Middle Cambrian ctenophores from the Stephen Formation, British Columbia, Canada

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SUMMARY

The Ctenophora are a marine phylum of gelatinous swimmers and crawlers, with a minimal fossilization potential. To date only two acceptable fossil specimens are known, both from the Devonian Hunsrück Slate. Here we re-describe the single specimen of *Fasciculus vesanus* from the Phyllopod bed of the Burgess Shale (Middle Cambrian). The globose body bore two sets of comb-rows: one elongate and estimated to total ca.16, the other shorter and totalling ca. 64, so giving a total of ca. 80. Internally there were at least two and possibly four prominent organs, each consisting of an elongate series of lobes. *Xanioascus canadensis* gen. nov., sp. nov. is recorded from a horizon low in the Stephen Formation, from the *Glossopleura* zone. It is more similar to extant ctenophores than *F. vesanus*, but the comb-rows total ca. 24. These converge on the aboral pole, where there is evidence for the polar fields. The comb-rows stop short of the oral area, which is poorly defined. Internally prominent ovoid bodies are sometimes present, but their significance is uncertain. *Ctenorhabdotus capulus* gen. nov., sp. nov. occurs in the *Bathyuriscus-Elrathina* zone of the Stephen Formation. It is best known from the Raymond Quarry of the Burgess Shale, but also occurs in the underlying strata, including the Phyllopod bed. The comb-rows appear to have totalled 24, and converged towards the aboral pole, adjacent to which they amalgamate as groups of three rows each. In the fossils the comb-rows then join eight strands, possibly representing the meridional canals, that meet as a ring. In addition, in each group of three comb-rows the central row appears to have been conspicuously shorter than those flanking it. The aboral pole also bore a prominent capsule, presumably housing the statocyst. The oral area, which lacks the comb-rows, bore a voluminous mouth, apparently surrounded by a folded margin with possible musculature. These Cambrian ctenophores differ from the Devonian and Recent taxa in a number of ways. They have a larger number of comb-rows and apparently an absence of tentacles. In addition, structures found in the Cambrian ctenophores, such as the lobed organs of *F. vesanus* and the ovoid bodies of *X. canadensis* lack obvious counterparts in living species. The wider affinities of the ctenophores remain mysterious, but they probably evolved very early in the metazoan radiations, perhaps from an animal with an anterio–posterior axis and a ciliated surface.

Abbreviations

Abor. Re.	aboral region	?Ga. Re.	possible gastric region
Ap. Or.	apical organ	La.	lath-like structures in oral region
Cap.	capsule, housing probable statocyst (in *Ctenorhabdotus* gen. nov.)	Lo. Or.	lobate organ (in *Fasciculus*)
Co. Ro.	comb-rows of fused cilia and underlying polsters	Or. Re.	oral region
Co. Ro. (Opp. Si.)	comb-rows on opposite side of animal (in *Fasciculus*)	Ov. Bd.	ovoid bodies (in *Xanioascus* gen. nov.)
		?Stom.	possible stomodaeum
		1...24, I...IV	number of comb-rows (asterisks refer to opposite side of *Fasciculus* specimen)

1. INTRODUCTION

Ctenophores are an important group of largely pelagic diploblastic metazoans. Here only an outline of ctenophore anatomy is given, but excellent reviews are available (Krumbach 1925, 1927; Hyman 1940; Pianka 1974; Harbison & Madin 1982; Tamm 1982; Harbison 1985; Hernandez-Nicaise 1991). For the most part these marine animals are readily recognizable on account of the eight elongate bands composed of numerous transverse rows of cilia (the ctenes or comb-rows). In some taxa the comb-rows extend along almost the entire length of the animal, whereas in others some or all of the eight rows may be conspicuously shorter. The cilia move in metachronal waves with the power strokes serving to propel the animal, although in many forms this beating is supplemented by the action of muscular lobes to impart a stronger swimming motion. With the exception of groups such as the beroids, which engulf their prey and slice captured material with lips equipped with fused cilia (Swanberg 1974), cteno-

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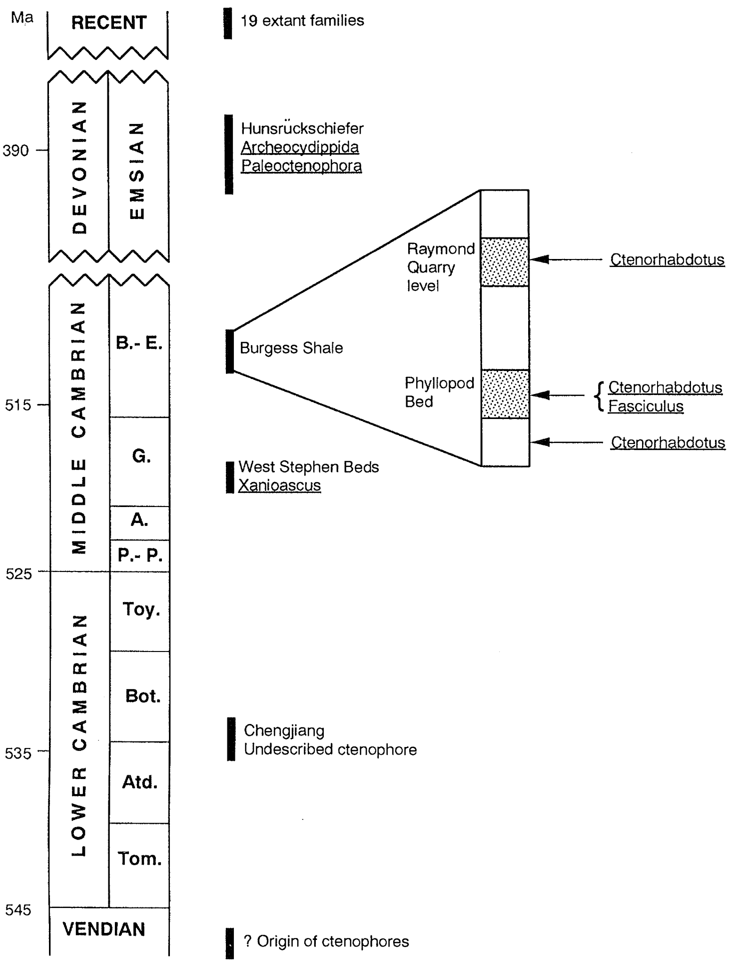

Figure 1. Stratigraphic distribution of ctenophores, highlighting their occurrences in the Cambrian (Canada and China, latter courtesy of Chen Jun-yuan, personal communication) and Devonian (Germany). The abbreviations in the Lower Cambrian refer to the standard stage divisions based on the Siberian platform: Tommotian (Tom.), Atdabanian (Atd.), Botomian (Bot.) and Toyonian (Toy.). The sub-divisions for the Middle Cambrian refer to polymeroid trilobite zonations employed in North America: *Plagiura–Poliella* (P.–P.), *Albertella* (A.), *Glossopleura* (G.), and *Bathyuriscus–Elrathina* (B.–E.) zones. The Emsian is a stage within the Lower Devonian.

phores ensnare food with a pair of tentacles equipped with colloblasts, specialized cells with sticky properties. These tentacles usually trail behind the animal, but in all but a few forms (e.g. thalassocalycids) they can be retracted into pouches. At the aboral end of the animal, where the comb-rows converge, the distinctive aboral or apical organ consists of a statocyst and other sensory cells situated beneath a dome of fused cilia. Extending from the apical organ in either direction is a ciliated loop (the polar fields). The mouth at the opposite end is capable of voluminous dilation and leads to a spacious digestive cavity, which in at least some taxa possesses anal pores. Apart from the nervous system, the other principal internal feature is a complex series of gastrovascular canals that extend from the gastric cavity. Although the comb-rows define an octomeral symmetry, the canals reflect a strong biradial symmetry. The phylum shows a wide range of morphologies that includes the ribbon-like cestids (Venus' Girdle), the extraordinary ocyropsids with their prominent oral lobes, and the benthic platyctenids which as adults have lost the comb-rows.

Ctenophores are often allied with the cnidarians, as the Coelenterata. This is on account of a shared diploblastic organization and spacious digestive cavity (coelenteron). Despite this similarity there is wide agreement that ctenophores and cnidarians are not closely related (e.g. Mills & Miller 1984). All suggestions of ctenophores bearing cnidae, other than by capture from cnidarian hosts, have been refuted (Carré *et al.* 1989). Moreover, the long-standing debate concerning the status of *Hydroctena* and its supposed intermediacy between ctenophores and cnidarians has finally been resolved and dismissed (Nielsen 1987). Although ctenophores are generally referred to as diploblastic, there are anal pores and the mesoglea contains muscle fibres and thus shows some differentiation towards a tissue grade. This suggests that the ctenophores can be regarded as a separate approach towards a triploblastic condition, but derived from a very early stock of primitive metazoans. On the other hand, Nielsen (1995) was so impressed with the mesoderm-like nature of the mesoglea and the evidence for its embryological origin that he proposed the ctenophores to be the sister-group of the deuterostomes (chordates, echinoderms, and related phyla). This places them considerably higher in the tree of metazoan evolution, but as yet this hypothesis receives little

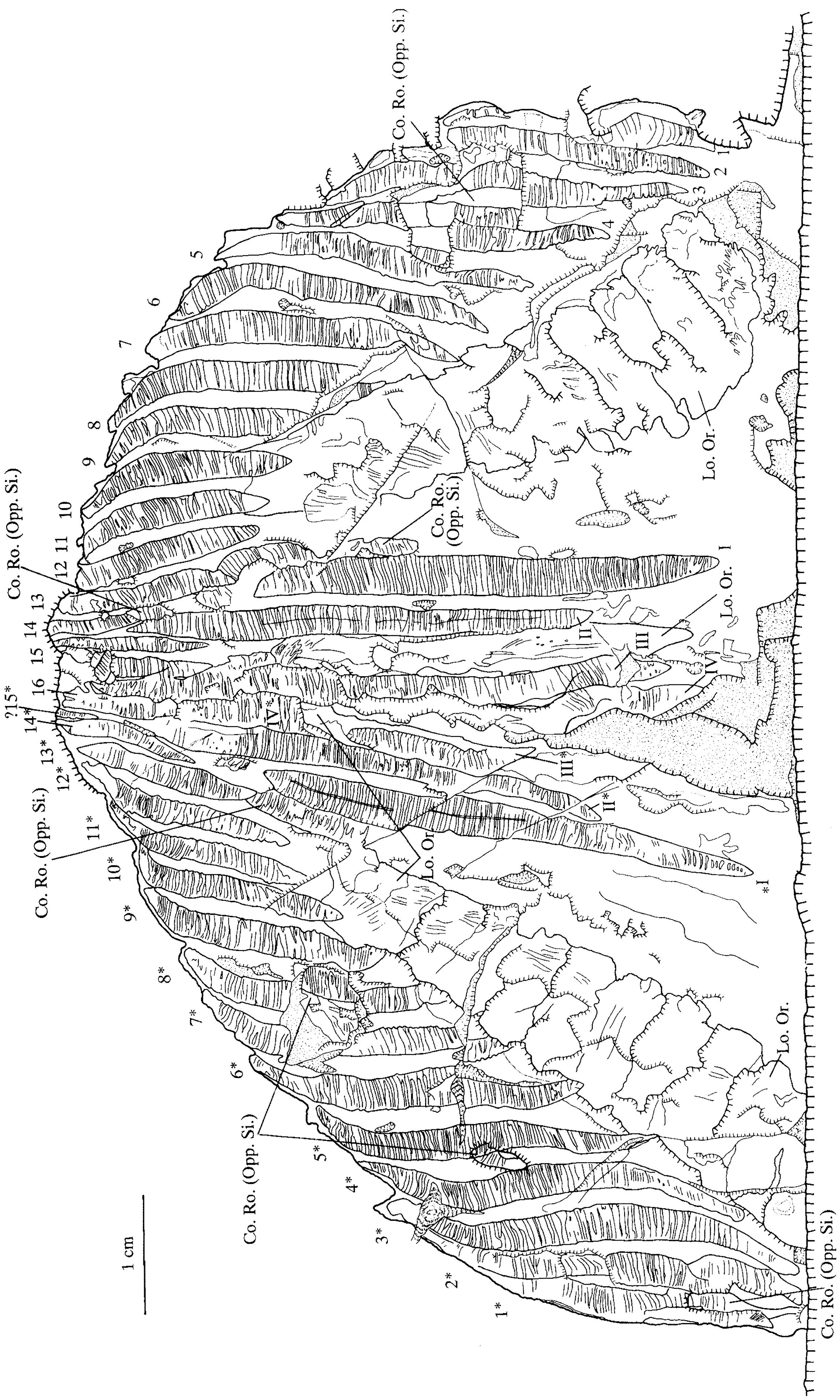

Figure 2. Interpretative drawing of USNM 139215 (counterpart), with some information transferred from the part. For photographic comparison see page 282, figure 3.

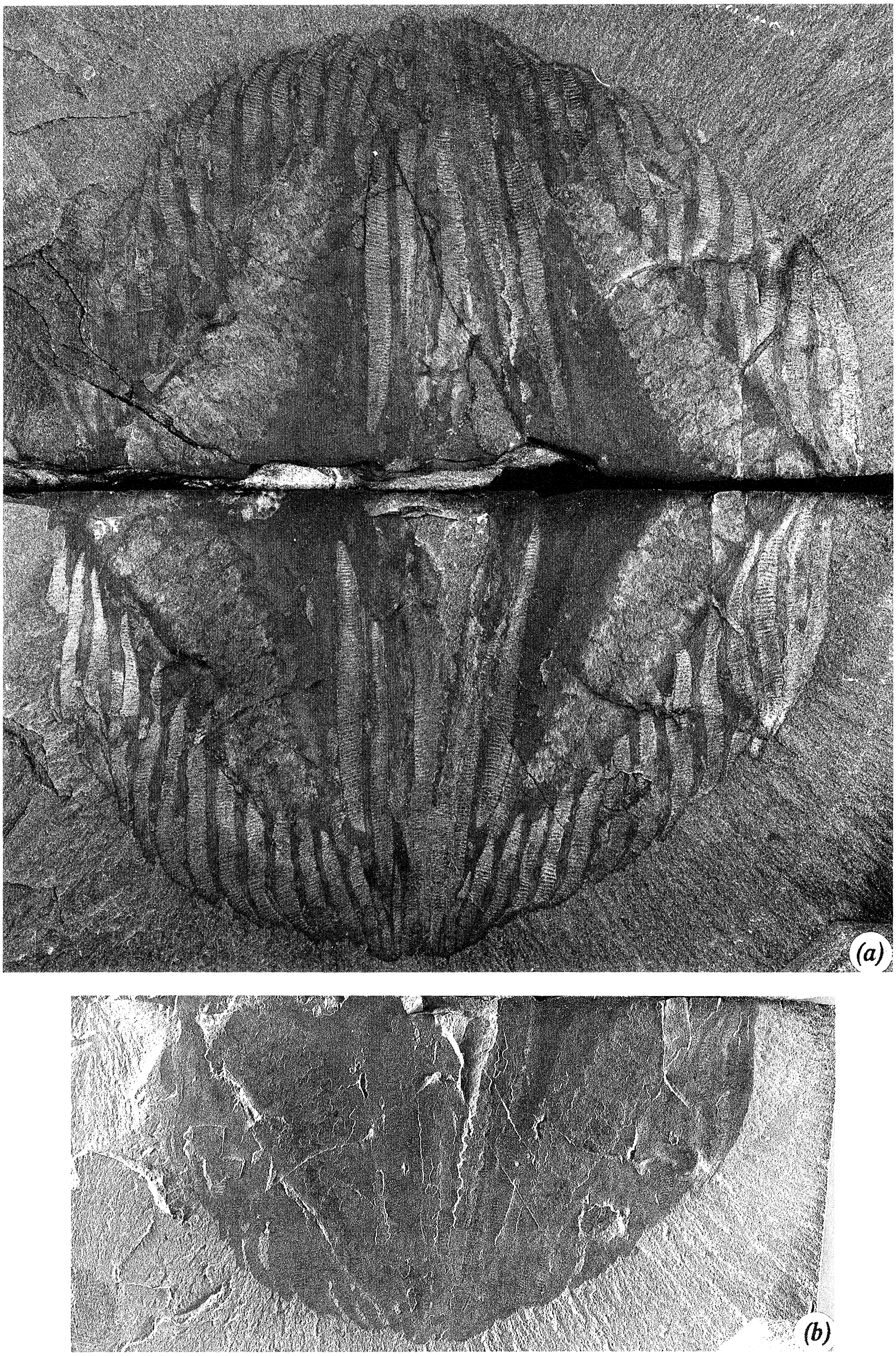

Figure 3. For description see opposite.

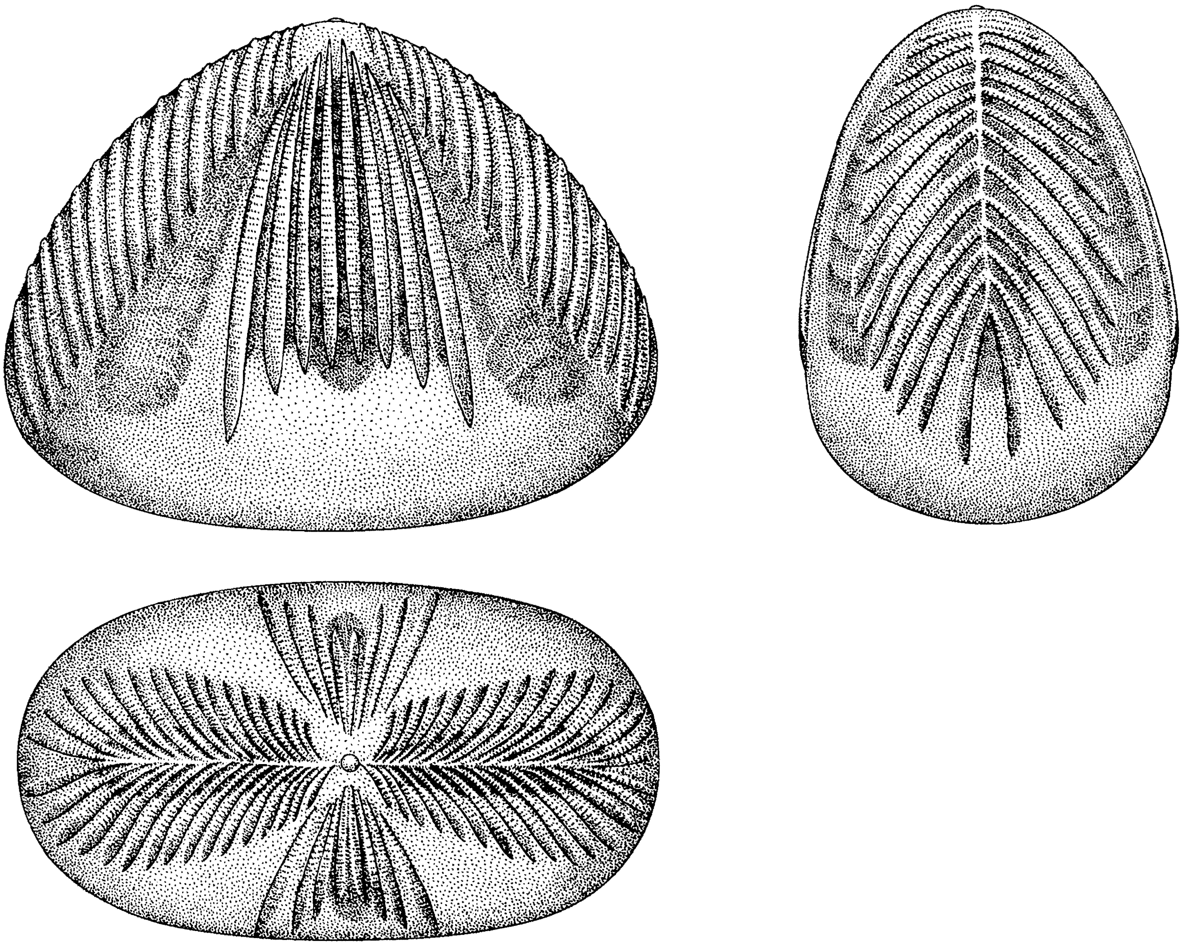

Figure 4. Reconstruction of *Fasciculus vesanus* in lateral and aboral views.

support from other lines of evidence. As this paper shows their fossil history can be traced at least as far back as the Middle Cambrian. However, their range is probably even longer because examples appear to be present in the Lower Cambrian Chengjiang biota of Yunnan, China (see below).

The fossil record of ctenophores is extremely sparse, and most of the existing claims for fossil ctenophores may either be rejected or are decidedly unproven. This is scarcely surprising given their delicate gelatinous construction which makes the collection of even living specimens exceptionally difficult. A hitherto unsuspected wealth of living ctenophores has now been seen in submersible dives, revealing ctenophores that are normally destroyed in collecting nets (e.g. Harbison *et al.* 1978). This absence of hard-parts and a predominantly pelagic mode of life that removes the animals from benthic processes help to explain a negligible fossil record.

At an early stage of the investigation of the Ediacaran assemblages from Namibia, the German investigator Gürich (1930, 1933) proposed that taxa such as *Rangea* might be referred to the Ctenophora, but this was decisively rejected by his compatriot Richter (1955). Since then our knowledge of Ediacaran taxa has greatly increased as has the debate concerning their affinities. Although the discussion covers extensive ground, broadly two camps exist which are divided in their interpretation of these fossils. One regards them as being primitive metazoans (e.g. Glaessner 1984; Gehling 1991; Jenkins 1992; Conway Morris 1993*a*), whereas the other proposes that they are an extinct group of multicellular eukaryotes referred to as the Vendobionta (e.g. Seilacher 1992). Even proponents of the former hypothesis, however, have not reinvoked a ctenophoran affinity for any Ediacaran fossil. This might be premature because there are a number of bag-like fossils, notably *Platypholina* (Fedonkin 1985, plate 19, figures 5 & 6) and *Protechiurus* (Glaessner 1979, figure 1) for which a ctenophore affinity cannot be dismissed. Although their most compelling comparison with younger organisms is with the Cambrian fossil and probable cnidarian *Mackenzia costalis* (Conway Morris 1993*a*), the only known specimen of *Protechiurus* has eight longitudinal ridges. These were interpreted as muscle bands by Glaessner (1979), but

Figure 3. *Fasciculus vesanus* Simonetta & Delle Cave, Stephen Formation (Burgess Shale), Walcott Quarry, Field, British Columbia, USNM 139215 (holotype). (*a*) Part (upper) and counterpart (lower), x1.4. (*b*) Part, photographed in low angle light, x1.1.

Figure 5. Interpretative drawing of ROM 43186 (counterpart), with some information transferred from part. For photographic comparison, see page 286, figure 7.

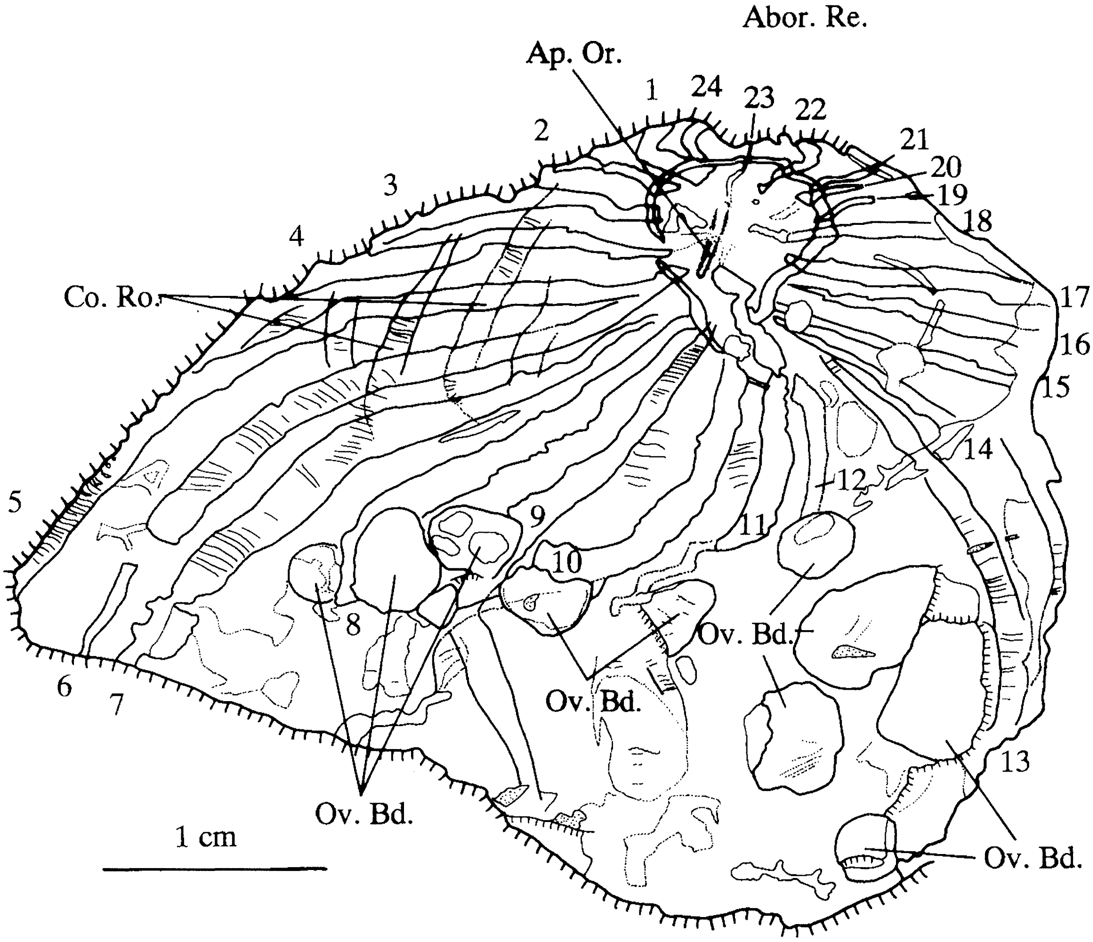

Figure 6. Interpretative drawing of ROM 43191.

one can speculate that these eight ridges are the remains of comb-rows. Below, however, it is suggested that the reduction of the comb-rows to eight was a post mid-Cambrian event.

In terms of the possible record of Phanerozoic ctenophores Ziegler (1991) has tentatively suggested that the hitherto enigmatic *Laffonia helvetica* from the Upper Jurassic of Switzerland may be a ctenophore. This worker also synonymized this taxon with *Pseudocaudina brachyura* from the late Jurassic Solnhofen Limestone of south Germany. As described this latter fossil has enjoyed a chequered career, being assigned first to holothurians (Broili 1926) and then to the actinarians (Heding 1932). Although the overall shape of *Laffonia* and the elongate striated rows are consistent with a ctenophore bearing comb-rows, the style of preservation and lack of other anatomical details make this assignment tentative. Caster & Brooks (1956) described a small ribbon-like fossil (*Cestites mirabilis*) from the Lower Ordovician of Tennessee as a ctenophore comparable to *Cestus*. The specimen is small and has no structures to support placement in the Ctenophora (see also Häntzschel 1975, p.W149). Even less credible is Gislen's (1947) identification of calcareous fossils (*Peridionites*) from the Middle Cambrian of Queensland as calcified ctenophores. The true nature of these remains, as part of an eocrinoid (Echinodermata), has been explicated by Smith (1982).

To our knowledge the only convincing published examples of fossil ctenophores are the genera *Ctenorhabdotus* gen. nov., *Fasciculus* and *Xanioascus* gen. nov. from the Middle Cambrian Stephen Formation and two specimens referred to respectively as *Paleoctenophora* (*P. brasseli*) and *Archeocydippida* (*A. hunsrueckiana*) from the Devonian (Emsian) Hunsrück Slate of north-west Germany (Stanley & Stürmer 1983, 1987; see also pp. 63–65 in Bartels & Brassel 1990) (figure 1). These latter fossils are pyritized and so amenable to radiography. The bodies of these Devonian ctenophores are more or less globose and bear comb-rows, the details of which are clearer in *A. hunsrueckiana*. Stanley & Stürmer (1983, 1987) also presented evidence for tentacles and tentacle sheaths, and concluded that both were cydippids.

These interpretations of the Hunsrück fossils, however, found little favour with Otto (1994, p. 59) who, as part of a wider attack on current interpretations of the Hunsrück Slate and its soft-part preservation, argued that *P. brasseli* 'obviously represents the shell of a small brachiopod', whereas *A. hunsrueckiana* might be some sort of sedimentary structure. The specimen of the former taxon is admittedly the more poorly preserved of the two Hunsrück specimens and the associated tentacle may be fortuitously superimposed, but Otto's (1994) comparison with a brachiopod is not very compelling. In the case of *A. hunsrueckiana* the quality of preservation is somewhat better, and we accept the identification of the principal organs,

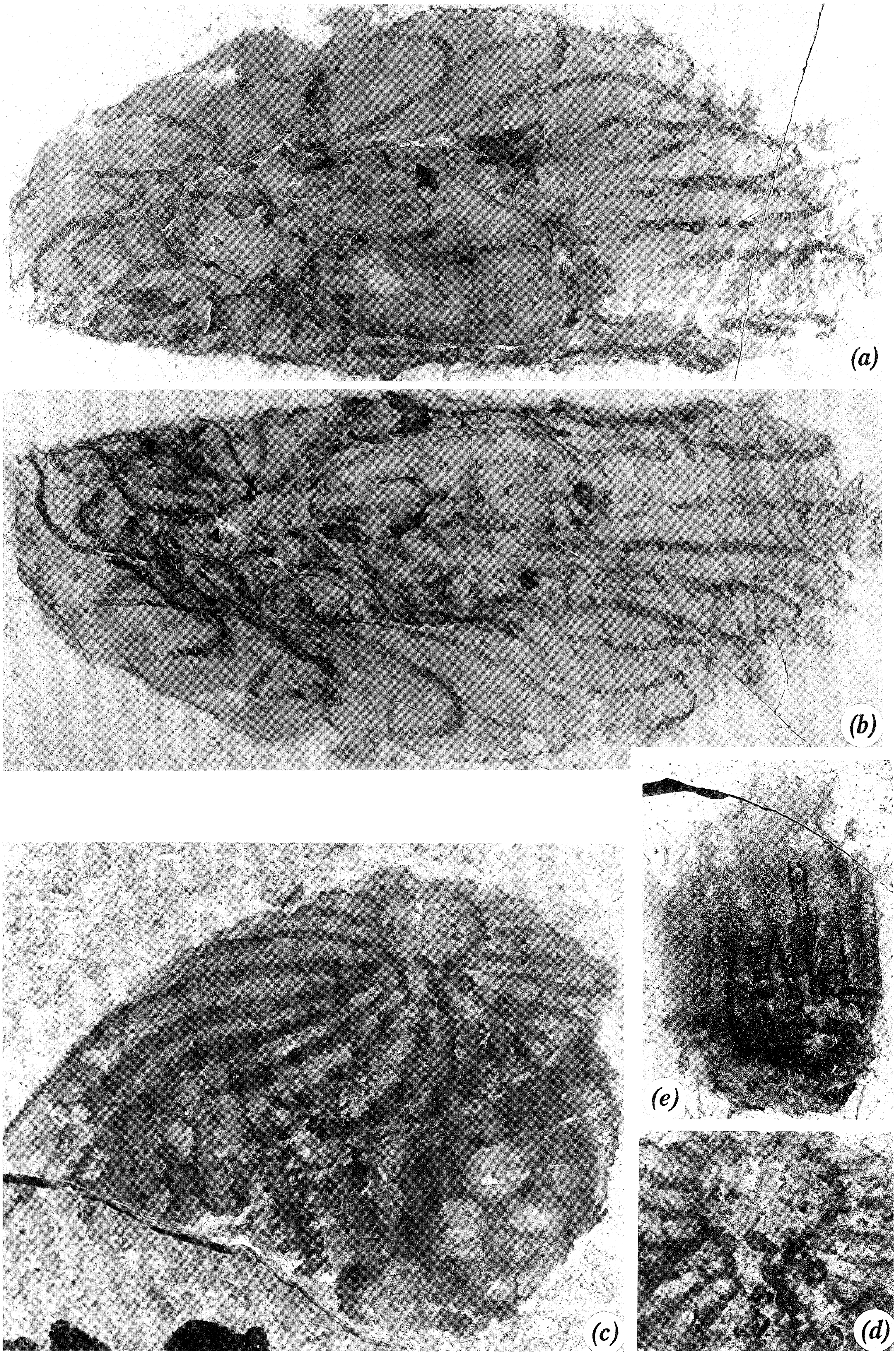

Figure 7. For description see opposite.

notably the comb-rows. In an earlier publication Stürmer *et al.* (1980, plate 1, figure 2) illustrated a purported ctenophore, but as Otto (1994) points out this specimen is more convincingly assigned to the chondrophorines that were assessed in detail by Yochelson *et al.* (1983). The Hunsrück material has been studied by radiography. Although this has some advantages, such as allowing stereoscopic viewing of the fossils, the relative coarseness of the pyrite replacement leads to some ambiguous interpretations. In contrast, the Cambrian specimens, although greatly compacted, do show a wide range of anatomical detail.

Specimens of a fossil ctenophore apparently comparable to *Ctenorhabdotus* gen. nov. have also been collected from the Lower Cambrian (Upper Atdabanian-Lower Botomian) Burgess Shale-type fauna at Chengjiang in Yunnan province, south China (J. -Y. Chen, personal communication). This material, however, does not seem to be comparable to the purported ctenophore depicted in an earlier reconstruction of the Chengjiang biota and referred to as 'a ribbon-shaped species similar to living cestid forms of comb-jellies' (Chen *et al.* 1991, p. 15, figure 3).

To date, the fossil record of ctenophores has been too scanty to add much material to our understanding of ctenophore phylogeny. Stanley & Stürmer (1983, 1987) commented that the Devonian material showed an affinity with the cydippids, while as discussed below *Ctenorhabdotus* gen. nov., *Fasciculus* and *Xanioascus* gen. nov. may throw some light on earlier stages of ctenophore diversification. Their Palaeozoic record is also consistent with data from molecular biology, especially ribosomal RNA sequences. These latter data confirm inferences based on classical anatomy for a ctenophore affinity, albeit remote, with the Cnidaria and an origination early in metazoan history (e.g. Christen *et al.* 1991).

2. HISTORY OF RESEARCH AND STRATIGRAPHIC CONTEXT

The first two specimens (USNM 139215 (figures 2 & 3), 468031 (figures 10*a*, *b*)) to be collected were obtained by C. D. Walcott and now reside in the National Museum of Natural History, Smithsonian Institution, Washington D.C. The first of these, which was to be designated as the holotype of *Fasciculus vesanus* by Simonetta & Delle Cave (1978), is known to have been collected in 1917 because a sketch was made by Walcott in his diary on the day of discovery (Sunday, August 19). Walcott never published an account of these specimens, and to date the only information available is the brief report by Simonetta & Delle Cave (1978) on the holotype and only known specimen of *Fasciculus*. These authors were uncertain as to the affinities of *Fasciculus*, but mentioned (Simonetta & Delle Cave 1978, p. 47) the possibility of 'Some affinities to the Cnidaria'. The other of Walcott's specimens has remained undescribed. A third specimen (MCZ 101681, figures 12 & 15*a*) is in the collections of the Museum of Comparative Zoology, Harvard University. This specimen must have been collected either during one of P. E. Raymond's Harvard Summer School courses in field geology that visited the Burgess Shale quarry in 1924, 1925 and 1927, or during 15 days of excavation in 1930. In this enterprise Raymond led a four-man Harvard party, reopened Walcott's quarry and opened another quarry 'higher up the mountain' (Raymond 1930, p. 32). The most likely source was the upper quarry, now called Raymond's quarry, or adjacent float (see below) because this level has yielded most of the other specimens of this species described here. Renewed impetus for a more thorough account of these ctenophores has arisen from continuing field-work by the Royal Ontario Museum (ROM), commencing in 1981.

All eight specimens of *Xanioascus* gen. nov. come from a locality informally called the 'West Stephen beds' on the west-facing slope of Mount Stephen, approximately 5 km south of the Walcott quarry on Mount Field. This site is equivalent to locality 9 of Collins *et al.* (1983), and has already attracted attention on account of arthropods such as *Sanctacaris uncata*, which is interpreted as a very early chelicerate (Briggs & Collins 1988). The first specimen (ROM 43186, holotype, figures 7*a*, *b*) was collected on July 6, 1982 by David Rudkin from surficial excavation at the site. The remainder were all collected during full-scale excavation of the site between July 12 and August 26, 1983. Three specimens, and possibly a fourth, were found on one bedding plane, whereas a fifth specimen occurred on a bedding surface 0.5 m lower amongst a number of similar-sized structureless 'blobs' that may also represent ctenophores (figure 21*e*). Originally thought to be approximately the same age as the Burgess Shale (Collins *et al.* 1983), the discovery of the trilobite *Glossopleura in situ* (Collins, 1986), indicates that this site is significantly older, falling in the next lower trilobite zone (figure 1).

In July and August of 1991, 1992 and 1993, eleven specimens of *Ctenorhabdotus* gen. nov. were excavated by ROM parties from the Raymond quarry bed, approximately 21 m stratigraphically above the base of Walcott's quarry. The eleven specimens occurred singly over a thickness of 2.3 m, with only two coming from the same level. The MCZ specimen probably came from this bed as well. In contrast, presumably the specimen of *Ctenorhabdotus* gen. nov. collected by Walcott came from the Phyllopod bed. This is because although the specimen occurs on a weathered surface it is associated with a specimen of an agnostoid trilobite, which are common in the Walcott Quarry, but very rare in the Raymond Quarry bed. In any event a downward extension of the stratigraphic range of *Ctenorhabdotus* gen. nov. is confirmed because the one specimen collected by the 1994 ROM party came from

Figure 7. *Xanioascus canadensis* gen nov., sp. nov., Stephen Formation, Mount Stephen, Field, British Columbia. (*a*–*b*) ROM 43186, part and counterpart, x3.4. (*c*–*d*) ROM 43191. (*c*) Entire specimen, x2.5. (*d*) Detail of aboral region, x3.5. (*e*) ROM 43192, juvenile specimen, x3.0.

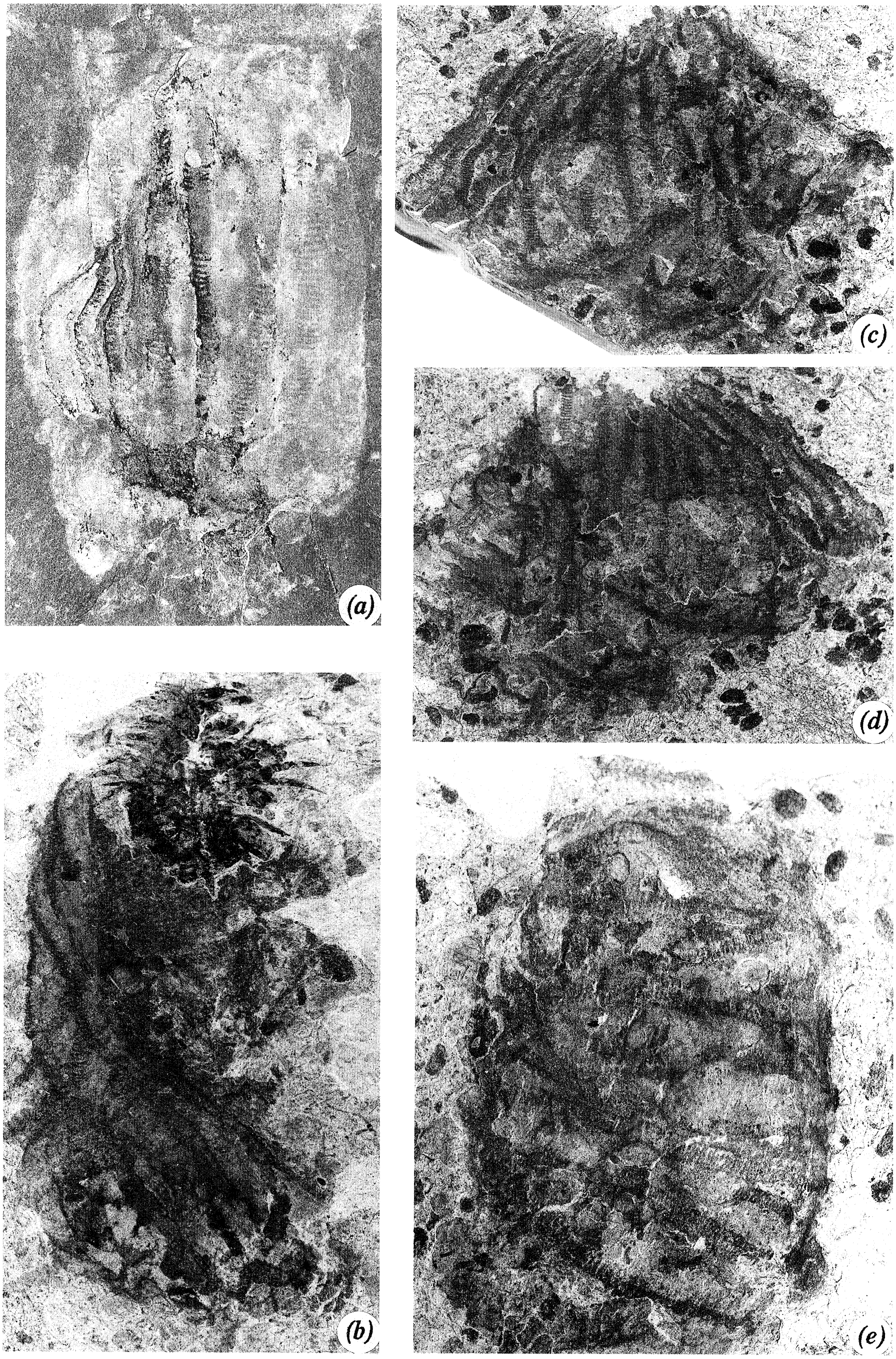

Figure 8. For description see opposite.

a level 1.3 m below the base of the Phyllopod bed. Two of the four specimens collected during the 1995 ROM season came from the base of the Phyllopod bed in the Walcott Quarry (equivalent to Walcott's (1912, p. 152) layer 12 or 'great *Marrella splendens* layer'). The other two specimens are from outcrops immediately to the south of the Walcott Quarry. Although these horizons are most likely equivalent to the Phyllopod bed, their precise correlation with this informal stratigraphic unit cannot be established owing to small-scale faulting and an absence of marker beds. The one specimen of *Fasciculus* is presumed to come from the Phyllopod bed.

3.THE TAXONOMIC STATUS OF CTENORHABDOTUS GEN. NOV., FASCICULUS AND XANIOASCUS GEN. NOV.

Passing mention of the likely ctenophore affinities of *Fasciculus* have been made by various workers (Collins *et al.* 1983; Conway Morris 1985, 1993*b*; Collins 1986). A more circumspect view was offered by others (Briggs & Conway Morris 1986), and Stanley & Stürmer (1987) were even more sceptical by concluding that *Fasciculus* was better regarded as 'a problematic cnidarian, defying classification with extant groups'. The place of these Cambrian animals in the ctenophores largely depends on the prominent elongate rows with transverse bar-like structures being correctly identified as the remains of the diagnostic comb-rows. Each row consists of the actual cilia (the comb-plates or ctenes) and supporting structures that underlie them. These underlying units form bar-like structures, and are composed of tall ciliated cells (polsters) that form a basal cushion to the fused cilia of the combs. Direct evidence for the fused cilia in *Fasciculus* and the other ctenophores described here does not appear to be present. There appear to be two possible explanations as to why the cilia are not evident. Less likely, perhaps, is that they detached shortly after death and before fossilization in a manner similar to that observed in Recent ctenophores. In correspondence (letter, 4 March 1995) Dr R. Harbison informed us that 'When recent ctenophores die and decompose, the comb plates are the first to drop off, leaving marks where they were attached in the comb rows'. The extent of decay in these ctenophores and the Burgess Shale fossils in general is quite difficult to assess, although in some specimens of *Xanioascus* gen. nov. decay is more evident (see below). Despite their spectacular preservation there is in fact widespread evidence for decay in the fauna, most notably in the prominent 'dark-stain' associated with most specimens of the arthropod *Marrella* (Whittington 1971). It remains arguable whether there might be a taphonomic distinction between the preservability of cilia and the underlying polster cells. The latter, however, have a well-developed cytoskeleton (Hernandez-Nicaise 1991), and this might enhance their preservation potential. The alternative possibility is that direct evidence of the cilia has been destroyed by the very high degree of compression experienced by these fossils. The Burgess Shale specimens appear to have been reduced to carbon films which in at least some cases are less than 10 μm thick (Butterfield 1990*a*, figure 4). Butterfield (1990*b*) was able to show, by careful isolation after acid digestion of the sediment, that the Burgess Shale fossils sometimes preserved ultrastructural details. This is typical, however, of quasi-hard parts such as the sclerites of *Wiwaxia*, the chaetae of *Canadia*, and arthropod cuticles. Other material is more featureless (Butterfield 1990*a*, figure 1A), and the likelihood of identifying ultrastructural details in isolated fragments of either *Fasciculus* or the other ctenophores described here may be low. More significant is the observation that on a macroscopic scale fine details are not necessarily preserved in the Burgess Shale fossils. A notable example is the presence of eyes in many of the arthropods and related organisms such as *Opabinia* and perhaps *Nectocaris*. It may be reasonably inferred that they were compound, but are typically preserved as either very dark or reflective areas and seldom show clear evidence for the individual lenses.

It is concluded that the transverse structures in *Fasciculus* and the other Cambrian ctenophores are best compared with the comb-rows. It seems most likely that the structures visible in the fossils largely represent the basal polsters. Note also that the spacing of these structures is comparable to that observed in living ctenophores. Finally, it should also be stressed that, to the best of our knowledge, apart from the ctenophores no other metazoan phylum (see Nielsen 1995) has bar-like structures remotely like the ones described here.

The only formal description of *Fasciculus* is based on a single specimen (part and counterpart) from the Burgess Shale, which Simonetta & Delle Cave (1978) referred to *F. vesanus*. It is our belief that all the other specimens ($n = 26$) cannot be referred to this species, and accordingly are placed in *Ctenorhabdotus* gen. nov. and *Xanioascus* gen. nov. The decision to recognize three genera is not straightforward, because the holotype and only known specimen of *Fasciculus vesanus* appears to be incomplete owing to rock breakage. Thus the possibility remains that its supposed distinctiveness is in fact a result of taphonomic alteration or even original teratology. Incompleteness of this specimen makes it difficult to judge its original shape, but as preserved this unique specimen differs by its broadly flaring outline. The principal reason for the generic separation of this specimen, however, is the unique arrangement of the comb-rows which differs from the remaining specimens in three respects: (i) clear bilateral or possibly biradial symmetry; (ii) differentiation into long and short varieties; and (iii) a much larger total (see below for a more detailed description). In addition, the specimen of *Fasciculus* differs from

Figure 8. *Ctenorhabdotus capulus* gen. nov., sp. nov., Stephen Formation, Raymond Quarry, Field, British Columbia. (*a*) ROM 50823, x2.8. *Xanioascus canadensis* gen. nov., sp. nov., Stephen Formation, Mount Stephen, Field, British Columbia. (*b*) ROM 50824, x2.0. (*c–d*) ROM 43195, part and counterpart, x1.8. (*e*) ROM 43193, x2.1.

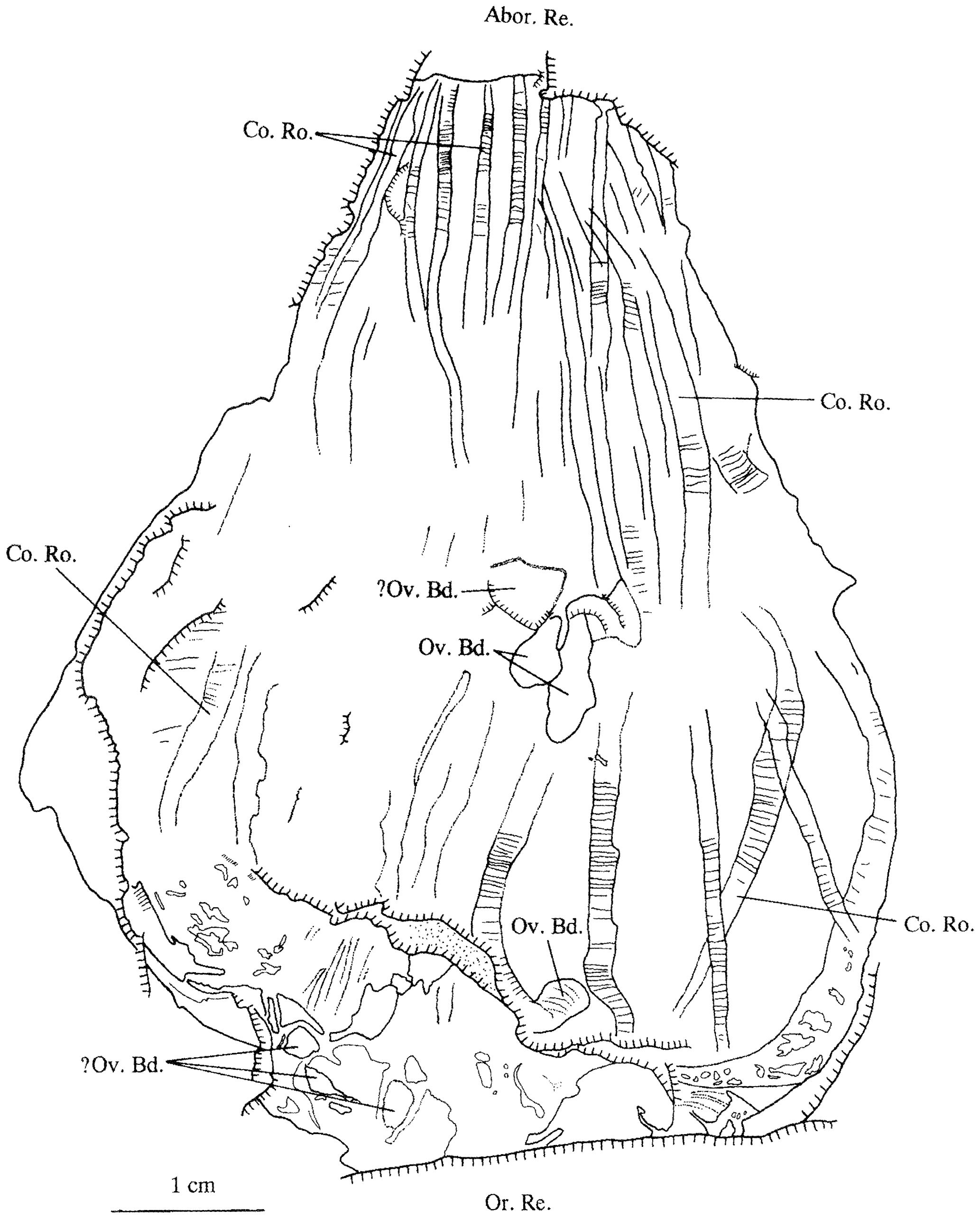

Figure 9. Interpretative drawing of ROM 43190 (part), with some information transferred from the counterpart. For photographic comparison see page 292, figure 10*b*.

those of *Ctenorhabdotus* gen. nov. and *Xanioascus* gen. nov. in possessing unique internal organs and lacking the so-called ovoid bodies present in many specimens of the latter genus.

4. METHODS

Nearly all the material was collected by quarrying. One specimen (figure 15*a*), which occurs on a weathered surface and has no counterpart, may have been collected as float by Raymond. Where necessary very limited preparation with a dental microdrill served to remove small areas of sediment. Specimens were photographed in white light. In some cases immersion in alcohol enhances detail (e.g. figures 7*a–c*). Camera-lucida drawings are placed opposite some of the photographs as a guide to our interpretation of the specimens.

5. SYSTEMATIC PALAEONTOLOGY

(*a*) *Systematic section*

(i) *Phylum*

Ctenophora Eschscholtz, 1829.

(ii) *Revised diagnosis of phylum*

Metazoans characterized by rows of cilia, eight in Recent and Devonian taxa, but up to ca. 80 in Cambrian forms. Apical organ with statocyst present, tentacles sometimes. Mouth leading to gastric cavity and internal canal system.

(iii) *Class and order*

Uncertain.

(iv) *Family*

Fasciculidae fam. nov.

(v) *Diagnosis*

Ctenophores with probable biradial symmetry, with two sets of comb-rows. One set totals ca. 16, elongate. Second set consists of ca. 64, increasing in length away from first set. Two, probably four, internal lobate organs. Body globose, oral region not known.

(vi) *Genus* Fasciculus *Simonetta & Delle Cave*, 1978

Type and only known species Fasciculus vesanus Simonetta & Delle Cave, 1978. Original designation, p.47.

Diagnosis As for family.

Fasciculus vesanus Simonetta & Delle Cave, 1978

1978	*Fasciculus vesanus* Simonetta & Delle Cave, pp. 45, 47, figures 1,2.
1985	*Fasciculus vesanus* Conway Morris, p.347.
1985	*Fasciculus vesanus* Whittington, pp.53, 127, 135
1986	*Fasciculus vesanus* Briggs & Conway Morris, pp. 167, 172.
1987	*Fasciculus vesanus* Stanley & Stürmer, pp. 61, 62.
1993*b*	*Fasciculus* Conway Morris, p.222.
1994	*Fasciculus vesanus* Briggs *et al.*, p.95, figure 45.
1994	*Fasciculus vesanus* Nudds & Sepkoski, p.122.

Holotype and only known specimen USNM 139215 (figure 3), original of Simonetta & Delle Cave (1978, figures 1,2).

Locality and stratigraphy Walcott quarry, Fossil Ridge north of Field, British Columbia. Stephen Formation (Phyllopod bed, Burgess Shale), *Bathyuriscus-Elrathina* zone, Middle Cambrian.

(*b*) **Preservation**

The only known specimen (part and counterpart; figure 3*a*) appears to be incomplete. As preserved the outline of the specimen (figure 3*b*) is approximately semi-circular, with a maximum width of about 103 mm and greatest depth of approximately 58 mm. Much of the specimen is preserved as a single film, but a substantial original thickness may be inferred from a separate level of splitting that forms a deeper horizon (exposed in isolated areas) in the part (defined by Simonetta & Delle Cave 1978, p. 46), and corresponding outliers in a higher position in the counterpart.

(*c*) **Morphology**

The orientation of the specimen is not certain, but in living ctenophores (also *Ctenorhabdotus* gen. nov. and *Xanioascus* gen. nov., see below) the comb-rows converge on the aboral pole and extend varying distances towards the mouth. This suggests that the closure of the specimen outline represents the aboral pole.

Simonetta & Delle Cave (1978) commented on the striking bilateral symmetry of the specimen which is evident from both the elongate structures interpreted as comb-rows, and structures referred to here as the lobate organs (figures 2 & 3). The comb-rows are clearly preserved and fall into two zones (figures 2 & 3). The central zone is composed of elongate comb-rows and these are flanked on either side by a set that forms the marginal zones. The precise disposition of the comb-rows in the central zone is difficult to establish because of their closeness and partial obscuration by the corresponding set of comb-rows from the opposite side of the animal; the latter are visible on a separate level of bedding. There appear to be four comb-rows on each side of the mid-line, making an estimated total in the animal of about 16. All the central comb-rows are rather elongate and of approximately the same length, albeit with points of origination that approach the aboral pole towards the midline. The comb-rows of each marginal zone are substantially shorter, but show a gradual increase in length away from the mid-line of the specimen. Because of overlap in the comb-rows and the small size of those closest to the centre of the lower edge, it is difficult to count the precise number of comb-rows in each of the marginal zones, but 16 rows are visible on the left-hand side of the counterpart, and 15 or 16 on the right side (figures 2 & 3). As there would have been a corresponding series of flanking comb-rows on the other side of the animal (represented by the largely concealed layer in the part), it is estimated that the original total of this series was approximately 64 (4 x 16) (figure 4).

In both the central and marginal zones each comb-row has sub-parallel sides for most of its length, but tapers to an acute point at either end. The curvature of the rows, especially pronounced towards the margins, may be in part original, but is believed to be largely a reflection of their traversing the curved surface of the animal. All the comb-rows share the characteristic of appearing as prominent transverse bar-like structures. Details are not easy to discern, but there is some evidence for each unit possibly consisting of two transverse bars that meet at either end.

A number of the comb-rows also display a reflectively preserved central strand. The significance of this structure is not clear, but it is perhaps comparable to the similarly placed giant axons of the living ctenophore *Euplokamis* (Mackie *et al.* 1992, figure 2). This feature appears to be a novelty of *Euplokamis*, and if the central strands in *Fasciculus* are of comparable origin this is unlikely to be of phylogenetic importance.

The other principal organ in the only known specimen are segmented structures, which increase in width in the presumed oral direction (figures 2 & 3). Two are clearly visible, occupying the region between the central and marginal zones of the comb-rows. There are, however, traces of what appear to be an additional pair of these lobate organs, nested in the central region of the specimen. These two strands are narrow, and presumably represent an end-on view, suggesting that originally each lobate organ may have been compressed in cross section. The presence of four lobate organs suggests, of course, a biradial (or tetraradial) symmetry. The detailed structure of the lobate organs is difficult to resolve, but they appear to consist of a segmented series of imbricated units, each one of which has a feathery appearance. In places this texture may be resolved into an apparently tentacular structure. It would be tempting to compare these

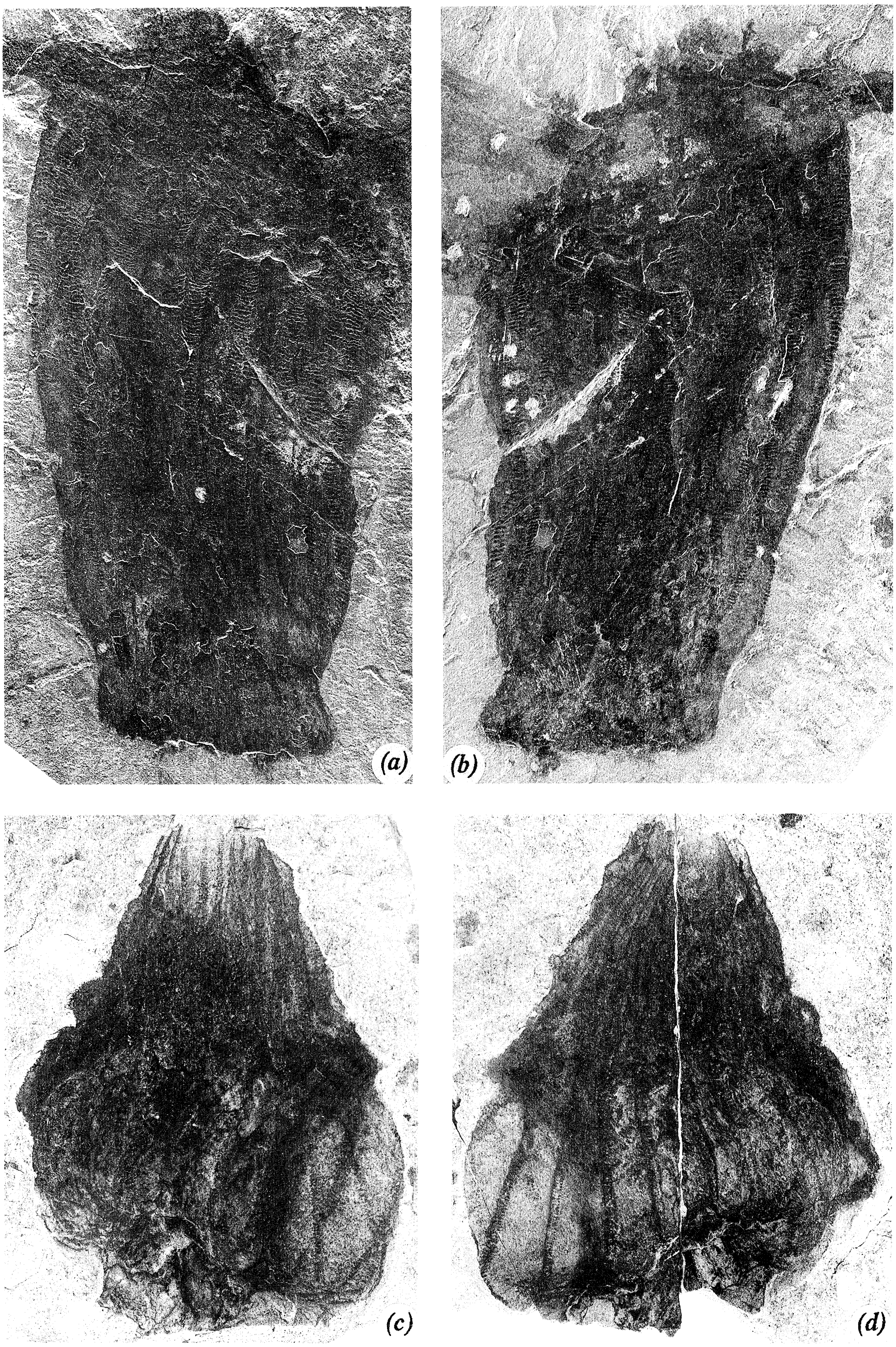

Figure 10. For description see opposite.

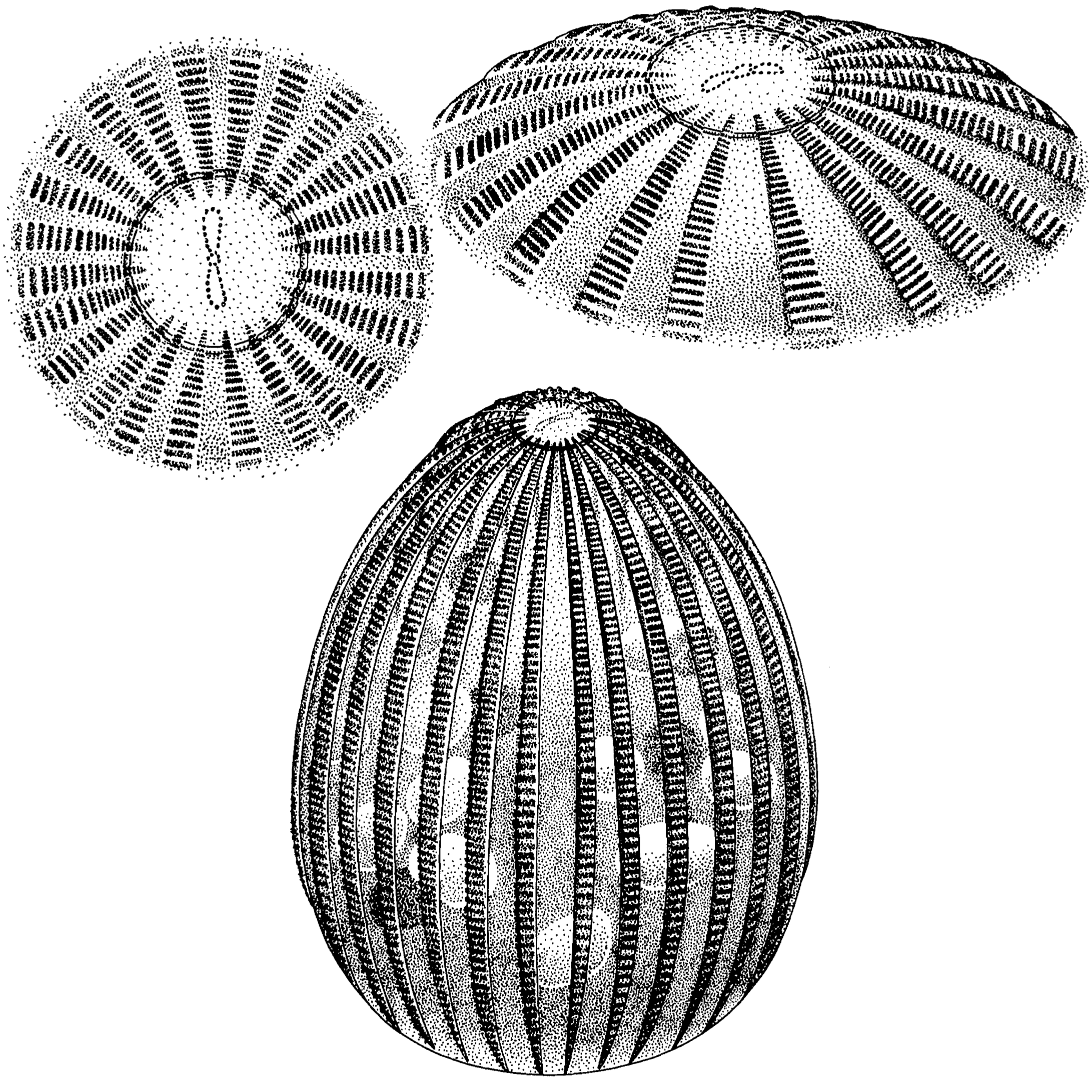

Figure 11. Reconstructions of *Xanioascus canadensis* gen. nov., sp. nov. The drawings show the entire animal (lower, with diagrammatic indications of the enigmatic enclosed ovoid bodies), and vertical and oblique views of the aboral region (upper left and right respectively).

lobate organs with the feeding tentacles of living ctenophores, but the former appear to be considerably more massive.

(*d*) *Systematic section*

(i) *Family*

Xanioascidae fam. nov.

(ii) *Diagnosis*

Sac-like ctenophores bearing c.24 comb-rows that extend close to oral area. Polar fields and presumed apical organ present. Mouth probably large. Internal ovoid bodies.

(iii) *Genus* Xanioascus *gen. nov.*

Type and only known species *Xanioascus canadensis* sp. nov.

Etymology The generic name is a compound to indicate the animal's sac-like nature (Gr. *askos*) and the comb-rows (Gr. *xanion*).

Diagnosis As for family.

(iv) Xanioascus canadensis *sp. nov.*

1983 *Fasciculus* Collins *et al.*, p.165, figure 4, Table 1
1986 *Fasciculus* Collins p.37, bottom figure
1987 *Fasciculus* Stanley & Stürmer p.61

Etymology The specific name refers to the country of origin.

Material Holotype ROM 43186. Paratypes ROM 43190–43193, 43195, 43199, 50824.

Locality and stratigraphy West-facing slope, 1500 m southwest of the north shoulder of Mount Stephen, near Field, British Columbia (locality 9 of Collins *et al.* 1983). Stephen Formation, *Glossopleura* zone, Middle Cambrian.

Figure 10. *Ctenorhabdotus capulus* gen. nov. Stephen Formation (Burgess Shale), ?Walcott Quarry, Field, British Columbia. (*a*–*b*) USNM 468031; object traversing upper part of specimen is an example of the priapulid *Ottoia prolifica*, x2.0. *Xanioascus canadensis* gen. nov., sp. nov., Mount Stephen, Stephen Formation, Field, British Columbia. (*c*)–(*d*) ROM 43190. (*c*) Part, x1.3. (*d*) Counterpart, x1.4.

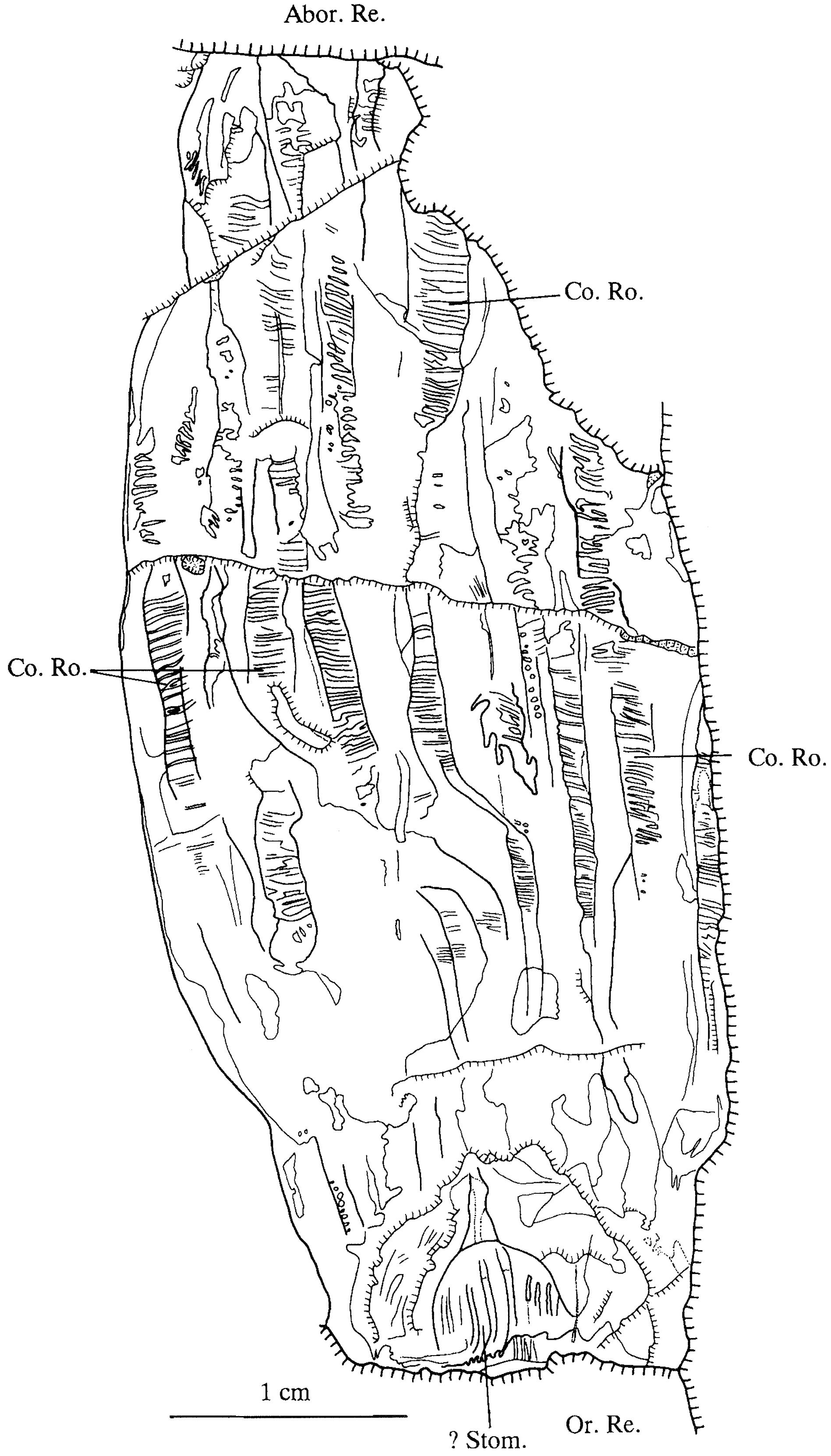

Figure 12. Interpretative drawing of MCZ 101681. For photographic comparison see page 296, figure 15*a*.

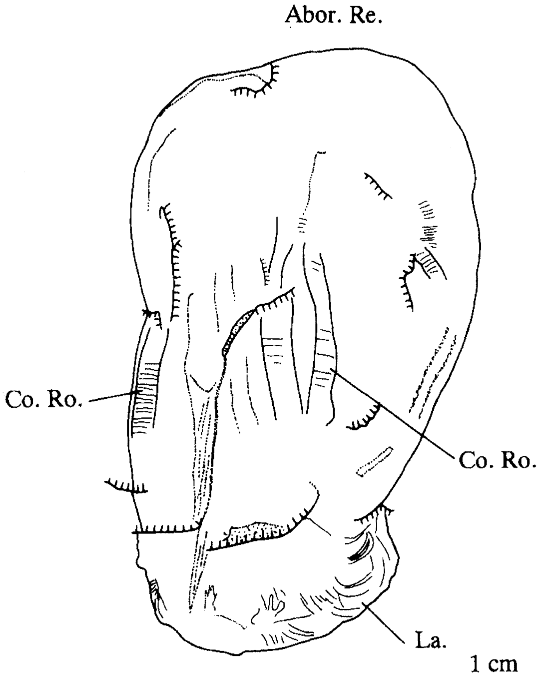

Figure 13. Interpretative drawing of ROM 50821. For photographic comparison see page 296, figure 15*d*.

(*e*) *Preservation*

Specimens are preserved in pale-coloured shale. Evidence of decay is available in some specimens (figures 8*b*–*d*), where the body outline is disrupted and incomplete. Immediately associated biota includes *Wiwaxia* cf. *corrugata* (figure 8*b*) and algae similar to *Morania* sp. (figures 8*c*, *d*).

(*f*) *Morphology*

Variation in shape is difficult to assess because preservation tends to be relatively poor. Some differences in shape can be attributed to the attitude of the specimens at the time of burial. The oval outline of ROM 43186 (figures 5 & 7*a*, *b*) may be in part because it is buried with its aboral-oral axis more or less at right angles to bedding. Specimens buried in side-view vary from approximately quadrate (in the juvenile ROM 43192, figure 7*e*) to pear-shaped in ROM 43190 (figures 9 & 10*c*, *d*) with its swollen ?oral end tapering markedly towards the opposite pole. Overall *Xanioascus* gen. nov. appears to have been sac-like, with a flexible body capable of considerable distortion in life. Size range is considerable, although the variation in shape and attitude make simple comparisons difficult. The smallest specimen is ROM 43192 (figure 7*e*), with a height of approximately 21 mm. The other specimens are substantially larger, but only two are complete enough to be measured. ROM 43190 (figures 9 & 10*c*, *d*) has a height of 75 mm, whereas the maximum diameter of ROM 43186 (figures 5 & 7*a*, *b*) is 48 mm.

The comb-rows form the most prominent feature. Their precise total is difficult to determine, not least because nearly all the specimens are either incomplete or buried obliquely so obscuring a substantial portion of the surface. In ROM 43186 (figures 5 & 7*a*, *b*), where end-on burial facilitates a fairly accurate count, at least 18 comb-rows are clearly discernible, and the original total perhaps is many as ca. 24. Folding about the ambitus and poorer preservation on one margin, however, makes tracing and recognition of some of the rows difficult. In the smaller ROM 43191 (figures 6 &

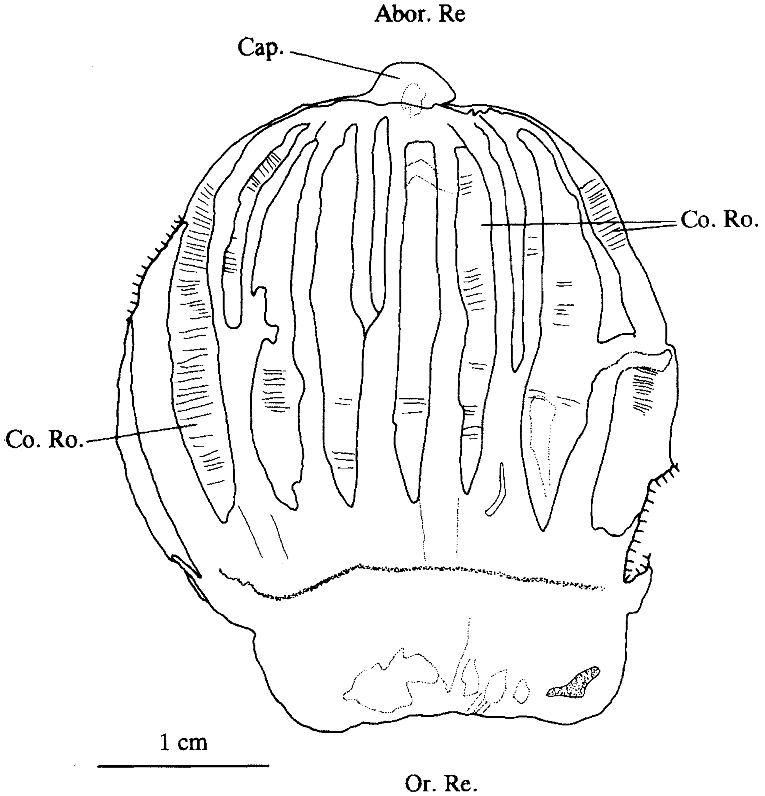

Figure 14. Interpretative drawing of ROM 50822. For photographic comparison see page 296, figure 15*d*.

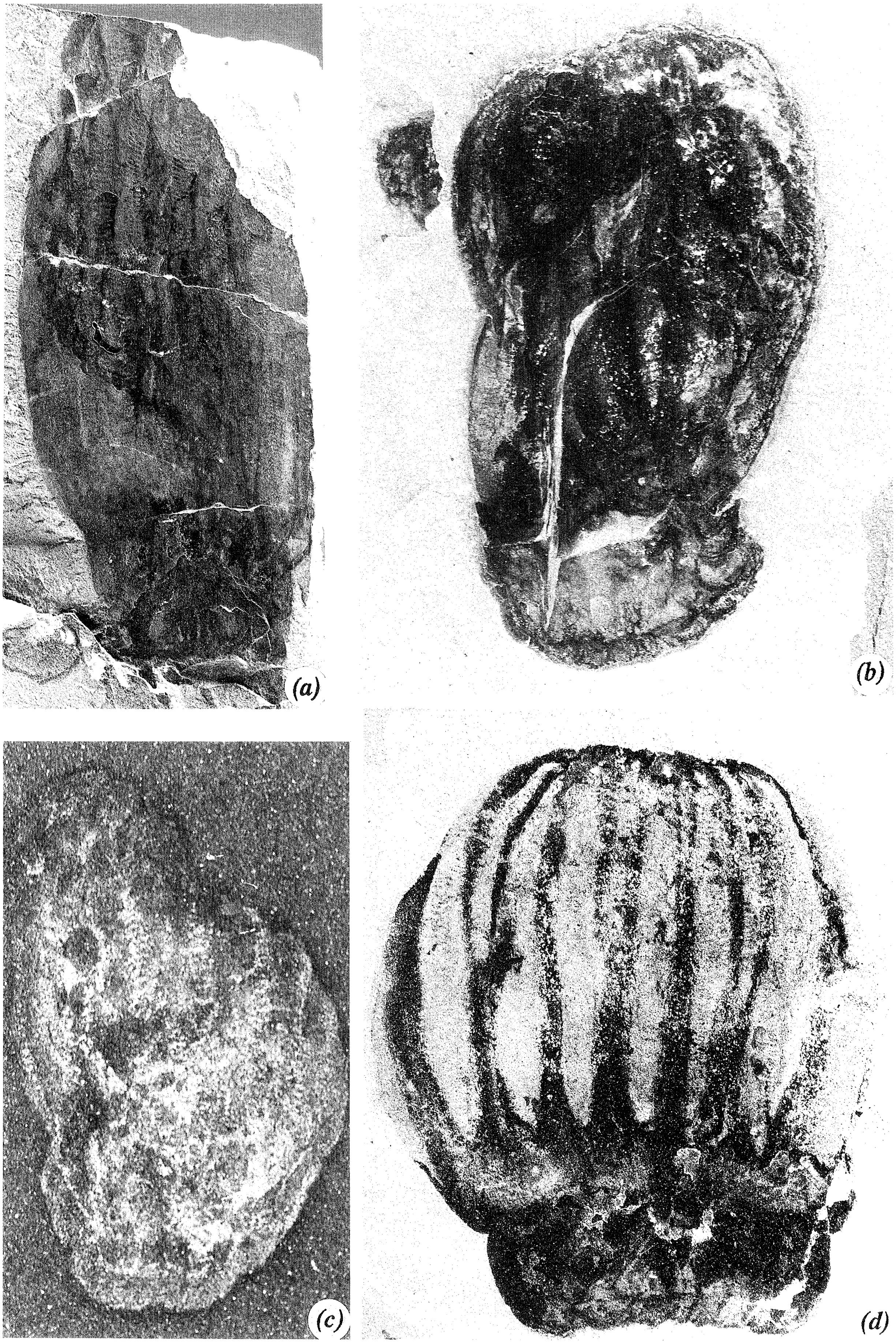

Figure 15. For description see opposite.

7*c*), where the comb-rows can be seen converging on the aboral end, the total number of rows appears more reliably to be 24. So far as can be determined the individual comb-rows do not coalesce adjacent to the aboral pole in a manner similar to *Ctenorhabdotus* gen. nov., where there is a convergence of the 24 comb-rows into eight primary strands (see below). The comb-rows of *Xanioascus* appear to resemble those of *Fasciculus* in overall structure, but are all of more or less equal length. They extend most of the length of the animal, but in the juvenile ROM 43192 (figure 7*e*) there appears to be a recognizable oral region without comb-rows.

In addition to the convergence of the comb-rows one specimen shows additional features in the aboral region. On the apex of ROM 43191 (figures 6 & 7*d*) there is an elongate structure, composed of what may have been minute pits, with a looped enclosure at one end. This structure appears to be comparable to the ciliated structures known as the polar fields that flank the apical organ (Hyman 1940, figure 209B, C). Presumably in the central region there was an apical organ but for this there appears to be no direct evidence. Assuming such a structure was present, as in living ctenophores, it would have been quite small and thus not comparable to the much larger capsule-like organ of *Ctenorhabdotus* gen. nov. Encircling the aboral pole in ROM 43191 (figures 6 & 7*d*) is a dark annulus, not quite complete, that presumably underlay the comb-rows. This structure may represent part of a canal system. Finally, in this specimen a conspicuously dark vermiform structure runs parallel to the comb-rows, but extends further towards the aboral tip and terminates adjacent to the apical organ. It may represent either part of a comb-row or be some other internal organ. Only two specimens show possible evidence for the oral region. The juvenile ROM 43192 (figure 7*e*) appears to provide some evidence in the form of a dark mass that presumably surrounded a voluminous mouth. What may be the same region could be represented in a crushed state by the sub-central elliptical zone in ROM 43186 (figures 5 & 7*a*, *b*).

A conspicuous, albeit enigmatic, feature of *Xanioascus* gen. nov. are approximately oval structures, termed here the ovoid bodies (figures 5, 6, 7*a–c*, 8*e*, 9 & 10*c–d*). They are typically dark in colour, and often show evidence of being bilayered, enclosing a wedge of sediment. Their nature is debatable, especially as there appears to be no counterpart of such structures in extant ctenophores. Of the three principal possibilities: food contents, reproductive tissue or embryos (or associated brood chambers), the first proposal seems less likely given their coherent shape and lack of identifiable components. In living ctenophores the reproductive tissue is disposed along the canals that run beneath the comb-rows. Stanley & Stürmer (1987) tentatively identified comparable reproductive organs in *Archeocydippida hunsrueckiana*. In any event, neither of their fossil specimens from the Devonian of Germany show structures equivalent to the ovoid bodies, and overall the arguments for their identification as reproductive tissue seems weak. In certain of the benthic platyctenids the embryos are brooded (e.g. Pianka 1974), unlike free-swimming species where the larvae are dispersed (Hyman 1940). Nevertheless, a comparison between the ovoid bodies of *Xanioascus* gen. nov. and the embryos or brood chambers of the platyctenids seems somewhat forced. This is because brooding of embryos is confined to the platyctenids, which are somewhat aberrant in terms of ctenophore anatomy and are widely regarded as very derived rather than primitive. In addition the brood chambers of the living platycenids are in general much smaller than the ovoid bodies of *Xanioascus*. Finally it should be noted no equivalent to the lobate organ of *Fasciculus* has been identified in *Xanioascus* gen. nov. (figure 11).

(*g*) ***Systematic section***

(i) *Family*

Ctenorhabdotidae fam. nov.

(ii) *Diagnosis*

Box-like to globose ctenophores bearing 24 comb-rows, converging in groups of three to form eight strands that meet in a ring surrounding the aboral pole. Each group of three comb-rows apparently consists of elongate rows flanking a central and shorter row. Apical organ and presumed statocyst present, housed beneath prominent capsule-like dome. Mouth large, flanked by lobate margin.

(iii) *Genus* Ctenorhabdotus *gen. nov.*

Type and only known species Ctenorhabdotus capulus sp. nov.
Etymology The generic name is based on Greek words and refers to the prominent stripe-like (rhabdotus) comb-rows (ctenos).
Diagnosis As for family.

(iv) *Ctenorhabdotus capulus* sp. nov.

Etymology The specific name refers to the prominent aboral capsule-like structure.
Material Holotype ROM 50822. Paratypes MCZ 101681, USNM 468031, ROM 50820, 50821, 50823, 50825–50830, 50866, 51047, 51439–51442.
Locality and stratigraphy Levels within the Phyllopod bed in the Walcott quarry, and 1.3 m beneath it, and two localities immediately to the south of the Walcott Quarry (informally referred to as 'Fault Wedge' and 'South of Fault') that appear to expose equivalents of the Phyllopod bed. In addition, this ctenophore is recorded from the Raymond quarry bed, 21 m above, Fossil Ridge, north of Field, British Columbia. Stephen Formation (Burgess Shale), *Bathyuriscus-Elrathina* zone, Middle Cambrian.

Figure 15. *Ctenorhabdotus capulus* gen. nov., sp. nov., Stephen Formation, Raymond Quarry, Field, British Columbia. (*a*) MCZ 101681, x2.2. (*b*) ROM 50821, x3.5. (*c*) ROM 50820, juvenile specimen, x6.9. (*d*) ROM 50822, x3.1.

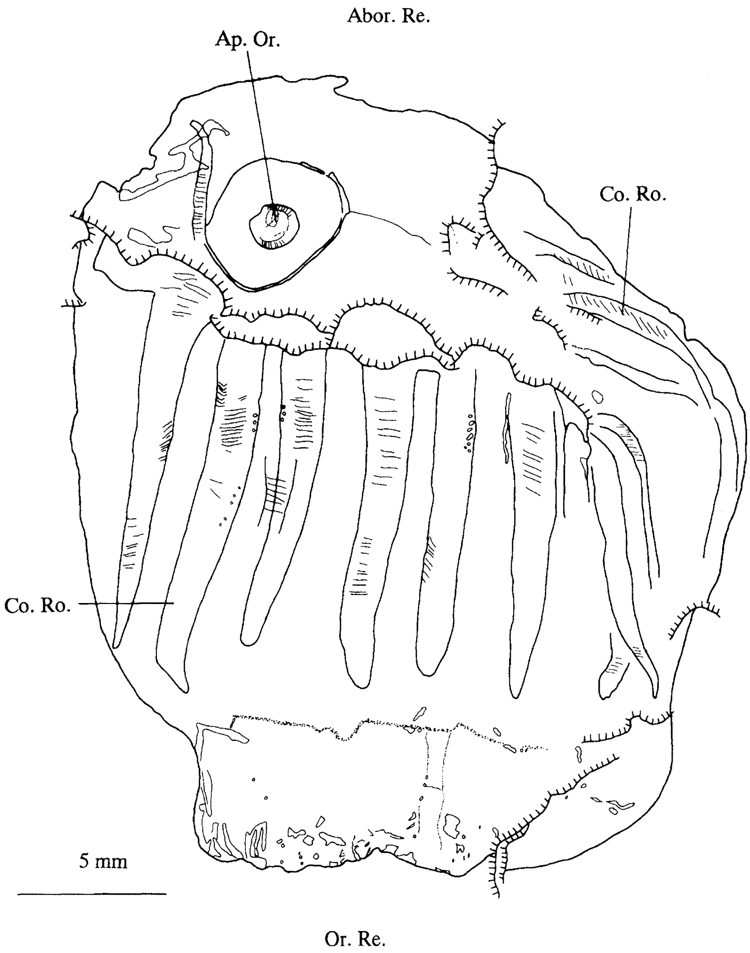

Figure 16. Interpretative drawing of ROM 50829.

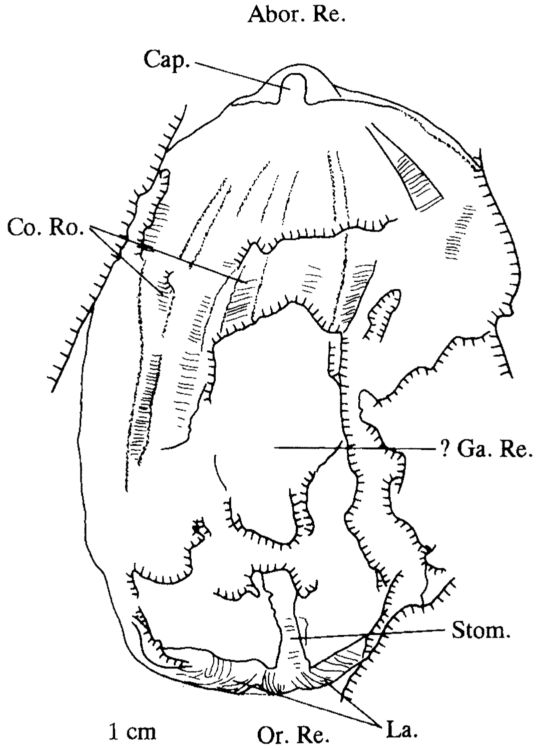

Figure 17. Interpretative drawing of ROM 50827.

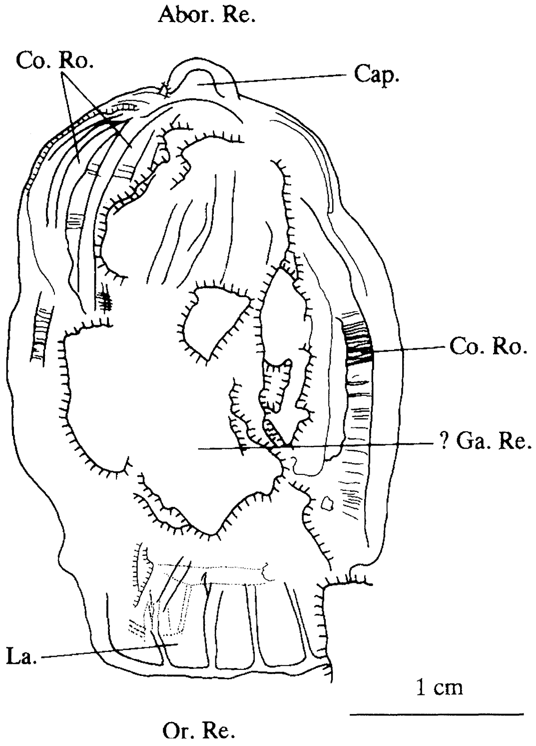

Figure 18. Interpretative drawing of ROM 50826.

Figure 19. *Ctenorhabdotus capulus* gen. nov., sp. nov., Stephen Formation, Raymond Quarry, Field, British Columbia. (*a–b*) ROM 50829, part and counterpart, x 3.4. (*c–d*) ROM 50827, part and counterpart, x2.1. (*e*) ROM 50826, x2.0. (*f–g*) ROM 50825, part and counterpart, x1.4. (*h*) ROM 50828, x1.7.

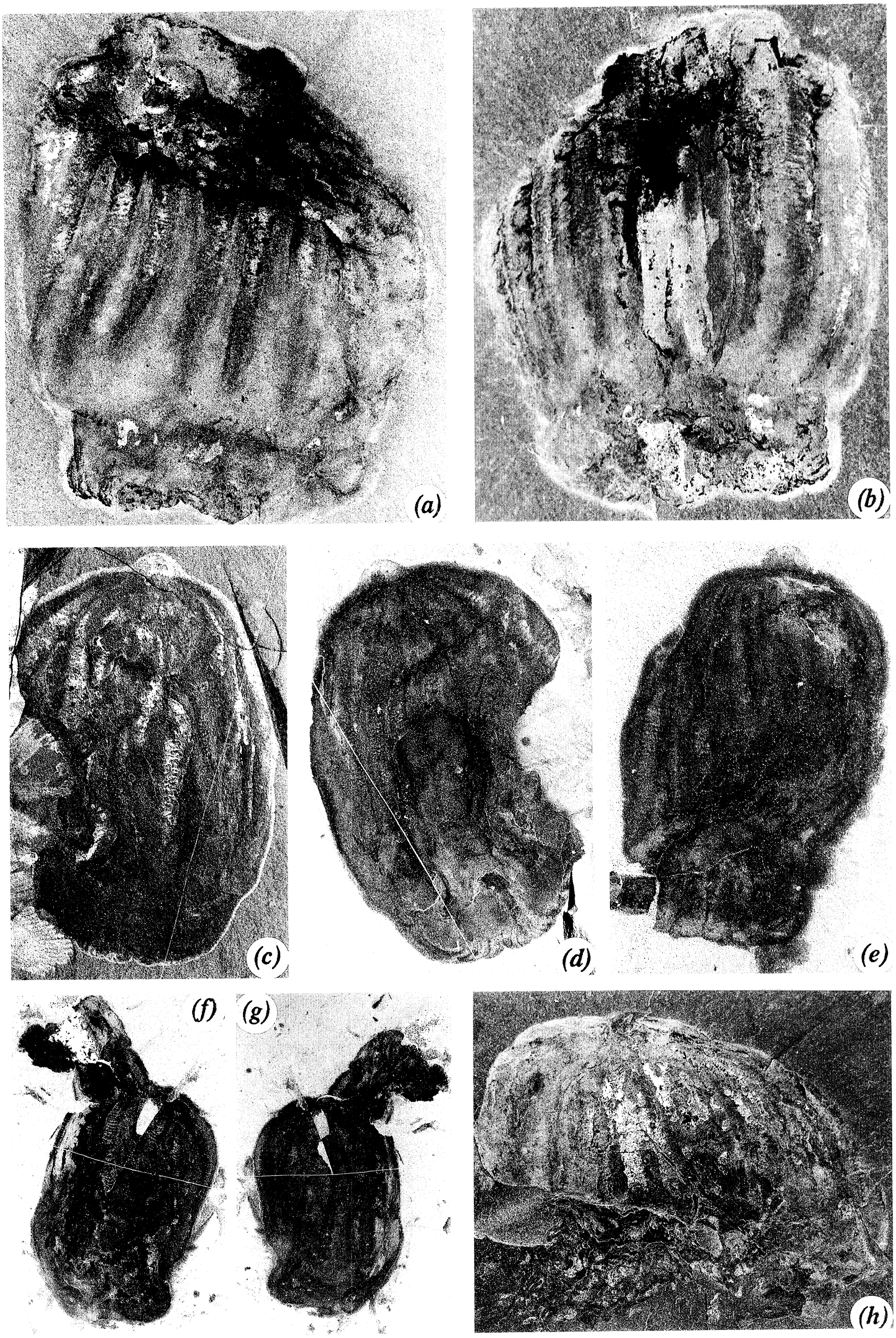

Figure 19. For description see opposite.

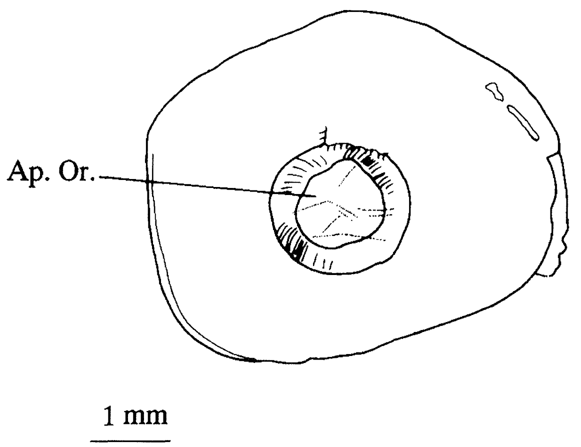

Figure 20. Interpretative drawing of possible apical organ and associated statocyst in ROM 50829.

(*h*) ***Preservation***

Specimens occur on slightly greenish shale surfaces when weathered, or dark grey if freshly exposed. Fossils show little evidence of decay (but see §5*c*), although the margins of ROM 50866 (not illustrated) appear to be somewhat incomplete. In ROM 50825 (figure 19*f*, *g*) what appears to be the aboral end forms a unique tongue-like extension. This feature conceivably represents a death reaction occurring during burial. Two specimens (ROM 51441 and 51442) are associated on the same slab; one is relatively relaxed (figure 23*f*), the other apparently more contracted. Taxa associated with *Ctenorhabdotus* gen. nov. include the arthropods *Leanchoilia superlata* (figure 19*c*) and *Canadaspis perfecta* (bivalved carapaces only), the priapulid worms *Ottoia prolifica* (figure 10*b*) and *Selkirkia columbia* (tubes only) (figure 23*f*), the sponge *Hazelia delicatula*, and agnostoid trilobites (*Peronopsis montis*).

(*i*) ***Morphology***

Specimens are typically quadrate in side view, with approximately flat oral and aboral regions, connected by sub-parallel sides (figures 8*a*, 10*a*, *b*, 12, 15*a*, 18 & 19*e*). Other specimens are more globose, and their more equal transverse and longitudinal dimensions suggest they are contracted (figures 13, 14, 15*b*, *d*, 17 & 19*c*,*d*). The smallest specimen (ROM 50820, figure 15*c*) is about 16 mm long, but relaxed i.e. quadrate, specimens reach 70 mm in length (i.e. parallel to the aboral–oral axis).

The comb-rows are a prominent feature (figures 8*a*, 10*a*, *b*, 12–14, 15*b*, *d*, 17, 18, 19*c*-*h*, 22*a* & 23*f*), and they appear to be somewhat broader than those of *Xanioascus* gen. nov. (figures 16 & 19*a*, *b*). In ROM 50826 (figures 18 & 19*e*) the rows can be seen to converge on the aboral pole, but the clearest details of the arrangement in this region is in ROM 51439 (figures 23*a*, *b*). This specimen shows a group of three comb-rows converging aborally, to join a single strand that then meets a well-defined ring-like structure (figures 23*c*, *d*). In ROM 51439 eight of these strands are discernible, although two are almost superimposed. On the reasonable assumption that every strand connected to three comb-rows, this implies that in life *Ctenorhabdotus* gen. nov. had the same number of comb-rows as *Xanioascus* gen. nov., i.e. 24. In addition, in ROM 50822 it appears that elongate comb-rows, that extended close to the oral area, flank conspicuously shorter comb-rows (figures 14 & 15*d*). Although the convergence of sets of three comb-rows is not clearly visible in this specimen, because of the attitude of burial, it seems likely that in life the central row was short and was flanked by an elongate row on either side. Thus *Ctenorhabdotus* is reconstructed as having a total of 8 short comb-rows and 16 elongate comb-rows (figure 24). All the remaining specimens are buried more or less on their side, so confirmation of the original comb-row total of 24 is not possible. In ROM 50829 (figures 16 & 19*a*, *b*) the aboral region appears to have been infolded and crushed. Although this allows more complete inspection of the comb-rows, a complete suite still cannot be counted.

The strands (and central ring) are reflectively preserved, and they do not carry the transverse structures that probably represent the polster cells (see §3). In all living ctenophores the comb-rows stop short of the aboral pole, but are connected to the central statocyst via narrow ciliated furrows. The strands in ROM 51439 are substantially thicker (figures 23*c*, *d*), and it is more likely that they represent not only these furrows, but more particularly the broader meridional canals that in living ctenophores underlie the comb-rows. The exact nature of the central ring is debatable, because in living ctenophores the meridional canals converge but do not meet. In ROM 51439 a direct connection between strands and ring is evident (figures 23*c*, *d*), and it is considered less likely that this latter structure represents some direct aboral extension of the stomach such as the anal canals or associated infundibulum. Located in between the central ring and the trifurcation of the comb-rows in ROM 51439 there is also a well-defined annular structure, demarcated in an adoral direction by reflectively preserved tissue.

Some evidence exists for an aboral apical organ (and statocyst), although no equivalent to the ?ciliated loop (polar fields) of *Xanioascus* gen. nov. has been recognized. What may represent the statocyst in top-view

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Figure 21. *Ctenorhabdotus capulus* gen nov., sp. nov., Stephen Formation, Field, British Columbia. (*a*) ROM 50829, possible statocyst and surrounding area, including comb-rows, x 11.0. (*b*) ROM 50827, detail of capsule surrounding presumed statocyst, x 14.1. (*c*) ROM 50826, detail of capsule surrounding presumed statocyst, x 12.8. (*d*) ROM 50828, possible statocyst, x 13.6. *Xanioascus canadensis* gen nov., sp. nov., Stephen Formation, Mount Stephen, Field, British Columbia. (*e*) Bedding surface exposed in field with ROM 43191 (see figures 9*c*, *d*), which is arrowed, and numerous other 'blobs' that may represent ctenophores. Water-spray cylinder (upper right) is ca. 15 cm across.

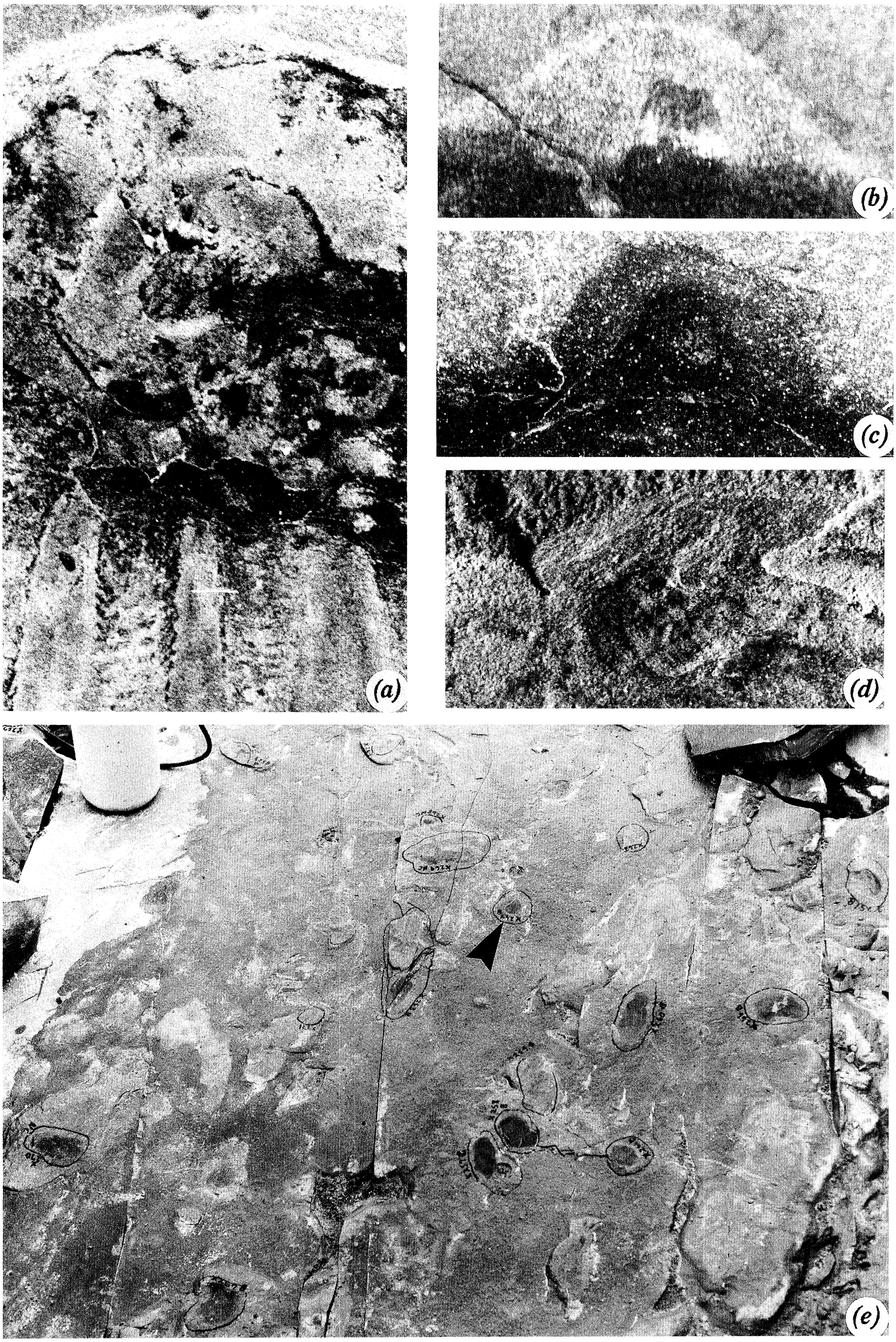

Figure 21. For description see opposite.

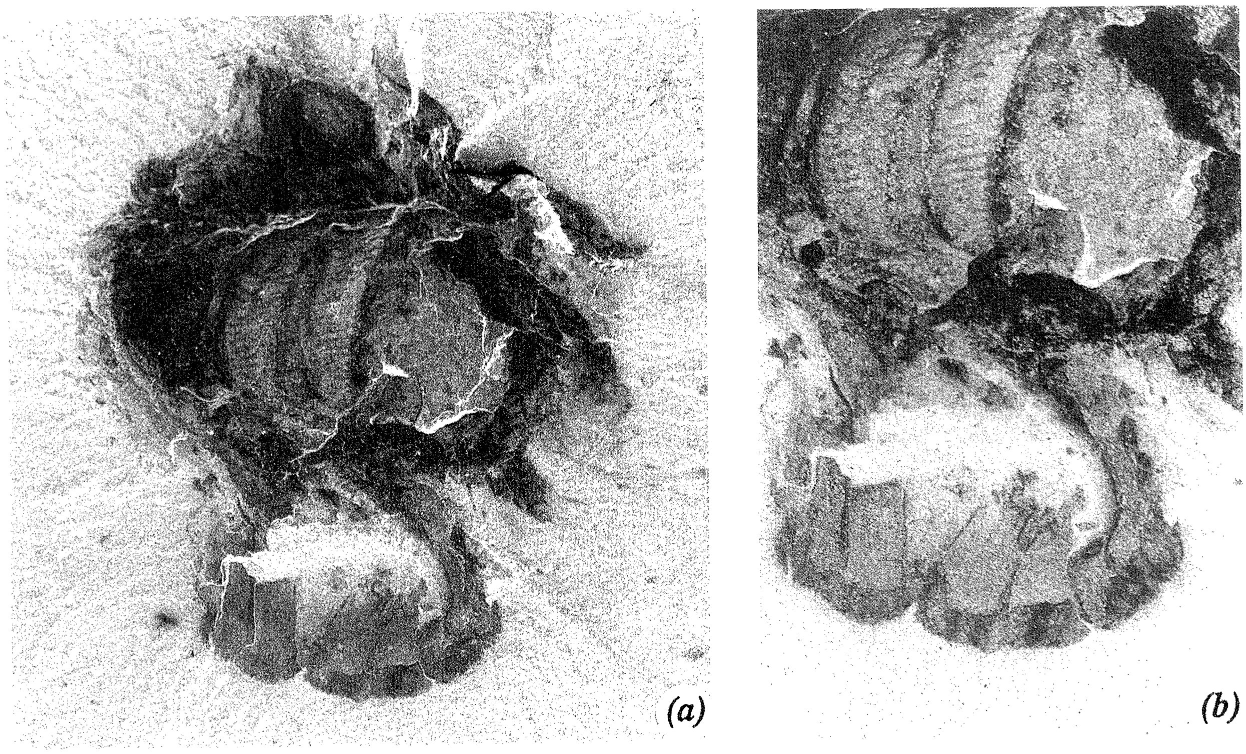

Figure 22. *Ctenorhabdotus capulus* gen. nov., sp. nov., Stephen Formation, Raymond Quarry, Field, British Columbia. (*a–b*) ROM 51047 (*a*) part, x 4.1. (*b*) Detail of oral region, x 5.6.

occurs in two specimens. In ROM 50828 (figures 19*h* & 21*d*) a small circular area (ca. 1.5 mm diameter) in the aboral region is identifiable. It bears oblique striations, but inspection of the counterpart suggests these may be an artefact of mineral growth. More puzzling, perhaps, is ROM 50829 (figures 16, 19*a*, *b*, 20 & 21*a*), where a broad disc (ca. 4 mm diameter) with a well-defined margin, perhaps equivalent to the annular structure in ROM 51439 (figures 23*c*, *d*), encloses a smaller circular area. This latter region has an annular zone with impressed radial structures while the central-most region contains spicule-like elements, although these latter items may well be artefacts of diagenesis. In the opinion of D.H.C. this area (figures 20 & 21*a*) in ROM 50829 also houses minute oval structures that may be interpreted as the statoliths themselves. In preparing the camera-lucida drawing of this region (figure 20), however, S.C.M. was unable to discern clearly these structures in the fossil. Their original presence is certainly likely, but their depiction in the reconstruction (figure 24) of *Ctenorhabdotus* gen. nov. is taken as hypothetical by S.C.M.

In side-view the aboral end of ROM 50827 (figures 17, 19*c*, *d* & 21*b*) and ROM 50826 (figures 18, 19*e* & 21*c*) projects as a distinct papilla, herein referred to as the capsule. A comparable arrangement, albeit preserved at a more oblique angle, is evident in ROM 51440 (figure 23*e*). In this specimen the capsule has a microstructure similar to ROM 50828 (figures 19*h* & 21*d*). This capsule is somewhat similar to the dome that houses the centrally located statocyst in living ctenophores, but is substantially larger than is normally the case in extant ctenophores. The exception to this is in the case of some larvae where the dome is relatively enormous (figure 7.7a of Tamm 1982), and even more prominent than it is in *Ctenorhabdotus*. The well-defined central region within the capsule conceivably represents a compacted version of the central statolith and associated balancers (see Tamm 1982; Hernandez-Nicaise 1991), but precise details are difficult to discern.

An alternative proposal concerning the capsule is based on the observation that in living ctenophores the dome, which is composed of fused cilia, is likely to detach from the rest of the body (R. Harbison, personal communication), perhaps shortly after death, in a manner hypothesised for the ciliary comb-plates (see above). Thus it might be argued that the dome is unlikely to be present in fossil examples. Many living ctenophores, however, bear aboral papillae, in various configurations. Dr R. Harbison has suggested that it would be better to compare the capsule in *Ctenorhabdotus* with such aboral papillae. Nevertheless, the apparently

Figure 23. *Ctenorhabdotus capulus* gen. nov., sp. nov., Stephen Formation, Walcott Quarry or immediately adjacent localities, Field, British Columbia. (*a–d*) ROM 51439 (a) Part, x3.7 (*b*) Counterpart, x3.5 (*c*) Aboral pole of part, x8.4 (*d*) Aboral pole of counterpart, x8.7 (*e*) ROM 51440, part, x5.2. (*f*) ROM 51441, part, x1.8; the extremity of the associated specimen ROM 51442 is visible on the right-hand side.

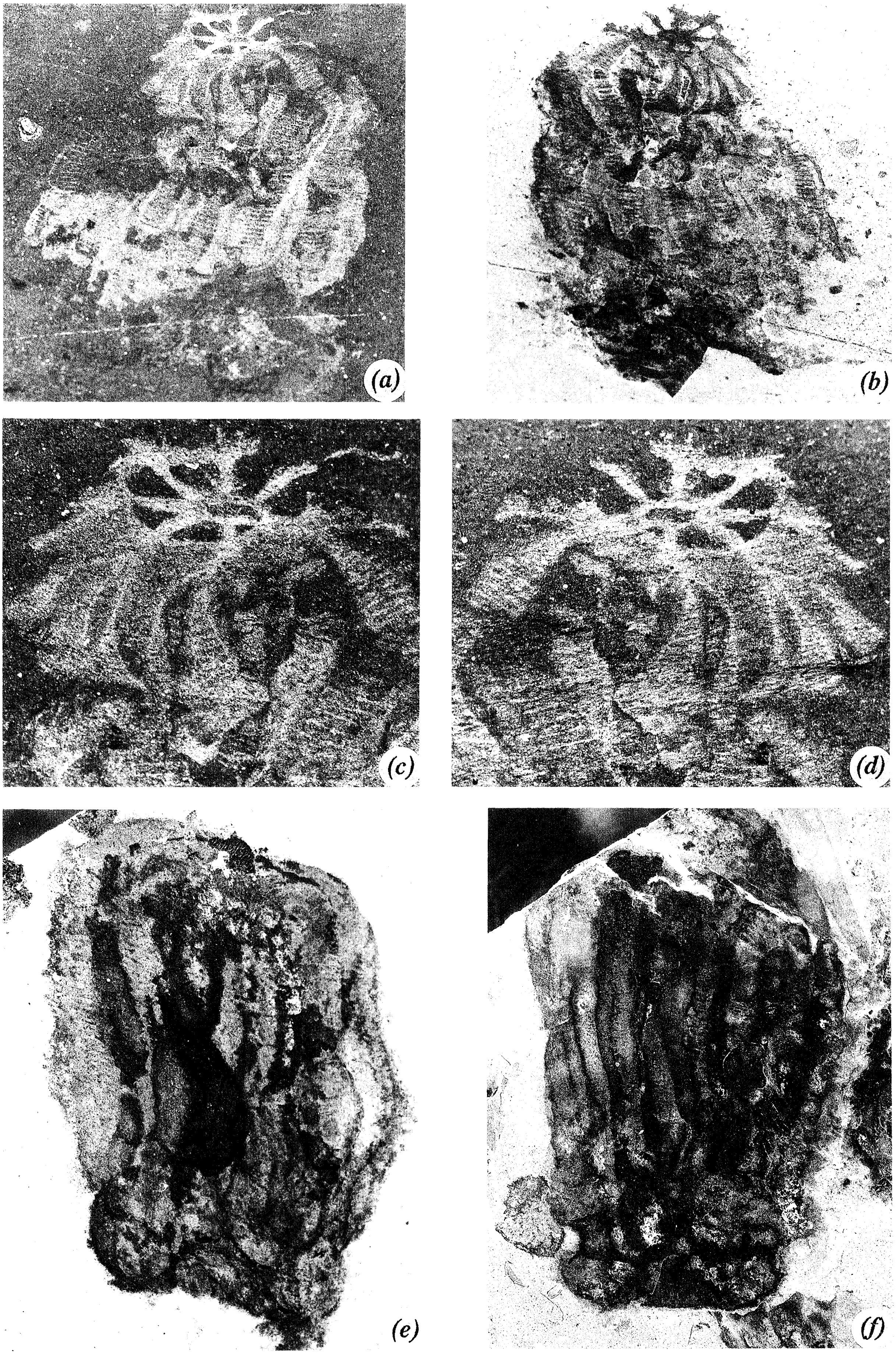

Figure 23. For description see opposite.

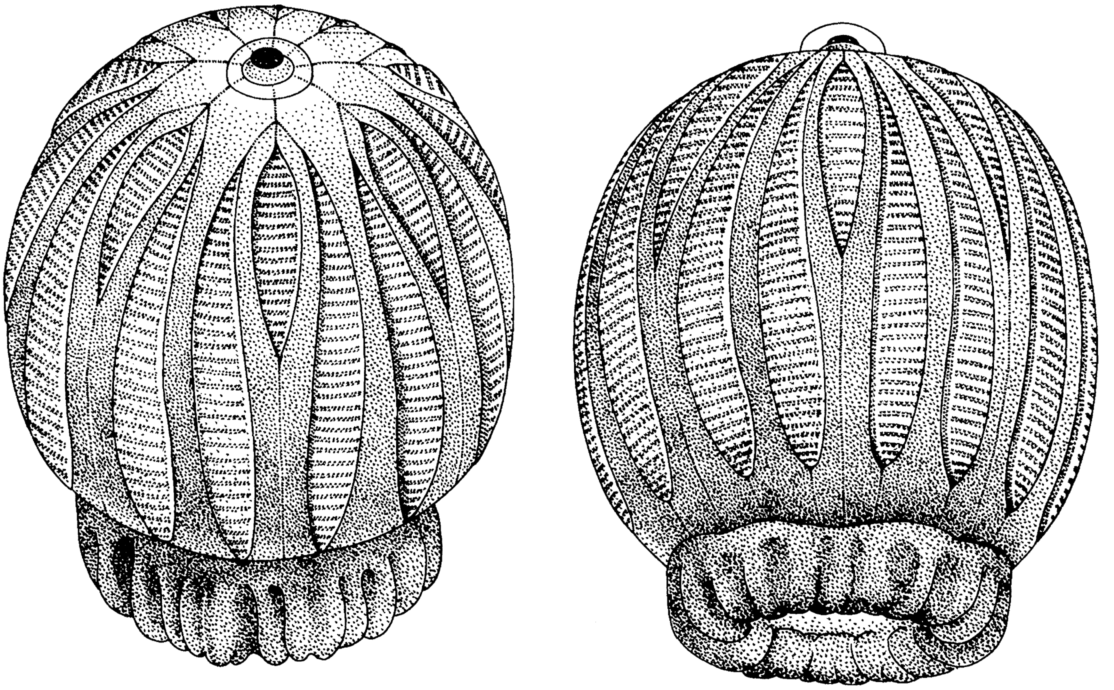

Figure 24. Reconstruction of *Ctenorhabdotus capulus* gen. nov., sp. nov.

central position of the capsule (figure 17, 18 & 19*c–e*) appears to be more consistent with it being equivalent to the dome housing the statocysts (figure 24).

The oral region is discrete, appears to lack the comb-rows, and in some specimens (figures 14, 15*d*, 19*a*, *b* & 23*f*) is demarcated by a constriction. Overall this area evidently consisted of a voluminous mouth surrounded by a velum-like structure. In this latter region different specimens show a variety of features that may represent the same basic structure preserved in a number of ways. Thus in ROM 50826 the oral area bears approximately triangular structures (figures 18, 19*e*). A somewhat similar arrangement is visible in ROM 51047 where the distinction between the oral region and the rest of the body is especially pronounced (figure 22*a*). In detail the oral region of this specimen has a prominent dark rim and a series of longitudinal structures (figure 22*b*). Somewhat different are recurved structures on the oral rim of several specimens (figures 13, 15*b*, 17 & 19*c*, *d*).

The interpretation of these structures is not entirely satisfactory. R. Harbison (personal communication) has suggested that the various longitudinal structures could have arisen as part of the process of disintegration of the oral region. More specifically he proposed the longitudinal lines themselves ‘could be traces of meridional canals (or they could simply be folds of tissue)’. The nature of the dark margin in ROM 51047 (figure 22*b*) is more controversial. One possibility is that it represents a band of circular muscles (R. Harbison, personal communication). In contrast one of us (D.H.C.) prefers to interpret this band as more likely to be a cross-section through the wall of the oral region. In support of these observations might be: (i) its strong contrast in terms of density and boundary with the rest of the oral region; and (ii) the change in width of this band towards the right-hand edge of the oral region. The linear structures above the dark band are striking and reminiscent of those in ROM 50826 (figures 18 & 19*e*). In both cases they impart a lath-like appearance to the oral region. Whether these structures are in direct line with either the comb-rows or the intervening areas is not easy to determine. What may be the oral region in a retracted state is present in MCZ 101681 (figures 12 & 15*a*), where a cap-like structure with relatively prominent striations leads towards a longitudinal strand. This latter feature may be part of the stomodaeum, and equivalent structures appear to be present in ROM 50827 (figures 17 & 19*c*, *d*). Aboral to this putative stomodaeum the fossil film that comprises this specimen is conspicuously thick and may represent the remains of part of the gastric region, as may the central dark region of ROM 51440 (figure 23*e*).

6. ECOLOGY OF CAMBRIAN CTENOPHORES

Most living ctenophores are pelagic and active swimmers. The benthic platyctenids are highly modified, and it is questionable if fossilized remains would be recognized. The prominent comb-rows in *Ctenorhabdotus* gen. nov., *Fasciculus* and *Xanioascus* gen. nov. suggest they were also active swimmers, possibly aided by muscular contractions. How they fed is more conjectural. There is no direct evidence for tentacles, and in *Xanioascus* gen. nov. and more convincingly in *Ctenorhabdotus* gen. nov. prey may have been engulfed by the voluminous mouth in a way comparable to living beroids which employ fused arrays of macrocilia to hold and cut food (Swanberg 1974; Tamm & Tamm 1993). The absence of a preserved oral region in *Fasciculus* precludes speculation on its method of feeding.

7. DISCUSSION

(*a*) *Are* **Ctenorhabdotus** *gen. nov.*, **Fasciculus** *and* **Xanioascus** *gen. nov. ctenophores?*

In reviewing occurrences of fossil ctenophores Stanley & Stürmer (1987) were highly sceptical that these Cambrian fossils could be interpreted as ctenophores. What are interpreted here as the comb-rows were regarded as 'a plethora of tentacles', with the implicit assumption that they should be compared with the tentacles of extant cnidarians. Stanley & Stürmer's (1987) comment that there is no trace of statocysts is of questionable relevance in that their claim for identifying statocysts in the Devonian *Paleoctenophora brasseli* on the basis of a pyritic mass in the aboral region seems suspect. The evidence for an apical organ, in the form of the prominent capsule-like structure and possible statocysts in *Ctenorhabdotus* gen. nov., is reviewed above. Although not free of controversy, these structures seem to be best understood in the context of this organ. Similarly, what appears to be the polar fields in *Xanioascus* gen. nov. are also consistent with ctenophore anatomy.

Apart from the possible apical organ and associated statocyst, the compelling reason for identifying these Cambrian fossils as ctenophores are the structures interpreted as comb-rows. The problems of identifying the actual ciliary combs and the preservational context of these soft-bodied fossils are reviewed above (§3). Overall, however, the elongate structures present in these fossils seem to be strikingly similar to the comb-rows of extant ctenophores. The obvious difference is that all living ctenophores (and probably the Devonian forms) invariably have eight rows, whereas in *Xanioascus* gen. nov. there were 24 rows, whereas in *Fasciculus* the number was substantially higher. *Ctenorhabdotus* also possessed 24 rows, but there is a strong link with Recent ctenophores because of their coalescence into eight aboral strands. The arrangement of the comb-rows in *Ctenorhabdotus* gen. nov. and *Xanioascus* gen. nov. is generally more similar to that of living forms, whereas their division into discrete zones in *Fasciculus* has no counterpart in any Recent taxon. Although these differences distinguish the Cambrian species from non-tentaculate modern ctenophores such as the beroids, their significance for classification is much less than that of the possession of comb rows which is unique to the Ctenophora. Other differences, notably the apparent absence of the gastric canals, may have more to do with preservation than an original contrast in anatomy between Cambrian and Recent ctenophores. In particular, the case for the eight prominent strands in ROM 51439 (figures 23*c*, *d*) representing the aboral section of the system of meridional canals seems reasonable. As noted above, however, these canals in extant ctenophores do not unite in a ring, and this structure (figures 6, 7*c*, *d*, 20, 21*a* & 23*c*, *d*) may be a significant point of difference.

(*b*) *The origin and phylogeny of ctenophores*

Given the controversial nature of discussions of early metazoan evolution, there is a rare unanimity concerning ctenophores: they are primitive but highly distinctive, their antecedents are effectively unknown, and their degree of anatomical separateness gives few clues to their ancestry. Unfortunately the embryological development also appears to throw little light on their relationships. Earlier notions of a link to the turbellarians have been abandoned, and the relationship to the cnidarians is also now widely questioned (e.g. Mills & Miller 1984; Harbison 1985). The present consensus (but see Nielsen 1995) regards ctenophores as diploblastic, arising from a primitive stock but evolving towards the triploblastic condition at least in terms of the musculature (Hernandez-Nicaise 1991) if not the nervous system, but representing a dead-end rather than a staging post to the triploblast bilaterians (e.g. Hyman 1940). Even so, molecular biology suggests that the closest living relatives are the cnidarians (Christen *et al.* 1991).

The role of these Cambrian ctenophores in elucidating early ctenophore evolution remains somewhat problematic. The most obvious feature in these Cambrian genera is the substantially greater number of comb-rows than in younger forms. These are estimated to be 24 in *Ctenorhabdotus* gen. nov. (figure 24) and *Xanioascus* gen. nov. (figure 11), and approximately 80 in *Fasciculus* (figure 4), with the last genus showing the further peculiarity of two discrete zones of comb-rows with the shorter set totalling about 64. In contrast all extant ctenophores have 8 comb-rows, and although the respective lengths may not be equal they show nothing like the regionation of *Fasciculus*. Although the precise number is difficult to discern, the Devonian ctenophore *Archaeocydippida* appears to have 8 comb-rows (Stanley & Stürmer 1983, 1987; in contrast *Paleoctenophora* is too poorly preserved to give any reliable indication of possible comb-row totals), so presumably this characteristic had stabilized by at least 400 Ma BP.

The route to such stabilization, however, is more conjectural and in part depends on assumptions of body symmetry and which Cambrian genus is the more derived. Extant ctenophores show biradial symmetry, which is most clearly defined by the interior gastric canals. It is likely that those structures were present in the Cambrian taxa, but apart from the eight strands in a specimen of *Ctenorhabdotus* sp. nov. (figures 23*a*–*d*), no unequivocal evidence of them is fossilized. In *Xanioascus* gen. nov. the only clue to a biradial symmetry is the putative details of the polar fields (figures 6 & 7*d*). This and the radial arrangement of the comb-rows suggest that *Ctenorhabdotus* gen. nov. and *Xanioascus* gen. nov. may be closer to extant ctenophores than is *Fasciculus*.

In *Fasciculus* there is some evidence for tetraradial or biradial symmetry as expressed by the lobate organs. Two of the lobate organs are very clear, but the other two appear to be preserved end-on. Such an arrangement seems to be more consistent with a biradial symmetry (figure 4). As noted above the division of the comb-rows into two discrete sets is a unique character which may be more primitive, although a stratigraphically older occurrence in Chengjiang (figure 1) appears to be more similar to *Ctenorhabdotus* gen. nov. Accepting this as a provisional hypothesis there seems to be no simple way to decide whether the condition of 24 comb-rows in *Ctenorhabdotus* gen. nov. and *Xanioascus* gen. nov. was obtained from the *Fasciculus*-like state by reduction of the short and/or long set. Indeed, an alternative proposal is that *Fasciculus* is an early off-shoot in ctenophore evolution, somewhat isolated from the main lineage represented by *Ctenorhabdotus* and *Xanioascus*. The further reduction, from 24 comb-rows to the invariable total of 8 in all living ctenophores, is easier to envisage. So far as can be determined each of the 24 comb-rows in *Xanioascus* has a separate termination (figures 5, 6 & 7*a–d*). In contrast, in *Ctenorhabdotus* the comb-rows coalesce in groups of three. It is possible, therefore, to imagine suppression of two flanking comb-rows in each set, leaving the central row, so leading to the standard arrangement of 8 rows. Alternatively, the central row of each set may have been suppressed, so that the next stage of ctenophore evolution was via a condition of 16 comb-rows, which in turn was reduced to 8 either by further reduction or coalesence. This hypothesis may be more likely in as much as the central row of each group of three is already shorter, so *Ctenorhabdotus* could represent a transitional form towards the 16 row condition.

Reasons for the reduction to eight comb-rows are speculative, but one possibility is the enhanced degree of nervous control over a smaller number and hence greater manoeuvrability in the three-dimensional environment of the pelagic ctenophores. This in itself may be sufficient to explain the constancy of eight comb-rows in all living ctenophores. Similar examples of anatomical stabilization occur in other groups, most notably perhaps in the five-fold symmetry of practically all extant echinoderms. The other feature that may have been more or less coincident with the final reduction to eight comb-rows was the development of the feeding tentacles. Reasonable evidence exists in the Devonian fossils for these structures, and they are present in practically all living ctenophores save the beroids.

Much more difficult to assess is the phylogenetic significance of the lobate organs in *Fasciculus* and the ovoid bodies of *Xanioascus* gen. nov. As noted above neither of these structures has an obvious counterpart in either extant ctenophores or the Devonian taxa. Nor can equivalents to these organs be recognized in other phyla, and thus at present we are unable to suggest possible clues to the wider inter-relationships of the ctenophores.

Despite these uncertainties it seems worth speculating briefly on the precursors of the ctenophores. Dr R. Harbison has suggested to us that the initial stage was represented by a gelatinous animal that was little more than a ciliated sac with at first uniform ciliation over its surface, which only subsequently coalesced into a series of longitudinal strips or comb-rows. At first these were numerous, as seen in the Cambrian material, but subsequently were reduced to eight rows. Several plausible routes, with *Fasciculus* either an off-shoot or an intermediate form, could be proposed. In any event, a phylogenetic lineage leading from *Xanioascus* to modern (and Devonian?) ctenophores via *Ctenorhabdotus* with progressive reduction from 24 to 8 comb-rows seems plausible. The first ctenophores probably ingested prey, possibly employing macrocilia, and this general scenario is consistent with the beroids being the closest approximation to the primitive condition in living ctenophores (Harbison 1985, figure 6.9b).

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REFERENCES

Bartels, C. & Brassel, G. 1990 Fossilien im Hunsrückschiefer. Dokumente des Meereslebens im Devon. *Mus. Idar-Oberstein* **7**, 1–229.

Briggs, D. E. G. & Conway Morris, S. 1986 Problematica from the Middle Cambrian Burgess Shale of British Columbia. In *Problematic fossil taxa* (ed. A. Hoffman & M. H. Nitecki), pp. 167–183. New York: Oxford University Press.

Briggs, D. E. G. & Collins, D. 1988 A Middle Cambrian chelicerate from Mount Stephen, British Columbia. *Palaeontology* **31**, 779–798.

Briggs, D. E. G., Erwin, D. H. & Collier, F. J. 1994 *The fossils of the Burgess Shale*. Washington: Smithsonian Institution Press.

Broili, F. 1926 Eine Holothurie aus dem Oberen Jura von Franken. *Sber. bayer. Akad. Wiss* 1926, 341–351.

Butterfield, N. J. 1990*a* Organic preservation of non-mineralizing organisms and the taphonomy of the Burgess Shale. *Paleobiology* **16**, 272–286.

Butterfield, N. J. 1990*b* A reassessment of the enigmatic Burgess Shale fossil *Wiwaxia corrugata* (Matthew) and its relationship to the polychaete *Canadia spinosa*. *Paleobiology* **16**, 287–303.

Carré, C. & Carré, D. 1993 *Ctenella aurantia*, genre et espèce nouveaux de cténophore tentaculé (Ctenellidae fam. nov.) méditerranéen sans colloblastes et avec ventouses labiales. *Can. J. Zool.* **71**, 1804–1810.

Carré, D., Carré, C. & Mills, C. E. 1989 Novel cnidocysts of narcomedusae and a medusivorous ctenophore, and confirmation of kleptocnidism. *Tiss. Cell* **21**, 723–734.

Caster, K. E. & Brooks, H. K. 1956 New fossils from the Canadian-Chazyan (Ordovician) hiatus in Tennessee. *Bull. Am. Paleont.* **36**, 157–199.

Chen, J. Y., Bergström, J., Lindström, M. & Hou, X. 1991 Fossilized soft-bodied fauna. *Natl. Geog. Res. Explor.* **7**, 8–19.

Christen, R., Ratto, A., Baroin, A., Perasso, R., Grell, K. G. & Adoutte, A. 1991 An analysis of the origin of metazoans, using comparisons of partial sequences of the 28S RNA, reveals an early emergence of triploblasts. *EMBO J.* **10**, 499–503.

Collins, D. 1986 Paradise revisited. *Rotunda* **19**, 30–39.

Collins, D., Briggs, D. & Conway Morris, S. 1983 New Burgess Shale fossil sites reveal Middle Cambrian faunal complex. *Science, Wash.* **222**, 163–167.

Conway Morris, S. 1985 Non-skeletalized lower invertebrate fossils: a review. In *The origins and relationships of lower invertebrates* (ed. S. Conway Morris, J. D. George, R. Gibson & H. M. Platt), pp. 343–359. Oxford: Clarendon Press.

Conway Morris, S. 1993*a* Ediacaran-like fossils in Cambrian Burgess Shale-type faunas of North America. *Palaeontology* **36**, 593–635.

Conway Morris, S. 1993*b* The fossil record and the early evolution of the Metazoa. *Nature, Lond.* **361**, 219–225.

Eschscholtz, F. 1829 *System der Acalephen. Eine ausführliche Beschreibung aller Medusenartigen Strahlthiere.* Berlin: Ferdinand Dümmler.

Fedonkin, M. A. 1985 Systematic description of Vendian Metazoa. In *The Vendian system, Vol.* 1 *Palaeontology* (ed. B. S. Sokolov & A. B. Iwanowski), pp. 70–106. Moscow: Nauka (In Russian. English translation by Springer-Verlag 1990, pp. 71–120.)

Gehling, J. G. 1991 The case for Ediacaran fossil roots to the metazoan tree. *Geol. Soc. India Mem.* **20**, 181–224.

Gislen, T. 1947 On the Haplozoa and the interpretation of *Peridionites*. *Zool. Bidr. Upps.* **25**, 402–408.

Glaessner, M. F. 1979 An echiurid worm from the late Precambrian. *Lethaia* **12**, 121–124.

Glaessner, M. F. 1984 *The dawn of animal life. A biohistorical study.* Cambridge University Press.

Gürich, G. 1930 Die bislang ältesten Spuren von Organismen in Südafrika. *Int. geol. Congr.* (*Pretoria*) **15**, 670–680.

Gürich, G. 1933 Die Kuibis-Fossilien der Nama-Formation von Südwestafrika. *Paläont. Zeit.* **15**, 137–154.

Häntzschel, W. 1975 Supplement 1. Trace fossils and problematica. In *Treatise on invertebrate paleontology* (ed. C. Teichert), pp. W1–W269. Boulder: Geological Society of America and Lawrence: University of Kansas Press.

Harbison, G. R. 1985 . On the classification and evolution of the Ctenophora. In *The origins and relationships of lower invertebrates* (ed. S. Conway Morris, J. D. George, R. Gibson & H. M. Platt), Systematics Association Special, vol. 28, pp. 78–100. Oxford: Clarendon Press.

Harbison, G. R. & Madin, L. P. 1982 Ctenophora. In *Synopsis and classification of living organisms* (ed. S. P. Parker), pp. 707–715. New York: McGraw-Hill.

Harbison, G. R., Madin, L. P. & Swanberg, N. R. 1978 On the natural history and distribution of oceanic ctenophores. *Deep Sea Res.* **25**, 233–256.

Heding, S. G. 1932 *Paracaudina* nom. nov. a correction, together with some remarks concerning the supposed fossil holothurian *Pseudocaudina brachyura* Broili. *Vidensk. Meddr dansk naturh. Foren.* **92**, 455–456.

Hernandez-Nicaise, M.-L. 1991 . Ctenophora. In *Microscopic anatomy of invertebrates, vol.* 2: *Placozoa, Porifera, Cnidaria and Ctenophora* (ed. F.W. Harrison & J.A. Westfall), pp. 359–418. New York: Wiley-Liss.

Hyman, L. H. 1940 *The invertebrates: Protozoa through Ctenophora.* New York: McGraw-Hill.

Jenkins, R. J. F. 1992 Functional and ecological aspects of Ediacaran assemblages. In *Origin and early evolution of the Metazoa* (ed. J. H. Lipps & P. W. Signor), pp. 131–176. New York: Plenum.

Krumbach, T. 1925 Ctenophora. In *Handbuch der Zoologie* (ed. W. Kükenthal & T. Krumbach),vol. 1, pp. 905–995. Berlin Leipzig: Walter de Gruyter.

Krumbach, T. 1927 Ctenophora. In *Die Tierwelt der Nord- und Ostsee* (ed. G. Grimpe & E. Wagler), vol. 7, pp. 1–50. Leipzig: Akademische Verlagsgesellschaft.

Mackie, G. O., Mills, C. E. & Singla, C. L. 1992 Giant axons and escape swimming in *Euplokamis dunlapae* (Ctenophora: Cydippida). *Biol. Bull. mar. biol. Lab., Woods Hole* **182**, 248–256.

Mills, C. E. & Miller, R. L. 1984 Ingestion of a medusa (*Aegina atrea*) by the nematocyst-containing ctenophore *Haeckelia rubra* (formerly *Euchlora rubra*): phylogenetic implications. *Mar. Biol.* **78**, 215–222.

Nielsen, C. 1987 *Haeckelia* (= *Euchlora*) and *Hydroctena* and the phylogenetic inter-relationships of Cnidaria and Ctenophora. *Z. zool. Syst. Evolutionsforsch.* **25**, 9–12.

Nielsen, C. 1995 *Animal evolution. Interrelationships of the living phyla.* Oxford University Press.

Nudds, J. R. & Sepkoski, J. J. 1994 Coelenterata. In *The fossil record 2* (ed. M. J. Benton), pp. 101–124. London: Chapman & Hall.

Otto, M. 1994 Zur Frage der 'Weichteilerhaltung' im Hunsrückschiefer. *Geol. Palaeont.* **28**, 45–63.

Pianka, H. D. 1974 Ctenophora. In *Reproduction of marine invertebrates* (ed. A. C. Giese & J. S. Pearse), pp. 201–265. New York: Academic Press.

Raymond, P. E. 1930 Report on invertebrate paleontology. *Rep. Mus. comp. Zool. Harv.* **1929–1930**, 31–33.

Raymond, P. E. 1931 Notes on invertebrate fossils, with descriptions of new species. *Bull. Mus. comp. Zool. Harv.* **55**, 165–213.

Richter, R. 1955 Die ältesten Fossilien Süd-Afrikas. *Senckenberg leth.* **36**, 243–289.

Seilacher, A. 1992 Vendobionta and Psammocorallia: lost constructions of Precambrian evolution. *J. geol. Soc. Lond.* **149**, 607–613.

Simonetta, A. & Delle Cave, L. 1978 Notes on new and strange Burgess Shale fossils (Middle Cambrian of British Columbia). *Mem. Soc. tosc. Sci. nat.* A **85**, 45–49.

Smith, A. B. 1982 The affinities of the Middle Cambrian Haplozoa (Echinodermata). *Alcheringa* **6**, 93–99.

Stanley, G. D. & Stürmer, W. 1983 The first fossil ctenophore from the Lower Devonian of West Germany. *Nature, Lond.* **303**, 518–520.

Stanley, G. D. & Stürmer, W. 1987 A new fossil ctenophore discovered by X-rays. *Nature, Lond.* **328**, 61–63.

Stürmer, W., Schaarschmidt, F. & Mittmeyer, H.-G. 1980 Versteinertes Leben im Röntgenlicht. *Kleine Senckenberg-Reihe* **11**, 1–79.

Swanberg, N. 1974 The feeding behavior of *Beroe ovata. Mar. Biol.* 24, 69–76.

Tamm, S. L. 1982 Ctenophora. In *Electrical conduction and behaviour in 'simple' invertebrates* (ed. G. A. B. Shelton), pp. 266–358. Oxford: Clarendon Press.

Tamm, S. L. & Tamm, S. 1993 Diversity of macrociliary size, tooth patterns, and distribution in *Beroe* (Ctenophora). *Zoomorphology* **113**, 79–89.

Walcott, C. D. 1912 Middle Cambrian Branchiopoda, Malacostraca, Trilobita, and Merostomata. *Smithson. Misc. Collns* **57**, 145–243.

Whittington, H. B. 1971 Redescription of *Marrella splendens* (Trilobitoidea) from the Burgess Shale, Middle Cambrian, British Columbia. *Bull. geol. Soc. Can.* **209**, 1–24.

Whittington, H. B. 1985 *The Burgess Shale*. New Haven: Yale University Press.

Yochelson, E. L., Stürmer, W. & Stanley, G. D. 1983 *Plectodiscus discoideus* (Rauff): A redescription of a chondrophorine from the early Devonian Hunsrück Slate, West Germany. *Paläont. Z.* **57**, 39–68.

Ziegler, B. 1991 . Was ist *Laffonia helvetica* Heer? *Stuttg. Beitr. Naturk.* **172**, 1–10.

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Figure 3. For description see opposite.

Figure 7. For description see opposite.

Figure 8. For description see opposite.

Figure 10. For description see opposite.

Figure 15. For description see opposite.

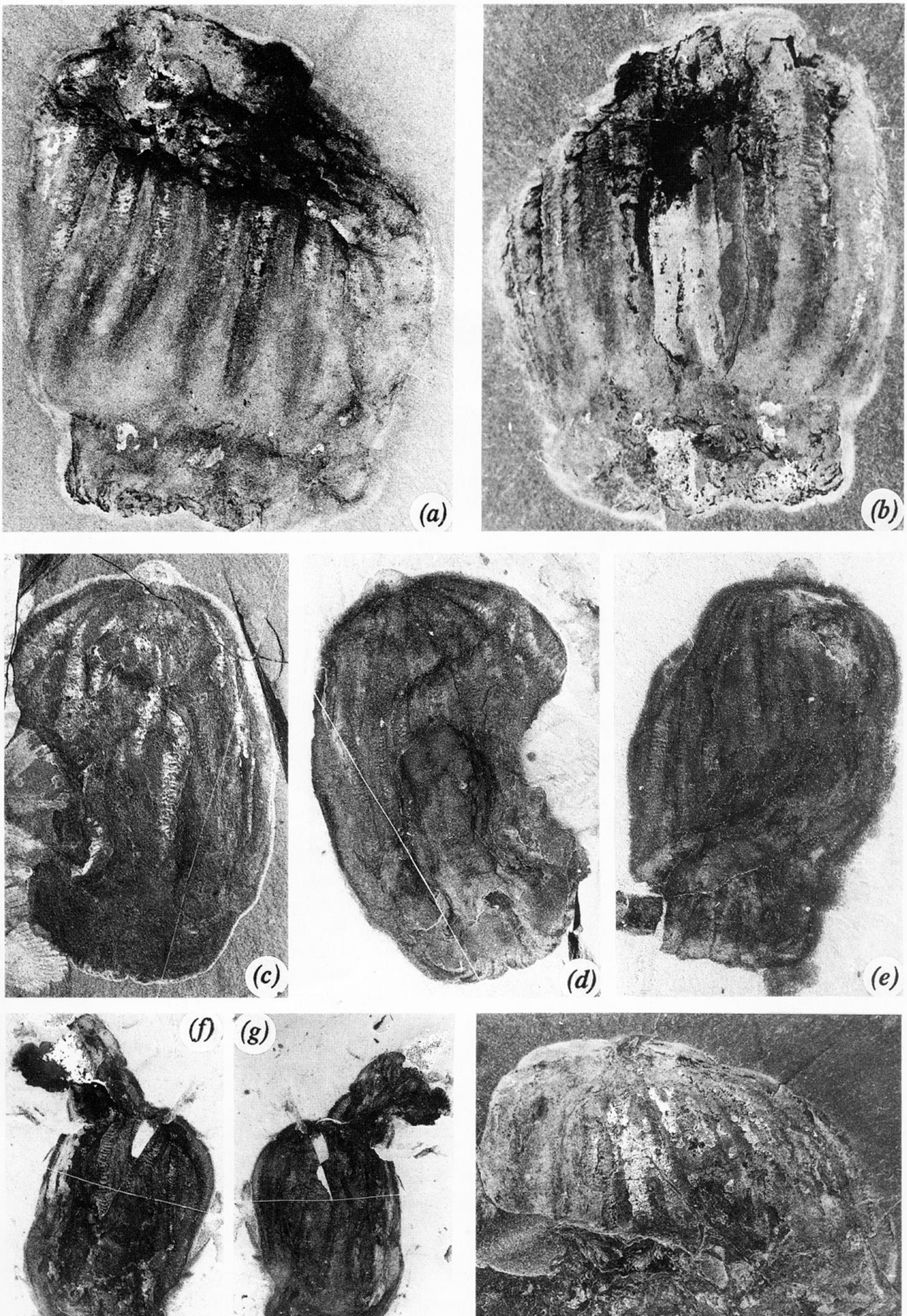

Figure 19. For description see opposite.

Figure 21. For description see opposite.

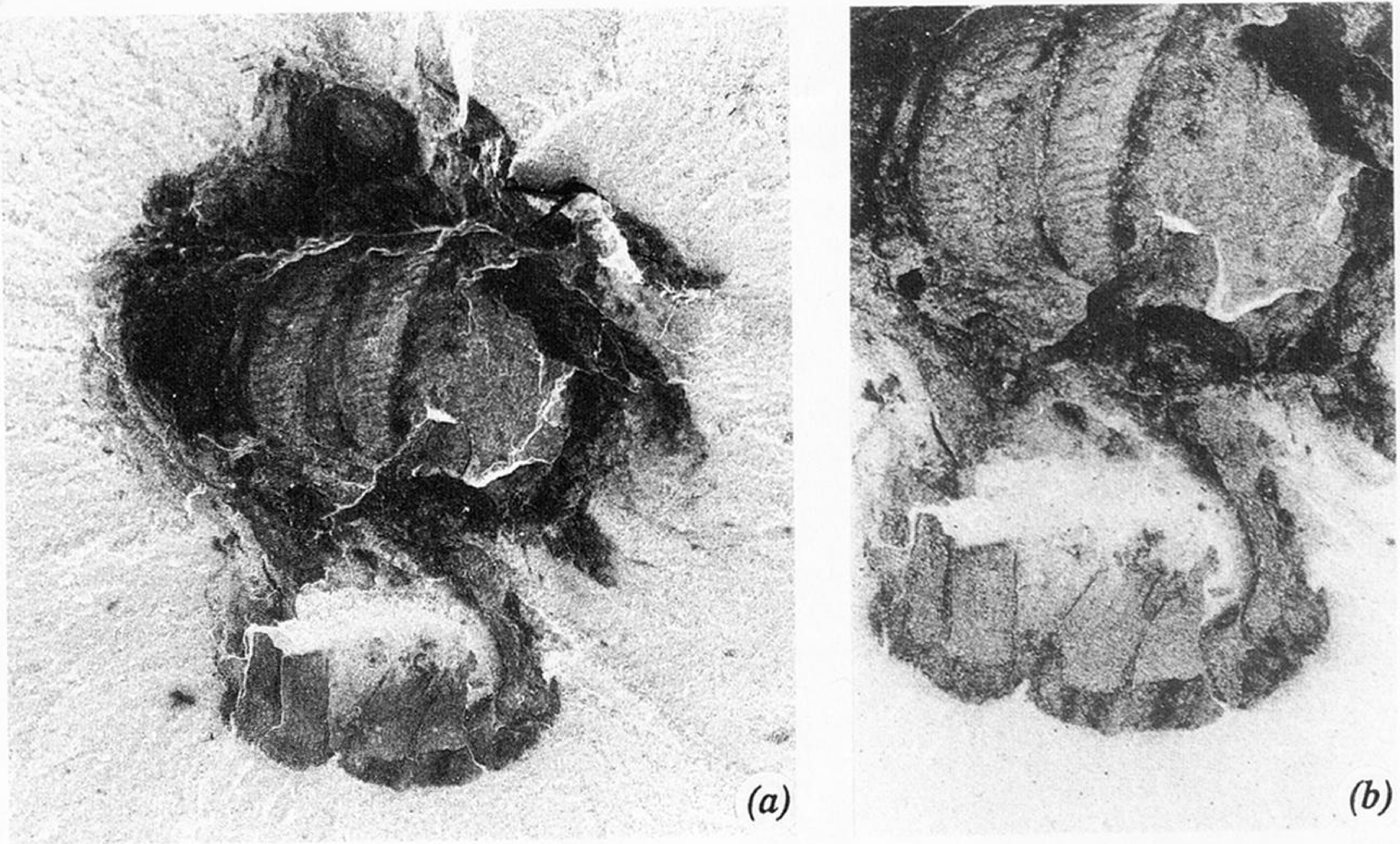

Figure 22. *Ctenorhabdotus capulus* gen. nov., sp. nov., Stephen Formation, Raymond Quarry, Field, British Columbia. (*a–b*) ROM 51047 (*a*) part, x 4.1. (*b*) Detail of oral region, x 5.6.

Figure 23. For description see opposite.