A NEW CAMBRIAN LOPHOPHORATE FROM THE BURGESS SHALE OF BRITISH COLUMBIA

by s. CONWAY MORRIS

ABSTRACT. A single specimen (part and counterpart) of a new genus and species, *Odontogriphus omalus*, from the Burgess Shale (middle Cambrian) is described. Despite poor preservation its affinities appear to lie with the lophophorates. The simple lophophore contains tooth-like elements that are similar to certain Cambrian conodonts. It is suggested that this new genus and species is an example of a conodontophorid.

DURING a search in March 1974 through the very extensive collections of Burgess Shale fossils in the National Museum of Natural History (formerly the U.S. National Museum), Washington, D.C., a sawn slab bearing the specimen described here was noticed and set aside for further study. Shortly afterwards the counterpart was found elsewhere in the collections. The specimen had evidently never been noted by any other worker. No other specimens have been found.

STRATIGRAPHY

The Burgess Shale was discovered by C. D. Walcott in 1910, a year after he had found a dislodged slab containing soft-bodied fossils. Quarrying of the rock unit that yielded the soft-bodied fossils, the 7 ft 7 in. (2·31 m) thick Phyllopod bed, continued intermittently until 1917. An enormous number of specimens (*c.* 50 000) was collected and shipped to the U.S. National Museum (USNM). The broad history of the discovery of the Burgess Shale and research on its fauna and flora has been reviewed by Whittington (1971). The Burgess quarry was reopened in 1966 and 1967 by a party from the Geological Survey of Canada (GSC), with the co-operation of authorities of the Yoho National Park and the Parks Canada, Department of Indian and Northern Affairs, Ottawa, and the fauna and flora is currently receiving critical and detailed study by several workers, based principally at Cambridge. This article is the first in a series which will deal with worms and miscellaneous other fossils from this famous locality.

The stratigraphic position of the Burgess Shale is now fairly well understood (Fritz 1971). The shale forms a lentil in the otherwise impure limestone and shale sequence of the Stephen Formation. The Phyllopod bed occurs near the base of the Burgess Shale (Walcott 1912*b*). The Stephen Formation was deposited in a basin that lay to the south of a prominent and steep carbonate bank whose trend was roughly north-north-west (McIlreath 1974). Fritz (1971) was able to show that the Burgess Shale itself was laid down in water several hundred feet deep. There is considerable evidence that the Phyllopod bed, at least, was deposited from a succession of mudflows or turbidites (Piper 1972; Whittington 1971).

A

The larger slab of rock, which bears the counterpart, is labelled 35k. This is the USNM locality number for the Phyllopod bed (Walcott 1912a). The specimen is associated with *Eldonia ludwigi* Walcott, 1911a, *Ottoia prolifica* Walcott, 1911b, semi-isolated scales of *Wiwaxia corrugata* Walcott, 1911b, arthropods, and un-identifiable debris of organic origin. GSC collections show that *E. ludwigi* is most abundant at the level 3 ft 7 in.–4 ft 0 in. (1·09–1·22 m) above the base of the quarry, and Walcott (1912a) noted a similar distribution. This strongly suggests that *Odonto-griphus omalus* also comes from this horizon.

SYSTEMATIC PALAEONTOLOGY

Superphylum LOPHOPHORATA
Phylum UNCERTAIN
Class CONODONTOPHORIDA Eichenberg, 1930?
Family ODONTOGRIPHIDAE fam. nov.
Genus ODONTOGRIPHUS gen. nov.

Type and only known species. Odontogriphus omalus sp. nov.

Derivation of name. Odontogriphus is derived from the Greek and means 'toothed riddle', a reference to its uncertain affinities.

Diagnosis. Bilaterally symmetrical, dorso-ventrally compressed lophophorate. Body tapering at posterior, head poorly differentiated from the annulated trunk. Head bears double-looped lophophoral apparatus containing tooth-like elements and a pair of lateral palps. Gut straight, mouth ventral, anus probably terminal. Lateral longitudinal muscles running along edges of trunk.

Odontogriphus omalus sp. nov.

Plates 30–34; text-figs. 1, 2, and 4

Derivation of name. The trivial name *omalus* (Latin) refers to its originally dorso-ventrally compressed nature.

Diagnosis. As for the genus.

Holotype and sole specimen. USNM 196169, and counterpart 196169a. The new species is from the Stephen Formation (middle Cambrian), Burgess Shale Member (*Pagetia bootes* faunule of the *Bathyuriscus-Elrathina* Zone: Fritz 1971). The Phyllopod bed (7 ft 7 in., 2·31 m) lies within division h. of the Burgess Shale (Walcott 1912b). The Phyllopod bed is exposed in the Burgess quarry, which is situated on a ridge connecting Wapta Mountain to Mount Field at an elevation of about 7500 ft (2286 m). The Burgess quarry is 3 miles (4·8 km) north of Field, southern British Columbia.

A note on the photography and interpretation of the specimen

The part and counterpart have been photographed in air with ordinary white light using Ilford N5/31 film (Pl. 30, fig. 1; Pl. 31, fig. 1; Pl. 32, fig. 1) and ultra-violet light using Panatomic-X film (Pl. 33, figs. 1–3; Pl. 34, figs. 1–2), and under alcohol with white light using Ilford N5/31 film (Pl. 30, fig. 2; Pl. 31, fig. 2; Pl. 32, fig. 2). The white light was produced by four lamps, two intensity lamps, and a directional spot lamp. Alcohol was used because some details of the specimen which are obscure or invisible when dry become obvious when wet. The ultra-violet light was produced from a directional lamp. The lamp was inclined to the horizontal specimen at about 60°, the specimen was then tilted through about 10° towards

the lamp until maximum reflectivity, as observed down a focusing tube, was obtained. Focusing was undertaken in ordinary light.

Camera-lucida drawings are placed beside or with Plates 30, 31, 33, and 34 as a guide to their interpretation.

Preservation and morphology

The surface of the shale is slightly weathered, and there are scattered browny-yellow spots of iron oxide that presumably derive from iron pyrites. The specimen itself is poorly preserved and has been disrupted by compaction scarps. The fossil consists of a thin film that is darker than the surrounding rock. The anterior apparatus and palps are preserved in slight relief. Partial decay prior to fossilization is probably responsible for the poorly defined margins of the specimen. The processes of decay may have been instrumental in allowing details of internal anatomy to become more easily visible (Pls. 30–32). In a later paper evidence derived from study of the priapulid *Ottoia prolifica* will be presented to show that varying degrees of decay resulted in different anatomical features becoming visible.

The probable appearance of *Odontogriphus omalus* in life is shown in text-fig. 3. The anterior end was not clearly delimited from the trunk as a definite head. The body was about 6 cm long and some two and a half times longer than broad. It appears to have been dorso-ventrally compressed. The composition of the body may have been predominantly gelatinous. Although the edges of the body are indistinctly preserved the general outline is clear. The anterior margin was slightly convex, and the smooth lateral margins were more or less parallel to one another. The posterior part of the specimen is twisted so as to lie at right angles to the anterior part, and behind the locus of twisting the width of the body decreases (Pl. 31; text-fig. 2). This decrease is believed to be an original feature. The twisting of the body may have occurred when gentle currents disturbed the specimen on the sea-floor. If the twisting had taken place during transport in a mudflow the two parts of the body might be expected to be separated by a layer of sediment, as has been noted by the author in twisted specimens of the laterally flattened worm *Pikaia gracilens* Walcott, 1911*b*. The distortion was presumably purely passive rather than a death reaction.

The fine transverse lines (*c.* 1 mm apart) crossing part of the specimen are taken to represent annulations rather than true segmentation (Pl. 30, fig. 2; Pl. 31, fig. 2; Pl. 32, fig. 2; text-figs. 1, 2) as discussed below. Although only about ten of the annuli are preserved there is no reason to doubt that they originally occurred over most of the body. They may have totalled about fifty. The only other external details that have been preserved are the anterior apparatus and the palps (Pls. 30–34; text-figs. 1, 2, and 4).

The anterior apparatus is taken to be a feeding apparatus. Its suitability for this purpose is plain. The apparatus is situated at the end of a broad medial tube that was almost certainly the gut, judging by its similarity to the fossilized gut of other specimens from the Burgess Shale. The apparatus is bilaterally symmetrical and is sited on the midline of the animal. It most probably lay on the ventral surface of the body. Its form is that of a shallow U opening forward with the closure gently flexed anteriorward, and the ends tending to coil inward (Pls. 33, 34; text-fig. 4). The ends do not appear to fuse. The apparatus as now preserved is about 4 mm across and 2 mm long. It carries the remains of about twenty-five 'teeth' (Pl. 33; text-fig. 4) (the reasons
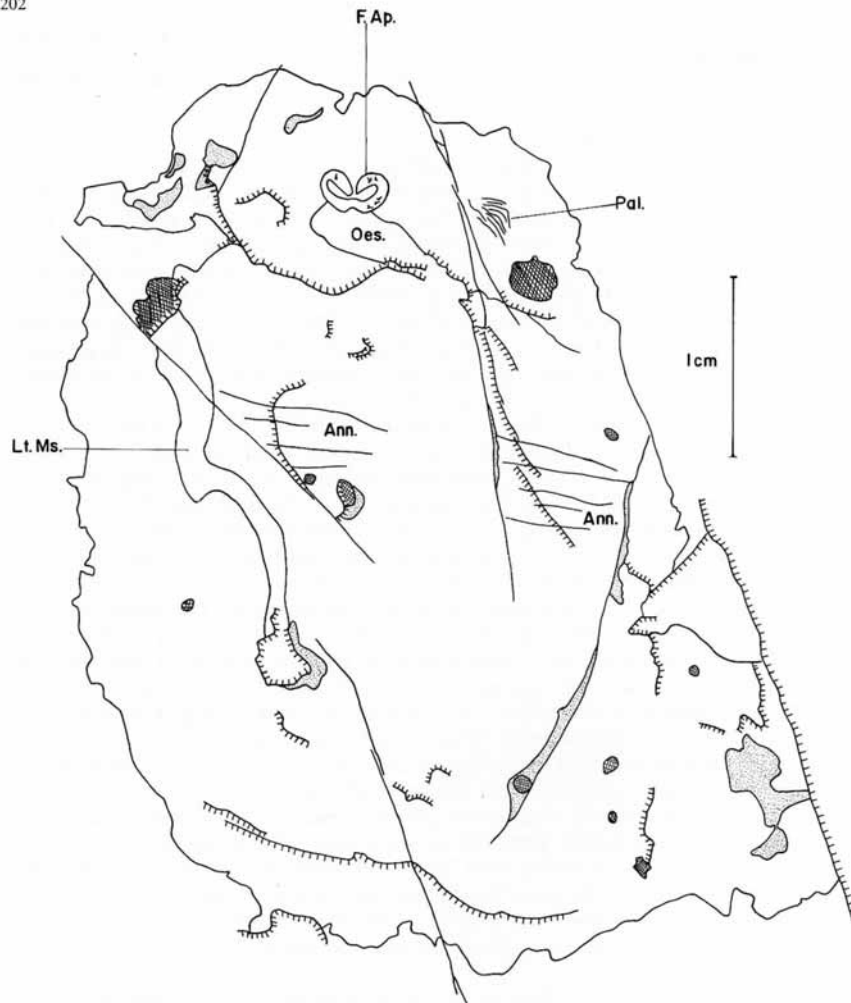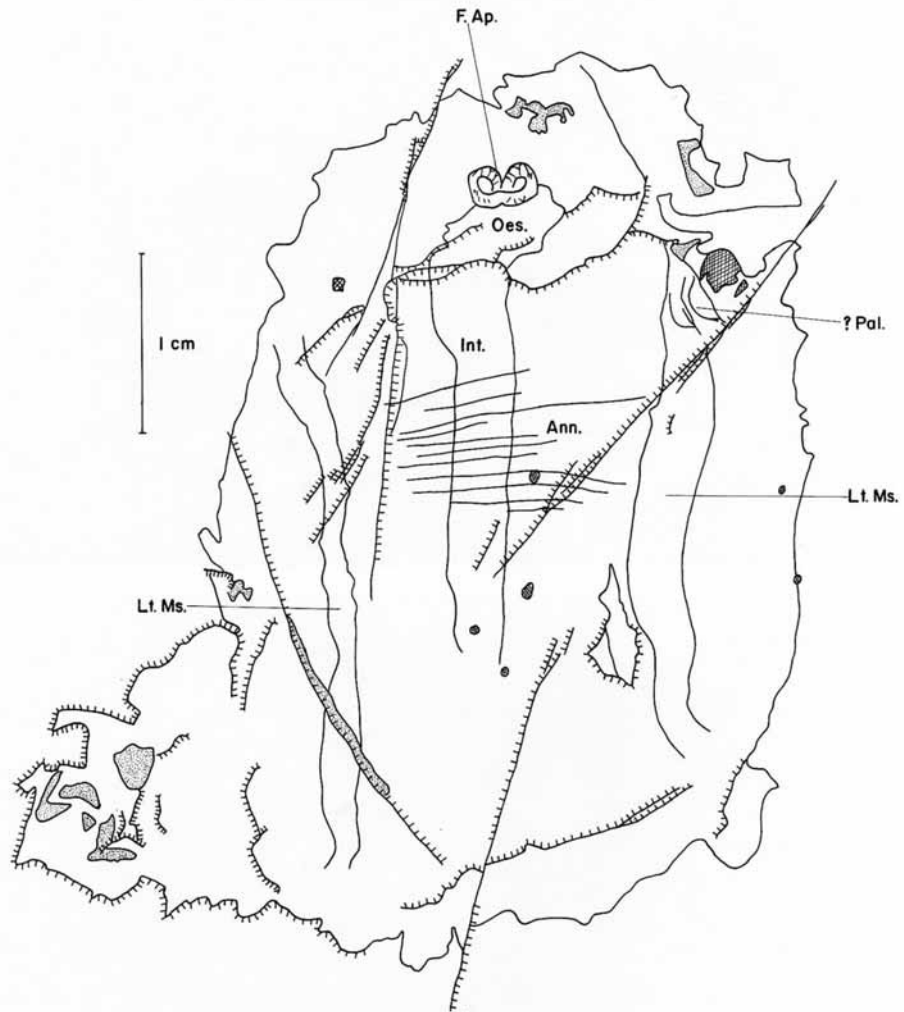
TEXT-FIG. 1. Camera-lucida drawing of the part (USNM 196169). With the exception of labelled features, all the lines crossing the specimen are the products of compression. Lines with hachures indicate definite breaks in slope, the hachures being directed downslope. Stippled areas represent rock, cross-hatched areas those parts rich in iron oxide and coloured browny-yellow. Ann., Annulations; F. Ap., Feeding apparatus; Lt. Ms., Lateral muscle; Oes., Oesophagus; Pal., Palp.

EXPLANATION OF PLATE 30

Figs. 1-2. *Odontogriphus omalus* gen. et sp. nov. Part of holotype (USNM 196169). Whole specimen in ordinary light from south-west, ×2·8. 1, in air. 2, under alcohol.
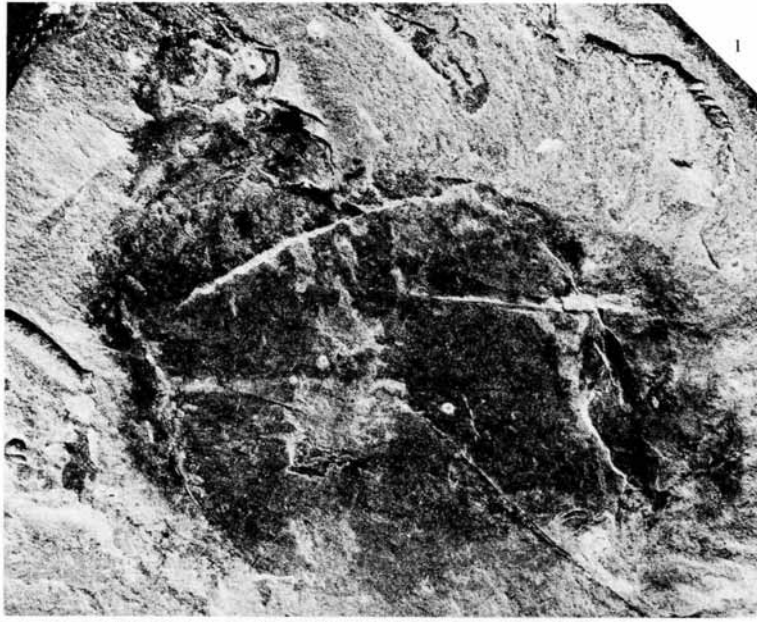
PLATE 30

1

2
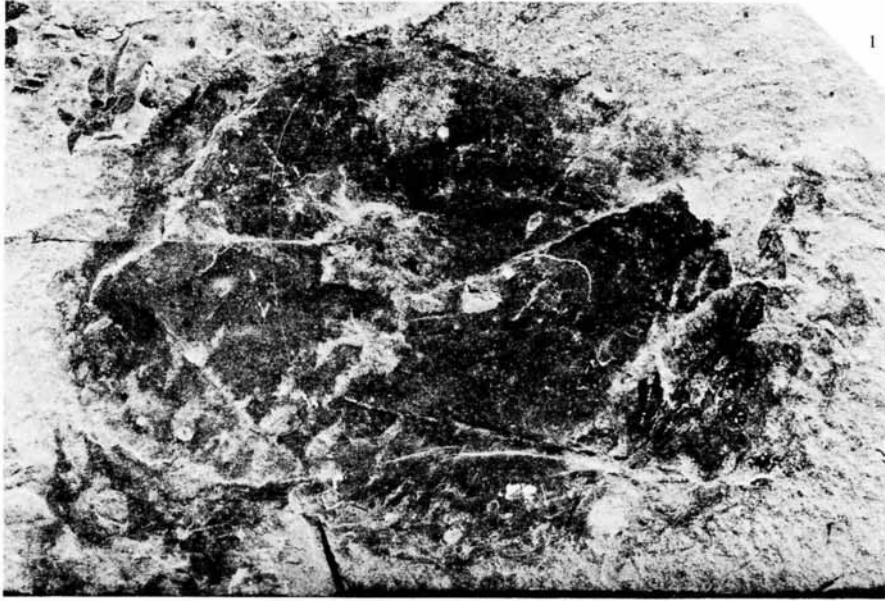
CONWAY MORRIS, Cambrian lophophorate

TEXT-FIG. 2. Camera-lucida drawing of the counterpart (USNM 196169a). See explanatory notes for
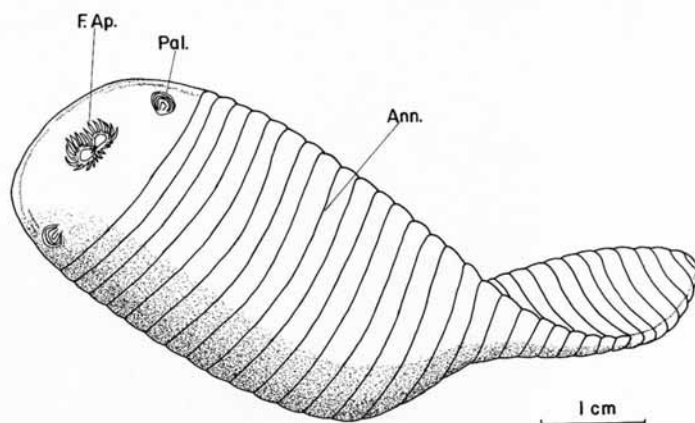text-fig. 1. Int., Intestine.

EXPLANATION OF PLATE 31

Figs. 1–2. *Odontogriphus omalus* gen. et sp. nov. Counterpart of holotype (USNM 196169a). Whole
specimen in ordinary light from north-north-east, ×2·1. 1, in air. 2, under alcohol.

PLATE 31

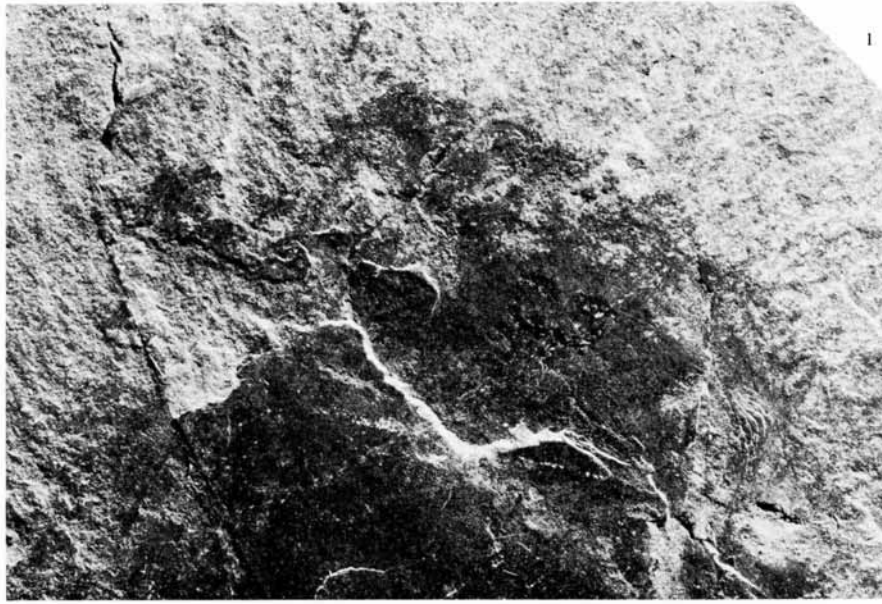
CONWAY MORRIS, Cambrian lophophorate

TEXT-FIG. 3. Reconstruction of appearance of *Odontogriphus omalus* gen. et sp. nov. in life. Anterior shows the ventral surface carrying the feeding apparatus and palps. The narrower posterior part of the trunk is twisted so as to reveal the dorsal surface. Abbreviations as for text-fig. 1.

for considering them to be other than true biting or rasping teeth are given below). With one possible exception the 'teeth' themselves have been leached away during diagenesis leaving external moulds or flattened, reflectively preserved impressions. Leaching of calcareous components of other members of the fauna, such as articulate brachiopods, has been noted by Whittington (1971). One 'tooth' (D in text-figs. 4A and 8), however, is preserved as a structureless whitish mineral. This mineral may be the original material, or a degraded remnant of the 'tooth', or a subsequent infilling of the mould. Three 'teeth' in the posterior part of the apparatus, including the 'tooth' preserved in the white mineral, are preserved sufficiently well and in such an orientation for much of their detail to be apparent (text-fig. 4B). They consist of a distinct expanded base (or root) that gives rise to a long thin cusp, the cusp itself being about six times longer than wide. These 'teeth' are about 0·4 mm long. The cusp is between 0·02 and 0·07 mm (maximum) wide and the expanded base is about 0·2 mm broad. In outline the basal edge is convex upward beneath the cusp, which suggests that the basal surface of each mould is domed upwards. This implies that there was a shallow central cavity, but it does not appear to have any pre-sedimentary filling. Furthermore, in the 'tooth' nearest the midline the expanded base is almost equally
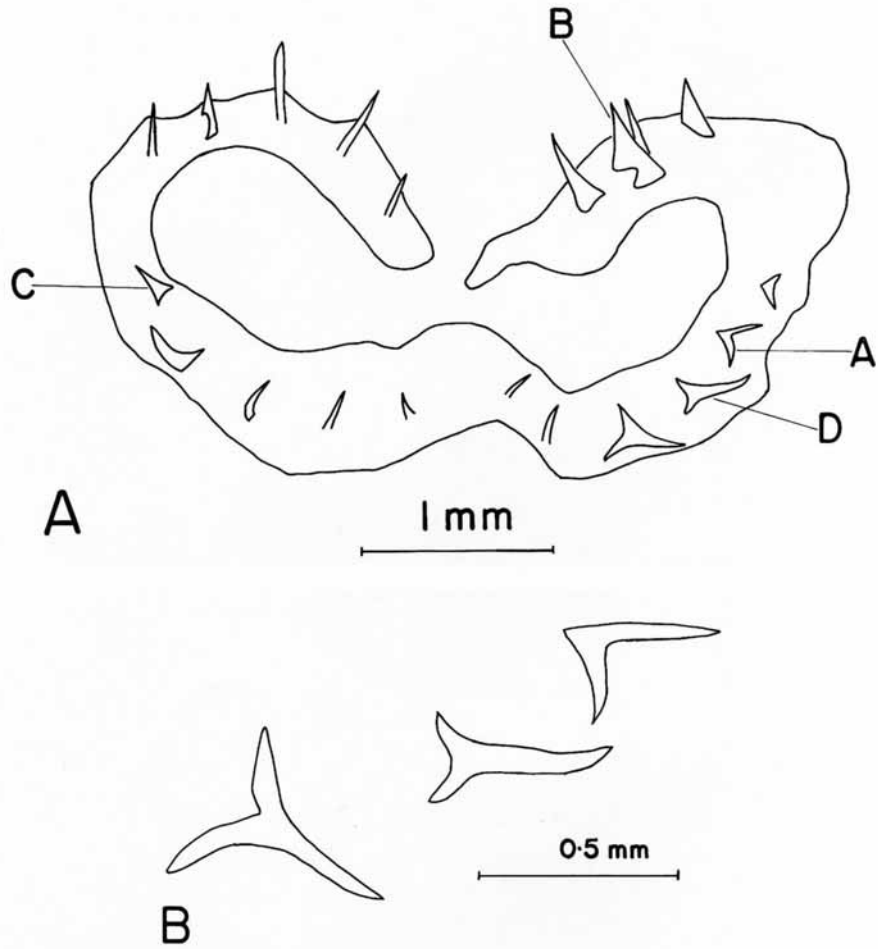
PLATE 32

CONWAY MORRIS, Cambrian lophophorate

TEXT-FIG. 4. A, camera-lucida drawing of the feeding apparatus of the part (USNM 196169). The letters A–D refer to four well-preserved 'teeth', see text-fig. 8. Anterior of apparatus towards the top of page. B, enlargement of three 'teeth' including A and D from the posterior loop of the apparatus to show possible symmetry transition. Midline on left-hand edge.

EXPLANATION OF PLATE 33

Figs. 1–3. *Odontogriphus omalus* gen. et sp. nov. Enlargement of the feeding apparatus of part of holotype (USNM 196169) in ultraviolet light, ×23·5. 1, light from east. 2, light from north-east. 3, light from south-west.

PLATE 33
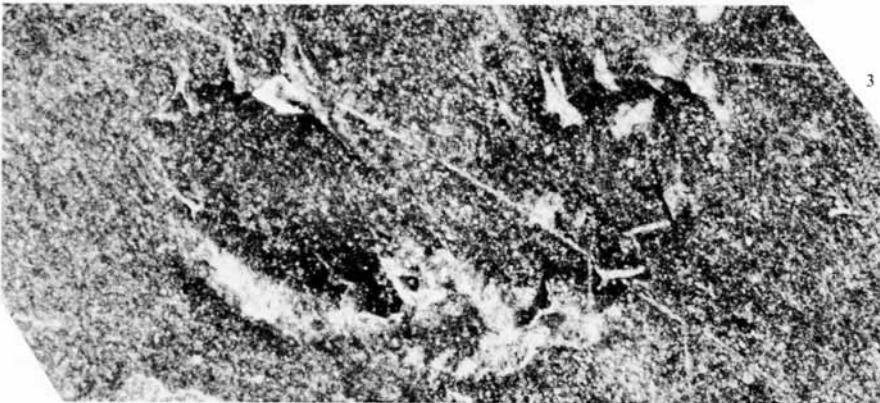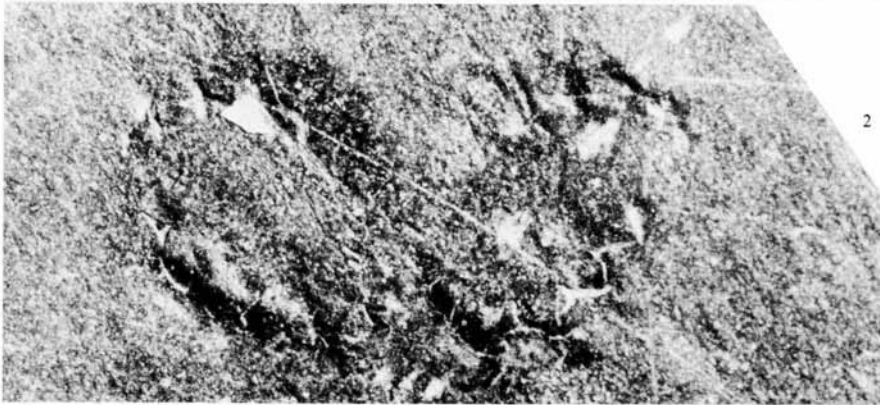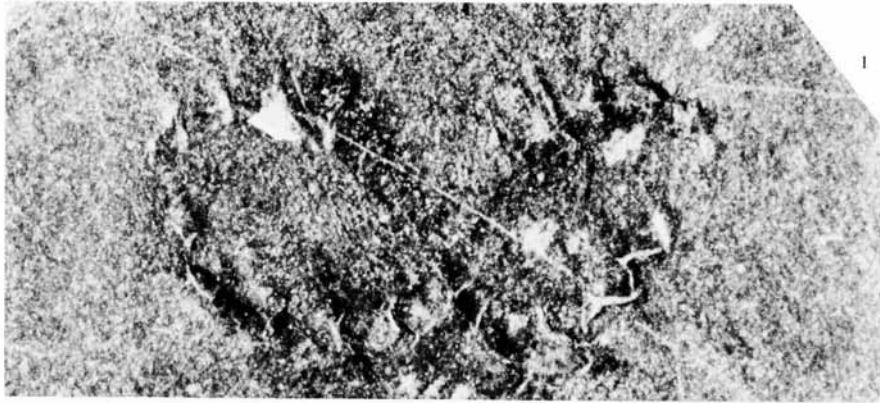
CONWAY MORRIS, Cambrian lophophorate

well developed on either side of the cusp, whereas the two more abaxial ones appear to have the base on the inner side of the apparatus reduced in size. Other 'teeth' within the anterior loop of the apparatus appear as simple cones (text-fig. 4A). Two explanations of the variations in shape are possible:

1. The suppression of one side of the expanded base may represent an original symmetry transition—from almost symmetrical 'teeth' beside the midline to increasingly asymmetrical 'teeth' abaxially.

2. The 'teeth' may lie at slightly different angles to the bedding plane so that different sections through one 'tooth' type are now seen. The 'teeth' may not originally have had the same orientation along the length of the apparatus, and it is possible that they were rotated by a regular amount along the length of each loop of the apparatus. Alternatively, during decay the 'teeth' may have fallen at different angles to the bedding plane.

These two explanations are not mutually exclusive. The author prefers to consider that the 'teeth' within the anterior and posterior parts of the apparatus represent two aspects, at right angles to one another, of one 'tooth' type. The aspects were determined by the way the 'teeth' came to lie with respect to the loop. Thus, the 'teeth' in the posterior part of the apparatus lie parallel to the loop, whereas the 'teeth' in the anterior are at right angles to the loop. It is not possible to determine whether the apparent symmetry transition of the three well-preserved 'teeth' is an original feature. The exact degree of variation among the 'teeth' cannot be established, but it is evident that they were in all cases relatively simple cones.

In the counterpart evidence of 'teeth' is almost entirely lacking. This is probably because the specimen split more or less through the middle, with the more ventral part of the apparatus coming away with the counterpart. The apparatus of the counterpart does, however, bear regularly spaced (four per 1 cm) depressed areas (0·4 mm across) (Pl. 34) which are faintly visible as raised areas in the part (Pl. 33, fig. 1). They are believed to represent decayed, and possibly retracted, remains of tentacles. The retracted tentacles of some entoprocts (Atkins 1932, fig. 3), for instance, are similar in appearance. The exact position and extent of the mouth cannot be determined, but it was almost certainly located within the loops of the apparatus. The probable appearance of the feeding apparatus in life is shown in text-fig. 5.

Slightly posterior to the apparatus and near one side of the ventral surface there is a palp (3 mm long, 2 mm across) consisting of about six layers that apparently were originally plates of tissue disposed parallel to the surface and fused adaxially in a common base. The layer closest to the surface of the animal is the largest and the size of the layers decreases away from the body (Pl. 30; Pl. 32, fig. 1; text-fig. 1). It is possible that this palp was formed by rock compression, but its regularity suggests that it is some genuine feature of the anatomy. On the counterpart the palp is much

---

EXPLANATION OF PLATE 34

Figs. 1–3. *Odontogriphus omalus* gen. et sp. nov. 1, 2, enlargement of the feeding apparatus of counterpart of holotype (USNM 196169a) in ultraviolet light, ×21·8. 1, light from north. 2, light from east. 3, camera-lucida drawing of above figures. Lines with hachures indicate definite breaks in slope, the hachures being directed downslope. Tt., rounded areas which probably represent tentacles.
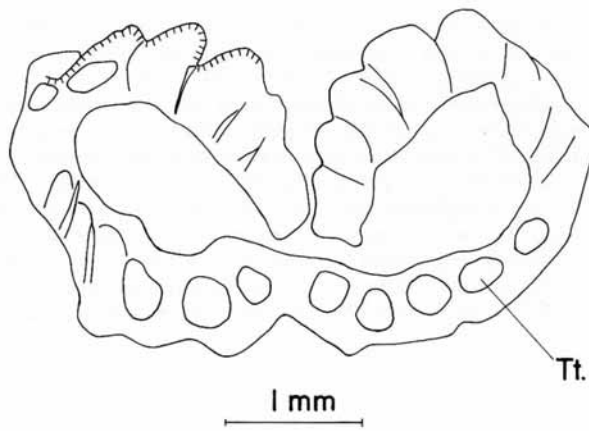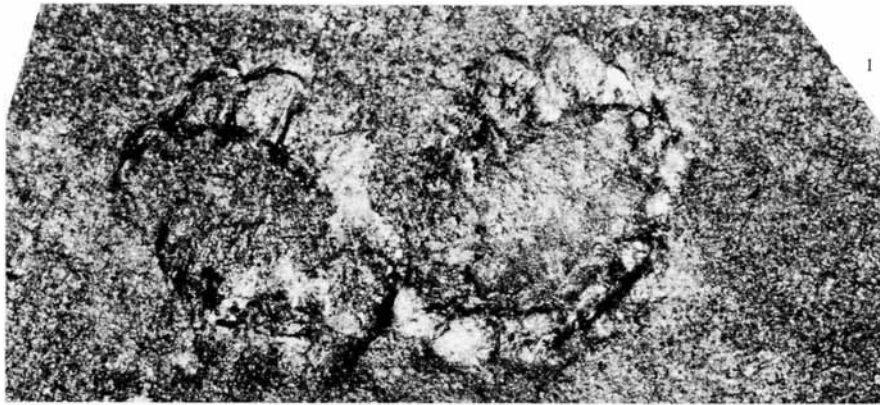
PLATE 34

1 mm

CONWAY MORRIS, Cambrian lophophorate
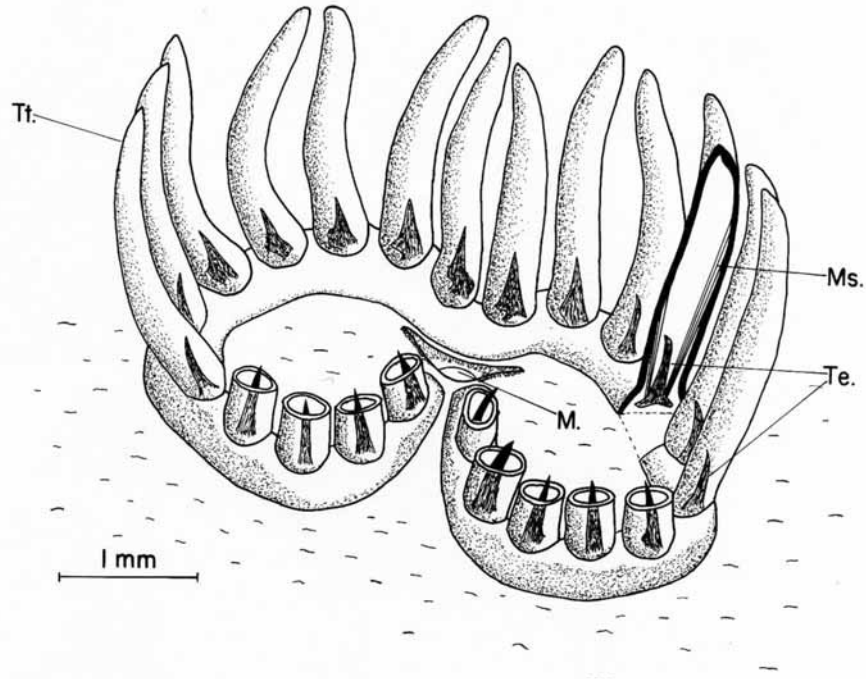
TEXT-FIG. 5. Reconstruction of appearance of the feeding apparatus in life from the anterior. The anterior tentacles have been cut away near the base to avoid obscuring detail. A section of the loop including part of a tentacle has also been removed to reveal hypothetical internal details. M., Mouth; Ms., Muscle; Te., 'Teeth'; Tt., Tentacles. The exact position of the mouth and presence of muscles is hypothetical.

less well preserved and its identification remains uncertain (Pl. 31; Pl. 32, fig. 2; text-fig. 2). When the counterpart is combined, by reversal, with the part the specimen can be seen to have possessed a pair of ventro-lateral palps.

A few details only of the internal anatomy have survived. Immediately behind the feeding apparatus there is a swollen, slightly reflective area which continued as a narrow parallel sided band (3 mm across) running down the middle of the trunk. After about 2·5 cm it fades away posteriorly (Pl. 31, fig. 2; text-fig. 2). These features are interpreted as an oesophagus and a narrower intestine. The anus is assumed to have been terminal. There is no evidence that the gut was recurved. No gut contents have been noted. Along each side of the body there is a dark longitudinal band (1·5–3 mm wide) which probably represents lateral longitudinal muscles (Pl. 30, fig. 2; Pl. 31, fig. 2; text-figs. 1, 2). The annulations could reflect underlying circular muscles.

DISCUSSION

Mode of life

The animal appears to have been dorso-ventrally compressed. This, together with its possibly gelatinous composition, suggests that it was pelagic. Its extreme rarity within the Burgess Shale indicates that, being pelagic, its chances of becoming involved in the mudflows that went to form the Phyllopod bed were slight. The absence of fins and the poor streamlining imply that it floated or else swam only sluggishly. Alternating contractions of the lateral longitudinal muscles on each side could have produced a wave-like rippling of the body edges that would have aided locomotion. The body may have been capable of more general undulations as well. A modern analogue of this animal might be seen in the bathypelagic nemertines (see e.g. Coe 1926, 1935, 1945, 1954). They have been found at depths of 200 m, but generally occupy depths of about 1000 m. Their distribution tends to be stratified with particular species occurring in greatest numbers at definite depths. The population density is, however, very low. Their dorso-ventrally compressed bodies are mostly composed of firm gelatinous tissues and many of the species are similar in shape to *O. omalus*. The majority of species appear to float or swim poorly by slow undulations.

It is unlikely that the apparatus was used as a rasping tool. In the molluscan radula the teeth are uniformly directed posteriad and are sited on an elongate pad of tissue. The shape of the apparatus, on the other hand, is such that some of the 'teeth' could not have effectively contributed to rasping activities. Furthermore, the slenderness of the 'teeth' with their consequent fragility makes their use in rasping or biting improbable. The apparatus instead appears to have affinities with the tentacular lophophore of the lophophorates. It is suggested that the apparatus bore food-gathering tentacles that were supported internally by the 'teeth' (text-fig. 5). *O. omalus* probably fed in a similar manner to the modern lophophorates. Water currents may have been promoted by cilia that covered the tentacles. The looped shape of the apparatus could have induced water vortices which channelled food towards the mouth.

The palps are rather small to have acted as efficient respiratory organs, and they were probably sensory. Respiration may have been carried out over the entire body, with gases diffusing through all parts of the body wall.

Zoological affinities

The relationships of *O. omalus* are not easy to determine. It can be excluded from most groups of worms on various grounds. The flattened nature of the body does not compel reference to the platyhelminthes (the flat worms) or to pelagic nemertines, because none of the representatives of these phyla has a comparable feeding apparatus. The apparatus is not a radula, so that there is no indication of any affinity with the Mollusca. Comparisons with annelid jaws or with armed mouths of other invertebrate phyla such as the Gnathostomulida (Riedl 1969) achieve equally little.

The shape of the apparatus is, however, very much reminiscent of the tentacular lophophore that characterizes the lophophorate phyla, i.e. the Brachiopoda, Phoronida, and Ectoprocta or Bryozoa (text-fig. 6A–C). A valuable general account of the
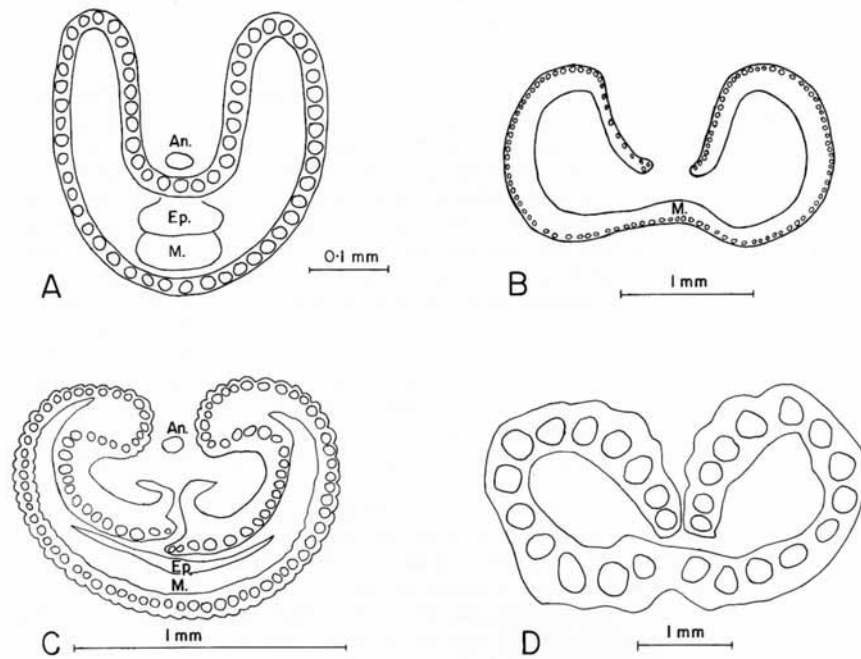
TEXT-FIG. 6. Comparison of the lophophores of A, phylactolaemate ectoproct (from Harmer 1896, fig. 236.3). B, articulate brachiopod (adapted from Atkins 1958, fig. 9). C, phoronid worm (from Benham 1889, pl. 10, fig. 12). D, the feeding apparatus of *Odontogriphus omalus* gen. et sp. nov. Circles indicate tentacles. An., Anus; Ep., Epistome; M., Mouth. The likely position of the mouth in D is given in text-fig. 5.

Lophophorata is given by Hyman (1959), and much of the following information is derived from her work. These three phyla differ in many respects, but the lophophore common to all remains a remarkably constant structure. The phoronids and ecto-procts have a recurved gut with the anus opening close to, but outside, the lophophore. The gut of the articulate brachiopods is blind, and that of the inarticulates is generally recurved. The phoronids are sessile worms occupying chitinous tubes, whereas the brachiopods and ectoprocts have well-developed calcareous, phosphatic, or chitinous exoskeletons. The lophophore in these animals is composed of one or two ridges bearing rows of tentacles and it partly or entirely encircles the mouth. The mouth is usually partially covered by a flap of tissue, the epistome. The lophophore of the phoronids and phylactolaemate (freshwater) ectoprocts consists of two parallel ridges bearing tentacles, with the mouth located between the two ridges. In the brachiopods and gymnolaemate (marine) ectoprocts there is a single ridge, which is basically circular and embraces the mouth. The ciliated tentacles are used to trap food. The primitive shape of the lophophore was probably that of a horseshoe, although circular and crescentic shapes are also known (Hyman 1959). The lopho-

phores of some of the modern phoronids, brachiopods, and phylactolaemate ecto-procts are sometimes modified by inturning or even multiple coiling of the ends. The single-ridged apparatus of *O. omalus* compares well (text-fig. 6D), suggesting that this organ is indeed a lophophore. Further, there is evidence that it may have borne short tentacles. Apart from the presence of the lophophore, however, *O. omalus* has no significant feature in common with the known lophophorates. An important difference between the modern lophophore and that of *O. omalus* is that no present-day examples have internal 'teeth' for support of the tentacles. The entire lophophore in the articulate brachiopods is, however, often supported by a brachidium and the lophophoral tentacles or filaments of some of the terebratulids (brachiopods) carry numerous minute perforated calcareous plates (Steinich 1963a, b; Rowell and Rundle 1967; Williams 1968). Such cases are rare, and as the tentacles of recent lopho-phorates are almost without exception supported by coelomic fluid, it is pertinent to inquire why supporting 'teeth', if that was their function, were necessary in *O. omalus*. One possible explanation is that the coelom was greatly reduced or even obliterated by the dorsal-ventral compression and perhaps by ingrowth of occluding gelatinous tissue as well. The 'teeth' could have supplemented or even replaced fluid support of the tentacles. The body cavity of the terebratulids, however, does not appear to be reduced and their lophophoral spicules must impart some rigidity to tentacles. The exact function of these spicules is obscure however. They may represent a response to excess $CaCO_3$ secretion. Little direct comparison of the 'teeth' and spicules is possible, because the latter are much more numerous, asymmetric in distribution, more or less random in shape, and are also usually to be found in the mantle tissues (A. Williams pers. comm.). In contrast, each tentacle of *O. omalus* appears to have been supported by a single 'tooth' and the distal ends of the tentacles may have been flexible. An additional function of the 'teeth' might have been to act as insertion points for tentacular muscles (text-fig. 5).

In this context the views of Lindström (1973, 1974) on the nature of the conodont animal or conodontophorid are of particular relevance. Conodonts are minute teeth-like objects whose maximum dimension is usually of the order of a few milli-metres. They are composed principally of calcium phosphate. Their range runs from late Precambrian to Triassic, and possibly to the Cretaceous (Diebel 1956; Müller and Mosher 1971). Cambrian conodonts are mostly simple cones, and such forms continue to occur through most of the Palaeozoic. Many more highly diversified conodonts appear in post-Cambrian rocks. The soft parts that held the conodonts have not been definitely identified, and their affinities have been the subject of much speculation. Lindström (1973) has argued in favour of relating the conodontophorid to the lophophorates, but he did not suggest firm reference to any of the three extant phyla. He proposed that the conodonts supported tentacles which formed a lopho-phoral ring around the mouth. This hypothesis of Lindström's is only one of several advanced in recent decades, although it is the most cogently argued. Reviews of the problem of affinity are available in Rhodes (1954), Hass (*in* Moore 1962), Lindström (1964), and Globensky (1970). The affinities are often thought to lie with the anne-lids or chordates, especially fish. Further recent hypotheses have suggested an alliance with the chaetognaths (Rietschel 1973), the conulariids (Bischoff 1973), the gnathostomulids (Ochietti and Cailleux 1969; Rodgers 1969), and the aschelminthes,

B

in particular the kinorhynchs and rotifers (Hofker 1974). None of these proposals is especially appealing and some workers have suggested that the conodonts belong to a new group. The only generally accepted features of the conodontophorid are that it was 'soft-bodied, bilaterally symmetrical, marine and pelagic' (Hass 1962, p. W33). Whether it was entirely pelagic is not completely certain. Distribution of Ordovician conodonts suggest that, with the exception of simple cones, they may have belonged to nekto-benthonic animals. The Cambrian conoidal conodonts, however, probably derive from pelagic conodontophorids (Barnes and Fåhraeus 1975).

There is one record of supposed fossilized soft parts of a conodont animal. This is the soft-bodied chordate-like material, containing conodonts, discovered in the Namurian of Montana (Melton and Scott 1973; Scott 1973) (text-fig. 7). The
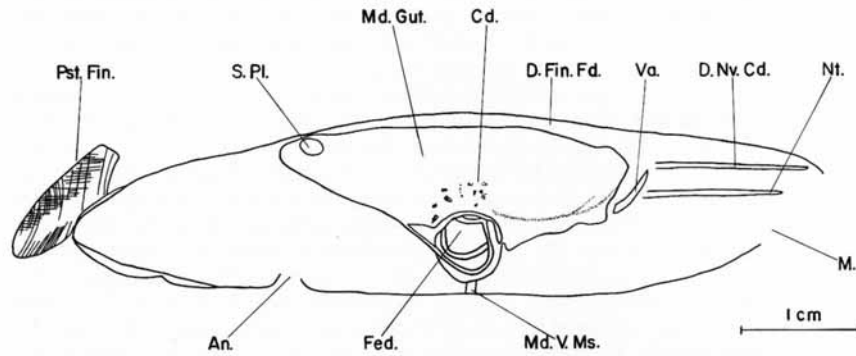
TEXT-FIG. 7. Slightly simplified interpretation of the chordate-like fossils (conodontochordates) from the Bear Gulch Limestone, Montana (from Scott 1973, fig. 6). An., Anus; Cd., Conodonts; D. Fin. Fd., Dorsal fin fold; D. Nv. Cd., Dorsal nerve cord; Fed., Ferrodiscus; M., Mouth; Md. Gut., Midgut (delta-enteron); Md. V. Ms., Midventral muscle; Nt., Notostyle?; Pst. Fin., Posterior fin; S. Pl., Sieve plate?; Va., Valve to midgut?

few specimens found are not very well preserved, but the soft-part morphology appears to be almost invariable among these specimens. The slight differences that exist can be attributed to preservational factors. They have, however, been divided into three genera on the basis of the enclosed conodonts. The over-all shape was elongate. The mouth appears to have been sub-terminal, and although the connection cannot be traced it must have joined the expanded midgut, the deltaenteron, where the conodonts are found. The anus appears to have been ventral, and there was a large finned post-anal tail. A complex organ, the ferrodiscus, was located beneath the deltaenteron and may have been involved with circulatory and respiratory activities. These authors also presented evidence for an anterior notostyle and dorsal nerve cord. Lindström (1974) discussed these findings and suggested that there must be some doubt as to whether the animals were conodontophorids rather than conodontophages. In these fossils the conodont assemblages are variable in composition, although hindeodellids are always the commonest (Table 1). Also, the conodonts are rather scattered within each specimen. This suggests that the conodonts were ingested,

TABLE 1. Distribution of various conodont elements within the conodonto-chordate specimens from the Bear Gulch Limestone (Namurian), Montana. Each vertical column refers to one specimen. Data from Melton and Scott (1973) and Scott (1973).

| Element type	*Lewistownella lowerae*	*Lochriea wellsi*			*Scottognathus elizabethi*	
Hindeodellids	12	10	9+	12	10+	12
Ozarkodinids	2	1	0	0	3	3
Synprioniodinids	0	0	0	0	2	0
Neoprionoidinids	3	3	1	3	0	0
Platforms	4	3	0	1	4	3

because in other cases, in which there are no associated soft parts, assemblages with a more regular and coherent arrangement have been identified.

It may be suggested that *O. omalus* is an example of a conodont animal. This conclusion is based on two principal lines of reasoning.

1. The 'teeth' of the feeding apparatus have a strong resemblance to some Cambrian conodonts (text-fig. 8). The earliest conodont-like fossils are found in late Precambrian and early Cambrian rocks (Poulsen 1966; Missarzhevsky 1973; Landing 1974; Matthews and Missarzhevsky 1975). Reviews of the record of Cambrian (especially upper Cambrian) conodonts have been produced by Müller (1971) and Barnes *et al.* (1973). Certain other Cambrian phosphatic microfossils, called para-conodonts, are perhaps related to the true conodonts (Müller 1971; Müller and Nogami 1971). Although some of the Cambrian conodonts have bizarre shapes, e.g. *Westergaardodina*, the majority are more or less conical. Conoidal conodonts continue to occur into the Devonian and perhaps the Carboniferous (Ellison 1972). The great predominance of cones in the Cambrian strongly suggests that the apparatuses of most of the Cambrian conodontophorids bore only this type of conodont. Such monoconoidal apparatuses probably continued into the Ordovician (Sweet and Bergström 1972) and perhaps to the Devonian (Klapper and Philip 1972), although some of the conoidal forms found in the Devonian may only have been one constituent of an apparatus (type 4 apparatus in Klapper and Philip 1971) that contained other, more complex, elements. Most examples of conical conodonts in natural assemblages are as fused clusters (Barnes 1967; Pollock 1969), but Miller and Rushton (1973) have noted a bilaterally symmetrical assemblage of approximately twelve elements from the Cambrian of Warwickshire.

Given the state of preservation of the 'teeth' of *O. omalus*, it is impossible to obtain information on the full shape and extent of the basal cavity or on the presence of carinae or striations, i.e. on any of the characters by which the majority of the genera and species of Cambrian conodonts are defined. Hence, no exact comparisons with known forms can be suggested. There is, nevertheless, a clear general resemblance to distacodontids such as *Scandodus* Lindström, 1955, emend. Lindström, 1971 (text-fig. 8), and the two are in much the same order of size.

It is not possible to establish whether the 'teeth' resemble paraconodonts rather than conodonts because no histological information is obtainable. The leaching of the 'teeth', with resultant moulds, raises questions concerning their composition. It may be noted that cases are known in which conodonts, originally phosphatic,
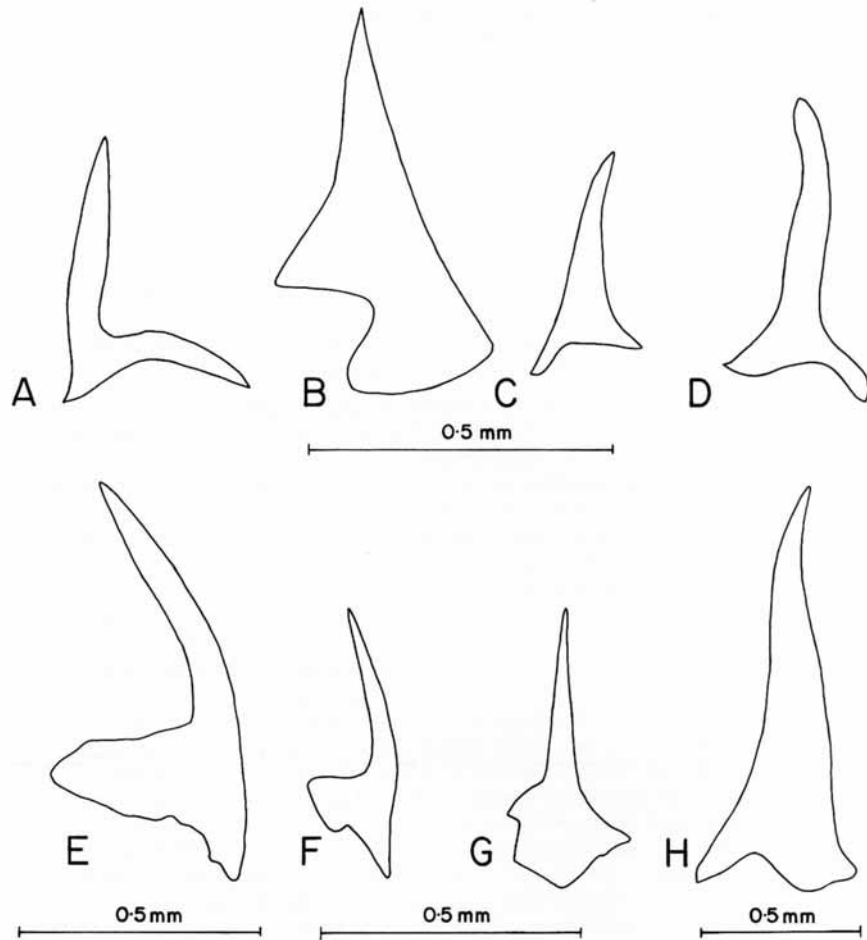
TEXT-FIG. 8. Comparison between 'teeth' of the feeding apparatus (A–D, for location in apparatus see text-fig. 4A) and three specimens (E, F and G, H) in various aspects of the upper Cambrian conodont *Scandodus tortilis* Müller (from Müller 1959, pl. 12, figs. 10, 7a and b, and 8 respectively).

have been leached during diagenesis, leaving either moulds or else a white or brown degradation product (Matthews 1969a, b; Matthews *et al.* 1972). It may be significant that these cases noted by Matthews are from dark siliceous shale (Lower Carboniferous) that is comparable to the Phyllopod bed in sedimentary character. Considering possible vulnerability during diagenesis, it is worth remembering that the ratio of organic material to phosphate is believed to have been relatively

high in Cambrian conodonts (Clark and Miller 1969; Müller and Nogami 1971). The presence of appreciable amounts of organic matter may have helped to promote destructive leaching of the 'teeth' of *O. omalus*.

2. A second reason for regarding *O. omalus* as a possible conodontophorid lies in the fact that the lophophore apparatus shows considerable agreement with the hypothetical conodont apparatus proposed by Lindström (1974). The appearance of Lindström's hypothetical animal does not, however, tally closely with *O. omalus*. In the animal he envisaged almost the entire surface is occupied by the lophophore. In criticism of this proposal it may be pointed out that it would be unusual for an animal to devote a major part of its outer surface to the activities of feeding. Further, Lindström's animal is too large to have floated (judging by the behaviour of similarly sized aquatic creatures today) and some sort of post-lophophoral body to be used in propulsion is presumably necessary. There are few animals which manage to make use of one organ system for locomotion and simultaneously for feeding. Although the free-living crinoid, *Antedon*, for instance, employs its flexible arms in both feeding and locomotion, it feeds only when stationary (Hyman 1955). It is, therefore, unlikely that the tentacles of Lindström's animal served, at any one time, for both feeding and swimming. There is also a difference in size between *O. omalus* (length 6 cm) and Lindström's hypothetical animal (length 1 cm). Lindström (1974) came to this value by supposing that the 7 cm long conodontochordates described by Melton and Scott would have been unable to ingest animals of any size larger than about 1 cm. However, some animals are known to be capable of eating prey of their own size.

These apparent differences of size may not be very significant. It is quite possible that post-Cambrian conodontophorids were smaller than late Precambrian and Cambrian forms in which the conodonts could on occasion be relatively large (see lengths of the order of 2 mm reported in Poulsen 1966). The number of conodonts in the apparatus may also have varied, but the 'teeth' total about twenty-five in *O. omalus* and it may be significant that the largest number of conodonts recorded in an assemblage is twenty-two (Rhodes 1962). Presumably, with increasing diversity of conodont form in post-Cambrian time, increasingly complex configurations of the lophophore arose. The lophophore as portrayed by Lindström (1974), for example, is much more elaborate than noted in *O. omalus*. It is likely that this diversification of the conodonts led to looped and branched lophophores, in a way analagous to the development in increasingly complex lophophores in many brachiopods (Hyman 1959; Rudwick 1970, fig. 79), thus greatly increasing the surface area available for feeding.

The systematic position of O. omalus

In attempting to establish the systematic position of *O. omalus* the following points should be borne in mind:

1. In his 1973 paper Lindström regarded the conodontophorid as being distantly related to other lophophorates, in particular the brachiopods. He drew attention to a similar development of pitted microstructure in conodonts and in the inarticulate calcareous brachiopod *Crania*. He suggested that the polygonal pattern, known to be characteristic of muscle insertion areas in *Crania* (Williams and Wright 1970),

had the same significance in conodonts. It has been suggested above that the 'teeth' too may have had muscles inserted on them (text-fig. 5). It may be significant, moreover, that *Crania* is regarded as one of the most primitive brachiopods and could have retained features lost in other more advanced members of this phylum (Hyman 1959).

2. Although other groups such as the endoprocts and sipunculids have a lophophore-like organ, the author prefers to regard the lophophore of *O. omalus* as indicating an affinity with the superphylum Lophophorata. This new form cannot readily be accommodated in any of the three constituent phyla, and nor is it easy to indicate to which of the three *O. omalus* is most closely related. It may be marginally closer to the vermiform phoronids, which Hyman (1959, p. 603) noted 'seem to come nearer a presumed type plan' and are believed to have some 'characteristics of the common lophophorate ancestor' (Hyman 1959, p. 604) than to the brachiopods or ectoprocts. None of the modern lophophorates have multiple segmentation such as the annelids possess. If *O. omalus* is genuinely related to the lophophorates, its annulations are most probably superficial rather than a reflection of true segmentation.

3. If *O. omalus* is taken to belong within the Lophophorata brief speculation on the ancestral form of this superphylum is relevant. The stock that produced *O. omalus* is unlikely to be ancestral to the other lophophorates, because it has specialized features such as the lophophoral 'teeth'. One would presume also that the common ancestor must have existed before the appearance of the late Precambrian conodonts. *O. omalus* might, nevertheless, have primitive features now obscured or lost in the other lophophorates. Hyman (1959, p. 229) stated that 'Presumably the ancestral type of Lophophorata was a vermiform animal with body regionated into head, lophophoral region, and trunk, but the head appears to have undergone practically complete degeneration, probably as a consequence of a sessile or sedentary mode of life'. It is tempting to suggest that the area anterior to the lophophore represents the ancestral head, retained in this animal because of its active way of life. It is impossible to determine whether the pre-lophophoral area was the protosome containing the protocoel, being separated from the lophophoral region by a distinct septum. The protocoel is considered by some authors (e.g. Hyman 1959) to be absent from the modern lophophorates, but more recent evidence suggests that it exists as the greatly reduced cavity within the epistome (e.g. Ryland 1970; Zimmer *in* Larwood 1973). It is very probable that the feeding apparatus of *O. omalus* was ventral rather than dorsal. If the pre-lophophoral area became so reduced that the feeding apparatus was located at the anterior end, the apparatus would then have the orientation the lophophore has in modern forms, with the convex side ventral to the mouth. The straight gut with apparently terminal anus of *O. omalus* may also be primitive. Hyman (1959, p. 230) noted that the 'median posterior position of the anus is seen only in the brachiopod genus *Crania*, where it may be primitive'. The recurved gut of the ectoprocts and phoronids may be an adaptation to a sedentary way of life. The shape of the apparatus deviates only slightly from the primitive horseshoe shape of the basic lophophore (Hyman 1959).

REFERENCES

ATKINS, D. 1932. The ciliary feeding mechanism of the entoproct polyzoa, and a comparison with that of the ectoproct polyzoa. *Q. Jl microsc. Sci.* **75**, 393–423.

—— 1958. A new species and genus of Kraussinidae (Brachiopoda) with a note on feeding. *Proc. zool. Soc. Lond.* **131**, 559–581.

BARNES, C. R. 1967. A questionable natural conodont assemblage from Middle Ordovician limestone, Ottawa, Canada. *J. Paleont.* **41**, 1557–1560.

—— and FÅHRAEUS, L. E. 1975. Provinces, communities, and the proposed nektobenthonic habit of Ordovician conodontophorids. *Lethaia*, **8**, 133–149.

—— REXROAD, C. B. and MILLER, J. F. 1973. Lower Paleozoic conodont provincialism. *Spec. Pap. geol. Soc. Am.* **141**, 157–190.

BENHAM, W. B. 1889. The anatomy of *Phoronis australis*. *Q. Jl microsc. Sci.* **30**, 125–159.

BISCHOFF, G. C. O. 1973. On the nature of the conodont animal. *Geologica et Palaeontologica*, **7**, 147–174.

CLARK, D. L. and MILLER, J. F. 1969. Early evolution of conodonts. *Bull. geol. Soc. Am.* **80**, 125–134.

COE, W. R. 1926. The pelagic nemerteans. *Mem. Mus. comp. Zool. Harv.* **34**, 1–244.

—— 1935. Bathypelagic nemerteans collected within a 25 mile circle near Bermuda. *Zool. Anz.* **111**, 315–317.

—— 1945. Plankton of the Bermuda oceanographic expeditions. XI. Bathypelagic nemerteans of the Bermuda area and other parts of the north and south Atlantic oceans, with evidence to their means of dispersal. *Zoologica, N.Y.* **30**, 145–168.

—— 1954. Bathypelagic nemerteans of the Pacific Ocean. *Bull. Scripps Instn Oceanogr. tech. Ser.* **6** (7), 225–286.

DIEBEL, K. 1956. Conodonten in der Oberkreide von Kamerun. *Geologie*, **5**, 424–450.

EICHENBERG, W. 1930. Conodonten aus dem culm des Harzes. *Paläont. Z.* **12**, 177–182.

ELLISON, S. P. 1972. Conodont taxonomy in the Pennsylvanian. *Geologica et Palaeontologica*, SB **1**, 127–146.

FRITZ, W. H. 1971. Geological setting of the Burgess Shale. *In* Extraordinary fossils. *Symp. North Amer. Paleont. Conv.* 1969, Pt. I, 1155–1170.

GLOBENSKY, Y. 1970. The nature of conodonts. *Naturaliste Can.* **97**, 213–228.

HARMER, S. F. 1896. Polyzoa. *In* HARMER, S. F. and SHIPLEY, A. E. (eds.). *The Cambridge Natural History*, **2**, 465–533.

HASS, W. H. 1962. Conodonts. *In* MOORE, R. C. (ed.). *Treatise on invertebrate paleontology*, W (Miscellanea), W3–W69.

HOFKER, J. 1974. Eine mögliche Tiergruppe, welche die Trägerin der sogenannten Conodonten war. *Paläont. Z.* **48**, 29–35.

HYMAN, L. H. 1955. *The Invertebrates: Echinodermata*. Vol. IV. New York, 763 pp.

—— 1959. *The Invertebrates: Smaller coelomate groups*. Vol. V. New York. 783 pp.

KLAPPER, G. and PHILIP, G. M. 1971. Devonian conodont apparatuses and their vicarious skeletal elements. *Lethaia*, **4**, 429–452.

—— —— 1972. Familial classification of reconstructed Devonian conodont apparatuses. *Geologica et Palaeontologica*, SB **1**, 97–114.

LANDING, E. 1974. Early and Middle Cambrian conodonts from the Taconic allochthon, eastern New York. *J. Paleont.* **48**, 1241–1248.

LINDSTRÖM, M. 1955. Conodonts from the lowermost Ordovician strata of south-central Sweden. *Geol. För. Stockh. Förh.* **76**, 517–604.

—— 1964. *Conodonts*. Amsterdam. 196 pp.

—— 1971. Lower Ordovician conodonts of Europe. *Mem. geol. Soc. Am.* **127**, 21–61.

—— 1973. On the affinities of conodonts. *Spec. Pap. geol. Soc. Am.* **141**, 85–102.

—— 1974. The conodont apparatus as a food-gathering mechanism. *Palaeontology*, **17**, 729–744.

MCILREATH, I. A. 1974. Stratigraphic relationships at the western edge of the Middle Cambrian facies belt, Field, British Columbia. *Geol. Surv. Pap. Can.* **74-1** (Part A), 333-334.

MATTHEWS, S. C. 1969a. A Lower Carboniferous conodont fauna from east Cornwall. *Palaeontology*, **12**, 262-275.

—— 1969b. Two conodont faunas from the Lower Carboniferous of Chudleigh, south Devon. Ibid. 276-280.

—— and MISSARZHEVSKY, V. V. 1975. Small shelly fossils of late Precambrian and early Cambrian age: a review of recent work. *Jl geol. Soc. Lond.* **131**, 289-304.

—— SADLER, P. M. and SELWOOD, E. B. 1972. A Lower Carboniferous conodont fauna from Chillaton, southwest Devonshire. *Palaeontology*, **15**, 550-568.

MELTON, W. and SCOTT, H. W. 1973. Conodont-bearing animals from the Bear Gulch Limestone, Montana. *Spec. Pap. geol. Soc. Am.* **141**, 31-65.

MILLER, J. F. and RUSHTON, A. W. A. 1973. Natural conodont assemblages from the upper Cambrian of Warwickshire, Great Britain. *In* North-Central section, 7th annual meeting, *Geol. Soc. Am., Abstr.* **5** (4), 338-339.

MISSARZHEVSKY, V. V. 1973. Conodontiform organisms from beds close to the Precambrian-Cambrian boundary on the Siberian Platform and in Kazakhstan. *In* ZHURAVLEVA, I. T. (ed.). *Palaeontological and biostratigraphical problems in the Lower Cambrian of Siberia and the Far East*, 53-57. [In Russian.]

MÜLLER, K. J. 1959. Kambrische Conodonten. *Z. dt. geol. Ges.* **111**, 434-485.

—— 1971. Cambrian conodont faunas. *Mem. geol. Soc. Am.* **127**, 5-20.

—— and MOSHER, L. C. 1971. Post-Triassic conodonts. Ibid. 467-470.

—— and NOGAMI, Y. 1971. Über den Feinbau der Conodonten. *Mem. Fac. Sci. Kyoto Univ.* series Geology and Mineralogy, **38**, 1-87.

OCHIETTI, S. and CAILLEUX, A. 1969. Comparaison des conodontes et des mâchoires de Gnathostomulides. *C.r. hebd. Séanc. Acad. Sci., Paris*, **268** (ser. D), 2664-2666.

PIPER, D. J. W. 1972. Sediments of the Middle Cambrian Burgess Shale, Canada. *Lethaia*, **5**, 169-175.

POLLOCK, C. A. 1969. Fused Silurian conodont clusters from Indiana. *J. Paleont.* **43**, 929-935.

POULSEN, V. 1966. Early Cambrian distacodontid conodonts from Bornholm. *Biol. Meddr*, **23** (15), 1-10.

RHODES, F. H. T. 1954. The zoological affinities of the conodonts. *Biol. Rev.* **29**, 419-452.

—— 1962. Recognition, interpretation, and taxonomic position of conodont assemblages. *In* MOORE, R. C. (ed.). *Treatise on invertebrate paleontology*, W (Miscellanea), W70-W83.

RIEDL, R. J. 1969. Gnathostomulida from America. *Science, N.Y.* **163**, 445-452.

RIETSCHEL, S. 1973. Zur Deutung der Conodonten. *Natur Mus., Frankf.* **103**, 409-418.

RODGERS, J. 1969. Gnathostomulida: is there a fossil record? *Science, N.Y.* **164**, 855-856.

ROWELL, A. J. and RUNDLE, A. J. 1967. Lophophore of the Eocene brachiopod *Terebratulina wardenensis* Elliott. *Paleont. Contr. Univ. Kans.* **15**, 1-18.

RUDWICK, M. J. S. 1970. *Living and fossil brachiopods*. London. 199 pp.

RYLAND, J. S. 1970. *Bryozoans*. London. 175 pp.

SCOTT, H. W. 1973. New Conodontochordata from the Bear Gulch Limestone (Namurian, Montana). *Publs Mich. St. Univ. Mus.* Paleontological series, **1**, 81-100.

STEINICH, G. VON. 1963a. Fossile spicula bei Brachiopoden der Rügener Schreibkreide. *Geologie*, **12**, 604-610.

—— 1963b. Drei neue Brachiopodengattungen der subfamilie Cancellothyrinae Thomson. Ibid. 732-740.

SWEET, W. C. and BERGSTRÖM, S. M. 1972. Multielement taxonomy and Ordovician conodonts. *Geologica et Palaeontologica*, SB **1**, 29-42.

WALCOTT, C. D. 1911a. Middle Cambrian holothurians and medusae. Cambrian geology and paleontology, II. *Smithson. misc. Collns*, **57**, 41-68.

—— 1911b. Middle Cambrian annelids. Cambrian geology and paleontology, II. Ibid. 109-144.

—— 1912a. Middle Cambrian Branchiopoda, Malacostraca, Trilobita and Merostomata. Cambrian geology and paleontology, II. Ibid. 145-228.

—— 1912b. Cambrian of the Kicking Horse Valley, B.C. *Rep. geol. Surv. Can. for 1911*, 188-191.

WHITTINGTON, H. B. 1971. The Burgess Shale: history of research and preservation of fossils. *In* Extraordinary fossils. *Symp. North Amer. Paleont. Conv.* 1969, Pt. I, 1170-1201.

WILLIAMS, A. 1968. A history of skeletal secretion among articulate brachiopods. *Lethaia*, **1**, 268-287.

—— and WRIGHT, A. D. 1970. Shell structure of the Craniacea and other calcareous inarticulate Brachiopoda. *Spec. Pap. Palaeontology*, **7**, 51 pp.

ZIMMER, R. L. 1973. Morphological and developmental affinities of the lophophorates. *In* LARWOOD, G. P. (ed.). *Living and fossil Bryozoa*, 593-599.

S. CONWAY MORRIS
Department of Geology, Cambridge University
Cambridge CB2 3EQ