annuli.

Priapulites konecniorum Schram, 1973

Plate 29, figs. 4–7; Plate 30, figs. 1–3

1973 *Priapulites konecniorum* Schram, pp. 985, 987, 989, pl. 1, figs. 1–4; text-fig. 1A.

Diagnosis. As for the genus.

Holotype. PE 21555.

Paratypes. PE 21412, H 125, HTP 3265 (counterpart PE 25135), unnumbered specimen in Popp Collection (private). Abbreviations H and HTP refer to private collections, see Schram (1973) for details.

Other material. PE 12789, 20069, 22487 (counterpart 32481), 24287, 24411, 32758–32760, an unnumbered specimen.

History of research and stratigraphy. P. konecniorum was described by Schram (1973) who noted details of its morphology and systematic position. The specimens, in common with the rest of the soft-bodied fauna of the Mazon Creek area (north-eastern Illinois), were found in siderite nodules of the Francis Creek Shale, Middle Pennsylvanian.

Morphology. Eleven specimens, including the holotype, were examined. The average length of the body was about 3·9 cm, although specimens with lengths of up to 6·3 cm are known. The proboscis was about 1·1 cm long and occupied about 30% of the length of the body. The proboscis had about twenty longitudinal rows (Pl. 29, fig. 4) (Schram

1973), although poor preservation and the high degree of curvature of the edges of the proboscis suggests that the total may have been higher. The proboscis rows bore scalids (the 'warts' noted by Schram 1973) which were apparently simple cones and were probably arranged in about five series per row (Pl. 29, fig. 4). Each series consisted of about six scalids that decreased in size posteriorly (Pl. 29, fig. 5). No pharyngeal armature is preserved, although the peribuccal collar is sometimes visible. The trunk had between thirty and forty annuli, which may have borne surface ornamentation (Pl. 29, figs. 4, 6, 7; Pl. 30, figs. 1-3) (Schram 1973). Schram (1973) remarked that although there were apparently two caudal appendages, most specimens have only one preserved (see also Schram, pl. 1, figs. 2, 3). The author's studies indicate that only one specimen (PE 25135) has a caudal appendage that might conceivably be interpreted as double, although preservation is too poor to be certain (Pl. 30, fig. 1). The other specimens either have one definite caudal appendage (Pl. 29, figs. 6, 7), or are not well enough preserved to reveal any details (Pl. 29, fig. 4; Pl. 30, figs. 2, 3). It is concluded that *P. konecniorum* was monocaudal. The author found no evidence to support the depiction by Schram (1973, his text-fig. 1A) of a papillate appendage. It appears to have been fairly smooth and possibly divided by transverse furrows (Pl. 29, fig. 6), which could conceivably represent relict annulations.

Systematic position. As is discussed below *P. konecniorum* would appear to be most closely related to the modern *Priapulus* (Priapulidae).

THE INTERRELATIONSHIPS OF FOSSIL AND MODERN PRIAPULIDS AND THEIR AFFINITIES WITH RELATED ASCHELMINTHES

THE details for placing *Ottoia prolifica*, *Selkirkia columbia*, *Louisella pedunculata*, *Ancalagon minor*, and *Fieldia lanceolata* within the Phylum Priapulida are given below. The position of *Priapulites konecniorum* has already been established (Schram 1973). *S. rara* is almost completely ignored here because it is based on a single incomplete specimen. Exact comparison with the other archaeopriapulids is somewhat tentative. Similarly, *L. simplex* is not considered here because its affinities with the archaeopriapulids cannot be definitely established. Each genus is sufficiently distinct from the others to warrant placing it in a separate family. The feature common to the archaeopriapulids is the spiny or hooked proboscis. It has the same basic structure in these Cambrian priapulids as well as in the modern priapulids. It can be divided into three distinct zones (text-fig. 33) (to avoid confusion of tenses when comparing modern and extinct forms in this section the features of the archaeopriapulids are referred to in the present tense).

Zone I. This, the proximal zone of the fully everted proboscis, carries hooks (in *O. prolifica*, *A. minor*, and *F. lanceolata*), spines (in *S. columbia*), or papillae (in *L. pedunculata*). The variation in the type of armature of this zone as well as zones II and III, while significant for familial diagnosis, does not exclude these worms from the Priapulida. The equivalent armature of the modern priapulids, the scalids, also shows considerable variation.

Zone II. The chief characteristic of this zone is that, with the exception of a proximal row of elongate spines in *O. prolifica*, *S. columbia*, *L. pedunculata*, and possibly

F. lanceolata, it is unarmed and smooth. These spines could be considered as modified distal armature zone I but they are so distinctive that a separate zone is recognized.

Zone III. This is the most distal zone and it is capable of complete eversion in *O. prolifica*, *S. columbia*, and *L. pedunculata*. The proximal half is armed with teeth disposed in quincunxes. In *O. prolifica*, *S. columbia*, and all modern priapulids the teeth are multispinose. The teeth of *L. pedunculata* and probably *F. lanceolata* are, however, simple spines, while those of *A. minor* are hooks. Despite this variation in the three latter species, as compared with the other priapulids, the similarity of the teeth in arrangement and relative position on the proboscis demonstrates that they are almost certainly homologous.

Notwithstanding the common proboscis structure, a separate family is proposed to accommodate each archaeopriapulid genus. Comparison of the archaeopriapulids with the three extant families of priapulids, i.e. the Priapulidae, Tubiluchidae, and Maccabeidae, shows that none of the archaeopriapulids can be placed in these modern families. Furthermore, the characters used to separate the archaeopriapulid families are of comparable importance to those used to divide the recent priapulid families. *S. rara* and *L. simplex* are not sufficiently understood to merit formal establishment of new families to accommodate these worms.

Description of Archaeopriapulid families

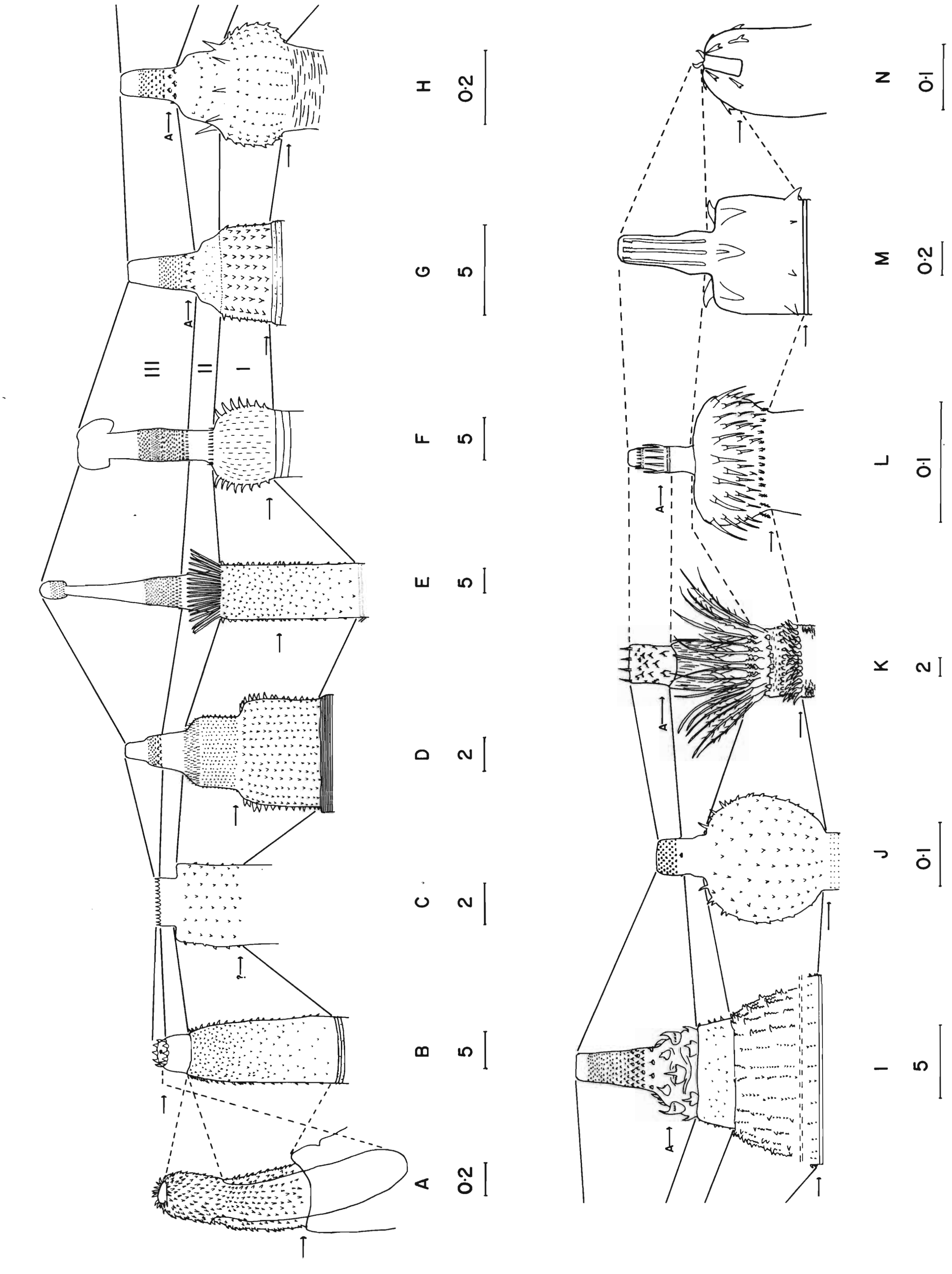
Ottoiidae Walcott, 1911. Nom. correct Howell, 1962. Emend. herein

This family is here emended to include only *O. prolifica*. *A. minor*, *O. tenuis*, and *Banffia constricta*, which were included by Walcott (1911*c*), are removed. *A. minor* is the sole representative of a new family of priapulids, the Ancalagonidae. *O. tenuis* and *B. constricta* are unrelated to the priapulids (Conway Morris 1976*b*). The Ottoiidae is the most closely related archaeopriapulid family to the Priapulidae, and acts as an intermediate group between the extant Priapulidae and the other archaeopriapulids. The Ottoiidae is, however, distinguished from the latter family by the presence of zone II proboscis spines (except in the post-larva of *Priapulopsis bicaudatus*), posterior hooks and a bursa, as well as the ability to evert completely zone III of the proboscis. The arrangement and morphology of the proboscis armature of the Ottoiidae is, however, so similar to that of the Priapulidae that the placement of the former family in the priapulids is certain.

The Ottoiidae differs from the other archaeopriapulids by absence of trunk spines and the possession of posterior hooks.

Selkirkiidae fam. nov.

Walcott (1911*c*) included *Selkirkia columbia* within the Canadiidae (Polychaeta) Walcott, 1911, nom. correct Howell, 1962, although in the same paper he stated (p. 118) that this family contained only the genus *Canadia*. Moreover, his diagnosis for the Canadiidae shows that *S. columbia* cannot belong to this family. A new family, the Selkirkiidae, is proposed. Discussion of other possible members in addition to *S. columbia* will be found below. The spinules of zone III are similar to those of the Ottoiidae and modern priapulids, although the rest of the proboscis armature is rather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different. Although both the Selkirkiidae and Maccabeidae are tubicolous, the two families differ in most details and are not closely related.

Differences with the other archaeopriapulids include possession of an annulated tube and having zone I of the proboscis divided into two sub-zones.

Miskoiidae Walcott, 1911

Walcott (1911*c*) placed only one species, *Miskoia preciosa*, in this family. Another species of *Miskoia*, *M. placida* Walcott, 1931, is synonymous with *O. prolifica*. The synonymy of *M. preciosa* with *L. pedunculata* has been discussed above. In keeping with principles of zoological nomenclature, the original family name is retained as Walcott (1911*b*) did not name a family to contain *L. pedunculata*. The relationship of the Miskoiidae with modern priapulids stems from the common proboscis structure. Otherwise they have few details in common.

The Miskoiidae is distinguished from other archaeopriapulids by a papillate zone I and small spines on the distal part of zone III of the proboscis. In addition the trunk carries two rows of papillae.

Ancalagonidae fam. nov.

A. minor is removed from the Ottoiidae because of the substantial differences with the type species *O. prolifica*. A new family, the Ancalagonidae, is proposed to accommodate *A. minor*. The affinity of the Ancalagonidae with modern priapulids is based, as with the Miskoiidae, on the proboscis structure. This family may also be fairly close to the ancestors of the acanthocephala.

TEXT-FIG. 33. Diagram showing homology between probosces of archaeopriapulids (B–F) and modern priapulids (G–K). Each proboscis can be divided into three zones: I–III; see text for full explanation. The variation in proboscis armature is given in Tables 2 and 3. The attempt to homologize the acanthocephalan proboscis (A) with the priapulid proboscis is by taking zone I as equivalent to the hooked proboscis and zone III to the proboscis receptacle. The zones cross each other because the proboscis receptacle never everts, whereas the apparently equivalent zone III does, or can be induced to, in the priapulids. The kinorhynch proboscis (L) may be equivalent to that of the priapulids. The probosces of the nematomorphs *Gordius* (M) and *Nectonema* (N) are probably homologous to one another. They are included here because their basal hooks may belong to zone I, whilst the stylets and pincers could be placed in zone III. As in the Acanthocephala, a counterpart to zone II cannot be clearly identified. →, furthest observed point of eversion of proboscis; A →, point beyond which proboscis does not normally evert so that artificial eversion has been used to reveal the distal part of zone III. A, *Centrorhynchus globocaudatum* (Acanthocephala), from Yamaguti 1963, fig. 565. B, *Ancalagon minor* gen. nov. (Ancalagonidae). C, *Fieldia lanceolata* (Fieldiidae). D, *Selkirkia columbia* sp. nov. (Selkirkiidae). E, *Louisella pedunculata* (Miskoiidae). F, *Ottoia prolifica* (Ottoiidae). G, *Halicryptus spinulosus* (Priapulidae), based on Théel 1906, pl. 2, fig. 12. H, *Priapulopsis bicaudatus* (Priapulidae, larval form) from Sanders and Hessler 1962, fig. 5C. I, *Priapulopsis bicaudatus* (Priapulidae), from Théel 1906, pl. 2, fig. 10. J, *Tubiluchus corallicola* (Tubiluchidae), from Calloway 1975, fig. 1.2 and Land 1970, fig. 52. K, *Maccabeus tentaculatus* (Maccabeidae), from Por and Bromley 1974, fig. 1 and unpublished photograph by C. B. Calloway. L, generalized kinorhynch based on *Echinoderes*, from Remane 1936, figs. 211 and 240.2. M, *Gordius* (Nematomorpha), from Mühldorf 1914, pl. 2, fig. 21 and Dorier 1965, fig. 1003. N, *Nectonema munidae* (Nematomorpha), from Huus 1931, fig. 3*a*. Scale lines with values beneath are in mm.

The details of the proboscis are sufficiently different from the other families to justify erection of this new family. In particular the armature of zone III is reduced to a small number of basal hooks.

Fieldiidae *fam. nov.*

This family is established to hold *Fieldia lanceolata.* Comparison with modern priapulids is via the basic structural similarity of the proboscis. The Fieldiidae is distinguished by the spiny trunk and enlarged sediment-filled midgut.

Other than placing these five families in the Priapulida, no satisfactory way of amalgamating them into higher taxa has been found. Each family has certain similarities with others but no consistent pattern emerges. *A. minor* is the most isolated, and *F. lanceolata* may represent a form intermediate between *A. minor* and the other archaeopriapulids. The common spinule (zone III) structure of *O. prolifica* and *Selkirkia columbia* may be significant, whilst the over-all morphology of the probosces of *O. prolifica* and *L. pedunculata* is similar. *Scolecofurca rara* may be closest to *L. pedunculata.* Spiny trunks are common to *L. pedunculata*, *A. minor*, and *F. lanceolata.* The differences between the genera are, however, such that coherent grouping is impossible. The order Miskoa Walcott, 1911*c* cannot be utilized.

Salvini-Plawen (1974) divided the extant priapulids into two orders: the Priapulimorpha, which includes the Tubiluchidae and Priapulidae, and the Seticoronaria which includes the Maccabeidae. His diagnosis for the two orders were: 'Order (nov.) Priapulimorpha: free-living Priapulida, introvert with longitudinal rows of separate hook-to-spine-shaped scalids; frequently with one or two body appendages; forward locomotion with help of introvert. Order (nov.) Seticoronaria: semi-sessile Priapulida with introvert armature in oblique rows (and circles), the foremost being setae and those behind as differentiated scalids; tactile bristles around the mouth; backward locomotion with help of posterior end.' The archaeopriapulids share characteristics with both orders. The validity of these orders as now understood cannot be upheld.

Immediate relationships of the Archaeopriapulids

Relationships to polychaetes, sipunculids, and echiuroids. As some authors have discussed the affinity of some of the archaeopriapulids with worms other than priapulids it is necessary to make some brief comments.

Walcott (1911*c*) considered *L. pedunculata* (as *M. preciosa*) and *Selkirkia columbia* to be polychaetes. Robison (1969) agreed with Walcott's assignation of *S. columbia.* Madsen (1957) interpreted *L. pedunculata* (*sensu* Walcott 1911*b*) as a terebellid polychaete. Walcott (1911*c*) mistook the trunk papillae of *L. pedunculata* for parapodia, but neither this species nor *S. columbia* has any definite polychaete features. Walcott (1911*c*) tentatively placed *O. prolifica* and *A. minor* within the Gephyrea, which comprises the Priapulida, Sipunculida, and Echiuroidea. He realized that they possessed both similarities and differences with modern Gephyrea, and he implied that the ancestors of the Gephyrea, such as *O. prolifica*, were annulated. Walcott also indicated that the affinity of *Ottoia* was greatest with the sipunculids. The Gephyrea is now considered to be an artificial group (e.g. Hyman 1959), and its three members are usually taken to be separate phyla. Following the dismantling of the Gephyrea, *Ottoia* was assigned to the sipunculids (Howell 1962).

O. prolifica has some similarities with the sipunculids (Banta and Rice 1976). The proboscis, termed the introvert in the sipunculids, has a terminal mouth and retractor muscles in both groups. This similarity is without phylogenetic significance because the proboscis is an organ common to burrowing worms with a fluid-filled body cavity (Clark 1964). Moreover, the sipunculid introvert bears tentacles, and although a few species (e.g. *Onchnesoma steenstrupii*) lack these tentacles, there is no evidence that they are primitive (Shipley 1892). *Golfingia* is believed to be the most primitive sipunculid (Clark 1969). Although the introvert often carries hooks and papillae (e.g. Shipley 1892, 1893; Théel 1905), which have a superficial resemblance to the proboscis armature of the archaeopriapulids, they are never arranged in the basic three zones of the archaeopriapulid proboscis. The gut of archaeopriapulids is straight and not systematically coiled and recurved like that of the sipunculids (Meyer 1933). The anus of the sipunculids is located near the base of the introvert, whereas it is terminal in the archaeopriapulids.

The echiuroids possess a non-retractable unarmed proboscis with the mouth at its base. The trunk bears a pair of anterior setae and sometimes a posterior circle or semi-circle of setae as well (text-fig. 16). Their closest relations are with the annelids (Clark 1969), albeit rather distant (Newby 1940). Although the posterior setae of *Urechis caupo* are arranged in a semi-circle (Fisher and MacGinitie 1928*a*) like the posterior hooks of *Ottoia prolifica*, there is no evidence that they are homologous. The absence of anterior setae and the entirely different proboscis of the archaeopriapulids strengthens Meyer's (1933) opinion that there is no affinity between the two groups.

Walcott (1911*c*, p. 111) suggested that *Ottoia* and *Banffia* could 'link the Chaetopoda and Hirudinea' within the Annelida. It is generally accepted, however, that the leeches are derived from oligochaetes (e.g. Clark 1969). The archaeopriapulids bear no significant resemblance to oligochaetes or polychaetes and, as would be expected, no similarity to leeches or fossils (*Epitrachys* and *Palaeohirudo*) interpreted as leeches by Kozur (1970).

Relationships to priapulids. Nearly all discussion on the affinity of *O. prolifica* has led to a relationship with the priapulids being established, although some authors have also noted similarities with the kinorhynchs and acanthocephala (Meyer 1933; Størmer 1944; Lang 1953; Gekker and Ushakov 1962; Banta and Rice 1976). None of these workers, however, placed *O. prolifica* actually within the Priapulida; indeed, Lang (1953) considered that the presence of posterior hooks in *O. prolifica* removed it from the priapulids.

There is a marked similarity between the probosces of *O. prolifica* and modern priapulids, and in both groups the proboscis can be divided into the three zones (text-fig. 33). The distal zone III of the everted archaeopriapulid proboscis bears spinules, spines, or hooks that are equivalent to the pharyngeal teeth of modern priapulids (Table 2). In particular, the spinules of *O. prolifica* (Banta and Rice 1976) and *S. columbia* are very similar to the teeth of recent priapulids (text-figs. 8, 9, 23). They are both multispinose with a large central cusp flanked by smaller ones. Their morphology, moreover, varies along the length of zone III in both archaeo- and recent priapulids.

TABLE 2. Comparative morphology of everted zone III armature in priapulids

	Number of proximal pentagonal circles	First (proximal) row of teeth	Middle rows of teeth	Last (distal) rows of teeth
Ancalagonidae	?None	Hooks	Absent	Absent
Fieldiidae	None	Spines	?Absent	?Absent
Selkirkiidae	None	Multispinose	Multispinose, decreasing in size	Probably multispinose
Miskoiidae	None	Spines	Spines, decreasing in size	Probably small spines
Ottoiidae	None	Conical with fringe of spines (type A)	Multispinose and spinose (types B and C)	Multispinose (type D)
Priapulus caudatus (Priapulidae)	7, largest teeth in fourth circle	Slightly reduced, multispinose	Multispinose, decreasing in size	Spines
Priapulopsis bicaudatus (Priapulidae)	5, largest teeth in third circle	Greatly reduced	Multispinose, decreasing in size	Spines
Halicryptus spinulosus (Priapulidae)	6, largest teeth in second and third circles	Unreduced	Multispinose, decreasing in size	Spines
Tubiluchidae	?1	?Papillae	Pectinate, all of same size	Fimbrillae
Maccabeidae	6 or ?7	?Sclerotized trabeculae	Multispinose, about same size, all in pentagons	Very elongate spines

The first five to seven rows of teeth in the Priapulidae are arranged in pentagonal circles (text-fig. 1c) and these proximal circles evert during feeding. The more distal teeth are disposed quincunxially and they never normally evert. All the zone III armature of the archaeopriapulids is, however, arranged quincunxially. It is proposed that the quincunxial arrangement is primitive and the basal pentagons of teeth are a post-Cambrian development, unless the ten circum-oral hooks of *A. minor* formed two pentagonal circles. The reasons for adopting pentagonal symmetry are not clear. The basal pentagons alternate with one another so that the corners of one pentagon are opposite the edges of the adjacent one, i.e. a quincunxial arrangement persists (text-fig. 1c). It is suggested that some teeth were enlarged for more effective predation, whilst the intervening ones were suppressed. The primitive quincunxial pattern was, however, maintained so that there are ten 'teeth locations' around the mouth. Thus the pentagonal symmetry is a response to the problem of 'squaring a circle' with a limited number of quincunxially arranged teeth. Furthermore, teeth of a single pentagon on opposite sides of the mouth cannot interfere (Nichols 1967). The most proximal circle of teeth in most of the Priapulidae, especially *Priapulopsis*, has a somewhat different morphology to that of the succeeding rows (Land 1970, figs. 24–25), and thus the teeth are comparable to the distinctive type A spinules of *O. prolifica*. Calloway (1975) suggested that the five anteriormost buccal or collar papillae of adult *Tubiluchus* were homologous to the five sclerotized trabeculae located on the margin of the buccal tube and pharynx of *Maccabeus* (Por and Bromley, 1974). The author suggests that these papillae and trabeculae represent the first pentagonal circle of greatly modified pharyngeal teeth. Most of the other teeth in the Priapulidae and Maccabeidae are similar to the type B spinules of *O. prolifica* and spinules of *S. columbia*. In these two archaeopriapulids as well as the Priapulidae the teeth decrease in size forwards in the fully everted zone III. The most distal teeth of *Priapulus* (Ehlers, 1861, pl. 20, fig. 8; Hammond 1970*a*), *Halicryptus* (Ehlers, 1862, pl. 34, fig. 11), and *Maccabeus* (Por and Bromley, 1974, pl. 3, fig. *c*) consist of single spines and so are comparable to the type C spinules of *O. prolifica*. No extant priapulid has spinose teeth succeeded by multispinose teeth, unlike *O. prolifica* where the spinose type C is followed by type D spinules. The structure of the pectinate teeth and more distal fimbrillae of *Tubiluchus* differs from the other priapulids (Land 1970; Kirsteuer and Rützler 1973). The spinules of *O. prolifica* and *S. columbia* appear to be closer to the teeth of priapulids other than *Tubiluchus*.

The zone III armature of the other archaeopriapulids, i.e. oral spines of *L. pedunculata*, proboscis hooks of *A. minor*, and proboscis spines of *F. lanceolata*, differ from the multispinose teeth of modern priapulids. Judging by its position on the proboscis this armature can, however, be regarded as strictly equivalent.

In modern priapulids the pharyngeal teeth are succeeded by a collar which on inversion forms the buccal tube. The collar carries a variable number of irregularly arranged minute papillae which in *Halicryptus* and *Priapulus* resemble minute scalids (Hammond 1970*a*; Land 1970). The pharyngeal teeth and proboscis scalids (see below) are so similar in shape and arrangement to the spinules (zone III) and proboscis hooks (zone I) respectively of *O. prolifica*, that the homology of the intervening proboscis zone II can hardly be doubted. In *O. prolifica*, *Selkirkia columbia*, *L. pedunculata*, and possibly *F. lanceolata*, the proximal end of zone II bears anteriorly directed spines. Most modern priapulids lack prominent armature on this part of the proboscis, but some have noticeable spines or papillae on the proximal part. The rest of the collar has inconspicuous armature, and the number of papillae is very variable (Land 1970). In the archaeopriapulids the distal part of zone II appears to be unarmed. Although the prominent zone II armature could be interpreted as specialized zone I scalids, the author regards them as distinct for the following reasons: they are always located on the proximal part of the collar; in modern priapulids, unlike the scalids, they are not arranged in twenty-five fold symmetry; they are usually elongate. A recent priapulid with prominent zone II armature is the larva of *Pr. bicaudatus* (= *P. atlantisi* Sanders and Hessler, 1962, see Land 1970) which has eight elongate collar papillae. Por and Bromley (1974) and Salvini-Plawen (1974) suggested that the eight trigger spines of *Maccabeus* are homologous to the collar papillae of other modern priapulids. Calloway (1975) proposed, however, that the eight papillae that surround the oral area of *Tubiluchus* represent the first row of scalids, and are equivalent to the larval papillae of *Pr. bicaudatus* and the trigger spines of *Maccabeus*. The author would propose, however, that the papillae of *Tubiluchus* are also collar (zone II) armature. The eightfold symmetry of the prominent collar armature is striking. If the zone II spines of the archaeopriapulids are homologous, there must have been a reduction from the total of forty to fifty spines observed in *O. prolifica* and other archaeopriapulids. It is conceivable that the zone II proximal armature of the archaeopriapulids is a multiple of eight. Zone II of *A. minor*, and perhaps *F. lanceolata*, lacks conspicuous armature and is similar to the poorly armed collar of most recent priapulids. It is clear from the above discussion how inappropriate Banta and Rice's (1976) term 'collar hooks' is for the zone I proboscis hooks of *O. prolifica*.

The proximal part of the proboscis in modern priapulids bears twenty-five longitudinal rows of papillae, spines, or hooks that, despite their variation in morphology, are termed scalids (Land 1970). The scalids can be arranged either in one longitudinal set, as in adult *Halicryptus*, *Tubiluchus*, and all the larval priapulids (Sanders and Hessler 1962; Land 1970), or in numerous longitudinal sets that are separated from one another by distinct gaps, as in the adult *Priapulus* and *Priapulopsis* (Land 1970). Each set consists of a number of scalids, typically about seven, that decrease in size posteriorly. Banta and Rice (1976) stated that the 'priapulids lack obvious counterparts to the . . . spine-hook rows (of *O. prolifica*)'. It is difficult to see, however, what more likely counterpart there is than the proboscis scalids. Not only are they situated on the same part of the proboscis, i.e. zone I (text-fig. 33), but their shape, arrangement, and number, especially amongst the Priapulidae is directly comparable to the proboscis hooks of *O. prolifica*. The scalids of modern priapulids are not of a constant form (Table 3). In *Maccabeus*, for example, the scalids form specialized glandular, trifid, sensory, and tentacular spines (Por and Bromley 1974) that have little superficial similarity to the scalids of other priapulids. Thus, although the proboscis hooks of *O. prolifica* are not identical to the scalids, there is no reason to doubt their basic affinity. The variety of scalids present in recent priapulids is paralleled by the spines, hooks, and papillae on zone I of the archaeopriapulid proboscis (text-fig. 33).

TABLE 3. Comparative morphology of proboscis and trunk in priapulids and possibly related aschelminthes

	Zone III (phaeyngeal teeth)	Zone II (collar)	Zone I (scalids)	Trunk
Acanthocephala	?Proboscis receptacle	?	Hooks	Smooth or annulated, with or without spines
Ancalagonidae	Hooks	Unarmed	Spinose hooks	Annulated, setae ?in concentric rows
Fieldiidae	Spines	Unarmed	Hooks	Spines, some in concentric rows
Selkirkiidae	Multispinose teeth	Proximal spines	Spines	Anterior rows of papillae, otherwise smooth
Miskoiidae	Spines	Proximal spines	Papillae	Spines in concentric rows, two longitudinal rows of papillae
Ottoiidae	Multispinose teeth	Proximal spines	Hooks	Annulated, with posterior hooks
Priapulites (?Priapulidae)	Unknown	Unknown	Conical scalids	Annulated
Priapulus (Priapulidae)	Multispinose teeth	Tiny papillae	Conical scalids	Annulated, with papillae and posterior ring papillae and warts
Priapulopsis (Priapulidae)	Multispinose teeth	Tiny papillae	Telescopiform scalids	Annulated, with papillae, tumuli, and posterior ring papillae
Halicryptus (Priapulidae)	Multispinose teeth	Tiny papillae	Curved scalids	Annulated, with spines
Tubiluchidae	Pectinate teeth and fimbrillae	Papillae	Complex scalids	Tumuli in rows, with flosculi and tubuli
Maccabeidae	Multispinose teeth	Proximal spines	Four types of scalid	Tubercules in roughly concentric rows
Kinorhyncha	Spines	?Oral styles	Scalids	Zonites, with spines
Gordioidea	?Triple stylets	?Unarmed	?Spines	Annulated, with posterior spines
Nectonematoidea	?Pincers	?Unarmed	?Hooks	Smooth

Apart from variations in size, the zone I archaeopriapulid armature has a more or less constant form in any species, unlike *Maccabeus* where distinctly different types of scalid co-exist. A difference between modern priapulids and *O. prolifica* is that in the former the scalids are arranged in twenty-five longitudinal rows (Calloway 1975), whereas the proboscis hooks of *O. prolifica* form about thirty longitudinal rows. If the rows of spines between the hooks represent reduced hooks the total would be doubled to about sixty. The anomalous figure of sixteen for the single row of sensory scalids in *Maccabeus* (Por and Bromley, 1974) was replaced by a total of twenty by Salvini-Plawen (1974). Land (1970) also noted twenty rows of scalids in *Tubiluchus*, although Calloway (1975) cited twenty-five. A quincunxial pattern is recognizable in the zone I armature of *O. prolifica* and *Selkirkia columbia*, although it is less discernible in the other archaeopriapulids. The quincunxial pattern of the zone I armature, like that of the zone III teeth, appears to be primitive, and the longitudinal rows of scalids present in most modern priapulids represents a more recent development.

The probosces of *O. prolifica*, *S. columbia*, and *L. pedunculata* can be everted further than those of extant priapulids. Thus, whereas in the latter group the proboscis never naturally everts beyond the proximal teeth of zone III, all of zone III in these archaeopriapulids can be exposed. A possible explanation why eversion is restricted in modern priapulids is that little adjustment is required for the proboscis to change from burrowing to eating positions, whereas in *O. prolifica* and *L. pedunculata* the proboscis would have to invert substantially in *O. prolifica* from stage 6 to stage 3 (text-figs. 12, 29).

The trunk of modern priapulids is variously ornamented (Land 1970). The trunk of the Priapulidae is annulated, whereas those of the Tubiluchidae and Maccabeidae are not. Similarly, amongst the archaeopriapulids only *O. prolifica* and *A. minor* have annulated trunks. The trunk spines of *L. pedunculata* and *F. lanceolata*, and probably those of *A. minor* are arranged in an annular fashion, as are the trunk tubercules of *Maccabeus* (Por and Bromley, 1974; Salvini-Plawen 1974) and the anterior tumuli of *Tubiluchus* (Calloway, 1975). The trunk specializations of the archaeopriapulids appear to be simple spines. Although poor preservation may have obscured fine details, no definite equivalent to the flosculi, tumuli, and other cuticular specializations of some priapulids (especially tubiluchids) (Land 1970; Kirsteuer and Land 1970; Kirsteuer and Rützler 1973; Por and Bromley 1974) has been noted. The trunk tubercules of the tube-dwelling *Maccabeus* (Por and Bromley, 1974) are not similar to the anterior trunk papillae of *S. columbia*.

A definite counterpart of the posterior hooks of *O. prolifica* has not been identified in recent priapulids. The 'anal hooks' of *Halicryptus* (Banta and Rice 1976) are, in fact, two setae (Théel 1906, pl. 2, fig. 13). They are not comparable to the posterior hooks, although they may have an affinity with the two posterior spines flanking the anus of *Maccabeus* (Por and Bromley, 1974; Salvini-Plawen 1974). *Maccabeus* also has a posterior circlet of forty-five to sixty hooks (Por and Bromley 1974; Salvini-Plawen 1974). Although the posterior hooks of *O. prolifica* form only a semi-circle, they would seem to approach the condition in *Maccabeus* fairly closely.

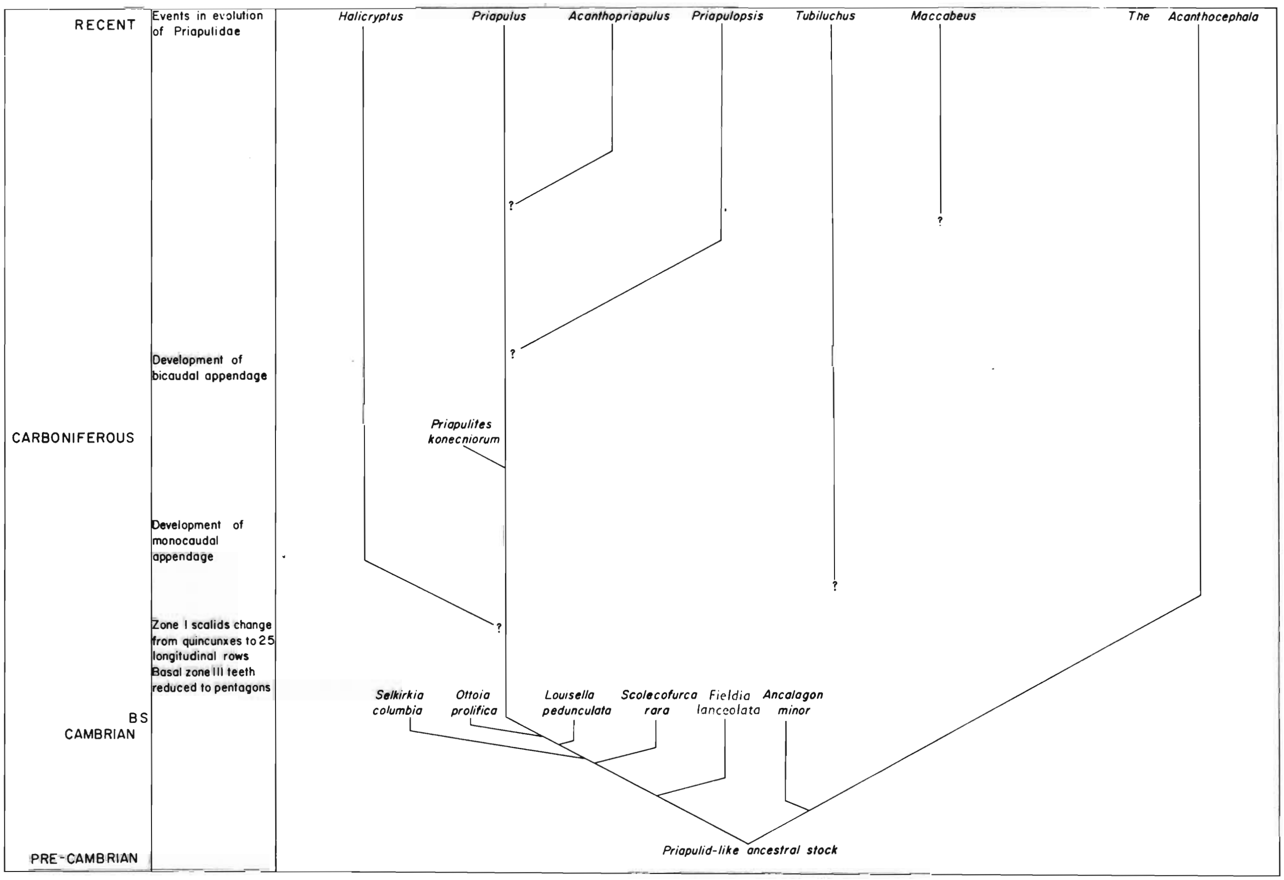
The eversible extension of the posterior trunk of *O. prolifica* (the bursa) and *L. pedunculata* (trunk division D) is not comparable to the caudal appendage of some priapulids because the latter does not carry the gut and is not invertible.

The detachment of the cuticle from the body wall noted in some archaeopriapulids suggests that they moulted. The modern priapulids also moult (Lang 1948*a*; Carlisle 1959; Shapeero 1962*a*, *b*; Land 1970; Por and Bromley 1974).

The evidence outlined above gives strong support to previous suggestions that *O. prolifica* is related to the priapulids. So great is the resemblance that the author has no hesitation in including this species in the priapulids. The discovery of *Tubiluchus* (Land, 1968, 1970) and *Maccabeus* (Por, 1972; Por and Bromley 1974; Salvini-Plawen 1974) has shown the diversity of modern priapulids to be greater than previously realized. *O. prolifica* is the most closely related of the archaeopriapulids to the recent priapulids, and it acts as an intermediate form between the two groups. The other more diverse archaeopriapulids have distinct priapulid characteristics and should also be placed within this phylum.

It is probable that the Cambrian witnessed an evolutionary radiation of the priapulids. The other soft-bodied Cambrian faunas, e.g. from Emu Bay Shale (Glaessner 1976), Kinzer Shale (Resser and Howell 1938), and Spence Shale (Robison 1969) appear to lack, with the possible exception of *Selkirkia*, fossil priapulids, but as is discussed below all have yielded the annelids *Protoscolex* or *Palaeoscolex*. These annelids are absent from the Burgess Shale and their possible mutual exclusion with archaeopriapulids may be due to ecological conditions such as substrate and oxygen concentrations. Additional evidence for the postulated radiation of the priapulids may, however, be forthcoming from study of Cambrian trace fossils. The marked eversion of the probosces, together with the use of the swollen distal end, in *O. prolifica* and *L. pedunculata* (text-figs. 12, 29) suggests their trace may have been comparable to the distinctive burrowing trace left by *Sipunculus* (Schäfer 1972, fig. 160). The other archaeopriapulids may have left burrows similar to those of modern priapulids (Schäfer 1972, fig. 136). Search in Cambrian rocks for such trace fossils may well prove profitable. They apparently became the dominant macro-worm group in at least some muddy marine sediments, as can be seen by the relative abundance of the archaeopriapulids as compared with other groups of worms in the Burgess Shale. Polychaetes predominate in deep-sea marine sediments today (e.g. Sanders and Hessler 1969) and the priapulids are either absent from or form an insignificant part of most benthonic faunas. The Priapulidae exist in cold waters and often in anaerobic muds which are inhospitable to most metazoans (Wesenberg-Lund 1929; Fänge and Åkesson 1952; Land 1970), whilst *Tubiluchus* and *Maccabeus* are members of the meiobenthos (Land 1970; Por and Bromley 1974). Hence, the Priapulida has found protected niches that avoid competition with more successful worms (Land 1970).

The finding of a Pennsylvanian (Upper Carboniferous) priapulid, *Priapulites konecniorum* Schram, 1973, in conjunction with the knowledge of recent priapulids allows some considerations on priapulid phylogeny (text-fig. 34). Schram (1973) noted that this worm differed noticeably from *Halicryptus*. He failed to distinguish *Priapulopsis* from *Priapulus* treating them together under the latter genus, and noted that *Priapulites konecniorum* differed 'in having fewer proboscis ridges, fewer trunk annulae, and a relatively shorter proboscis'. The author believes, however, that considerable affinity exists with *Priapulus*. In particular there is the similarity of the monocaudal appendage, number of annuli, scalid type and arrangement, and proportion of proboscis to trunk. Differences include the apparent absence of papillae



TEXT-FIG. 34. Phylogeny of the Priapulida and Acanthocephala. The six genera from the Burgess Shale (BS) demonstrate the Cambrian radiation of the priapulids. The stratigraphic position of *Priapulites konecniorum* is from Schram (1973). The age of the branching of the modern genera from the central stock is very uncertain. The *Halicryptus* stock probably evolved in pre-Carboniferous times, the *Priapulopsis* stock in post-Carboniferous times. The origins of the *Tubiluchus* and *Maccabeus* stocks are uncertain. The Acanthocephala are shown to be derived from a Precambrian priapulid which was probably not far removed from *Ancalagon minor* gen. nov.

on the caudal appendage and apparently fewer rows of scalids, although as discussed above the total may have been greater, perhaps equalling twenty-five rows. The generic distinction between *Priapulites* and *Priapulus* is valid, but it is possible that the former genus should be placed in the Priapulidae. The early occurrence (Carboniferous) of the monocaudal condition suggests that the bicaudal appendage of *Priapulopsis* may have arisen by fission after the Pennsylvanian. Additional evidence that *Priapulopsis* is more evolved than *Priapulus* includes the greater number of series of scalids. The author considers *Acanthopriapulus* to be derived, if at all, from the *Priapulus* stock rather than vice versa. This is based on the following facts: *Acanthopriapulus* has a specialized monocaudal, spiny appendage; the arrangement of the scalids is loose with little trace of longitudinal rows, and none of the primitive quincunxial pattern remains.

O. prolifica has a greater similarity to *Halicryptus* than to any other genus of the Priapulidae, although they differ in size with *O. prolifica* averaging 8 cm and *Halicryptus* 3 cm (see Ehlers 1862). The author has, however, noted specimens of the latter worm up to 9 cm long in the USNM. The two genera have the following features in common: both lack a caudal appendage and have numerous (about a hundred) annulations, whereas the other Priapulidae possess one or two caudal appendages and have fewer annulations. The proboscis of *Halicryptus* and the equivalent zones in *O. prolifica* occupy only about 10% of the total length of the animal; the proportion of the proboscis is greater in the remaining Priapulidae. Both genera have only one longitudinal set of scalids (= proboscis hooks), and the posterior scalids have lateral flanges of spines, although only *Halicryptus* has bifid teeth at the distal ends of these scalids. The other Priapulidae possess numerous sets of scalids, none of which bear lateral flanges of spines. Finally, neither genus has posterior ring papillae (see Land 1970) unlike the other genera. Por and Bromley (1974) and Salvini-Plawen (1974) suggested, however, that the posterior hooks of *Maccabeus* are homologous with the ring papillae. If the posterior hooks of *O. prolifica* have an affinity with those of *Maccabeus*, a connection with the ring papillae is conceivable.

It is suggested, on the strength of the similarities between *O. prolifica* and *Halicryptus*, that the *Halicryptus* stock arose before the evolution of the caudate Priapulidae; possibly before the Pennsylvanian. *Halicryptus* would seem to be the most primitive of the extant Priapulidae. The absence of *Halicryptus* from normal marine environments suggests that it was unable to compete with the other Priapulidae (Land 1970).

The origins of *Tubiluchus* and *Maccabeus* are difficult to determine. The adult *Tubiluchus* appears to retain some primitive features. These include the quincunxial arrangement of the pharyngeal teeth with the possible exception of a basal pentagonal circle, although the larva has several such circles of teeth (Land 1970). The scalids form a single series in longitudinal rows (like *Halicryptus*), but a quincunxial pattern is still clearly recognizable (Calloway 1975). The ability of the pharynx to evert further than in other modern priapulids may also be primitive. *Tubiluchus* has, however, individual features such as the distinctive teeth which are probably specialized adaptations to its meiobenthonic habit (Land 1968, 1970). It is uncertain why the larva should have the apparently more advanced feature of pentagonally arranged teeth which are similar to those of the Priapulidae (Land 1970). It is considered unlikely that the primitive features of the adult would have persisted if the *Tubiluchus* stock had derived directly from a primitive *Priapulus* type. The *Tubiluchus* stock may have arisen from a Cambrian ancestor, possibly not too distant from the *Ottoia–Halicryptus* stock, which suggests that its monocaudal condition arose by parallel evolution. *Maccabeus*, on the other hand, appears to have advanced features (Por and Bromley 1974), such as the specialized scalids, and few primitive characteristics. The lack of the caudal appendage may be secondary and due to its semi-sessile mode of life, unlike *Halicryptus* where its absence is probably primitive. All the teeth of *Maccabeus* are arranged in pentagonal circlets, with the exception of the last row which consists of fifteen (= 5 × 3) teeth (Por and Bromley 1974). It was suggested above that pentagonal symmetry was imposed on originally quincunxially arranged teeth, and in *Maccabeus* this process has nearly reached completion. If it is assumed that the five pharyngeal trabeculae represent teeth, they are among the most modified first circlet known in the priapulids. *Maccabeus* is not closely related to the tubicolous *S. columbia*. The tube of the former genus is formed from agglutinated plant fragments and is unannulated (Por and Bromley 1974), whereas in *S. columbia* it is secreted entirely by the animal and is annulated. The proboscis morphology of these two genera also differs considerably in detail. Størmer's (1944) suggestion that the tube of *S. columbia* is comparable to the lorica that encases larval priapulids would appear to be unfounded although both are cuticular products. The lorica is longitudinally ridged, unannulated, usually bears tubuli, and sometimes has anterior accessory plates (see Land 1970).

The stocks that included *S. columbia*, *L. pedunculata*, and *F. lanceolata* apparently became extinct and have left no recognizable descendants (text-fig. 34). *A. minor*, whilst belonging to the archaeopriapulids, appears to have affinities with the phylum Acanthocephala and may be close to the ancestors of that phylum. The priapulids, especially the archaeopriapulids, are rather isolated from each other. The evolution of the Priapulida probably produced many other forms.

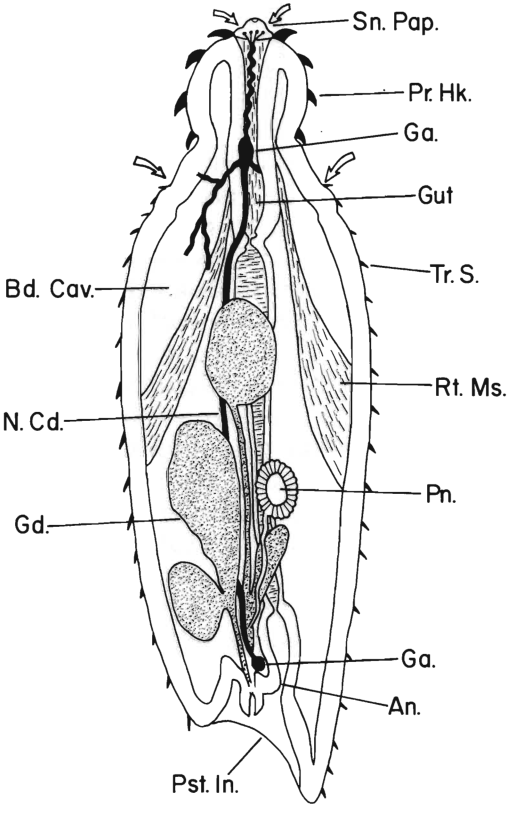
It is worth speculating when the priapulids were relegated to the minor role that they have in modern infaunal communities. The majority of archaeopriapulids were carnivorous. The appearance of scolecodonts in the Ordovician belonging to eunicid-like polychaetes suggests that they replaced the archaeopriapulids as the major infaunal predators at this time. The persistence of carnivorous polychaetes suggests that the priapulids never recovered their dominance. The septate nature of the polychaetes, which permitted more efficient burrowing, must have also been a factor in superseding the aseptate priapulids. The priapulids have remained infaunal and, unlike the polychaetes, have never managed to diversify into other habitats.

Wider relationships of the archaeopriapulids to other groups. The priapulids may belong to the larger group of Aschelminthes, which also includes the kinorhynchs, gordioids, rotifers, gastrotrichs, nematodes, and possibly more distantly the acanthocephala (Hyman 1959). Possible affinities of the archaeopriapulids with some of the aschelminthes are now discussed.

Relationships to Acanthocephala. O. prolifica has also been allied with the acanthocephala (Meyer 1933; Golvan 1958). The acanthocephala are a completely endoparasitic phylum of worms, with a life cycle alternating between vertebrate and arthropod hosts (see Hyman 1951; Yamaguti 1963; Nicholas 1967, 1973; Bullock 1969). They have a characteristic hooked proboscis that can introvert into a receptacle (text-fig. 33). A neck separates the trunk (frequently spiny) from the proboscis. Internally there is no gut, but the reproductive organs are prominent. The body cavity is extensive and is lined with a non-nucleated membrane. Some authors have suggested that the acanthocephala are related to the platyhelminthes (Chitwood 1950; Petroschenko 1952) and in particular the parasitic cestodes (Van Cleave 1941*a*). Such similarities that exist are most probably due to convergence of these two specialized parasitic groups (Golvan 1958; Nicholas and Hynes 1963; Nicholas 1971; Whitfield 1971*b*) and there are significant differences (Monné 1959; Crompton and Lee 1965; Lee 1966). Other authorities could not discern a clear relationship with any other phylum (Hyman 1951), although complete divorce from other groups is unlikely. Another school of thought places them close to at least some of the aschelminthes (Haffner 1950; Whitfield 1971*a*, *b*) and the priapulids in particular (Meyer 1928, 1933, 1938; Lang 1953, 1963; Golvan 1958). This latter opinion is adopted here. Comparison of the acanthocephala to the priapulids is, however, necessarily difficult, because the former group is so completely adapted to a parasitic way of life. The fullest discussion on the relationship between the two groups is by Golvan (1958). One of the points of difference which he considered important, i.e. unlike the priapulids the cuticle of the acanthocephala is not moulted, may not be relevant as Cable (1968) has reported moulting in acanthocephala.

Meyer (1933), Lang (1953), and Golvan (1958) placed *O. prolifica* closest to the acanthocephala, especially on the basis of the common possession of a spiny anterior. *O. prolifica* was compared by Meyer and Golvan to *Corynosoma*, *Bolbosoma*, and *Centrorhynchus*, although these genera do not appear to be primitive. Attempts to homologize the probosces of priapulids and acanthocephala are difficult. The proboscis receptacle of acanthocephala is believed to be directly derived from the foregut (Haffner 1950), and as such could be homologous to the priapulid pharynx (zone III) (Lang 1963). The hooked acanthocephalan proboscis may be equivalent to the scalid-bearing zone I of the priapulid proboscis (Lang 1953). The opinion of Meyer (1933) and Golvan (1958) that the proboscis hooks (zone I) of *O. prolifica* are situated on the anterior trunk, and that only the narrower anterior part of the proboscis is equivalent to the acanthocephalan proboscis is considered here to be incorrect. The quincunxial arrangement of the proboscis hooks of the acanthocephala is also found in the proboscis hooks of *O. prolifica* and proboscis spines of *Selkirkia columbia*, although the zone I armature of the other archaeopriapulids appears to be less regular. Haffner's (1950) assertion that a difference between priapulids and acanthocephala is that the scalids of the former group are not arranged quincunxially is unimportant. This is because the development of longitudinal rows of scalids is a more recent development. The distinctive anterior blade-like hooks of the young acanthocephala (see Grabda-Kazubska 1964) bear less resemblance to the proboscis hooks of *O. prolifica* than the adult. Contrary to the statement by Banta and Rice (1976) the posterior spines of acanthocephala, such as *Corynosoma*, *Telosentis*, and *Illiosentis* (Van Cleave 1918, 1923; Van Cleave and Lincicome 1939) are not hooks and are not bilaterally arranged. They have little resemblance to the posterior hooks of *O. prolifica* and are better regarded as a remnant of spines that once covered the entire trunk (Golvan 1959). The suggestion by Banta and Rice (1976) that the gut of *O. prolifica* was invested by a membranous tube is not supported by the researches of the author. This negative evidence is important because in acanthocephala a ligament sac surrounds the ligament strand. The ligament strand is believed to be derived from the mid-gut (Haffner 1942, 1950). If the membranous tube existed in *O. prolifica* it could have been interpreted as a proto-ligament sac.

The ancestors of the acanthocephala must have been free-living. Haffner (1950) and Golvan (1958) illustrated a hypothetical reconstruction of a free-living ancestral acanthocephala: the proto-acanthocephala (text-fig. 35). If this proto-acanthocephala is compared with the archaeopriapulids it is clear that its general morphology is like that of *A. minor*. The proboscis of the latter worm, however, has numerous spinose hooks rather than the relatively 'few large hooks' (Golvan 1958) which the proto-acanthocephala possesses. Van Cleave (1941*b*, 1952) has also suggested that the primitive acanthocephala has few proboscis hooks. The hooks of the proto-acanthocephala are arranged quincunxially (Haffner 1950; Golvan 1958). While the proboscis hooks of *A. minor* may have this arrangement, there is no doubt that the proboscis hooks of *O. prolifica* are so disposed. As in the proto-acanthocephala the probosces of the archaeopriapulids, perhaps with the exception of *A. minor*, can invert. The trunk spines of acanthocephala are a primitive feature (Van Cleave 1952; Golvan 1959; Golvan and Deltour 1964), and the spiny trunk of the proto-acanthocephala has its counterpart in trunk spines of *L. pedunculata*, *A. minor*, and *F. lanceolata*. The lacunar system within the body wall of acanthocephala is believed to have arisen as a



TEXT-FIG. 35. Hypothetical longitudinal section through the free-living proto-acanthocephala which was ancestral to the recent parasitic Acanthocephala. Arrows mark points of invagination of anterior of body. Slightly simplified from Golvan (1958, fig. 10). No scale was given by Golvan.

response to the lack of a gut (Haffner 1950). It is absent from the proto-acanthocephala and archaeopriapulids. A spacious body cavity is common to both groups. In acanthocephala the body cavity is restricted along much of the trunk by the ligament sac but it expands at either end (Haffner 1950). It may be significant that the body cavity of *A. minor* appears to show the same feature. The lemnisci, elongate lobes of tissue hanging from the neck into the body cavity, are characteristic of modern acanthocephala and probably arose late in their evolutionary history and are missing in the proto-acanthocephala (Haffner 1950; Golvan 1958). The proto-acanthocephala are free-living and therefore they have a gut. Haffner (1950) suggested that the mouth was located in the side of the proboscis, whereas Golvan (1958) positioned it, as in the archaeopriapulids, terminally. *O. prolifica* (and presumably the other archaeopriapulids) and the proto-acanthocephala possess a longitudinal nerve cord. Preservation is not good enough in any archaeopriapulid to permit unequivocal identification of a urinogenital system like that of the proto-acanthocephala. The proto-acanthocephala is also equipped with a posterior invagination that carries the gut and urinogenital openings. Upon protrusion, this invagination would give a bursa with openings at its tip. Some species of male acanthocephala possess a genital bursa (Van Cleave 1945), whilst the bursa of *O. prolifica* carries the gut although there is no definite evidence that it was genital. Furthermore, the acanthocephalan bursa may also represent the remains of the posterior gut (Haffner 1942). Some acanthocephala (Van Cleave 1945), *L. pedunculata* and, to a more limited extent *O. prolifica*, can also invert part of the posterior trunk. The proto-acanthocephala is believed, like the archaeopriapulids, to have been a burrower in marine sediments (Haffner 1950; Whitfield 1971*a*), and Nicholas (1971) proposed that the ancestral acanthocephala belonged to the interstitial fauna of sandy marine sediments. Whitfield (1971*a*) also drew attention to similarities between larval acanthocephalans, gordioids, and kinorhynchs. He suggested that these groups had a common burrowing ancestor.

It is concluded that the archaeopriapulids show suggestive similarities to the Acanthocephala and its hypothetical free-living ancestors. Comparing the modern acanthocephala, with their extreme modifications, to the evolved priapulids is difficult (Lang 1953). Comparison of the archaeopriapulids, which retain primitive features, to the hypothetical free-living proto-acanthocephala is, in some ways, more fruitful. *A. minor* has the strongest superficial resemblance to the proto-acanthocephala, although it differs in a number of respects. *A. minor* is rather isolated from the other archaeopriapulids and is considered to be the closest of them to the acanthocephalan stem group (text-fig. 34). In particular the proboscis is simpler, with the usually extensive zone III armature being reduced to a few hooks at the base of the zone. Zone III apparently could not evert further than the hooks. The disappearance of the hooks, together with the closure and atrophy of the gut, would result in an animal remarkably like an acanthocephala. *A. minor* itself is probably too large to have become parasitic on Cambrian arthropods, but Nicholas (1971) has suggested that the ancestral acanthocephala were very small. The other archaeopriapulids differ by too much to be considered as candidates for acanthocephalan ancestry.

It is suggested that the priapulids and acanthocephala had a common ancestor in the late Precambrian. The ancestor had a proboscis divided into three zones: zone I had hooks, zone II was unarmed, and zone III bore hooks or spines and was normally inverted as the first part of the gut. All the proboscis armature was disposed quincunxially. Neither Haffner (1950) nor Golvan (1958) suggested that the pharynx of the proto-acanthocephala was armed, but the affinity with the archaeopriapulids makes this conclusion reasonable. The trunk bore concentric rows of spines. The gut was straight with terminal openings. The complete adaptation of the acanthocephala to parasitism shows that this way of life was adopted long ago, possibly in the early Palaeozoic (Van Cleave 1947; Golvan 1958; Crompton 1975).

The acanthocephala were probably the first of the aschelminthes to become parasitic (Golvan 1958). The spiny proboscis, which was used for burrowing, represents an important pre-adaptation for gripping the gut wall of the host (Whitfield 1971*a*). The parasitic gordioids and nematodes arose later (Golvan 1958). Evolution amongst the acanthocephala themselves is highly speculative. There is no general agreement on which of the classes is the most primitive. A review of acanthocephalan classification is given by Bullock (1969). The Archiacanthocephala (Haffner 1950), Eoacanthocephala (Petroshenko 1956), and Palaeacanthocephala (Lang 1953; Golvan 1959) have all been identified as the most primitive, although within the Eoacanthocephala it is accepted that the Gyracanthocephala is more primitive than the Neoacanthocephala (Van Cleave 1947; Golvan 1959). Van Cleave (1947) suggested that the evolution paralleled that of their vertebrate hosts, but this view is not supported elsewhere (Golvan 1959; Golvan and Deltour 1964). The original primary host of the acanthocephala may have either been an arthropod or a vertebrate (Haffner 1950). It is possible that the earliest acanthocephala utilized Cambrian arthropods (Van Cleave 1947), which as the Burgess Shale fauna shows were very diverse, before the evolution of the vertebrates.

Despite evidence linking the priapulids and acanthocephala, there are unresolved difficulties. For instance, Whitfield (1971*b*) showed that although spermatozoa of acanthocephala is comparable to some aschelminth spermatozoa, priapulid sperm appears to be rather distinct. The peritoneal membrane of the Priapulidae apparently contains scattered nuclei (Shapeero 1961) which suggests that they are truly coelomate. This led Shapeero to regard the priapulids as an isolated phylum without close relatives because the other aschelminthes and acanthocephala appear to lack these nuclei. However, in *Maccabeus* and *Tubiluchus* no peritoneal nuclei were found, although in the former genus coelomic amoebocytes are sometimes found adfixed to the membrane lining the body cavity (Por and Bromley 1974; Calloway 1975). Furthermore, in the acanthocephala the primary body cavity forms from a mesodermal split and is not a blastocoelic cavity (Meyer 1928; Nicholas and Hynes 1963). The origin of the body cavity in other aschelminthes is also diverse (Remane 1963). The peculiar acanthocephalan body wall (Crompton and Lee 1965) may be an adaptation to parasitism and the lack of a gut.

Relationships to kinorhynchs. The nearest relatives of the priapulids are generally regarded as the Kinorhyncha (Hammarsten 1915; Lang 1948*b*, 1953, 1963; Land 1968, 1970). The kinorhynchs are minute marine animals (length about 0·5 mm) with an introversible spiny proboscis and a trunk consisting of twelve or thirteen distinctive plated ‘segments’ or zonites which usually bear spines. The musculature is reduced because of their small size. Circular muscles are confined to the first two zonites and the remainder are converted into dorso-ventral muscles. The two pairs of longitudinal muscles act anteriorly as proboscis retractors. Although the segmentation is superficial, the nerve cord is ganglionated. Like the priapulids the cuticle is moulted (Remane 1928; Lang 1949; Hyman 1951).

The probosces of the kinorhynchs and priapulids are similar (Meyer 1933) (text-fig. 33). The scalids (zone I) of the priapulids may be homologous with those of the kinorhynchs (Land 1970). Comparing the rest of the proboscis is, however, more difficult. The pharyngeal teeth, which are normally inverted, are perhaps equivalent to those of the priapulids on zone III (Lang 1963). The oral styles number eight (Remane 1928) or nine (Merriman and Corwin 1973). They are reminiscent of the zone II spines which in recent priapulids total eight. The latter spines, however, are located at the base of zone II, whereas the oral styles are a little more distal.

The early stages of development (Kozloff 1972) do not appear to throw additional light on the affinities of kinorhynchs.

Relationships to nematomorphs. The nematomorphs are also believed to have an affinity with the priapulids (Hyman 1951). They are divided into the Gordioidea and Nectonematoidea. The latter are marine and are more closely related to the nematodes than the former group. The poor fossil record consists only of adults (Voigt 1938; Sciacchitano 1955). The adult is a fusiform, free-living worm and the affinity with the priapulids is only clear with the parasitic larva (see e.g. Montgomery 1904; Mühldorf 1914; Dorier 1930, 1965; Inoue 1958; Zapotosky 1974). After hatching, the larva attaches itself with the aid of the spiny proboscis in the arthropod host. It gradually changes into a juvenile worm and leaves the host to become free-living.

The proboscis armature of the tiny gordioid larva (about 150μ long) is arranged in three concentric rows consisting of six, six, and seven spines. These spines, and presumably the short proboscis spines of the larval *Nectonema* (Huus 1931), may be equivalent to the zone I armature of the priapulids. The relative positioning of the three stylets of the gordioids and the pincers of *Nectonema* is uncertain. They cannot be assigned definitely to either zone II or III. Although the larval gordioids sometimes possess one or two pairs of posterior spines, there is no compelling reason to support Banta and Rice's (1976) view that they are comparable to the posterior hooks of *O. prolifica.*

Many of the differences between the larval nematomorphs and the priapulids, such as the blind gut and specialized glandular cells, are due to the parasitism of the former group.

Relationships to other aschelminthes. Affinities are also believed to lie between the aschelminthes discussed above and the remaining members, i.e. the Rotifera, Gastrotricha, and Nematoda. Haffner (1950), Remane (1963), Whitfield (1971*b*), and Storch and Welsch (1969) placed the acanthocephala closest to the rotifers, although other authors (Hyman 1951) regarded the rotifers as primitive and not far removed from the mollusc-annelid and flatworm stocks. The gastrotrichs are generally accepted to be closest to the nematodes (Hyman 1951; Golvan 1958). Golvan (1958) regarded the nematodes as the successful main-stock of the aschelminthes. There has been considerable discussion on the nature of the protonematode (e.g. Keilin 1926; Chitwood and Chitwood 1933; Chitwood 1950; Chabaud 1955; Inglis 1962; Maggenti

1963). Unfortunately the sparse body and trace-fossil record sheds no light on the matter (Taylor 1935; Dollfus 1950; Størmer 1963; Voigt 1957; Moussa 1970; Schram 1973). Study of the archaeopriapulids has not clarified the affinities of these aschelminthes or shed light on the protonematode.

Other fossils described as Ottoia *and* Selkirkia. A number of other fossils, mostly from the Cambrian, have been placed by Walcott and other workers in the archaeopriapulid genera *Ottoia* and *Selkirkia*. As is discussed in this section these assignations, with two possible exceptions, are untenable.

Walcott (1911*c*) described two other species with the type species *O. prolifica*. They are *A. minor* (Walcott) (= *O. minor* Walcott) which is described above, and *O. tenuis* Walcott which will be described elsewhere because it is entirely unrelated to the priapulids. The author knows of two other specimens, both located in the USNM, that have been described as *Ottoia*.

One specimen is labelled *O. inopinata* and consists of a poorly preserved part and counterpart (Pl. 30, figs. 6, 7). The counterpart has a label attached with 219a written on it. This is the USNM locality number for 'Lower Ordovician, Canadian (Levis Shales), 0·5 mile (0·8 km) NE. of east railway station, opposite Levis iron foundry, Quebec, Canada' (quoted from Resser locality file in the USNM). The identification label with the specimen gives the same information. It was apparently collected by Walcott in 1889, but has never been described. The end of the specimen that is taken to be the anterior is apparently surrounded by a dark organic stain, possibly comparable to that associated with the great majority of specimens of *M. splendens* (Whittington 1971*a*, *b*). The specimen is about 8·7 cm long, and although its shape is reminiscent of *Ottoia* there is no evidence of proboscis or posterior hooks. The animal appears to have been annulated and there are traces of the gut. It is concluded that this specimen cannot be referred to *Ottoia* and its wider relationships remain obscure.

The other specimen (USNM 90784) was described by Resser and Howell (1938, pl. 1, fig. 1) from the Kinzer Shale as *Ottoia* sp. (Pl. 30, fig. 5). These shales are of Lower and Middle Cambrian age (Resser and Howell 1938; Campbell 1971). Although the specimen is not very well preserved the annulations at one end are associated with minute papillae (Pl. 30, fig. 5). It is, therefore, comparable to members of the poorly defined papillate *Protoscolex* (in part)—*Palaeoscolex* group. This is a distinctive assemblage of Lower Palaeozoic worms that has not previously been recognized as a separate group, although Whittard (1953) noted that *Protoscolex* and *Palaeoscolex* were probably related. In 1878 Ulrich described from the Eden Series, Economy Formation (Ordovician) of Covington, Kentucky, four species of worms within the new genus *Protoscolex*: *P. covingtonensis* (the type species), *P. tenuis*, *P. simplex*, and *P. ornatus*. The author re-examined Ulrich's specimens which are in the USNM. *P. tenuis* is entirely smooth, whereas *P. covingtonensis* and *P. simplex* are annulated, but otherwise smooth and only *P. ornatus* bears one or two rows of papillae per segment. There can be little doubt that the last species is only very distantly, if at all, related to the others which are not considered further here because their taxonomic positions remain very uncertain. *P. ornatus* is however, comparable to the *Palaeoscolex* (*Pa.*) Whittard, 1953 and may even belong to this genus. Until a definitive reappraisal of this group is undertaken it would seem best, however, to maintain this and the other papillate species discussed below in *Protoscolex* (*P.*) (in part). Other worms with the characteristic rows of papillae encircling the body have been noted by Miller and Faber (1892, pl. 1, figs. 5, 6 as *P. magnus* from the Eden Series, Fulton Shale (Ordovician) of Cincinnati, Ohio), Bather (1920, text-figs. 1, 2 as *P. latus* from the Lower Ludlow Shales (Silurian) of Herefordshire), Ruedemann (1925*b*, text-figs. 27–29; pl. 14, figs. 1, 2 as *P. batheri* from the Lockport Limestone (Silurian) of Gasport, New York), Whittard (1953, pl. 4, figs. 1–3; pl. 5, figs. 1–5 as *Palaeoscolex piscatorum* from the Shineton Shales (Tremadocian) of Shropshire and Breadstone Shales (Tremadocian) of Gloucestershire), Robison (1969, pl. 138, figs. 1, 2 as *Pa. ratcliffei* from the Spence Shale (Middle Cambrian) of Utah), Glaessner (1976 as *Pa.* sp. nov. from the Emu Bay Shale (uppermost Lower Cambrian) of South Australia) and possibly Roy and Croneis (1931, pl. 44, fig. 4 as *P.* (?) *ruedemanni* from the Upper Lockport Shale (Silurian) of Illinois). In addition, Ruedemann described *P.* cf. *covingtonensis* and *P. gigantus* (1925*a*, text-figs. 63, 64 and pl. 9, fig. 8 respectively, from the transitional beds between the Utica and Frankfort beds (Ordovician) of Holland Patent, New York and Frankfort Shale near Rome, New York; see also Cisne 1973), but neither of these species can be referred to the papillate varieties of *Protoscolex*. The precise definition of *Protoscolex* (papillate forms) and *Palaeoscolex* requires examination. Table 4 reviews characteristics of some of these species. Judging by the descriptions there are several distinctive groups, all, however, characterized by two (rarely one) transverse rows of papillae per metamere. The number of papillae per row varies, but all metameres appear to be papillate. It is generally assumed that the papillae bore setae, although in no specimen have actual remains of setae been noted. The ends of the animal are conical and lack appendages. It is likely that the particular details of morphology noted by Whittard (1953) in *Pa. piscatorum* are at least partly a reflection of fine preservation, rather than especially important taxonomic differences with the other species. The *Protoscolex* (in part)–*Palaeoscolex* group ranges from Lower Cambrian (Kinzer Shale, Resser and Howell

TABLE 4. Comparisons between various species of *Protoscolex* (P.) and *Palaeoscolex* (Pa.)

	Maximum length (mm)	Approximate number of segments	Number of papillae per row	Number of rows per segment	Height of segment (mm)	Width of body (mm)
P. batheri Ruedemann 1925	118	170	60–80	2	0·7	4·3
P. ornatus Ulrich 1878	60	150	25–30	2(1)	0·23	2
P. latus Bather 1920	6·9	275	40	2	0·25	3
P. magnus Miller and Faber 1892	44	150	12–16	1	0·12	0·15
P. (?) *ruedemanni* Roy and Croneis 1931	28·5	80	?	?	0·75	1
Pa. piscatorum Whittard 1953	49	450	60–80	2	0·1	1·5
Pa. ratcliffei Robison 1969	125	400	50–80	2	0·3	2–5
P. sp. Kinzer Fm. Resser and Howell 1938	34	100	34	?	0·5	2·5–3

1938; Emu Bay Shale, Glaessner 1976) and Middle Cambrian; (Spence Shale, Robison 1969) to the Upper Silurian (Lower Ludlow, Bather 1920). These worms have been placed within the polychaetes (e.g. Ulrich 1878) and oligochaetes (Bather 1920; Ruedemann 1925*b*), although Whittard (1953) considered neither assignation likely and Stephenson (1930) rejected the proposed alliance with the oligochaetes. Although several polychaete families have become lumbricinid with reduced parapodia so that the setae arise direct from the body wall, e.g. the Capitellidae, the setae are never arranged in a continuous row around the body as probably occurred in the *Protoscolex* (in part)-*Palaeoscolex* group. In some oligochaetes, however, the setae do arise from around most of the body (the perichaetine condition). Stephenson (1930), however, noted that this arrangement is a recent adaptation and cannot be regarded as primitive. Moreover, the double row of papillae on each metamere seen in most members of the *Protoscolex* (in part)-*Palaeoscolex* group is unknown in the oligochaetes, even when secondary annuli form. Furthermore, if the simple jaws described in *Pa. piscatorum* (Whittard, 1953) were common to the group, this would represent another difference with the oligochaetes. The suggestion by Eastman (1927) and Roger (1952, 1959) that *Protoscolex* belongs to the order Miskoa Walcott, 1911*c* is untenable. The validity of the Miskoa was discussed above.

Nevertheless, if the papillae did bear setae, it would be reasonable to include this group within the Annelida on the basis of the representatives having numerous, similar, setigerous metameres. Details of the prostomium remain uncertain. This group cannot be accommodated in any of the modern classes of annelids, and its taxonomic status is uncertain. The author considers that it forms a coherent group above the family level and that it may even represent a new class of annelids. No formal diagnosis is given at present. Thus Whittard's (1953) erection of the family Palaeoscolecidae is valid, but not taxonomically high enough to define the entire group. The *Protoscolex* (in part)–*Palaeoscolex* group may have arisen from a common ancestor with the polychaetes. The ancestor of the polychaetes is believed to have been oligochaetoid (Fauchald 1974), and may have arisen from within the oligochaete stock (Clark 1964, 1969). Hence, the *Protoscolex* (in part)–*Palaeoscolex* group may be closer to this ancestral group of annelids than the polychaetes, although it is unlikely to have been the ancestral group itself as definite polychaetes are known from the Middle Cambrian (Walcott 1911*c*) and possibly earlier.

In addition to the type species, renamed herein *S. columbia* sp. nov., Walcott (1911*c*) described two other species of *Selkirkia: S. fragilis* and *S. gracilis* (now interpreted as a junior synonym of '*S.*' *major*, see above) (Walcott 1911*c*, pl. 19, figs. 8, 9). These species will be described in detail elsewhere. It will suffice to note here that because of major differences of the tube and soft parts they cannot be included within *Selkirkia* or even the priapulids.

Resser and Howell (1938) described some annulated fossil tubes from the Kinzer Shale (USNM locality no. 22L) as *S. pennsylvanica.* The author examined the two illustrated specimens in the USNM. The paratype (Resser and Howell 1938, pl. 4, fig. 10) may be a juvenile specimen of *Selkirkia*, conceivably *S. columbia.* As no soft parts are preserved identification remains uncertain. The holotype (Resser and Howell 1938, pl. 5, fig. 8) is comparable to the species *Tubulella flagellum* (Matthew) (= *Urotheca flagellum* Matthew, 1899, pl. 1, fig. 1*a–c*; *Hyolithellus flagellum* (Matthew) Walcott

1908, pl. 1, fig. 8, 8*a*; name emended by Howell 1949), which is also known from the Burgess Shale.

Robison (1969) restudied the six USNM syntypes of *S. spencei* Resser, 1939 from the Spence Shale (Middle Cambrian). He claimed that one specimen showed expansions and contractions in its diameter of between 4·0 and 5·5 mm, and came to the conclusion that the specimens were burrows of a vagrant animal rather than tubes of a sedentary organism. During the author's re-examination of the syntypes, he noted that the alternating diameter of one of the specimens was due to an overgrowth of $CaCO_3$, which upon removal exposed the fossil beneath (Pl. 30, fig. 8). With the exception of one specimen which probably is a burrow (Pl. 30, fig. 4), the others appear to be tubes (Pl. 30, fig. 8). The specimens have sharp boundaries and some of them show distinct tapering. Occasionally some of the annulations are preserved (Pl. 30, fig. 8). The placement by Resser (1939) of this species in *Selkirkia* is reasonable but definite proof is lacking.

A note on photography

With the exception of Plate 29, figs. 1–3 and Plate 30, fig. 5, which were photographed in ordinary white light, all the photographs were taken in ultra-violet light from a directional lamp. Specimens were photographed in either high- or low-angle ultra-violet light. Unless stated otherwise high-angle light was used in which the lamp was inclined to the specimen table at about 65°. The specimen was then tilted through about 10° until maximum reflectivity, as observed down the focusing tube, was obtained. In low-angle light the specimen was placed as horizontal as possible, and the angle of incident light was about 30°. After the specimen had been correctly orientated, focusing was undertaken in ordinary white light. The direction given in the plate explanations refers to the origin of the light, the top of the page being north.

Some specimens were immersed in distilled water and photographed in ultra-violet light (Pl. 17, fig. 4), or in alcohol and photographed in ordinary white light (Pl. 29, figs. 1–3). This procedure was adopted because some details of the specimens which are obscure or invisible when dry become obvious when wetted. Except for Plate 29, figs. 1–3, which were taken on Ilford N5/31 film, Panatomic-X film was used for all plate-figures.

By way of explanation some of the plate-figures have corresponding camera-lucida drawings (text-figs. 36–99) placed opposite them. Lines with hachures indicate definite breaks in slope, the hachures being directed downslope. Some of the breaks in slope result from the use of dental microdrill to remove rock that overlies a specimen (e.g. Pl. 2, fig. 7; Pl. 3, fig. 4; Pl. 5, fig. 1; Pl. 7, fig. 1; Pl. 10, fig. 2; Pl. 13, fig. 6; Pl. 21, fig. 1; Pl. 25, figs. 4, 5). Stippled areas represent rock. The linear areas filled with chevron or U-shaped lines refer to compaction ridges and grooves respectively. Unless stated otherwise all specimens are from the Burgess Shale, British Columbia.

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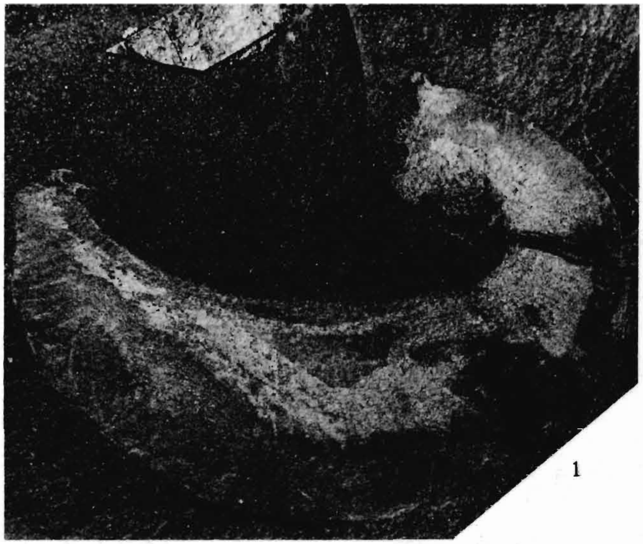
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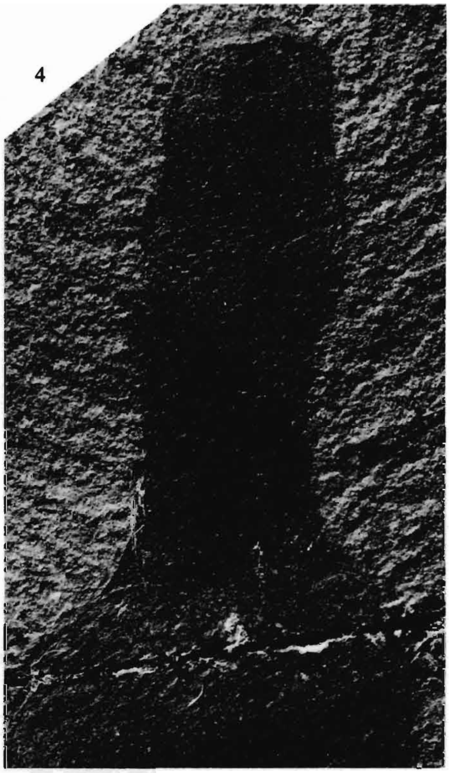
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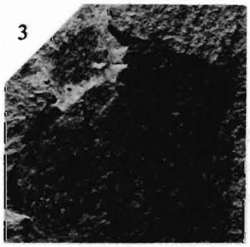
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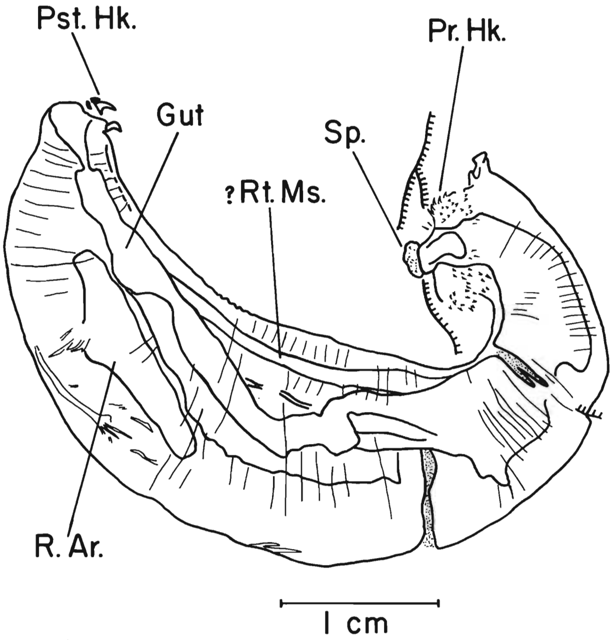
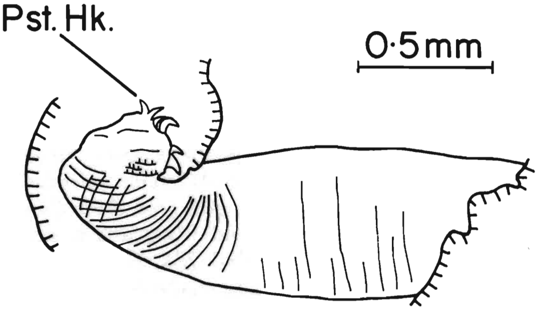
CONWAY MORRIS, *Ottoia prolifica*



TEXT-FIG. 36



TEXT-FIG. 37

EXPLANATION OF PLATE 1

Ottoia prolifica Walcott.

Fig. 1. USNM 57619. Lectotype, light from north, × 2, see text-fig. 36, original of Walcott 1911*c*, pl. 19, fig. 1.

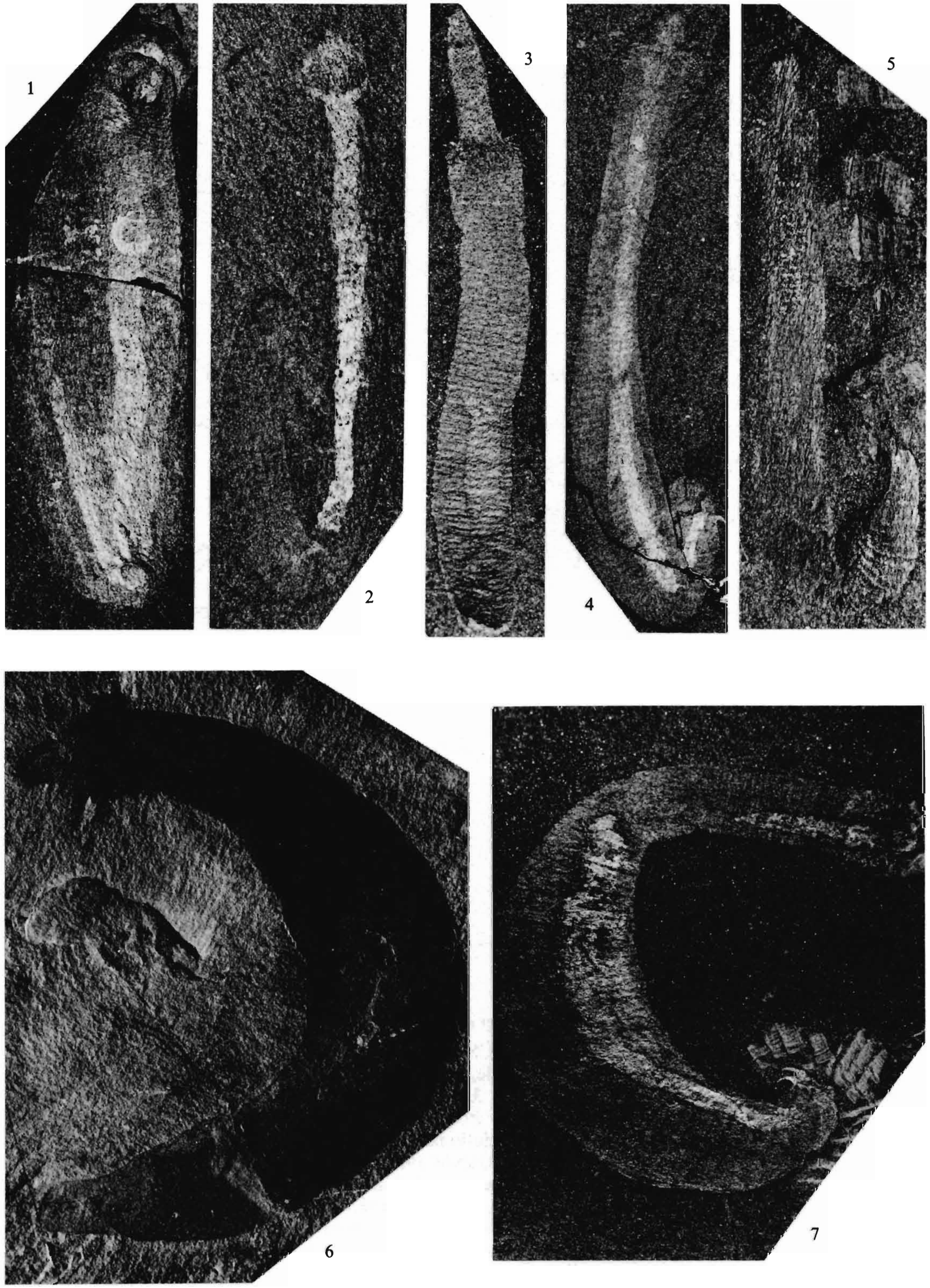
Figs. 2, 3. USNM 57620. 2, paralectotype, low-angle light from north, × 1·3, original of Walcott 1911*c*, pl. 19, fig. 2. 3, enlargement of proboscis, low-angle light from north, × 2·6.

Fig. 4. USNM 57622. Paralectotype, proboscis everted to stage 5 (see text-fig. 12), low-angle light from north, × 5·6, original of Walcott 1911*c*, pl. 19, fig. 4.

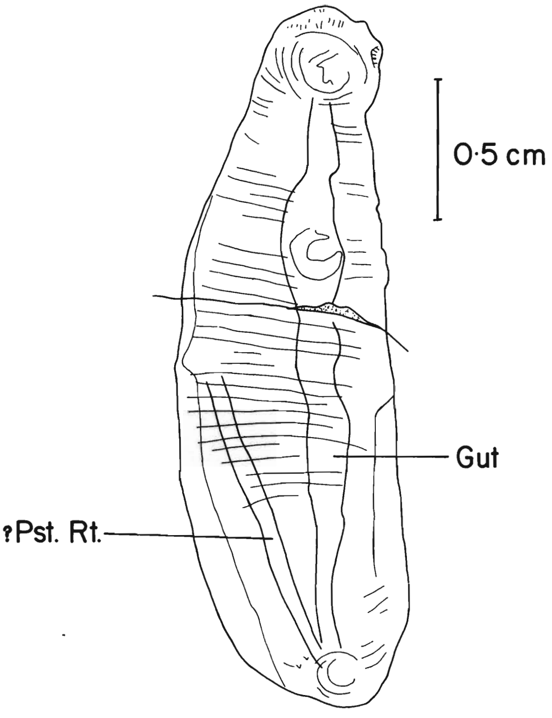
Fig. 5. USNM 57621. Paralectotype, posterior trunk with hooks, light from east, × 3·8, see text-fig. 37, original of Walcott 1911*c*, pl. 19, fig. 3.

Fig. 6. USNM 57486. Folded and decayed specimen with posterior hooks, light from north, × 2·7, original of Walcott 1911*a*, pl. 3, fig. 1.

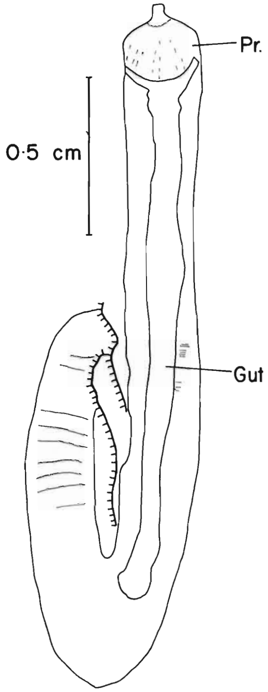
PLATE 2



CONWAY MORRIS, *Ottoia prolifica*



TEXT-FIG. 38



TEXT-FIG. 39

EXPLANATION OF PLATE 2

Ottoia prolifica Walcott.

Fig. 1. USNM 57647. Specimen with both ends upturned, light from east, × 3·8, see text-fig. 38, original of Walcott 1911*c*, pl. 22, fig. 6.

Fig. 2. USNM 83939b. Poorly preserved juvenile specimen, light from west, × 5, see text-fig. 39, original of Walcott 1931, pl. 9, fig. 2.

Fig. 3. USNM 198565. Juvenile specimen with proboscis at stage 5 (see text-fig. 12), light from west, × 6.

Fig. 4. USNM 188617. Posterior gut flanked by reflective area that may represent urinogenital organ, light from east, × 2·2.

Fig. 5. USNM 83939d. Juvenile specimen, light from north-east, × 6·6, original of Walcott 1931, pl. 9, fig. 4.

Fig. 6. USNM 57623. Paralectotype, note contraction of posteriormost trunk, low-angle light from west, × 1·3, original of Walcott 1911*c*, pl. 19, fig. 5.

Fig. 7. USNM 188616. Proboscis at stage 3 (see text-fig. 12) and arc of posterior hooks partially visible, light from north, × 4·8.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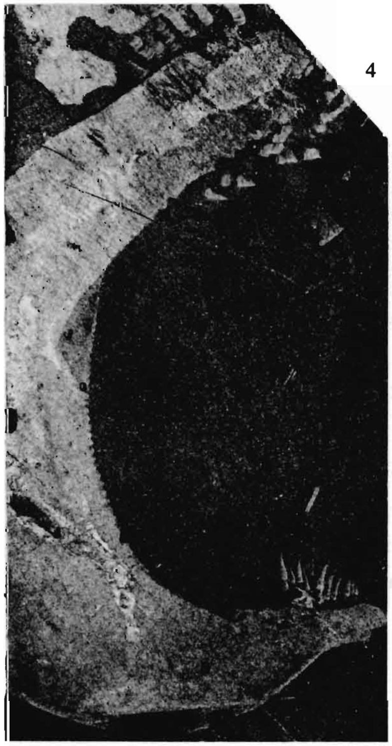
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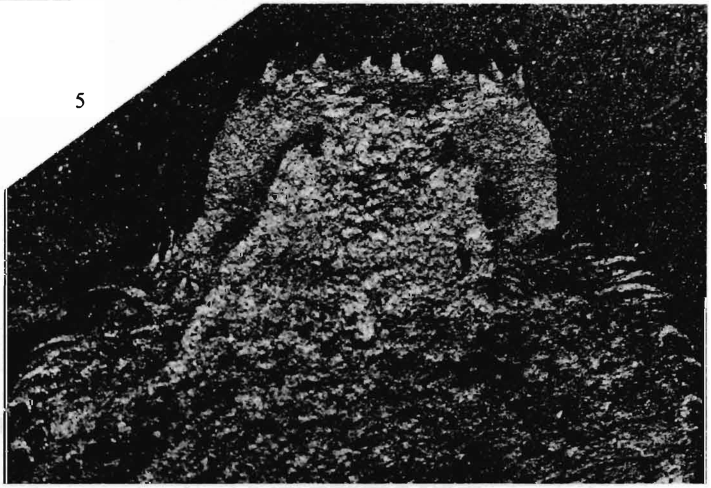
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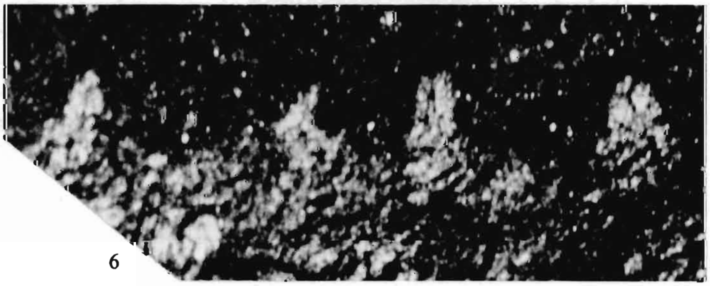
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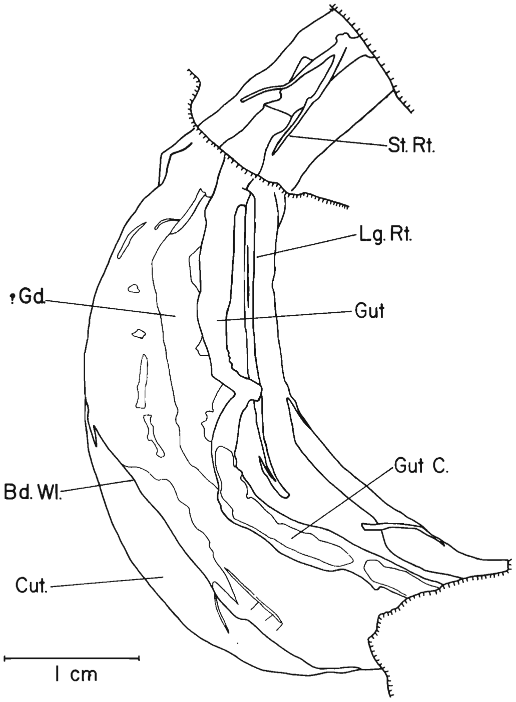
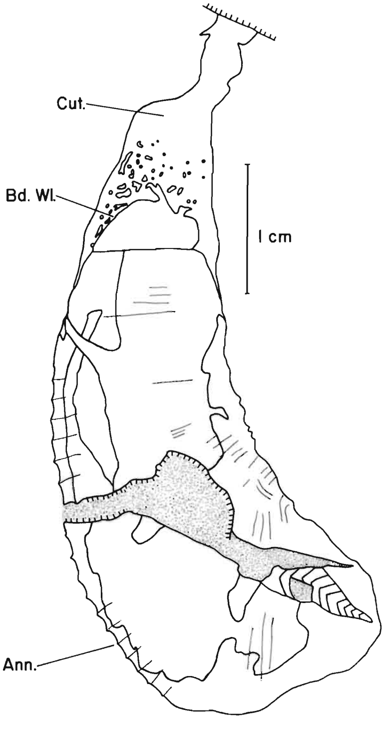
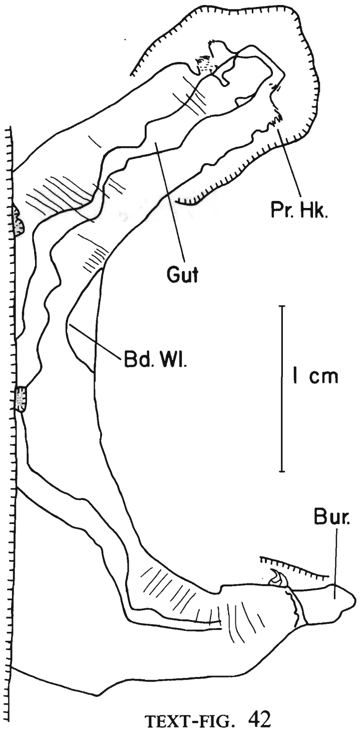
CONWAY MORRIS, *Ottoia prolifica*



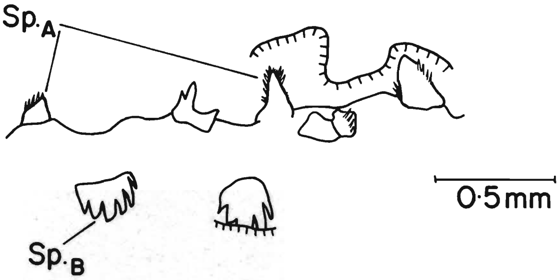
TEXT-FIG. 40



TEXT-FIG. 41



TEXT-FIG. 42



TEXT-FIG. 43

EXPLANATION OF PLATE 3

Ottoia prolifica Walcott.

Fig. 1. USNM 198589. Specimen with body wall detached from cuticle, light from east, × 2, see text-fig. 40.

Figs. 2, 3. USNM 198592. 2, contracted specimen, low-angle light from east, × 1·8, see text-fig. 41. 3, enlargement of annulations, light from west, × 15.

Fig. 4. USNM 198582. Proboscis at stage 3 (see text-fig. 12) and bursa everted, light from south-west, × 2·3, see text-fig. 42.

Figs. 5, 6. USNM 198591. 5, proboscis with type A spinules everted, light from north, × 7·6. 6, enlargement of type A spinules, light from west, × 40, see text-fig. 43.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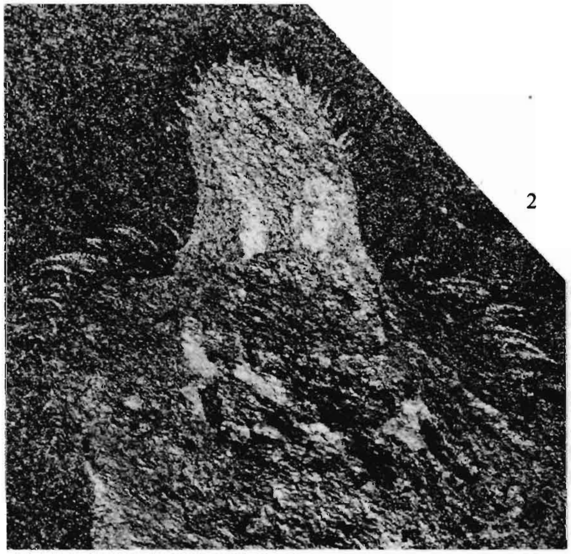
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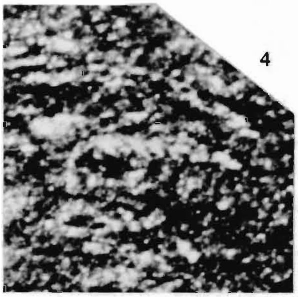
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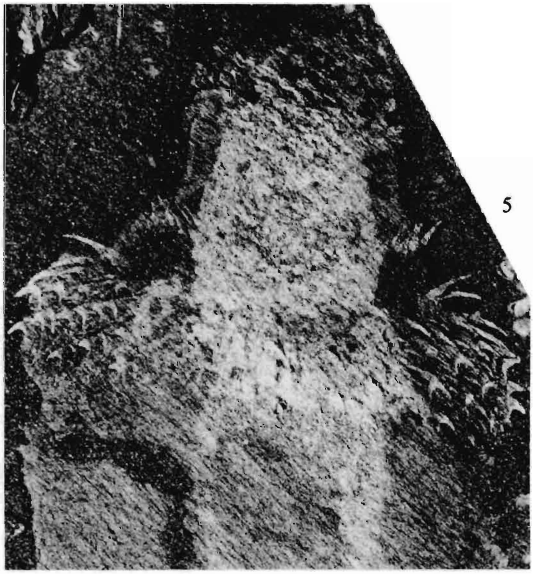
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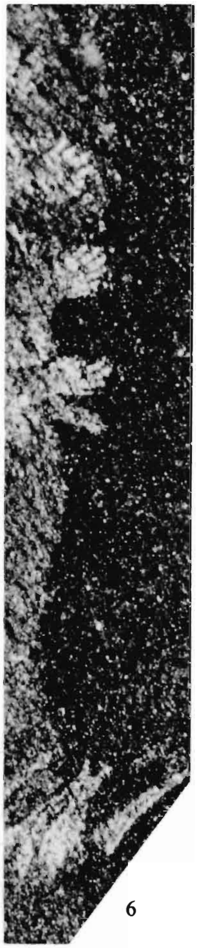
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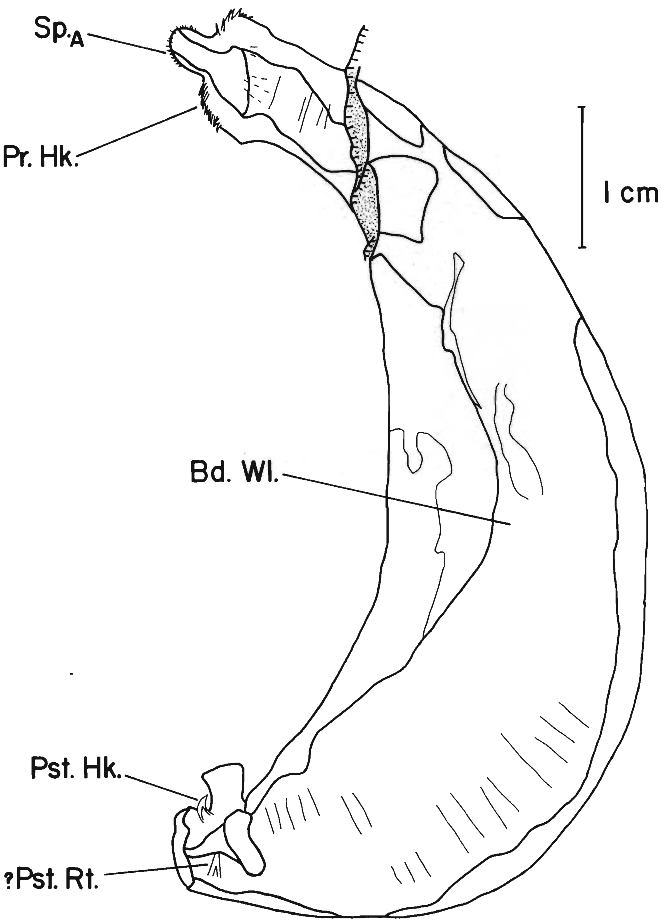
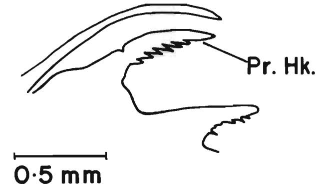
CONWAY MORRIS, *Ottoia prolifica*



TEXT-FIG. 44



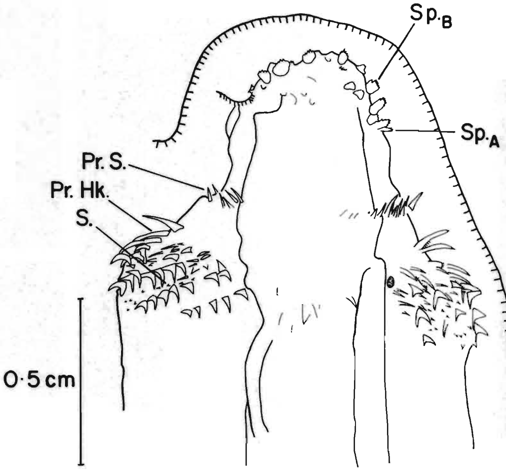
TEXT-FIG. 45

EXPLANATION OF PLATE 4

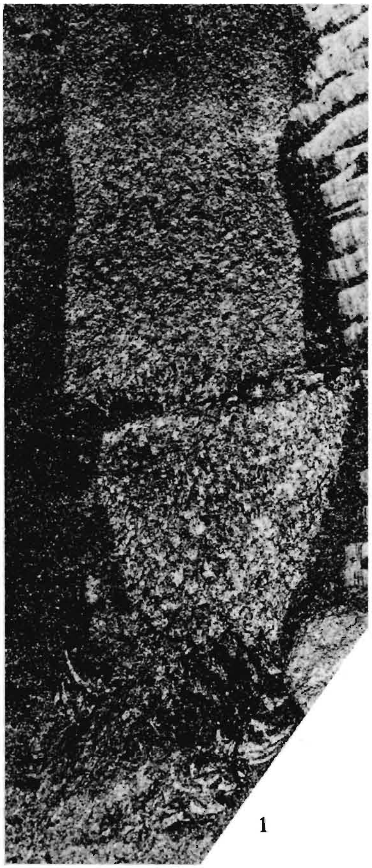
Ottoia prolifica Walcott

Figs. 1–4. USNM 188609. 1, specimen with reflectively preserved body wall obscuring internal anatomy, light from east, × 1·7, see text-fig. 44. 2, counterpart, proboscis with type A spinules everted, light from north, × 8·6. 3, enlargement of posterior trunk with possible posterior retractor muscle, light from west, × 8. 4, enlargement of proboscis hooks with lateral spines, light from north, × 38, see text-fig. 45.

Figs. 5, 6. USNM 198818. 5, proboscis at stage 4 (see text-fig. 12), light from west, × 5·6, see text-fig. 46. 6, enlargement of proboscis spinules and spines, light from west, × 22.



TEXT-FIG. 46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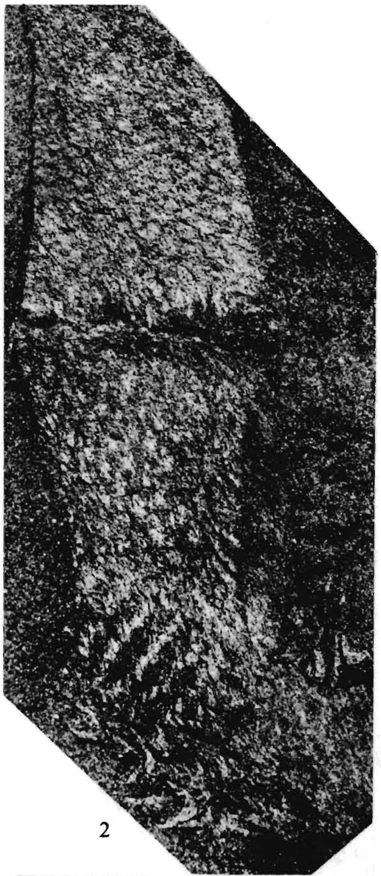
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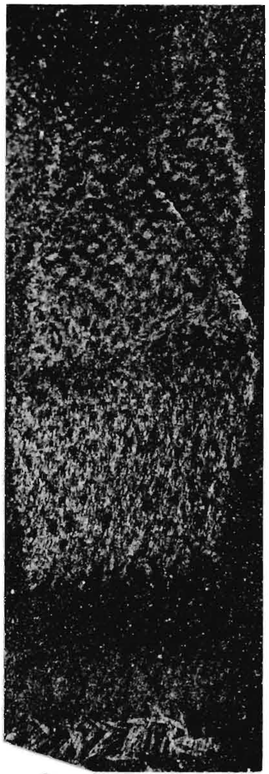
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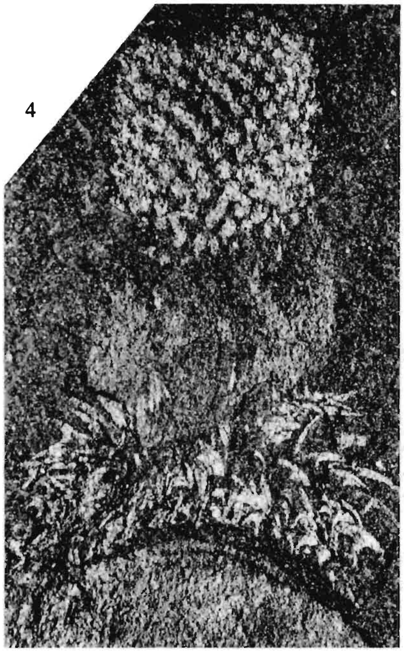
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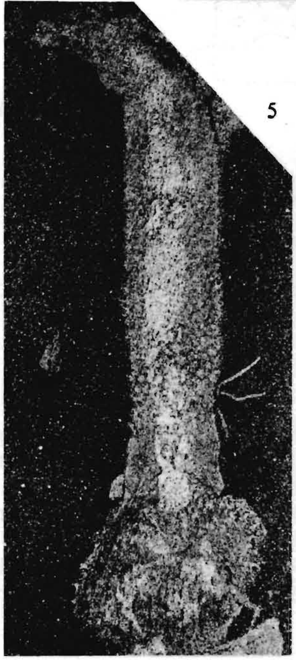
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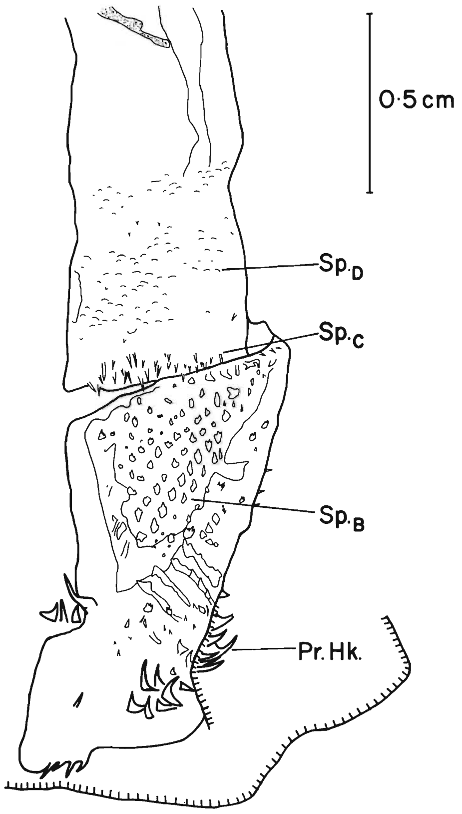
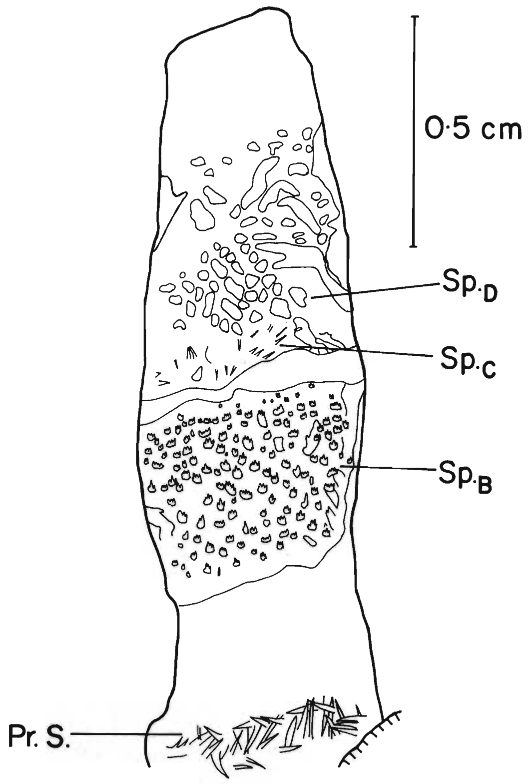
CONWAY MORRIS, *Ottoia prolifica*



TEXT-FIG. 47



TEXT-FIG. 48

EXPLANATION OF PLATE 5

Ottoia prolifica Walcott.

Figs. 1, 2. USNM 198578. 1, proboscis with hooks and spinule types B, C, and D, light from south-east, × 6·3, see text-fig. 47. 2, counterpart, light from south-west, × 7.

Fig. 3. USNM 198579. Proboscis with spines and spinule types B, C, and D, light from west, × 6·6, see text-fig. 48.

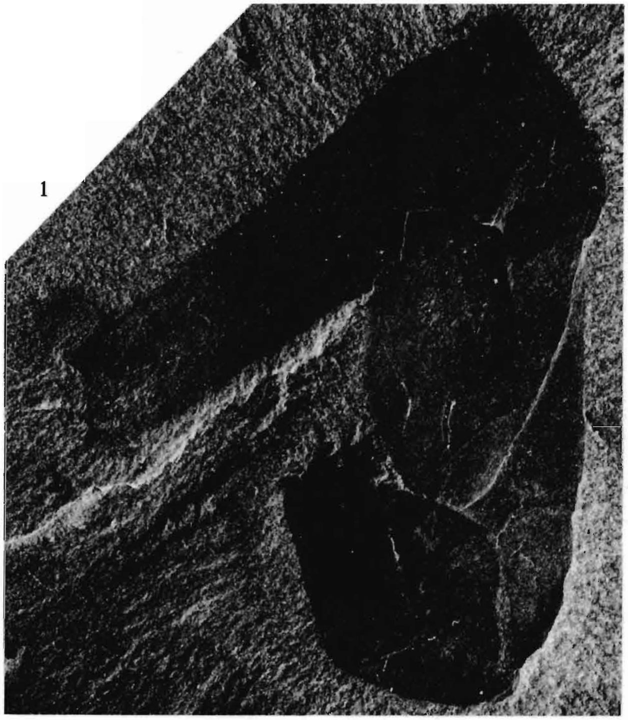
Fig. 4. USNM 172985. Proboscis at stage 4 (see text-fig. 12), light from west, × 9, original of Banta and Rice 1976, fig. 19.

Fig. 5. USNM 198594. Proboscis at stage 5 (see text-fig. 12), light from east, × 2·6.

Fig. 6. USNM 196106. Proboscis with spinules and posteriorly directed proboscis spines, light from west, × 8·2.

PLATE 6

1



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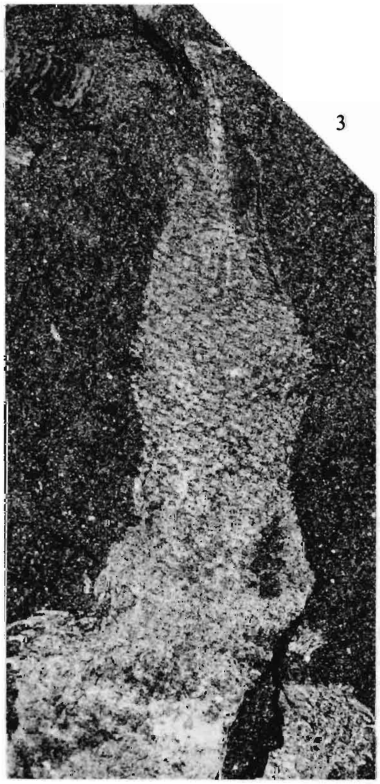

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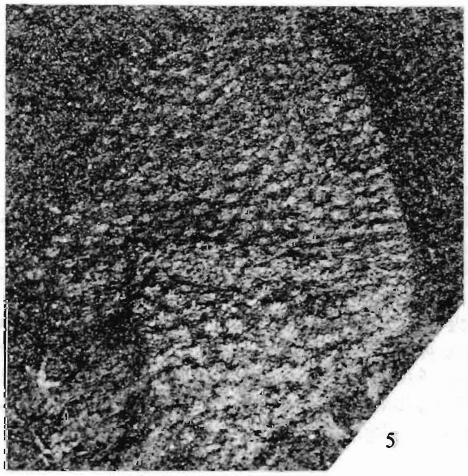

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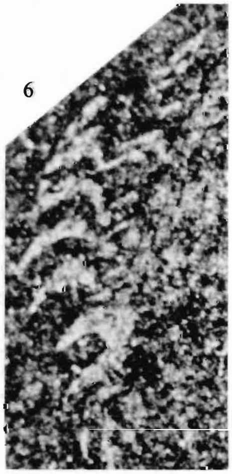
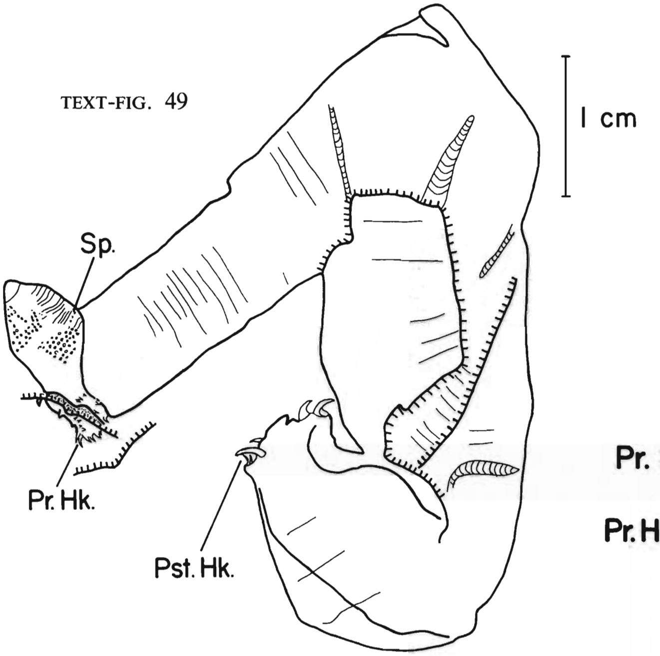
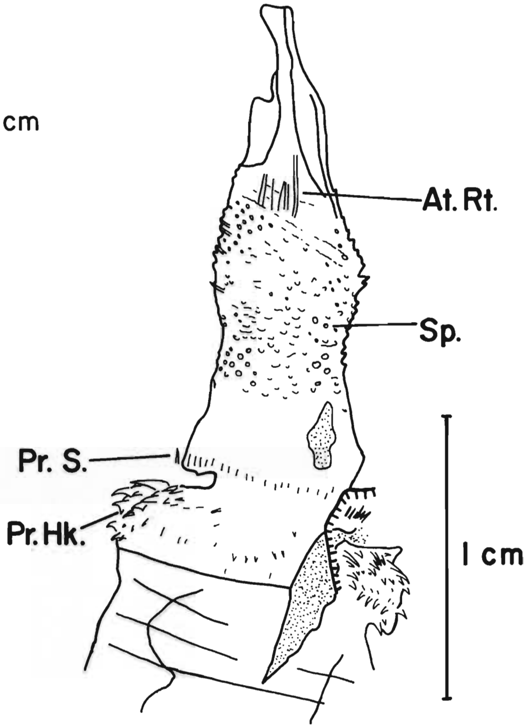


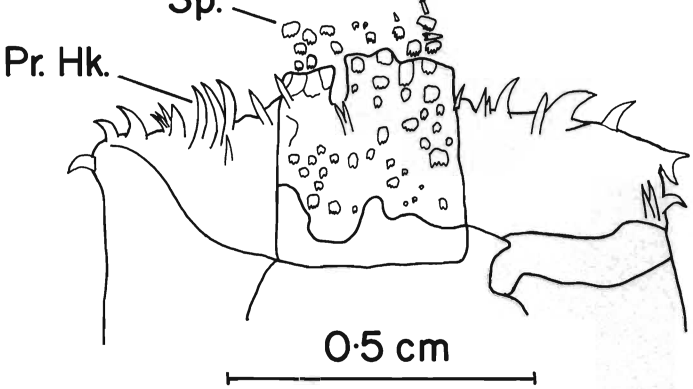
CONWAY MORRIS, *Ottoia prolifica*



TEXT-FIG. 49



TEXT-FIG. 50



TEXT-FIG. 51

EXPLANATION OF PLATE 6

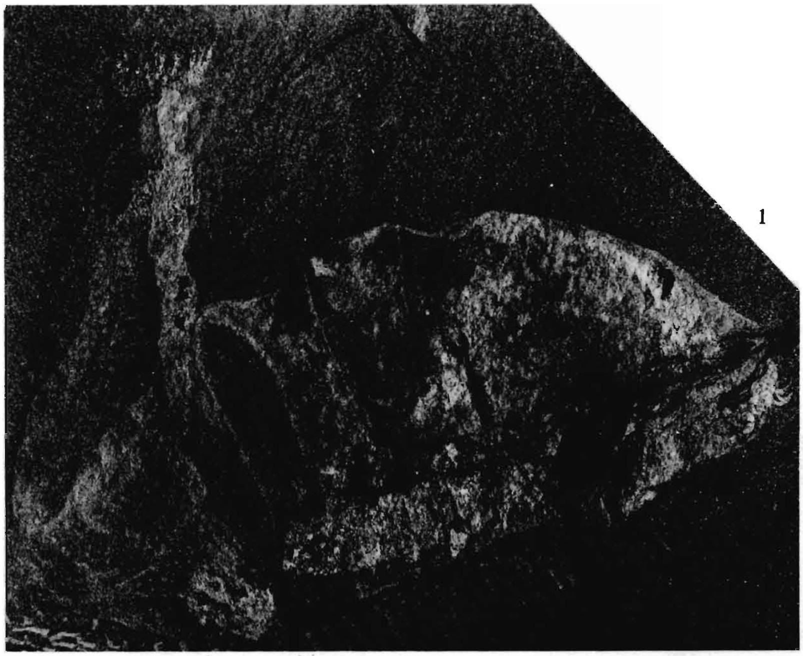
Ottoia prolifica Walcott.

Figs. 1, 5. USNM 188637. 1, specimen crumpled and distorted by decay, low-angle light from west, × 1·9, see text-fig. 49. 5, enlargement of proboscis, light from west, × 8·4.

Figs. 2, 6. USNM 198570. 2, anterior trunk and proboscis with retractor muscles preserved as reflective strands flanking the gut, light from west, × 5. 6, enlargement of proboscis hooks and associated row of fine spines to the right-hand side, light from west, × 17.

Fig. 3. USNM 188607. Proboscis with anterior retractor muscles, light from east, × 4·4, see text-fig. 50.

Fig. 4. USNM 198586. Proboscis partially inverted by 'neck' retractor muscles (see text-fig. 11), light from north-east, × 10, see text-fig. 51.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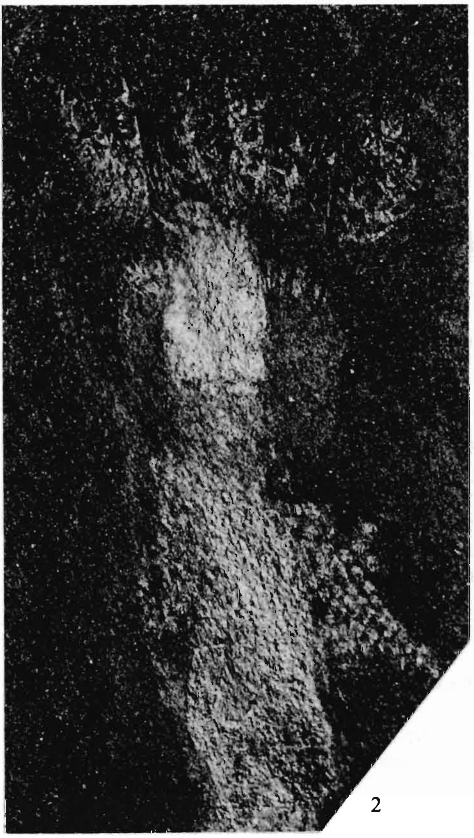
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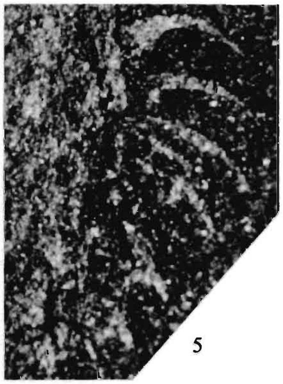
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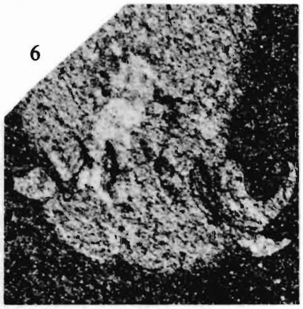
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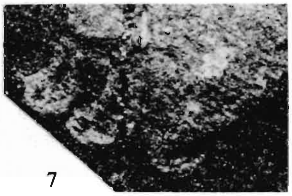
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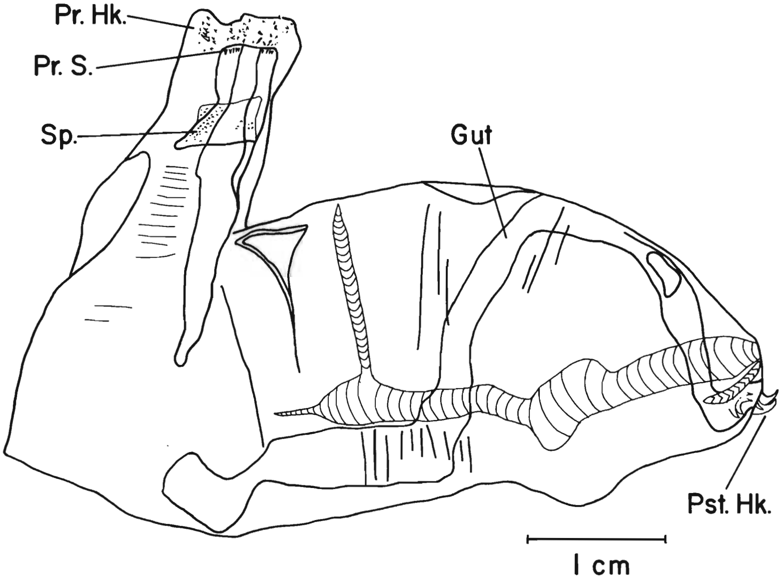
CONWAY MORRIS, *Ottoia prolifica*



TEXT-FIG. 52

EXPLANATION OF PLATE 7

Ottoia prolifica Walcott.

Figs. 1, 2. USNM 198593. 1, rather decayed specimen with proboscis at stage 1 (see text-fig. 12), light from north-east, × 1·8, see text-fig. 52. 2, counterpart, enlargement of retracted proboscis, light from east, × 7.

Fig. 3. USNM 188597. Proboscis at right angles to trunk so exposing about twenty-eight rows of proboscis hooks, light from south-east, × 8·2.

Figs. 4, 5. USNM 188594. 4, anterior proboscis at stage 6 (see text-fig. 12), light from north-east, × 4·2. 5, counterpart, enlargement of proboscis hooks, light from north-east, × 14.

Fig. 6. USNM 198585. Six posterior hooks arranged across the trunk, light from south, × 12·4.

Fig. 7. USNM 172977. Posterior hooks showing excavation of concave side, light from north, × 11, original of Banta and Rice 1976, fig. 25.

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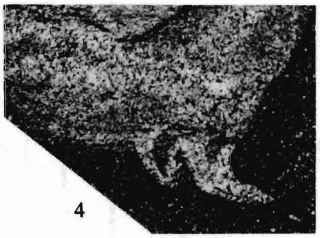

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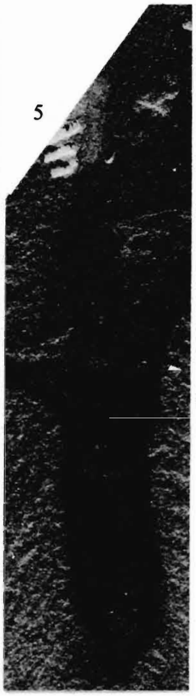

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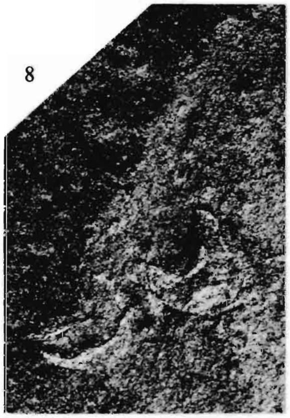

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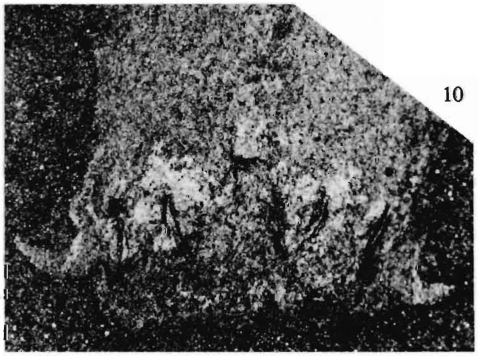

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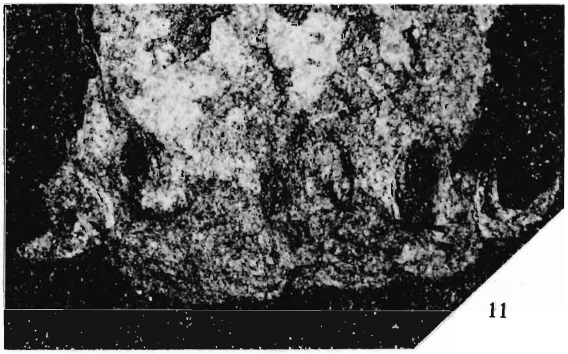

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CONWAY MORRIS, *Ottoia prolifica*

EXPLANATION OF PLATE 8

Ottoia prolifica Walcott.

Figs. 1, 2. USNM 172986. 1, anterior trunk and proboscis prior to cleaning of specimen, × 2, original of Banta and Rice 1976, fig. 22. 2, specimen after cleaning: note disappearance of dark lines on trunk, light from east, × 2.

Figs. 3, 4. USNM 188608. 3, proboscis at stage 2 (see text-fig. 12), light from west, × 7·6. 4, posterior hooks showing excavation of concave side, light from east, × 11.

Fig. 5. USNM 188593. Counterpart, posterior hook, and bursa everted, low-angle light from south, × 3·6.

Fig. 6. USNM 188595. Posterior hooks and inflated bursa, light from north, × 4·4.

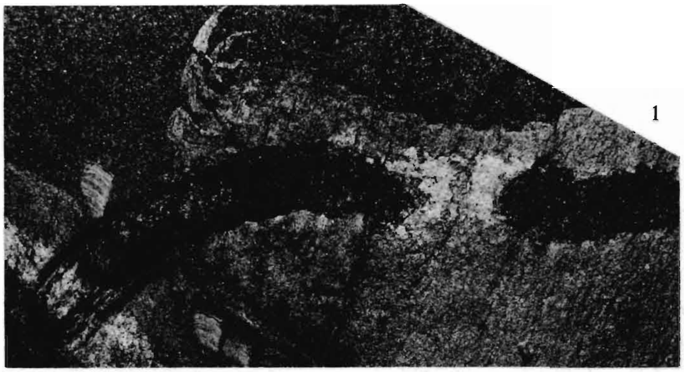
Fig. 7. USNM 188614. Posterior hook and swollen bursa, light from south, × 3.

Fig. 8. USNM 172987. Posterior hooks, light from south-east, × 9, original of Banta and Rice 1976, fig. 24.

Fig. 9. USNM 198580. Counterpart, posterior hooks showing excavation of concave side, light from south, × 12.

Fig. 10. USNM 188634. Six posterior hooks arranged across the trunk, light from east, × 8.

Fig. 11. USNM 172989. Posterior hooks on either side of trunk separated by central unarmed gap, light from east, × 9, original of Banta and Rice 1976, fig. 27.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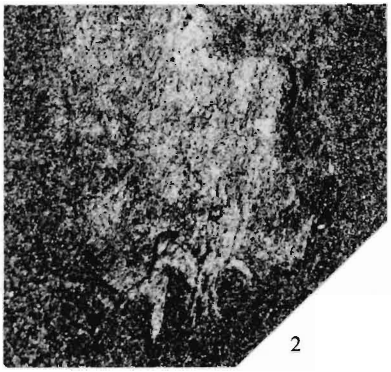
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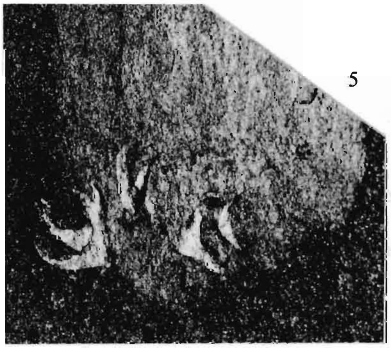
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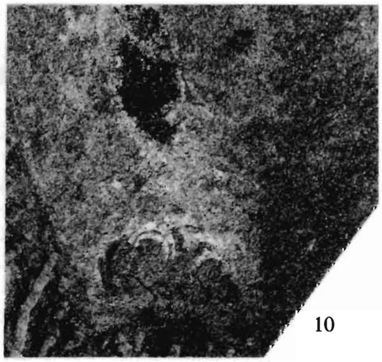
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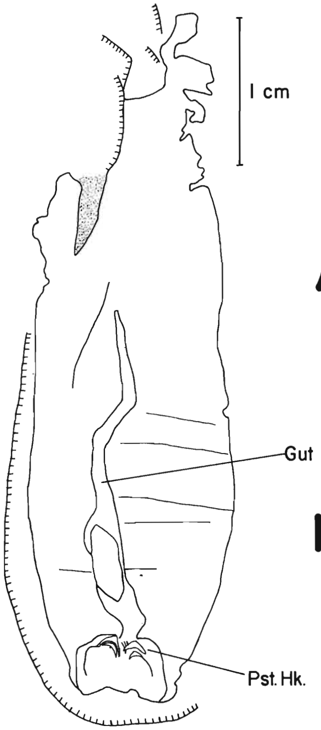
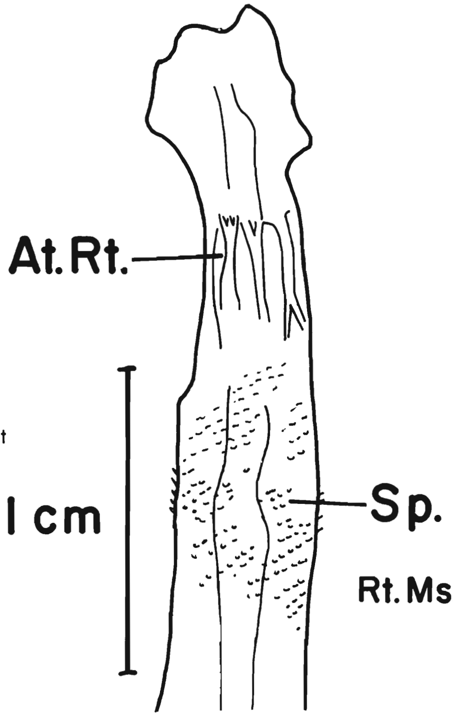
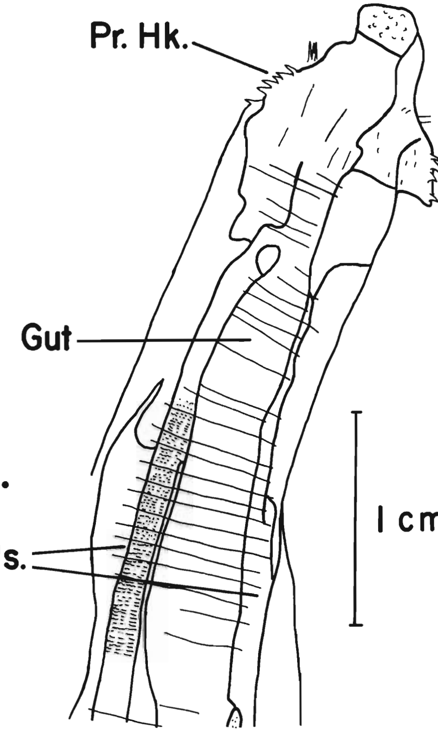
CONWAY MORRIS, *Ottoia prolifica*



TEXT-FIG. 53



TEXT-FIG. 54



TEXT-FIG. 55

EXPLANATION OF PLATE 9

Ottoia prolifica Walcott.

Fig. 1. USNM 188639. Posterior hooks, trunk, and bursa with gut contents, light from north, × 5·6.

Fig. 2. USNM 188612. Posterior hooks on the point of eversion (see text-fig. 14), light from west, × 7·8.

Figs. 3–5. USNM 83928. 3, entire animal with anterior retracted, light from east, × 1. 4, low-angle light from south-west, × 1, original of Walcott 1931, pl. 2, fig. 1. 5, enlargement of six posterior hooks, light from east, × 7·4.

Figs. 6, 10. USNM 198581. 6, posterior trunk fading into rock anteriorly, low-angle light from north-east, × 2, see text-fig. 53. 10, enlargement of inverted posterior hooks (see text-fig. 14), light from west, × 3·5.

Fig. 7. USNM 198569. Proboscis with anterior retractor muscles, light from west, × 3·8, see text-fig. 54.

Fig. 8. USNM 188620. Anterior trunk with retractor muscles flanking gut, light from east, × 3, see text-fig. 55.

Fig. 9. USNM 172988. Posterior hooks and slightly everted bursa, light from south, × 6·5, original of Banta and Rice 1976, fig. 26.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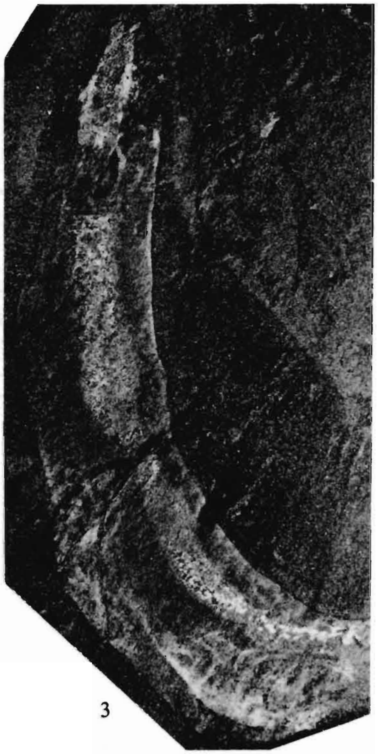
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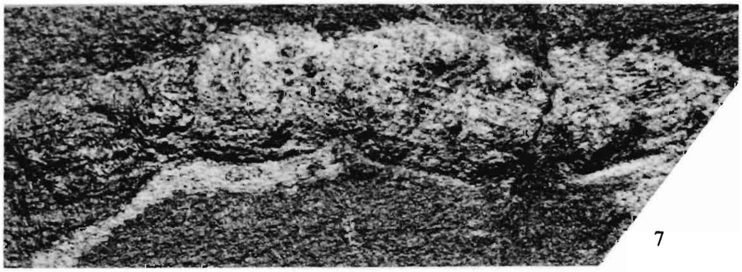
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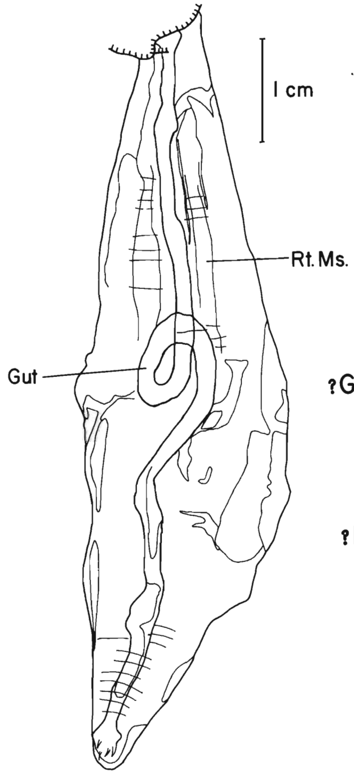
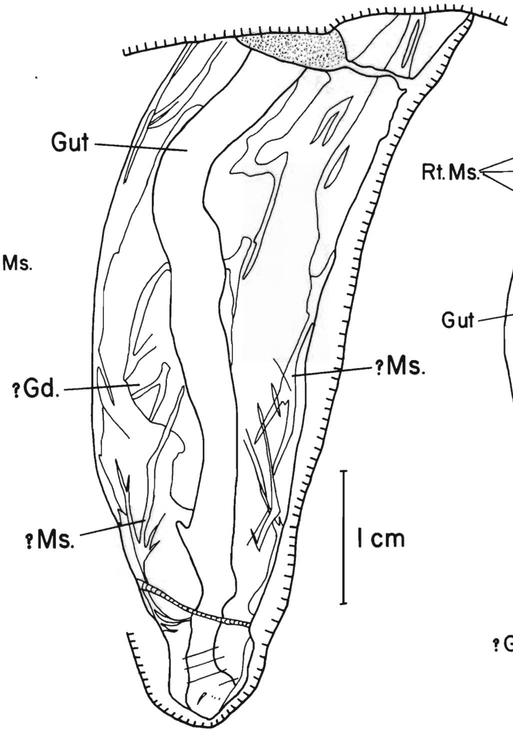
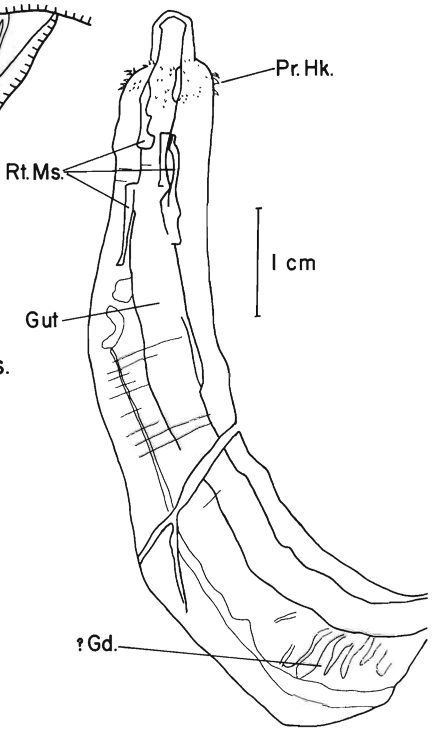
CONWAY MORRIS, *Ottoia prolifica*



TEXT-FIG. 56



TEXT-FIG. 57



TEXT-FIG. 58

EXPLANATION OF PLATE 10

Ottoia prolifica Walcott.

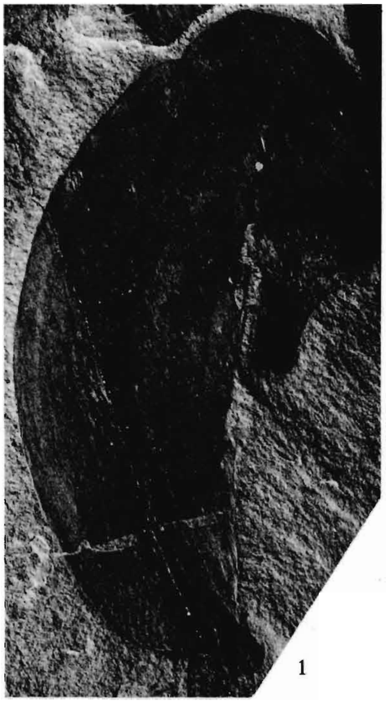
Fig. 1. USNM 198577. Trunk with looped gut flanked by retractor muscles, light from west, × 1·8, see text-fig. 56.

Fig. 2. USNM 198571. Trunk with possible muscles and urinogenital organ, light from west, × 2·2, see text-fig. 57.

Figs. 3, 4. USNM 188618. 3, anterior of animal with possible urinogenital organ, light from east, × 1·5, see text-fig. 58. 4, enlargement of proboscis and trunk with retractor muscles, light from east, × 3·4.

Figs. 5, 6. USNM 188599. 5, proboscis at stage 5 (see text-fig. 12) and anterior trunk containing striated mass that may represent a gizzard, low-angle light from south-east, × 3. 6, enlargement of possible gizzard, low-angle light from north, × 6·2.

Fig. 7. USNM 188593. Intestine wall lineations impressed on to gut contents, light from north, × 8·8.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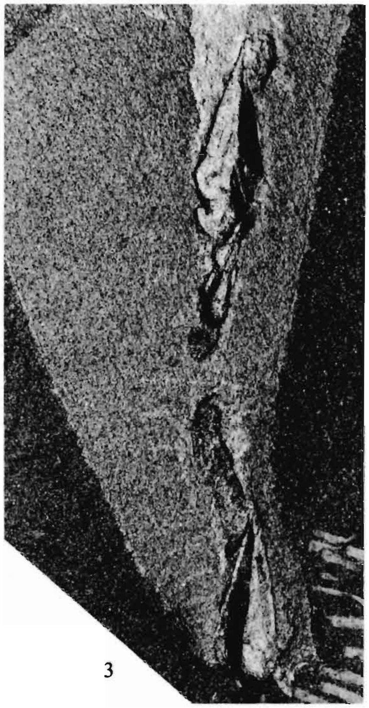
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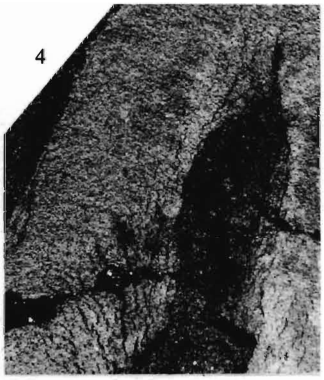
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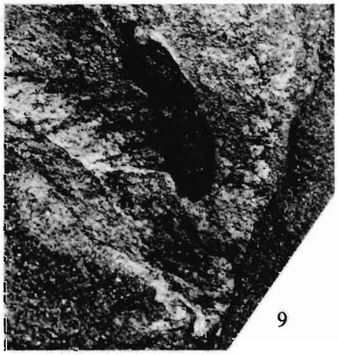
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CONWAY MORRIS, *Ottoia prolifica*

EXPLANATION OF PLATE 11

Ottoia prolifica Walcott.

Fig. 1. USNM 172979. Body wall detached from cuticle along sides of trunk, low-angle light from west, × 1·8, original of Banta and Rice 1976, fig. 4.

Fig. 2. USNM 172976. Specimen with slight anterior dark stain, low-angle light from west, × 1·4, original of Banta and Rice 1976, fig. 1. N.B. Banta and Rice have printed fig. 1 in reverse.

Figs. 3, 4. USNM 188604. 3, posterior gut containing three hyolithids with apices anteriorward, light from west, × 3·5. 4, cracks in the fossil film surrounding a major compaction tear, light from south, × 3·6.

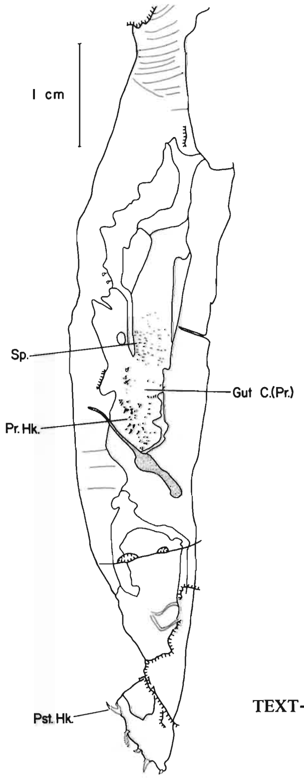
Fig. 5. USNM 198922. Trunk with gut containing proboscis of another specimen of *Ottoia prolifica*, light from east, × 1·7, see text-fig. 59.

Fig. 6. USNM 196204. Gut containing hyolithid and brachiopod, light from south, × 2.

Fig. 7. USNM 188606. Cutaneo-visceral muscles arising from intestine, light from north, × 6·2.

Fig. 8. USNM 198587. Gut with macerated contents along much of its length, low-angle light from north-east, × 1·2.

Fig. 9. USNM 199101. Posterior gut with faecal bolus that may contain sediment, light from north, × 2·5.



TEXT-FIG. 59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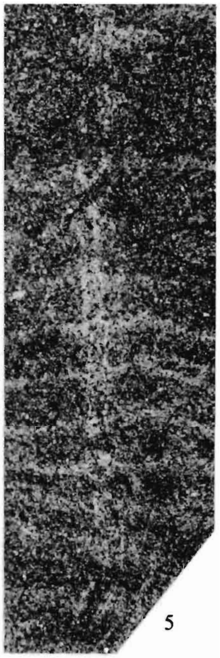
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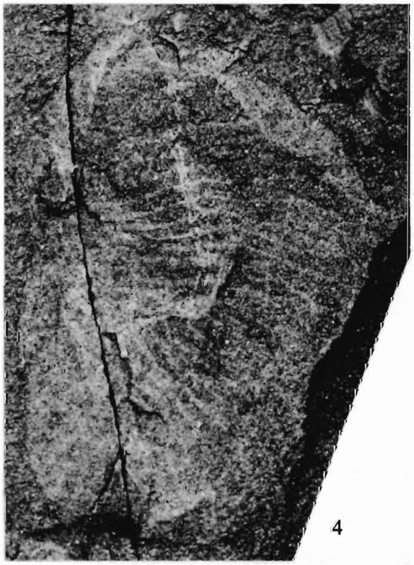
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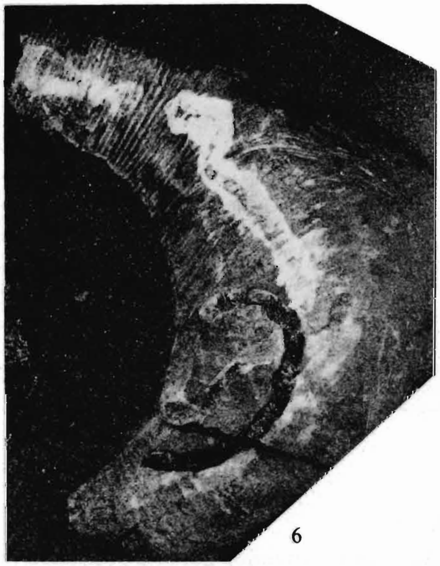
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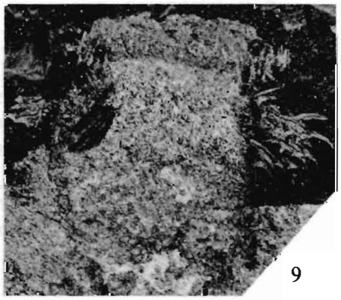
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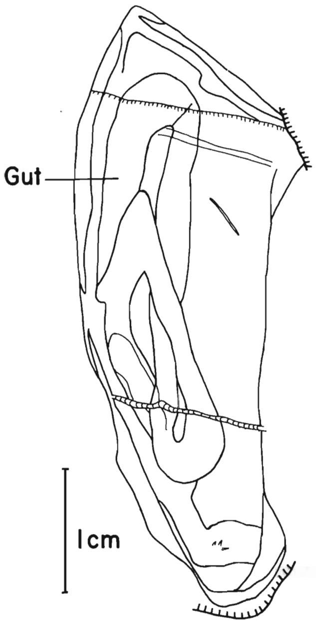
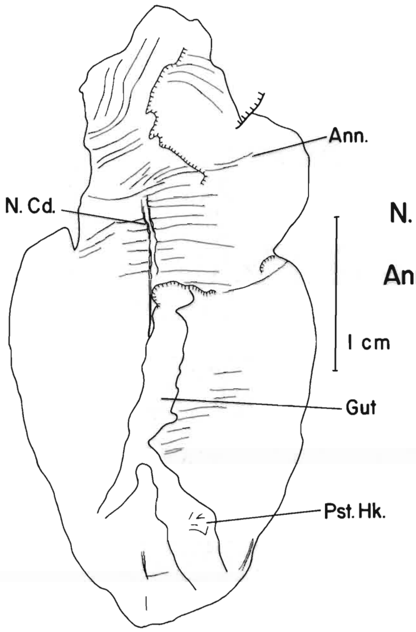
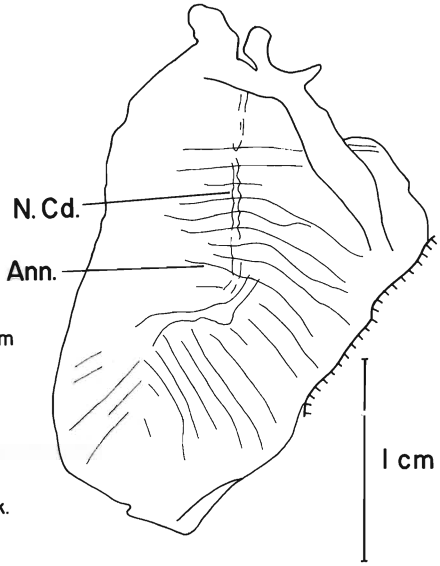
CONWAY MORRIS, *Ottoia prolifica*



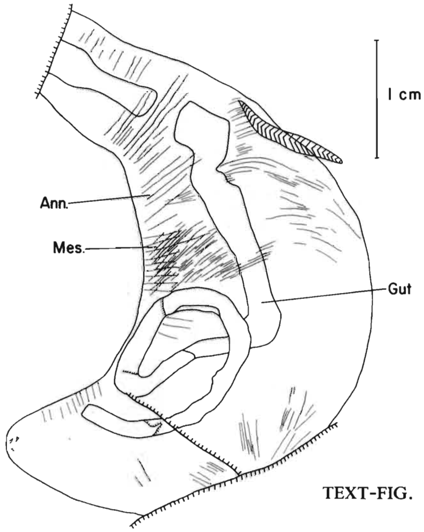
TEXT-FIG. 60



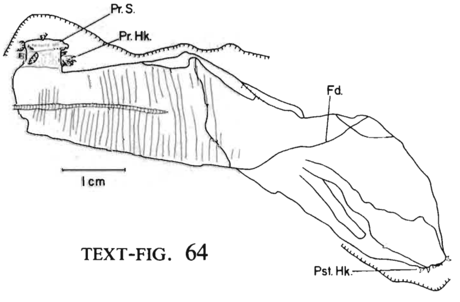
TEXT-FIG. 61



TEXT-FIG. 62



TEXT-FIG. 63



TEXT-FIG. 64

EXPLANATION OF PLATE 12

Ottoia prolifica Walcott.

Fig. 1. USNM 198568. Specimen with proboscis and anterior retracted, light from east, × 2, see text-fig. 60.

Figs. 2, 3. USNM 188636. 2, decayed specimen with incomplete gut and nerve cord, light from south-east, × 2·2, see text-fig. 61. 3, enlargement of nerve cord, light from east, × 8.

Figs. 4, 5. USNM 188635. 4, decayed specimen with nerve cord, light from north, × 2·6, see text-fig. 62. 5, enlargement of nerve cord, light from west, × 10.

Fig. 6. USNM 199413. Specimen with looped gut and mesenteries, light from east, × 1·8, see text-fig. 63.

Fig. 7. USNM 188610. Trunk containing gut and possible muscles, light from east, × 2·2.

Figs. 8, 9. USNM 198572. 8, decayed specimen consisting mostly of fossilized cuticle with the posterior trunk folded over, light from north, × 1·4, see text-fig. 64. 9, enlargement of proboscis at stage 3 (see text-fig. 12), light from north, × 5.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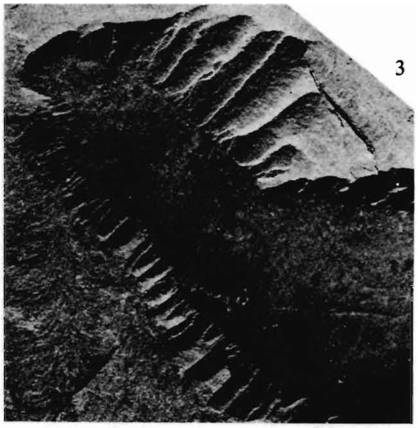
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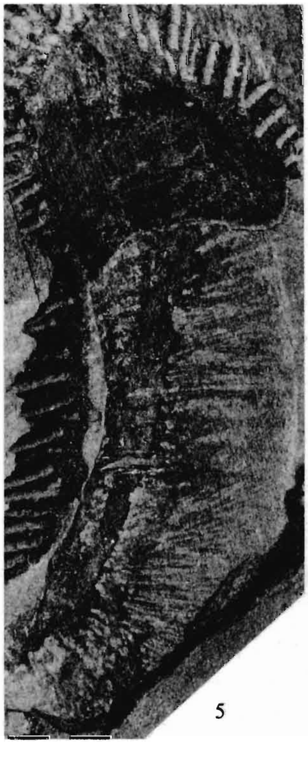
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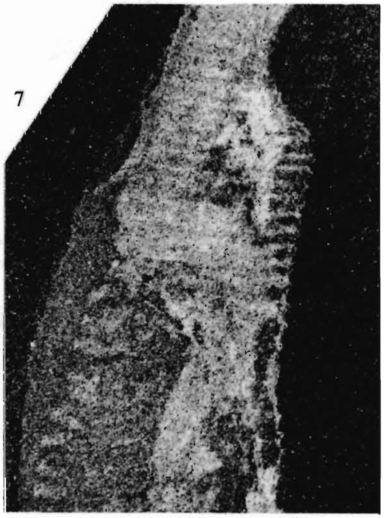
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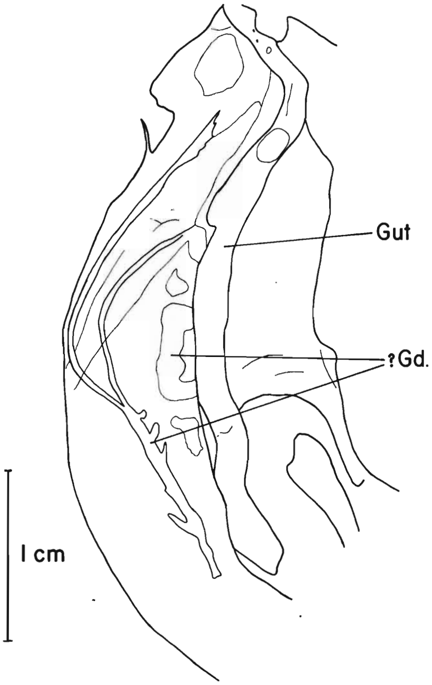
CONWAY MORRIS, *Ottoia prolifica*



TEXT-FIG. 65

EXPLANATION OF PLATE 13

Ottoia prolifica Walcott.

Fig. 1. USNM 188603. Trunk containing gut and possible urinogenital organ, light from west, × 2·9, see text-fig. 65.

Fig. 2. USNM 188638. Decayed specimen with posterior hooks, light from north-east, × 1·6.

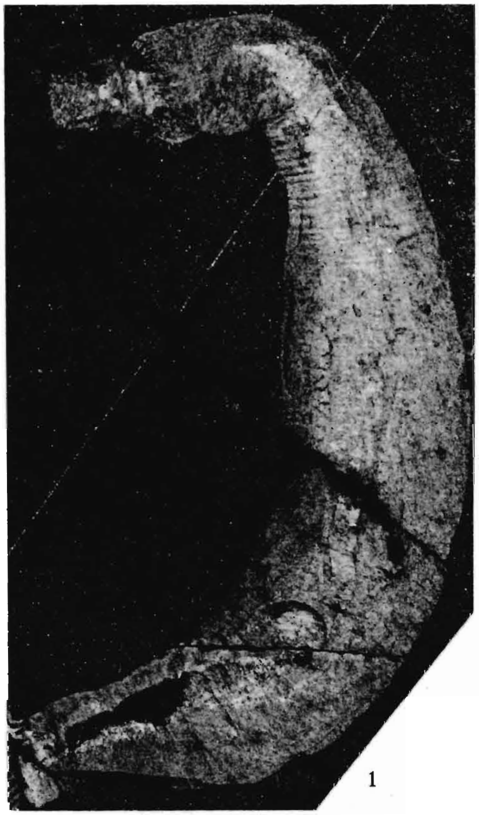
Fig. 3. USNM 188619. Specimen surrounded by fracture planes, light from north-east, × 1·6.

Fig. 4. GSC 45326. Specimen with elongated anterior trunk, light from west, × 1.

Fig. 5. GSC 45324. Mesenteries running from right-hand side of gut, light from west, × 3. Contrast of specimen heightened by immersion in 15% hydrofluoric acid for 15 seconds (cf. Whittington 1971*b*, pl. 16, fig. 2).

Fig. 6. GSC 45325. Posterior trunk and everted bursa of abnormal length, light from west, × 3.

Fig. 7. USNM 198588, retractor muscle cut by annulations giving it pseudo-segmented appearance, light from west, × 2·4.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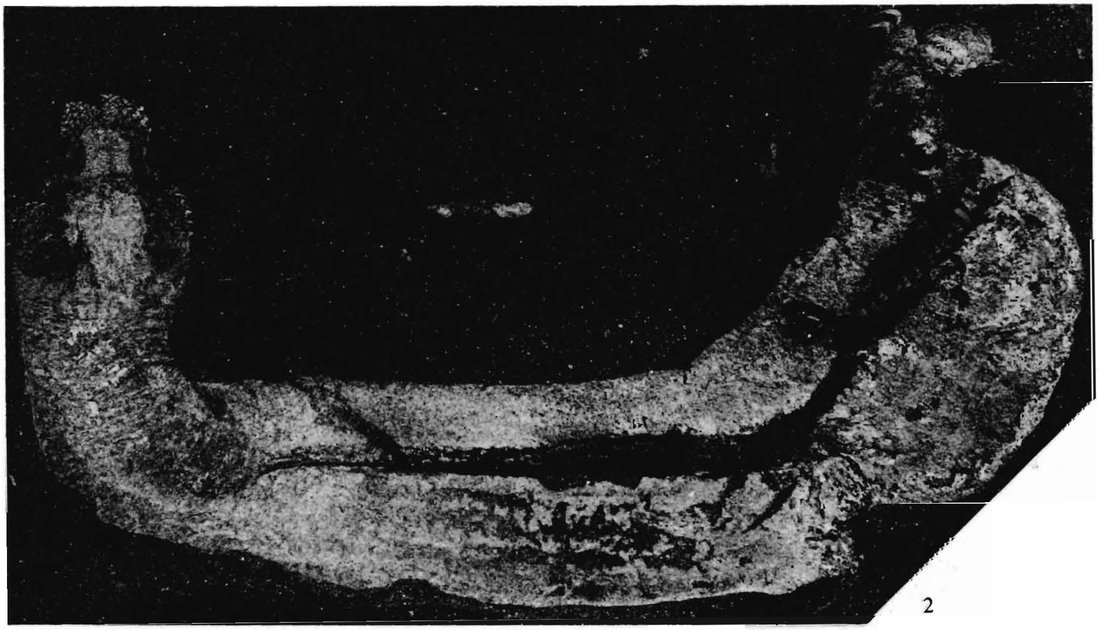
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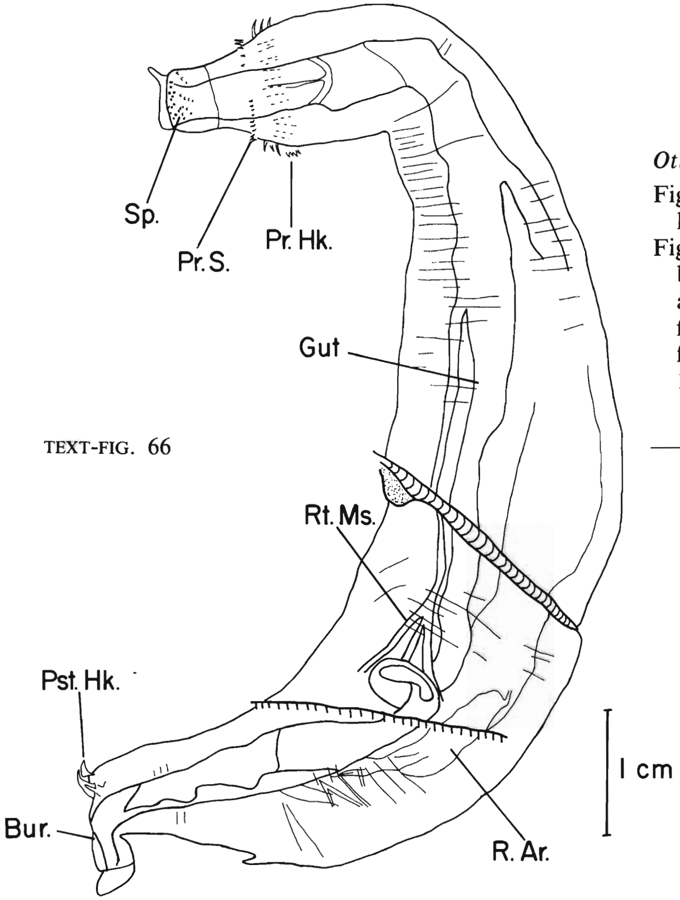
CONWAY MORRIS, *Ottoia prolifica*



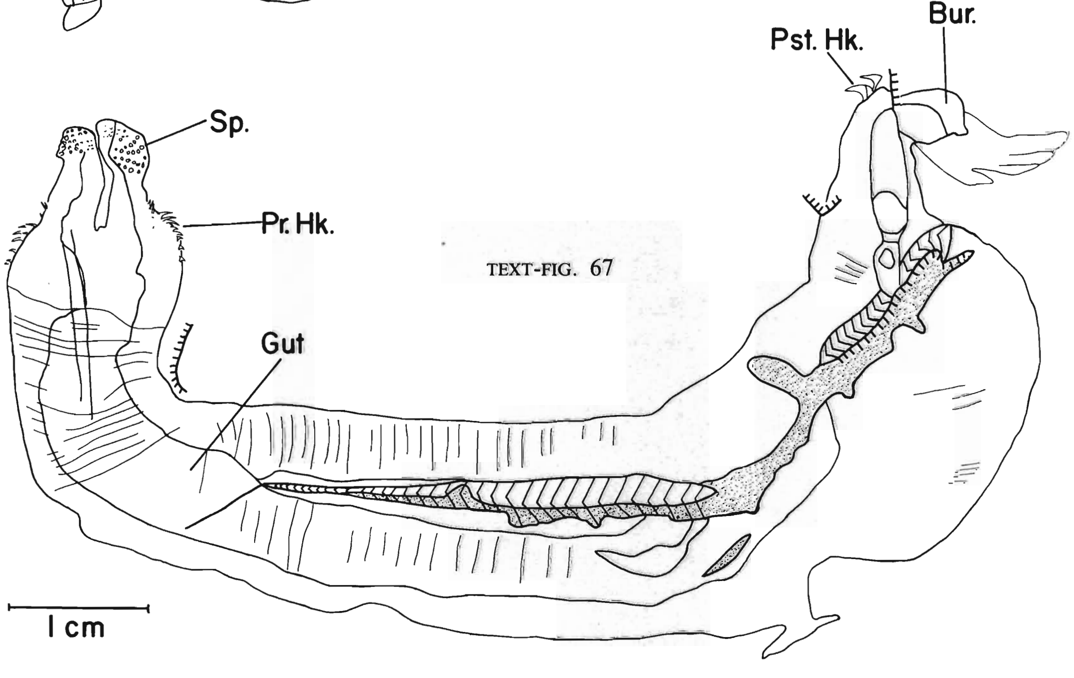
TEXT-FIG. 66

EXPLANATION OF PLATE 14

Ottoia prolifica Walcott.

Fig. 1. GSC 45322. Well-preserved specimen, light from east, × 1·5, see text-fig. 66.

Figs. 2, 3. GSC 40972. 2, specimen with body wall obscuring most of the internal anatomy, light from south, × 2, see text-fig. 67. 3, enlargement of proboscis, light from west, × 5·5, original of Crompton 1975, pl. 3, fig. C.



TEXT-FIG. 67

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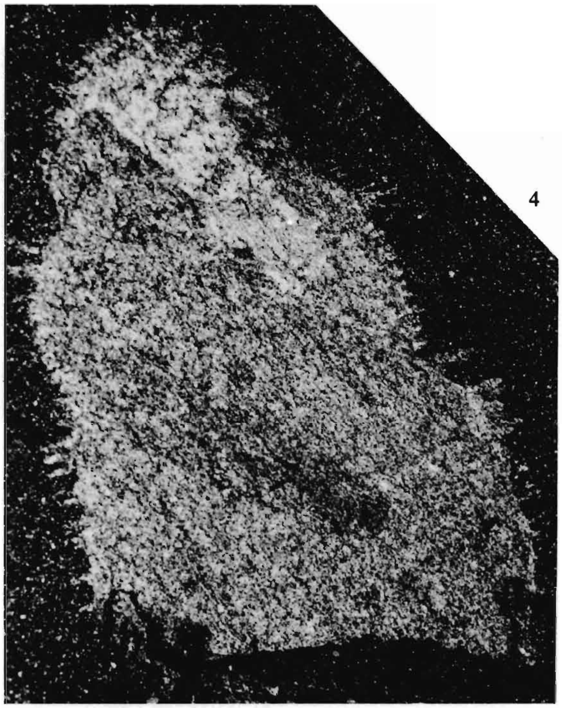

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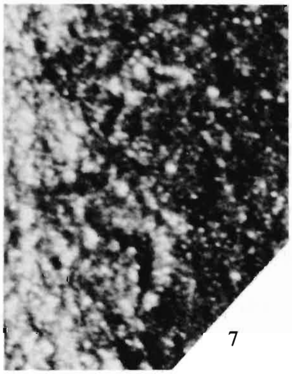

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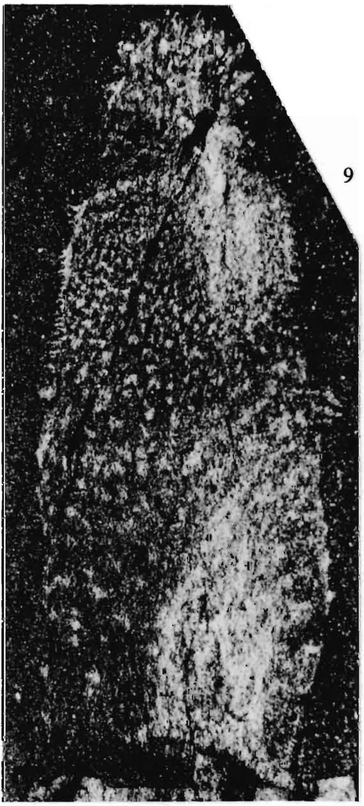

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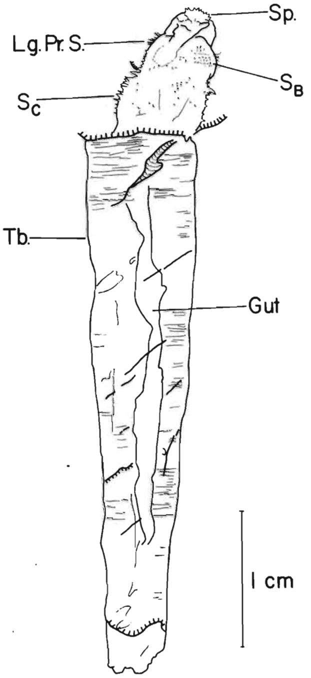
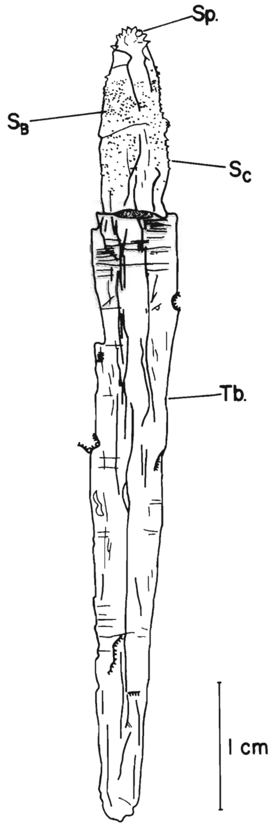
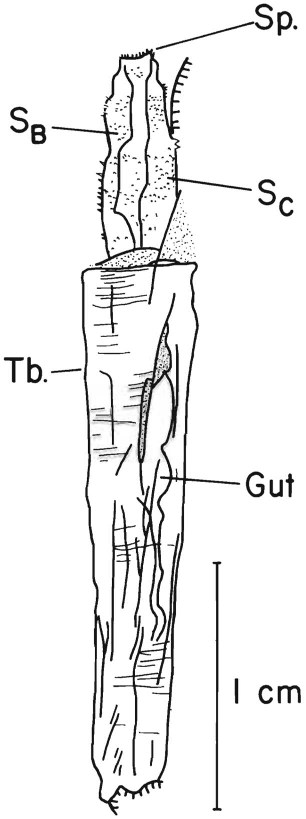
CONWAY MORRIS, *Selkirkia*



TEXT-FIG. 68



TEXT-FIG. 69



TEXT-FIG. 70

EXPLANATION OF PLATE 15

'Selkirkia' major Walcott. Fig. 1. *Selkirkia columbia* sp. nov. Figs. 2–10.

Fig. 1. USNM 96542. Holotype, slender tube lacking soft parts, light from east, × 1·4, original of Walcott 1908, pl. 1, fig. 11.

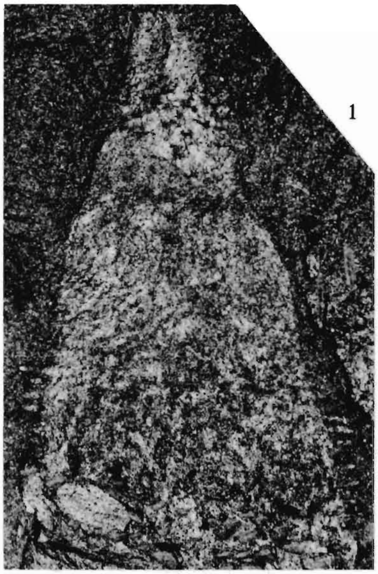
Figs. 2–4, 7. USNM 83941a. 2, paratype, well-preserved specimen in broad aspect, light from north-west, × 2, see text-fig. 68, original of Walcott 1931, pl. 10, fig. 1. 3, counterpart, light from north-west, × 2·2. 4, counterpart, enlargement of proboscis, light from east, × 9. 7, counterpart, enlargement of multidentate proboscis spinules (see text-fig. 23), light from north, × 48.

Fig. 5. USNM 193892. Juvenile specimen, light from east, × 16.

Fig. 6. USNM 198630. Enlargement of posterior tube with two flaps, light from west, × 6.

Figs. 8, 9. USNM 83941b. 8, paratype, counterpart, well-preserved specimen in narrow aspect, light from east, × 1·8, see text-fig. 69, counterpart of original of Walcott 1931, pl. 10, fig. 2. 9, counterpart, enlargement of proboscis, light from east, × 7.

Fig. 10. USNM 57624. Holotype, specimen with creased tube, light from east, × 3·6, see text-fig. 70, original of Walcott 1911*c*, pl. 19, fig. 6.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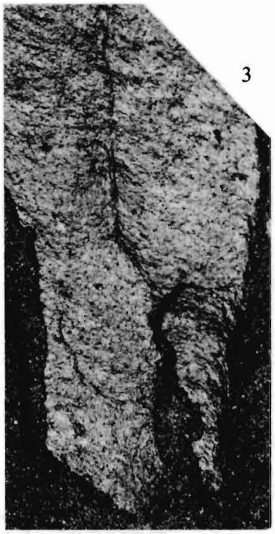
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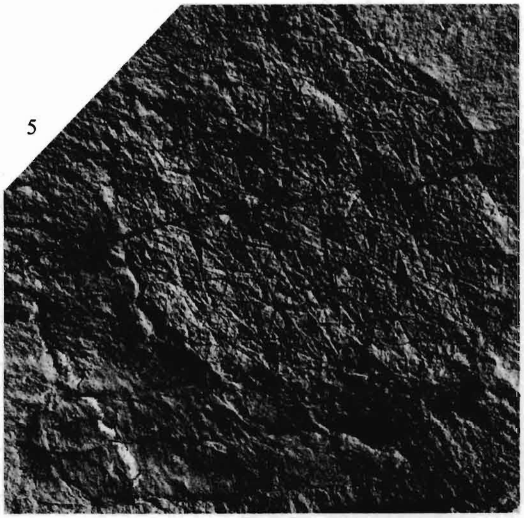
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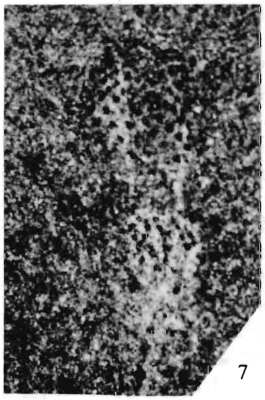
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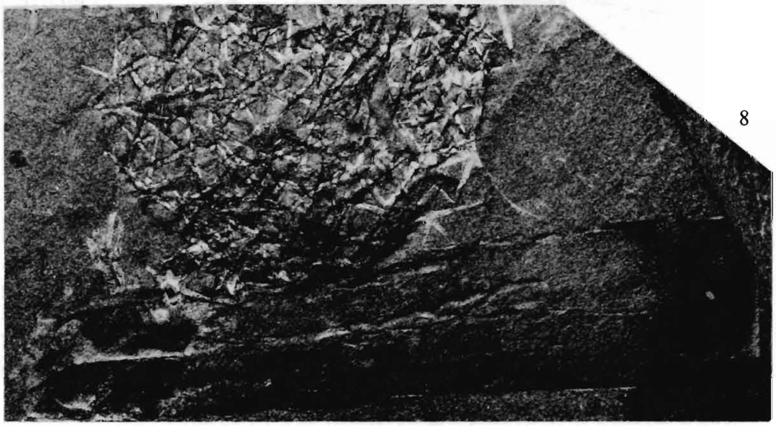
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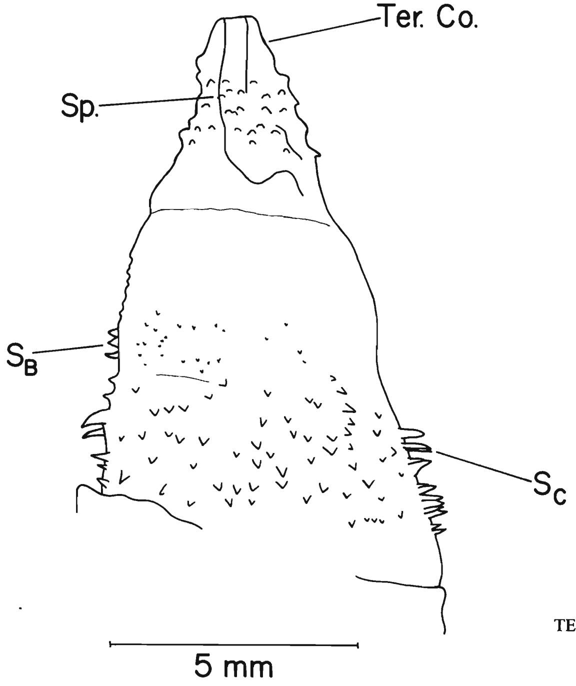
CONWAY MORRIS, *Selkirkia columbia*



TEXT-FIG. 71

EXPLANATION OF PLATE 16

Selkirkia columbia sp. nov.

Figs. 1–3. USNM 198617. 1, proboscis at stage 4 (see text-fig. 25), light from east, × 6, see text-fig. 71. 2, counterpart, enlargement of proboscis division C spines, light from east, × 22. 3, enlargement of posterior tube to show ends separated by sediment, light from east, × 6.

Fig. 4. GSC 45321. Tube with sponge (*Pirania muricata*) attached, low-angle light from north-east, × 1·4.

Fig. 5. USNM 66521. Tube with sponge (*Eiffelia globosa*) attached, light from south-west, × 2, syntype of *E. globosa*, original of Walcott 1920, pl. 86, fig. 1.

Fig. 6. USNM 198618. Specimen with proboscis at stage 3 (see text-fig. 25), light from north-west, × 3.

Fig. 7. USNM 198642. Partially decayed proboscis showing quincunxially arranged spinules, light from east, × 9.

Fig. 8. GSC 45327. Tube with sponge (*Eiffelia globosa*) and more posteriorly an indeterminate tubular organism attached, light from north, × 2·5.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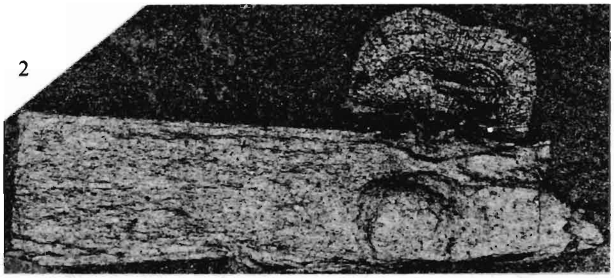
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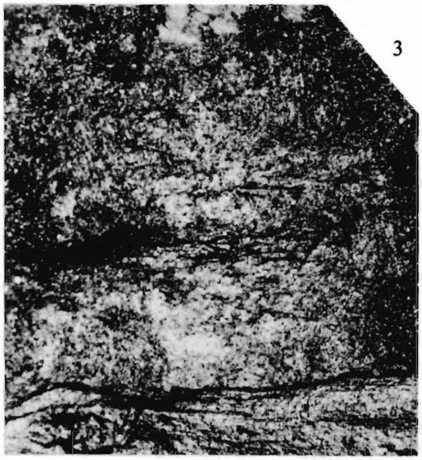
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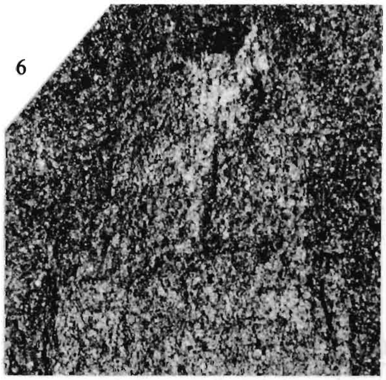
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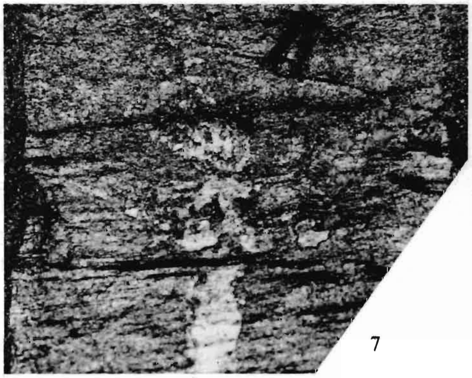
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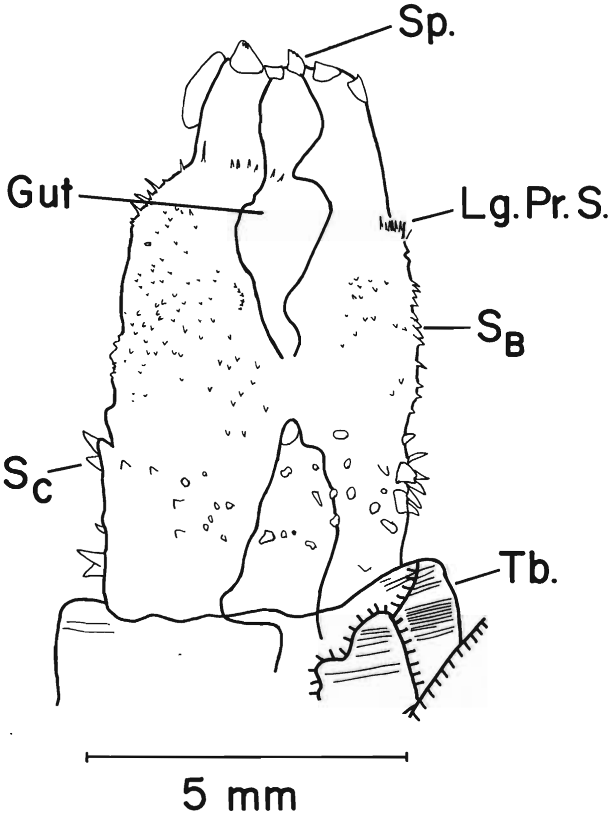
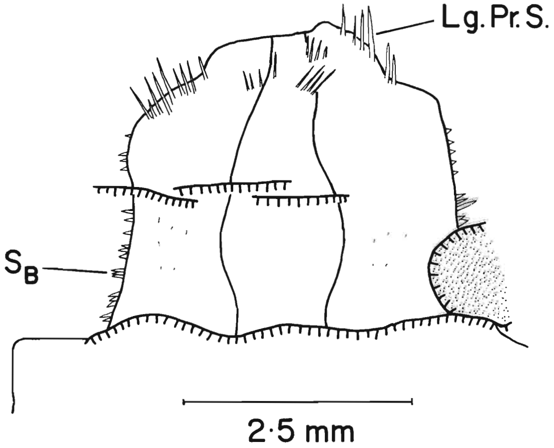
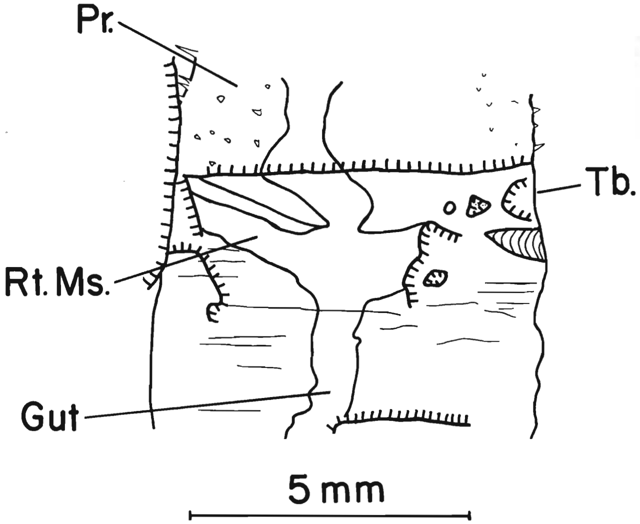
CONWAY MORRIS, *Selkirkia columbia*



TEXT-FIG. 72



TEXT-FIG. 73



TEXT-FIG. 74

EXPLANATION OF PLATE 17

Selkirkia columbia sp. nov.

Fig. 1. USNM 198626. Proboscis at stage 3 (see text-fig. 25), light from east, × 9·6, see text-fig. 72.

Fig. 2. USNM 198623. Tube with brachiopod (*Nisusia burgessenis*) attached, light from south, × 4·2.

Fig. 3. USNM 198619. Proboscis at stage 2 (see text-fig. 25), light from west, × 11, see text-fig. 73.

Fig. 4. USNM 198624. Poorly preserved proboscis and tube with anterior trunk papillae preserved as reflective rows of dots, light from west, photographed under distilled water, × 4·4.

Fig. 5. USNM 198633. Reflectively preserved paired retractor muscles running from gut, light from north-west, × 7·6.

Fig. 6. USNM 198627. Proboscis apparently at stage 1 (see text-fig. 25), light from east, × 10.

Fig. 7. USNM 198628. Paired retractor muscles running forward from the gut towards the base of the proboscis, light from south, × 9, see text-fig. 74.

Fig. 8. USNM 198621. Proboscis at stage 4 (see text-fig. 25) with division B spines in quincunxes, light from west, × 10·5.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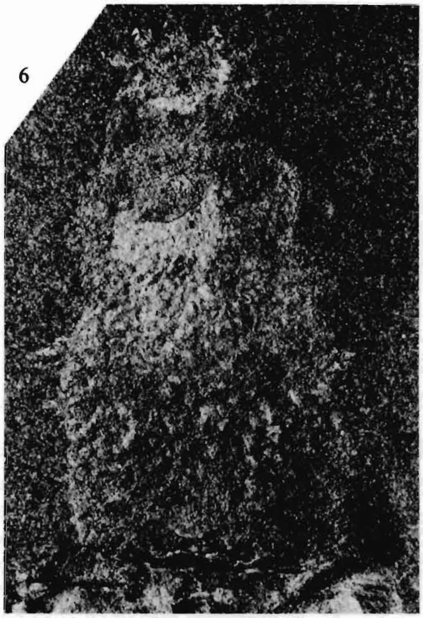
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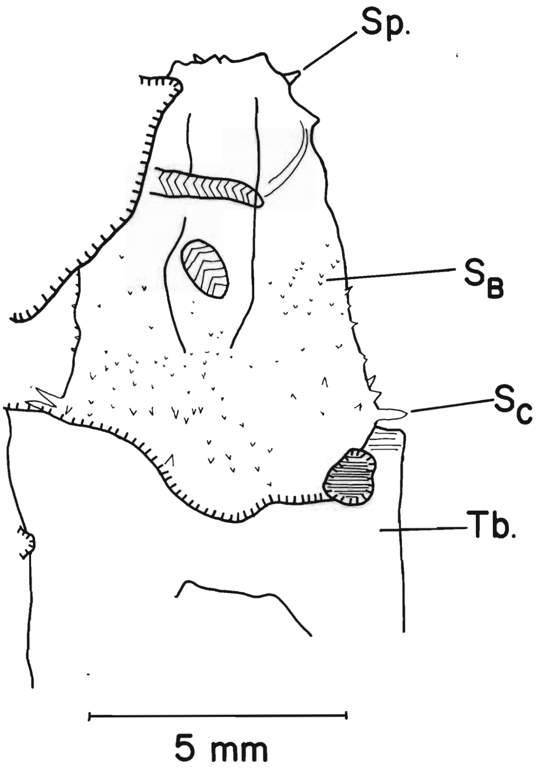
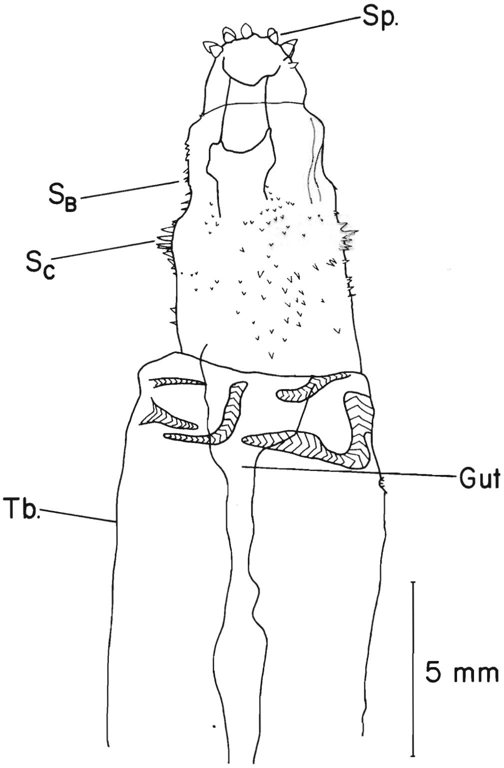
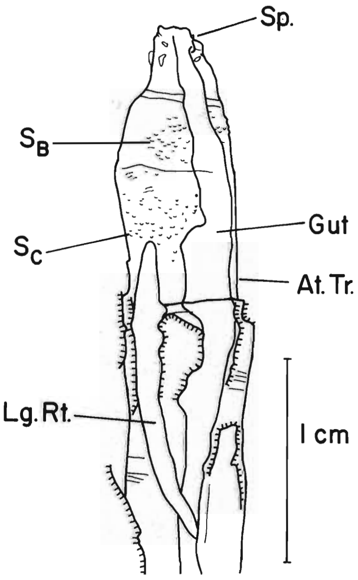
CONWAY MORRIS, *Selkirkia columbia*



TEXT-FIG. 75



TEXT-FIG. 76



TEXT-FIG. 77

EXPLANATION OF PLATE 18

Selkirkia columbia sp. nov.

Fig. 1. GSC 45329. Division C of proboscis almost entirely withdrawn into tube, light from west, × 8·2, see text-fig. 75.

Figs. 2, 3. USNM 198622. 2, enlargement of proboscis at stage 2 with division B long spines on point of eversion (see text-fig. 25), light from west, × 12. 3, complete specimen with gut displaced across tube, light from north-west, × 2·4.

Fig. 4. USNM 198620. Proboscis at stage 4 (see text-fig. 25), light from west, × 5.

Figs. 5, 6. GSC 45330. 5, complete specimen with crumpled anterior tube, light from west, × 2. 6, enlargement of proboscis at stage 3 (see text-fig. 25), light from west, × 7·8, see text-fig. 76.

Fig. 7. USNM 198632. Anteriormost trunk protruding beyond tube, gut, and probable retractor muscle, light from west, × 3, see text-fig. 77.

Fig. 8. USNM 198634. Poorly preserved specimen apparently with proboscis withdrawn into tube, light from south, × 1·6.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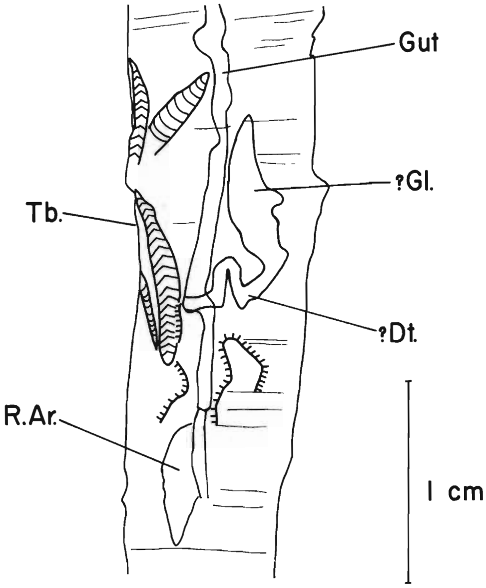
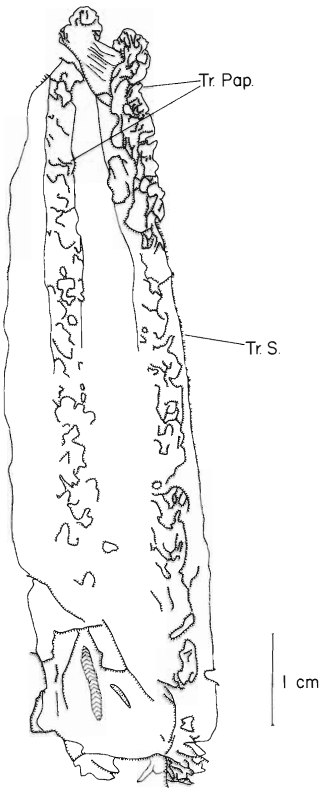
CONWAY MORRIS, *Selkirkia* and *Louisella*



TEXT-FIG. 78



TEXT-FIG. 79

EXPLANATION OF PLATE 19

Selkirkia columbia sp. nov. Figs. 1–3. *Louisella pedunculata* Walcott. Figs. 4–8.

Figs. 1, 2. USNM 198629. Possible gland with duct and another unidentifiable reflective area, light from north-west, × 3·8. 2, light from west, × 3·8, see text-fig. 78.

Fig. 3. GSC 45328. Proboscis apparently withdrawn into tube, light from west, × 3·5.

Fig. 4. USNM 57617. Paratype, counterpart, trunk division A, and proboscis with long spines radiating across bedding plane, light from west, × 1·9, counterpart of original of Walcott 1911*c*, pl. 18, fig. 3.

Figs. 5–7. USNM 57558. 5, holotype, specimen with ends folded beneath itself, light from north-west, × 1·3, see text-fig. 79, original of Walcott 1911*b*, pl. 13, fig. 4. 6, holotype, enlargement of terminal area to show trunk papillae and spines, low-angle light from west, × 2·6. 7, counterpart, note two rows of trunk papillae, low-angle light from east, × 1·7.

Fig. 8. USNM 57616. Paratype, counterpart, enlargement of distal proboscis, light from east, × 5.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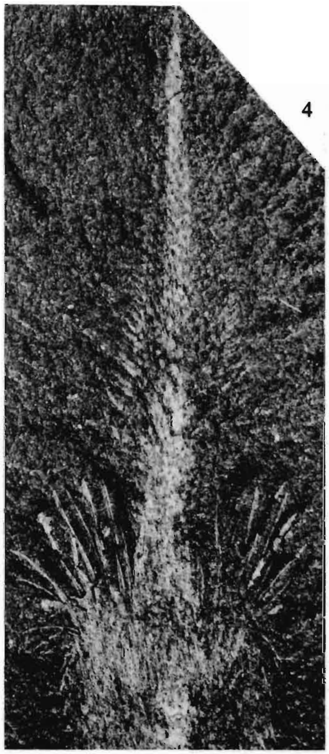
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CONWAY MORRIS, *Louisella pedunculata*

EXPLANATION OF PLATE 20

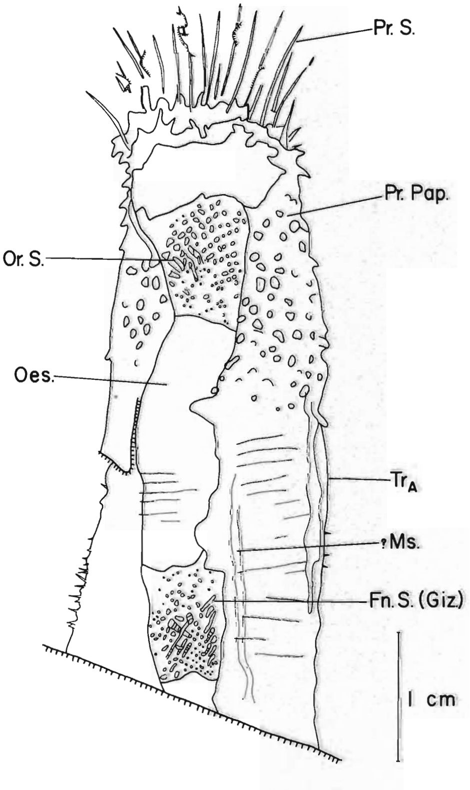
Louisella pedunculata Walcott.

Figs. 1–4. USNM 57616. 1, paratype, complete specimen with proboscis at stage 4 (see text-fig. 29), light from north-east, × 0·7, original of Walcott 1911*c*, pl. 18, figs. 1–2, 5. 2, paratype, low-angle light from south-east, × 0·7. 3, counterpart, light from north-east, × 0·7. 4, enlargement of proximal proboscis with oral spines, long spines, and papillae, light from east, × 3. See also Pl. 19, fig. 8 and Pl. 21, fig. 5.

Fig. 5. USNM 57618. Paratype, trunk with papillae, low-angle light from west, × 2·4.

Fig. 6. USNM 198644. Proboscis at stage 2 (see text-fig. 29), light from east, × 3·8, see text-fig. 80.

Fig. 7. USNM 198645. Proboscis at stage 2, distorted along right-hand side by compaction, showing long spines and papillae, light from south-east, × 5·6.



TEXT-FIG. 80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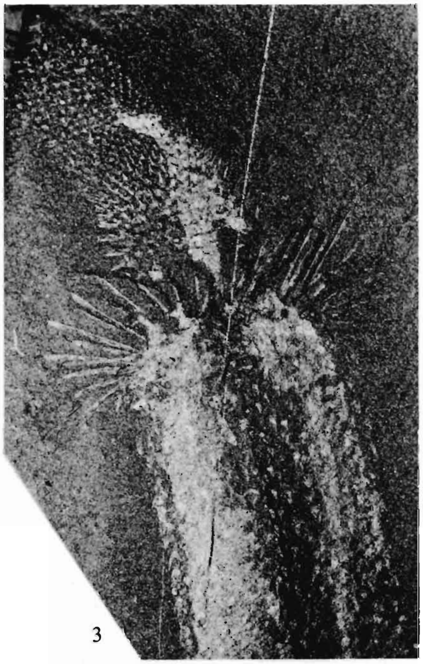
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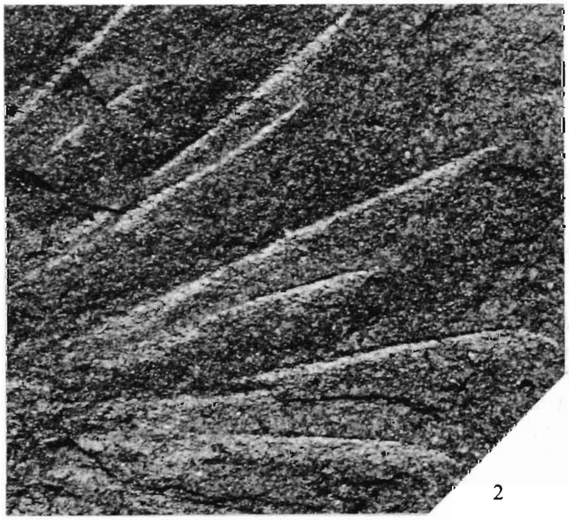
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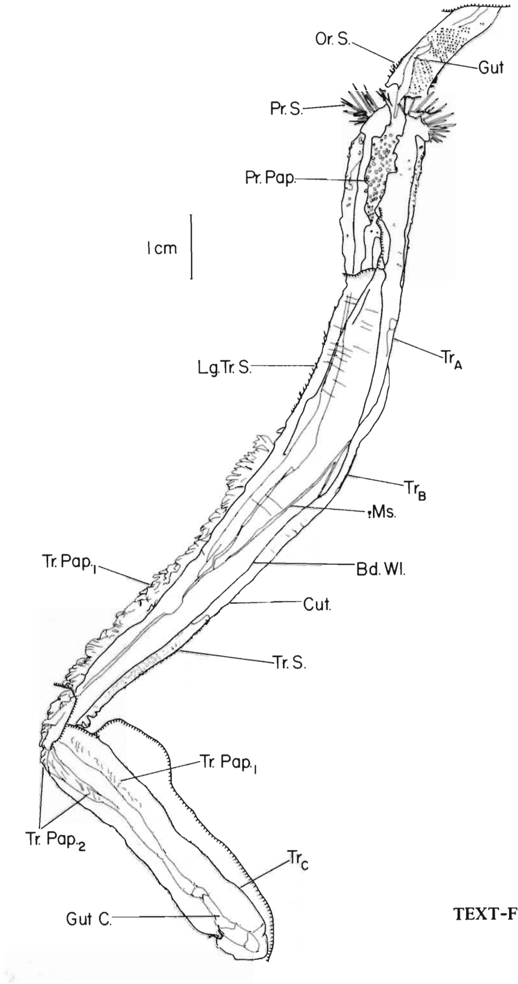
CONWAY MORRIS, *Louisella pedunculata*



TEXT-FIG. 81

EXPLANATION OF PLATE 21

Louisella pedunculata Walcott.

Figs. 1–4. USNM 198648. 1, well-preserved specimen with proboscis at stages 3–4 (see text-fig. 29), low-angle light from west, × 0·8, see text-fig. 81. 2, enlargement of long proboscis spines, note reflective leading edge and trailing blade, light from south, × 12. 3, counterpart, enlargement of proboscis, light from west, × 2·5. 4, enlargement of oral spines, light from west, × 9.

Fig. 5. USNM 57616. Enlargement of possible anterior gut contents, light from east, × 3·2.

Fig. 6. USNM 198650. Trunk completely twisted over with two parts separated by sediment, low-angle light from east, × 3.

Figs. 7, 8. USNM 198643. 7, proboscis at stage 3 (see text-fig. 29), light from west, × 3·7. 8, counterpart, trunk division C (spinose) and D (smooth), light from west, × 2.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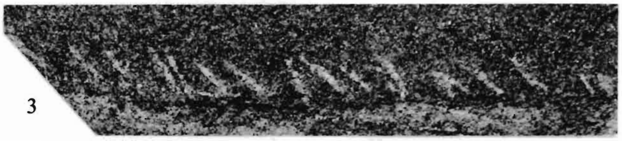
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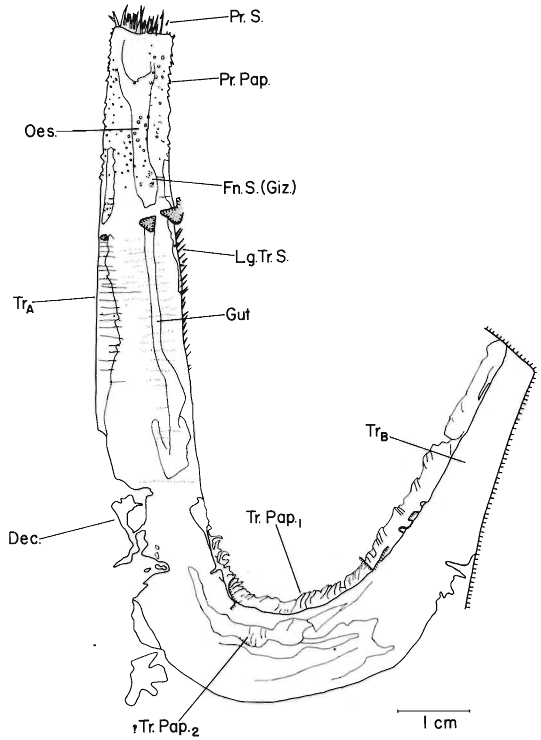
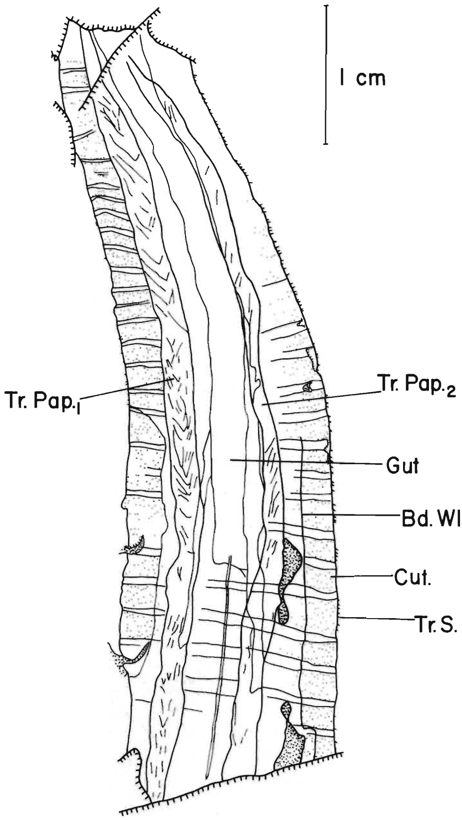
CONWAY MORRIS, *Louisella pedunculata*



TEXT-FIG. 82



TEXT-FIG. 83

EXPLANATION OF PLATE 22

Louisella pedunculata Walcott.

Figs. 1–3. USNM 198646. 1, slightly decayed specimen showing proboscis and trunk divisions A–B, light from north-east, × 0·9, see text-fig. 82. 2, enlargement of proboscis at stage 2 (see text-fig. 29), low-angle light from west, × 3. 3, enlargement of long spines of trunk division A, light from north, × 5·2.

Fig. 4. USNM 198656. Chevron arrangement of trunk papillae, light from west, × 5·2.

Figs. 5–7. USNM 198652. 5, trunk division **B** with the two rows of trunk papillae, low-angle light from west, × 1·8. 6, light from east, × 1·8, see text-fig. 83. 7, enlargement of spinose trunk wall with reflectively preserved body wall detached from cuticle, light from west, × 6·5.

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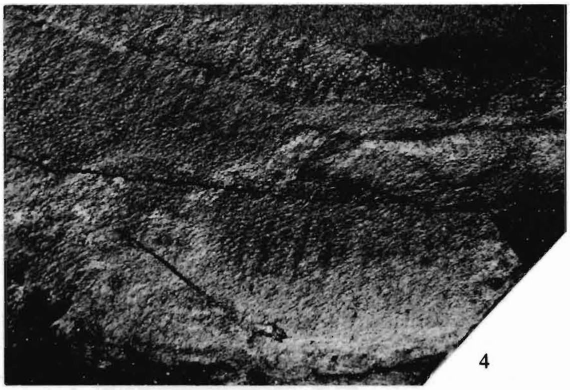

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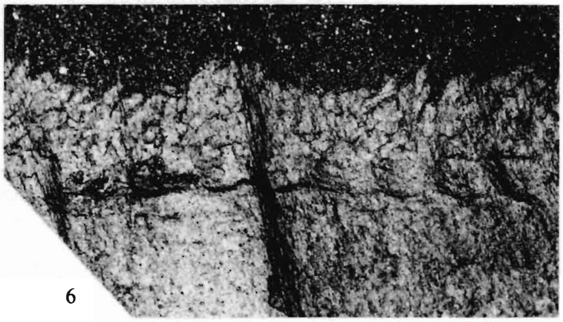

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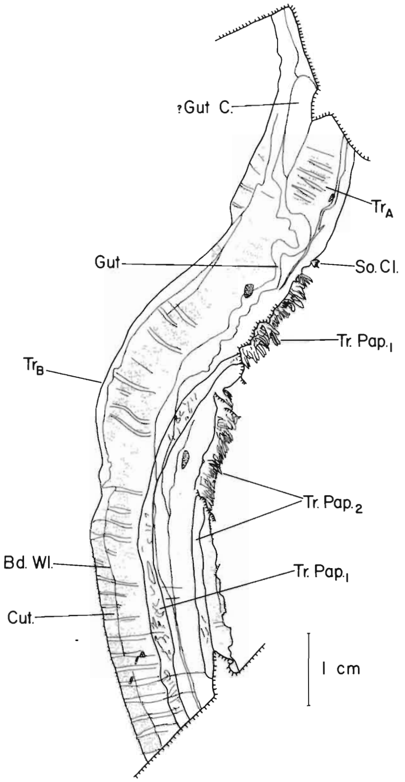
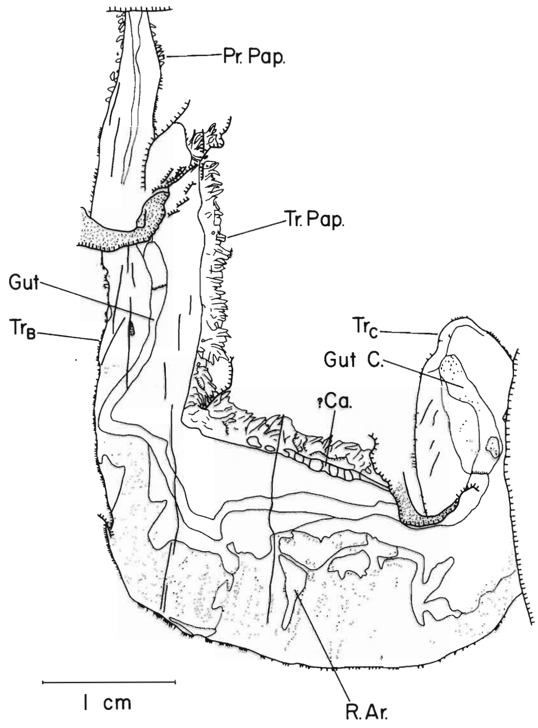
CONWAY MORRIS, *Louisella pedunculata*



TEXT-FIG. 84



TEXT-FIG. 85

EXPLANATION OF PLATE 23

Louisella pedunculata Walcott.

Figs. 1–4. USNM 198651. 1, trunk divisions A–B showing spiny surface and trunk papillae, light from south-east, × 1. 2, light from north-west, × 1, see text-fig. 84. 3, enlargement of trunk papillae, light from east, × 8·6. 4, enlargement of trunk division A showing alternate spiny and smooth zones, light from south, × 3.

Figs. 5, 6. USNM 198647. 5, contracted specimen, light from south, × 2, see text-fig. 85. 6, enlargement of trunk papillae and possible fluid feeder system represented by alternate rises and depressions, light from south, × 5·6.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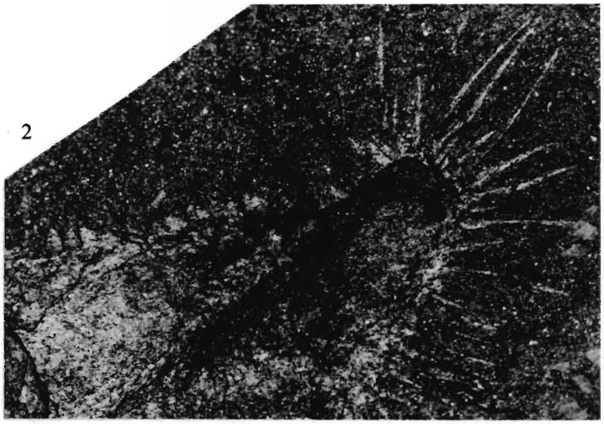
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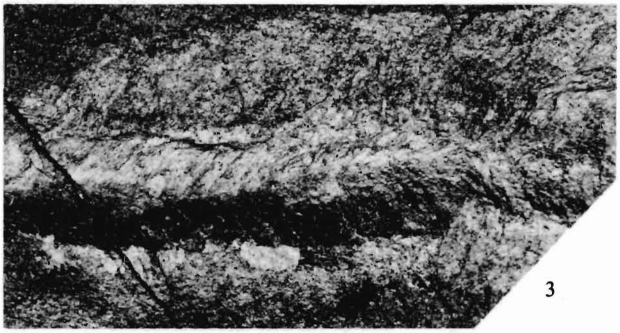
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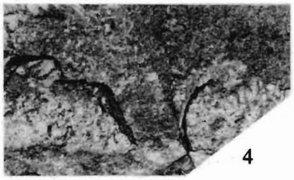
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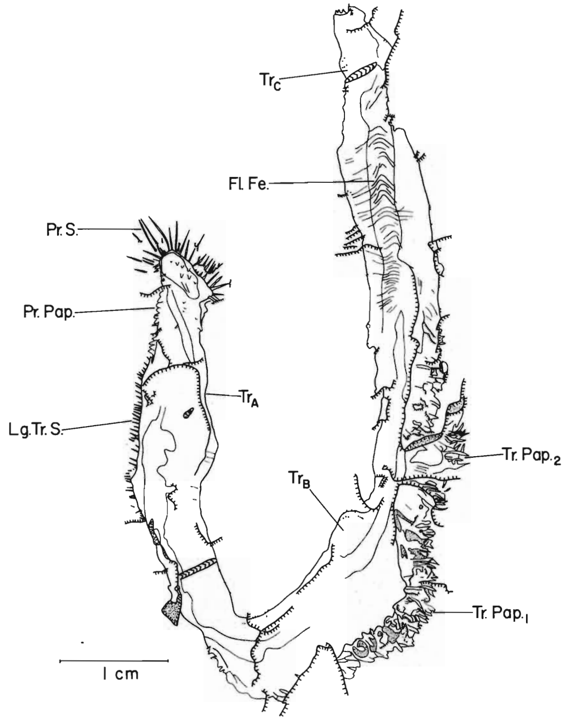
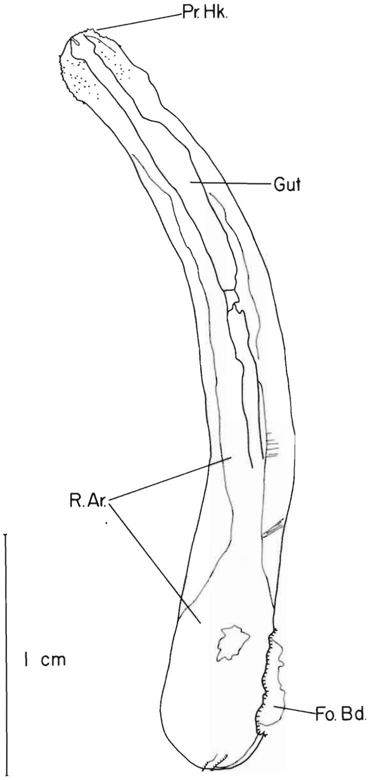
CONWAY MORRIS, *Louisella* and *Ancalagon*



TEXT-FIG. 86



TEXT-FIG. 87

EXPLANATION OF PLATE 24

Louisella pedunculata Walcott. Figs. 1–6. *Ancalagon minor* (Walcott) gen. nov. Figs. 7–9.

Figs. 1–4. USNM 198654. 1, specimen slightly distorted by sediment flowage, low-angle light from east, × 1·6, see text-fig. 86. 2, enlargement of proboscis showing proboscis papillae and long spines radiating over bedding plane, light from north, × 6. 3, enlargement of trunk division C showing furrow produced by flowage, light from south, × 5·4. 4, enlargement of trunk division B showing the two rows of trunk papillae separated by a layer of sediment, light from south, × 2.

Fig. 5. USNM 198653. Trunk division A and anterior of trunk division B, light from east, × 1·9.

Fig. 6. USNM 200596. Proboscis at stage 1 (see text-fig. 29), light from west, × 2·2.

Fig. 7. USNM 57646. Holotype, specimen with slight posterior dark stain and unidentifiable contents in posterior third of gut, light from west, × 1·3, original of Walcott 1911*c*, pl. 22, fig. 5.

Fig. 8. USNM 83939e. Paratype, young specimen, light from west, × 3·6, see text-fig. 87, original of Walcott 1931, pl. 9, fig. 5.

Fig. 9. USNM 188622. Specimen with swollen reflective areas at either end of body, light from east, × 1·5.

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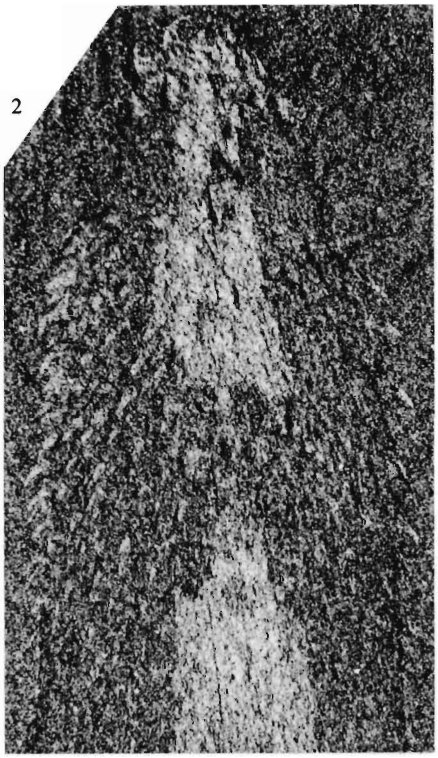

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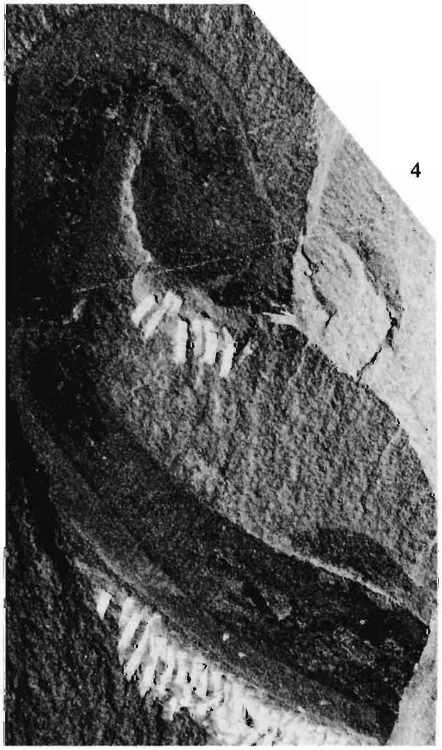

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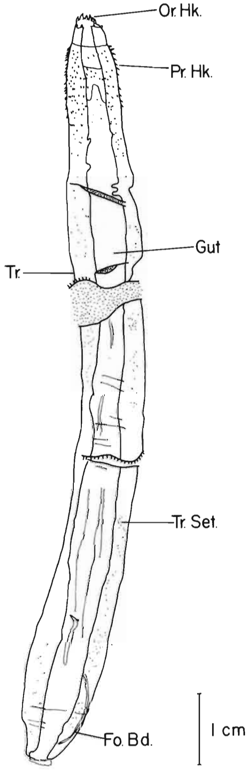
CONWAY MORRIS, *Ancalagon minor*



TEXT-FIG. 88

EXPLANATION OF PLATE 25

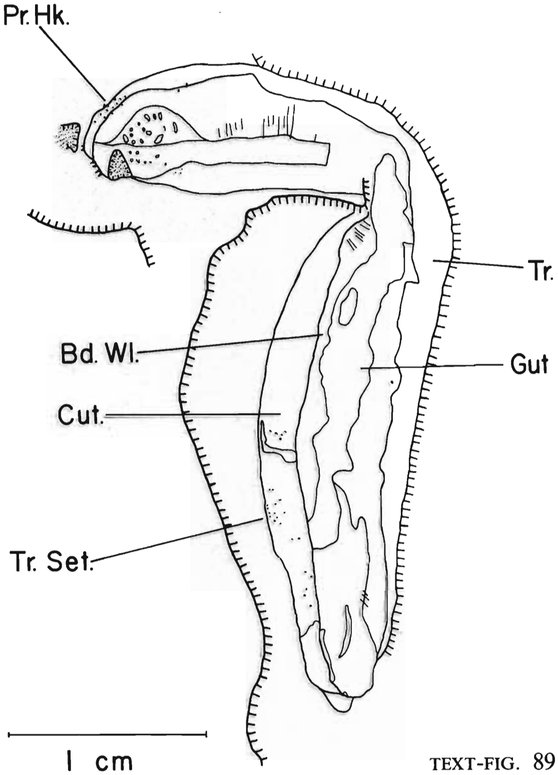
Ancalagon minor (Walcott) gen. nov.

Figs. 1–3. USNM 83939f. 1, paratype, well-preserved specimen, light from north-west, × 0·9, see text-fig. 88, original of Walcott 1931, pl. 9, fig. 6. 2, enlargement of proboscis, light from west, × 6·4, original of Walcott 1931, pl. 9, fig. 7. 3, counterpart, light from west, × 6·4.

Fig. 4. USNM 198610. Specimen with recurved ends, low-angle light from east, × 2·6.

Fig. 5. USNM 198609. Specimen with body wall detached from overlying cuticle, light from west, × 2·8, see text-fig. 89.

Fig. 6. USNM 198606. Posterior trunk apparently ruptured by decay, light from west, × 1·5.



TEXT-FIG. 89

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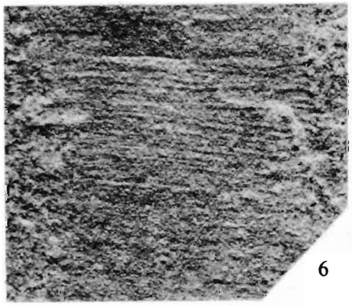

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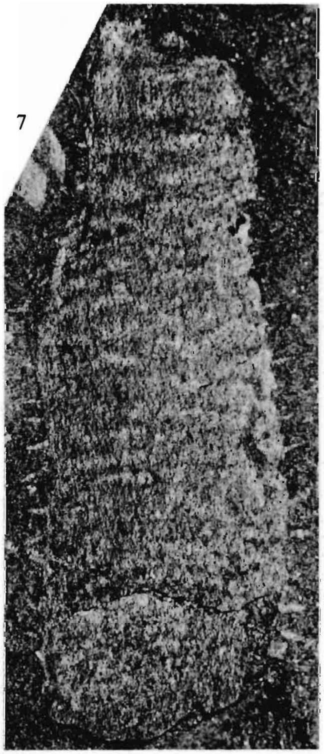

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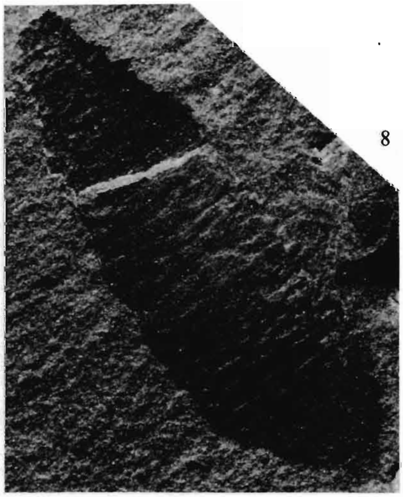

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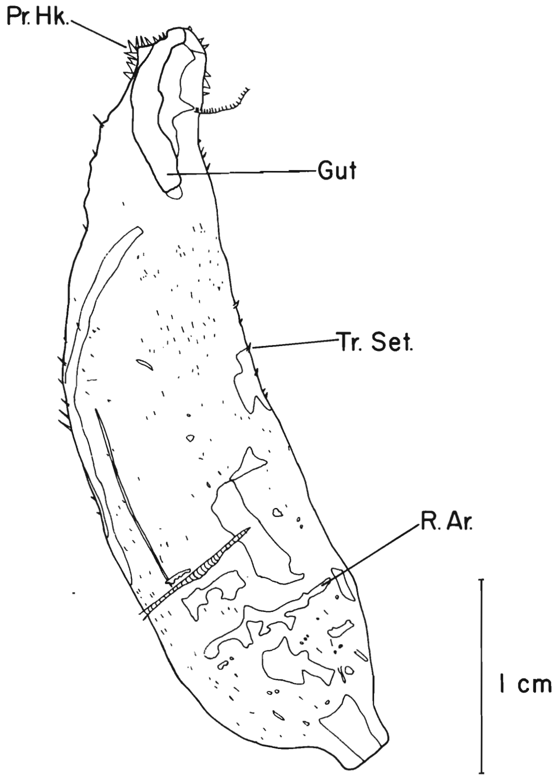
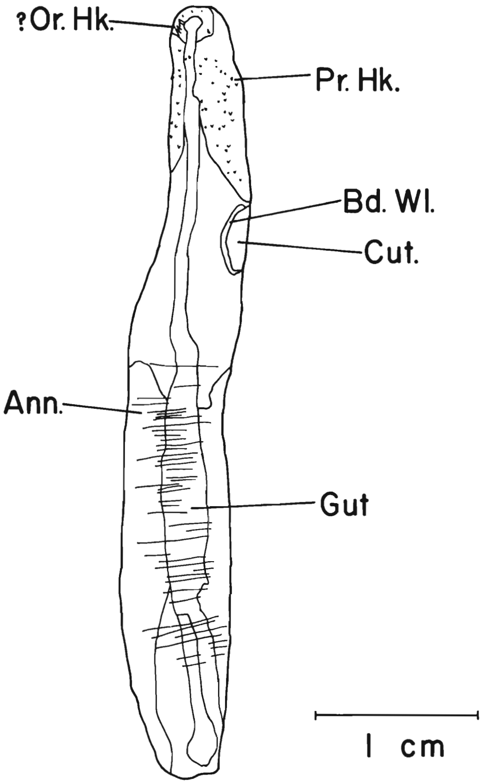
CONWAY MORRIS, *Ancalagon* and *Fieldia*



TEXT-FIG. 90



TEXT-FIG. 91

EXPLANATION OF PLATE 26

Ancalagon minor (Walcott) gen. nov. Figs. 1–6. *Fieldia lanceolata* Walcott. Figs. 7, 8.

Figs. 1, 2. USNM 198608. 1, counterpart, contracted specimen showing proboscis and setose trunk, light from north-west, × 2·9. 2, low-angle light from south-east, × 2·5, see text-fig. 90.

Figs. 3, 6. USNM 198607. 3, slightly decayed specimen, light from east, × 2·2, see text-fig. 91. 6, counterpart, enlargement of annulated trunk, low-angle light from north, × 5·3.

Figs. 4, 5. USNM 188621. 4, decayed specimen, light from west, × 1·5. 5, enlargement of proboscis with associated ostracod, low-angle light from east, × 7.

Fig. 7. USNM 83939c. Central trunk, light from east, × 6·6, original of Walcott 1931, pl. 9, fig. 3.

Fig. 8. USNM 198615. Central trunk broken open to reveal sediment infill, low-angle light from north, × 6·4.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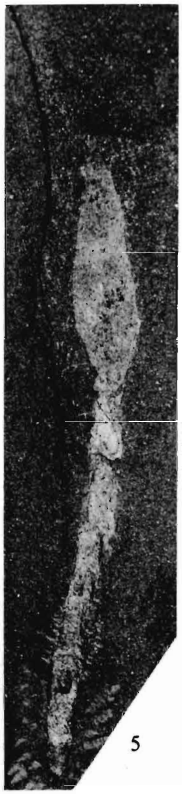
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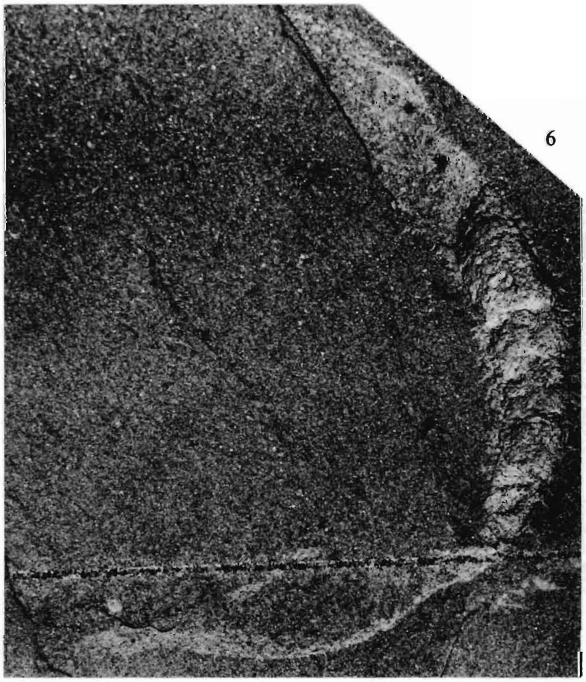
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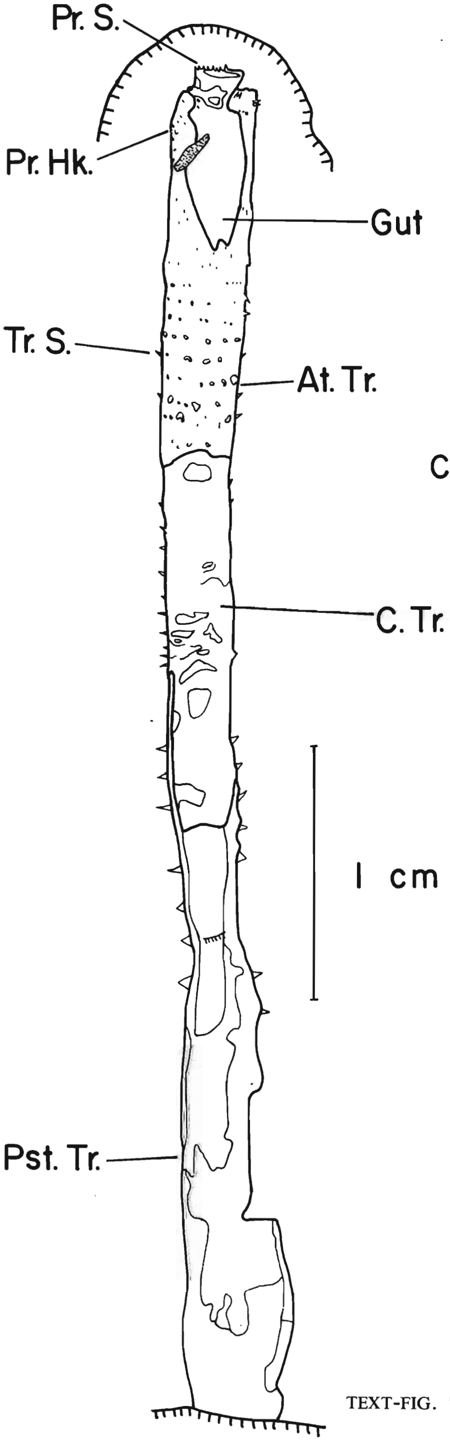
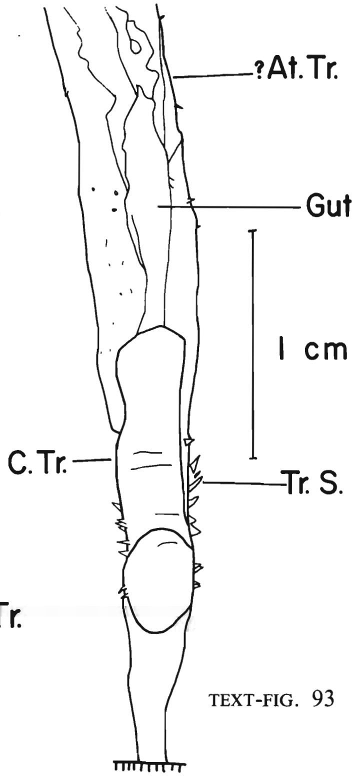
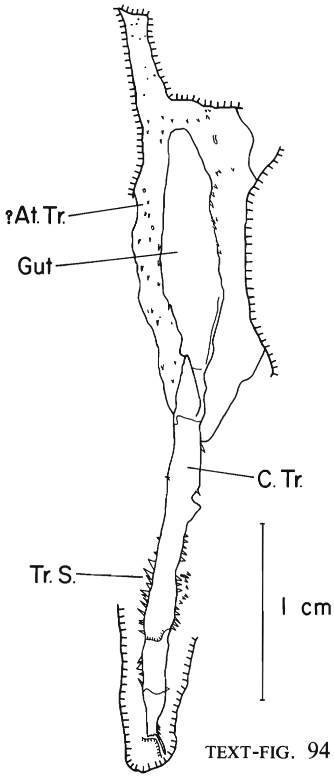
CONWAY MORRIS, *Fieldia lanceolata*



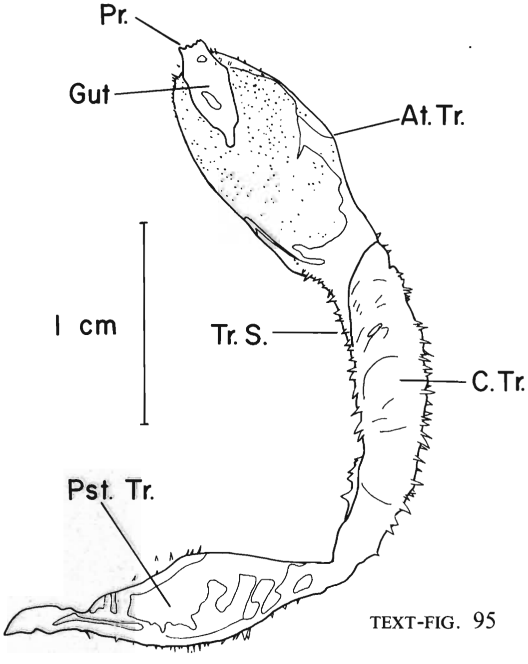
TEXT-FIG. 92



TEXT-FIG. 93



TEXT-FIG. 94



TEXT-FIG. 95

EXPLANATION OF PLATE 27

Fieldia lanceolata Walcott.

Figs. 1, 2. USNM 198597. 1. Well-preserved specimen, light from north-east, × 3·7, see text-fig. 92. 2, enlargement of proboscis, light from west, × 14.

Fig. 3. USNM 198602. Central and ?anterior trunk, light from east, × 3, see text-fig. 93.

Fig. 4. USNM 198603. Central and ?anterior trunk, light from south-west, × 2·9.

Fig. 5. USNM 198604. Central and ?anterior trunk, light from north-east, × 2·4, see text-fig. 94.

Figs. 6, 7. USNM 198605. 6, well-preserved curved specimen, light from north, × 3·2, see text-fig. 95. 7, counterpart, enlargement of proboscis and anterior trunk, light from west, × 6.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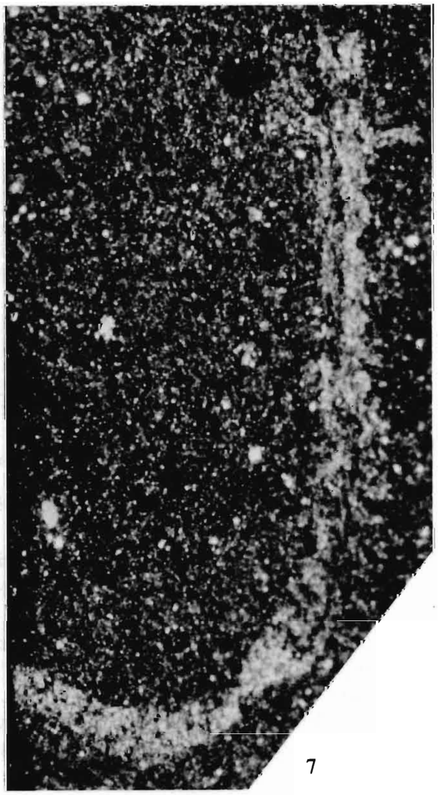
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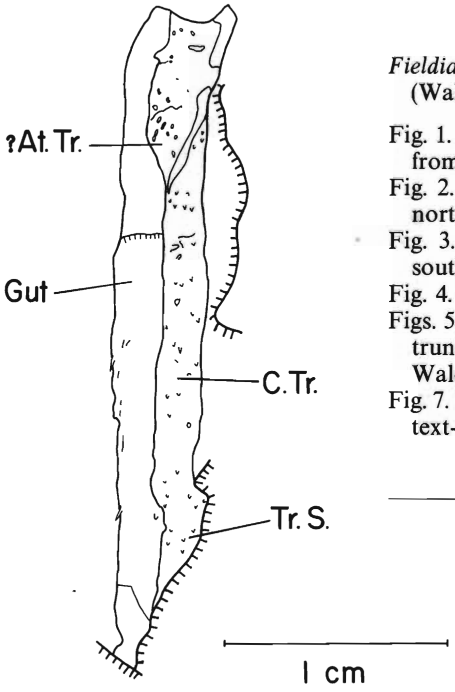
CONWAY MORRIS, *Fieldia* and *Lecythioscopa*



TEXT-FIG. 96

EXPLANATION OF PLATE 28

Fieldia lanceolata Walcott. Figs. 1–4. *Lecythioscopa simplex* (Walcott) gen. nov. Figs. 5–7.

Fig. 1. USNM 198601. Central gut flanked by spinose trunk, light from north-west, ×2·8.

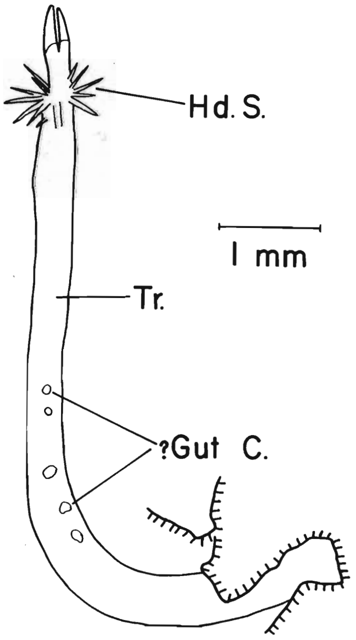
Fig. 2. USNM 198598. Central and ?posterior trunk, light from north-west, ×2·2.

Fig. 3. USNM 188633. Central and ?anterior trunk, light from south-west, ×3·2, see text-fig. 96.

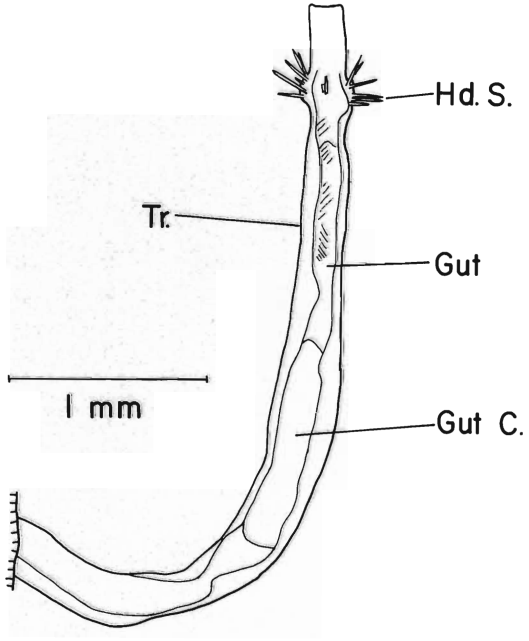
Fig. 4. USNM 198600. Central trunk, light from east, ×4.

Figs. 5, 6. USNM 83937. 5, specimen with spinose head and long trunk, light from north-west, ×16, see text-fig. 97, original of Walcott 1931, pl. 9, fig. 9. 6, counterpart, light from east, ×16.

Fig. 7. USNM 198714. Specimen with gut, light from east, ×28, see text-fig. 98.



TEXT-FIG. 97



TEXT-FIG. 98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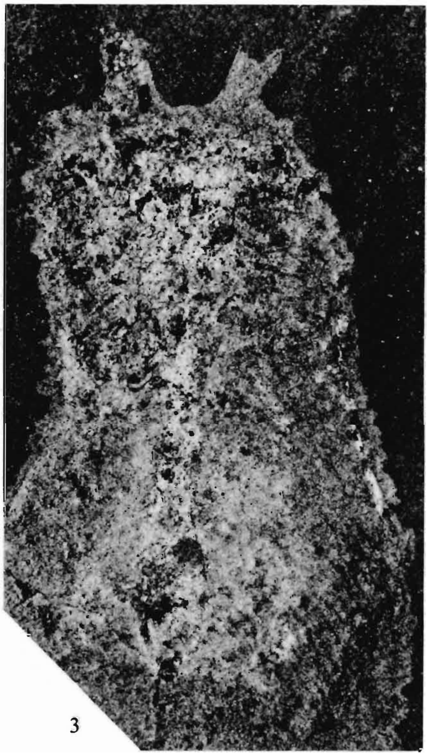
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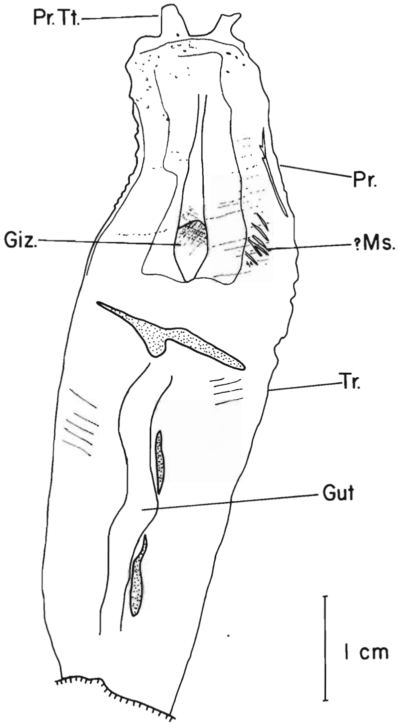
CONWAY MORRIS, *Scolecofurca* and *Priapulites*



TEXT-FIG. 99

EXPLANATION OF PLATE 29

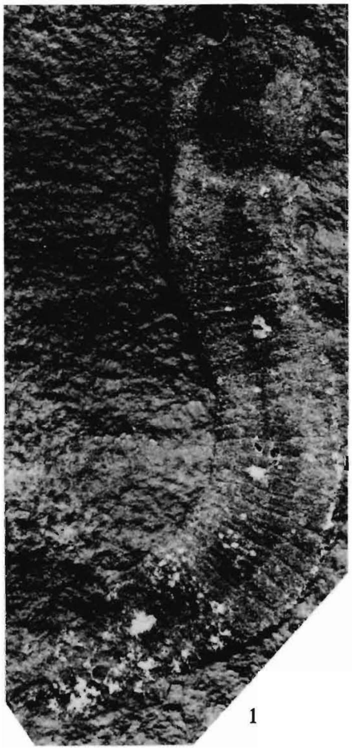
Scolecofurca rara gen. et sp. nov. Figs. 1–3. *Priapulites konecniorum* Schram. Francis Creek Shale (Pennsylvanian) Illinois. Figs. 4–7.

Figs. 1–3. GSC 45331. All photographed in ordinary white light under alcohol. 1, holotype, entire specimen, × 1·4, see text-fig. 99. 2, counterpart, × 1·4. 3, holotype, enlargement of proboscis with pair of tentacles, × 3·4.

Figs. 4, 5. PE 21555. 4, holotype, specimen consisting of slightly swollen proboscis and annulated trunk, light from north, × 2, original of Schram 1973, pl. 1, fig. 1. 5, enlargement of series of proboscis scalids, light from south-west, × 18.

Fig. 6. PE 32758. Specimen with monocaudal appendage, light from north, × 2·8.

Fig. 7. PE 32760. Specimen with apparent monocaudal appendage, light from north-east, × 2·6.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CONWAY MORRIS, *Priapulites*, *Selkirkia*, and *Protoscolex*

EXPLANATION OF PLATE 30

Priapulites konecniorum Schram. Francis Creek Shale (Pennsylvanian), Illinois. Figs. 1–3. *Selkirkia spencei* Resser. Spence Shale (Cambrian), Idaho and Utah. Figs. 4, 8. *Protoscolex* sp. Kinzer Shale (Cambrian), Pennsylvania. Fig. 5. Indeterminate worm ('*Ottoia inopinata*'). Levis Shale (Ordovician), Quebec. Figs. 6, 7.

Fig. 1. PE 25135. Complete specimen, light from south, × 2·8, counterpart of original of Schram 1973, pl. 1, fig. 4.

Fig. 2. PE 32759. Specimen with possible remains of gut, light from north-west, × 2·4.

Fig. 3. PE 24411. Specimen with proboscis replaced by a white mineral, light from north-east, × 1·3.

Figs. 4, 8. USNM 96493. Syntypes. 4, possible burrow, light from south-west, × 3. 8, tube with annulations at anterior, light from south-west, × 3·7.

Fig. 5. USNM 90784. Worm with papillate segments, ordinary white light, × 5·6, original of Resser and Howell 1939, pl. 1, fig. 1.

Figs. 6, 7. USNM (unnumbered). 6, complete specimen, light from east, × 1·2. 7, counterpart, light from east, × 1·2.