Articulated halkieriids from the Lower Cambrian of North Greenland and their role in early protostome evolution

S. CONWAY MORRIS[1] AND J. S. PEEL[2]

[1] *Department of Earth Sciences, University of Cambridge, Downing Street, Cambridge CB2 3EQ, U.K.*
[2] *Institute of Geology, Department of Historical Geology and Palaeontology, University of Uppsala, Norbyvägen 22, Uppsala, Sweden*

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SUMMARY

Articulated halkieriids of *Halkieria evangelista* sp. nov. are described from the Sirius Passet fauna in the Lower Cambrian Buen Formation of Peary Land, North Greenland. Three zones of sclerites are recognizable: obliquely inclined rows of dorsal palmates, quincuncially inserted lateral cultrates and imbricated bundles of ventro-lateral siculates. In addition there is a prominent shell at both ends, each with radial ornamentation. Both sclerites and shells were probably calcareous, but increase in body size led to insertion of additional sclerites but marginal accretion of the shells. The ventral sole was soft and, in life, presumably muscular. Recognizable features of internal anatomy include a gut trace and possible musculature, inferred from imprints on the interior of the anterior shell.

Halkieriids are closely related to the Middle Cambrian *Wiwaxia*, best known from the Burgess Shale: this clade appears to have played an important role in early protostome evolution. From an animal fairly closely related to *Wiwaxia* arose the polychaete annelids; the bundles of siculate sclerites prefigure the neurochaetae whereas the dorsal notochaetae derive from the palmates. *Wiwaxia* appears to have a relic shell and a similar structure in the sternaspid polychaetes may be an evolutionary remnant. The primitive state in extant polychaetes is best expressed in groups such as chrysopetalids, aphroditaceans and amphinomids. The homology between polychaete chaetae and the mantle setae of brachiopods is one line of evidence to suggest that the latter phylum arose from a juvenile halkieriid in which the posterior shell was first in juxtaposition to the anterior and rotated beneath it to provide the bivalved condition of an ancestral brachiopod. *H. evangelista* sp. nov. has shells which resemble those of a brachiopod; in particular the posterior one. From predecessors of the halkieriids known as siphogonuchitids it is possible that both

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chitons (polyplacophorans) and conchiferan molluscs arose. The hypothesis of halkieriids and their relatives having a key role in annelid–brachiopod–mollusc evolution is in accord with some earlier proposals and recent evidence from molecular biology. It casts doubt, however, on a number of favoured concepts including the primitive annelid being oligochaetoid and a burrower, the brachiopods being deuterostomes and the coelom being an archaic feature of metazoans. Rather, the annelid coelom arose as a functional consequence of the transition from a creeping halkieriid to a polychaete with stepping parapodial locomotion.

1. INTRODUCTION

Approximately 550 Ma ago, a major revolution in life effectively set the agenda for the evolution of life to the present day, at least in the marine realm. This event, colloquially referred to as the 'Cambrian explosion', does not mark the origination of animals which can be traced to at least the late Proterozoic Ediacaran faunas (Jenkins 1992; Conway Morris 1993*a*). Nevertheless, it represents a quantum leap in organization as is apparent from the abrupt appearance of hard skeletal parts and a major diversification of soft-bodied animals. The latter is most apparent from a substantial diversification of trace fossils (e.g. Crimes *et al.* 1977), but is more dramatically encoded by the remarkable process of Burgess Shale-type preservation. Although these categories of fossil occurrence remain useful for discussion, it is evident that the Cambrian explosion will be difficult to comprehend without an integrated approach that draws on all lines of palaeontological evidence.

One reason for this is that a significant number of the early skeletons were composed of numerous sclerites, so that on death the entire structure (scleritome) readily dispersed into their component parts. In the absence of exceptional preservation, such as occurs in a Burgess Shale-type fauna (Conway Morris 1989*a*), the exercise in reconstructing the articulated appearance is fraught with imponderables. Similarly, the precise connection between the various Cambrian metazoans and the type of trace fossil they may have made is tenuous, yet if established would enhance our understanding of ancient behaviour.

Although the core of the Cambrian fauna is well documented in the form of groups such as trilobites, molluscs, brachiopods, sponges (including archaeocyathids), echinoderms and various soft-bodied groups (notably priapulids and annelids), there remain a significant quotient of presently enigmatic taxa, especially in the early Cambrian. Many are represented by disarticulated sclerites whose taxonomy is confused by excessive use of form-taxa, failure to recognize taphonomic variants and uncertainties concerning the nature of the original scleritome. Here, we provide a description of superbly preserved halkieriid scleritomes from the Lower Cambrian of north Greenland. We conclude that halkieriids and near relatives such as the siphogonuchitids are part of an early radiation of the protostomes that ultimately led to the annelids, brachiopods and molluscs.

2. HISTORY OF RESEARCH

(*a*) *Halkieriids*

This group was first recognized on the basis of a small number of isolated sclerites, recovered from phosphatic nodules in the 'Green Shales' exposed in the banks of two small streams (Lilleå, Grødbyå) in south Bornholm (Poulsen 1967), an island within the south Baltic. This material was redescribed by Bengtson (1985), who concluded that the fossils were most likely of lower Atdabanian age. The original describer, Poulsen (1967), was uncertain of the taxonomic relationships of his Bornholm material, but provisionally considered a position within the hyoliths. With the renaissance in the study of early skeletal fossils from the Lower Cambrian, it became clear that halkieriid sclerites are widespread and a significant component of many assemblages (e.g. Missarzhevsky & Mambetov 1981; Qian & Bengtson 1989; Bengtson *et al.* 1990). An important development was the recognition of a relationship between *Wiwaxia corrugata*, best known from the celebrated Burgess Shale (Conway Morris 1985*a*), but also recorded from elsewhere in the Lower and Middle Cambrian of North America (Collins *et al.* 1983; Conway Morris & Robison 1988; Butterfield 1994), and South China (Zhao *et al.* 1994) and the halkieriids (Jell 1981; Bengtson & Missarzhevsky 1981). Using the information on the distribution of sclerites in articulated specimens of *Wiwaxia* from the Burgess Shale Bengtson & Conway Morris (1984) proposed a reconstruction of a halkieriid based on isolated sclerites (and one articulated array of three sclerites), largely from a sample collected in the Pestrotsvet Formation exposed at the Dvortsy section on the Aldan River, Siberia (hereafter the Siberian halkieriid, see figure 50). In particular, they recognized two distinctive types of sclerite (cultrate and palmate) and, more provisionally, a spiniform variety. At this time the cultrates and palmates were considered to be equivalent to the dorsal and lateral sclerites respectively of *Wiwaxia*, and no convincing counterpart to the curved ventro-laterals of the Burgess Shale form could be identified. Subsequently, unequivocal equivalents (known as siculates) have been identified in rich halkieriid assemblages from South Australia (Bengtson *et al.* 1990). Subsequent work on early skeletal fossils continued to yield halkieriid assemblages which could be accommodated in the schema proposed by Bengtson & Conway Morris (1984), but a rigorous testing of the hypothesis was only possible with the discovery of articulated halkieriid scleritomes from the Lower Cambrian Buen Formation of Peary Land, North Greenland (Conway Morris & Peel 1990).

(*b*) *The Sirius Passet fauna*

The potential for exceptionally preserved fossil faunas in North Greenland became apparent during a major programme of mapping undertaken by the

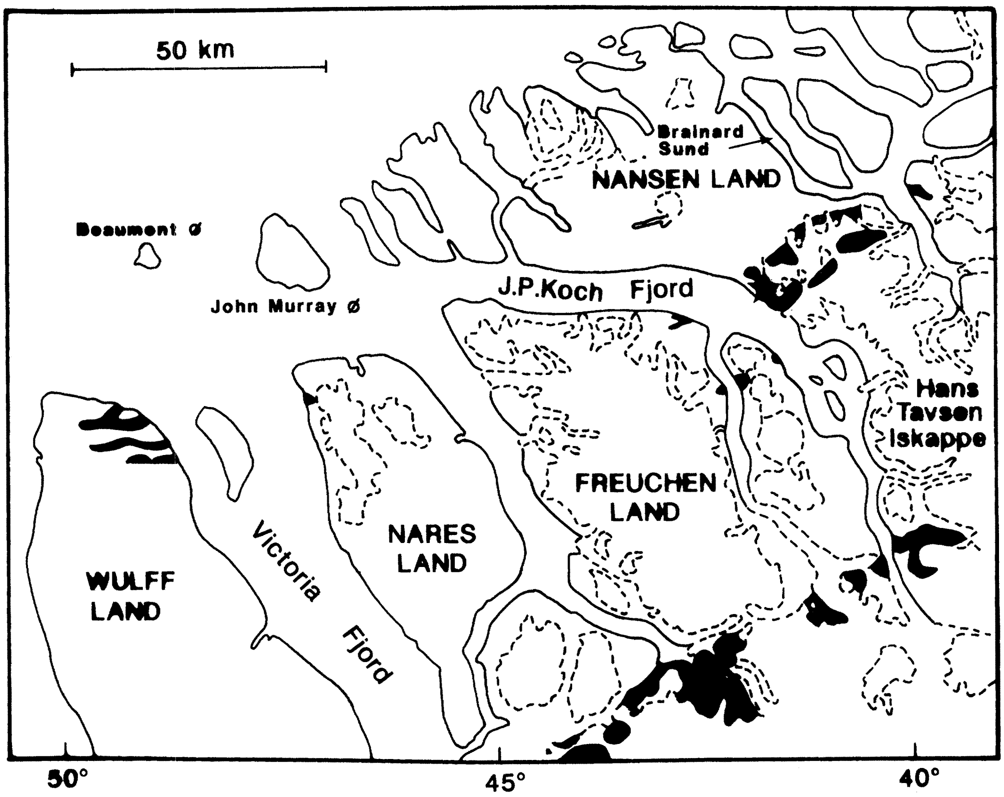

Figure 1. Locality map of Sirius Passet fauna (starred), Peary Land and the adjacent outcrop (in black) of the Buen Formation. Dashed areas enclose permanent ice (redrawn from Higgins *et al.* 1992).

Geological Survey of Greenland (Henriksen 1985), between 1978–1980 and 1984–1985. In 1984 N. J. Soper and A. K. Higgins were engaged in a geological traverse to the east of J. P. Koch Fjord (see figure 1). They collected a number of well preserved fossils, including sponges (Rigby 1986), from a hillside exposing the Buen Formation. The following year A. K. Higgins and N. C. Davis returned to the region and found abundant fossil material on the opposite side of the hill to that visited in 1984. A preliminary description of this fauna, which was clearly of Burgess Shale-type aspect (see Conway Morris 1989*a*), was provided by Conway Morris *et al.* (1987). Time for collecting in 1985 was extremely limited and a four-man expedition returned in 1989. Despite poor weather a substantial collection was made that included abundant arthropods, sponges, palaeoscolecidans, polychaete annelids, incertae sedis and halkieriids. One of the finest specimens, herein designated the holotype (MGUH 19728, see figures 6 and 9*a*–*e*), was located by M. P. Smith on the first day (9 July) of collecting in 1989. Overall the season yielded 21 specimens. A second season of collecting in 1991 provided another 31 specimens and in 1994 another 16 specimens were obtained. Three counterparts of specimens collected in 1989 were obtained during the 1991 season, including that of the holotype. Of the 68 halkieriid specimens available, 13 consist of part and counterpart (see, for example, figure 30*a*, *b*) and with few exceptions they were collected off the talus slopes on separate occasions. Other details of the first two expeditions are given by Peel *et al.* (1992).

In 1994 a new soft-bodied locality was discovered on the north side of the hill, somewhat to the east of the area first explored by Soper and Higgins. Five of the halkieriids (see figures 43 and 45*a*, *e*) collected during this season come from this new locality, that appears to be stratigraphically slightly higher than the main outcrop. On the west side of J. P. Koch Fjord in Lauge Koch Land (see figure 1) a locality that appears to be in the upper part of the Buen Formation has yielded well preserved sponges (Rigby 1986) and the trilobite *Alacephalus ?davisi* (Lane & Rushton 1992). This locality was visited in 1994, but despite further collections of sponges and trilobites, soft-part preservation was not observed. Still further west, in Wulff Land, equivalent horizons have yielded well preserved sponges (Rigby 1986).

The research programme into the Sirius Passet fauna is at a fairly preliminary stage. Apart from the initial announcement (Conway Morris *et al.* 1987), the halkieriid (Conway Morris & Peel 1990) and a remarkable, primitive arthropod (Budd 1993) the only other work yet published concerns the sponges (Rigby 1986), a single species of trilobite (Blaker 1988) and the palynology (Vidal & Peel 1993). The latter is part of a wider survey and a point worth nothing is that despite the sometimes fine preservation of the acritarchs in the Buen Formation in outcrops to the south-east in southern Peary Land, at Sirius Passet itself they are absent and only poorly preserved bacteria were recovered.

Although the local stratigraphy is complex, Peel *et al.* (1992) concluded that the Sirius Passet assemblage

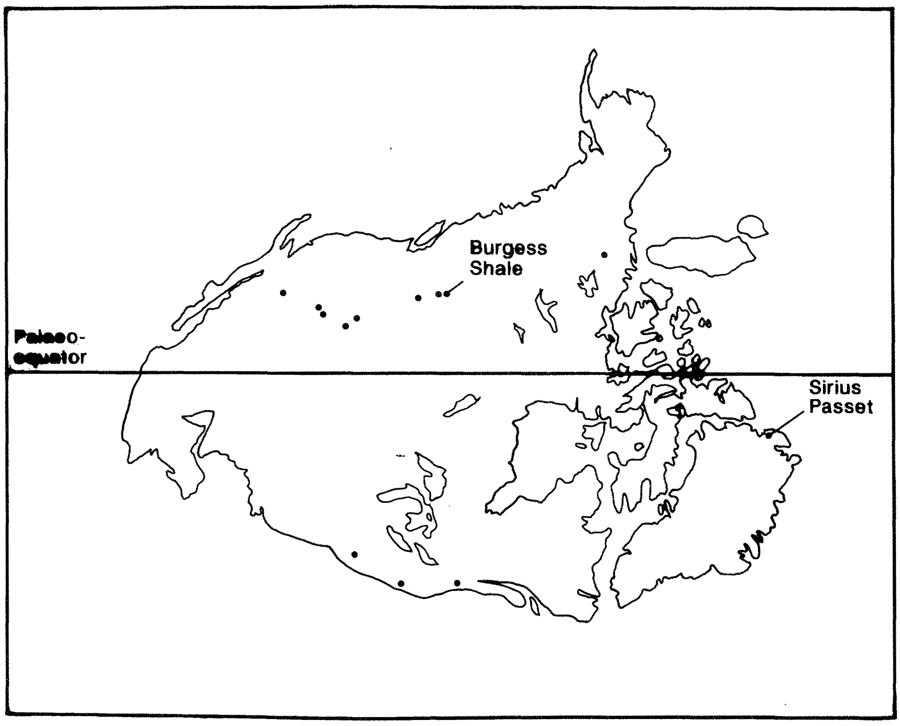

Figure 2. Distribution of Lower and Middle Cambrian Burgess Shale-type faunas from the Laurentian craton (see Conway Morris 1989*a* and Butterfield 1994 for data sources). Note the concentric distribution of the faunas and the general tendency for them to be located in the region facing the open ocean. This aspect is less clear along the western Cordillera on account of post-Cambrian accretion to the craton combined in some examples with eastward movement on thrust-sheets. Projection is for the Middle Cambrian, cylindrical equidistant.

was deposited immediately adjacent to the carbonate platform (defined by the Portfjeld Formation) and thus faced the open ocean in a setting reminiscent of many of the other Burgess Shale-type faunas (Conway Morris 1989*a*; see also figure 2). It appears that the Sirius Passet fauna lies in the basal part of the Buen Formation.

Concerning the age of the Sirius Passet fossils, it is now possible to amplify the initial conjectures given in Conway Morris *et al.* (1987). The only known trilobite in the Sirius Passet *Buenellus* (Blaker 1988) is interpreted by Palmer & Repina (1993) as a normal nevadiid and so indicative of the *Nevadella* Zone of the North American standard and thus equivalent to the uppermost Atdabanian (see figure 48). This estimate is consistent with the occurrence higher in the Buen Formation of *Olenellus* (*Mesolenellus*) *hyperboreus* which is indicative of a Botomian age (Palmer & Repina 1993). The acritarchs from the Buen Formation (Vidal & Peel 1993) are in accordance with these ages, although no diagnostic palynomorphs occur in the Sirius Passet assemblage itself.

3. PRESERVATION AND TAPHONOMY

The stratigraphy and regional character of the Buen Formation were reviewed by Vidal & Peel (1993). The clastic sequence demonstrates a variety of facies ranging from near-shore sands to deeper water muds in which the Sirius Passet fauna is located. Many, although not all, Burgess Shale-type faunas are located in deeper-water settings. In the case of the North American (Laurentia) craton these faunas have a concentric distribution in sites that generally face the open ocean (see figure 2). Thus there is a measure of predictability about new discoveries. Limited reconnaissance along the outcrop of the Buen Formation (see Higgins *et al.* 1992) earlier had revealed two other occurrences with well-preserved sponges (Rigby 1986), but a specific search both north of Navarana Fjord and along the south side of Sirius Passet towards Brainard Sund (see figure 1) failed to reveal new soft-bodied occurrences. Although the taphonomy of Burgess Shale-type faunas show some features in common, the limited information to hand suggests significant variations. Little is yet known about the taphonomy of the Sirius Passet fauna, although it is evident that the sediment has been subjected to fairly pronounced metamorphism (Vidal & Peel 1993). More immediately, it is not clear whether the fauna is either effectively autochthonous and owes its preservation to adverse environmental conditions impinging on the sea-floor or is allochthonous, having been transported by storm action or turbidity currents to a hostile milieu that favoured soft-part preservation. Subtle differences in the lithology in which the halkieriids are embedded, which typically are slightly silty shales but range to fine silts, suggest varying energy of depositional processes possibly consistent with distal tempestites. With one exception all the halkieriids are buried effectively parallel to the bedding planes, but one juvenile specimen (see figure 12*g*) is twisted over, perhaps due to transport. This parallel orientation also characterizes most other taxa in the fauna, although the occasional arthropod and some of the palaeoscolecidan worms are buried at an angle to the sediment surface. Deposition, therefore, is inferred to have been a moderate process, rather than a turbulent event that characterized the Phyllopod bed fauna of the Burgess Shale (Whittington 1971; Piper 1972). The specimens occur isolated on separate slabs, with one exception (see figure 45*e*) where there appears to be superposition of two specimens.

There is some evidence that burial (or whatever process was responsible) did not instantly kill the animals. The polychaete worms are sometimes tightly coiled and more open-to-tight coiling also occurs in some of the palaeoscolecidans (cf. Whittard 1953; Robison 1969). Such coiling has been observed in modern worms stored in anoxic sediments (Dean *et al.* 1964) and appears to represent entry into metabolic stasis. Absence of such coiling in the Phyllopod bed (Burgess Shale) worms may be indicative of rapid death, during or immediately upon burial (Conway Morris 1986). A characteristic feature of the halkieriids is a curved anterior region, sometimes tightly recurved (see figures 6, 8, 9*a*, *g*, 10, 12*a*, 28, 30*a*, *b*, 31, 34 and 35*a*, *f*). Of the 38 suitably preserved specimens, 25 (66%) show some degree of curvature. This attitude may be a response to anoxia. This conclusion is consistent with the comments of Vidal & Peel (1993) who inferred low oxygen conditions for the Sirius Passet fauna on the basis of its palynology and comparison with other dysaerobic sediments.

No trails are associated with the halkieriids, which are assumed to have been benthic (§6), although in the soft sediment these trails may have had a low preservation potential. Nevertheless, unequivocal trace fossils consisting of simple infaunal burrows are frequent in the fauna. These traces await detailed study, but are broadly divisible into two types: relatively large with spreite subparallel to the walls, and minute narrow burrows. In addition, somewhat massive beds in the section display more extensive bioturbation. The nature of the original animals that were able to survive in this hostile milieu is not known. These traces are often associated with the exceptionally preserved body fossils, but the cross-cutting (see figures 13 and 16*a*, *c*) appears to be fortuitous and there is no evidence in the halkieriids that the trace makers sought out the carcasses as scavengers. Evidently the trace and body fossils lay at different levels and have been superimposed by compaction.

The halkieriids are strongly compressed, but both sclerites and shells show relief (see, for example, figures 27*g* and 39*c*) and are inferred to have been mineralized, presumably with calcium carbonate as is the case in other halkieriid sclerites (see, for example, Bengtson & Conway Morris 1984; Bengtson *et al.* 1990). Support for the Sirius Passet halkieriids having calcareous biomineralization comes from the associated metazoans known to have had originally calcareous skeletons (trilobites and much rarer hyoliths) which are consistently decalcified. In the halkieriids normally only the outer sclerite surfaces are preserved, but MGUH 19733 is unusual because the internal cavities of the sclerites are infilled with a brown mineral, that also reveals the lateral canals (see figure 22*b*, §5*c*). Mineralization also occurs in nodular to elongate patches which are interpreted as gut contents (see, for example, figures 11, 12*d*, 19 and 22*e*).

With four exceptions all the specimens are preserved entire, effectively with no disruption of the sclerites or shells. In MGUH 19731 (see figures 11 and 12*d*) two groups of cultrate sclerites have been displaced from the right side. Near the anterior the margin is disrupted, whereas the second clump is located about 10 mm from the rest of the body. Although collected incomplete SM X24905 shows more extensive disruption, including considerable disturbance of the right side and a lengthwise split through the anterior shell (see figures 18 and 22*c*, *d*). In both MGUH 19731 and SM X24905 the observed disruption is attributable to decay. In SM X24931 (see figures 44 and 45*c*) part of the left-hand side of the anterior region is excavated as an arcuate area. Adjacent to this area are disrupted sclerites and beneath the body the crumpled remains of the anterior shell. It is, however, in positive relief indicating that the shell has not been simply folded beneath the animal. SM X24931, therefore, appears to have been a victim of predation, presumably by one of the co-occurring arthropods. Finally in SM X24930 the scleritome is intact, except that the posterior shell has been rotated (see figures 43 and 45*a*, *b*).

Neither isolated sclerites nor shells have been recognized on bedding planes. This may be due to oversight, but the relative scarcity of trilobite fragments as against intact exoskeletons suggests that calcareous debris may have been subject to rapid post-mortem dissolution, possibly because of the acidity of the muds. In contrast isolated sclerites of *Wiwaxia* are widespread in the Phyllopod bed of the Burgess Shale (Conway Morris 1985*a*; Mankiewicz 1992).

4. METHODS

Specimens were collected from the talus slopes above J. P. Koch Fjord, trimmed and packed in foam-lined boxes. In the laboratory limited preparation with a dental microdrill was employed to remove overlying sediment. For photography specimens were coated with ammonium chloride sublimate. In a few cases (see figures 12*c* and 22*b*) specimens were photographed in ultraviolet radiation, in the manner used in Burgess Shale studies (see, for example, Conway Morris 1979*a*, 1985*a*). For ultrastructural studies latex pulls of selected areas were taken, gold-coated and examined in a JEOL-28 scanning electron microscope. Where appropriate drawings of specimens are placed opposite the relevant photographs as a guide to our interpretations. Hachured lines indicate either breaks in slope or lines of rock fracture, with the hachures being directed downslope.

5. SYSTEMATIC PALAEONTOLOGY

(*a*) *The concept of* Halkieria

The taxonomic assignment of the Sirius Passet halkieriids presents some difficulties because of incomplete knowledge of scleritome organization in this group. The type material of *Halkieria* from Bornholm (Poulsen 1967) is known only from cultrate sclerites (Bengtson 1985) and although the absence of other sclerite types is most likely taphonomic, the possibility remains that this material had a markedly different scleritome from other halkieriids. In addition, Poulsen (1967) did not describe any material that could be plausibly compared to halkieriid shells. A further complication is that even where halkieriid scleritomes were moderately well understood (e.g. Bengtson & Conway Morris 1984; Qian & Bengtson 1989; Bengtson *et al.* 1990; Landing 1991), the recognition of the shells as an integral part of the skeleton (Conway Morris & Peel 1990) will necessitate a radical revision of halkieriid taxonomy (see also Bengtson 1990, 1992). Possible cases of isolated halkieriid shells are reviewed below, but a potentially important consideration is whether the sclerites are relatively invariant whereas the shells show greater morphological variation. Ultimately the shells may be more useful, not only for taxonomic discrimination, but also with respect to tracing phylogenies.

At present the following genera of halkieriids are recognized: *Halkieria* Poulsen, 1967; *Thambetolepis* Jell, 1981 and *Sinosachites* He, 1980. A number of synonymous genera are discussed by Qian & Bengtson (1989, pp. 40–47), but the poor quality of many descriptions and a lack of awareness of halkieriid sclerites originally forming a scleritome means that their taxonomy is still unsettled. The Sirius Passet cultrate sclerites approach closely previously described equivalents in *Halkieria*, although differences exist with the palmates and perhaps the siculates (see §5*c*). The relatively short lateral canals of the cultrates (see figure 22*b*) also find counterparts in other material of *Halkieria* (e.g. Bengtson *et al.* 1990), whereas in *Thambetolepis* (Jell 1981; Bengtson *et al.* 1990) and apparently *Sinosachites* (Qian & Bengtson 1989) the lateral canals are more extensive. Although the position of the Sirius Passet halkieriids in the genus *Halkieria* cannot be regarded as entirely secure, at present there seems to be less justification for erecting a new genus. These halkieriids, however, cannot be readily compared to any known species and accordingly *Halkieria evangelista* sp. nov. is erected.

(*b*) *Systematic section*

(i) *Family Halkieriidae Poulsen 1967*

Diagnosis (modified from Qian & Bengtson 1989, p. 40, and Bengtson *et al.* 1990, p. 71)

Bilaterally symmetrical lepidote metazoans with calcareous sclerites disposed in several longitudinal zones. Principal types include lateral cultrates and dorsal palmates and at least sometimes ventro-lateral siculates and perhaps dorso-lateral spiniforms. Sclerites housed soft-tissue in central cavity that extended into lateral canals of varying length and was connected to body via basal foramen of restricted diameter. Sclerites consist of a blade and basal region. Blade compressed in cultrates and palmates, sub-cylindrical in siculates. Base usually sharply folded towards lower side of cultrates and palmates, more continuous with blade in siculates. Surface ornamentation comprises longitudinal ribs and sometimes transverse ribbing or tubercles on upper side of blade, on lower side more subdued with transverse striations. At least one shell present.

(ii) *Genus* Halkieria *Poulsen, 1967*

Type species

Halkieria obliqua Poulsen, 1967. Original designation p. 30.

Diagnosis (modified from Qian & Bengtson 1989, p. 41)

Halkieriids with siculate, cultrate and palmate sclerites, short lateral canals. Anterior and posterior shell present.

Halkieria evangelista sp. nov.

1990	'Articulated halkieriids' Conway Morris & Peel, pp. 802–805, figures 1–4.
1991	'Articulated halkieriid' Peel, pp. 6–8, figure 2
1991	Halkieriid Erwin, p. 32
1992	*Halkieria* sp. Bengtson, figure 1
1992*b*	'Articulated halkieriids' Conway Morris, figure 22.8*d*, *e*
1993*b*	'Articulated halkieriid' Conway Morris, pp. 223–224, figure 4*c*
1993	*Halkieria* Dzik, figure 11*a*
1994	*Halkieria* Conway Morris, figure 2D

Derivation of specific name

The name is chosen as an indication of the fossil's explanatory power for Lower Cambrian palaeontology, and also as a pun on Johann, one of the pilots who assisted in field-work.

Diagnosis

A species of halkieriid with an estimated maximum length of about 80 mm. Siculates form imbricating rows, each consisting of a fan-like array, apparently arising from a lobe. Imbricated cultrates flank lateral, anterior and posterior regions, increasing in size adaxially. Palmates arrayed in elongate rows, imbricating in posterior and adaxial direction. Shells convex dorsally, prominent growth lines and radial ornamentation. Anterior shell subquadrate, posterior shell more ovate, less convex and stronger radial ornamentation. Internal anatomy includes prominent rods beneath dorsal surface, running adaxially in an anterior direction. Straight gut, possibly with anterior feeding apparatus, sub-terminal anus.

Material

MGUH (Geological Museum, University of Copenhagen, Denmark) 19728–19734, SM (Sedgwick Museum, University of Cambridge) X24901-X24935. The holotype is designated as MGUH 19728.

(*c*) *Morphology*

(i) *Dimensions and attitudes*

To the first approximation all specimens are buried in a dorso-ventral attitude. Thirteen specimens are known as part and counterparts (see, for example, figure 30*a*, *b*), the former being designated by the side

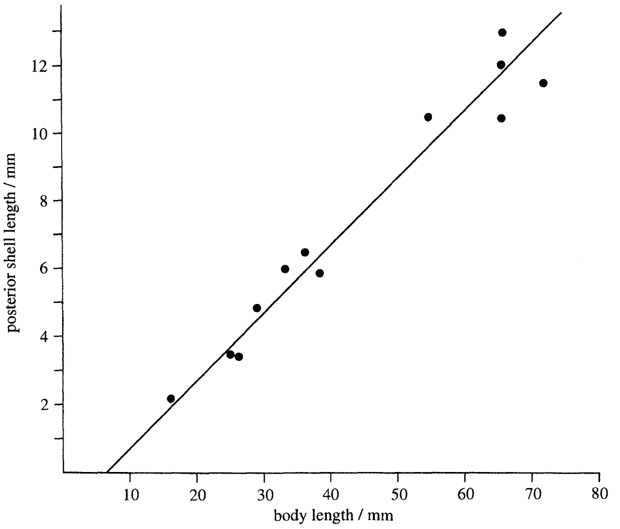

Figure 3. Bivariate plot showing relation between length of both body and posterior shell in 12 available specimens of *Halkieria evangelista* sp. nov. Regession statistics: $y = 6.4332 + 4.9589x$; $r^2 = 0.954$.

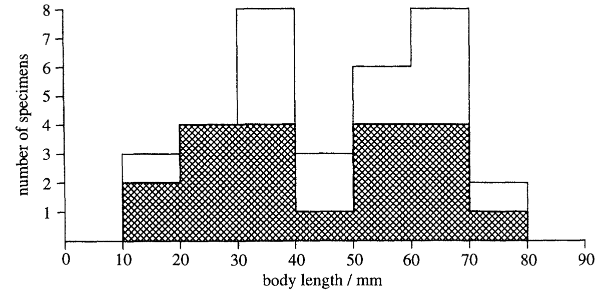

Figure 4. Size–frequency histogram of length of the 34 specimens of *Halkieria evangelista* sp. nov (mean = 40.1 mm, s.d. = 20.6 mm). Cross-hatched zone refers to specimens complete enough to measure ($n = 20$). The total includes specimens whose length has been estimated from length of posterior shell (see figure 3).

showing positive relief. The remainder are disassociated parts or counterparts. Way-up of collected slabs is not known, but the great majority appear to be dorsal-side up on the bedding surface. Rare ventral specimens are identified by the preservation of either soft-tissues associated with the concave surface of the anterior shell (see figures 29, 30*e*, *g*, 32, 33 and 35*d*, *e*) or the sole region flanked by siculates (see figures 23 and 27*a*–*c*). In dorsoventral aspect the anterior and posterior ends of the body have rounded outlines, although the former extends into a short cone-like structure. The lateral margins of the animal are effectively parallel (see figures 6, 9*a*, 11, 12*d*, *g*, 13 and 16*a*).

Of the 68 specimens only 20 are complete enough to provide length measurements (note that the five specimens collected from the new locality discovered in 1994 (§2*b*) are included in the main sample for all measurements). Fairly reliable estimates of length, however, can be obtained from 14 incomplete specimens with well-preserved posterior shells, on the basis that lengths of body and shell are directly proportional (see figure 3). Such a compilation echoes the size-frequency obtained from entire specimens and overall the size-frequency histogram shows a strong bimodal distribution (see figure 4). The smallest entire specimens are SM X24932 (see figure 45*d*) and X24934, each approximately 16 mm long. MGUH 19732 (see figure 12*g*) and SM X24929 are the next smallest in length recovered, at 25 mm and 26 mm, respectively. The incomplete SM X24923 (see figures 37 and 39*d*) had an original length estimated to be approximately 18 mm as judged from a faint impression in the underlying sediment that was presumably made by the now-missing section, a value in agreement with an estimate based on the size of its posterior shell (see figure 3). The largest entire specimen (MGUH 19729, figures 13 and 16*a*) is 71 mm long, and this almost coincides with the estimate (see figure 3) derived from the largest posterior shell in the incomplete SM X24926 (see figures 38 and 39*g*, *h*) at approximately 72 mm. The absence of specimens less than approximately 15 mm may be an oversight during collecting, although in the Phyllopod bed (Burgess Shale) a significant number of taxa lack juvenile representatives (Conway Morris 1986).

The configuration of the specimens is variable. Some are either effectively straight (see figures 13 and 16*a*), gently curved (see figures 11 and 12*d*) or sinuous (see figures 29 and 30*e*). Most characteristic, however, is curvature of the anterior region which ranges from open (see, for example, figures 41 and 42*b*), to more or less strongly recurved (see figures 6, 9*a*, 10, 12*a*, 31, 34, 35*a*,*f*, 45*e*). Many specimens are too incomplete to judge overall configuration, although where only the posterior is available it is usually straight (see, for example, figures 14, 16*e*, 19, 22*e*, and 30*d*) and rarely curved (see, for example figures 21 and 22i). One unique specimen (figure 12*a*) has the anterior twisted over. These various configurations suggest that despite its coating of sclerites the body was relatively flexible, although the frequency of the recurved anterior may have resulted from death in anoxic conditions (see §3).

(ii) *Sclerites*

The external skeleton of *H. evangelista* consists of three zones of sclerites and two shells (anterior and posterior). Siculate sclerites occupy the margins of the animal and abut the ventral soft-bodied sole. Cultrates mantle the sides of the animal, extending along the sides of the trunk and overlapping the outer edges of the anterior and posterior valves. The central zone of dorsal surface is occupied by palmates, and these abut the trailing and leading margins respectively of the anterior and posterior shells. In addition to the external skeleton of sclerites and shells there is evidence for an internal skeleton of obliquely orientated rods.

The dorsal surface on which the palmates were inserted appears to have been gently convex, except along the midline which is marked by a narrow, prominent groove (see figures 6, 7, 9*a*, *b*, *f*, 12*g*, 20, 22*h*, 29, 30*d*, *e*, 41 and 42*b*). The palmates were inserted in closely spaced rows, each one of which ran towards the midline in an oblique and posterior direction (see figure 9*c*). Along each row there were, in adult specimens, approximately 6–7 sclerites which increased in size towards the margin and imbricated in the opposite adaxial direction. Adjacent rows are largely separated, but imbricate in a posterior di-

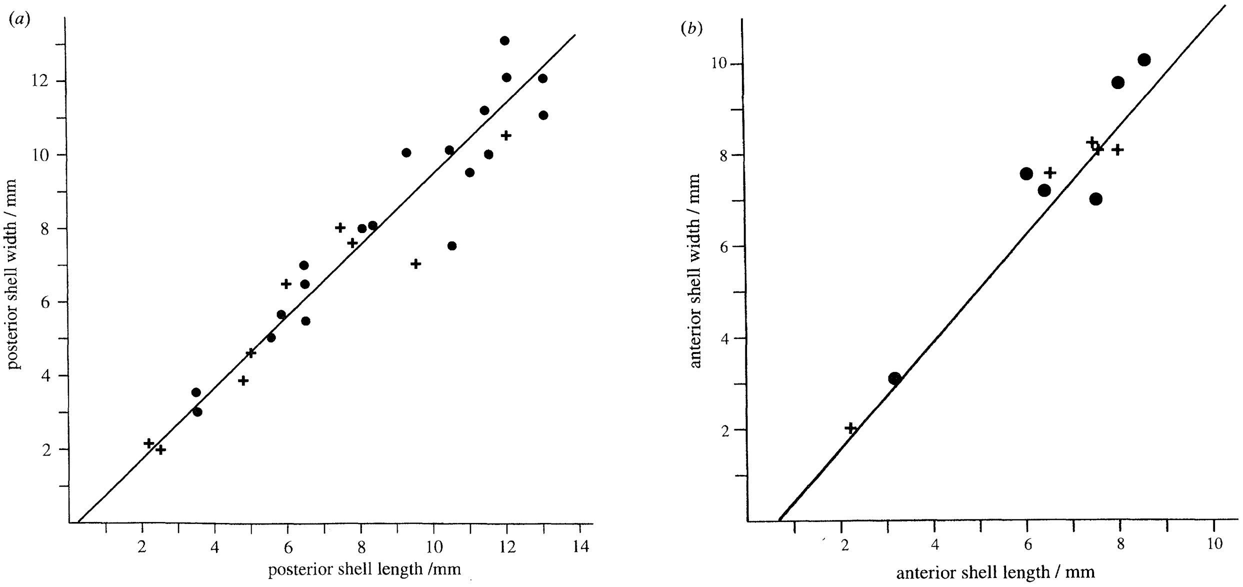

Figure 5. Bivariate plots showing relationship between maximum length and width in posterior (*a*) and anterior (*b*) shells of *Halkieria evangelista* sp. nov. Filled circles, measured; crosses, estimated. Regression statistics: (*a*) $y = 0.32538+1.0222x$, $r^2 = 0.914$, $n = 28$; (*b*) $y = 0.71707+0.81354x$, $r^2 = 0.927$, $n = 11$.

rection. Imbrication of the palmates, especially along each row, means that in the absence of either folding over or disarticulation of this region, only the distal portion of the upper surface of each sclerite is visible. As preserved each sclerite appears to have been symmetrical with prominent ribbing, consisting of a median rib flanked on either side by about four ribs together with a marginal thickening. Overlap also precludes accurate length estimates, but in a row maximum width varies from approximately 0.75–1.2 mm in an abaxial direction.

In the holotype (see figures 6 and 9*a*) it is estimated that each side of the palmate zone bore about 42 rows, giving an approximate total of 550 palmates. The first rows arise immediately behind the anterior shell but because of crushing and other distortion the precise arrangement is not clearly visible in any specimen. The palmate zone terminates in the rows that abut the leading margin of the posterior valve. This region is well preserved in the holotype (figure 9*a*), where about four rows abut the shell with the number of sclerites in each row reduced posteriorly as the shell expands in width.

The cultrate sclerites mantle the entire margin of the animal, totally enclosing the dorsal zone that bears the palmate sclerites and shells. In the specimens the cultrates occur in one of two configurations. The first (normal configuration) is abutting the palmate zone, with the sclerites pointing adaxially along the lateral margins and towards the anterior shell at the front of the animal (see figures 6, 9*a*, *e*, 10, 12*a*, 15, 16*h*, 19, 20, 21, 22*e*, *h*, *i*, 24, 27*e*, *h*, 28, 30*a*, *b*, 31, 35*a*, 43 and 45*a*). Alternatively, the cultrates are splayed outwards (splayed configuration) and in the part the sclerites are preserved in negative relief (see figures 11, 12*d*, 38, and 39*g*). Intermediate examples are also known where the outer i.e. most adaxial, row is splayed, but the remainder are adpressed to the body with their distal terminations still directed towards the midline (see figures 25 and 27*i*).

The cultrate zone consists of about four rows of imbricated sclerites, with (in normal configuration) a progressive size increase towards the midline. The largest sclerites are about 3 mm in length (see figures 24, 27*e*, *h*, 31, 35*b*, 36 and 39*b*). The pattern of imbrication is such that the rows alternate in position (figure 27*g*) and although the pattern is not precisely regular, overall it is quincuncial. The posterior cultrates overlap the trailing edges of the posterior shell (e.g. figures 6, 9*a*, *d*, 10, 12*b*, 21, 22*i*, and 39*f*), but the equivalent overlap of the frontal margin of the anterior shell is usually less clearly preserved (e.g. figures 24 and 27*h*). At the anterior the cultrates sweep towards the mid-line to form an imbricated panel (figures 24 and 27*h*). In some specimens the splayed configuration of the cultrates extends around the anterior margin (see figures 11, 12*d*, 13 and 16*a*, *d*). Although the anterior margin of the animal usually appears to be continuous, in several specimens there is a distinct triangular extension or cone covered with tiny sclerites (see figures 24, 27*h*, 31, 34 and 35*a*, *g*). Abaxial to the main zone of cultrates there is slight evidence in one specimen for a region occupied by more elongate, even lanceolate, sclerites that run subparallel to the longitudinal axis (see figure 16*a*, *b*), but similar structures have not been observed elsewhere.

The cultrate sclerites are elongate, symmetrical and strongly convex on the upper side which also bears prominent ribs (see figures 12*e* and 42*h*). In rare cases of a specimen in splayed configuration (see figures 38 and 39*g*) or more clearly in a specimen showing partial disarticulation (see figures 11 and 12*d*) the entire sclerite is visible. The sides are subparallel, the base rounded and with a circular structure that presumably represents the foramen (figure 12*e*). A narrow extension extending away from the base may represent an attachment stalk (figures 39*j* and 42*g*).

The unusual replacement in MGUH 19733 (figure 22*a*) reveals internal details of the cultrate sclerites. In general, the brown mineral appears to infill the cavity that is believed to have been originally filled by soft-tissue. In a few sclerites both this filling and the outer wall are visible, and can be seen to be connected by a series of short canals, approximately 0.1 mm in length (figure 22*b*).

Whereas the disposition of the palmate and cultrate sclerites is relatively clear, the arrangement in the siculates zone is somewhat more problematic because this zone is preserved in a variety of ways. These include a very narrow zone with strong relief and the sclerites subparallel to the longitudinal axis (e.g. figures 15 and 16*h*) or a somewhat wider array defined by an apparently serial row of arcuate siculates (e.g. figures 6, 7, 8, 9*e,f,g*, 10, 12*a*, 20, 22*h*, 27*k*, 28, 30*a, b*, 32, 35*d*, 36 and 39*a*). In other specimens this arcuate array forms the outer margin and is separated from the cultrates by a convex region of closely packed siculates that impart a pitted appearance to this region (see figure 35*b*). In yet other specimens the siculates underlie other regions of the body with the arcuate zone reversed such that the siculates are now convex towards the midline (see figures 13 and 16*a, b*). Where the siculates underlie the margins of the body, the cultrates are always in the splayed configuration (figure 39*g*). All these aspects of the siculate zone are resolved in specimens that show the arcuate sclerites to have arisen in distinct bundles, each somewhat similar to a bunch of bananas. These bundles arose in a closely spaced series, the transverse axis of each array arising obliquely to the midline (figures 21, 22*j*, 23 and 27*d*). The bundles imbricated in a posterior direction. Particularly important is the preservation of a siculate bundle in SM X24906 (figures 19 and 22*f*) where the sclerites appear to arise from a discrete lobe. The exact shape of these siculates, apart from their arcuate nature, is difficult to establish, but they may have had a subcircular to subtriangular cross section. There is no evidence for the prominent ribbing similar to that of the palmates and cultrates. The siculate zone appears to have encircled most of the animal. They are clearly visible along the lateral margins, and also at the posterior end where the sclerites of each side meet at the midline (see figures 11, 12*d,g*, 16*f*, 38, 39*e–h* and 45*e*). At the anterior the sclerites can be traced well past the margin of the anterior valve (see figures 6 and 9*a*) and although this region usually displays cultrate sclerites the siculates are assumed to converge close to the anterior tip, beneath the cultrates.

Despite the post-mortem flattening of the specimens, which is often less accentuated in juvenile specimens, the arrangement of the cultrate and siculates is consistent with the former occupying the steep sides of the animal and being separated from the siculates by a prominent groove (see figures 6, 9*e*, 12*g*, 15, 16*h*, 20, 22*h*, 24, 27*e*, 29, 30*e*, 31, 32, 35*b, d*, 44 and 45*c*). The frequency of underfolding (for example, figures 13, 16a, 29 and 30*e,f*) of the siculate-bearing margins, which may characterize both sides or one side only, suggests that this region of the body formed a flexible flap or skirt. The prominent groove presumably served to separate the flap from the rest of the body, and when the body was so enrolled some or all of the cultrate sclerites were forced into the splayed configuration.

(iii) *Shells*

The anterior and posterior shells differ somewhat in shape but both grew by accretion as is evident from the growth lines. They are assumed to have been composed of calcium carbonate, a notion supported by evidence of brittle behaviour in the anterior shell whose more convex profile presumably made it more prone to fracturing during compaction (e.g. figures 11 and 12*f*). In the partially decayed SM X24905 the anterior shell has split open (figures 18 and 22*d*), suggesting that it was also rather thin. This is consistent with an incomplete juvenile (SM X24935) in which the anterior shell is quite strongly distorted.

The margins of the anterior shell are often obscured by cultrate sclerites and this combined with crushing and other distortion make the exact shape of the shell difficult to establish (see figures 6, 9*a*, 18, 22*d*, 31, 32, 34, 35*a, c, d,f*, 36, 39*c*, 41, 42*b* and 45*e*). In well preserved material (e.g. figures 12*f* and 16*d*), however, the shell in dorsal outline tends to be slightly wider than it is long. It has a rounded anterior margin, slight wing-like extensions on either side and a backwardly projecting umbonal region that presumably overhung its posterior margin (see figures 12*f* and 16*d*). All the well preserved shells are in adult specimens but the configuration of the growth lines shows that in earlier ontogenetic stages it was more rectangular. Adult growth appears to have been effectively isometric (figure 5*b*). The growth lines are divisible into prominent examples, which are occasional and irregularly spaced, separated by finer increments (figure 39*c*). The growth lines show a few minor irregularities, of which a notch-like deflection in one line of SM X24922 presumably reflects local damage to the shell margin (figure 39*c*). In addition to the growth lines some specimens display subdued radial ornamentation that is more apparent in the posterior shell. In apparent contrast to the posterior shell the anterior one was presumably firmly attached to the body via secretory mantle and probably also via musculature (see §5*c* (v)). It appears, however, that the anterior region could be protruded because in MGUH 19729 there is a smooth quadrate area in front of the shell (see figures 13 and 16*a, d*). This appears to correspond to the outline of the shell and is rimmed by cultrates in a splayed configuration, suggesting downward folding of the anterior margins.

The posterior shell (figures 6, 9*d*, 10, 12*b*, 13, 16*c*, 19, 21, 22*g, i*, 25, 26, 27*i,j*, 30*d*, 37, 38, 39*d, e,f, h* and 45*e*) was considerably less convex, except in the early stages of ontogeny when it is more cap-like. SM X24930 (figures 43 and 45*a, b*) is unique in that the shell is rotated, through about 120°. The rest of the preserved scleritome (the anterior is absent owing to rock breakage) in this specimen is undisrupted, so this rotation suggests the posterior shell was relatively weakly attached to the rest of the body, perhaps on account of an hypothesized cavity beneath it (see §6). In shape the posterior shell is oval, with growth again effectively isometric (figure 5*a*). The umbo is well developed, and although compaction of the margin that lies immediately to its anterior makes it difficult to discern details, there is an indication that this region

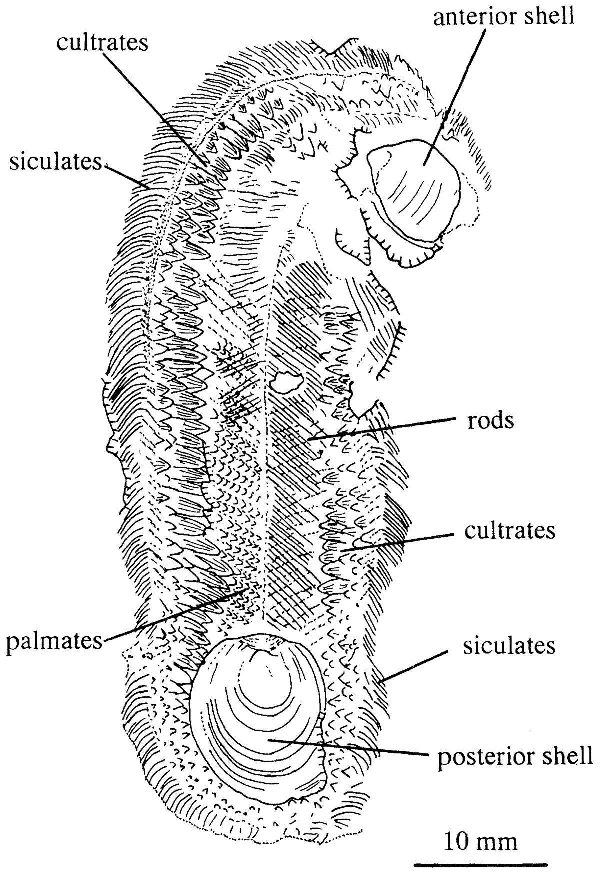

Figure 6. Interpretative drawing of MGUH 19728.

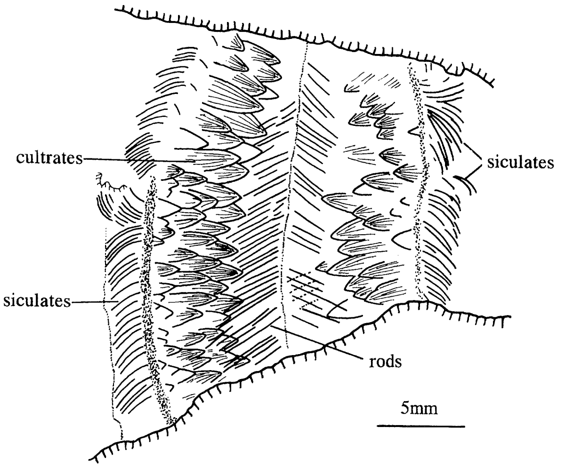

Figure 7. Interpretative drawing of MGUH 19734.

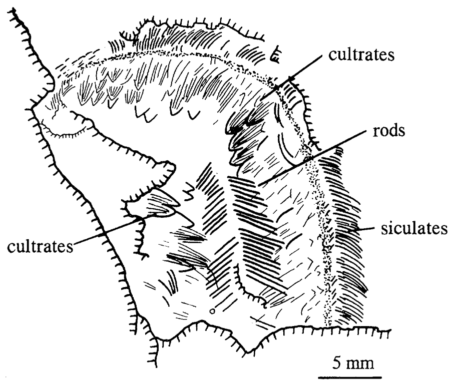

Figure 8. Interpretative drawing of SM X24901.

was not completely straight but on the midline raised as a low arch (see figures 26, 27*j*, 38 and 39*h*). As in the anterior shell, the growth lines include strongly defined increments separated by finer lines. Very few specimens (see figures 11, 12*d*, 13 and 16*a*) have both shells well enough preserved to compare the pattern of growth lines, but it appears that there is no direct correspondence between growth increments at either end of the animal, at least so far as major lines are concerned. The radial ornamentation (figures 12*c* and 42*j*) is well developed on the posterior shell. It is defined by very narrow ridges (approximately 40 per mm) that radiate from the umbo across the entire shell. Those that run to the anterior margin diverge widely either side of the midline, whereas in the opposite direction the radial ridges overlap in the median area to give a lattice-like arrangement (figure 12*c*).

Although the calcium carbonate of the shells appears to have been removed, examination of the interior of the anterior shell of SM X24920 (see figure 35*d*) via a latex peel (see §4) reveals somewhat irregular re-entrants of low relief (figure 42*e*,*f*) that are interpreted as impressions of shell ultrastructure. Similar features have been documented on phosphatic steinkerns of Cambrian molluscs and other early skeletal fossils (Runnegar 1985, 1989; Bengtson *et al.* 1990). Because of the irregularity of the putative ultrastructure in the halkieriid shell any comparison with known fabrics is tentative, but either aragonitic nacre or foliated calcite is a possibility.

(iv) *Rods*

Traversing the palmate zone in a direction at right angles to the rows of sclerites, i.e. obliquely forward, are prominent rod-like structures (see, for example, figures 6, 7, 8, 9*a*–*c*,*f*,*g*, 10, 11, 12*a*,*d*, 13, 14, 15, 16*a*, *b*,*e*,*h*, 21, 22*j*, 24, 27*e*,*f*,*h*, 30*a*,*b*,*h*, 31, 35*a*, 37, 38, 39*d*,*g*, 40, 41, 42*a*,*b*, 43 and 45*a*). They are elongate and form a prominent chevron-like array, meeting along the midline with an acute angle to the posterior. In the majority of specimens the median ends of each rod appear to lie opposite each other, but in SM X24903 they overlap slightly to give a zig-zag pattern (figure 16*g*). The rods are closely spaced

Figure 9. *Halkieria evangelista* sp. nov., Buen Formation, Sirius Passet fauna, J. P. Koch Fjord, Peary Land, Greenland. (*a*)–(*e*) MGUH 19728, holotype. (*a*) Entire specimen, anterior recurved to right, × 2.8. (*b*) Central zone with palmates, posterior to right, × 5.0. (*c*) Details of palmates, left-hand side, × 10.0. (*d*) Posterior shell, × 4.9. (*e*) Detail of left-hand side to show siculates, cultrates and abaxial palmates, × 5.0. (*f*) MGUH 19734, incomplete specimen showing mid-region of body, note bunched arrangement of siculates at front right, × 3.0. (*g*) SM X24901, mid-portion of body, anterior recurved left, × 2.7. All specimens coated with ammonium chloride sublimate.

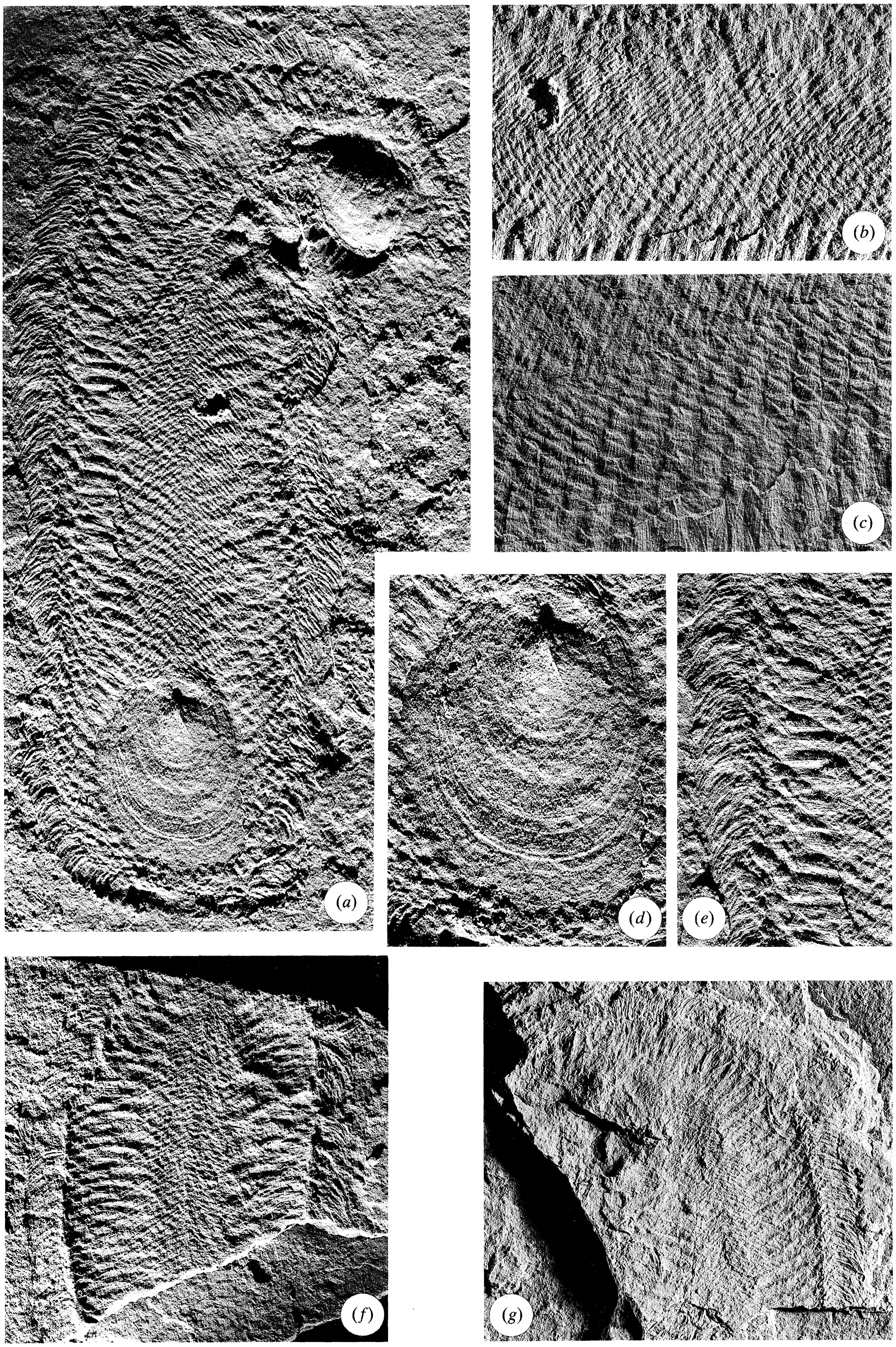

Figure 9. For description see opposite.

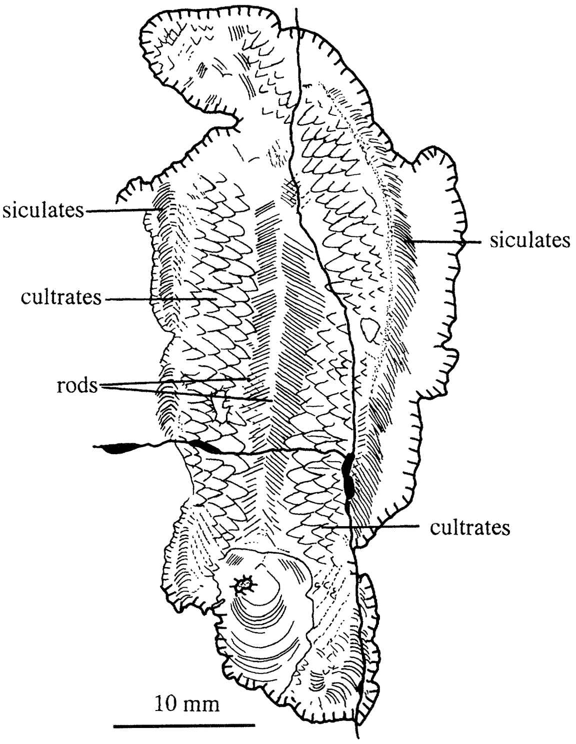

Figure 10. Interpretative drawing of MGUH 19730.

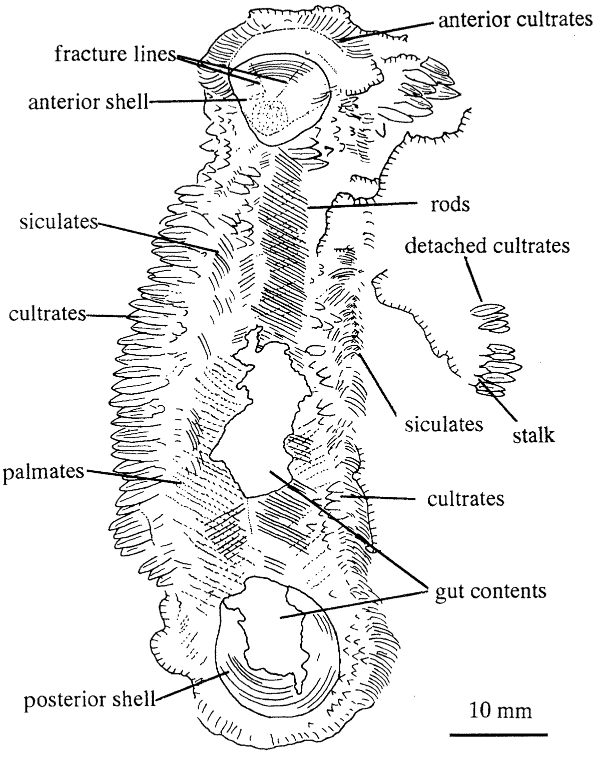

Figure 11. Interpretative drawing of MGUH 19731.

(approximately 30 per cm in MGUH X24911) and appear to have had flat upper surfaces. They evidently lay beneath the palmates and have been impressed on them by compaction. Their precise nature is not known, but presumably they were embedded in the dorsal body wall and composed of resistant material, perhaps cartilaginous. In SM X24911 (figure 27*f*) there appears to be an additional set of rods, more nearly parallel to the antero-posterior axis, underlying the adaxial region of cultrates.

(v) *Soft-tissues*

Relatively little is known about the soft-parts, with the available evidence sporadically distributed in a few specimens. The sclerites and shells entirely covered the dorsal and lateral areas, but the ventral region was evidently a soft-bodied sole, presumably comparable to the muscular foot of molluscs such as snails and chitons. This ventral sole is most apparent in SM X24910, in which the siculate sclerites border a smooth dark area through which in places can be seen faint impressions of the palmate and cultrate sclerites (see figures 23 and 27*a*, *b*). On the margins of the sole there are transverse wrinkles (figure 42*i*). These do not appear to represent impressions of underlying siculates, nor are they readily comparable to gill-like structures such as molluscan ctenidia. They may nevertheless represent a respiratory surface. Otherwise the sole is more or less featureless.

In two other specimens evidence for soft-parts is preserved in the region of the anterior valve, concave-up presumably because burial was ventral-side up. In MGUH X24917 (figures 29 and 30*g*) a narrow (150 μm) channel immediately to the anterior of this valve is interpreted tentatively as part of the foregut. Within the concavity of the valve itself there is a series of radiating strands which might represent musculature, perhaps associated with the anterior gut. Also in this region is a faint branched structure, conceivably an external palp. Impressed onto the concave interior of the anterior valve in SM X24920 (see figures 32 and 35*d*) are a series of structures. Most obvious are digitate impressions, preserved in positive relief, situated near the lateral margin of the valve (figures 32, 33, 35*e* and 42*c*, *d*). These probably represent muscle-scars. Nearer the midline and subparallel to the antero-posterior axis are a faint series of transverse bars (see figures 33 and 35*e*), also in positive relief. It seems unlikely that these bars represent part of the feeding apparatus as the structure is somewhat removed from the midline and it has a dorsal position. For a similar reason the prominent channel that runs along the midline of the anterior shell may be more likely to represent a dorsal blood sinus rather than a trace of the

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Figure 12. *Halkieria evangelista* sp. nov., Buen Formation, Sirius Passet fauna, J. P. Koch Fjord, Peary Land, Greenland (*a*)–(*c*) MGUH 19730. (*a*) Entire specimen, anterior recurved to left, × 3.0. (*b*) Posterior shell, × 5.3. (*c*) Posterior shell, detail of radial ornamentation, × 20.0. (*d*)–(*f*) MGUH 19731. (*d*) Entire specimen, gut traces in mid-region and posterior shell, and displaced group of sclerites beyond right-hand margin (arrowed), × 2.3. (*e*) Detail of cultrate sclerites in displaced mass, with preserved bases, compare to figure 42*g*, × 14.5. (*f*) Detail of anterior shell, note fracture lines induced by compression, × 4.4. (*g*) MGUH 19732, entire specimen with anterior end twisted over, × 3.8. All specimens coated with ammonium chloride sublimate, except for (*c*) which was photographed under ultraviolet radiation.

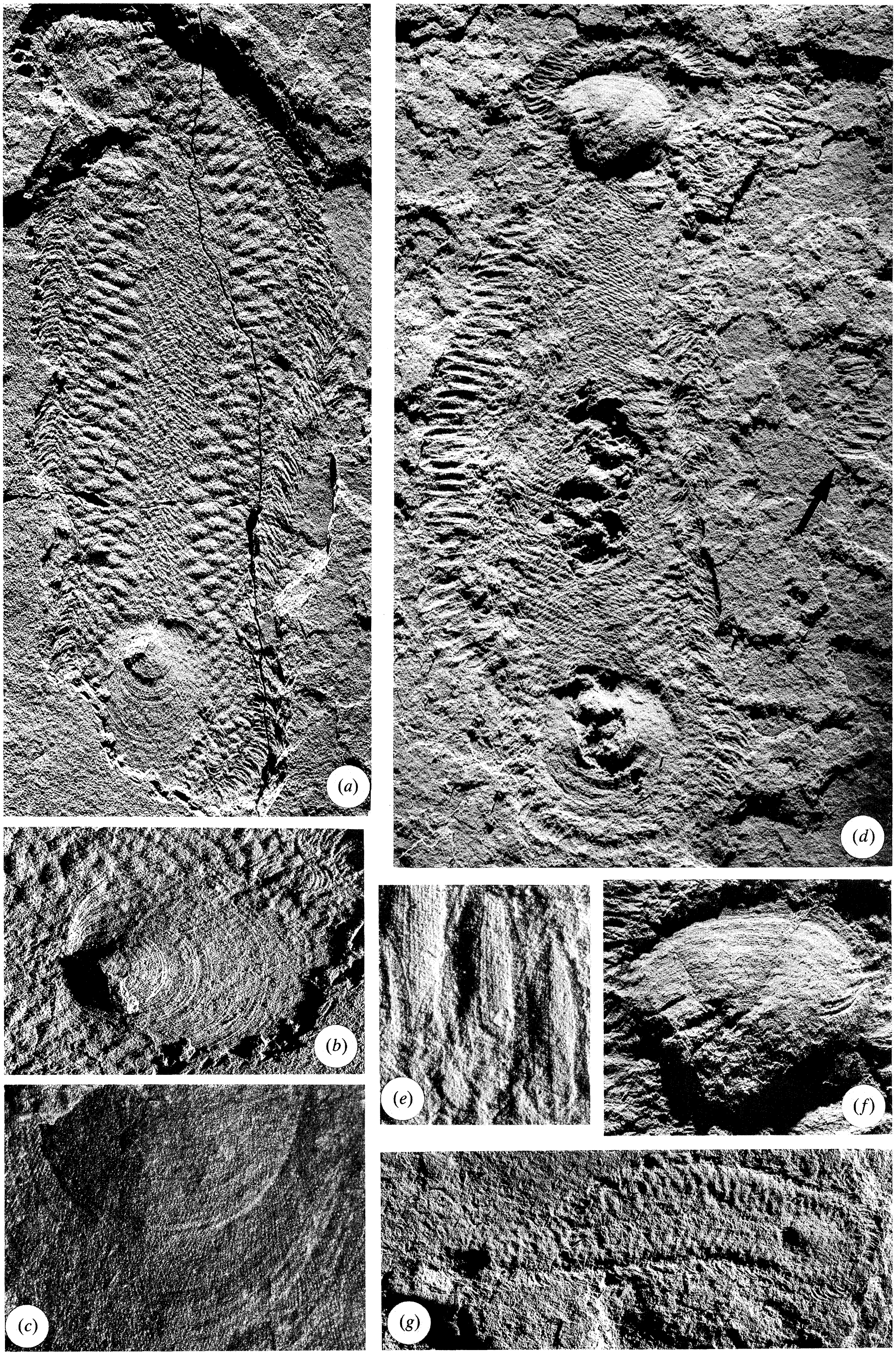

Figure 12. For description see opposite.

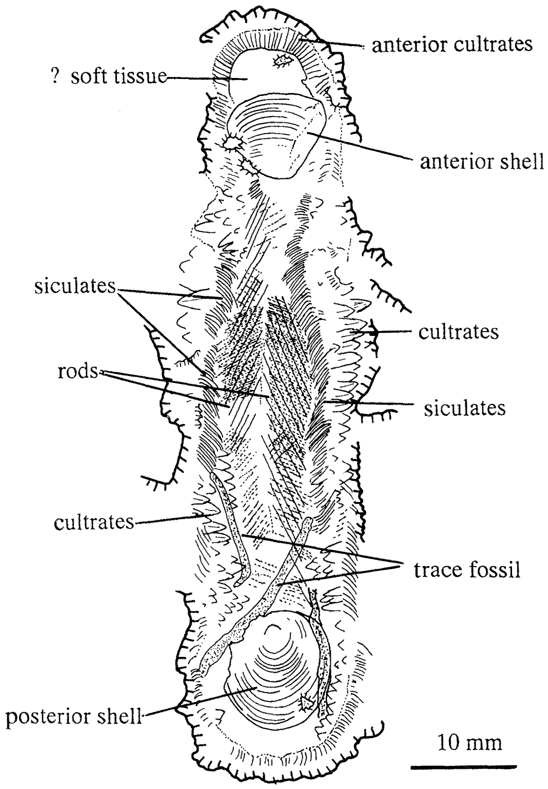

Figure 13. Interpretative drawing of MGUH 19729.

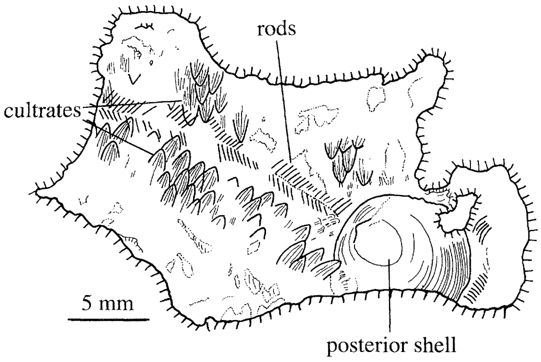

Figure 14. Interpretative drawing of SM X24902.

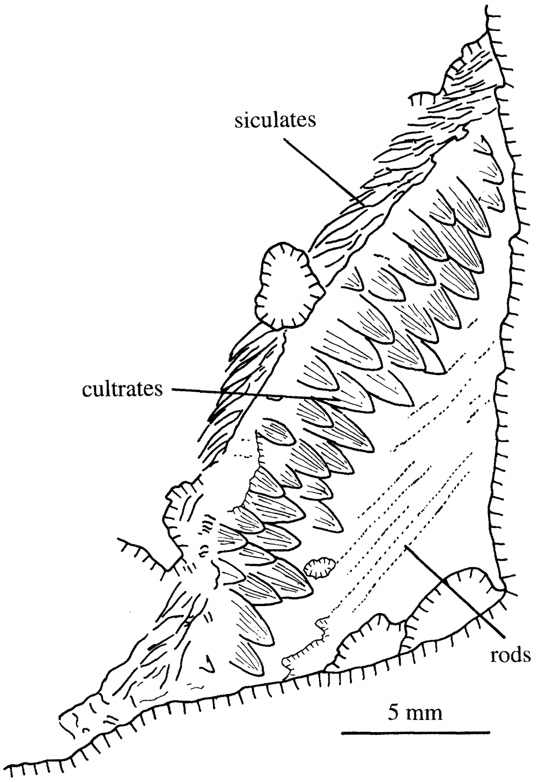

Figure 15. Interpretative drawing of SM X24904.

gut. Also present on the inner surface of this shell are a series of very faint grooves and striations, the significance of which remains uncertain. At the anterior tip of SM X24911 a narrow tube-like structure extends along the midline (figures 24 and 27*h*), partly obscured by the cultrate sclerites. As the mouth was probably sub-terminal it seems less likely that this structure was part of the foregut. Immediately posterior to the anterior valve SM X24923 is an area of longitudinal folds (figures 36 and 39*a*) that appears to be too centrally located to represent underfolded siculates. It could represent part of the gut, possibly a crop-like structure. In approximately the same region, however, SM X24926 (figure 39*g*) shows a narrow tubular structure, beneath the palmate sclerites, that appears to contain posteriorly directed denticle-like units (figures 38 and 39*g*, *i*). Details are difficult to discern, but this structure could represent a retracted and folded array of teeth used as a feeding apparatus. In a number of specimens central and posterior regions of the body contain nodule-like masses, presumably representing diagenetically altered gut contents (figures 11, 12*d*, 19 and 22*e*). Some of these nodular masses extend close to the posterior margin, suggesting the anus was subterminal. In nearly all cases the putative gut contents are unidentifiable, but in a few specimens (e.g. SM X24917) possible remains of bradoriid arthropods are identified on the basis of their prominent end-spines (see Conway Morris *et al.* 1987, figure 2*d*).

6. ECOLOGY

Halkieria evangelista (figure 46) was almost certainly benthic and it appears ill-adapted for swimming. Most probably it crawled across the seabed. Conceivably the animal burrowed, but there is little in its anatomy to

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Figure 16. *Halkieria evangelista* sp. nov., Buen Formation, Sirius Passet fauna, J. P. Koch Fjord, Peary Land, Greenland. (*a*)–(*d*) MGUH 19729. (*a*) Entire specimen, note trace fossils superimposed at posterior, × 2.0. (*b*) Mid-region of body showing palmates and siculates on either side recurved under body, × 2.4. (*c*) Posterior shell, with superimposed trace fossils, × 4.0. (*d*) Anterior shell, retracted from zone of splayed cultrates, × 6.7. (*e*) SM X24902, entire specimen showing posterior shell and adjacent region, including rods, × 3.7. (*f*)–(*g*) SM X24903. (*f*) Imbricated rows of siculate sclerites at posterior, × 6.6. (*g*) Rods along mid-line, × 14.2. (*h*) SM X24904, incomplete specimen showing left-hand side with marginal siculates and cultrates, × 4.5. All specimens coated with ammonium chloride sublimate.

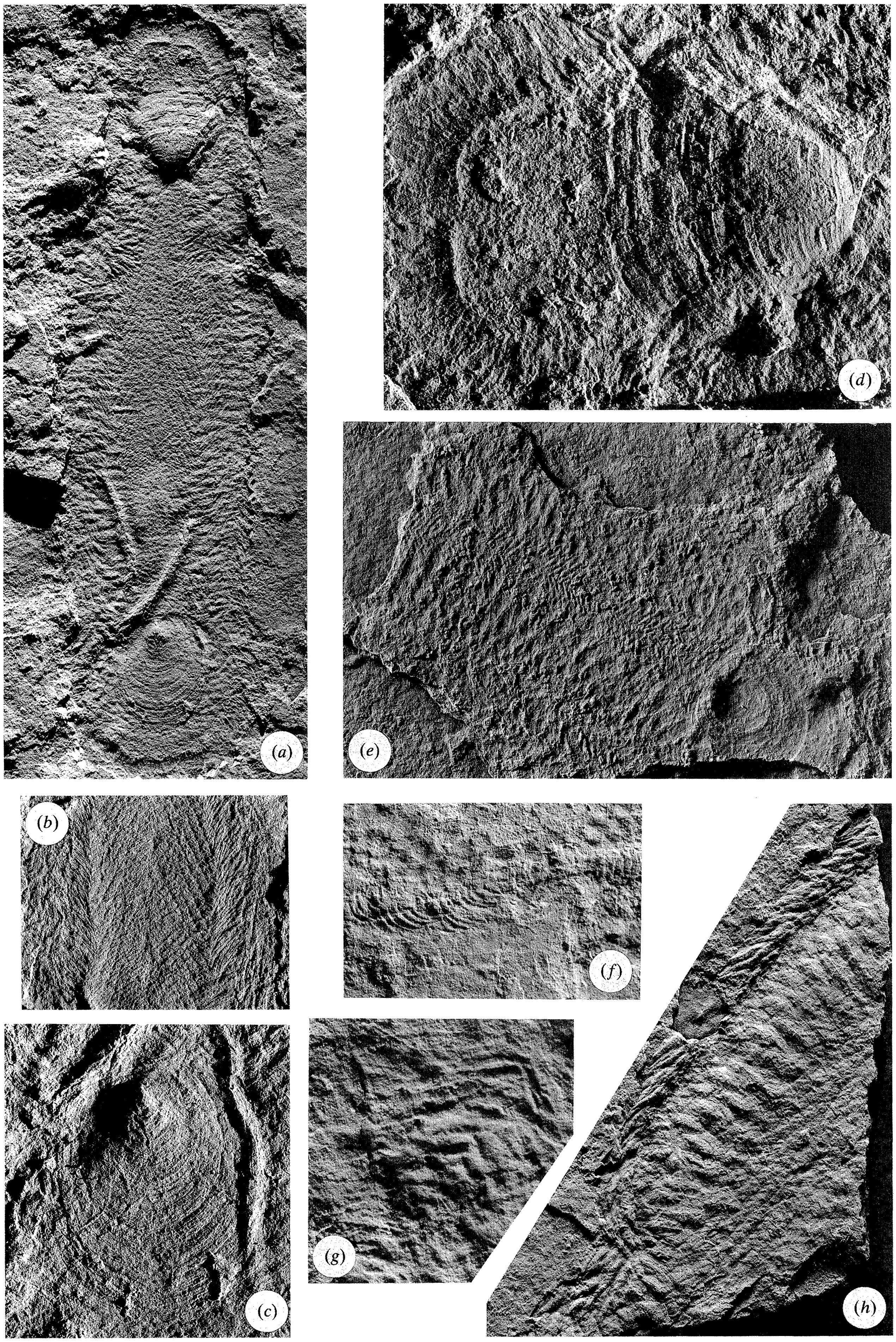

Figure 16. For description see opposite.

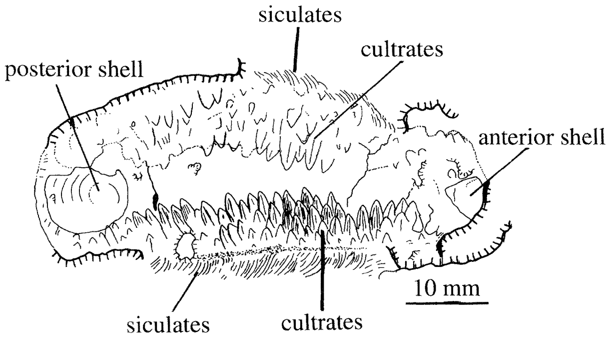

Figure 17. Interpretative drawing of MGUH 19733.

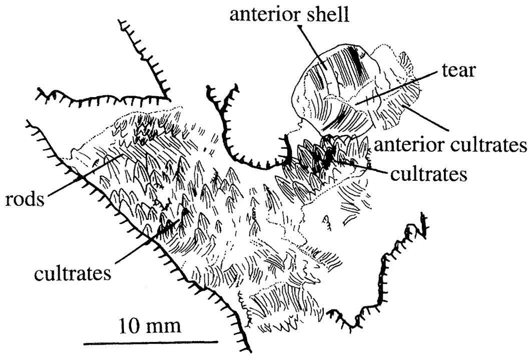

Figure 18. Interpretative drawing of SM X24905.

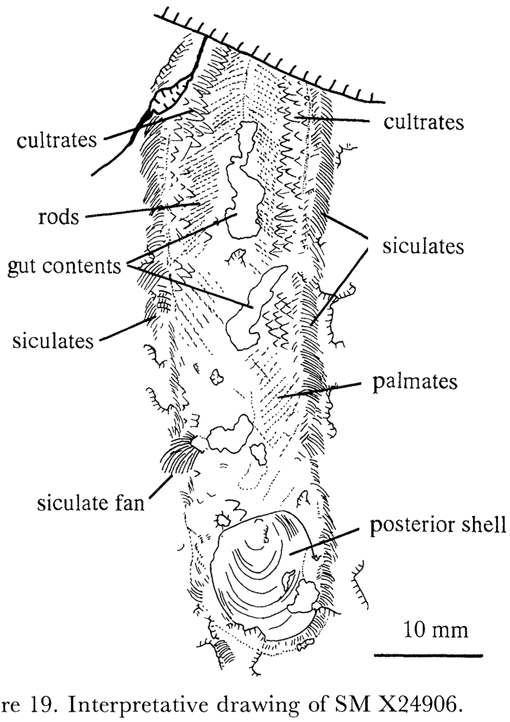

Figure 19. Interpretative drawing of SM X24906.

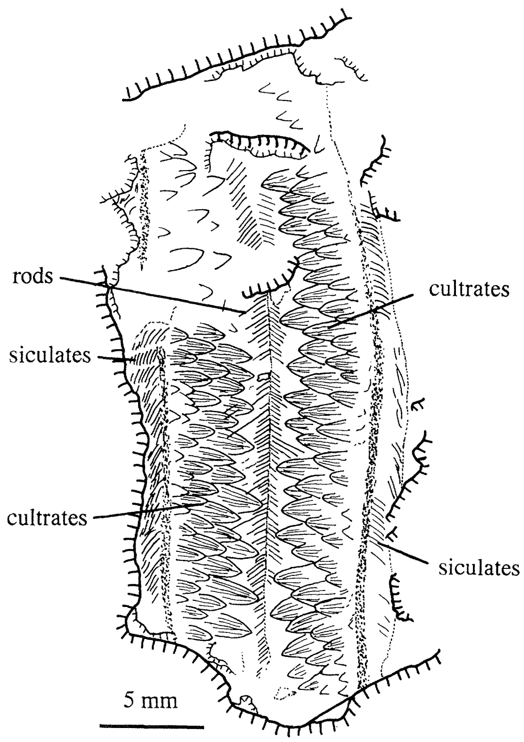

Figure 20. Interpretative drawing of SM X24907.

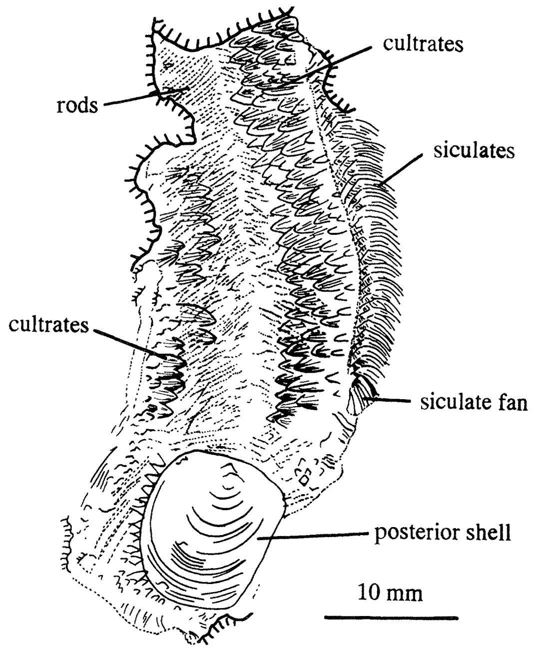

Figure 21. Interpretative drawing of SM X24908.

Figure 22. *Halkieria evangelista* sp. nov., Buen Formation, Sirius Passet fauna, J. P. Koch Fjord, Peary Land, Greenland. (*a*)–(*b*) MGUH 19733. (*a*) Entire specimen, anterior to right, × 2.5. (*b*) Detail of cultrate sclerites showing lateral canals, × 30.0. (*c*)–(*d*) SM X24905. (*c*) Entire specimen, with evidence for partial decay, × 2.0. (*d*) Detail of anterior shell, showing split, and adjacent cultrates, × 6.3. (*e*)–(*g*) SM X24906. (*e*) Entire specimen, showing mid-region and posterior, × 1.7. (*f*) Detail of bundle of siculates, attached to lobate base, × 10.0. (*g*) Posterior shell and adjacent siculate sclerites, note enigmatic circular structures impressed onto lower right of shell (arrowed), × 4.6. (*h*) SM X24907, entire specimen, mid-region of body, × 2.5. (*i*)–(*j*) SM X24908. (*i*) Entire specimen showing mid-region and posterior, × 1.7. (*j*) Detail of mid-section of body, showing siculates in fan-like bundles, cultrates and palmates, × 3.2. (*k*) SM X24909, entire specimen, showing anterior end, × 2.1. All specimens coated with ammonium chloride sublimate, except for (*b*) which was photographed under ultra-violet radiation.

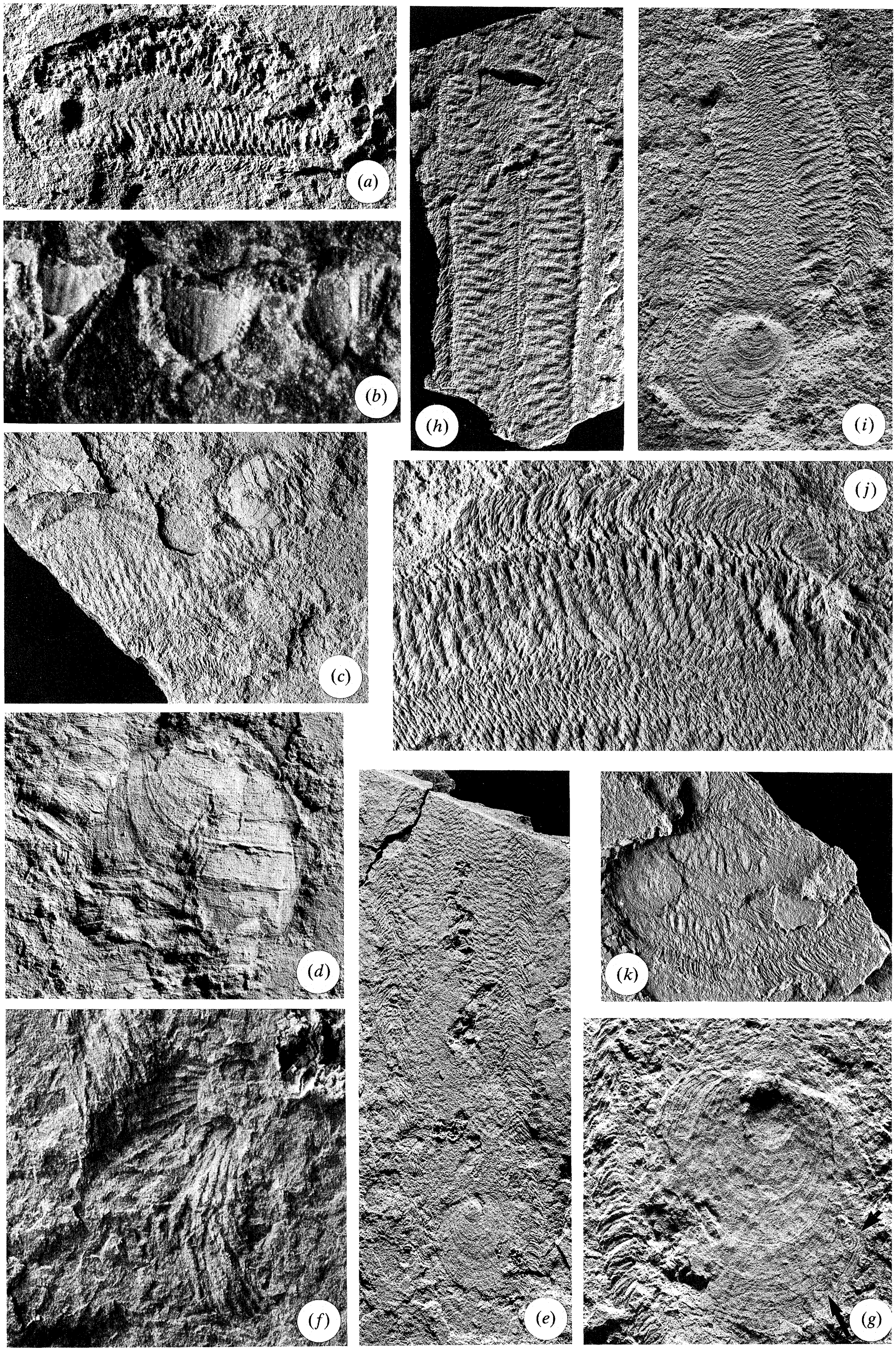

Figure 22. For description see opposite.

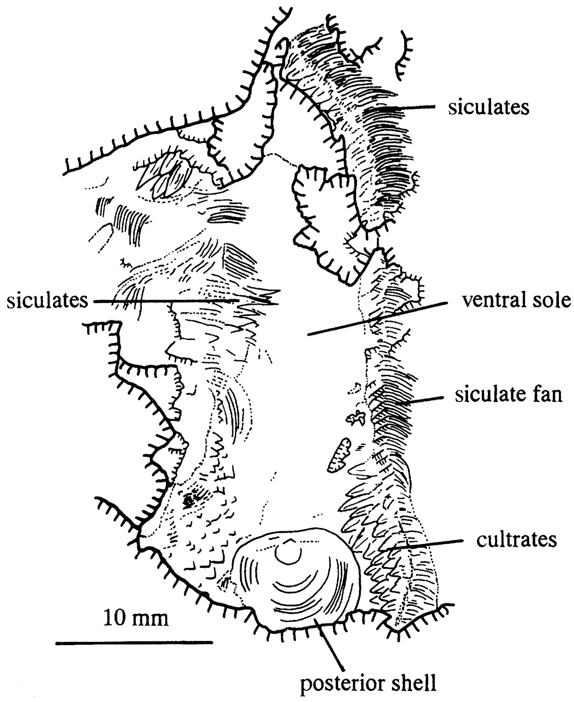

Figure 23. Interpretative drawing of SM X24910.

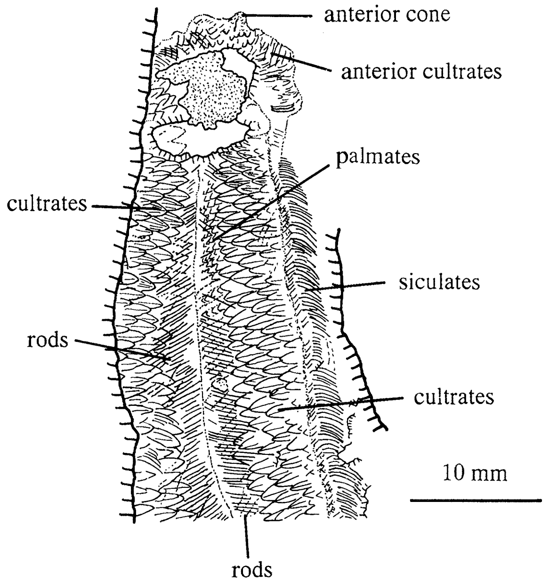

Figure 24. Interpretative drawing of SM X24911.

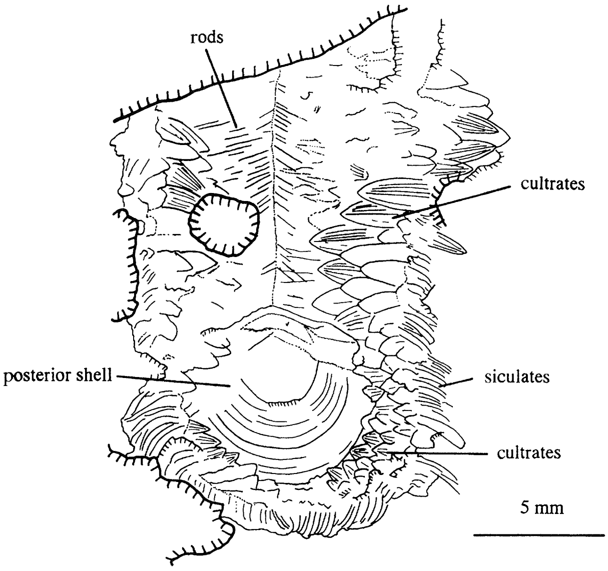

Figure 25. Interpretative drawing of SM X24912.

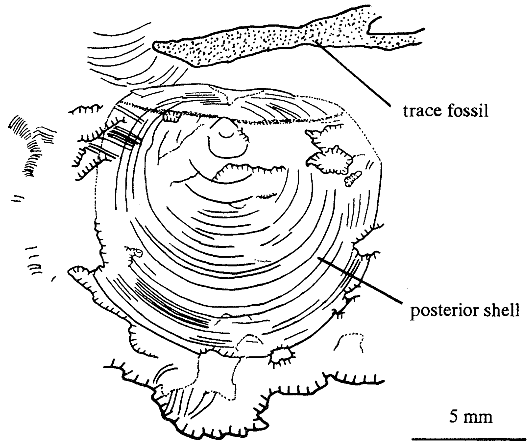

Figure 26. Interpretative drawing of SM X24913.

suggest such activity was routine. Locomotion is inferred to have been executed by locomotory waves moving along the muscular sole. There is no evidence for discrete locomotory appendages comparable, for example, to either the parapodia of polychaete annelids or other limb-like extensions that could act as levers. The backward projecting sweep of the bundles of siculates presumably acted as analogues to skis during locomotion. In addition, the imbricated arrangement of these bundles (figure 27*d*) would act as a ratchet-like anchor against slippage.

The close packing of the sclerites, especially the palmates and cultrates, presumably restricted the contractibility of the body. Nevertheless, the body was evidently capable of some shortening as may be judged from measurements of the chevron angle made by the rods which varies from approximately 50° (elongate, minimum width, see for example, figures 13 and 16*a*, *b*) to 120° (most contracted, see, for example figures 10 and 12*a*). Other evidence for flexibility comes from those specimens with underfolding of the siculates and the cultrates in splayed configuration, so indicating that the body could enrol longitudinally above the sole.

Figure 27. *Halkieria evangelista* sp. nov., Buen Formation, Sirius Passet fauna, J. P. Koch Fjord, Peary Land, Greenland. (*a*)–(*d*) SM X24910. (*a*) Entire specimen showing posterior body and ventral sole flanked by siculates, × 1.8. (*b*) Detail of siculates, left-hand side, × 3.9. (*c*) Detail of siculates, right-hand side, × 4.7. (*d*) Detail of siculates, right-hand side, showing imbricated series of bundles, × 14.5. (*e*)–(*h*) SM X24911. (*e*) Anterior of specimen, × 2.7. (*f*) Detail of cultrates and rods beneath palmates, × 11.5. (*g*) Detail of cultrates, note inclined rows of insertion, × 9.4. (*h*) Detail of anterior, × 4.4. (*i*) SM X24912, entire specimen showing posterior body, × 3.4. (*j*)–(*k*) SM X24913. (*j*) Posterior shell, × 3.4. (*k*) Detail of siculates on right-hand side, × 5.9. All specimens coated with ammonium chloride sublimate.

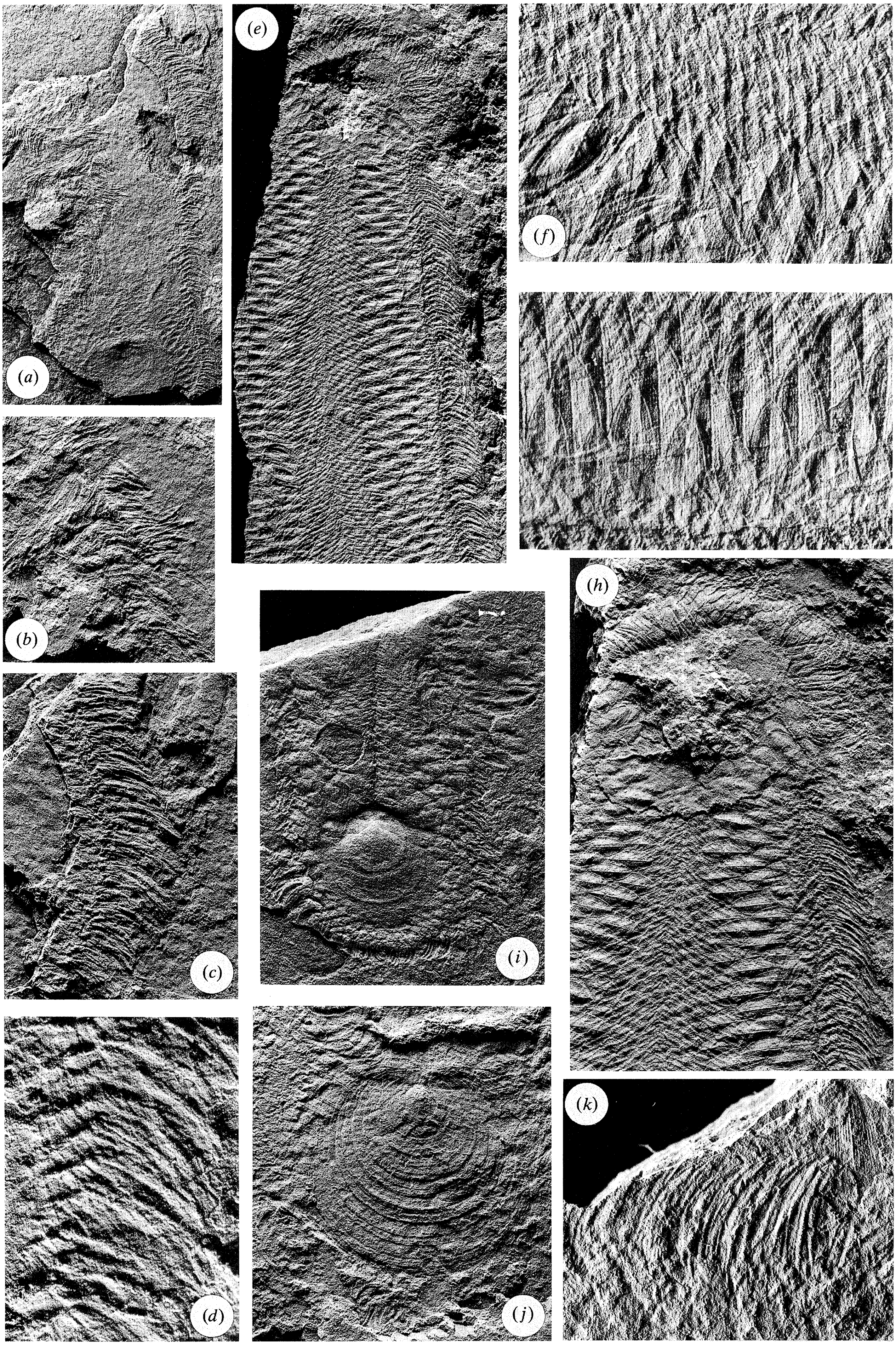

Figure 27. For description see opposite.

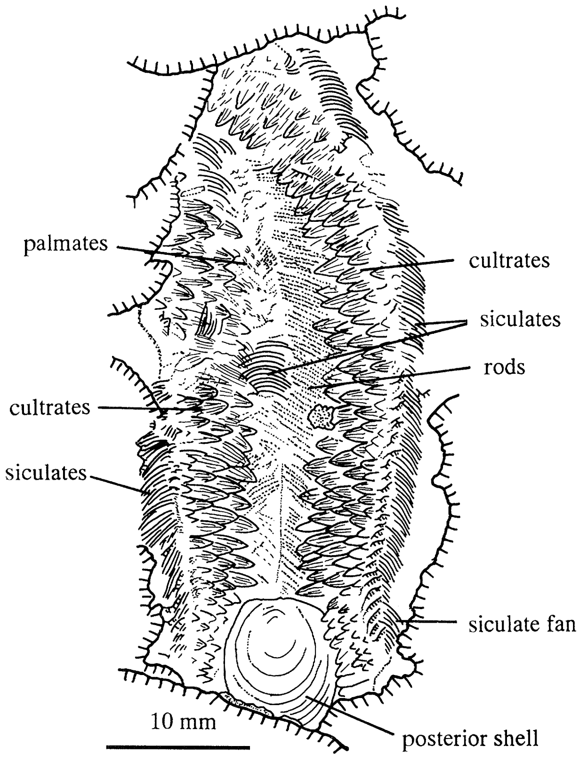

Figure 28. Interpretative drawing of SM X24914.

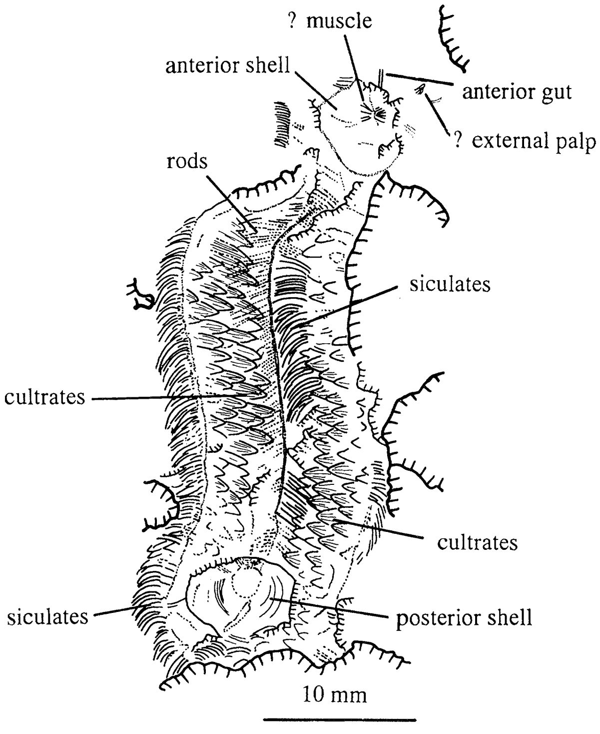

Figure 29. Interpretative drawing of SM X24917.

The outward projection of the cultrates and enclosure of the soft ventral area may have contributed to protection from predators.

The function of the shells is contentious, although there is little reason to accept Dzik's (1993, p. 366) gloomy assessment that 'It is hard to imagine any function of these two structures which could not be satisfactorily performed by the scale-like sclerites covering the rest of the body...they must have been rudimentary, nonfunctional organs.' Bengtson's (1990) proposal that they could have acted to plug the entrances of a U-shaped burrow is ingenious, and echoes earlier suggestions that the enigmatic *Mobergella* (Bengtson 1968) acted as the operculum (which may also be unfounded). It does not explain, however, why the shells have markedly different shapes when they had identical functions, and it also presupposes a high degree of longitudinal curvature in a somewhat inflexible animal. To date, none of the burrows present in the Sirius Passet fauna (see § 3) appears to correspond to the activities of the halkieriid. Nevertheless, satisfactory explanations for the function of the two shells are not easy. Given that the sclerites probably imparted effective protection, such a role for the shells is likely to have been secondary. Evidence for the insertion of various organ systems, perhaps including musculature (figures 33, 35*e* and 42*c*, *d*), onto the inner surface of the anterior shell suggests that its principal function may have been to provide a stable attachment surface for the concentration of anterior organs. The function of the posterior shell is seen as rather different, perhaps connected with respiration (Peel 1991, p. 7), and the rotation of the shell in SM X24930 (figures 43 and 45*a*, *b*) was used to argue for a looseness of attachment and the possibility of an underlying cavity. The sclerites formed a dense imbricated array over the entire surface in contact with sea-water. Although some gas exchange presumably occurred here and may have been facilitated by elevating tracts of sclerites the primary purpose of the scleritome appears to have been to provide a cataphract array to maximize protection. If rudimentary gills were housed beneath the posterior shell these could have provided the principal surface for respiratory exchange. The margin of the posterior shell in *H. evangelista*, however, appears to be entire. The overlap of the cultrates around the trailing margins of the posterior shell at first sight may appear to be one difficulty with this respiratory hypothesis but inhalant channels may have been narrow and possibly opened by elevation of the surrounding sclerites. In times of danger the sclerites could have been clamped against the shell margin to provide an effective seal.

Figure 30. *Halkieria evangelista* sp. nov., Buen Formation, Sirius Passet fauna, J. P. Koch Fjord, Peary Land, Greenland. (*a*)–(*b*) SM X24914, part and counterpart of entire specimen, × 2.6 and × 2.2 respectively. (*c*) SM X24915, entire juvenile, × 3.6. (*d*) SM X24916, juvenile specimen, posterior section, × 3.4. (*e*)–(*g*) SM X24917. (*e*) Entire specimen showing body in sinuous configuration, × 2.3. (*f*) Detail of right-hand side showing cultrates and bundles of siculates recurved beneath body, × 8.3. (*g*) Detail of anterior region showing possible soft-tissues preserved beneath anterior shell, including gut trace (top arrow) and putative musculature (bottom arrow), × 10.8. (*h*) SM X24918 entire specimen, with well preserved rods, × 2.0. All specimens coated with ammonium chloride sublimate.

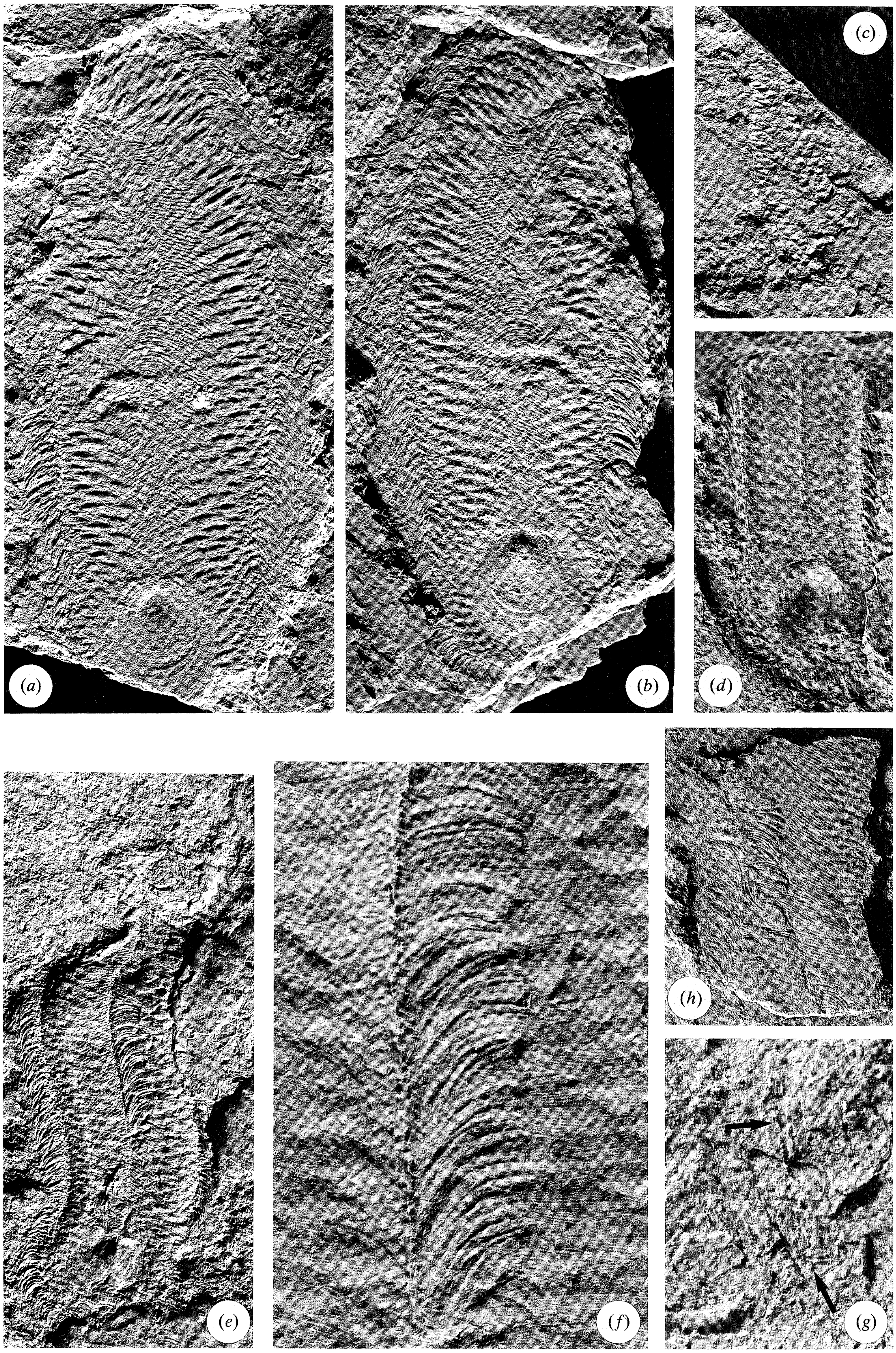

Figure 30. For description see opposite.

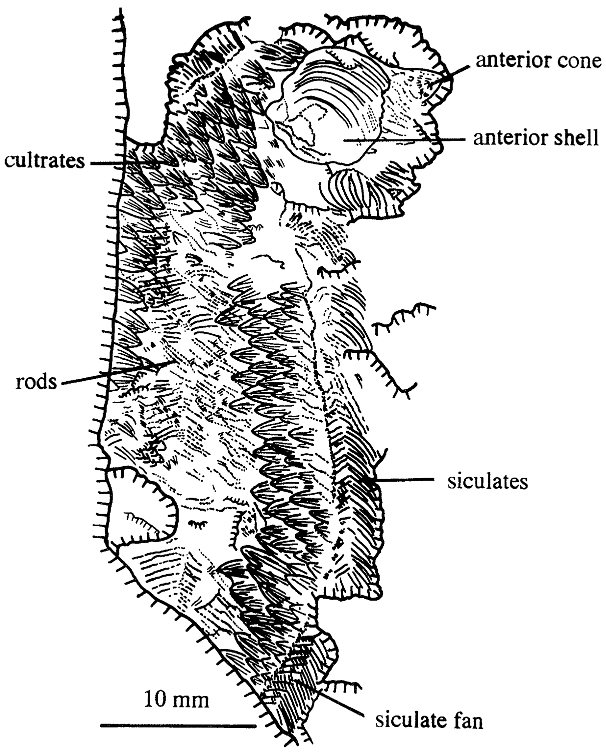

Figure 31. Interpretative drawing of SM X24919.

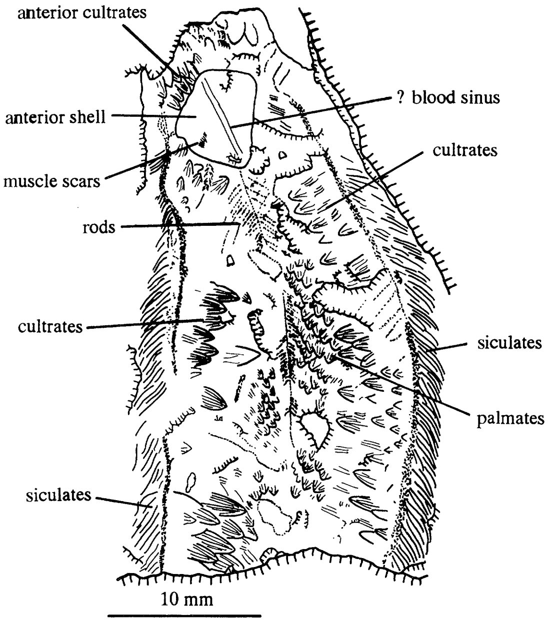

Figure 32. Interpretative drawing of SM X24920.

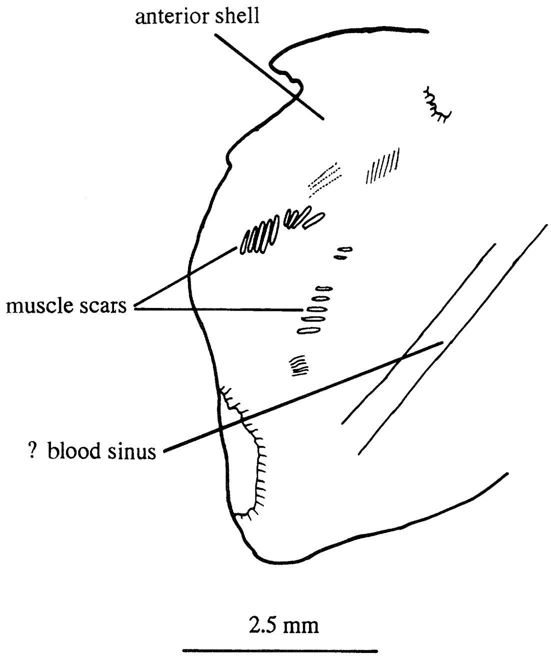

Figure 33. Interpretative drawing of SM X24920, anterior shell.

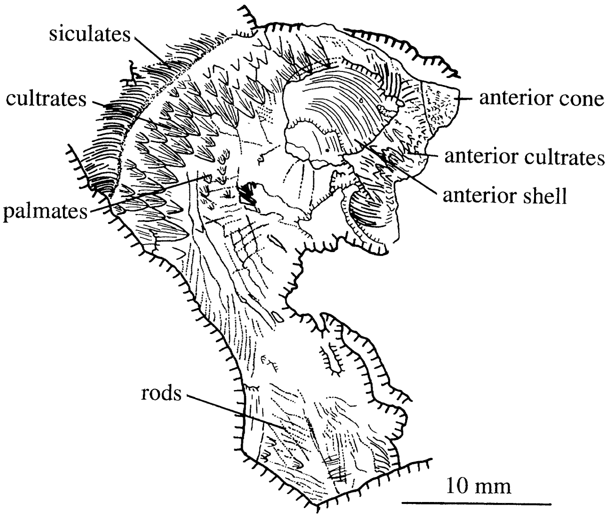

Figure 34. Interpretative drawing of SM X24921.

7. THE PHYLETIC POSITION OF HALKIERIIDS

(*a*) *Introduction*

The presence of prominent shells, an imbricated coat of sclerites, and a broad foot have been taken to indicate that the halkieriids (see figure 49) lie close to the Mollusca (Conway Morris & Peel 1990; Peel 1991; Bengtson 1992). Halkieriids are also believed to be closely related to *Wiwaxia corrugata*, best known from

Figure 35. *Halkieria evangelista* sp. nov., Buen Formation, Sirius Passet fauna, J. P. Koch Fjord, Peary Land, Greenland. (*a*)–(*c*) SM X24919. (*a*) Entire specimen showing anterior and mid-region, × 2.7. (*b*) Anterior shell, × 4.6. (*c*) Detail of right-hand side showing siculates and cultrates, × 7.0. (*d*), (*e*) SM X24920. (*d*) Entire specimen showing anterior region, × 3.3. (*e*) Detail of interior of anterior shell showing possible muscle scars (top-left arrow, compare figure 42*c*, *d*) and ?blood sinus (central arrow), × 9.0. (*f*), (*g*) SM X24921, entire specimen, showing anterior region × 3.4. (*g*) Anterior tip showing cultrates and cone-like extension (arrowed), × 8.0. All specimens coated with ammonium chloride sublimate.

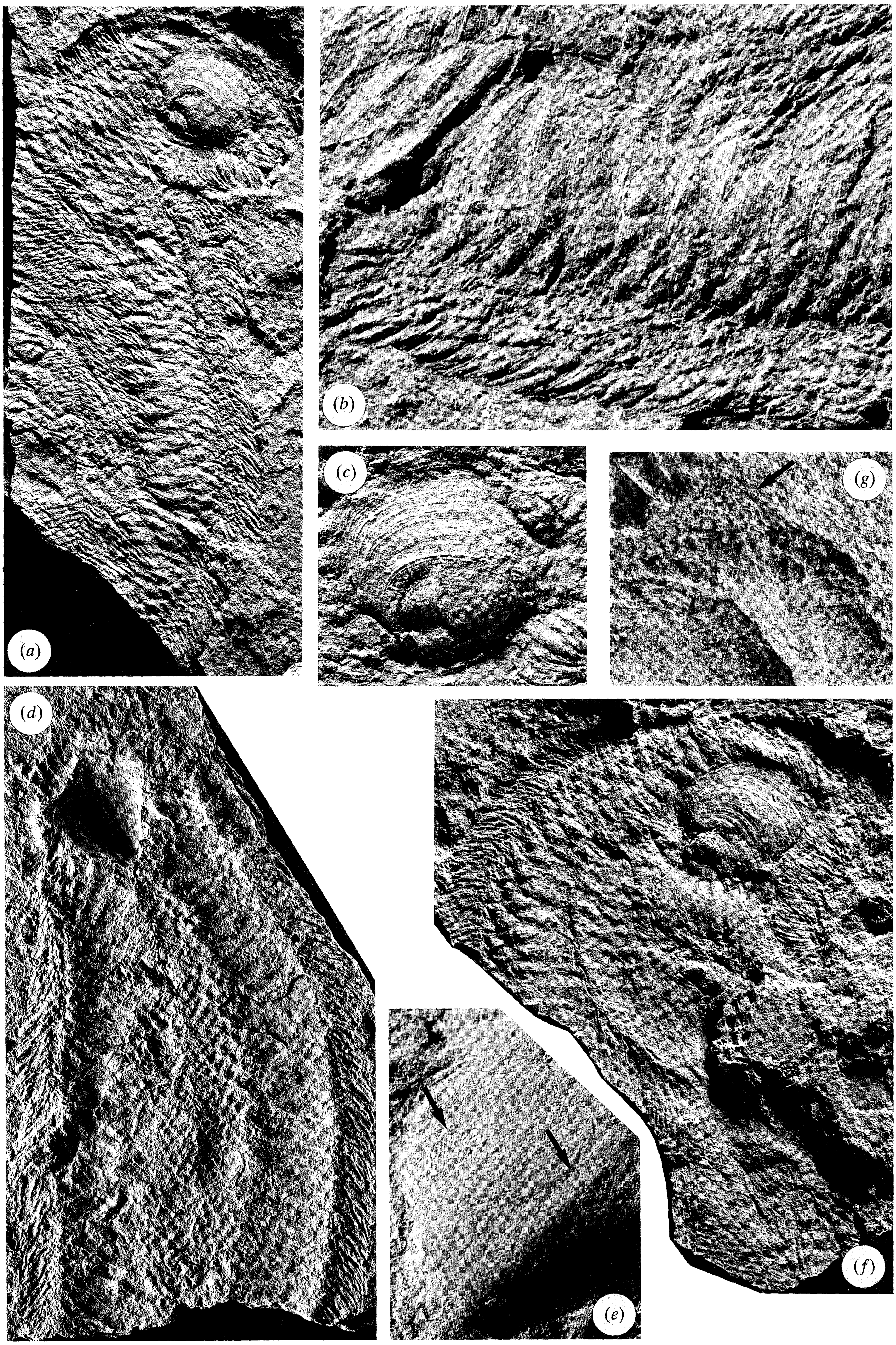

Figure 35. For description see opposite.

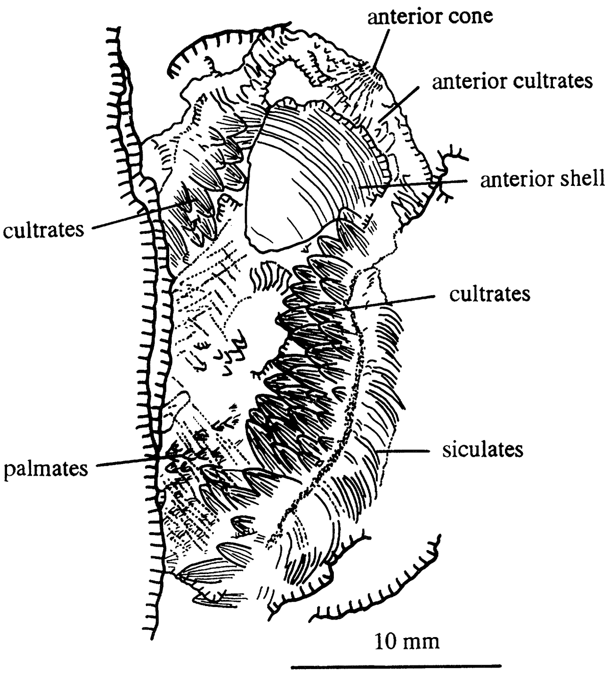

Figure 36. Interpretative drawing of SM X24922.

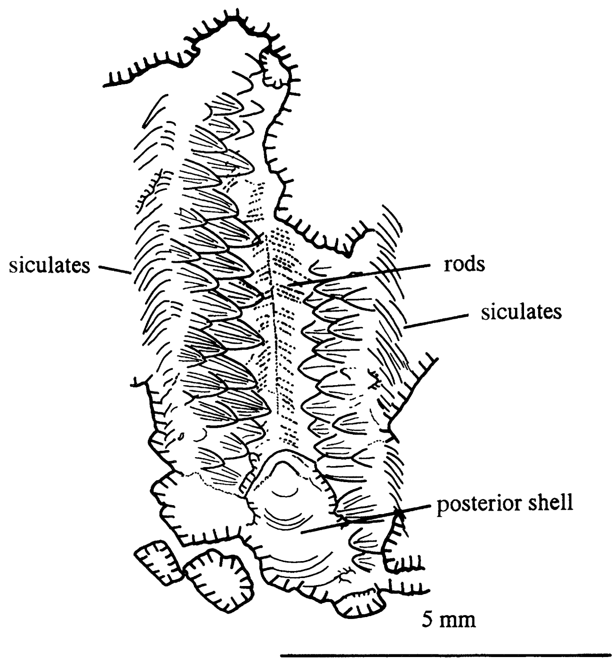

Figure 37. Interpretative drawing of SM X24923.

the Burgess Shale and interpreted by Conway Morris (1985) as most probably a relative of the molluscs. In contrast, Butterfield (1990) placed *Wiwaxia* firmly within the polychaete annelids and argued that there were significant similarities with the Burgess Shale polychaete *Canadia spinosa* (see Conway Morris 1979*a*). Nevertheless, Butterfield's (1990) proposal that *Wiwaxia* is a true polychaete remains controversial. Detailed arguments given below draw on recurrent suggestions of a relationship between the Annelida and Mollusca (see, for example, Ghiselin 1988; Eernisse *et al.* 1992) to argue that the halkieriids (and *Wiwaxia*) are relevant to understanding the origins of not only those two phyla, but also the Brachiopoda, an idea that has been largely neglected for more than a century (Morse 1873).

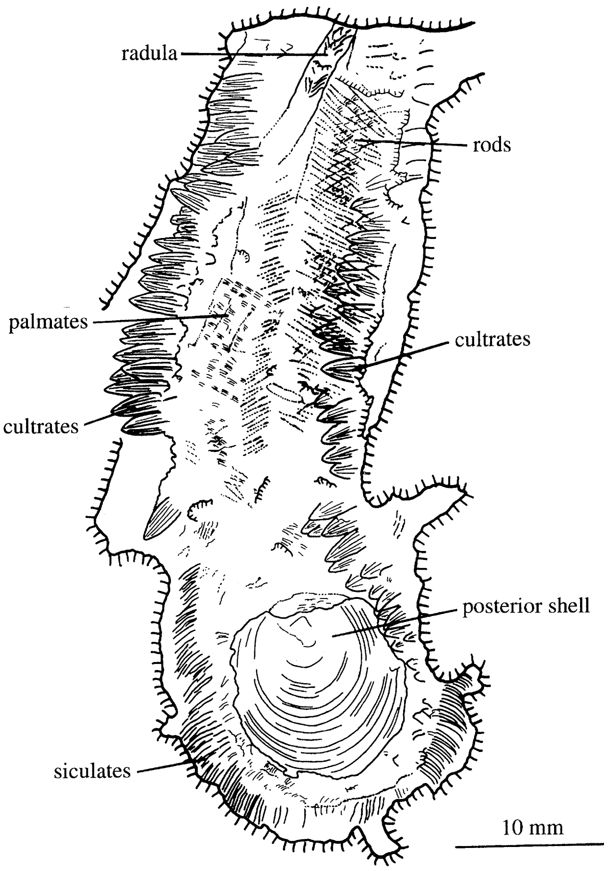

Figure 38. Interpretative drawing of SM X24926.

The detailed arguments for these proposals are presented below and the proposed tree of relationships is given in figure 50. Some aspects of our discussion may remain controversial, but three particular aspects deserve emphasis. First, our results are broadly congruent with newly-obtained data from molecular biology (Lake 1990; Adoutte & Philippe 1993; see also Wägele & Wetzel 1994). Second, our proposals throw new light on hitherto puzzling similarities, such as the identical structure of annelid chaetae and the setae of brachiopods (Orrhage 1973). Inevitably, one must also infer that other features, presently believed to be of

Figure 39. *Halkieria evangelista* sp. nov., Buen Formation, Sirius Passet fauna, J. P. Koch Fjord, Peary Land, Greenland. (*a*)–(*c*) SM X24922. (*a*) Entire specimen showing anterior, × 2.9. (*b*) Details of siculate and cultrate sclerites on right hand side, × 7.5. (*c*) Anterior shell, × 7.4. (*d*) SM X24923, entire juvenile specimen showing posterior, × 8.5. (*e*) SM X24924, posterior shell and surrounding siculate sclerites, × 5.3. (*f*) SM X24925, entire specimen showing posterior, × 2.0. (*g*)–(*j*) SM X24926. (*g*) Entire specimen showing mid-region and posterior, × 1.7. (*h*) Posterior shell surrounded by siculates, × 3.7. (*i*) Possible radula in anterior section (arrowed), × 12.9. (*j*) Cultrate sclerites from left-hand, note possible stalk (arrowed), × 8.0. All specimens coated with ammonium chloride sublimate.

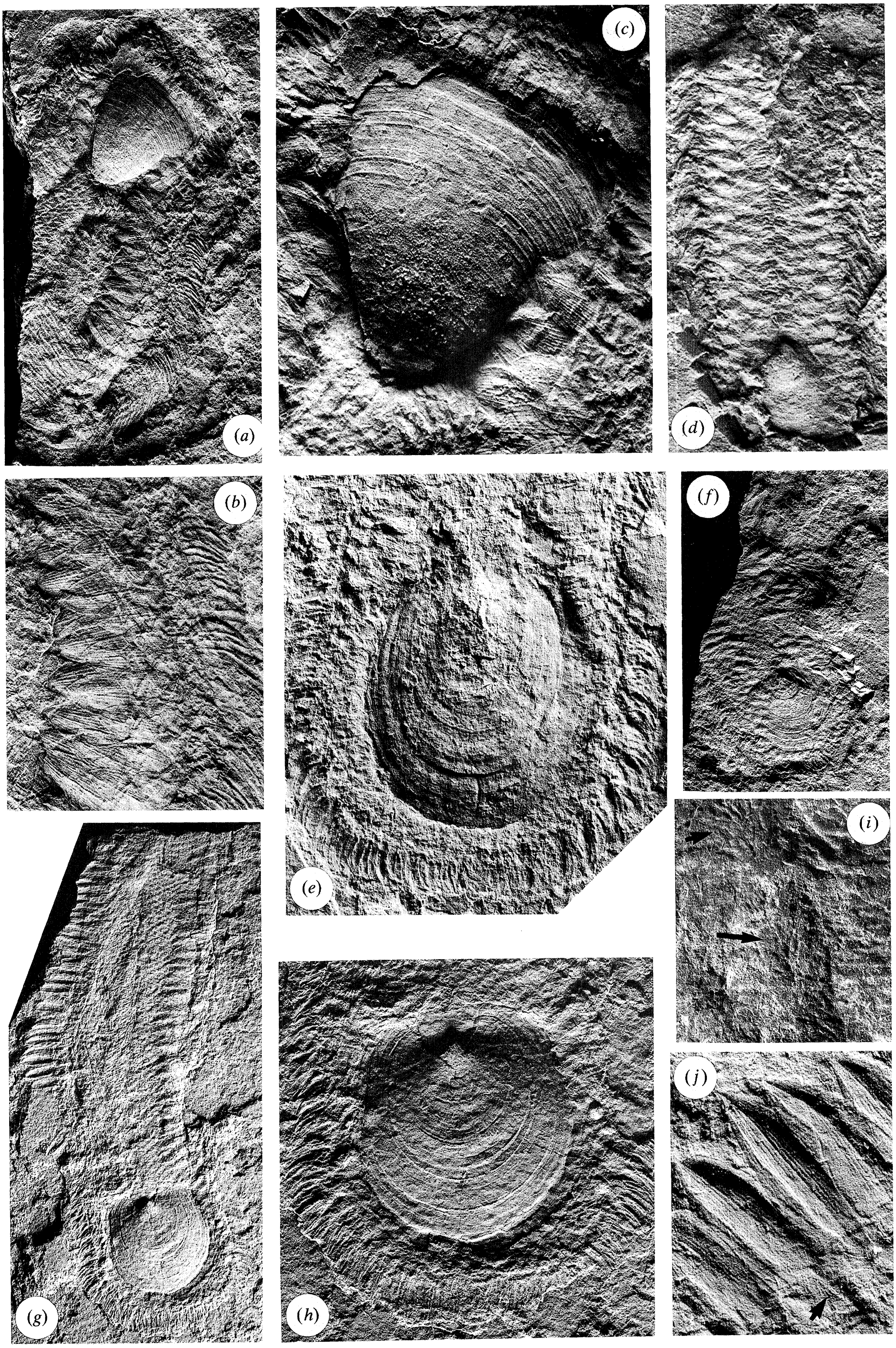

Figure 39. For description see opposite.

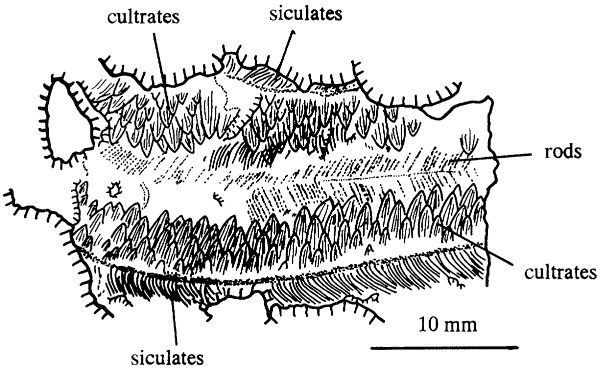

Figure 40. Interpretative drawing of SM X24927.

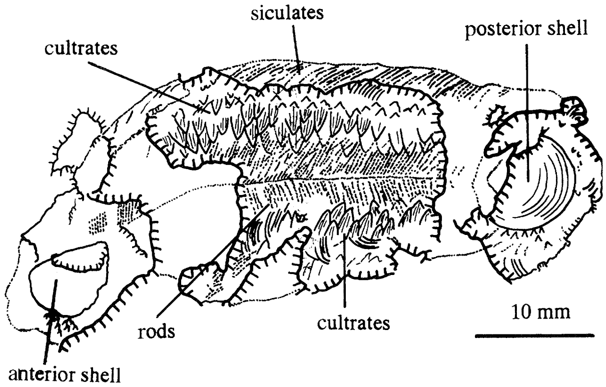

Figure 41. Interpretative drawing of SM X24928.

phylogenetic significance, such as the similarity between the lophophores of brachiopods and pterobranch hemichordates (see Halanych 1993) are actually convergent. The literature we cite is, therefore, selective and it is not our purpose to present an exhaustive review of early discussions of protostome phylogeny. Third, the arguments here are crucially based on data from two extinct taxa (*Halkieria evangelista* and *Wiwaxia corrugata*) in conjunction with the crown groups of annelids, brachiopods and molluscs. Much of what is inferred in the various stem lineages (see figure 50) will be testable as and when new articulated material emerges.

(*b*) *Are halkieriids related to* Wiwaxia?

These groups appear to be related (Conway Morris & Peel 1990), but with *Wiwaxia* (figure 47*e*) the more derived and closer to the polychaetes (figure 50). The distribution of sclerites into the palmate, cultrate and siculate zones of halkieriids finds an apparent equivalence in *Wiwaxia*. Using the terminology of Conway Morris (1985*a*) the corresponding zones in *Wiwaxia* are dorsal (= palmate), upper lateral (= cultrate) and ventro-lateral (= siculate). Many other metazoans are spicule-bearing and include platyhelminthes, nemerteans, gastropods (acochlidiaceans, rhodopids), aplacophorans and polyplacophorans (see, for example, Rieger & Sterrer 1975), but in none of these is the spicule distribution comparable to the distinctive and equivalent zones in the halkieriids and *Wiwaxia*. The palmate and cultrate sclerites of *Wiwaxia* have prominent longitudinal ribs (Conway Morris 1985*a*), and by careful palynological extraction of isolated sclerites Butterfield (1990) was able also to recognize knobs and denticles running longitudinally (see also Mankiewicz 1992, figure 9.6). Closely similar ribs and denticles are widespread on halkieriid sclerites (e.g. Jell 1981, figure 5*a*–*c*; Bengtson *et al.* 1990, figure 50J), although the latter may have a variety of other ornamentations that are comparable to various sachitids, especially *Hippopharangites dailyi*.

Nevertheless halkieriids and *Wiwaxia* are by no means identical. Some differences are believed to be relatively trivial. The Sirius Passet halkieriid is elongate and bears multiple transverse rows of sclerites, the possibly segmental nature of which is discussed below. In contrast *Wiwaxia* (figure 47*e*) has many fewer segments; in the adult there are about eight transverse rows of palmates as compared to an approximate total of 40–50 in the halkieriid (see figure 49). Despite the close equivalence of sclerite zones, a seemingly notable difference between the Sirius Passet halkieriid and *Wiwaxia* (cf. figures 9*a* and 47*e*) is the absence in the former animal of the elongate dorso-lateral spines and perhaps also the equivalents to the lower lateral sclerites. The spines, however, are presumably modified cultrate sclerites and their generation would involve a minor developmental shift towards elongation. Support for this notion comes from their irregular insertion along either side of *Wiwaxia*, consistent only with the spines forming an effective defensive array. In any event, there is no evidence from the Burgess Shale fossils for the spines arising in a regular segmental manner, such as depicted by Dzik ((1986) figure 12A; Dzik (1993) figure 11b) and inferred by Butterfield (1990, p. 301).

More significant differences between halkieriids and *Wiwaxia* include the presence of shells and mineralized sclerites in the former animals. A specific search for shells in *Wiwaxia*, including semi-articulated specimens where the sclerites are dispersed (see Conway Morris 1985*a*), failed to reveal any associated shell, with one possible exception. USNM 199936 (figures 46 and 47*a*, *b*) is a small semi-articulated specimen consisting of

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Figure 42. *Halkieria evangelista* sp. nov., Buen Formation, Sirius Passet fauna, J. P. Koch Fjord, Peary Land, Greenland. (*a*) SM X24927, entire specimen, × 2.2. (*b*) SM X24928, entire specimen, × 1.8. (*c*)–(*f*) SM X24920 interior of anterior valve. (*c*) Possible muscle scars (arrowed), × 30. (*d*) Detail of left-hand set in (*c*), × 60. (*e*), (*f*) Possible impressions of shell ultrastructure, × 240 and × 400 respectively. (*g*), (*h*) SM X24926, cultrate sclerites. (*g*) Cultrates with possible attachment stalks, × 17. (*h*) Detail of longitudinal ribs, × 80. (*i*) SM X24910, ventral surface with linear array of folds along margin, × 23. (*j*) MGUH 19728, posterior shell, detail of radial ornamentation, × 43. (*a*) and (*b*) are coated with ammonium chloride sublimate, and (*c*)–(*j*) are scanning electron micrographs of gold-coated latex pulls.

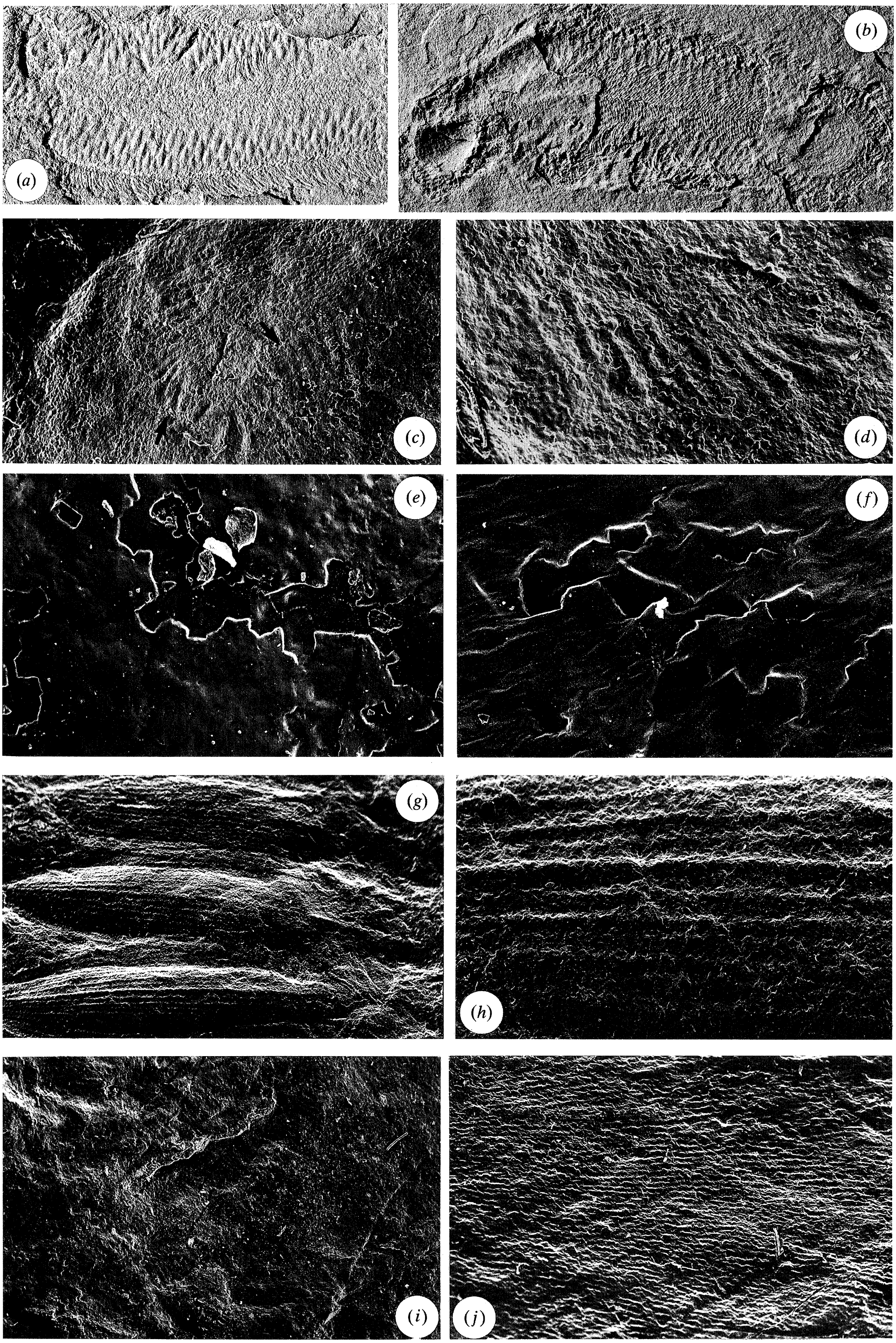

Figure 42. For description see opposite.

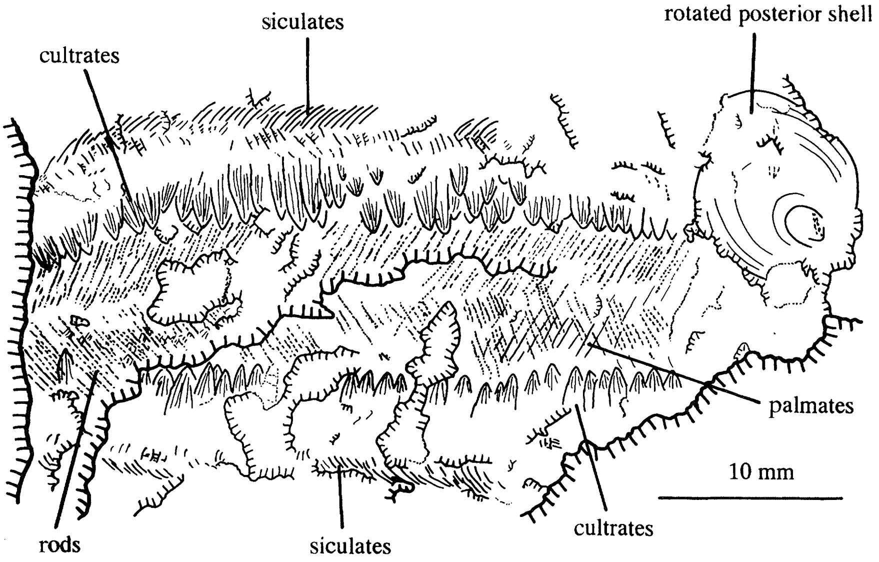

Figure 43. Interpretative drawing of SM X24930.

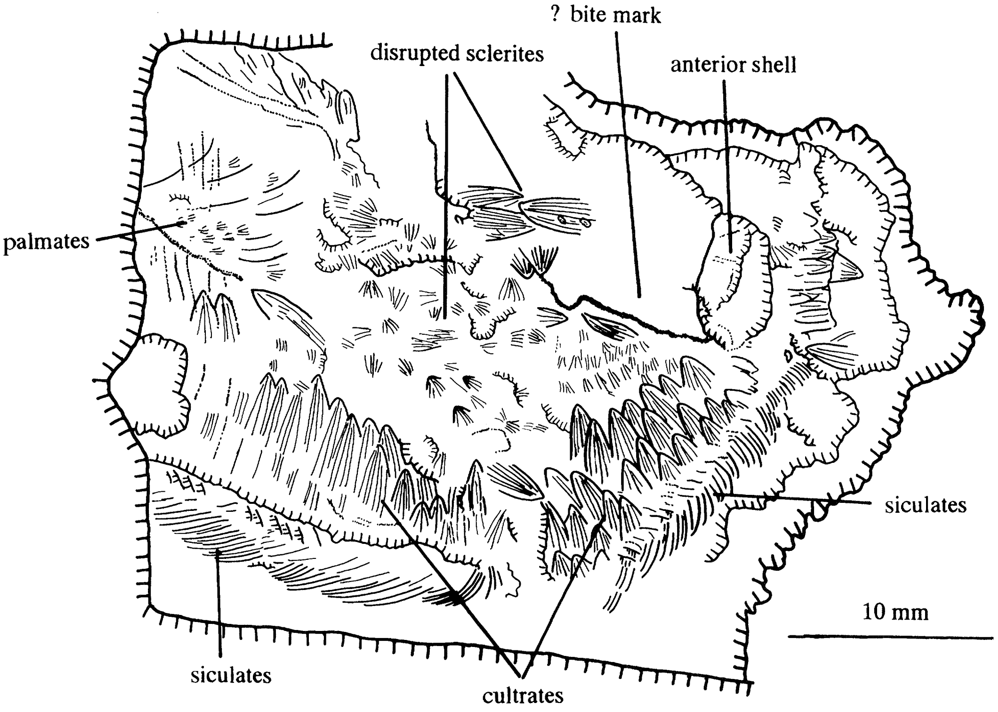

Figure 44. Interpretative drawing of SM X24931.

several sclerites (principally palmates (= dorsal of Conway Morris 1985*a*)) and a small (approximately 2.5 mm) convex structure, vaguely reminiscent of a brachiopod, with relatively prominent concentric ornamentation (figure 47*c*, *d*). Brachiopods from the Burgess Shale are in need of revision (Conway Morris 1979*b* gives a review of available work; see also Jin *et al.* 1993), but the shell-like structure in close association with the sclerites of *Wiwaxia* appears not to be a brachiopod. It is tentatively interpreted as a vestigial shell.

The sclerites of *Wiwaxia* (figure 47*a*, *b*, *e–h*) were unmineralized (Conway Morris 1985*a*), whereas halkieriids had a relatively thick calcareous wall that originally was probably aragonitic (Bengtson & Conway Morris 1984). The nature of the soft-tissue within the halkieriid sclerites is speculative, other than it presumably included secretory cells and occupied internal canals of varying complexity (see Bengtson *et al.* 1990). Butterfield (1990) emphasized these differences, especially the hollow nature of halkieriid sclerites versus what he identified in the Burgess Shale as flat and solid wiwaxiid sclerites in unequivocal terms: 'the blades are decidedly *not* hollow…the structure does *not* define or include an open internal space' (Butterfield (1990) p. 288, his emphases). He concluded, therefore, that the overall similarity between the respective sclerites was a result of convergence. More recently, Butterfield (1994) has described new examples of isolated *Wiwaxia* sclerites from the Mount Cap Formation in the Lower Cambrian (see figure 45). Although not discussed in the text, Dr

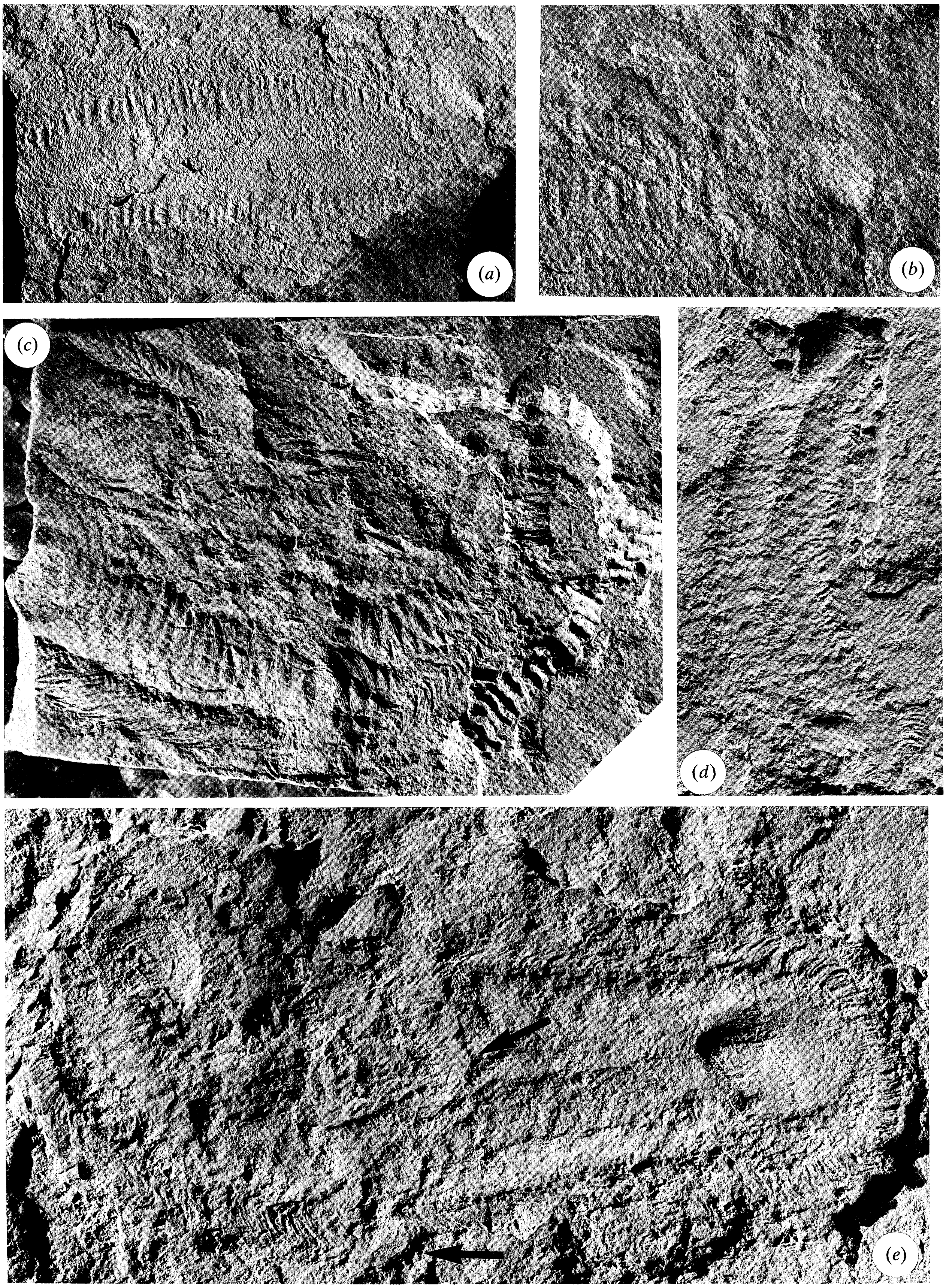

Figure 45. *Halkieria evangelista* sp. nov., Buen Formation, Sirius Passet fauna, J. P. Koch Fjord, Peary Land, Greenland. (*a*)–(*b*) SM X24930. (*a*) Entire specimen showing mid-section and posterior of body, with posterior shell rotated forwards by about 120°, ×2.1. (*b*) Detail of rotated posterior shell, ×3.6. (*c*) SM X24931, anterior of specimen showing possible evidence for predation, ×2.6. (*d*) SM X24932, entire juvenile specimen, ×5.9. (*e*) SM X24933, entire specimen, apparently superimposed on second halkieriid (arrowed), ×5.8.

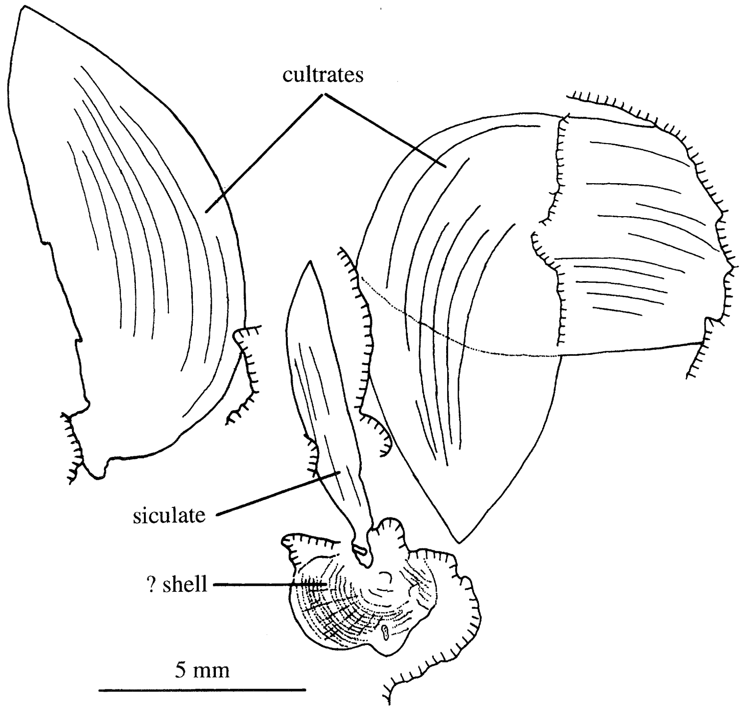

Figure 46. Interpretative drawing of USNM 199936.

Butterfield tells us that these sclerites are unequivocally hollow. Moreover, careful focusing on some of the Burgess Shale sclerites suggests that where the ribbing consists of fine and thick varieties (cf. figures 47*f*–*h*) these ribs appear to occur at two levels, perhaps representing the upper and lower walls of the sclerite. A transition, therefore, between the sclerites of halkieriids and *Wiwaxia* may be envisaged by loss of calcareous walls leaving a mass of tissue bounded by cuticle. As discussed below this need not negate the derivation of polychaete chaetae from the sclerites of a *Wiwaxia*-like animal.

Halkieriids are widespread in Tommotian and Atdabanian strata and the postulated age of the Sirius Passet fauna (figure 48) is close to the last reliable reports of disarticulated sclerites from acid resistant residues. Post-Atdabanian strata have received relatively little investigation for such fossils, but recent studies (see, for example, Müller & Hinz 1992; Brock & Cooper 1993) have revealed rich assemblages of small shelly fossils but no halkieriids. The first record of *Wiwaxia*, which we postulate is descended from a halkieriid (§ 7 *b*), is not known until higher in the Lower Cambrian (Butterfield 1994), but the fossilization potential for wiwaxiid sclerites may have been considerably lower than for equivalent mineralized halkieriids. To date only two occurrences of *Wiwaxia* sclerites (both isolated) are known between the Mount Cap first appearance and the articulated material in the Burgess Shale: the Kaili Formation (Zhao *et al.* 1994) and Spence Shale (Conway Morris & Robison 1988). The present stratigraphic gap between the last known halkieriids and first *Wiwaxia* (figure 47) may be an artefact of sampling.

Using *Wiwaxia* as a guide and having to hand a well-preserved Tommotian assemblage of disarticulated sclerites Bengtson and Conway Morris (1984) reconstructed the likely appearance of an entire halkieriid, unaware of the prominent shells since identified in the Sirius Passet specimens. A scleritome-based approach to reconstructing halkieriids only known from disarticulated sclerites and shells is still in its infancy. There is little doubt, however, that the Sirius Passet specimens can provide only an approximate guide to the group as a whole. A number of assemblages of disarticulated sclerites seem to lack siculate sclerites (Bengtson & Conway Morris 1984) and/or have two discrete types of palmate sclerite (S. Conway Morris & B. Xiao, unpublished data). In addition, there is some evidence that there is variation in the type of shells carried. It is also possible that some halkieriids either lacked shells (as may also be the case in *Wiwaxia*) or possessed shells but were otherwise aspiculate (Conway Morris 1995).

(*c*) ***Halkieriids and molluscs***

(i) *Introduction*

The proposed relationship between halkieriids and

Figure 47. (*a*)–(*h*) *Wiwaxia corrugata* (Matthew), Stephen Formation (Burgess Shale,), Walcott Quarry, near Field, British Columbia, Canada. (*a*)–(*d*) USNM 199936. (*a*)–(*b*) Partially articulated specimen showing possible vestigial shell (arrows) in high and low angle ultra-violet radiation, × 4.6 and × 3.6, respectively. (*c*)–(*d*) Detail of shell, × 15.3. (*e*) USNM 57635, entire specimen in dorsal aspect, × 2.1. (*f*) MCZ 9501-15, × 19. (*g*) MCZ 9501-14, × 19. (*h*) MCZ 101680, × 19. (*i*) *Canadia spinosa* Walcott, USNM 83929c, detail of ctenidial-like respiratory appendage (arrowed) and adjacent neurochaetae, × 8.

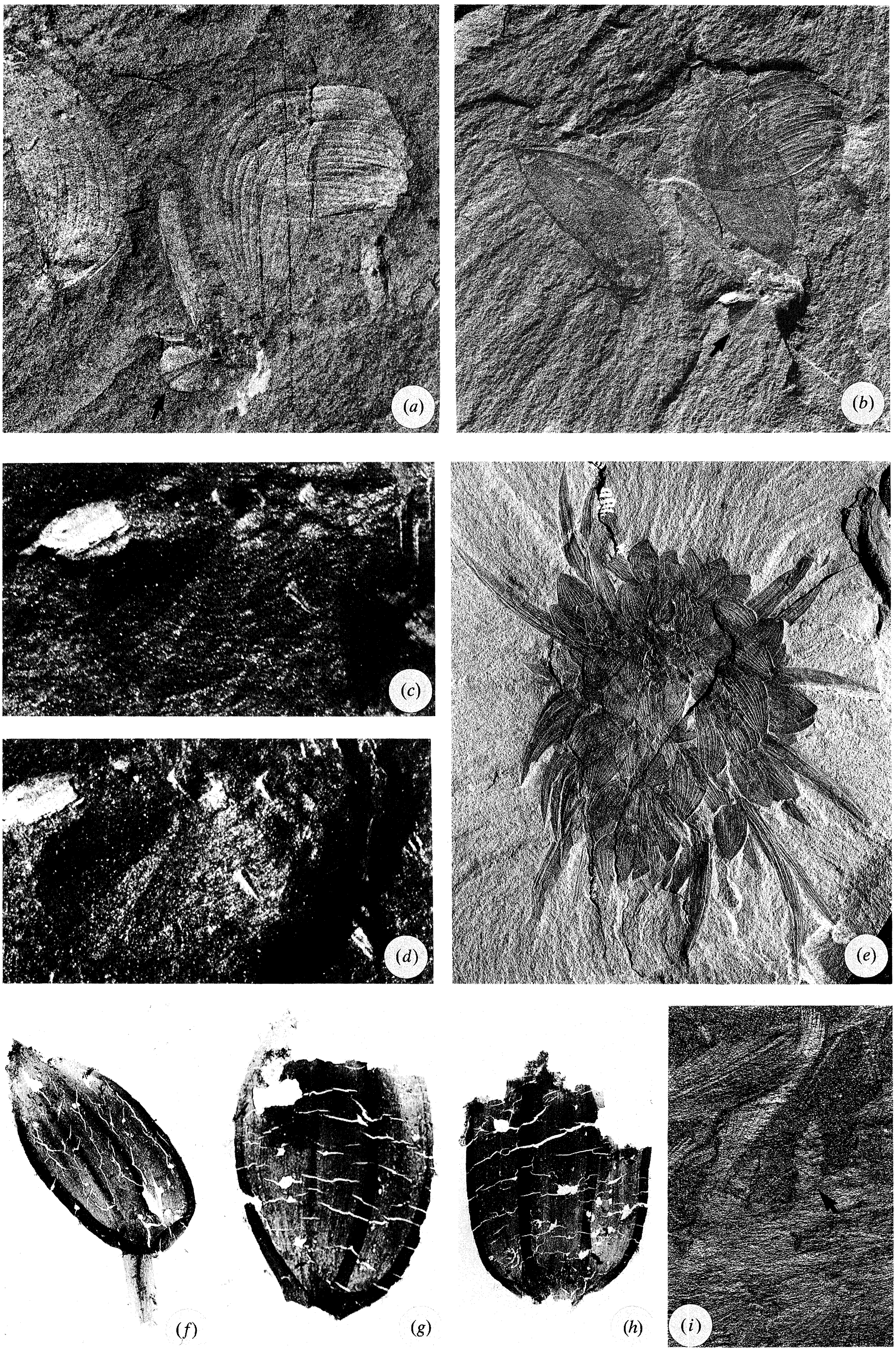

Figure 47. For description see opposite.

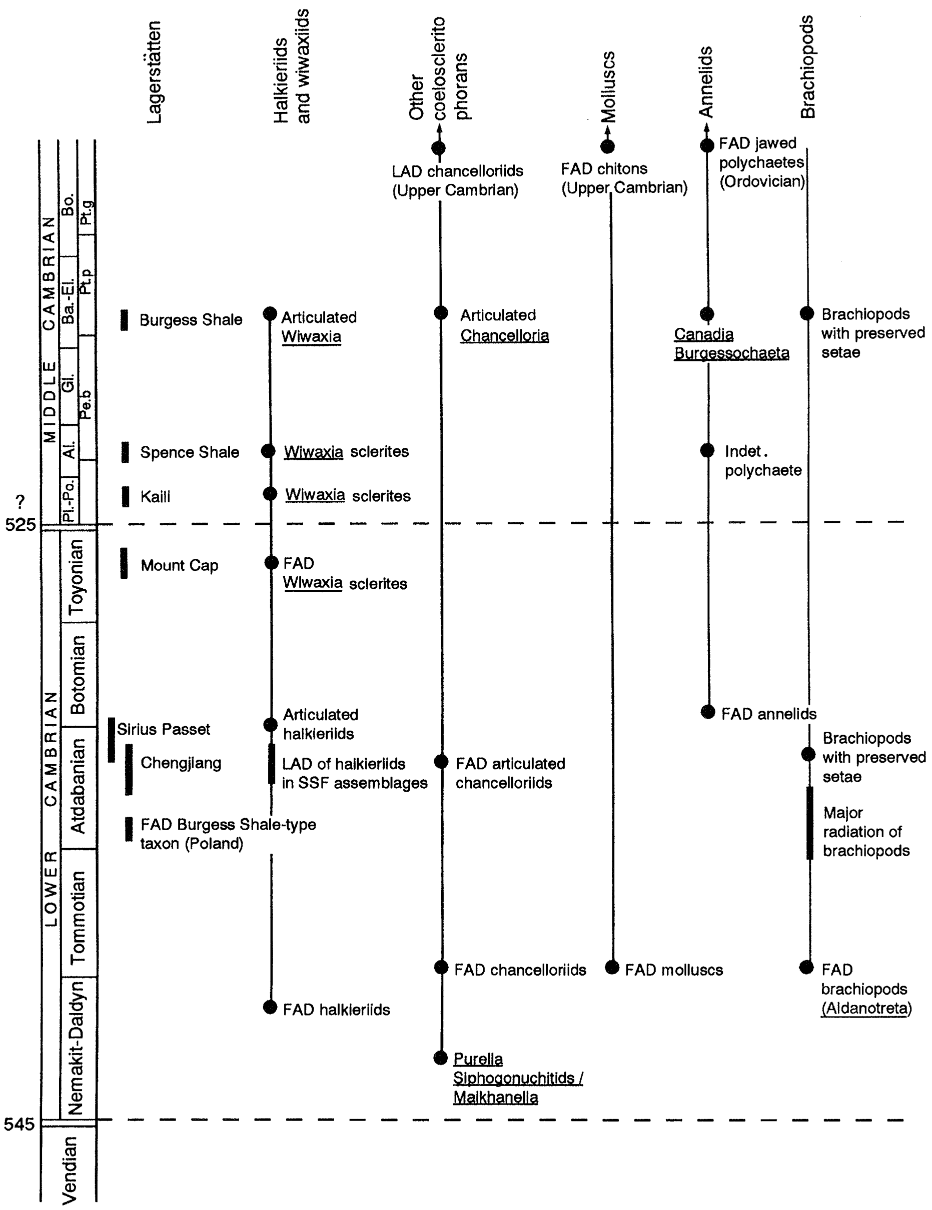

Figure 48. Lower and Middle Cambrian stratigraphy and key events relevant to halkieriid evolution, including distribution of principal lagerstätten, first appearance datum (FAD), last appearance datum (LAD) of wiwaxiids, annelids, brachipods, and molluscs and notable examples intermediate between FAD and/or LAD. The Lower Cambrian stratigraphy is based on the Siberian standard, whereas that of the Middle Cambrian follows the scheme of stratigraphy erected for the Laurentian area in terms of polymeroid and agnostoid trilobites (see Conway Morris 1989*a* for further explanation).

molluscs (Conway Morris & Peel 1991; Peel 1991) is based on its slug-like appearance with inferred muscular ventral sole or foot and a dorsal epithelium bearing calcareous structures in the form of two prominent shells, beneath the posterior of which may have resided gills (perhaps equivalent to ctenidia), and a cataphract array of sclerites. Evidence for a radula is equivocal (figure 39*i*), but the better known feeding apparatus of *Wiwaxia* has been compared with the molluscan radula (Conway Morris 1985*a*). Amongst the Mollusca overall the halkieriids resemble most closely the aplacophorans (caudofoveates and solenogasters) and chitons, both which are widely regarded as primitive in contrast to the more derived conchiferans (monoplacophorans (inclusive Helcionelloida and Tergomya), gastropods, cephalopods, bivalves, scaphopods and the extinct rostroconchs; see Runnegar & Pojeta (1985) and Peel (1991)).

(ii) *Chitons*

If chitons were to be derived from halkieriids then the two principal steps in terms of scleritome arrangement presumably would be duplication of the shells along the length of the body to provide the characteristic arrangement of eight valves and alteration of the hollow sclerites to solid spicules embedded in the leathery girdle. Neither of these steps appear to have been straightforward. The shells in the Sirius Passet halkieriids do not resemble closely any of the different value types of chitons. Apart from presumably being calcareous with an inner layer composed to possibly foliated calcite (see §5*c* (iii)) the structure of

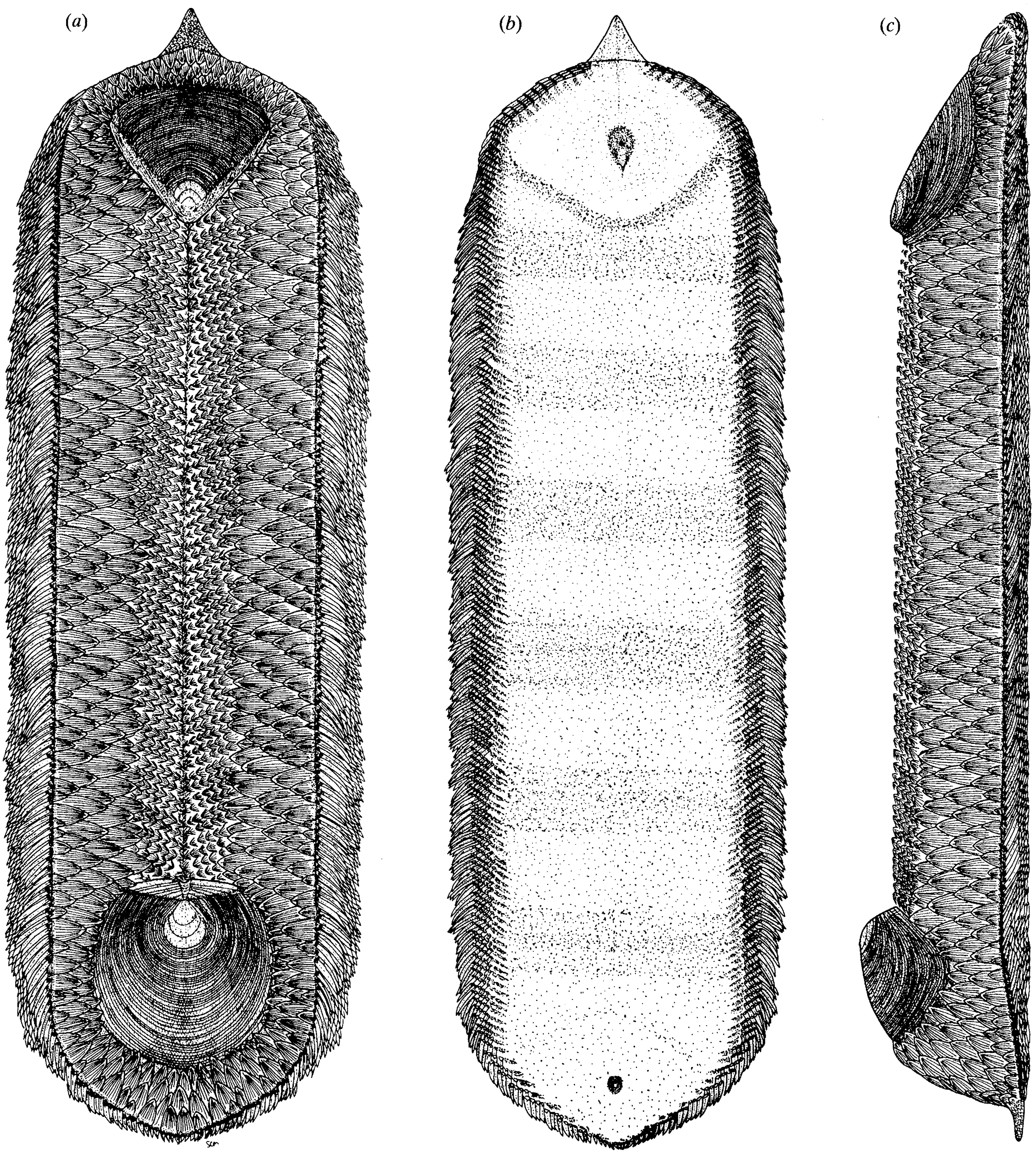

Figure 49. Reconstruction of *Halkieria evangelista* sp. nov. in (*a*) dorsal, (*b*) ventral, and (*c*) lateral views. In ventral view the location of mouth and anus are estimates, and the dark bands on the sole refer to inferred waves of monotaxic muscular contraction during locomotion.

the halkieriid shells is not known. There is no reason, however, to think that they approach in organization the shell structure of chiton valves (e.g. Haas 1972, 1977, 1981; Currie 1992), which have a complexity of shell layers unrivalled in the Mollusca. Because the shells of the Sirius Passet halkieriid are little like chiton valves, there is no obvious reason to homologize the two halkieriid shells with any of the eight (or seven, if the embryological condition (e.g. Christiansen 1954) recapitulates an earlier phylogenetic stage (Salvini-Plawen 1981); see also Rolfe (1981)) valves, other than on the basis of their anterior and posterior positions. In this context the shell *Triplicatella disdoma* deserves mention. The type occurrence is from the Lower Cambrian of Australia (Bengtson *et al.* 1990, see figures 157–158). Its similarity to a chiton valve led Yates *et al.* (1992) to interpret it as the earliest known example, whereas Conway Morris (1993*b*) speculated that its co-occurrence with the halkieriid *Thambetolepis* was consistent with it belonging to the same scleritome. Recent evidence, however, suggests that the original interpretation of it being an operculum (Bengtson *et al.* 1990) is more plausible (A. Yates, personal communication).

Whereas the transition between halkieriid and wiwaxiid sclerites appears to be relatively straightforward, transformation between halkieriid sclerites and the spicules embedded in the girdle of a chiton is also less easy to imagine. Bengtson (1992, p. 417) has discussed in outline this transition, drawing attention to possible mineralogical similarities. The method of spicule secretion is discussed by Haas and co-workers (Haas & Kriesten 1975, 1977; Haas 1977, 1981). Any transformation presumably would involve the secretory cells of a halkieriid sclerite coming to occupy a basal position and developing into the cup-like structure, with a pronounced zone of microvilli adjacent to the calcareous base, which in chitons houses the solid spicules. Such a transition may seem less implausible if the evolutionary steps of halkieriid sclerite → wiwaxiid sclerite → polychaete chaeta is accepted (see §7*d*) in as much as there is a similar development of cup (follicle) and microvilli at the root of the chitinous chaeta. Nevertheless, there is no direct evidence, either from the available fossil record or embryological studies (see Haas 1981, p. 409, figure 8), to support the derivation of the girdle spicules of chitons from halkieriid sclerites. Although some spicules superficially resemble sclerites (e.g. Haas & Kriesten 1975, figure 1A; 1977, figure 1, plate 1, figures 5–12; Saito & Okutani 1992, figure 3A), particularly in terms of either longitudinal ribbing or on occasion an approximation to base and blade (e.g. Scheltema 1985) no equivalence to the halkieriid sclerite zones is apparent in the chiton girdle.

It may also be worth considering whether there is no direct connection between the sclerites and spicules of halkieriids and chitons, respectively, with the latter representing newly evolved structures. This is because in a subsequent section (see § 7*d*) the possible homology between chaetae of polychaetes (as well as setae of brachiopods) and halkieriid sclerites will be explored. It may be significant that similar chaetal structures have also been reported in molluscs. Most convincing is Kölliker's organ, which is a structure composed of setae and found only in juvenile octopods (Cephalopoda) (Brocco *et al.* 1974). These setae have a similar ultrastructure to those of annelids, although they differ in showing periodic cleaving off the distal tips of the microvilli. Cephalopods, and more especially octopods, are generally regarded as amongst the more derived of molluscs (Engeser 1990) and survival of this primitive feature (as may also be the case for the segmented series of gills and a chitin-rich shell (Peters 1972)) is noteworthy. It is of interest, therefore, that setal structures have been reported also in chitons (Leise & Cloney 1982; see also Morse 1873). Although chitinous and with a cortex similar to that of polychaete chaetae, the central medulla contains dendritic bundles that extend upwards from the basal cell and may have a sensory function. The case for these structures being homologous with chaetae, but modified as receptors, seems possible.

(iii) *Aplacophorans*

Despite the fact that aplacophorans are generally regarded as the most primitive of extent molluscs, with either the caudofoveates the sister group of solenogastres and Polyplacophora (e.g. Salvini-Plawen 1981, 1990) or the two aplacophoran groups being a sister group to the polyplacophorans (e.g. Scheltema 1988, 1993; Scheltema *et al.* 1994), beyond being vermiform and spiculate there seem to be few specific and precise similarities between this extant group (which lacks a fossil record; see Briggs *et al.* 1987 for effective refutation of one proposal) and the halkieriids. The spicules of aplacophorans may superficially resemble halkieriid and wiwaxiid sclerites (e.g. Morse 1979, figures 2, 6, 10; Scheltema 1989, figures 2, 7; 1990, figure 2; Morse & Norenburg 1992, figures 2, 7, 8; Scheltema *et al.* 1994, figure 4D), but their mode of secretion is closely similar to the spicules of chitons (Hoffman 1949; Haas 1981; Scheltema *et al.* 1994) and so different from halkieriids. Some spicules are hollow and Bengtson (1992) drew specific comparisons between such spicules and halkieriid sclerites, albeit concluding (p. 417) that 'More problematic, however, is the direct comparison of the internal cavities: in the coeloscleritophorans [which include halkieriids] these were apparently filled with active, secretory tissue, whereas the cavity in *Proneomenia* [an aplacophoran] spicules form passively, by the blocking of secretory activity by the cuticular boss.' Moreover, the hollow spicules in aplacophorans are regarded as derived rather than primitive (Scheltema 1988). The absence of specific divisions of spicules comparable to the sclerite zones in halkieriids is another obvious point of difference. Attempts to draw comparisons between the halkieriid arrangement and specific features in some aplacophorans such as spinose zones or imbricated arrays of spathulate spicules adjacent to the foot in *Meiomenia* (Morse & Norenburg 1992, figure 13) are probably superficial. Aplacophorans lack shells, although in *Nematomenia protecta*, which is regarded as a primitive solenogaster, the spicules of the dorsum coalesce to form three dorsal shields (Thiele 1913). Although this occurrence may echo how the conchiferan shell could have formed by amalgamation of spicules (e.g. Carter & Aller 1975), in these shields the spicules remain distinct (Thiele 1913, plate 4, figure 19) and there is no similarity to the shells of halkieriids. The presence of ctenidia in halkieriids remains highly speculative, but a significant point concerning the ctenidia of aplacophorans and possibly comparable structures in the Burgess Shale polychaete *Canadia* is returned to below.

(iv) *Early mollusc evolution*

Aplacophorans and chitons share a number of significant similarities but the data from halkieriids do little to resolve further their phylogeny. Indeed, the halkieriids may be too derived to cast much direct light on mollusc origins (figure 50). More relevant might be the related siphogonuchitids. Bengtson (1992) reconstructed the siphogonuchitid scleritome as being a cap-like shell, generally referred to as *Maikhanella*, that is patently composed of fused sclerites embedded in shell-like material. Siphogonuchitids appear to be quite closely related to halkieriids, but evidently had a simpler scleritome (two types of sclerite referred to respectively at present as *Siphogonuchites* and *Lopochites* (see Qian & Bengtson 1989; S. Conway Morris & B. Xiao, unpublished observations)). This group is probably more primitive, although the precise homologies between the scleritomes of siphogonuchitids and

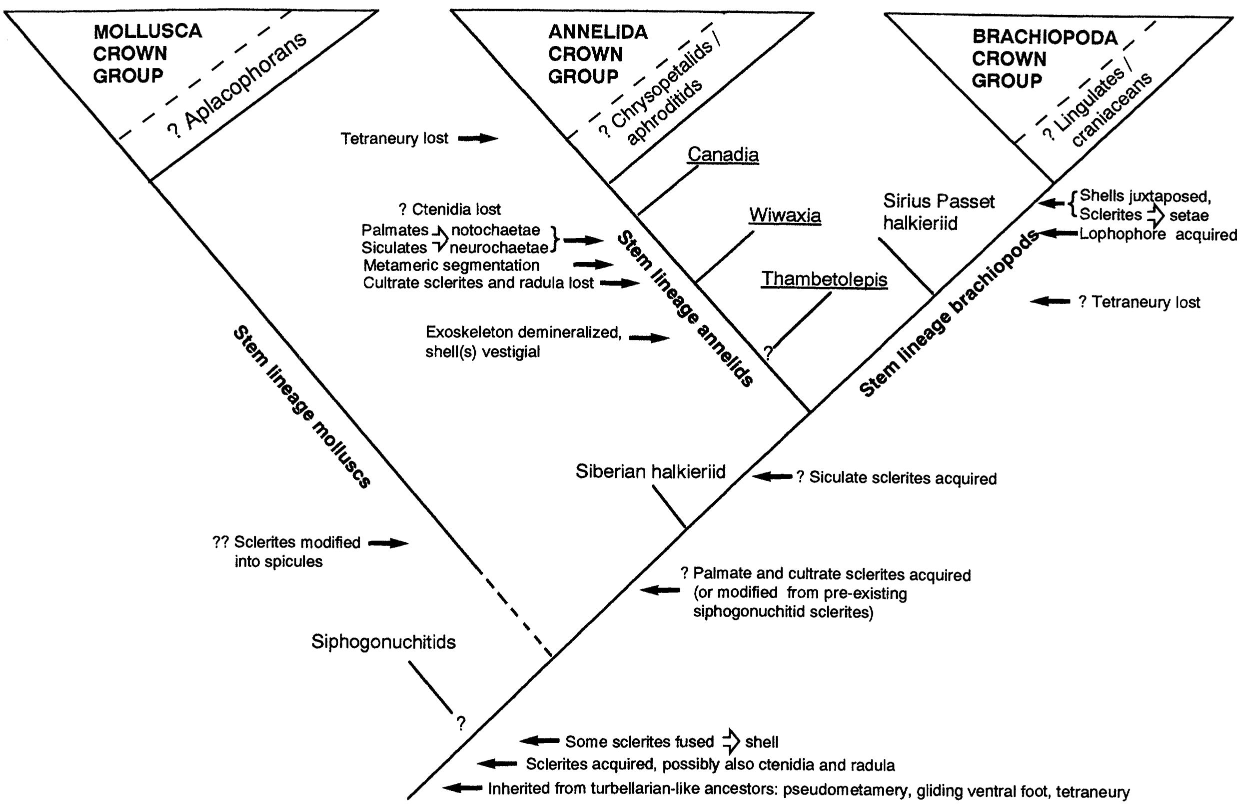

Figure 50. Evolutionary tree of annelid-brachiopod-mollusc evolution showing possible positions of extinct Cambrian taxa, including halkieriids, siphogonuchitids, *Wiwaxia* and *Canadia*. Characters acquired (or lost) along the extinct stem lineages leading to the crown groups (the last common ancestor of all living taxa and all its descendants) are also depicted. The most primitive clade in each of the three crown groups is taken to be the aplacophorans in molluscs, chrysopetalids or the related aphroditids in annelids, and either the lingulates or craniaceans in the brachiopods. The insertion of various taxa in the stem lineages is highly provisional.

halkieriids remain to be explored. In terms of stratigraphic appearances siphogonuchitids arise in the basal-most Cambrian (Nemakit-Daldyn; figure 48) and in general appear to precede the slightly later appearance of the halkieriids (see Khomentovsky & Karlova 1993). If aplacophorans are very primitive molluscs (e.g. Salvini-Plawen 1990) they may represent descendants of a stock close to the siphogonuchitids (figure 50), but before a true shell was secreted (see also Haas 1981). As with halkieriids, however, direct comparisons between aplacophoran spicules and siphogonuchitid sclerites are not straightforward. Alternatively, aplacophorans may have evolved from early molluscs developing spicules in a manner closely comparable to the chitons but in contrast losing all traces of their shells, possibly as a consequence of their specialized modes of life. A concept related to these two proposals is introduced by Scheltema (1993) who envisages the aplacophorans arose from a pre-chiton + conchiferan molluscan stock. Third, and perhaps least likely, the apparent primitiveness of aplacophorans is in fact a reflection of at least some clades being highly derived (see also Freeman & Lundelius 1992) from one or more groups of conchiferan molluscs. This would parallel the development of spicule-bearing groups, such as the acochlidiaceans (e.g. Swedmark 1968; Morse 1976, 1987) and rhodopids (Salvini-Plawen 1991) in the gastropods. In either of the second two cases derivation could be by processes such as progenesis (see Scheltema 1993; Scheltema *et al.* 1994).

A further complication is the relatively late appearance of chitons, despite the consensus that they (with the aplacophorans) precede the conchiferans. The earliest chitons may not appear until the Upper Cambrian in the guise of *Matthevia* (Runnegar *et al.* 1979) and *Preacanthochiton* (Bergenhayn 1960). Considerable confusion, however, has been engendered by claims for chitons from the Lower Cambrian of China (e.g. Yu 1987). Critical restudy (e.g. Qian & Bengtson 1990) suggests that while some of these cap-shaped shells may be derived either from halkieriids and near-relatives (Bengtson 1992), none is derived from a true chiton.

There are obvious difficulties in a straightforward derivation of the conchiferans from the chitons, not least in comparison of shell-types (see Haas *et al.* 1979; Wingstrand 1985; Scheltema 1988; Haszprunar 1992). In principle reduction of a halkieriid scleritome to a single shell could give rise to different types of monoplacophoran (see Peel 1991). The posterior shell of *H. evangelista* is reminiscent of the tryblidiid (tergomyan) monoplacophorans, which have flat cap-shaped and ovoid shells, evidently exogastric (Peel 1991). Such molluscs are often envisaged as the nearest approach to the ancestral conchiferan, but Peel (1991, p. 20) emphasizes that tryblidiids 'are conspicuously less common in the Early and Middle Cambrian than members of the class Helcionelloida'. Early conchiferan evolution remains complex (see Peel (1991), figure 4*b*; Geyer 1994), but as noted above halkieriids may transpire to be too derived to throw direct light on the origins of these more advanced molluscs. Comparisons are complicated yet further because although living monoplacophorans are taken as models of the primitive conchiferan state, much of their anatomy appears to be derived (Stuber & Lindberg 1989; Padian *et al.* 1994).

(v) *Halkieriid shells*

After the discovery of the Sirius Passet material, Peel (1991) and Bengtson (1992) listed a number of shells as potential candidates for components of either halkieriid or related scleritomes. Within the Australian material attention should be drawn to taxa presently described as Ornamental Cones form A, B and C (Bengtson *et al.* 1990, figures 99, 100). Form A was compared by Bengtson *et al.* (1990, p. 155) to the Chinese *Canopoconus* and Siberian *Purella*, both of which are now considered to derive from scleritomes (Bengtson 1992). Form A has an arched posterior margin, that is characteristic of other such shells (see Qian & Bengtson 1990, figures 59, 59), while the flatter form B has a general resemblance to cap-shaped shells with a scaly exterior. In both cases, however, any associated sclerites remain unknown. Form C has a strongly developed ornamentation that is somewhat reminiscent of the sachitid *Hippopharangites dailyi* (Bengtson *et al.* 1990), and it conceivably derives from the same scleritome.

A survey of the literature on early skeletal fossils no doubt would yield a number of other possibilities for consideration, although lack of data such as necessary information on associated sclerites and poor illustration make this a difficult exercise. Nevertheless, there is a wide variety of shell-like fossils from the Lower Cambrian, and possibly the Middle Cambrian (Conway Morris 1995), some of which almost certainly derive from halkieriid or related scleritomes (Conway Morris & Peel 1990; Bengtson 1992). Some degree of conjecture is inevitable given the putative shells are disassociated from co-occurring sclerites, but halkieriids (and their near-relatives) may have secreted a substantial range of shell-types. A few possible examples include those illustrated by Khomentovsky & Karlova (1991, plate 4, figures 2–4), although their referral of this material to *Triplicatella* may be incorrect, and the fossil referred to by Shaw (1955, plate 76, figure 12) as an 'undetermined brachiopod' from the Lower Cambrian Parker Slate of Vermont. None of these appears to be closely similar to those of the substantially larger Sirius Passet halkieriids, but this need not be of particular significance. Although the Sirius Passet shells are relatively enormous in comparison to the isolated shells derived from disarticulated scleritomes of halkieriids, the latter are typically replaced by diagenetic phosphate and extracted as parts of insoluble residues by acid digestion of calcareous sediments. It is clear that such assemblages are taphonomically biased in favour of smaller specimens, and possibly taxa (e.g. Dzik 1991*a*).

As noted above, derivation of the molluscs might be better considered in the context of the siphogonuchitids (figure 50). Construction of their shell may represent an intermediate stage before secretion was solely by accretion and the enclosed sclerites were discarded. A recurrent proposal is that the shell of conchiferan molluscs is derived from the aggregation of spicule-like elements (Salvini-Plawen 1980, 1981). Evidence for such a derivation might be sought in the larval development of the aplacophoran *Nematomenia banyulensis* where the seven transverse calcareous bands are composed of spicules (Pruvot 1890; see also Salvini-Plawen 1981). This feature, however, has not been detected in the early ontogeny of other aplacophorans (see reviews by Wingstrand 1985 and Scheltema 1988) and there is no evidence in the Sirius Passet halkieriids that the shells are so derived. It is also clear that, contrary to earlier reports, the valves of chitons are secreted as continuous rods rather than forming from the fusion of spicules (Haas *et al.* 1979; Kniprath 1981; Haas 1981; Scheltema 1988).

Work on assemblages of isolated sclerites with associated shells believed to derive from the same scleritomes is continuing, and new information is becoming available from surface outcrops in Xinjiang (China; S. Conway Morris & B. Xiao, unpublished data) and British Columbia (Canada; S. Conway Morris 1995), as well as borehole material from Oxfordshire, U.K. (S. Conway Morris & A. W. A. Rushton, unpublished data). Models of scleritome organization should improve, but a number of enigmatic shells still await assessment. The need for more examples of articulated scleritomes from Burgess Shale-type faunas is overwhelming.

(vi) *Conclusion*

Despite generalized similarities to molluscs the Sirius Passet halkieriid and *Wiwaxia* (Conway Morris & Peel 1990) may be too derived to be directly informative about mollusc origins (figure 50). More relevant, possibly, are the more primitive siphogonuchitids (Bengtson 1992). Nevertheless, their scleritome arrangement is conjectural and the transitions between the siphogonuchitid sclerites and the chitons, or between the siphogonuchitid shell and any equivalent in either the chitons and conchiferans is conjectural.

(*d*) *Halkieriids and annelids*

(i) *Introduction*

Accepting the relationship between halkieriids and wiwaxiids (§7*b*), and taking Butterfield's (1990) demonstration of the structural similarity between the sclerites of *Wiwaxia* and the chaetae of the polychaete annelids *Canadia* (Butterfield 1990; and *Burgessochaeta* (N. J. Butterfield, personal communication)) as a genuine homology then there is the potential to document how annelids might have arisen, at least in outline. Here we argue that annelidan chaetae are ultimately derived from halkieriid sclerites. Transformation from a halkieriid to a polychaete involved a number of other significant changes, most obviously development of discrete parapodia and loss of the shells (with the possible exception of sternaspid polychaetes).

(ii) *Origin of neurochaetae and notochaetae*

In halkieriids the siculate sclerites form an imbricated array (figures 21, 22*j*, 23 and 27*d*), with each 'segment' giving rise to a transverse bundle, evidently a prominent fan, attached to a lobate base (figures 19 and 22*f*). This arrangement is comparable to the lobate fascicle of neurochaetae in *Canadia spinosa* (see Conway Morris 1979*a*, figures 64 and 47*i*). The two sets of structures are suggested to be homologous. Nevertheless, their functions were by no means comparable. In *Halkieria* the recurved shape of individual sclerites suggests that this zone helped to act as a type of snowshoe (see Conway Morris 1992*a*, p. 633), while the closely imbricated arrangement of the siculate bundles (e.g. figure 27*d*) may have provided a ratchet to prevent backward slippage of the animal, in a manner reminiscent of the terrace lines employed by various invertebrates including some arthropods and mitrate echinoderms (see Jefferies 1984; Savazzi 1994). In any event the close spacing and lack of evidence for rotation suggests that the siculate bundles were unlikely to act as effective levers in the manner that characterizes the stepping pattern of the neuropodia in polychaetes (e.g. Storch 1968; Mettam 1971). The palmate sclerites in the Sirius Passet halkieriids arose in oblique rows, whereas in *Wiwaxia* the presumed equivalents (dorsal sclerites of Conway Morris 1985*a*) are larger, reduced in number and have closely spaced points of insertion that are more or less transverse to the body. This latter array is taken to be equivalent to the notochaetae of polychaetes, and more specifically the paleae coverings of such groups as the chrysopetalids. If neurochaetae and notochaetae are derived respectively from arrays of siculate and palmate sclerites, this implies that the intervening cultrates that cover the lateral margins of halkieriids and wiwaxiids must have been lost in the polychaetes (figure 50). This region is now represented by the inter-ramal recess that presumably arose as a result of the development of notopodium and neuropodium. In contrast, Butterfield (1990) evidently regarded the entire suite of sclerites in *Wiwaxia* as equivalent to the notochaetae and identified minute spines, sometimes with a spinose ornamentation, co-occurring in the same acid-residues that had released undoubted sclerites of *Wiwaxia*, as the neurochaetae. Similar spines were reported in two of the five samples from the Mount Cap Formation (figure 48) which yielded isolated *Wiwaxia* sclerites (Butterfield 1994). Apart from the apparent absence of these spines in semi-articulated specimens of *Wiwaxia* (see Conway Morris 1985*a*), a difficulty with this hypothesis is a lack of ultrastructure comparable to that identified in *Wiwaxia* (Conway Morris 1992*a*). Butterfield (1990, p. 295), however, also included a prescient proposal by T. Perkins that the siculates of *Wiwaxia* 'actually represent modified neurosetae', although here we propose the reverse in that the chaetae are taken to be modified sclerites.

In considering the hypothesis of equivalence between halkieriid sclerites and polychaete chaetae it is worth noting similarities between these sclerites and the distinctive paleae of chrysopetalids. Surface ornamentation of the two structures has some striking similarities in terms of ribs and tubercles (see illustrations of *Bhawania* in Katzmann *et al.* 1974 and Perkins 1985), although the generally broader shape of halkieriid (and *Wiwaxia*) sclerites must influence patterns of ornament. Another possibly significant similarity is the transverse ornamentation of *Paleaquor heteroseta* (Watson Russell 1986, figure 18), comparable to that seen in many halkieriid sclerites (e.g. Bengtson & Conway Morris 1984, figure 5A–C, F, 6D, B; Bengtson *et al.* 1990, figure 48A–D). Whereas surface ornamentation could well be a convergent feature the internal camerate structure defined by a series of canals may be a significant character shared by both sclerites and chaetae (compare Bengtson & Conway Morris (1984), figure 9C to Westheide & Watson Russell 1992, figures 1C, F, 2A, 3). Whether the sclerites of *Wiwaxia*, however, had a camerate interior is uncertain because the material isolated by Butterfield (1990, 1994) only preserves the outer cortex and its longitudinal canals. Nevertheless, Westheide & Watson Russell's (1992, p. 201) comments that 'Cameration ... could well be a plesiomorphic feature of the annelid chaetae' is consistent with a halkieriid ancestry. It is tentatively proposed that amongst halkieriids *Thambetolepis*, which has particularly prominent cameration (Bengtson *et al.* 1990), might be closer to the lineage leading to the annelids (figure 50). Attention might also be given to the amphinomid polychaetes such as the fireworm *Eurythoë*, because of repeated claims that the chaetae are calcareous (Gustafson 1930; Bobin 1948; Friedrich 1964; Schroeder 1984). Substantiation of this point is needed, and although the calcareous nature of the chaetae is probably a secondary feature, the possibility that it is a relict feature is intriguing given amphinomids have been regarded as primitive (§6*f* (v)).

(iii) *Modes of growth of sclerites and chaetae*

Despite the evidence for a link between halkieriids/wiwaxiids and polychaetous annelids, this hypothesis is not without its difficulties. One significant difference appears to be the modes of growth. In the Sirius Passet halkieriids an effective cover was evidently maintained in the growing animal by addition and interpolation of sclerites, combined with accretion around the margins of either shell. In contrast, the sclerite numbers of *Wiwaxia* do not show a significant increase during growth of an individual, and it may be that the final number of sclerites was laid down early in ontogeny. Resolution of sclerite numbers in juveniles of *Wiwaxia* is difficult because the specimens tend to preserve as a reflective mass (Conway Morris 1985*a*, plate 3, figures 42, 43; plate 4, figure 49; plate 7, figures 80, 81; plate 12, figure 123; plate 13, figure 134). However, in specimens about half the adult size the sclerite numbers are similar, if not identical, to fully grown individuals. Given that halkieriid growth was achieved by interpolation of generally larger sclerites, most obviously among the cultrates, whereas in wiwaxiids effective cover was maintained by sclerite enlargement, then how was the transition achieved? In the Sirius Passet material there is evidence that at least the cultrate sclerites (figures 39*j* and 42*g*) may have possessed an elongate stalk that extended from the base and presumably was embedded in the epidermis, perhaps in an invagination or follicle. Isolated sclerites lack evidence for such an attachment stalk, but it is possible that a comparable structure extended from the apertural region. Evidence from isolated sclerites (e.g. Bengtson & Conway Morris 1984; Bengtson *et al.* 1990), moreover, suggests that the sclerites were secreted at a given size, with the secretory tissue housed within an internal cavity variously divided by canals.

In wiwaxiids three alternative hypotheses of sclerite growth exist: moulting, periodic discarding or enlargement by accretion. A unique juvenile of *Wiwaxia* (Bengtson & Conway Morris (1984) figure 10; Conway Morris (1985*a*) pp. 533–534, plate 2, figures 17–19, 27) shows an enigmatic configuration of sclerites that was interpreted as an individual preserved in the act of moulting, with some sclerites in the process of re-inflation. The status of this specimen must remain unclear if the proposed transition between halkieriid sclerites and polychaete chaetae is accepted, as in neither group are the epidermal structures discarded by moulting. Another possibility in *Wiwaxia* is the shedding of smaller sclerites and replacement of larger ones capable of maintaining effective cover. Such a mechanism occurs in Recent chrysopetalids, a possibly primitive group of polychaetes that may be related to *Canadia spinosa*. Watson Russell (*in* Bhaud & Cazaux 1987; also personal communication) comments on adult replacement of chrysopetalid chaetae, especially in *Strepternos* where 'there is a continuous process of setal generation, replacement and loss during growth of the individual (her p. 664). If comparisons with polychaetes are accepted, then this might imply the generation of fresh follicles in as much as chaetal regeneration in polychaetes apparently does not occur in old follicles (Specht 1988). Continuous growth of the sclerite is an alternative possibility, although in polychaetes generation of new material is achieved via the microvilli inserted in the base of each follicle. Certainly the well-defined base of *Wiwaxia* sclerites (Conway Morris (1985*a*) plate 7, figure 78; plate 11, figure 114; plate 14, figure 143) suggests that they were housed in follicles comparable to those of polychaetes (see Specht 1988). This may also have been the case for the halkieriid sclerites to judge from the possible stalk (figures 39*j* and 42*g*).

(iv) *Vestigial shells*

Evidence of halkieriid-like shells in *Wiwaxia* remains equivocal (§7*b*) and there is no evidence for their persistence in any of the Cambrian polychaetes, including *Canadia* (see Conway Morris 1979*a*). Nevertheless, in this genus the notochaetae form a dense covering and careful excavation might reveal vestigial remains of a shell. Attention should also be drawn to the posterior plate or shield which characterizes the sternaspid polychaetes. Arising around the margins of this shield is a fan of chaetae while beneath it converge a series of retractor muscles that connect to these chaetae. Typically the plate consists of two halves with prominent radiating ribs that may give it a shell-like appearance (Malmgren 1868; Reitsch 1882; Augener 1918; Caullery 1944; Nonato 1966; Fauchald 1977; Bartolomaeus 1992). The plate is usually described as chitinous and according to Lowenstam (1972) it contains an amorphous ferric phosphatic mineral. More recently Bartolomaeus (1992) has provided a detailed description of the shield's ultrastructure. It is cuticular and very electron-dense, presumably because of the large quantities of iron. This ferrous precipitate occurs as clusters between a fibrillar network and increases in density towards the underlying basal cuticle. Iron was also detected (Bartolomaeus 1992, figure 9B) in the chaetae and in passing he (p. 250) commented on some close similarities with the ferrous biomineralization in the radula of chitons, but he declined to draw direct phylogenetic conclusions. The position of sternaspids in polychaete phylogeny is speculative and they are usually regarded as an isolated order (Fauchald 1977). Vejdovsky (1882) argued that sternaspids were very primitive, effectively linking the polychaetes to the sipunculans and echiuroids. As stated Vejdovsky's (1882) arguments are not especially convincing, although Dahl (1955) explored further the possibility of a relationship between sternaspids and sipunculans (§7*f* (vii)). In any event, the similarities of the shield with the posterior halkieriid shell may not be convergent, and the possibility of sternaspids being primitive should be investigated. In particular, although the evidence is slender there is quite a strong similarity between the sternaspid plate and the putative shell in *Wiwaxia* (figure 44*c*, *d*). In sternaspids the function of the ventral shield is regarded as protective, with the worm living head-down in the sediment and the shield acting to close the burrow entrance (Dales 1963; Day 1967, p. 648). A similar use was proposed for the halkieriid shells (Bengtson 1990), but is considered unlikely here (see §6). Goodrich (1897) noted, in addition, that another function of the sternaspid shield appeared to be acting as a rigid insertion for the ventral posterior retractor muscles, a function that may find a parallel in the anterior shell of the halkieriid (§5*c* (iii)).

(v) *Feeding apparatus*

In pursuing the argument that wiwaxiids were polychaetes Butterfield (1990, p. 295) attempted to compare the feeding apparatus of *Wiwaxia* to phyllodocidan jaws. In particular he questioned the transverse orientation of the feeding apparatus in *Wiwaxia*. However, his emphasis on the feeding apparatus being best exposed in oblique specimens, so indicating in his opinion a lateral attachment, is based on a simple misunderstanding of Burgess Shale taphonomy. Optimum exposure of the apparatus in the specimens is controlled by the levels of splitting (Conway Morris 1985*a*). The transverse nature of the apparatus is evident in dorso-ventral specimens (e.g. Conway Morris (1985*a*) plate 1, figures 6, 11, 12, plate 7, figures 72, 74, 75, plate 8, figures 84, 85, plate 9, figures 90, 93, 94, plate 12, figures 118–121, 126; see also figure 44*e* this paper), but in such orientations the level of splitting is usually along such a plane as to expose the sclerites and partially or totally conceal internal organs, including the feeding apparatus. In oblique specimens, in contrast, a relatively broad area of soft-tissues is often exposed and so usually the feeding apparatus is clearly revealed. The bilateral symmetry, close juxtaposition of either side of the toothed apparatus, and inferred ventral location are all reminiscent of molluscan radula (Conway Morris 1985*a*).

Polychaete jaws show considerable diversity, although none corresponds to that of *Wiwaxia*. Certainly those of chrysopetalids and aphroditaceans, perhaps the nearest relatives amongst the polychaetes to wiwaxiids (§7*f* (v)), are not comparable. In these polychaetes the jaw is typically a pair of stylets (e.g. Watson Russell 1991), far removed in form from the apparatus of *Wiwaxia*. Other annelids have a variety of jaws, based on either a denticulate pad or tongue (Jouin 1978; Purschke 1985, 1987*a*, 1988*a*, *b*; Purschke & Jouin 1988). These structures have a vague resemblance to radulae and the feeding apparatus of *Wiwaxia* but in no case does the similarity appear compelling. Other polychaetes, notably the dorvilleidids have an array of maxillae or maxillary plates (e.g. Purschke 1987*b*, 1988*b*; Hilbig 1991; Åkesson & Rice 1992, in particular figure 2A) that by themselves recall quite closely the arrangement in *Wiwaxia*, but unlike this Cambrian animal the jaw apparatus also consists of a corresponding set of mandibles. Moreover, in the retracted state the denticles of the maxillae usually point forwards, whereas in *Wiwaxia* the corresponding structures are posteriorly directed. However, despite Pelseneer's proposal (1899), a homology between the molluscan radula (and the corresponding feeding apparatus of *Wiwaxia*) and any one of the different types of polychaete jaws seems unlikely for at least two reasons. First, chitin occurs in both annelids (in the chaetae; see Schroeder 1984; Specht 1988) and molluscs (in the radula, e.g. Peters 1972; Salvini-Plawen & Nopp 1974), but in the former the jaw is variously sclerotized or even mineralized but it is not chitinous (e.g. Voss-Foucart *et al.* 1973; Vovelle 1982; Purschke 1988*b*). Second, despite the complexity and variety of different polychaetes jaws, none is comparable to the organization of the radula, including the method of tooth secretion (e.g. Purschke 1987*b*). Cambrian polychaetes, including *Canadia*, appear to lack jaws and annelids probably evolved these structures a number of times, beginning in the Ordovician, and independently of pre-existing structures that were present in wiwaxiids and their relatives. In contrast Ivanov & Tzetlin (1981) argued for a fundamental homology between molluscan radula and annelid jaw in terms of a common derivation from a ventral cuticular pad, but conceded that the details of jaw construction arose separately.

(vi) *Conclusion*

Halkieriids and the descendant taxon *Wiwaxia* are interpreted as providing key information on annelid origins. The Sirius Passet halkieriid provides information on overall scleritome arrangement, but may itself be closer to the lineage that led to the brachiopods (§7*e*). *Wiwaxia* is closer to the annelids, but retains primitive features such as cultrate sclerites and a radula-like feeding apparatus.

It is premature to review halkieriid phylogeny in detail. Tommotian examples from east Siberia (Bengtson & Conway Morris 1984) lack siculates and if this is an original rather than a taphonomic feature it is possible siculates were acquired subsequent to the palmates and cultrates (figure 50). In any event well-documented dispersed halkieriid scleritomes from South Australia (Bengtson *et al.* 1990) display the full complement of sclerite types.

(*e*) *Halkieriids and brachiopods*

(i) *Setae and sclerites*

The mantle setae of brachiopods are almost identical in terms of ultrastructure to polychaete chaetae (Schepotieff 1903; Gustus & Cloney 1972; Storch & Welsch 1972; Orrhage 1973; see also Nielsen 1991) as well as those of the related pogonophorans (e.g. George & Southward 1973, Orrhage 1973), myzostomids (Jägersten 1936) and echiurans (e.g. Orrhage 1971). Although this might represent a remarkable example of convergence (e.g. Orrhage 1971; Fauchald 1974; Dales 1977; Storch 1979), this similarity is accepted as being phyletically significant. The only principal difference appears to be the case where a new seta may start its development in a pre-existing follicle before branching off to initiate its own follicle (George & Southward 1973). Although the setae of brachiopods arise around the mantle margin in the adult, when they first appear in the early larva they have a more discrete organization. In particular in the larva of *Crania* the setae show a clear threefold segmentation that is also reflected in the newly-formed coelomic cavities (Nielsen 1991). The larva of *Crania* has been regarded as particularly primitive, but whether the craniaceans are the most primitive of the brachiopods (Carlson 1993*b*), as against *Lingula* and its allies (the Lingulata, see Bassett *et al.* 1993; Popov *et al.* 1993) is controversial. If the transition from halkieriid/wiwaxiid sclerites to chaetae is accepted (§7*d* (ii)), then one could hypothesize a transition between a halkieriid-like animal and an ancestral brachiopod. Recent molecular data suggesting the brachiopods lie firmly within the protostomes (Lake 1990; Adoutte & Philippe 1993; but see Nielsen 1991; Carlson 1993*a*) would also support this conjecture.

(ii) *Shells*

The posterior shell of the Sirius Passet halkieriids (figures 9*d*, 27*j* and 39*e*, *h*) is somewhat reminiscent of the valve of an inarticulate brachiopod, a point remarked upon in passing by Conway Morris & Peel 1990 (see also Yochelson 1993), who made, however, no phyletic deduction. How might a brachiopod evolve from a halkieriid-like animal? First, imagine a juvenile halkieriid with shells first in juxtaposition astride the transverse axis and subsequently folded together to define a posterior hinge line. In the case of the Sirius Passet specimens the outlines of two shells are fairly dissimilar, and it is *not* proposed that *H. evangelista* itself is ancestral to the brachiopods. Such an event occurred near to the base of the Cambrian (figure 48). With a change in function to a bivalved condition conformity of valve outline would be rapidly achieved, although in the so-called pseudobrachiopod *Apistoconcha siphonalis* from the lower Cambrian of South Australia there appears to be a marked discrepancy in valve outlines (Bengtson *et al.* 1990, figure 114). If this hypothesis is correct then the anterior shell remained dorsal (ultimately to give the brachial valve) and the posterior shell originally on the dorsum became ventral (ultimately the pedicle valve). A similar conclusion was reached by Nielsen (1991, p. 25) in a discussion of brachiopod embryology where he documented contraction and recurving in the larva of *Crania*. This worker also supported the notion of the ancestral form being a creeping metazoan with a straight gut. Concomitant with the juxtaposition of the shells was the reduction of the scleritome to an array arising from the margins of the shells. These sclerites prefigured the mantle setae of brachiopods. The posterior arch of what was to become the ventral valve would allow a muscular extension to protrude, ultimately to provide the pedicle. Certainly the solid pedicle of articulate brachiopods preserves little trace of this putative ancestral condition (see Richardson 1979; Stricker & Reed 1985*a*), but in the more primitive inarticulates the pedicle in lingulids retains a coelomic cavity (e.g. Morse 1902; Schaeffer 1926; Chuang 1964) and in early forms preserved in the Chengjiang lagerstätte is remarkably vermiform (see Jin *et al.* 1993). Shu *et al.* (1993, figure 3B) have even gone so far as to identify remains of the gut within the pedicle of one of the Chengjiang lingulids. Morse (1873) argued that the pedicle was derived directly from a worm (in his view an annelid), but this idea was received with scepticism (e.g. Schaeffer 1926). A related hypothesis that derives brachiopods from a polychaete ancestor is given by Gutmann *et al.* (1978). In detail, however, this proposal has few similarities to the halkieriid-brachiopod link proposed here, in that the German group hypothesize a phoronid-like intermediate and subsequent acquisition of the shells in a proto-brachiopod.

(iii) *Implications*

This hypothesis represents a radical departure from recent speculation that has derived the brachiopods from a phoronid-like ancestor (e.g. Valentine 1975; Wright 1979; Rowell 1982; Popov 1992; Popov *et al.* 1993). Although phoronids are usually regarded as primitive (e.g. Zimmer 1973), not all workers agree. On the basis of life-cycle studies, Jägersten (1972) has proposed brachiopods arose first, while Emig (1982) has argued that phoronids are the most highly derived forms, a view consistent with the more primitive sperm type of brachiopods (Afzelius & Ferraguti 1978; Willmer 1990). It is also consistent with evidence for evolutionary divergence between the annelids and phoronids as marked by independent acquisition of metanephridia (Bartholomaeus & Ax 1992). A yet more radical alternative is that the long-contested debate of whether the lophophorate phyla (brachiopods, ectoprocts, phoronids) are closer to the protostomes or deuterostomes is resolved by placing the first two groups in the protostomes, whereas the phoronids are an independent lineage allied to the deuterostomes (e.g. Nielsen 1977*a*, *b*; Zimmer 1973; Nielsen 1991).

Stratigraphic considerations do not appear to be in conflict with derivation of brachiopods from a halkieriid group (figure 48). The early history of brachiopods was reviewed by Popov (1992). Although he depicts the group originating in pre-Tommotian strata these early occurrences (as Heosomocelyphidae and Dolichomocelyphidae that together are placed in the order Heosomocelyphida) are based on Chinese material (Liu 1987) and their assignment to brachiopods is highly problematic. The next appearance are representatives of the Cryptotretidae, a group of paterinids that are known only from *Aldanotreta* and *Cryptotreta* (see Sokolov & Zhuravleva 1983). Moreover, if the *Purella*- and *Maikhanella*-groups are accepted as relatives of the halkieriids (see Bengtson 1992) then their appearance in the Nemakit-Daldyn stage, that underlies the Tommotian and is accepted by most workers as basal Cambrian, enhances their stratigraphic separation from the first brachiopods (figure 48).

(iv) *Ectoprocts*

The origin of the colonial ectoprocts by the aggregation and miniaturization of phoronid-like ancestors (e.g. Farmer *et al.* 1973; Farmer 1977) might also bear reconsideration, although Nielsen (1977*b*, 1991) remains sceptical that ectoprocts are close to either the brachiopods or phoronids. Rather he seeks a relationship to the entoprocts. Dzik (1991*b*) has presented evidence for the identification of solitary ectoproct ancestors in the form of cornulitid-like fossil tubes, although these derive from strata somewhat younger than the earliest unequivocal ectoprocts which appear in the early Ordovician. He suggested that cornulitids are closely related to the tubicolous tentaculitids, for which Towe (1978) presented evidence for their having a brachiopod-like shell structure.

Another line of investigation that should be reopened is the significance of the planktotrophic cyphonautes larva of ectoprocts, which is generally regarded as an archaic feature. In passing, however, it should be noted that the putative cyphonautes larvae from the Triassic of Spain (Boada & Diaz 1978) remain questionable, not least because of their relatively enormous size. In living cyphonautes particularly noteworthy is the bivalved 'chitinous' shell with mantle and adductor muscle and a ciliated foot-like structure (pyriform organ) that appears to secrete a mucous sheet upon which the settled larva explores the substrate prior to attachment and growth into the sessile colony (see Atkins 1955; Ryland 1964; Jägersten 1972; Farmer 1977; Stricker *et al.* 1988*a*, *b*; Stricker 1989). According to Jägersten (1972, p. 40) the shell is 'an ancient adult character, an immensely ancient heritage from one of the many ancestors in the phylogenetic line leading to the bryozoans'. Moreover he concluded (p. 41) that the shell-bearing 'ancestor question must be still older, and it must have been solitary'. Elsewhere Jägersten (1972, p. 61) suggested the pyriform organ came from 'an ancient organ of locomotion in the adult phase'. More specifically, could the former be a relic of a halkieriid shell and the pyriform organ a larval expression of the ancestral ventral sole?

In the context of this paper, moreover, it may be significant that the gizzard structure of the ectoproct *Bowerbankia* has been shown to be strikingly similar to the ultrastructure of polychaete chaetae (Gordon 1975), which as argued above (§7*d* (ii)) may be derived ultimately from halkieriid sclerites. Although a homology between polychaete chaetae (and their sclerite antecedents in halkieriids) and gizzard teeth in the bryozoan *Bowerbankia* may seem far-fetched, Gordon (1975) emphasized that the latter appear to be of ectodermal origin. Gizzard teeth are known to have a sporadic distribution among bryozoans, occurring most frequently in the ctenostomes (which include *Bowerbankia*), but also recorded in the cheilostomes and tubuliporates (Schäfer 1986). Schäfer (1986; see also Markham & Ryland 1987) considered the gizzard to be a convergent feature that evolved sporadically and several times in bryozoans. The primitive position of the ctenostomes (e.g. Taylor & Larwood 1990) suggests, however, that the gizzard ultrastructure of *Bowerbankia* (and possibly other ctenostomes) may be of phylogenetic significance.

(v) *Conclusion*

From a place close to the deuterostomes we propose a radical alternative for the derivation of the brachiopods from within the halkieriids, emphasizing the transformation of the shells and sclerites to a bivalved condition with the secretory mantle bearing chitinous setae. Other aspects of this hypothesis require exploration, including the following implications: was the musculature of brachiopods including the adductor/diductor system derived from pre-existing structures in halkieriids, including the anterior set of muscles that are hypothesized to have inserted onto the anterior shell (figures 33, 35*e* and 42*c*, *d*)? Is the mode of shell secretion of halkieriid, brachiopod (see Williams 1977; Stricker & Reed 1985*b*) and perhaps mollusc shells fundamentally homologous, with differences in mantle margin configurations a result of subsequent divergence (this is perhaps easier to envisage if the calcareous craniaceans (Carlson 1993*b*) preceded the phosphatic lingulates (Popov *et al.* 1993)); is the brachiopod lophophore a *de novo* acquisition and how might it be derived from a pre-existing ciliary trap?

(*f*) *Halkieriids as primitive protostomes*

(i) *Introduction*

The Sirius Passet halkieriids and the Middle Cambrian *Wiwaxia* are interpreted as descendants of the group that gave rise to both the molluscs, and are closer respectively to the lineages leading to the brachiopods and annelids (figure 50). This hypothesis has, therefore, a direct bearing on the protostome radiation. It is in agreement with recent molecular data, based on comparisons of ribosomal RNA sequences, of a close relationship between molluscs and annelids (Ghiselin 1988; Lake 1990). This hypothesis has a long pedigree (Pelseneer 1899; Wilhelmi 1944; Vagvolgyi 1967; Eernisse *et al.* 1992), but has been overshadowed by the notion of the Articulata, a supposed superphylum that houses the arthropods and annelids (e.g. Wheeler *et al.* 1993). The halkieriid hypothesis also revives a largely neglected proposal (Morse 1873) that argues for a close link between annelids and brachiopods.

This section, therefore, explores the wider significance of the halkieriids in the context of existing hypotheses of metazoan relationships. With so little known about the internal soft anatomy of halkieriids and wiwaxiids a number of important questions about the type of body cavity, circulatory arrangement, nervous system, and excretory organs must remain conjectural or be inferred from living, and perhaps much modified, descendants. Two items, however, merit discussion: the nature of the body cavities (coelomic or haemocoelic) and degree of segmentation, in particular whether metameric. Concerning the first there is evidence that both halkieriids and *Wiwaxia* crawled across the substrate on a muscular sole, possibly employing monotaxic waves of contraction (see Voltzow 1988). Even though the ventro-lateral siculates are hypothesized to be precursors of the polychaete neurochaetae, in halkieriids and *Wiwaxia* it appears that the siculates were unable to perform a stepping action that characterizes the locomotion of walking polychaetes. Thus halkieriids appear to have had a locomotory style more akin to molluscs, suggesting that any coelom was restricted (probably to the gono-pericardium, see Salvini-Plawen 1990) and fluid pressure was transmitted via a haemocoel, derived in turn from a primitive embryonic cavity.

(ii) *Coelom and locomotion*

If the transition from halkieriids to annelids (polychaetes) via an animal similar to *Wiwaxia* is accepted, then this implies that the annelid coelom is an evolutionary novelty (see also Vagvolgyi 1967, p.165) rather than an archaic feature that lies near the base of metazoan evolution, as proposed by the influential German school that has explored the consequences of the archicoelomate hypothesis (e.g. Siewing 1980; Rieger 1985; and Reisinger 1972; Willmer 1990 for reviews). Although it is possible that halkieriids had a mollusc-like coelom i.e. around the heart, there is less reason to think the ancestor can be regarded as coelomate (e.g. Scheltema 1988, p. 66; 1993). Equally, the comment by Ghiselin (1988, p. 82) that 'The coelom [of annelids] ceased to function as a hydrostatic skeleton, and was replaced as the main body cavity by a haemocoel' is the precise reverse of the halkieriid hypothesis (figure 50).

What then is the nature of the first annelids? There is considerable doubt whether any of the archiannelids are primitive (see e.g. Clark 1969; Dales 1977). This polyphyletic group is primarily adapted to a meiofaunal existence (see Clark 1969, 1978) and probably independently derived from a number of annelid groups by heterochrony (e.g. Westheide 1985). In contrast, identifying the primitive annelid as an epifaunal macroscopic creature with large parapodia (see Westheide 1985) bearing prominent fascicles of neurochaetae, presumably used for a stepping motion across the substrate and perhaps for occasional swimming and broad notochaetae (that provided a protective coat of paleae; see also Storch (1968)) questions the highly influential views of Clark (1964, 1969, 1978, 1979; see also Fauchald 1974; Bergström 1989; Salvini-Plawen 1990) of primitive annelids being oligochaetoid with the coelom evolving as a response to precise control of peristaltic movement in the burrowing cycle (see also Freeman & Lundelius 1992, p. 239). In terms of speculation on early metazoan evolution the hypothesis of Clark's has been repeatedly championed by Valentine (1975, 1991, p. 394; see also Brinkhurst & Nemec 1987; Bergström 1990). In exploring the hypothesis of R. B. Clark, Fauchald (1974) further argued that the original function of the chaetae was to assist anchoring the worm in a burrow. His proposal that they 'evolved as roughened thickenings of the cuticle to increase the friction between worm and burrow' (Fauchald 1974, p. 496) now seems less plausible. The fossil record appears to reveal a very different story. If the halkieriid to polychaete annelid transition is accepted, then it seems possible that originally the coelom evolved to facilitate movement and control of the parapodia as partially hydrostatic structures, with the chaetae being used for two purposes: locomotion by the neurochaetae and defence by the notochaetae. This view accords with earlier doubts on R. B. Clark's hydrostatic hypothesis expressed by Runnegar (1982). This worker pointed out that evidence for a large coelom in the Vendian *Dickinsonia* substantially predated the rise of trace fossils indicative of burrowing by peristaltic activity.

Runnegar (1982) also proposed that the origin of the coelom was connected with increase in body size, whereas here we propose a more direct connection with epifaunal, stepping locomotion. This latter view is supported by studies of locomotion in the amphinomids (Marsden 1966), the possibly primitive status of which is discussed below. In this group the parapodia are of unusual importance in walking, with the body lacking the sinuous movements that otherwise characterize the polychaetes. Marsden (1966) stressed how the neuropodia become turgid with coelomic fluid during the power-stroke. Although she was doubtful that this locomotory style was primitive, it can now be seen to be a logical development from the halkieriid precursor. Marsden (1966) also noted that a corollary of hydraulic parapodia was the necessity for watertight septa to isolate each segmental compartment. In any event the *de novo* origination of the annelid coelom is consistent with its development in the embryo by splitting within the mesoderm (schizocoelic).

As explained above the feeding apparatus of *Wiwaxia* seems comparable to a molluscan radula (Conway Morris 1985*a*), and proposed similarities with polychaete jaws (Butterfield 1990) are less compelling. The Burgess Shale polychaetes, including *Canadia spinosa*, which appears to be most similar to *Wiwaxia*, lack evidence for jaws (Conway Morris 1979*a*). This loss may be correlated from a crawling animal grazing with radula to a walking polychaete which no longer has its feeding area continuously adpressed to the substrate. The feeding habits of the Burgess Shale polychaetes are uncertain, but the prominent proboscis of *Canadia* is consistent with predation or scavenging (Conway Morris 1979*a*).

(iii) *Trace fossils*

The question of locomotory styles raises the possibility that Cambrian trace fossils may provide contributory evidence (see also Bergström 1990). It is not unusual for traces consisting of longitudinal furrows, especially taxa such as the late Vendian-early Cambrian *Didymaulichnus*, to be attributed to molluscs (e.g. Young 1972), if not gastropods (e.g. Crimes *et al.* 1977, p. 133), despite the body fossil evidence of their being mostly minute in the Cambrian. Attention should also be drawn to the Upper Cambrian *Climactichnites*, a large trace that is now attributed to a mollusc-like animal engaged in inter-tidal excursions (Yochelson & Fedonkin 1993). More problematic is the single specimen of *Bunyerichnus dalgarnoi* from the Brachina Formation of South Australia, a unit that underlies the Ediacaran bearing Pound Quartzite in the late Precambrian. Glaessner (1969) opined that this fossil might have been produced by either a neomenioid aplacophoran or a shell-less chiton-like animal. The former alternative was refuted by Salvini-Plawen (1990, p. 5), while subsequently Glaessner (1984, p. 69–70) interpreted the fossil as part of medusoid. In a recent compilation (Runnegar 1992, p. 1010–1011) listed *Bunyerichnus* as a dubiofossil.

A corollary of the evolution of annelids from halkieriids and the prior development of epifaunal strolling polychaetes is that early burrows, especially from the lowest Cambrian (Nemakit-Daldyn, Tommotian and Atdabanian, i.e. pre-Sirius Passet fauna, figure 48), are unlikely to represent the activities of infaunal annelids (cf. Valentine 1991, p. 394), but rather other groups such as priapulids (see Conway Morris 1977) or the nemerteans that are now identified as part of the protostome radiation (Turbeville *et al.* 1992) and are known to be effective burrowers (Turbeville & Ruppert 1983).

(iv) *Metameric segmentation*

The origin of metameric segmentation, and the related questions of whether: (i) this condition is genuinely realized in molluscs (see Lemche & Wingstrand 1959; Vagvolgyi 1967; Salvini-Plawen 1981, 1990; Russell-Hunter 1988); and (ii) its development in annelids and arthropods is homologous (Lemche & Wingstrand 1959) as a result of shared ancestry is open to renewed scrutiny. In halkieriids serial repetition is most evident in the rows of palmate and siculate sclerites (figure 49) and the internal rods. It remains conjectural whether this is metameric, but the regularity of spicule growth in turbellarians (see Rieger &

Sterrer 1975), from which the halkieriids are presumed to have arisen, cautions against uncritical acceptance. The styles of segmentation in molluscs and annelids, however, can be seen as emerging from the siphogonuchitid/halkieriid condition, rather than evolving from metameric ancestors (e.g. Lemche & Wingstrand 1959; Götting 1980). In molluscs the segmentation of organ system is most obvious in the chitons and monoplacophorans, but can also be traced in bivalves and cephalopods. This arrangement may be derived from the halkieriids but the irregular repetition suggests that it is not reduced from a more perfect metamery, a point already argued by various zoologists (e.g. Hammarsten & Runnström 1925; Steinböck 1963; Russell-Hunter & Brown 1965; Russell-Hunter 1988). This interpretation is an important departure from Lemche and Wingstrand's (1959; see also Lemche 1959*a*) notion that the molluscs, and specifically the tryblidiid monoplacophorans (Tergomya), show 'true segmentation' (Lemche 1959*b*, p. 380), but is more in keeping with Wingstrand's (1985) measured assessment of molluscan metamery which concedes that it is not directly comparable to the so-called eumetamery of annelids (see also Beklemischev 1958).

In annelids, however, metameric segmentation is interpreted as a further elaboration of halkieriid seriality and as with the development of the coelom is seen as a response to locomotory needs, specifically the development of ordered stepping movements of the neuropodia during the walking cycle. In this scenario the regularization of metamery arises from the metachronal waves of parapodial movement mediated via ordered bursts of neuronal firing from the ventral nerve chords.

(v) *Origin of annelids*

It will be apparent from the above discussion that to describe *Wiwaxia* as an unequivocal polychaete worm (Butterfield 1990, 1994; see also Edgecombe & Crisp 1991; Haszprunar 1992; Levinton 1992 for uncritical acceptances of this notion) neatly misses its true phyletic importance. It could be argued that the definition of polychaetes should be expanded to encompass *Wiwaxia*, but such a manoeuvre would obscure the evolutionary significance of transitions between what we choose to call phyla, and is unlikely to find favour among polychaete specialists when it is realized that in *Wiwaxia* there is neither an inter-ramal space nor parapodia, but rather in this region a continuous zone of cultrate sclerites. There is, moreover, apparently little reason to follow Butterfield (1990) in equating the entire set of sclerites in *Wiwaxia* (and thus halkieriids) to the paleal notochaetae of extant polychaetes, not least because of comparison of the neurochaetae with the discrete fan-like arrangement of the siculates (§7*d* (ii)). Concerning the fossil record of Cambrian polychaetes information is largely derived from the Burgess Shale (Conway Morris 1979*a*). The earliest polychaete appears to be an undescribed taxon from the lower Cambrian Sirius Passet fauna (figure 48). To date no polychaetes have been recovered from the Chengjiang fauna, which is probably slightly older (Conway Morris 1993*b*, figure 1). Which of the described Cambrian taxa is most primitive is conjectural, although leading candidates are *Burgessochaeta* and *Canadia*. Both are known to have chaetae with an ultrastructure identical to the sclerites of *Wiwaxia* (Butterfield 1990, personal communication). A primitive status for *Burgessochaeta* might be posited on account of the neuro- and notochaetae being identical. In the case of *Canadia*, however, a more immediate derivation of the chaetae from halkieriid sclerites, especially the prominent fans of neurochaetae from similarly disposed bundles of siculates, provides a strong argument for this genus being more primitive. A potentially important feature, hitherto overlooked, is the respiratory structures in *Canadia* that occupy the inter-ramal region of the parapodia (figure 47*i*). They were referred to as branchiae (Conway Morris 1979*a*), but these structures resemble none of the wide variety of body extensions that serve as gills in the polychaetes (e.g. Gardiner 1988; Storch & Alberti 1978). They do, however, bear a striking resemblance to the ctenidia, the characteristic respiratory organ of molluscs, including the caudofoveate aplacophorans (e.g. Salvini-Plawen 1968, figure 12, 1969, figure 11; Scheltema *et al.* 1994, figure 4C) and chitons. It is proposed that branchiae of *Canadia* conceivably represent relict organs, possibly present in halkieriids (? beneath the posterior shell, see above), lost in more derived polychaetes but otherwise retained in the descendant Mollusca, where at present they are regarded as a unique feature of the phylum (Russell-Hunter, 1988, p. 751).

The possible relationships between *Canadia* and the extant chrysopetalids was discussed by Conway Morris (1979*a*), and although the literature on the Recent group has continued to grow (e.g. Perkins 1985; San Martin 1986; Watson Russell 1986, 1991) the new information makes it no easier to decide whether the similarity is one of convergence or genuine phyletic affinity. Accepting the latter it is necessary, but not unreasonable, to invoke a greater cephalic complexity, acquisition of stylet-like jaws, loss of branchiae(? = ctenidia), development of compound neurochaetae, acquisition of dorsal and ventral parapodial cirri and frequently a restructuring of the insertion pattern of the notochaetae (paleae). Chrysopetalids are generally placed close to the aphroditaceans and although the latter are characterized by the sea-mouse *Aphrodita* the group also includes the paleae-bearing *Palmyra* which had earlier been housed within the chrysopetalids (Watson Russell 1989). Storch (1968) considered the aphroditaceans to be primitive but this view was disputed by Mettam (1971; see also Dales 1977; Clark 1979) who considered the complex musculature to be indicative of a highly derived state. Although the primitive status of the aphroditaceans appears to be broadly consistent with the phylogenetic thesis presented here, it may be significant that the paleae in *Palmyra* do not show the camerate interior that characterizes the chrysopetalids and might be homologous with the camerae of halkieriid sclerites. Although almost nothing is known of the musculature of either *Canadia* or *Burgessochaeta* (see Conway Morris 1979*a*), both taxa are reconstructed with a box-like cross section, reminiscent of the aphroditaceans. It is possible that these Cambrian polychaetes had a comparably intricate system of branching muscles (see Storch 1968) that served to brace the newly enlarged coelomic cavity.

Although based on the erroneous assumption that *Wiwaxia* was a genuine polychaete the comments by Westheide & Watson Russell (1992, p. 198; see also Westheide 1985; Watson Russell 1986, p. 39) that: 'We strongly favour the view of early annelid ancestors possessing a thickset dorsal cover of prominent chaetae for defensive and protective purposes. Together with the evolution of segmentation there might have taken place a separation into protective notochaetae and neurochaetae with functions related to locomotion', now appears to find confirmation in the fossil record. In principle a transitional phase between halkieriids and polychaete locomotion with muscular contractions of the sole and a stepping motion of the nascent neurochaetae arising from what may have been discrete lobes inflated hydraulically by coelomic fluid can be envisaged with the latter taking precedence as more energetically efficient. Interestingly some living polychaetes, including the amphinomids whose possibly primitive status is discussed below, still lubricate their passage over the substrate using ventral mucous glands (Marsden 1966).

If the clade that is hypothesized to include *Canadia*, chrysopetalids and aphroditaceans is accepted as among the most primitive of polychaetes, this has some important phylogenetic implications. An unusual feature of aphroditaceans (and amphinomids, whose primitiveness and relationship to aphroditaceans continues to be controversial (Marsden 1966)) is tetraneury, where the characteristic double ventral cord is paralleled by abaxial cords that supply the parapodia (note, in the chrysopetalids, whose possibly primitive status is discussed elsewhere, Ehlers (1864, p. 87) only noted a ventral nerve cord composed of two strands). The significance of tetraneury is debated. Gustafson (1930) proposed that this neural arrangement (in amphinomids) was a secondary feature and reflected the complex and specialized anatomy of the parapodia, whereas Storch (1912, 1913) and Storch (1968) proposed that this arrangement was primitive (see also Reisinger 1972). Although these latter views have been disputed by Mettam (1971; see also Dales 1977), the presence of tetraneury in molluscs (most clearly expressed in aplacophorans and chitons (Salvini-Plawen 1981, 1990)), as well as monoplacophorans (Lemche & Wingstrand 1959) suggests that this may indeed be a primitive condition (Reisinger 1972; Salvini-Plawen 1981) also present in the halkieriids and may be inherited from the 'orthogonal' pattern of their turbellarian ancestors (Hanström 1928; Reisinger 1972). Note, however, that there are histological similarities between the nervous system of annelids and molluscs which do not extend to the turbellarians (see Haszprunar 1992).

Much remains to be learnt about the annelid radiation but it is agreed that the initial appearance of jaws in Ordovician polychaetes and multiple evolution thereafter (e.g. Wolf 1980; Purschke 1987*a*, *b*, 1988*b*), the tubicolous habit with a calcareous or agglutinated skeleton in polychaetes such as serpulids and pectinariids respectively, the deviation of oligochaetes from polychaetes (possibly in association with the invasion of land; see Conway Morris *et al.* 1982; Manum *et al.* 1991) and the evolution of leeches from oligochaetes (see Purschke *et al.* 1993) are all landmarks to which the fossil record may contribute significantly.

(vi) *Origin of brachiopods*

The proposed link between halkieriids and brachiopods is discussed above (§7*e*), and only a few more general comments are given here. Although generally regarded as deuterostomes, overall the evidence is very equivocal (e.g. Willmer 1990). Recent molecular data (e.g. Lake 1990; Adoutte & Philippe 1993) also place the brachiopods firmly in the protostomes. Despite the problems inherent in biochemical phylogeny (see Mangum 1990), some evidence is also emerging to link the lophophorates with other protostomes. Specifically, the distribution of enzymes such as opine oxidoreductases not only place brachiopods, ectoprocts and phoronids together but indicates a significant relationship to molluscs (Hammen & Bullock 1991; see also Hammen & Fielding 1993). Such a placement had been revealed earlier for the brachiopods alone (Livingstone *et al.* 1983), but guided by preconceptions of orthodox phylogeny these authors had included the brachiopods in the deuterostomes. Other biochemical support for placing the brachiopods and ectoprocts in the protostomes is the common absence of sialic acids, in contrast to the deuterostome phyla (Warren 1963; Segler *et al.* 1978). This implies that various characters, especially embryological such as the fate of the blastopore, cleavage patterns and derivation of coelomic cavities are not of such fundamental phylogenetic significance as generally thought. The variability of these features within the deuterostomes and protostomes is reviewed by Nielsen (1985; see also Fioroni 1980). In particular, the supposed reliability of radial cleavage and the fate of the blastopore in embryology for phylogenetic determination have been thrown into serious doubt by Telford & Holland (1993; see also Wada & Satoh 1994) who demonstrated a position within the protostomes for the chaetognaths on the basis of molecular biology, so overturning their traditional placement in the deuterostomes. Derivation of the sessile brachiopods from a vagrant halkieriid suggests that suspension feeding and the development of the lophophore are *de novo* acquisitions, with the latter derived from ciliated extensions of ventral tissue adjacent to the anterior end. The presence of tentacular crowns in the sessile serpulid polychaetes would show a parallel development from a vagrant, jawed ancestor.

Such a proposal needs to be reconciled with the very strong similarity of such lophophores with those of the pterobranch hemichordates (Halanych 1993), whose place in the deuterostomes is not in doubt. That the lophophores are indeed convergent structures seems more likely as the molecular data (Ishikawa 1977*a*, *b*; Livingstone *et al.* 1983; Lake 1990; Hammen & Fielding 1993) is consistent with placing the brachiopods and their relatives in the protostomes. The purported derivation of the brachiopod shell from pre-existing structures in the halkieriids also argues for a fundamental homology rather than convergence with each other. Presumably, the halkieriids were equipped a mantle, at least one mantle lobe and a shell material capped with an organic periostracum.

(vii) *Protostome diversification*

The role claimed for halkieriids and relatives in the evolution of annelids, brachiopods and molluscs should not obscure the many problems that remain in understanding protostome evolution. It is argued below that the arthropods are a distinct protostomian clade, with no close relationship to the annelids. Arguments exist, however, for a number of other groups being related to the annelid-brachiopod-mollusc stock but whose derivations vary at present from uncertain to enigmatic. Perhaps least controversial in this category are the pogonophorans and vestimentiferans. Although at least the latter have been regarded as rather distant from the annelids (e.g. Jones 1985), recent evidence (e.g. Southward 1988; Kojima *et al.* 1993) has reinforced the closeness of these groups. On the other hand the status of the lobatocerebrids, an enigmatic group of worms that Rieger (1988; Haszprunar *et al.* 1991) argues may have arisen from close to the stem annelids, is no better resolved.

It is generally agreed that sipunculans and echiuroids are closely related to annelids (e.g. Clark 1969), whereas Scheltema (1993; see also Inglis 1985, p. 166) has vigorously reiterated possible connections between the sipunculans and molluscs (see Gerould 1907) emphasizing the so-called 'molluscan cross' in early development (but see Salvini-Plawen 1981, p. 237–238; Haszprunar 1992) and larval similarities (see Clark 1969 for a critical review). That a sipunculan-mollusc relationship should not be dismissed is also evident from biochemical evidence of the octopine pathway (Livingstone *et al.* 1983). Unfortunately the fossil record of echiuroids and sipunculans is almost non-existent (see Conway Morris 1985*b*), but in both cases their spacious coelom and effective absence of segmentation may reflect a sedentary existence (e.g. Clark 1969). The suggestion by Clark (1969, p. 15), however, that the sipunculans 'diverged from the preannelid stock' before the tetraneurous condition was acquired, now appears less plausible in view of its apparently primitive nature and inferred presence in halkieriids. In passing Clark (1969; see also Vejdovsky 1882; Dahl 1955) mentions various similarities between the sipunculans and the sternaspids (see also §7*d* (iv)) and even if these are without phylogenetic significance they may reflect parallel paths to effectively sessile worms with large undivided body cavities. Molecular evidence for a close link between brachiopods (as *Lingula*) and sipunculans (as well as priapulids) in terms of haemerythrin amino acid sequences (Curry & Runnegar 1990; Yano *et al.* 1991; Runnegar & Curry 1992) needs further exploration. It will be important to discover the corresponding sequences in polychaetes such as *Magelona*, which also possess haemerythrin.

The purported link between annelids and halkieriids throws further doubt on the popular notion of a close alliance between annelids and arthropods (e.g. Wägele & Wetzel 1994), notwithstanding Ghiselin's (1988, p. 68) comment that 'nobody contests the placement of the Arthropoda' with the Annelida. Nevertheless both belong to the great protostomian radiation and may be derived ultimately from turbellarian predecessors. In the case of halkieriids the evolutionary steps are effectively the same as those posited by various authors (e.g. Hammersten & Runström 1925; Fretter & Graham 1962; Steinböck 1963; Vagvolgyi 1967; Peters 1972; Stasek 1972; Freeman & Lundelius 1992, p. 237) to explain the transition from turbellarian to mollusc with the development of a dorsal mucoid coat, later calcified, marginal respiratory ctenidia, muscular locomotion, and radula. In contrast proposals for an alliance between the molluscs and arthropods have been generally muted (e.g. Lemche 1959*b*, 1966), although persistent mention is made of the shared feature of the blood pigment haemocyanin. This protein, however, very probably evolved independently in each phylum (Mangum 1990). The story of arthropod derivation from a turbellarian stock echoes rather than parallels that of the halkieriids. Amongst the Cambrian arthropods there is evidence for a significant radiation of lobopods (e.g. Hou *et al.* 1991; Ramsköld & Hou 1991) and some of the most primitive arthropods may be represented by this group and forms such as the Sirius Passet *Kerygmachela* which have dorsal gill-like extensions above the lobopods (Budd 1993). The action of the latter structures, used for walking in a manner reminiscent of the ventral neuropodia of polychaetes, presumably relied on enlargement of the haemocoel for their hydrostatic movement. Only subsequently were these appendages sclerotized to form the characteristic jointed limb that often retains a hydrostatic component, as in many spiders. Derivation of arthropods from a turbellarian ancestor via a lobopod radiation indicates a separate origin for metameric segmentation (Inglis 1985; Minelli & Peruffo 1991; Valentine 1991, 1994), albeit based ultimately on the pseudometamerism of turbellarians that via another avenue gave rise to partial segmentation in molluscs and metameric segmentation in annelids.

8. CONCLUSION

The extinct halkieriids and near relatives appear to have had a pivotal role in the origin of annelids, brachiopods and somewhat removed the molluscs, and indirectly a further suite of phyla that may include the pogonophorans (including vestimentiferans), ectoprocts and echiurans. The material from the Sirius Passet is invaluable because it allows inspection of the halkieriid scleritome; but the actual events that led to the rise of annelids, brachiopods and molluscs from halkieriid ancestors were evidently earlier in the Cambrian (figure 48). Whether the conchiferans (monoplacophorans and their descendants) arose from the chitons or from other types of siphogonuchitid/halkieriid is a moot point. Aplacophorans may represent an exceedingly primitive mollusc group, descendants of pre-halkieriids, but a more derived status seems a feasible alternative. Annelids are believed to have evolved from an animal close to *Wiwaxia*, with chrysopetalids among the most primitive of polychaetes. Other primitive groups appear to include amphinomids, aphroditaceans and possibly the sternaspids whose posterior plate may be a relic of the posterior shell in halkieriids and the questionable shell-like structure in *Wiwaxia*. Brachiopods probably evolved from a halkieriid more similar to *H. evangalista*, probably via a juvenile form. As knowledge of halkieriid taxonomy improves, so these proposed relationships (figure 50) may be tested more fully. In conclusion, the thesis that the phyla were already separated from each other in the Cambrian, recently restated by Bergström (1989, 1990), may not be entirely correct. The statement by Bergström (1990, p. 9) that: 'Various problematic fossils therefore are unlikely to be intermediate between phyla' is not consistent with the evidence from halkieriids.

An extensive review of the earlier literature on protostomian inter-relationships in the context of halkieriid evolution might satisfy historians of science, but is a largely redundant exercise when speculation and data are in such imbalance. Elements of the halkieriid/siphogonuchitid hypothesis of molluscan origins may, of course, be discerned in earlier work (e.g. Vagvolgyi 1967; Stasek 1972; Götting 1980; Salvini-Plawen 1980, 1981), but not surprisingly there remain significant differences. Likewise because the origin of annelids has largely been considered either in terms of a purported link with arthropods (Articulata) or as an oligochaetoid burrower (Clark 1964, 1969, 1979), their derivation from anything like a halkieriid has for the most part remained unconsidered. Thus for Vagvolgyi (1967, p. 156) to write: 'There is no evidence whatsoever for the assumption that annelids had ancestors with characteristic molluscan features, or that molluscs had ancestors with characteristic annelid feature [sic]' reveals the danger of relying too exclusively on data from extant forms. However, credit is certainly due to the group of workers (e.g. Hammarsten & Runnström 1925) who argued for a close relationship of annelids and molluscs with subsequent evolution of the annelidan coelom, and in Hammarsten & Runnström's (1925) view a common derivation from a turbellarian-like form (see also Vagvolgyi 1967). Similarly, the origin of brachiopods has been largely overshadowed by their supposed place close to or within the deuterostomes. In this context, therefore, the prescient discussion by Morse (1873) of a relationship between annelids and brachiopods deserves special note. The halkieriid hypothesis adds weight to recent data from molecular biology concerning a close relationship between molluscs and annelids, although Ghiselin's (1988, p. 81) proposal that: 'The molluscs evolved from something like an annelid' can now be seen to be effectively back-to-front (see Johansson (1952) and Valentine (1991) for similar conclusions; see also Vagvolgi 1967, p. 156 for a critical appraisal of the directionality of mollusc-annelid evolution). Moreover, despite the undoubtedly vital contributions of molecular biology to understanding metazoan evolution, it is important to realize; (i) sequence data may not provide unique solutions (see also Wägele & Wetzel 1994), especially during times of rapid diversification; and (ii) because inter-relationships are established on extant taxa that are highly derived, documenting the actual transitional forms that link what are now called phyla is only possible from the fossil record (Conway Morris 1993*b*).

Even though little is known about the internal anatomy of halkieriids and nothing directly of their embryology or larval development, it seems likely that the metameric segmentation and coelom of annelids emerged as a functional consequence of parapodial movement. Thus the coelom is unlikely to be an ancient feature of the bilaterans, rather it is polyphyletic and in the annelids its employment for burrowing is a secondary consequence (contra Clark 1964). Second, metamerism is almost certainly a grade and in its most developed metameric form appears to have been achieved at least three times: annelids, arthropods and chordates. The evolutionary steps that led from halkieriids to annelids seems to leave no room for arthropods (cf. Lemche & Wingstrand 1959; Lemche 1966), a conclusion in agreement with the recent analysis of comparative anatomy of extant forms of Eernisse *et al.* (1992). Rather the ancestry of arthropods may be traced to the lobopods and possibly related forms such as *Anomalocaris* and *Opabinia* (Budd 1993; see also Dzik & Krumbiegel 1989). The transition from a turbellarian-like worm to a primitive lobopod and pre-halkieriid bearing sclerites respectively seem feasible, but the closeness of the respective turbellarian stocks is unresolved.

Finally despite strong assertions that the phoronids and brachiopods belong to the deuterostomes (e.g. Zimmer 1973; Carlson 1993*a*), a critical review suggests the picture is much more equivocal (Willmer 1990). The proposal that brachiopods are indeed close to annelids is also supported by a variety of molecular data (Field *et al.* 1988; Lake 1990; Adoutte & Phillippe 1993; see also Ishikawa 1977*b*).

Several palaeontologists have explored early metazoan evolution in the context of the fossil record (e.g. Valentine 1975, 1991, 1994; Bergström 1989), but most of these schemes remain rather speculative. Thus much of Valentine's work has been strongly influenced by Clark's hypothesis of the origin of the coelom, which as formulated now appears to be in doubt. Bergström's (1989) invocation of a slug-like animal, pseudosegmented and showing spiral cleavage, giving rise to the majority of triploblastic phyla at first sight appears to accord well with the proposed role of the halkieriids and near relatives. A closer reading, however, shows that overall the correspondence is rather weaker, especially as the proposed 'procoelomates' of Bergström (1989, figure 5) are envisaged as giving rise to iterative stocks destined to be identified as the principal phyla recognized today. The fossil record has been generally regarded as silent on the problem of the origin of phyla, not least because proposals such as the role of the lobopod *Xenusion* and priapulids in protostome evolution (Dzik & Krumbiegel 1989) or the calcichordates in deuterostome diversification (e.g.

Jefferies 1990) remain deeply controversial.

It is more important to stress that although the recognition of the common ancestor of annelids, brachiopods and molluscs is not without interest, in principle the status of such a discovery is equivalent to the contribution palaeontology has made to understanding other evolutionary transitions such as those leading to amphibians (Coates & Clack 1990), reptiles (Smithson *et al.* 1994), mammals (Kemp 1982) and turtles (Lee 1993). In all these cases although the macroevolutionary consequences are plain to see, the processes by which phyla or other higher taxa arise appear to be step-like and gradual. A cardinal failure of proponents of macroevolutionary mechanisms to explain the origin of phyla (a concept largely dependent on the benefits of hindsight, see Conway Morris 1989*b*) seems to rest on an undue emphasis on the disparity of extant forms and an inability to envisage or identify the nature of transitional forms.

There is also a small irony to consider. In redescribing *Wiwaxia* one of us (Conway Morris 1985*a*, p. 572), while recognizing its molluscan affinities, regarded it as a distinct group and wrote: 'if the clock was turned back so metazoan diversification was allowed to re-run across the Precambrian-Cambrian boundary, it seems possible that the successful bodyplans emerging from this initial burst of evolution may have included wiwaxiids rather than molluscs'. On the basis of this statement an elaborate story of the significance of Burgess Shale fauna was presented by Gould (1990, p. 189) amongst which the hypothetical consequences of re-running this adaptive radiation and the purported role of macroevolutionary processes were writ large. It now seems that so far as the wiwaxiids (and halkieriids) are concerned there is no need to re-run anything, as the end-results are the familiar annelids, molluscs and perhaps more surprisingly the brachiopods.

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Figure 9. For description see opposite.

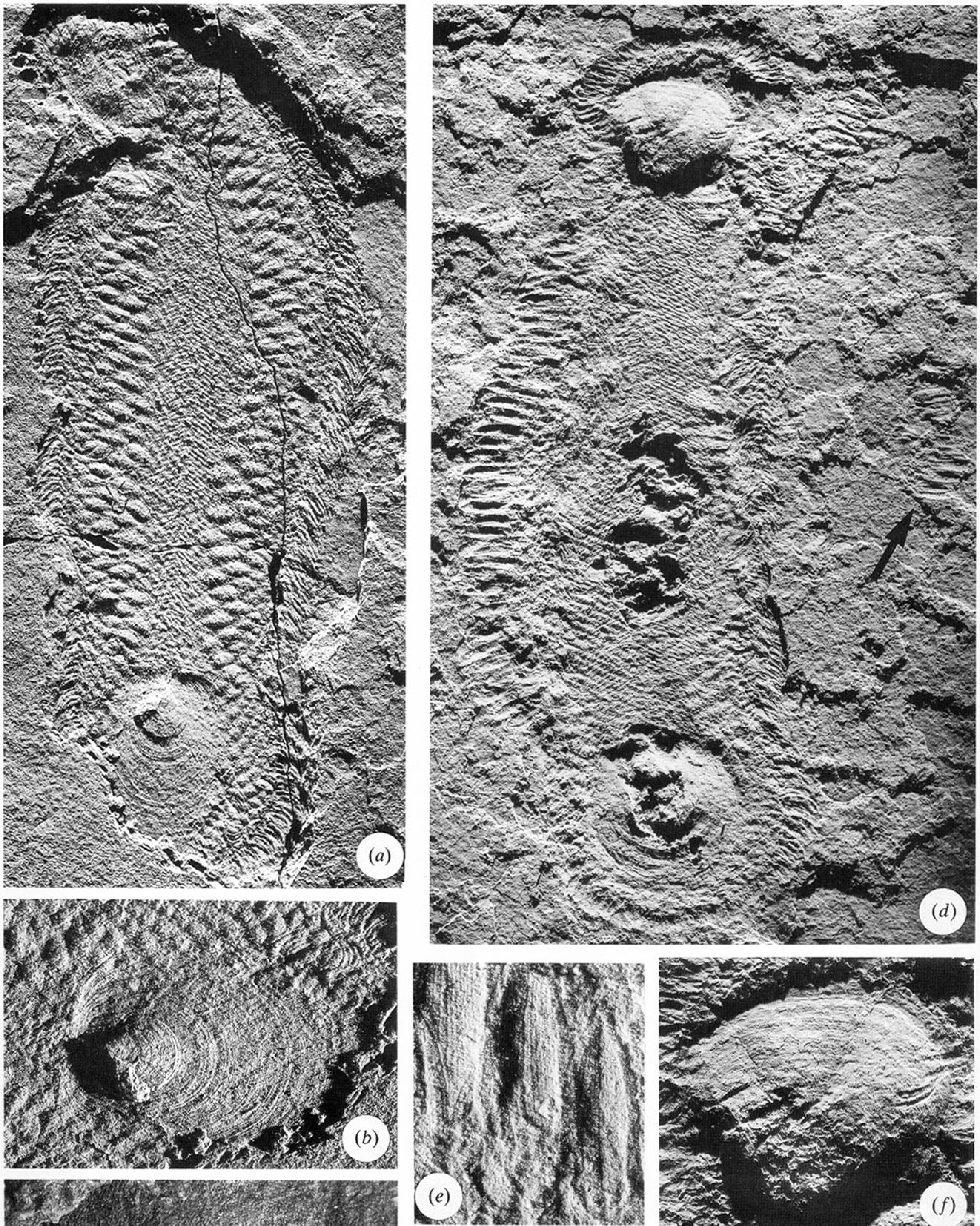

Figure 12. For description see opposite.

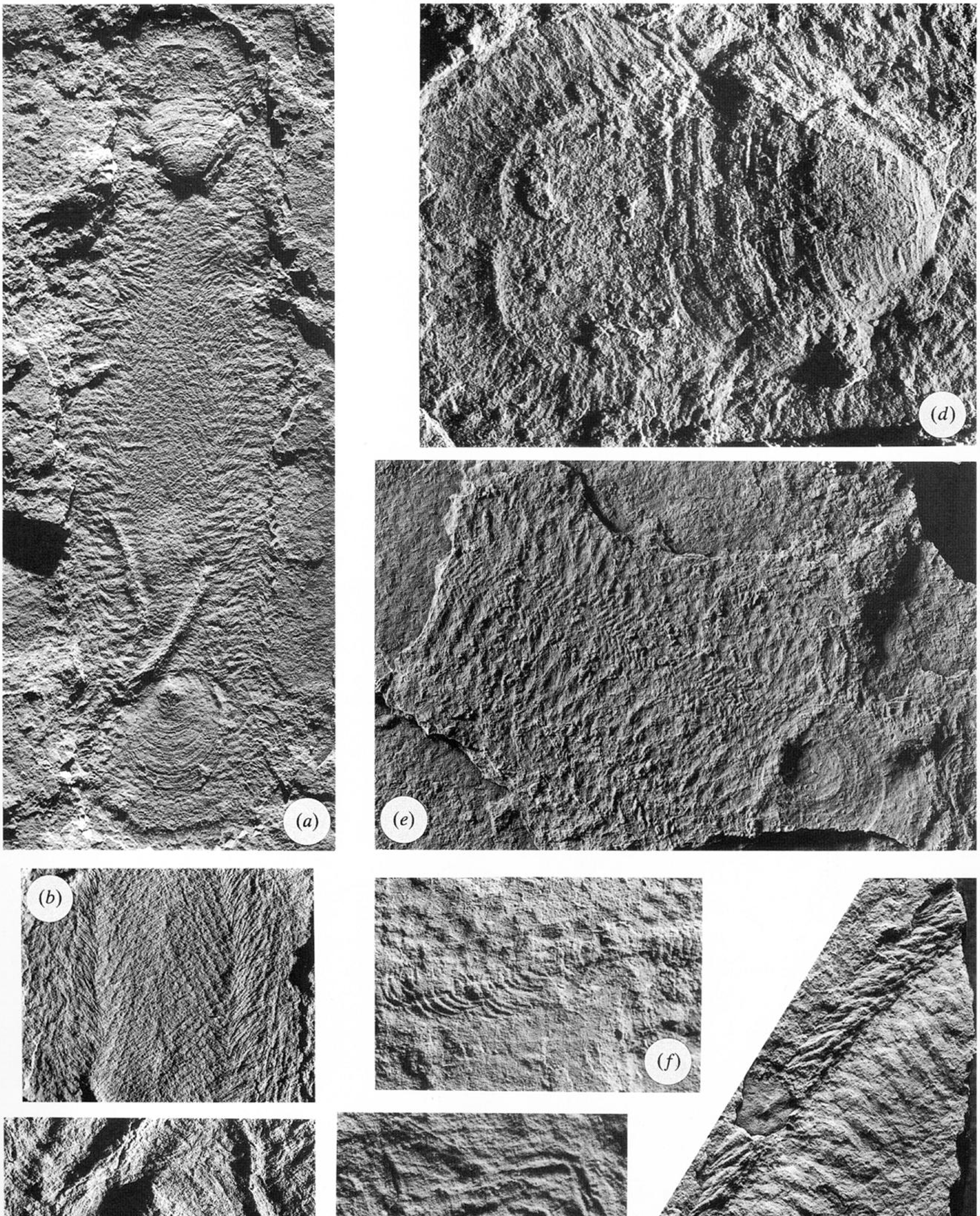

Figure 16. For description see opposite.

Figure 22. For description see opposite.

Figure 27. For description see opposite.

Figure 30. For description see opposite.

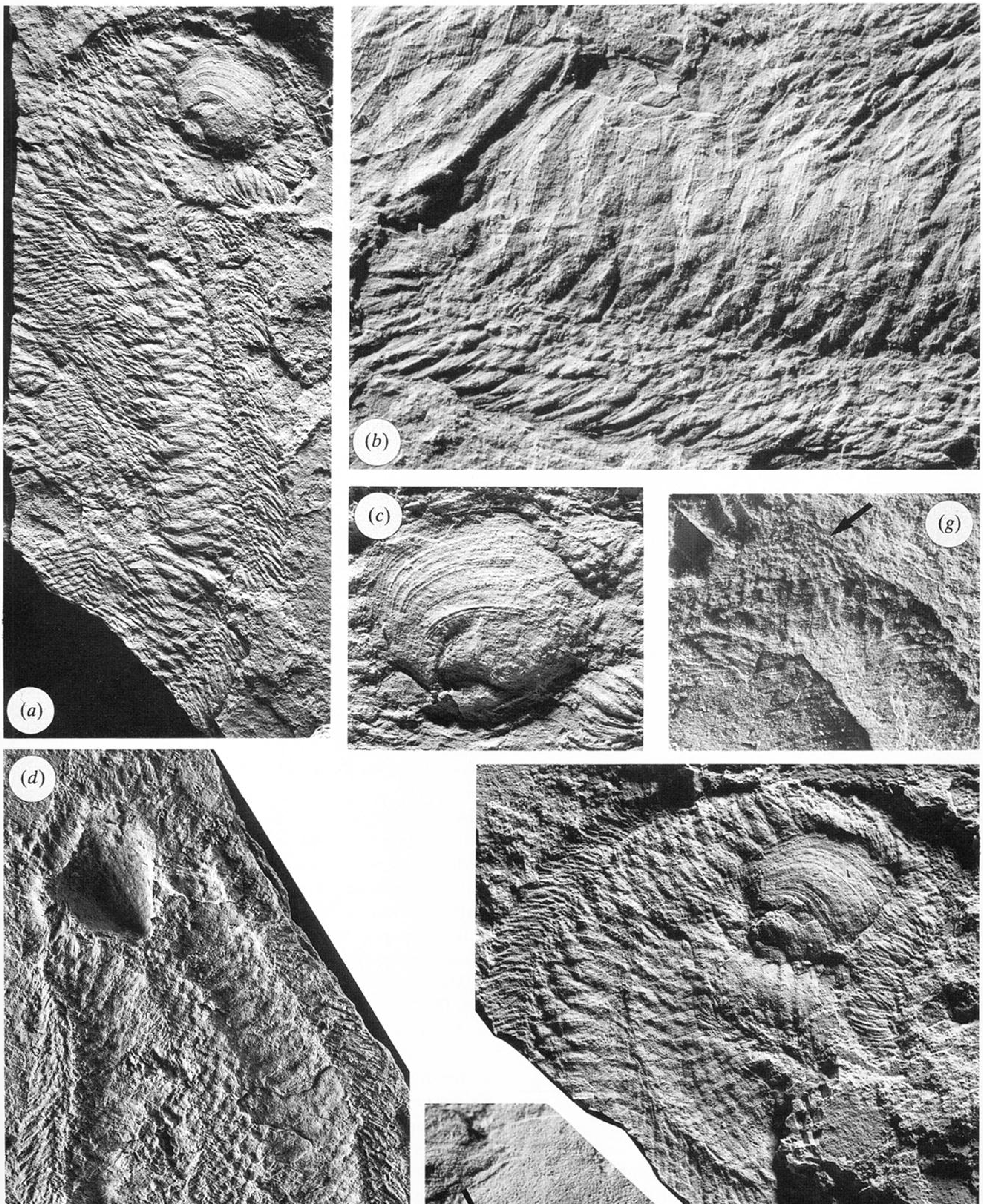

Figure 35. For description see opposite.

Figure 39. For description see opposite.

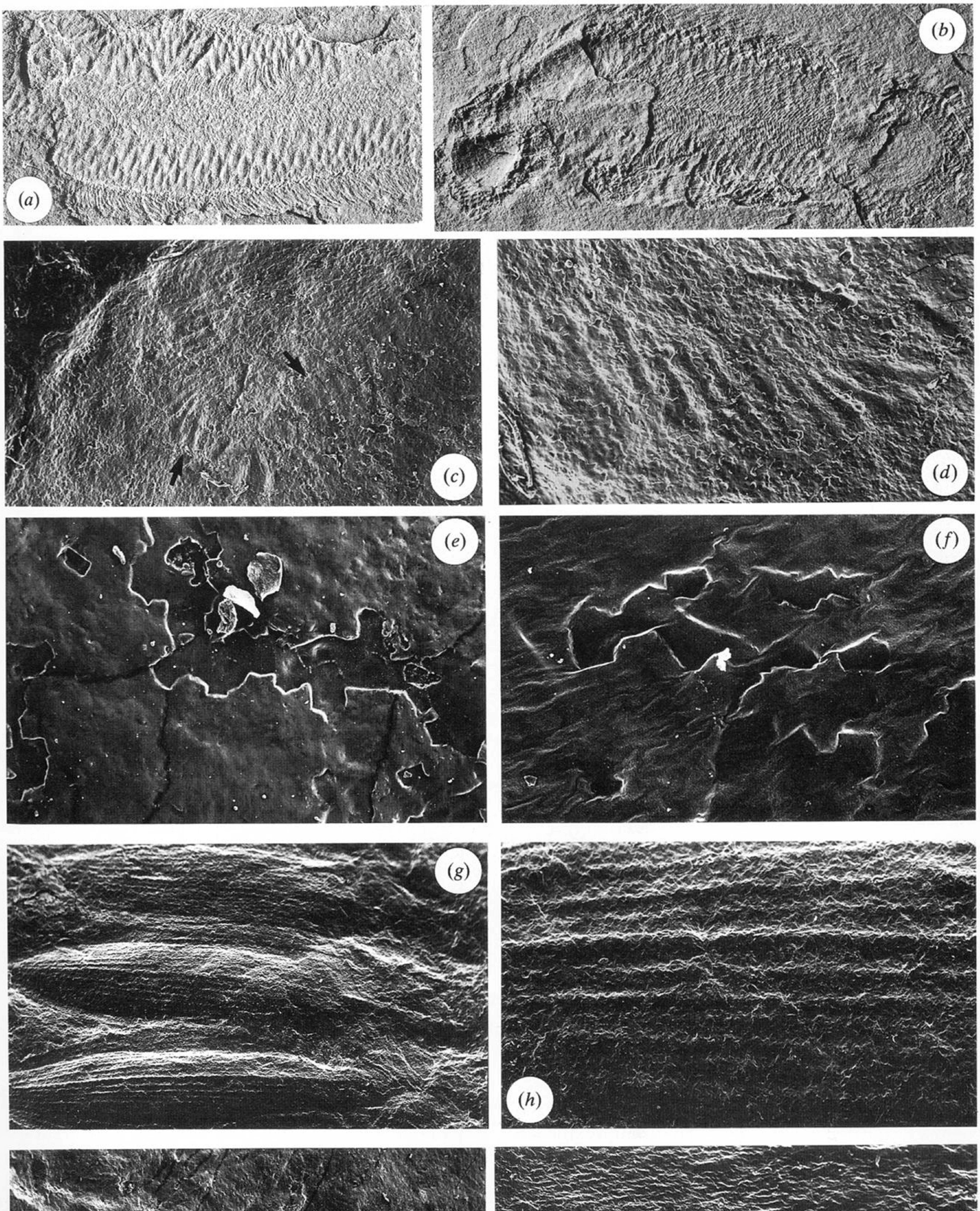

Figure 42. For description see opposite.

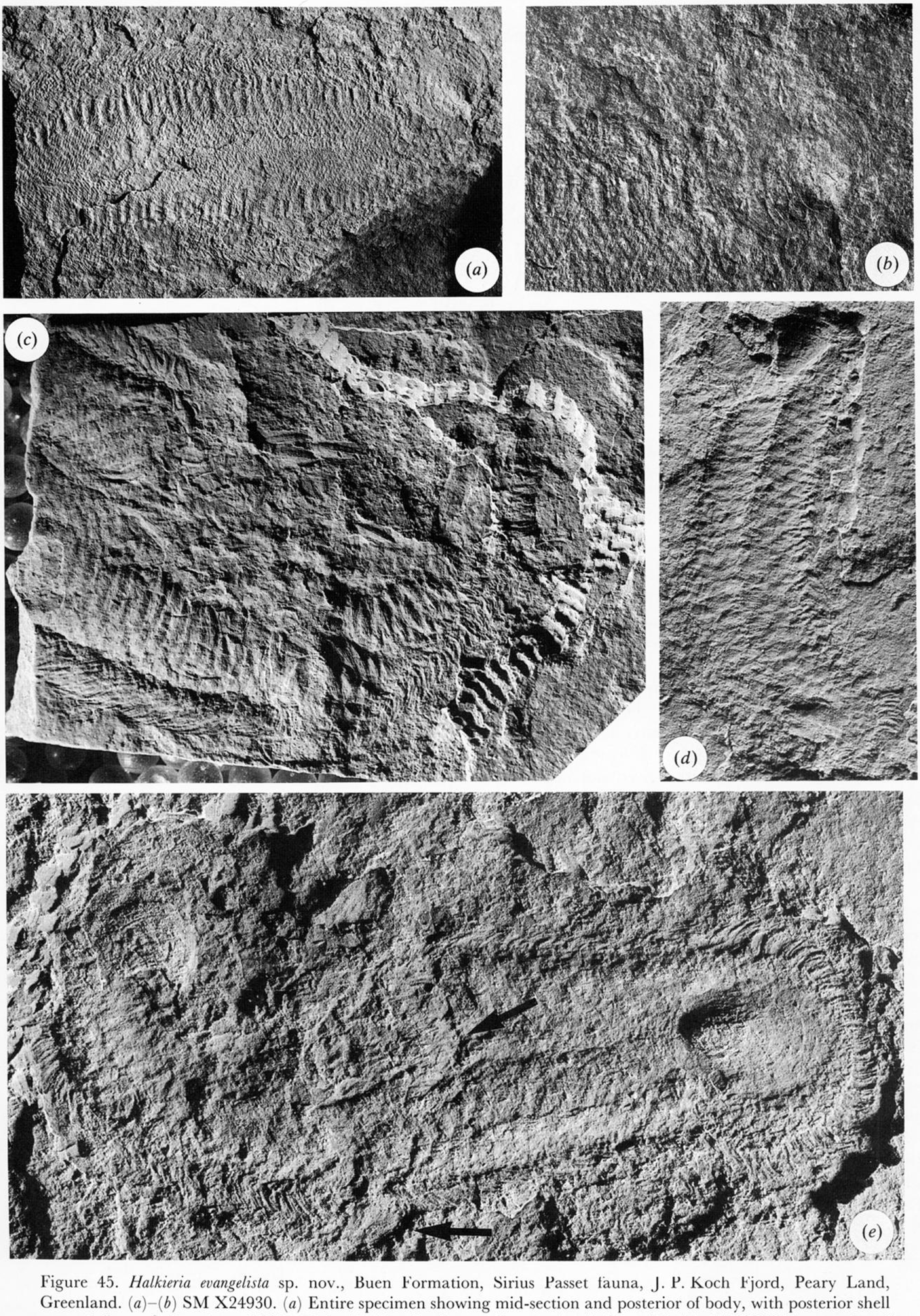

Figure 45. *Halkieria evangelista* sp. nov., Buen Formation, Sirius Passet fauna, J. P. Koch Fjord, Peary Land, Greenland. (*a*)–(*b*) SM X24930. (*a*) Entire specimen showing mid-section and posterior of body, with posterior shell rotated forwards by about 120°, × 2.1. (*b*) Detail of rotated posterior shell, × 3.6. (*c*) SM X24931, anterior of specimen showing possible evidence for predation, × 2.6. (*d*) SM X24932, entire juvenile specimen, × 5.9. (*e*) SM X24933, entire specimen, apparently superimposed on second halkieriid (arrowed), × 5.8.

Figure 47. For description see opposite.