



# The Classes Tergomya and Helcionelloida, and early molluscan evolution

John S. Peel

The broad spectrum of shell morphologies assigned to the molluscan Class Monoplacophora, and widespread inconsistency in application, have motivated abandonment of the term in formal systematics. Two classes, Tergomya and Helcionelloida, are recognised to include two of the major groups of untorted molluscs formerly united within the Monoplacophora by some recent authors.

The concept behind recognition of the Classes Tergomya and Helcionelloida is examined from the point of view of functional morphology. In the exogastric Tergomya, which includes the present day *Neopilina* Lemche, 1957 and its relatives, the apex of the generally low, cap-shaped shell is located anteriorly and the shell expands towards the posterior. More specialised tergomyans include tall hypseloconellaceans and strongly coiled cyrtonebellaceans. Three orders are recognised: Tryblidiida, Cyrtonebellida and Hypseloconida (nov.). The Class Helcionelloida includes endogastrically coiled shells in which the apex lies at the posterior and the shell expands anteriorly. Helcionelloids are probably ancestral to the Classes Rostroconchia and Scaphopoda, and may have given rise to the first cephalopods.

Recognition of Tergomya and Helcionelloida suggests that the Sub-phyla Diasoma and Cyrtosoma of recent authors may be polyphyletic; their use is discontinued.

Models for the evolution of the molluscs are discussed from the point of view of the early fossil record.

J. S. P., Geological Survey of Greenland, Øster Voldgade 10, DK-1350 Copenhagen K, Denmark.

The definition of the Monoplacophora by Knight (1952), on the basis of a suite of Palaeozoic fossils, in many ways acknowledged the expectation of molluscan workers for almost a century by establishing a taxon approximating to the 'archimollusc', the theoretical ancestor of the other shelled Mollusca favoured by many workers (cf. Morton, 1979, p. 12; Pojeta, 1980; see also Salvini-Plawen, 1980, 1981, 1985). Discovery of the living monoplacophoran *Neopilina* Lemche, 1957 placed Knight's description on a firm footing, adding detailed anatomical knowledge to a fossil group presumed extinct since the Devonian (Lemche, 1957; Lemche & Wingstrand, 1959; Wingstrand, 1985). Not surprisingly, the last three decades have seen considerable activity in the study of molluscan evolution, with the untorted, univalved molluscs referred to the Class Monoplacophora figuring prominently in theoretical studies, and with an ever increasing total of fossil monoplacophorans being described. As with most rapidly developing scientific fields, the study of fossil monoplacophorans has taken many twists and turns, with frequent new discoveries, and with conflicting views emerging concerning the scope of the class within the available fossil record.

## Monoplacophora: historical usage

Monoplacophorans were first described as fossils more than a century ago, but their significance was not at that time appreciated. Specimens from the Silurian of Gotland, Sweden, described by Lindström (1884) remain some of the best known and best preserved taxa, figuring prominently both in palaeontological studies (e.g., Knight, 1952; Knight & Yochelson, 1960; Peel, 1977a) and in the study of living forms by Lemche (1957) and Lemche & Wingstrand (1959). It is appropriate that Lemche (1957) derived the name of *Neopilina* from one of these Gotland forms, *Tryblidium unguis* Lindström, 1880, which Koken & Perner (1925) had earlier made type species of the new genus *Pilina* (Fig. 1).

Lindström (1884) described *Pilina unguis* and the contemporary *Tryblidium reticulatum* Lindström, 1880 as patelliform gastropods, noting the similarity of the multiple paired muscles of the two Gotland species with some specimens of extant patelliform gastropods in which the normally continuous muscle scar on the shell interior is broken into segments (Lindström, 1884, pl. 1,

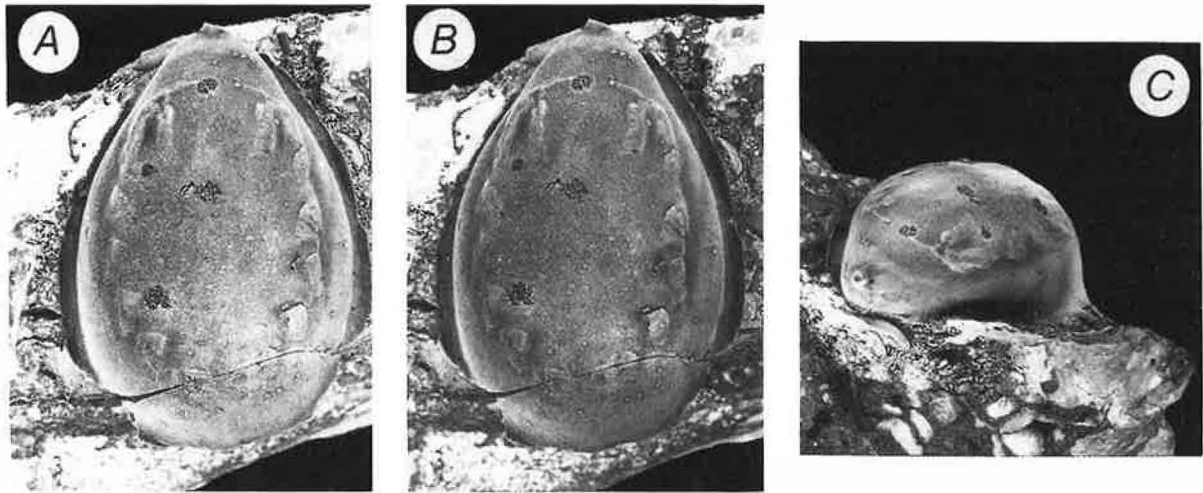


Fig. 1. *Pilina cheyennica* Peel, 1977, from the Late Ordovician Chimneyhill Limestone, near Ada, Oklahoma, U.S.A., YPM 74, holotype. A, B, stereo-pair of internal mould of a tryblidiacean tergomyan in dorsal view, oriented with anterior at the top and showing the paired, raised muscle scars; the small anterior tubercle represents the earliest growth stages,  $\times 1.3$ . C, oblique anterior view,  $\times 1$ . Note the external moulds of small bryozoan colonies which encrusted the interior of the dead shell.

fig. 32). Lindström's descriptions clearly indicated the essential shell characteristics of these 'original' mono-

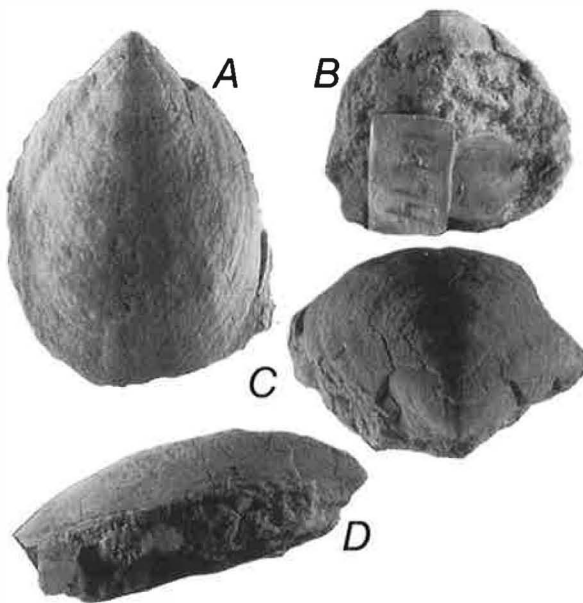


Fig. 2. *Tryblidium arcticum* Poulsen, 1974, a tryblidiacean tergomyan from the early Silurian of Washington Land, western North Greenland, MMH 13.674, holotype,  $\times 1$ . A, dorsal view. B, apico-ventral view showing the concave sub-apical surface below the overhanging apex. C, apico-dorsal view. D, lateral view showing the concave apertural plane with the resultant lateral emargination interpreted as the locus of the inhalant stream.

placophorans: the univalve, bilaterally symmetrical shell with the apex located near to the margin and the series of paired muscle scars on the shell interior, usually preserved as paired elevations on moulds of the shell interior (cf. Peel, 1977a and Figs 1, 2). Study of living *Neopilina* indicates that the monoplacophoran apex lies anteriorly and the shell thus expands towards the rear, i.e. the shell is exogastrically coiled. The anteriormost pair of muscles are large and composite, while subsequent pairs of muscles are subequal in size.

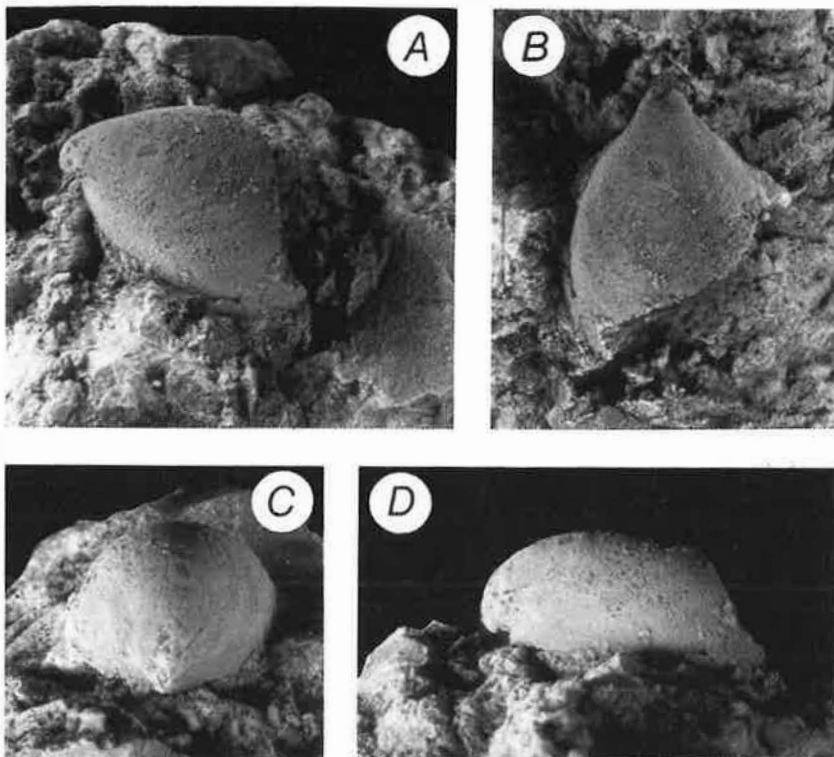
Lindström (1884) coined the term Tryblidia in referring collectively to various species resembling the Gotland forms and these monoplacophorans are usually placed within an Order Tryblidiida Lemche, 1957; they are frequently referred to as tryblidiaceans, tryblidians etc.

Wenz (1940) introduced the term Monoplacophora as an informal name for the tryblidiaceans to contrast their univalved shell with the multivalved shell of the Polyplacophora (cf. Geyer, 1986).

Knight (1952, p. 45) formally recognised the Monoplacophora as an order within the Sub-class Isopleura of an embracive Class Gastropoda. As the name suggests, the Isopleura retained "both in the shell and in the soft anatomy the primitive bilateral symmetry of the class." In addition to the Monoplacophora, Knight recognised the Polyplacophora (chitons) and Aplacophora as orders within the Isopleura, while the Sub-class Anisopleura contained the torted 'gastropods' which comprise the Class Gastropoda of current usage.

Knight (1952) established three families within the

Fig. 3. *Archinacella(?)* cf. *A.(?)* *elongata* (Cullison, 1944) from the Early Ordovician Poulsen Cliff Formation, Washington Land, western North Greenland, MGUH 18.970 from GGU collection 206483,  $\times 4$ . This supposed gastropod is shown in oblique dorso-lateral view (A), in dorsal view with the posterior apex located uppermost in the illustration (B), in oblique apico-dorsal view (C) and in lateral view with the strongly coiled apex overhanging the posterior margin (D).



Monoplacophora, namely Tryblidiidae, Hypseloconidae and Archinacellidae.

In the *Treatise on Invertebrate Paleontology* Knight & Yochelson (1960) included within the Class Monoplacophora three orders which many workers now assign to three distinct classes of Mollusca. Most genera within their Order Tryblidioidea (= Tryblidiida) are what

might be termed 'traditional monoplacophorans' such as *Pilina* and *Tryblidium* (Figs 1, 2). Their archinacelloideans (= Archinacellida; Fig. 3) are gastropods according to Starobogatov (1970), Harper & Rollins (1982), Yochelson (1988) and Peel (1990a), with Harper & Rollins also placing the cyrtoneleacean tryblidioideans of Knight & Yochelson (1960) in this class. Members of

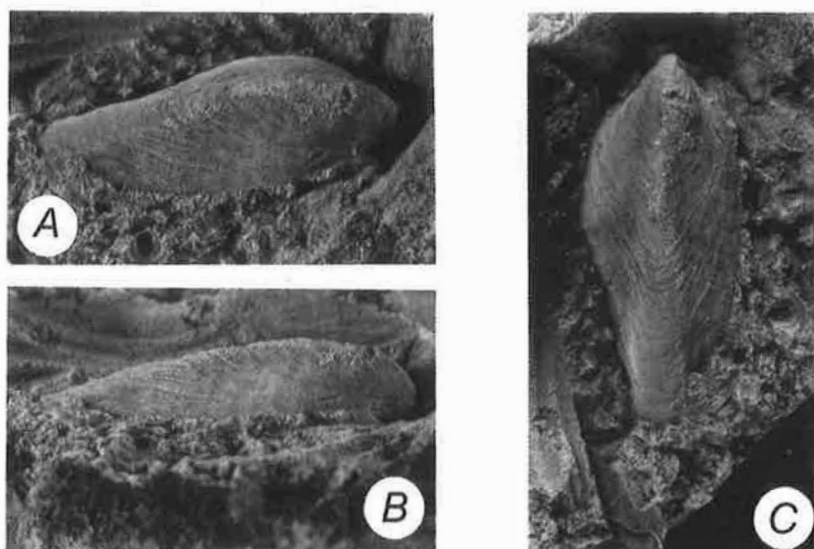


Fig. 4. *Stenothecoides groenlandicus* Peel, 1988 from the late Middle Cambrian Holm Dal Formation, Peary Land, central North Greenland, MGUH 18.676 from GGU collection 225561,  $\times 6$ . Oblique-lateral, lateral and plan views of a possible right valve.

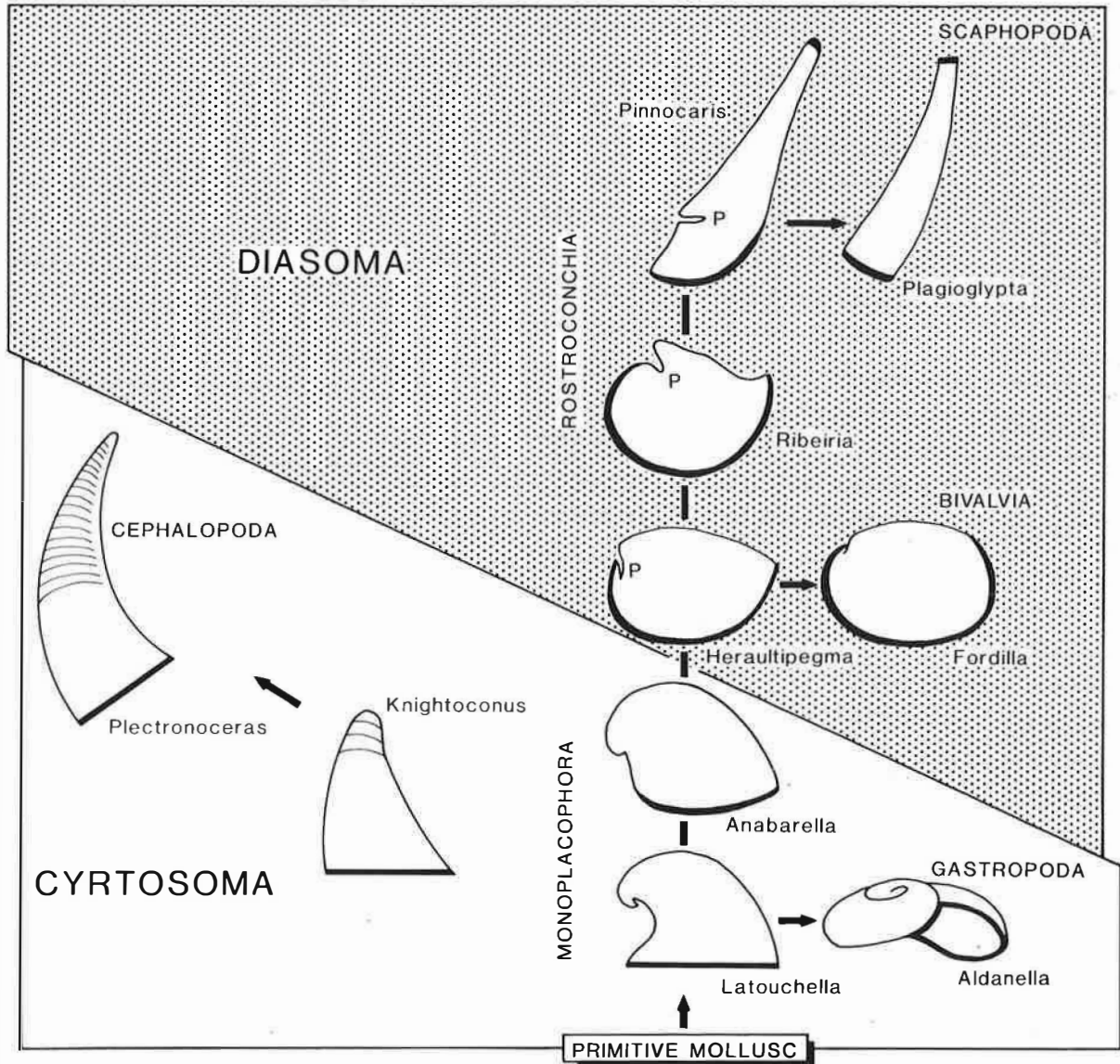


Fig. 5. Origin of the univalved and bivalved molluscs according to Runnegar & Pojeta (1974). Classes forming the Sub-phylum Diasoma (Rostroconchia, Bivalvia and Scaphopoda) are derived from the Class Monoplacophora. The Sub-phylum Cyrtosoma consists of the classes Monoplacophora, Gastropoda and Cephalopoda. Open apertures are indicated by thick black lines; p, pegma (redrawn from Runnegar & Pojeta, 1974, fig. 4). Runnegar & Pojeta (1974) considered the monoplacophorans *Latouchella* and *Anabarella* to be coiled exogastrically, i.e., with the shell coiled clock-wise when viewed laterally with anterior to the left as illustrated, while *Knightoconus* and its descendant cephalopods are endogastric, coiling anti-clockwise with the anterior to the left (cf. Fig. 12). In the present paper *Latouchella* and *Anabarella* are considered to be endogastric with the anterior to the right, as illustrated, while *Knightoconus* is interpreted as pseudo-endogastric, with the anterior to the left.

the Order Cambridioidea belong to the Class Stenothecoida (Fig. 4).

Horny (1965a, b), in part of a prolific series of papers concerning fossil monoplacophorans, proposed two sub-classes within the Monoplacophora, one of which (Sub-class Tergomya) corresponds to the traditionally

recognised tryblidiacean lineage. The Sub-class Cyclomya included the archinacelloideans and the more strongly coiled cyrtoneleacean tryblidioidaeans of Knight & Yochelson (1960). In the Tergomya, muscle scars form a ring located posterior to the shell apex, such that the apex lies outside of the muscle field, as in *Pilina*

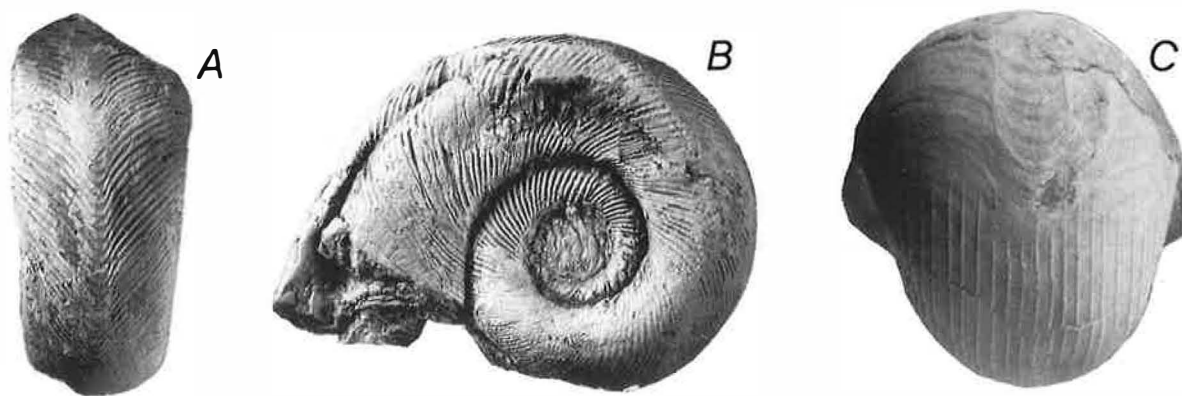


Fig. 6. Bellerophontiform molluscs. A, B, *Modestospira poulsoni* Yochelson, 1964 from the Lower Ordovician Orthoceras Limestone of Store Duegaard, Bornholm, Denmark. Holotype, MMH 9.953,  $\times 2$ , in dorsal and lateral views. *Modestospira* is characterised by its loosely coiled whorls, wide umbilici (B) and the median dorsal sinus (A). C, *Euphemites jacksoni* (Weir, 1931) from the Carboniferous (Namurian) of Congleton Edge, Cheshire, U.K. Topotype, MGUH 16.783,  $\times 4$ . In this globose bellerophontacean a broad slit generates a selenizone which, atypically for the group, is only visible in the latest part of the whorl due to the deposition of a strongly ribbed outer shell layer. In *Plectonotus* (Fig. 25A) this outer shell layer is not present and the selenizone is visible throughout the final whorl.

(Fig. 1; see also Fig. 13 and discussion below). In cyclomyans, which are often more strongly coiled, the shell apex lies within the muscle field.

The model of molluscan evolution presented by Runnegar & Pojeta (1974) and developed in a subsequent series of papers (e.g. Pojeta, 1980; Pojeta & Runnegar, 1976; Runnegar, 1978, 1983; Runnegar & Jell, 1976; Runnegar & Pojeta, 1985) depended largely on the adoption of a wide concept for the Class Monoplacophora which forms the stem-group for the other major taxa (Fig. 5) "thus expanding the original concept of the class to embrace most or all stem group molluscs that possessed an undivided shell (Conchifera)" (Runnegar in Bengtson *et al.*, 1990, p. 233). Apart from tryblidiaceans such as *Pilina*, *Tryblidium* and *Neopilina*, Runnegar & Pojeta (1985) formally assigned the helcionellids, hypseloconids, bellerophontids, archinacellids, pelagiellids, tuarangiids and cyrtoneillids to the class.

The Class Stenothecoida of Yochelson (1968, 1969, 1978) and Aksarina (1968; under the name *Probivalvia*; cf. Fig. 4), was dismissed by Runnegar & Pojeta (1974) as a group of bivalved monoplacophorans, without formal placement. Pojeta & Runnegar (1976, fig. 14) seemingly accept the class, but its constituent members are not included within the classifications given by Runnegar (1983) or Runnegar & Pojeta (1985).

One aspect of this large-scale expansion of the concept of the Class Monoplacophora, the assumption that all bellerophontiform molluscs (i.e. those strongly coiled, bilaterally symmetrical molluscs which morph-

ologically resemble the genus *Bellerophon* de Montfort, 1808; Fig. 6) were untorted, has led to protracted debate in the literature. One school accepts the hypothesis of Runnegar & Pojeta (1974) that all bellerophontiform molluscs are untorted (see also Salwini-Plawen, 1980, 1981). Another school insists that they are torted and hence gastropods (cf. Harper & Rollins, 1982) while a third group supported herein argues that the bellerophontiform molluscs include representatives of both torted and untorted molluscs (Berg-Madsen & Peel, 1978; Linsley, 1977, 1978; Yochelson, 1978, 1979; Horny, in press a, b). Interpretation of muscle scars in bellerophontiform molluscs has played a central part in this controversy.

While most of these groups assigned to the Monoplacophora by Runnegar & Pojeta (1985) share a pre-

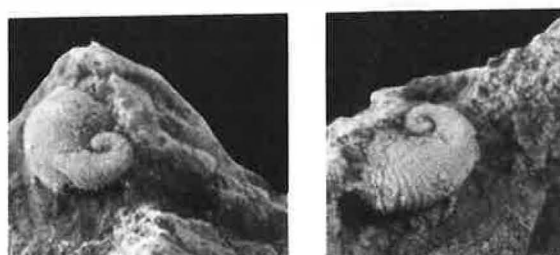


Fig. 7. *Costipelagiella kochi* Peel, 1988 from the late Middle Cambrian Holm Dal Formation, Peary Land, central North Greenland, MGUH 18.695 from GGU collection 225561, oblique apico-lateral views,  $\times 20$ .

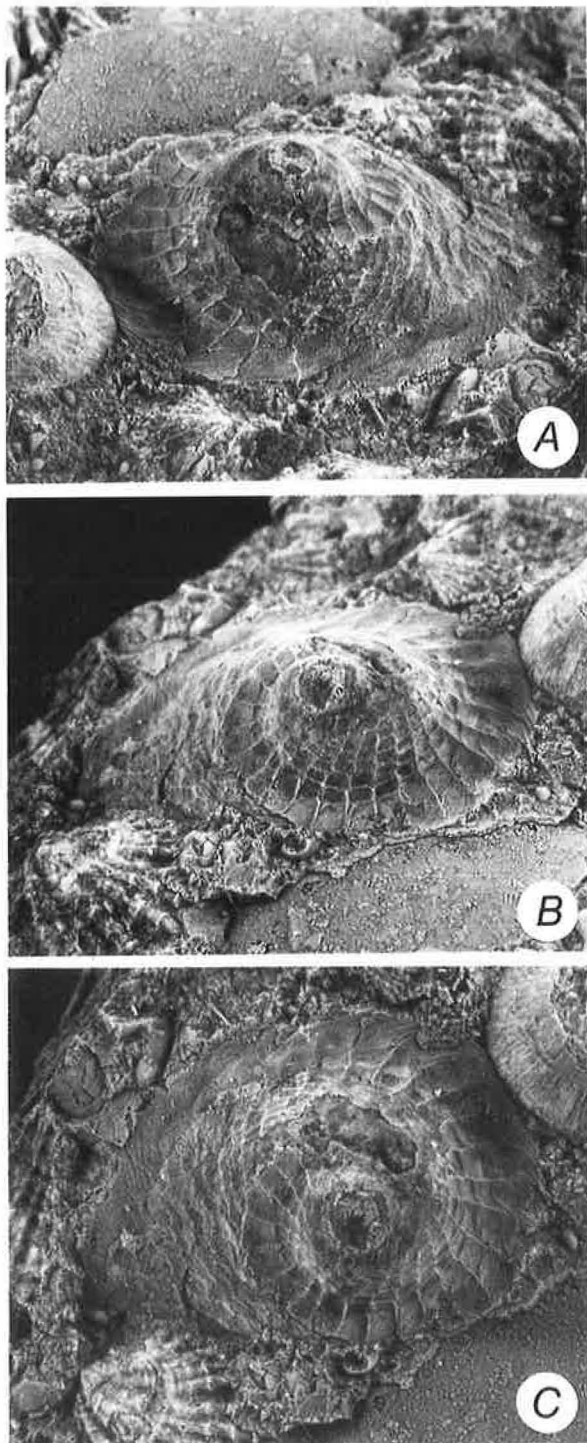


Fig. 8. *Clisospira ellitsgaardi* Peel, 1986 from the Early Silurian Cape Schuchert Formation, Kap Schuchert, Washington Land, western North Greenland, MGUH 16.778 from GGU collection 216482, holotype,  $\times 6$ . This member of the Class Paragastropoda is shown in oblique lateral views (A, B) and in apical view; note the sinistral coiling in contrast to the dextral coiling characteristic of most gastropods.

sumed basic untorted anatomy (except for the torted bellerophontids and archinacellids) and univalved shell (except for the tuarangiids), they clearly represent a broad array of adaptations in the earliest Palaeozoic history of the Mollusca. Indeed, Linsley & Kier (1984) considered pelagiellids (Fig. 7) to be part of their new Class Paragastropoda, together with the sinistrally coiled clisospirids (Fig. 8), macluritids and euomphalids, while MacKinnon (1982, 1985), Berg-Madsen (1987) and Krasilova (1987) thought that tuarangiids were bivalves.

Salwini-Plawen (1980, 1981) introduced the name Class Galeroconcha to include the Orders Tryblidiida (which he equated with Monoplacophora) and Bellerophontida (as Belleromorpha) which were considered to be untorted molluscs, although the Amphigastropoda Simroth, 1904 has a similar scope (see also Wenz, 1940 and Geyer, 1986). Galeroconcha is not used by Salwini-Plawen (1985; fig. 42).

Harper & Rollins (1982) reviewed the characters used by earlier workers in attempting to delimit the untorted monoplacophorans from the torted gastropods. They restricted the Class Monoplacophora to the tryblidiacean lineage, the Sub-class Tergomya of Horny (1965a, b), considering Horny's cyclomyans to be gastropods. By direct statement or implication, they excluded from this restricted Monoplacophora ten families of supposedly untorted molluscs which were placed in three orders within the Class Monoplacophora as defined by Runnegar & Jell (1976) and Runnegar & Pojeta (1985).

Geyer (1986) maintained a Class Monoplacophora but recognised that the helcionellids may represent a higher taxon separate from the tryblidiaceans.

#### Monoplacophora: current usage

It is apparent that the term Class Monoplacophora has not enjoyed stability since its inception. Thus, Peel (1991a) followed Wingstrand (1985) and others in recommending that Monoplacophora be abandoned as a class on account of this diverse and confusing usage. Peel could not accept the embracive usage of Class Monoplacophora employed by Runnegar & Jell (1976), Runnegar *in* Bengtson *et al.* (1990) and others. The Class Monoplacophora might have been restricted so as to be equivalent to the Class Tergomya of current usage, but this would scarcely alleviate the confusion in meaning present among contemporary writers. Sympathy is expressed for the plea of Horny (in press a) "...urgently interceding for the preservation of [Monoplacophora]" and restating his concept of Tergomya and Cyclomya as monoplacophorans. While the latter restatement is partly accepted, the intercession is reluctantly rejected.

Peel's (1991a) abandonment of the term Class Monoplacophora is restated and the Class Tergomya is further stabilised with the description of three constituent orders, below.

'Monoplacophoran' is an excellent term to cover the variety of untorted molluscs in a general sense, as an evolutionary grade, but this wide application is considered to be too great to accommodate within a single class. Haszprunar (1988) used the term at Super-class level, but to contain only a single Class Tryblidiida. Terms such as monoplacophoran, monoplacophore or monoplacophorous may prove to be useful descriptors for untorted molluscs with a single coiled or cap-shaped shell in general discussion.

Peel (1991a) developed ideas expressed in an earlier paper (Peel, 1988b) and recognised two major lineages of monoplacophorous molluscs separated mainly on the basis of their direction of shell coiling. The Sub-class Tergomya of Horny (1965a, b) was elevated to a full class to essentially replace Monoplacophora in the restricted sense of Harper & Rollins (1982), i.e. the *Pilina* and *Tryblidium* morphological group. The alternative term Tryblidiida has been employed by Wingstrand (1985), Haszprunar (1988) and others at a similar systematic level to the use of Tergomya, but without defini-

tion. Tryblidiida, however, has also been widely used as an order of the Class Monoplacophora and, as such, attributed to Lemche (1957) by many authors (e.g. Horny 1965a, b; Runnegar & Jell, 1976; Runnegar & Pojeta, 1985); this ordinal usage is preferred here. The concept of the Class Tergomya as expressed by Peel (1991a) is one of exogastrically coiled, untorted, univalved molluscs, usually with paired muscle insertions on the shell interior.

Peel (1991a) proposed a Class Helcionelloida to include the genera *Latouchella* Cobbold, 1921 (Figs 9, 10), *Helcionella* Grabau & Shimer, 1909 (Fig. 11) and their relatives which he distinguished from the tergomyans mainly in terms of their endogastric coiling (see Fig. 12).

In the present paper, the concept of exogastric Tergomya and endogastric Helcionelloida is further developed. The scope of the Tergomya is expanded from the original *Pilina* and *Tryblidium* group to take account of strongly coiled cyclomyans not discussed in the original proposal; three orders of Tergomya are recognised, one of which is new.

The idea of a major division within the untorted, bilaterally symmetrical, univalved molluscs (i.e. Monoplacophora in the sense now abandoned) based on dif-

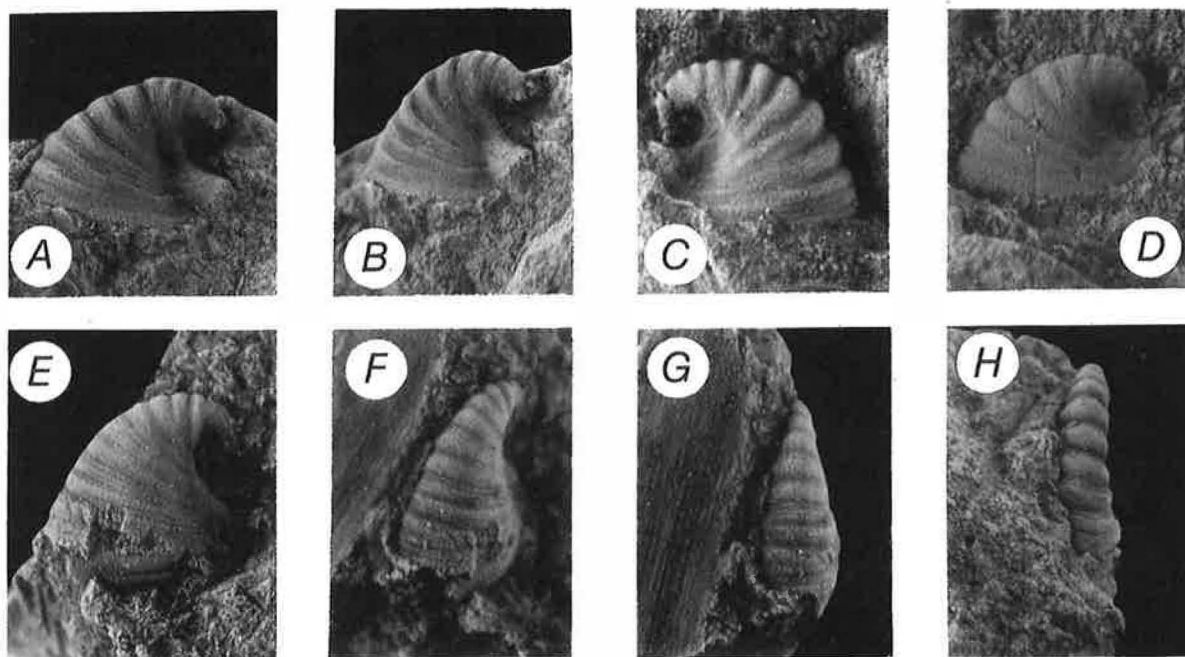


Fig. 9. *Latouchella holmdalense* Peel, 1988 from the late Middle Cambrian Holm Dal Formation, Gustav Holm Dal, Peary Land, central North Greenland, GGU collection 225535,  $\times 10$ . A, B, H, MGUH 18.678, the holotype in lateral, postero-lateral and anterior views, showing the prominent apertural fold on the posterior, sub-apical surface. C, MGUH 18.679 in lateral view with the anterior to the right. D, MGUH 18.680 in lateral view with the anterior to the left. E-G, MGUH 18.681 in lateral, antero-lateral and anterior views.

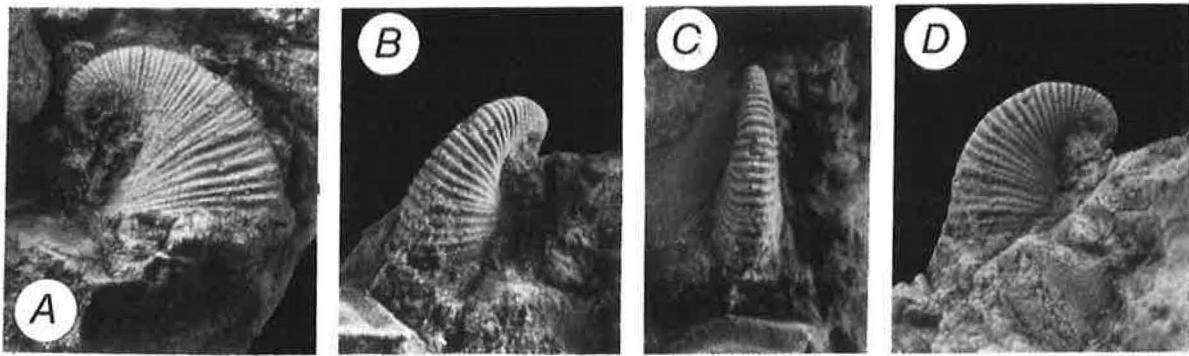


Fig. 10. *Latouchella pearylandica* Peel, 1988 from the late Middle Cambrian Holm Dal Formation, Gustav Holm Dal, Peary Land, central North Greenland, GGU collection 225561. A, MGUH 18.683 in lateral view with a shallow lateral emargination indicated by the concavity of the comarginal plications,  $\times 10$ . B-D, MGUH 18.684, the holotype in antero-lateral, anterior and lateral views,  $\times 13$ .

ferences in shell coiling is not new, although insufficient information has been published previously to give it credence or the ideas have not been fully developed. Yochelson (1978; 1979), Geyer (1986) and Peel & Yo-

chelson (1987) reconstructed helcionellids with endogastrically coiled shells, anticipating the formalisation proposed by Peel (1991a) and here.

Doguzhaeva (1981, p. 210) foresaw a dichotomy in a

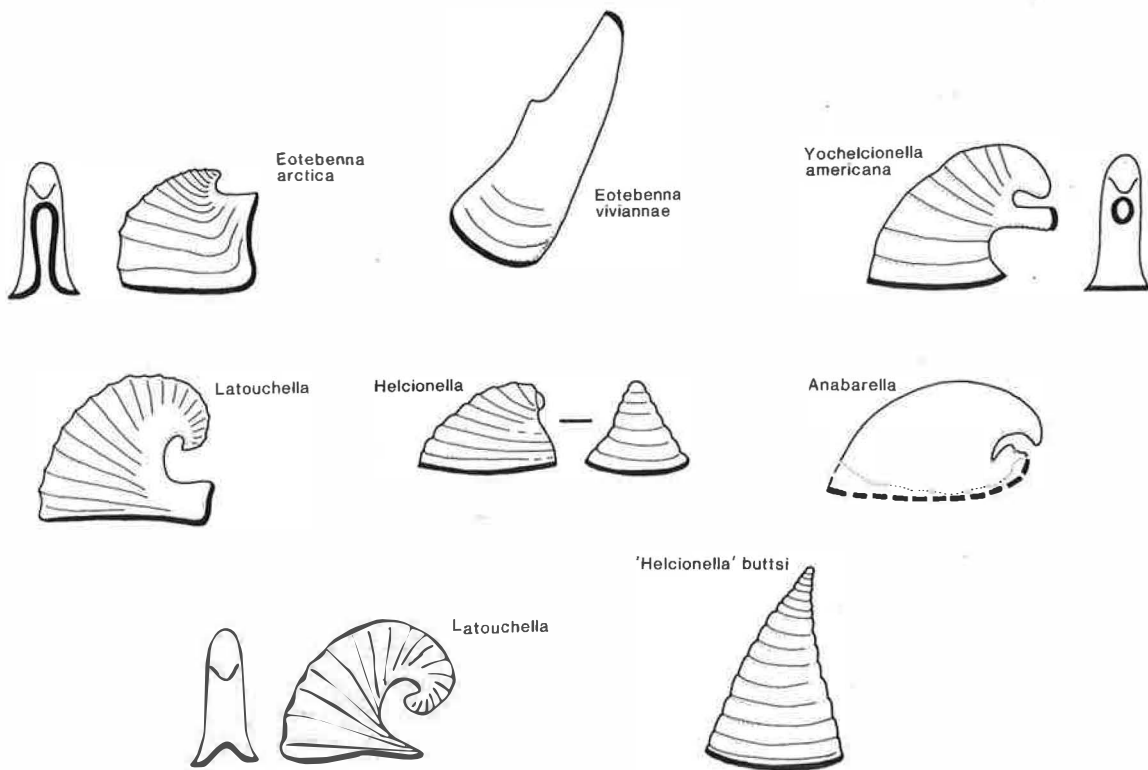
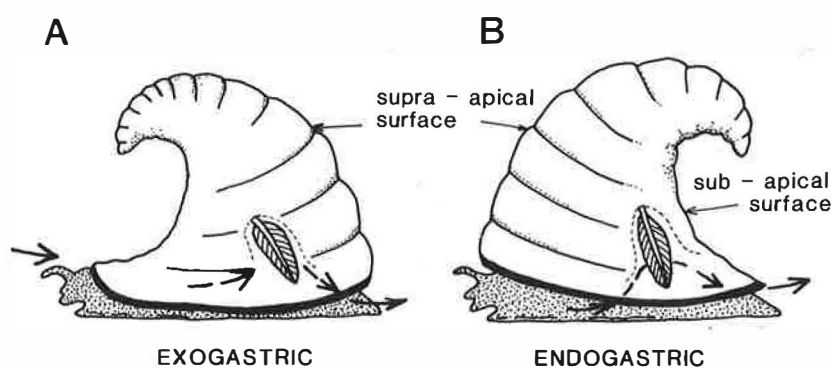


Fig. 11. Morphological variation within the Class Helcionelloida. All specimens are drawn in lateral view with the anterior to the left. *Helcionella* is shown in anterior and lateral views. Schematic drawings show the extent of the emargination in the posterior, sub-apical apertural margin in *Latouchella*, *Eotebenna arctica* and in *Yochelcionella*. The drawing of *Anabarella* is based on Runnegar (1983, fig. 4A); the preserved margin is shown by the stippled line and the inferred aperture by the heavy broken line. Apertural margins are indicated by thick black lines.



Fig. 12. Reconstructions of the helcionelloid *Latouchella*. A, Runnegar & Pojeta (1974), with inhalant water currents entering the shell anteriorly prior to postero-lateral exhalation. B, reconstruction favoured here. Inhalant currents enter the endogastric shell laterally while the exhalant stream leaves the mantle cavity along the median posterior margin. This reconstruction forms the basis of the Class Helcionelloida.



different context in proposing an Order Romaniellida for supposedly endogastric monoplacophorans (see Fig. 17, below). Her interpretation of an anal sinus in the sub-apical wall of Early Ordovician *Romaniella* Doguzhaeva, 1972 from the Soviet Union caused her to reinterpret this genus as endogastric and not exogastric, and to speculate that "...future studies of Monoplacophora will probably lead to the separation of ... three branches of development - three sub-classes within the Class Monoplacophora" [translated from Russian].

Doguzhaeva (1981) commented that *Latouchella* has much in common with *Romaniella* in terms of shell form and should not be treated as a gastropod as suggested by Knight *et al.* (1960), although contemporary authors already considered it to be untorted (cf. Runnegar & Jell, 1976). Uncertainty surrounding the status of *Romaniella* extends to many other cap-shaped and isostrophically coiled shells of similar age. It appears to be an unusual tergomyan; its reported broad emargination is not an unequivocal indicator of posterior since laterally compressed forms tend toward the development of lateral shields of the shell. Indeed, Stasek (1972, fig. 11A) inferred a hypothetical 'monoplacophoroid' ancestor to the Class Bivalvia with similar lateral shields and resultant, broad, anterior and posterior emarginations.

Doguzhaeva (1981) considered *Romaniella* to be some form of predecessor to the Order Archinacellida but archinacellids are here considered to be gastropods (see discussion below).

Yochelson *et al.* (1973, p. 286), while discussing the origin of cephalopods from tall monoplacophorans, correctly concluded that "one can not determine the anterior or posterior of a curved...or indeed any cap-shaped shell simply by observing the shell curvature." Peel (1988b) extended the discussion by noting that the position of the apex relative to the anterior and posterior margins in such shells also may be quite unconnected

with the direction of coiling, as partly illustrated by Rozov (1969, fig. 5) in considering exogastrically coiled shells (see also discussion below).

The need for functional morphological analyses of shell form in monoplacophorans of the type developed within the Class Bivalvia (e.g., Stanley, 1975; Allen, 1985; Vermeij & Dudley, 1985) and the Class Gastropoda (e.g. Linsley, 1977, 1978; Peel, 1974, 1984; Vermeij, 1975) to constrain interpretations of direction of coiling is evident. A number of relevant studies exist, e.g., Horny (1970) and Peel (1977a) discussed inhalant emarginations in fossil *Tergomya* while Rollins & Batten (1968), Peel (1980a), Linsley & Peel (1983) and Peel & Yochelson (1987) discussed more strongly coiled species. Linsley & Kier (1984) based their proposal of the molluscan Class Paragastropoda on functional morphological analysis while Peel (1991a) used this approach as the basis for formalising the separation of the two classes *Tergomya* and Helcionelloida.

### The question of size

Absolute size is one biological parameter which is often neglected in functional morphological interpretations of molluscs. Within the Gastropoda, shells with similar morphologies occur in widely separated environments where absolute size may be a limiting parameter. Thus, gastropod faunas which are supported by algal or other foliage at the present day rarely exceed 2 mm in length (Warmke & Almodovar, 1963; Brasier, 1975), a size limitation which encouraged Peel (1977b, 1978, 1984) to recognise possible foliage-supported gastropod faunas in the Silurian.

Runnegar & Jell (1976; see also Runnegar & Pojeta, 1985) noted the small size of early Cambrian molluscs, noting a subsequent increase in size as a conspicuous trend in molluscan evolution. To some extent this common size range of 1-2 mm in the Early Cambrian may

be a function of preservation or sampling bias since phosphatisation within coiled and cap-shaped forms is commonly restricted to near the apex. Thus, examination of phosphatic acid residues (a common form of study) may present an imperfect indication of true size ranges. Dzik (1991) demonstrated that centimetre-sized helcionelloids do occur in the earliest Cambrian of the U.S.S.R. even though most of their systematics is based on phosphatised internal moulds up to ten times smaller (cf. Missarzhevsky, 1989; Yu, 1987). Nevertheless, in a general sense, the observation of Runnegar & Jell (1976) appears to be correct and many of the Early and Middle Cambrian molluscs discussed here fall within this 1–2 mm size range (cf. Figs 23, 24, 27, 29, 31).

Specimens of this small size experience different physical and biomechanical constraints than molluscs ten times larger (and perhaps one hundred times more voluminous) and can only be interpreted functionally with great uncertainty when the larger morphologies serve as the functional reference point. The relationship to surface tension is critical, for example, in interstitial faunas (Swedmark, 1968).

In the present context mantle cavity reconstructions are discussed for a number of small helcionelloids, often

invoking models based on larger bellerophonacean gastropods. The validity of some of these reconstructions remains to be tested from the point of view of fluid mechanics. For example, it may prove unlikely that water could have been transported through the narrow snorkel of *Yochelcionella* (cf. Figs 28, 32, below), although the often minute distal opening of many small present-day scaphopods suggests that it was possible. Clearly, if the conduit in *Yochelcionella* was too narrow for water transport, the entire basis for the reconstruction is lost and the snorkel must be interpreted using another functional model.

The precept is followed that the mantle cavity reconstructions discussed below are possible in organisms of this small size. This approach is therefore the same as that employed by Runnegar & Pojeta (1974, 1985) and Pojeta & Runnegar (1976), although the conclusions offered below concerning the reconstruction of the helcionelloids are diametrically opposed. In the case of *Yochelcionella*, the former authors interpreted the function of the snorkel as inhalant while herein it is considered exhalant. Both interpretations assume that water transport was possible.

## Class Tergomya

The best known tergomyan lineage, the Tryblidiida, can be traced back from the present day *Neopilina*, through familiar fossil forms such as *Pilina* (Fig. 1) to the morphologically very similar Late Cambrian and Early Ordovician genus *Proplina* Kobayashi, 1933. Univalves from older Cambrian strata (e.g. *Kalbyella* Berg-Madsen & Peel, 1978 from the Middle Cambrian of Denmark and Australia) may extend the antiquity of this record.

Tryblidiidans are often considered to be the close descendants of the ancestral group of other conchiferous molluscs but possible members of the Tryblidiida are conspicuously less common in the Early and Middle Cambrian than members of the Class Helcionelloida.

### Cyclomya – gastropods or monoplacophores?

In association with the description of the Helcionelloida and Tergomya, Peel (1991a) recounted that Harper & Rollins (1982) had assigned the second of Horny's (1965a, b) sub-classes of the now abandoned Monoplacophora, the Sub-class Cyclomya, to the Class Gas-

tropoda. However, the status of most cyclomyan genera was not discussed by Peel in order to stress the fundamental difference in coiling between the endogastric Helcionelloida and the exogastric Tergomya. Exceptions were provided by the small group of genera centred around *Archinacella* Ulrich & Scofield, 1897, which were assigned to the Gastropoda in agreement with Starobogatov (1970), Harper & Rollins (1982), Yochelson (1988) and Peel (1990a), and by the Superfamily Hypseloconellacea of Stinchcomb (1986) which Peel considered to comprise atypically coiled tergomyans.

The decision to place the Hypseloconellacea within the Tergomya, and not within the Cyclomya as suggested by Harper & Rollins (1982), was based on ontogenetic studies of *Knightoconus* by Webers & Yochelson (1989) and Webers *et al.* (in press). *Knightoconus* and *Hypseloconus* were interpreted by Peel (1991a) as pseudo-endogastrically coiled tergomyans in which the unusually high shell (for a tergomyan) encompassed a change of coiling from the initial exogastric form to an ontogenetically later endogastric form (see discussion below).

Acceptance of *Hypseloconus* as a tergomyan may offer a clue to the affinities of other supposed cyclomyans, in particular members of the Order Cyrtoneillida Horny, 1963a in which the muscle scars have been excellently described by Horny (1963a; 1965a, b; see also Horny, 1990; in press a, b).

According to Horny (1965a, b), the fundamental difference between tergomyans and cyclomyans is the relationship between the circle of muscle scars and the apex of the shell. In tergomyans the apex lies outside of the dorsally placed muscle field while the apex lies within

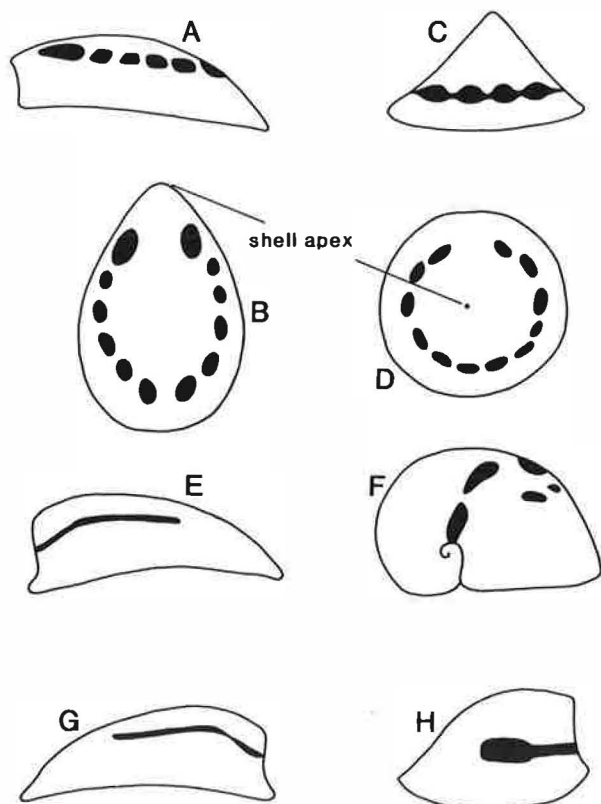


Fig. 13. Muscle scar patterns of 'tergomyan and cyclomyan-type' (cf. Horny, 1965a, b). A, B, internal mould of an untorted tryblidiid tergomyan shell exemplified by *Pilina* in lateral and dorsal views in which the circle of muscle scars lies on the dorsal surface and does not contain the shell apex ('tergomyan-type'). C, D, a cap-shaped shell in which the circle of muscle scars is arranged concentrically around the shell apex ('cyclomyan-type'). E, *Archinacella* interpreted as an untorted mollusc with the anterior to the left and the muscle scar of 'cyclomyan-type' passing below the shell apex. F, a cyrtoneillid with muscle scars of 'cyclomyan-type', anterior to left. G, *Archinacella* interpreted as a gastropod with the apex at the posterior and the anterior to the left. H, the patelliform gastropod *Metoptoma* oriented with the anterior to the left, for comparison with *Archinacella*.

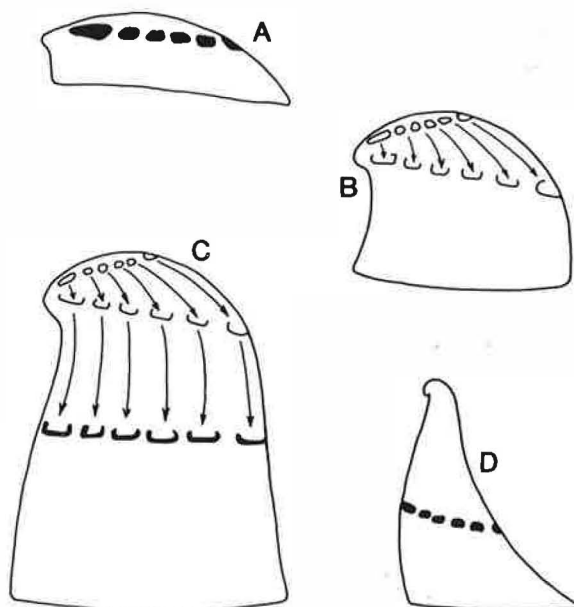


Fig. 14. Hypothetical derivation of a hypseloconid tergomyan such as *Knightoconus* (D) from a tryblidiid tergomyan such as *Pilina* (A). Increase in the tightness of coiling and height of the shell leads to migration of muscle scars from the 'tergomyan-type' (A) to 'cyclomyan-type' (B-D). The change is 'emphasised' by the change in coiling pattern from exogastric in the early growth stages to pseudo-endogastric in the adult (D).

the muscle scar cirlet in cyclomyans (Fig. 13A-D). The difference is striking when the tergomyan *Pilina* is compared with the supposed cyclomyan *Archinacella* of similar shell form (cf. Fig. 13A, E). *Archinacella*, however, is now considered to be a gastropod and not an untorted mollusc, with the result that the apex is not located anteriorly (Fig. 13E), as in *Pilina* (Fig. 13A), but posteriorly (Fig. 13G). The muscle scars of *Archinacella* thus resemble the sub-apical posterior muscle scars of limpet gastropods such as *Metoptoma* Phillips, 1836 or *Lepetopsis* Whitfield, 1882 (cf. Knight *et al.*, 1960, fig. 143; see Fig. 13H).

Most cyclomyans are morphologically distinct from the low, elongate shells of *Pilina*; the tall shells of hypseloconellaceans and the strongly coiled shells of cyrtoneillids (Fig. 13F) naturally require different patterns of muscle attachment than that present in *Pilina*. As shell growth parameters change, so will the disposition of muscle attachment sites, in response to changed biomechanical requirements. Muscle scars in *Knightoconus* can scarcely avoid changing from a tergomyan pattern in the juvenile to a cyclomyan pattern in the adult, as the tall pseudo-endogastric shell develops (Fig. 14A-D). Likewise, strong coiling through several whorls and a low rate of whorl expansion in some cyrtoneillids will

almost inevitably result in the acquisition of muscle scars of cyclomyan type (Fig. 15), although more rapidly expanding forms with fewer whorls such as *Cyrtoneilla* Hall, 1879 may well retain muscle scars which are more prominent on the dorsal surface (Rollins, 1969; Wingstrand, 1985, fig. 19).

Increase in coiling can clearly explain derivation of hypseloconellacean and cyrtoneillid muscle scar patterns from a tryblidiid shell (Figs 14, 15). However, the elongate tryblidiid form with its dorsal circlet of muscle scars may itself represent a strongly modified morphology rather than an ancestral form. Pronounced anterior displacement of the apex to produce a low, elongate shell of *Pilina* type, resulting from a rapidly expanding logarithmic spiral, may encourage migration of muscle scars from an originally circum-apical (cyclomyan) distribution to supra-apical (tergomyan) pattern (Fig. 16). Unfortunately, centralisation of an originally anterior apex could equally well lead to the assumption of a cyclomyan muscle field from an original tergomyan pattern.

#### The ancestral condition

Arguments concerning which morphology came first, the chicken or the egg, the cyclomyan or the tergomyan condition, must invoke other criteria than simple shape. A significant aspect in these discussions is geological age since some of the oldest cyclomyans (e.g. the hypseloco-

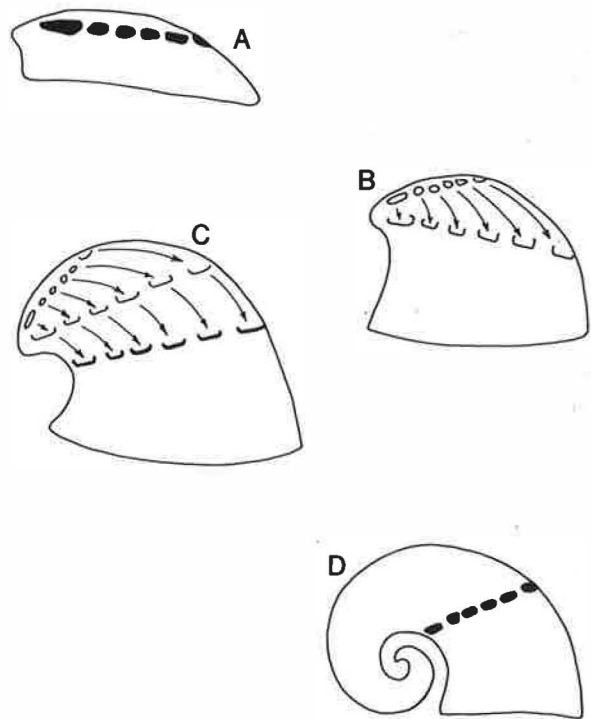


Fig. 15. Hypothetical derivation of a cyrtoneillid tergomyan (D) from a tryblidiid tergomyan (A). Tightening of the shell spiral and increased shell growth lead to derivation of muscle scars of 'cyclomyan-type' (D) from the original 'tergomyan-type' (A).

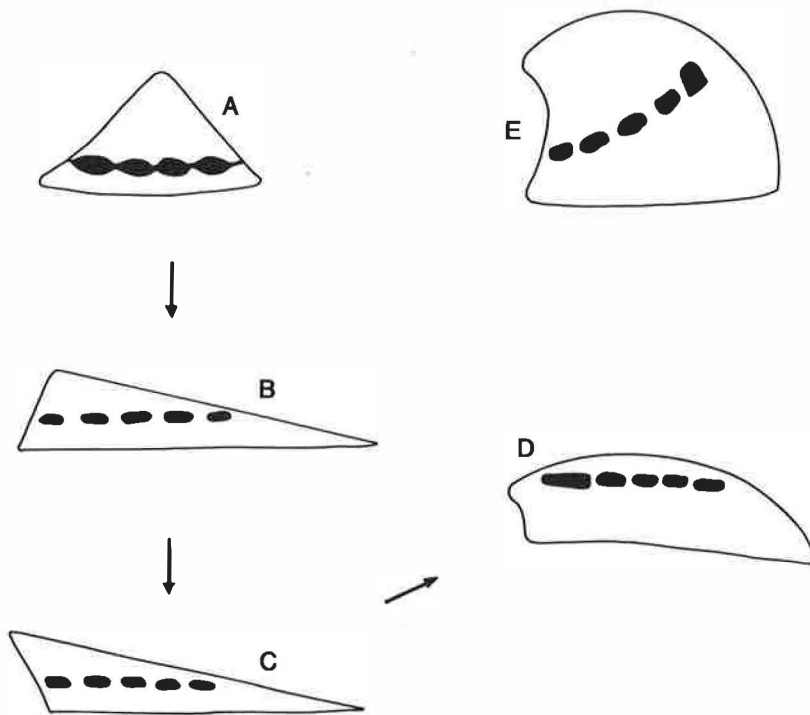
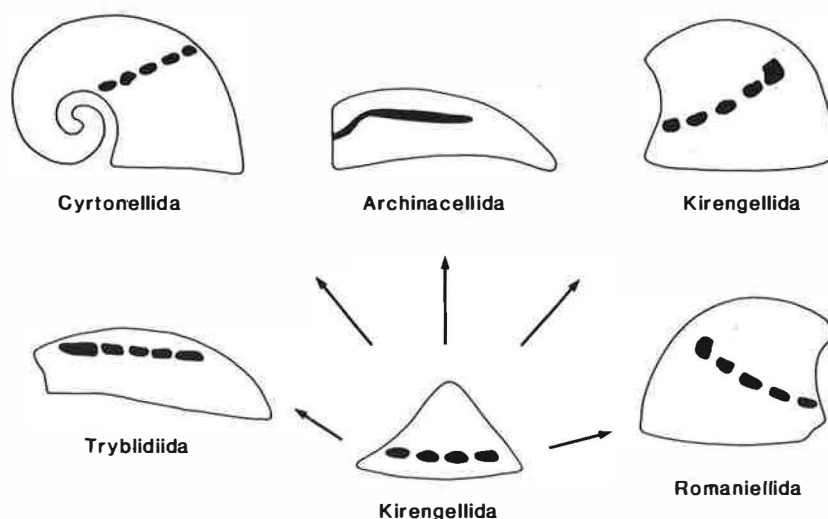


Fig. 16. Hypothetical derivation of a low, elongate, tryblidiid tergomyan (D) from a cap-shaped shell with muscle scars of 'cyclomyan-type' (A). Displacement of the apex to the anterior (A-C) and increase in coiling (D) tend to displace the circle of muscle scars addorsally. E, hypothetical member of the Order Kirengellida Rozov, 1975 in which muscle scars of 'cyclomyan-type' are associated with a tall, slightly coiled shell form.

Fig. 17. Radiation of un-torted molluscs ('monoplacophorans') from the ancestral kirengellid form according to Rozov (1975) and Doguzhaeva (1981).



nids from the late Middle Cambrian Holm Dal Formation of North Greenland described by Peel, 1988b) appear prior to the common appearance of univalves such as *Proplina* with muscle scars in a tergomyan pattern. However, the imperfections of the fossil record are notorious, as adequately documented by the absence of recognised trybliidiid tergomyans between the Devonian and the Cenozoic.

Rozov (1975) proposed that the 'primitive' monoplacophoran form was a cap-shaped or slightly coiled shell with muscle scars arranged concentrically around the apex (cf. Fig. 16A, E). He placed these shells in his new Order Kirengellida and derived other 'monoplacophoran' orders from this stock. Thus, he considered trybliidiids and archinacellids to be derived by anterior displacement of the apex and flattening of the shell, while cyrtoneilliids increased the degree of coiling. All orders were assumed to be exogastric (and consideration of helcinelloids was not given) but Doguzhaeva (1981) extended the concept by proposing that her new Order Romanielliida represented an endogastric branch from the original kirengellid stock (Fig. 17).

The model of Horny (1965a) implies derivation of the cyclomyan form with a central apex from an elongate ancestor to the Tergomya. The model also accords well with hypotheses recently stated by Salvini-Plawen (1985; see also Runnegar & Pojeta, 1985 and Wingstrand, 1985; see also Peel, 1991b) concerning the derivation of molluscs from a spiculate worm similar to living Aplacophora.

In a grossly simplistic sense, the morphological sequence from spiculate aplacophoran to multivalved polyplacophoran (by coalescence of spicules into a sequence of plates) may be argued to find its logical

continuation in the fusion of individual elements within the series of polyplacophoran valves to form the univalved, elongate tergomyan shell, with the serial muscle scars, gills and other organs representing the primitive condition. As noted by Wingstrand (1985, p. 61), however, such a direct sequence is neither necessary nor desirable; polyplacophorans and tergomyans were probably derived from a similar spiculate stock by separate events of spicule fusion. The halkieriid described by Conway Morris & Peel (1990; see also Peel, 1990b) and discussed in this volume (Peel, 1991b) possibly represents a third independent event even though its overall morphology suggests a tantalizing intermediate stage between the spiculate progenitor and eight-valved polyplacophorans. Rolfe (1981) has demonstrated that the supposed seven-valved polyplacophoran *Septemchiton* Bergenhayn, 1955 in fact has eight valves, although seven-valved forms still persist in the model of Salvini-Plawen, 1985). Again, the known geological distribution of both undoubted polyplacophorans and trybliidiid tergomyans shows a complicating late appearance of both groups near the Cambrian-Ordovician boundary. The simple model also neglects the effect of changing shell shape on differentiation of muscle scars.

#### *Sub-class Cyclomya abandoned*

The morphological scenario painted above casts doubt on the usefulness of the term *Cyclomya* in a phylogenetic classification, as a group of equivalent status to the Sub-class Tergomya, since it can be expected that 'cyclomyan' shells developed independently at different times and from different stocks within the Tergomya, in response to changes in coiling parameters. In

particular, the Hypseloconellacea may have little in common with the members of the Order Cyrtoneidida.

The terms *Tergomya* and *Cyclomya* have not gained wide acceptance as sub-classes of the Class Monoplacophora since their proposal by Horny (1965a, b) and were not employed by Starobogatov (1970), Runnegar & Jell (1976) or Runnegar & Pojeta (1985, but see Stasek, 1972; Morton, 1979). While *Tergomya* is now established at class level, *Cyclomya* is not employed. Consequently, the two orders which Horny (1965b) referred to the *Cyclomya* are relocated. The Order Cyrtoneidida Horny, 1963a is transferred to the Class *Tergomya* and the Order Archinacellida Knight & Yochelson, 1958 *sensu* Horny, 1965b is transferred to the Gastropoda.

#### Gastropods or retractile tergomyans

Most exogastrically coiled untorted molluscs can be readily placed within the cyrtoneidid *Tergomya*. However, the sinuitids (*Sinuites* Koken, 1896, *Strangulites* Horny, 1962 and *Sylvestrosphaera* Peel, 1980a) preserve muscle scar patterns which are difficult to reconcile with this assignment yet are not immediately reconcilable with the torted gastropod *Bellerophon*. The muscle attachment areas are not distributed around the whorl, as in *Cyrtoneidella* or *Sinuitopsis* (Fig. 18D-F), but consist of a single curved scar, or a pair of scars joined by a thin strand, near each umbilical shoulder, more than half a whorl back from the shell mouth (Fig. 18A-C). In position they resemble the scars of *Bellerophon*, although

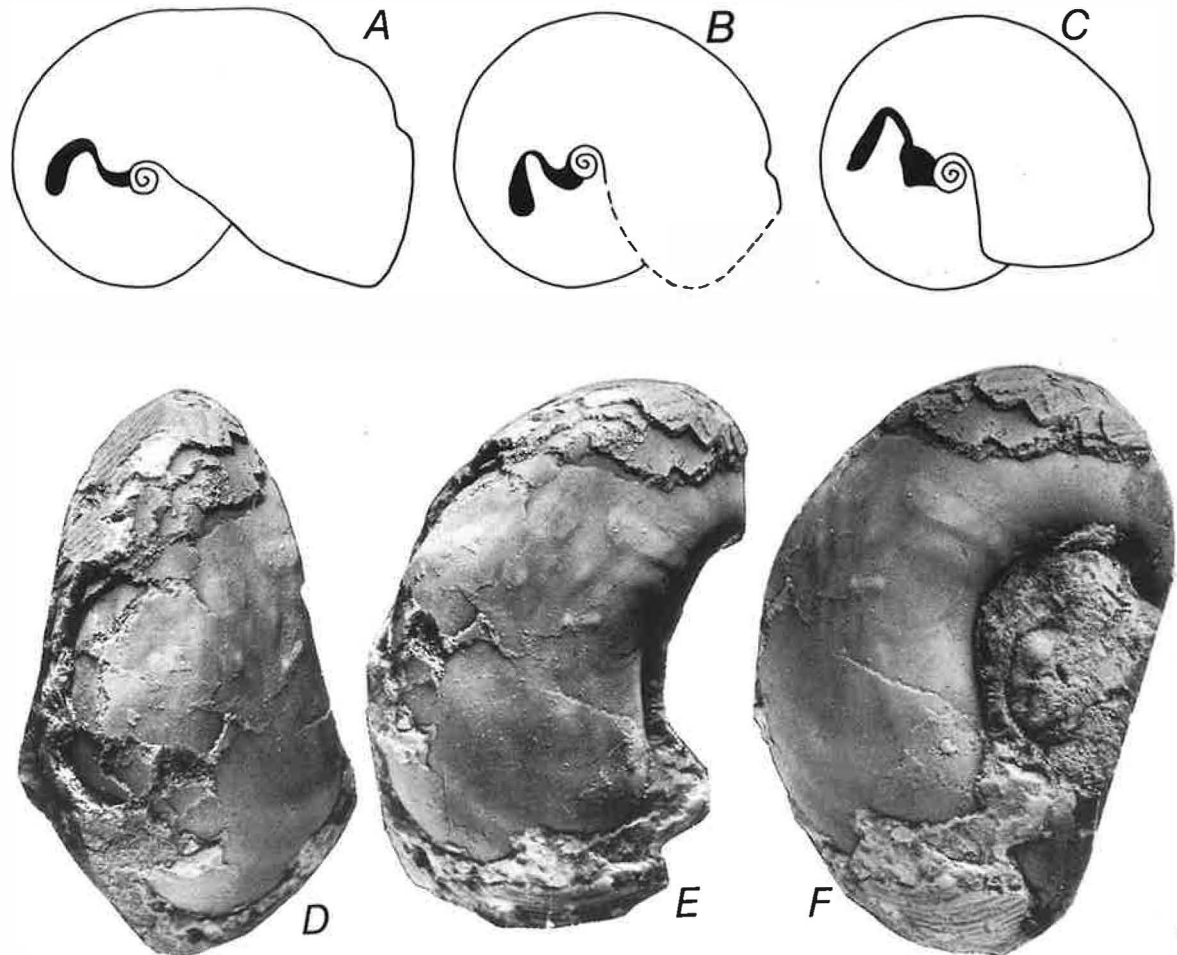


Fig. 18. Muscle scars in *Sinuites* (A), *Strangulites* (B) and *Sylvestrosphaera* (C), all shown in lateral view with the presumed anterior to the right (after Horny, 1990 and Peel, 1980a). D-F, *Sinuitopsis neglecta* Perner, 1903, partly exfoliated internal mould from the Lower Ordovician Zahotany Formation, Czechoslovakia, specimen P2 L 28633,  $\times 3.5$ . Note the deeply impressed multiple muscle scars represented by elevations on the internal mould; the lateral scar in F is repeated (photographs by Radvan J. Horny).

each of the single pair of muscle scars in the latter genus is V-shaped (cf. Peel, 1982). A suggestion by Peel (*in* Runnegar & Jell, 1980; Peel, 1980a, 1987; see discussion by Horny, 1990) that three pairs of muscle scars *may* have been present in *Sinuities* has not been substantiated by later work (Horny, 1990; *in press a, b*; personal communication, 1990; J. S. Peel, unpublished observations).

Knight (1947) described muscle scars in *Bellerophon* and *Sinuities*. He gave no indication that he considered the muscle scars in the two genera in any way to be different although both were considered to be gastropods and readily separable from the untorted *Cyrtoneilla* with its paired dorsal muscle scars. In 1976 Peel argued strongly for the similarity between muscle scars in these two genera, based on Knight's descriptions (see also Berg-Madsen & Peel, 1978) and an undescribed illustration of *Sinuities ammonoides* Koken, 1897 from the Baltic Ordovician (Koken & Perner, 1925, pl. 18, fig. 16). However, Peel (*in* Runnegar & Jell, 1980; Peel, 1980a, 1987) recanted his belief that *Sinuities* was a gastropod, considering the muscle scar pattern to indicate an untorted mollusc, a monoplacophoran of the then current usage. The muscle scars in *Sinuities* were considered to more closely resemble the muscle scars of *Cyrtoneilla* and other cyrtoneillid tergomyans (cf. Horny, 1963, 1965a, b) than the muscle scars of *Bellerophon* (cf. Peel, 1982), although this opinion was undoubtedly influenced by the now abandoned interpretation of three pairs of muscle scars in *Sinuities*.

Peel (1980a) described two pairs of muscle scars joined by a thin strand on the umbilical shoulders of a new Silurian genus, *Sylvestrosphaera* (Figs 18C, 19), noting its similarity to *Sinuities* (the dorsal area in the only known specimen was too poorly preserved to contribute decisively to the discussion concerning the third pair of muscles at that time believed to be present in *Sinuities*). Horny (1990) described similar muscle scars in *Strangulites* (Fig. 18B), placing all three genera within the Family Sinuitidae Dall *in* Zittel-Eastmann, 1913, confirming the earlier suggestion of Peel (1980a).

The deep placement of the muscle scars within *Sylvestrosphaera* lead Peel (1980a) to infer the ability to retract into the shell, by comparison with *Bellerophon* (cf. Linsley, 1978 and Peel, 1987, a much delayed publication). Horny (1990) extended this interpretation to *Sinuities* and *Strangulites*, noting that cyrtoneillids such as *Cyrtoneilla* and *Cyrtolites* probably clamped against the sediment surface instead of withdrawing into the shell.

Horny (1990) refrained from assigning the sinuitids to a molluscan class, although Peel (1980a) had argued that *Sylvestrosphaera* and *Sinuities* were retractile monoplacophorans (= Tergomya) and not bellerophontiform

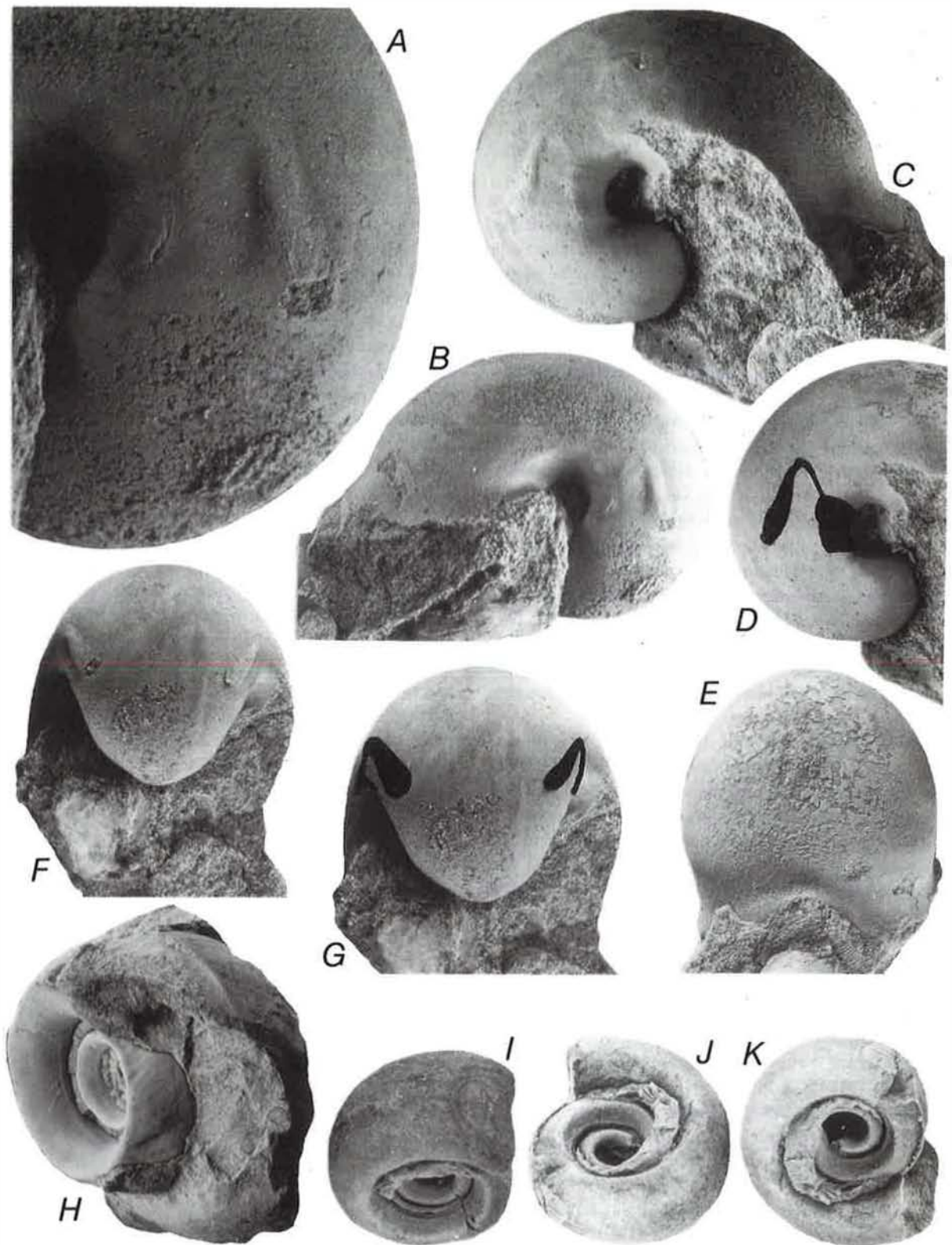
gastropods such as *Bellerophon*. This statement should be viewed in the light that Runnegar & Jell (1976) and Runnegar & Pojeta (1985) considered all bellerophontiform molluscs (i.e., cyrtoneillids, sinuitids and true bellerophontaceans) to be untorted monoplacophorans while Harper & Rollins (1982) considered them all to be torted gastropods. As stated previously (cf. Peel, 1976), the bellerophontiform molluscs are considered to be a mixture of untorted (cyrtoneillid Tergomya) and torted forms (bellerophontacean Gastropoda) but the status of the sinuitids is less clear.

The muscle scars in sinuitids resemble the cyrtoneillid Tergomya in terms of the shape of the scars and the presence of more than a single pair of muscle scars in *Sylvestrosphaera*. They resemble the muscle scars of bellerophontacean Gastropoda in comprising only a single pair of muscle scars in *Sinuities* and *Strangulites* (but not *Sylvestrosphaera*) and in their deep placement, although Horny (*in press a*) describes deeply placed scars from the cyrtoneillid tergomyan *Sinuitopsis*. However, differences in the shape of muscle scars in sinuitids when compared with the single pair of muscle scars in *Bellerophon* may be illusory, since described specimens of the latter genus with muscle scars are of Carboniferous age and therefore significantly younger than the Ordovician and Silurian sinuitids. It is thus readily argued that the *Bellerophon* condition represents a further simplification of the sinuitid muscle scar pattern and that the two groups are closely related. This argument is strengthened by the description by Horny (*in press b*) of muscle scars in *Sinuities* from the Lower Ordovician of Bohemia which show continuous migration tracks comparable to those seen in *Bellerophon*. As noted by Horny (*in press a*), muscle scars in the tergomyan *Sinuitopsis* (Fig. 18D-F) relocate by saltation (see also *Multifarites* Bjalyi, 1973).

Muscle scars which appear comparable to the *Bellerophon* condition have also been described in *Salpingostoma* Roemer, 1876 and *Megalomphala* Ulrich & Scofield, 1897 of similar age range to the sinuitids (Peel, 1972, 1976; 1991c; see Fig. 19). However, the whorl cross-section in these genera is morphologically quite distinct from the relatively globose, convex whorl profile of sinuitids and *Bellerophon*, and differences in muscle scar patterns may reflect variation in shell morphology.

It is imperative to bear in mind the warnings by Peel (1980a), Harper & Rollins (1982) and others about the dangers inherent in attaching undue significance to differences in muscle scar patterns between morphologically disparate coiling forms.

Linsley (1978) and Peel (1980a, 1987; see also Morton, 1979) pointed to the torsion potential of retractile





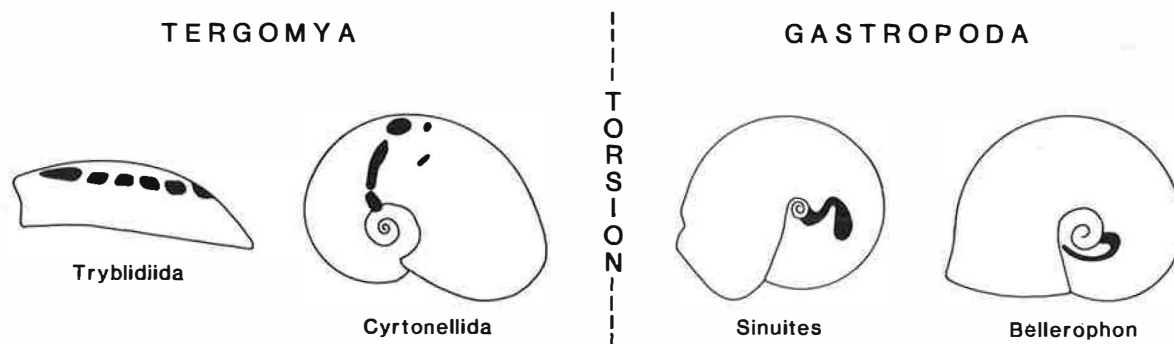


Fig. 20. Morphological sequence from Tergomya to bellerophontacean gastropod showing the possible origin of torsion. Musculature of 'tergomyan-type' in the Tryblidiida becomes 'cyclomyan' due to increased coiling in the Cyrtonebella. Concentration of muscle attachment areas moving by gradual anterior displacement (rather than the saltation characteristic of cyrtonebellids) in the umbilico-lateral area of *Sinuites* and *Bellerophon* characterises the post-torsional molluscs.

monoplacophorans (= Tergomya) and its relevance to discussions of the origin of the Gastropoda. Their independent conclusion that it was unlikely that torsion occurred in a cap-shaped shell of the type characteristic of tryblidiid tergomyans stands in contrast to the opinion of Haszprunar (1988).

Interpretation of *Sinuites* and *Sylvestrosphaera* as intermediates between cyrtonebellid tergomyans such as *Sinuitopsis* and bellerophontacean gastropods (Fig. 20) offers an attractive morphological series, although the Silurian *Sylvestrosphaera* is geologically too young to have filled this role phylogenetically (Peel, 1980a). The shape of the muscle scars in sinuitids, and in particular the composite form of the muscle scars in *Sylvestrosphaera*, may suggest that these molluscs were untorted

whereas *Bellerophon*, with its single pair of muscle scars elongated concentric to the axis of coiling, was torted. The biomechanical advantages of reducing muscle attachment to a single area on each umbilical shoulder may be equally valid for retractile tergomyan and gastropod alike.

It might also be proposed that the deep placement of muscle scars in sinuitids is a gastropod character but the ability to retract has equal protective advantages for both coiled tergomyans and gastropods (Peel, 1980a), as confirmed by the description of deeply placed muscle scars in *Sinuitopsis* by Horny (in press a).

The dilemma that it may be impossible to distinguish coiled retractile tergomyans from bellerophontacean gastropods on the basis of the number and placement of muscle scars alone (Peel, 1980a) possibly may be resolved by employing other shell characters, such as the shape of the muscle scars. Horny (1990; in press a, b) pointed out differences in the morphology and method of relocation of muscle scars in cyrtonebellid tergomyans and *Bellerophon*; he considered sinuitids to show greater similarity to *Bellerophon* on account of the gradual, non-saltating, relocation of muscle scars.

Other shell features cited in discussions of torsion in the bellerophontiform molluscs were reviewed by Harper & Rollins (1982; see also Yochelson, 1967) who admittedly found most of them to be individually non-diagnostic (the similar quandary facing attempts to delimit the Gastropoda as a class on the basis of a single shell feature is well known and merely demonstrates the need for a less simplistic model). Features such as the dorso-lateral supposedly inhalant emarginations of trilobed bellerophontaceans (Peel, 1974, 1977b, 1978, 1984) and *Knightites* Moore, 1941 (Knight, 1952) are difficult to dismiss as indicators of gastropod affinities (see discussion below), although the location of inhalant

Fig. 19. Muscle scars in the sinuitid *Sylvestrosphaera lemchei* Peel, 1980 and the bellerophontacean gastropod *Megalomphala taenia* (Lindström, 1884). A-G, *Sylvestrosphaera lemchei*, holotype, internal mould, OUM Geology, C. 16792, internal mould from the Late Silurian of Britain. A, detail of the muscle scar shown in B,  $\times 9$ ; B, C, lateral views with muscle scars,  $\times 3$  and  $\times 3.25$ , respectively; D, as C with muscle scar shaded,  $\times 2.5$ ; E, dorsal profile showing the broad anterior emargination and slightly constricted aperture,  $\times 2.5$ ; F, posterior view showing muscle scars on each umbilical shoulder,  $\times 2.5$ ; G, as F but with muscle scars shaded,  $\times 2.5$ . The use of anterior and posterior is based on the interpretation of *Sylvestrosphaera* as a gastropod. H-K, *Megalomphala taenia*, internal moulds from the Silurian of Gotland. H, MMH 13.037 in oblique antero-lateral view showing an elongate ridge associated with the muscle scar on the umbilical wall near the suture with the earlier whorl. A spiral ridge from the muscle scar in an earlier growth position is visible on the innermost visible whorl,  $\times 1$ . I-K, USNM 188177 in oblique lateral views showing similar ridges associated with musculature in the left (I) and right (J, K) umbilici,  $\times 1$ .

currents in sessile, morphologically bell-shaped, bellerophonacean gastropods may reflect other influences. Similarly, Horny (in press, a) describes umbilical sinuses in *Sinuitopsis* strongly indicative of tergomyan affinities. Functional morphological analysis of the type employed by Linsley (1977, 1978), Linsley & Peel (1983; see also Peel, 1974) and others offers a potential solution.

At the present time, the sinuitids are considered to be tortored retractile molluscs and, as such, they are assigned to the Gastropoda, largely following arguments presented by Horny (1990; in press a, b). Sinuitids represent part of a morphological continuum (Fig. 20) and placement of the torsion event in this series is to some extent arbitrary – a situation reminiscent of the separation of the classes Helcionelloida and Rostroconchia, discussed below. *Sylvestrosphaera* out of the three sinuitid genera is less confidently assigned to the Gastropoda than *Sinuites* and *Strangulites*. This lack of confidence is based partly on the clearly composite nature of each umbilico-lateral muscle scar complex and the unusual, inflated, shape of the whorl profile (Fig. 19E). *Sylvestrosphaera* is also considerably younger than other described sinuitids with muscle scars but is unfortunately only known from a single specimen (Peel, 1980a).

#### Tergomyan classification

Peel (1991a) presented a severe diagnosis of the Class Tergomya, based exclusively on members of the *Pilina* and *Tryblidium* morphological group, in order to stress the conceptual difference between exogastric tergomyans and the endogastric Helcionelloida. Discussion of the scope of both classes below the class level was purposely omitted, apart from general discussion concerning placement of hypseloconellaceans and members of the *Archinacella* group, noted above. Transfer of the Order Cyrtonegellida to the Class Tergomya (discussed above) and proposal of the new Order Hypseloconellida require emendation of the original diagnosis.

#### Class Tergomya

**Diagnosis** (emended). Generally bilaterally symmetrical molluscs in which the calcareous shell is usually planispirally coiled through about half a whorl to two or more whorls. The shell is often cap-shaped or ovoid, with an anterior apex which may vary from sub-central to overhanging the anterior margin; in other forms the shell may be a tall curved cone or coiled into a plane spiral with the coiled early growth stages carried ante-

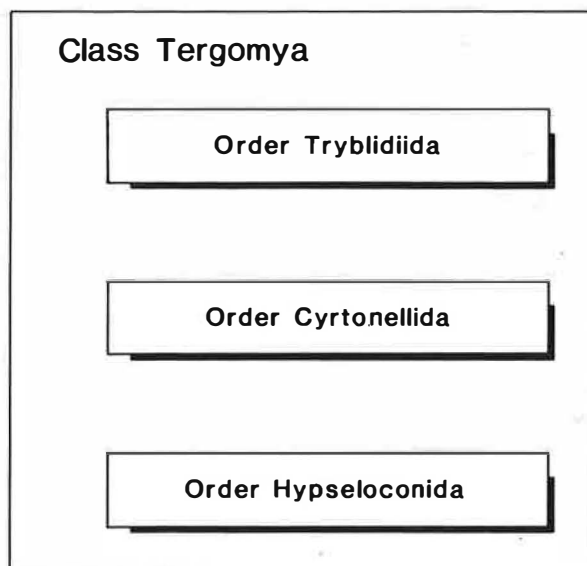


Fig. 21. Classification of the Class Tergomya.

riorly. The aperture is generally planar but may be slightly arched in lateral view in some cap-shaped forms (e.g., *Pilina*). Paired muscle scars on the shell interior of ovoid shells are typically grouped into a ring on the dorsal, supra-apical, surface with the apex lying outside of this ring. In strongly coiled shells and in unusually tall shells, paired muscle scars form a circle around the apex, varying in location from near the apertural aperture to about half a whorl back from the apertural margins. Ornamentation consists of radial and/or comarginal elements; prominent comarginal rugae are not widely developed.

**Discussion.** At this time, three orders are recognised within the Class Tergomya (Fig. 21): Tryblidiida, Cyrtonegellida and Hypseloconida (new).

#### Order Tryblidiida Lemche, 1957

This order includes those cap-shaped and ovoid shells related to *Neopilina*, *Pilina* and *Tryblidium* in which muscle scars are distributed in the tergomyan pattern of Horny (1965a, b; cf. Knight & Yochelson, 1960, in part; Horny, 1963b, c; 1970; Figs 13, 20). Runnegar & Jell (1976) placed the Archinacelloidea Knight & Yochelson, 1958 within their concept of the Tryblidiida but *Archinacella* and its relatives are here considered to be gastropods (Starobogatov, 1970; Harper & Rollins, 1982; Yochelson, 1988; Peel, 1990a).

### Order *Cyrtonegida* Horny, 1963a

The Order *Cyrtonegida* includes planispirally coiled shells (Fig 15D, 18D-F) such as *Cyrtolites* Conrad, 1838, *Cyclocyrtonegida* Horny, 1962, *Yochelsonella* Horny, 1962, *Cyrtonegida* and *Simitopsis* Perner, 1903 (Horny, 1963a, 1965a, b; Rollins & Batten, 1968; Rollins, 1969) in which several pairs of muscle scars form a circle around the shell, generally near to the aperture (Fig. 20). Starobogatov (1970) recognised an Order *Sinuitopsida* (alongside Orders *Tryblidiida* and *Cyrtonegida*) but this is here united with the *Cyrtonegida*. Runnegar & Jell (1976; see also Runnegar & Pojeta, 1985) placed the helcionelloids and hypseloconellaceans within their concept of *Cyrtonegida* while genera here regarded as members of the order were distributed between the *Cyrtonegida* and the Order *Bellerophonitida* of their usage (most *bellerophonitidans* are here considered to be gastropods).

The Orders *Kirengellida* Rozov, 1975 and *Romaniellida* Doguzhaeva, 1981 are not recognised and most of their genera are transferred to the *Cyrtonegida*.

### Order *Hypseloconida* (new)

The *Hypseloconida* is diagnosed as containing tall, slightly coiled, cyrticonic shells which are interpreted as pseudo-endogastrically coiled by comparison with *Knighoconus*. The single Superfamily *Hypseloconellacea* Stinchcomb, 1986 includes the genera *Hypseloconus*, *Knighoconus*, *Shelbyoceras* Ulrich & Foerste in Bridge, 1930 (cf. Stinchcomb & Echols, 1966), *Cambrioconus* Stinchcomb, 1986, *Cornuella* Stinchcomb, 1986, *Archeoconus* Stinchcomb, 1986 and *Yochelsonella* Flower, 1968. *Gasconadeoconus* Stinchcomb, 1986 and *Protoconus* Stinchcomb, 1986 do not appear to be hypseloconids, although originally included within the Superfamily *Hypseloconellacea* by Stinchcomb (1986). The latter author placed his superfamily within the Order *Archinacelloidea* of the Class *Monoplacophora* but, as noted elsewhere, *archinacelloids* are considered to be gastropods.

## Class *Helcionelloida*

Runnegar & Pojeta (1974) viewed the univalved and bivalved molluscs as belonging to two sub-phyla for which they proposed the names *Cyrtosoma* and *Diasoma* (Fig. 5). In the Sub-phylum *Cyrtosoma*, the shell is usually univalved and the gut bent into a U-shape or twisted on account of torsion; this sub-phylum includes the classes *Monoplacophora* of their usage, *Gastropoda* and *Cephalopoda*. The gut is essentially straight in the Sub-phylum *Diasoma* and the shell may be univalved or bivalved. The classes *Rostroconchia*, *Bivalvia* and *Scaphopoda* were assigned to the *Diasoma* by Runnegar & Pojeta (1974; see also Pojeta, 1980; Pojeta & Runnegar, 1976; Runnegar, 1978, 1983; Runnegar & Pojeta, 1985).

Runnegar & Pojeta (1974) derived the sub-phylum *Diasoma* from a group of univalved molluscs termed *helcionellaceans* which they assigned to the Class *Monoplacophora*. As noted above, they included a variety of molluscs within this class in addition to traditionally accepted *monoplacophorans* such as the *tryblidiaceans* *Pilina*, *Tryblidium* and the living *Neopilina* which Peel (1991a) placed within the Class *Tergomya*.

Runnegar & Pojeta characterised *helcionellaceans* in terms of the genus *Latouchella* (Figs 9–11), although this group of Early and Middle Cambrian molluscs de-

rives its name from *Helcionella* (Fig. 11). *Helcionella* is relatively more rapidly expanding and less strongly coiled than *Latouchella*.

In the *Treatise on Invertebrate Paleontology* Knight *et al.* (1960) placed *helcionellaceans* within the *archaeogastropod* *Prosobranchia* (Class *Gastropoda*) but Runnegar & Pojeta (1974) followed contemporary authors in considering *helcionellaceans* to be untorted molluscs. As with the *tryblidiaceans* (= Class *Tergomya* of present usage), Runnegar & Pojeta considered the *helcionellaceans* to be exogastrically coiled, i.e. the apex of the coiled shell was located anteriorly and the shell expanded posteriorly. Thus, the generally concave sub-apical surface was located anterior of the apex while the convex supra-apical surface was posterior (Fig. 12A).

Peel (1991a) considered that *helcionellaceans* represented a major lineage of untorted univalved molluscs distinct from the *Tergomya* and established a new class, the Class *Helcionelloida*. Peel considered *helcionelloids* to be endogastrically coiled (Fig. 12B), as suggested by Yochelson (1978; 1979), Geyer (1986) and Peel & Yochelson (1987), and thus distinct from the exogastric *Tergomya*. This conclusion was supported by interpretation of morphological features of the *helcionelloid* shell in terms of functional adaptation. The shell apex was

considered to be posterior and the shell expanded anteriorly in the Helcionelloida, as is the case also with the gastropods. Unlike gastropods, however, helcionelloids are interpreted as untorted molluscs.

### Order Eomonoplacophora

In a recent publication, not available to Peel (1991a), Missarzhevsky (1989) proposed Eomonoplacophora to contain *Helcionella* and its relatives, in a summary of Soviet Lower Cambrian helcionelloids. Missarzhevsky cited the importance of knowledge of muscle scars in classifying taxa within the Class Monoplacophora of his usage, approximately the Class Tergomya of this paper. He criticised Runnegar & Jell (1976) for only employing gross morphology as the basis for much of their classification, quoting as an example the unfortunate placement of *Protowenella* Runnegar & Jell, 1976, *Multifariites* Bjalyi, 1973 and *Bellerophon* within the same supposedly monoplacophoran order. Missarzhevsky placed *Bellerophon* with the gastropods, *Multifariites* with the Monoplacophora (= Tergomya) but found no conclusive evidence as to where he should place *Protowenella*.

Missarzhevsky (1989, p. 22) recommended that Monoplacophora should be restricted to those forms in which muscle scars clearly indicated this systematic position. He proposed Eomonoplacophora as an informal group of undefined systematic range to include Cambrian shells of monoplacophoran aspect but without preserved muscle scars. He defined several families on general morphological grounds.

Missarzhevsky expressed his conviction that Eomonoplacophora followed the general monoplacophoran body plan and were not gastropods. He suggested that muscle scars were not known in Eomonoplacophora on account of muscle insertion into an epithelial layer rather than directly to the shell. He considered direct muscle attachment to the shell to be a later evolutionary development in molluscan evolution.

Later in the same work, Missarzhevsky (1989, p. 171) formally erected Eomonoplacophora as a new order of the Class Monoplacophora.

Missarzhevsky interpreted members of the Eomonoplacophora as exogastric, in keeping with the placement within the Class Monoplacophora. Thus, he considered emarginations in the apertural margin of the concave sub-apical surface to be anterior and those in the supra-apical surface to be posterior (cf. Missarzhevsky, 1989, fig. 6). Following Runnegar & Pojeta (1974), the snorkel in *Yochelcionella* was also interpreted as anterior by Missarzhevsky (1989).

While Missarzhevsky's recognition of the integrity of the helcionelloids is to be applauded, his interpretation

of the group as exogastric can not be sustained. In consequence, the term Eomonoplacophora is not employed even though its generic content (but not its concept) corresponds quite closely to that of the Class Helcionelloida. Concept apart, it would also be confusing to maintain Eomonoplacophora for the present endogastric Helcionelloida after purposely replacing the exogastric Monoplacophora with Tergomya.

### Classification of helcionelloids

Two recent classifications of helcionelloid genera are available, but both view helcionelloids in different conceptual frameworks than that expounded here.

Runnegar & Jell (1976) assigned the families Helcionellidae, Scenellidae, Palaeacmaeidae, Yochelcionellidae, Procarinariidae, Hypseloconidae and Cyrtolitidae to their Superfamily Helcionellacea of the Order Cyrtoneidida, Class Monoplacophora. Procarinariidae was replaced by the new family name Stenothecidae by Runnegar & Jell (1980) for the same group of genera (*Anabarella* Vostokova, 1962; *Mellopegma* Runnegar & Jell, 1976, *Stenotheca* Hicks, 1872), but excluding the bivalve *Procarinaria* Perner, 1911.

Runnegar & Jell (1976) commented that the Palaeacmaeidae may not be untorted molluscs and this family does not appear in the list of helcionellacean families subsequently published by Runnegar & Pojeta (1985). Yochelson & Stanley (1981) interpreted *Palaelophacmaea* Donaldson, 1962, placed in the Family Palaeacmaeidae by Runnegar & Jell (1976), as a coelenterate (Hydrozoa).

In the present classification, the endogastric Helcionellacea and the exogastric Cyrtoneidida are referred to separate classes (respectively Helcionelloida and Tergomya), in direct conflict with the classifications of Runnegar & Jell (1976) and Runnegar & Pojeta (1985). Thus, the Helcionellacea as recognised here is removed from the Cyrtoneidida and does not contain the Family Cyrtolitidae which Runnegar & Jell (1976) placed here, although Runnegar & Pojeta (1985) placed it within another monoplacophoran order of their usage, Bellerophontida. Cyrtolitidae and Hypseloconidae are here considered to be Tergomya, although the latter family was also assigned to the Helcionellacea by Runnegar & Jell (1976) and Runnegar & Pojeta (1985).

The Scenellidae of Runnegar & Jell (1976) contains a variety of cap-shaped shells of moderate height ranging in age from Early Cambrian to Early Ordovician. The description of well preserved muscle scars in a specimen assigned to *Scenella* Billings, 1872 by Rasetti (1954) is of potentially great interest to interpretations of musculature in the Helcionelloida, as noted by Runnegar & Jell

(1976) and Runnegar & Pojeta (1974). However, the status of Rasetti's specimens both as members of *Scenella* and the Class Helcionelloida remains problematic. Yochelson & Gil-Cid (1984) suggested that *Scenella* was a chondrophore; this opinion is not endorsed although the status of many species assigned to the genus (also the genus *Marocella* Geyer, 1986) is problematic.

The systematic position of several Late Cambrian and Early Ordovician genera from the Soviet Union, *Kirengella* Rozov, 1968, *Lenaella* Bjalyi, 1973, *Moyerokania* Rozov, 1970 and *Romaniella* Doguzhaeva, 1972, which Runnegar & Jell (1976) assigned to the Scenellidae, remains uncertain; they appear to be tergomyans in which the muscle scar patterns reflect the relatively high, strongly coiled shell. Peel (1988b) described material from the late Middle Cambrian of Peary Land, North Greenland, which he assigned to *Kirengella* (inadvertently spelt *Kiringella* in perpetuation of an error in the American translation of Rozov's paper of 1968) within the Superfamily Hypseloconellacea (now order Hypseloconida of the Tergomya). Interestingly, Doguzhaeva (1981) interpreted *Romaniella* as endogastric on the basis of a shallow sinus in the sub-apical surface which she considered to indicate the location of the anus. Doguzhaeva placed *Romaniella* in a new Order Romaniellida of the Monoplacophora, pointing out its great similarity with *Latouchella*.

The helcionellids, yochelcionellids and stenothechids of Runnegar & Jell (1976) and Runnegar & Pojeta (1985) are readily retained within the Class Helcionelloida.

Missarzhevsky (1989, pp. 23–24 and table 2) recognised eight families of Eomonoplacophora for Soviet Lower Cambrian helcionelloids, five of which were new. Missarzhevsky (1989) employed a finer division than that employed by Runnegar & Jell (1976) and Runnegar & Pojeta (1985), although Helcionellidae and Yochelcionellidae are maintained. Mellopegmidae is proposed as a new family to contain *Mellopegma* and *Isitella* Missarzhevsky, 1989. The former genus was placed within the Stenothechidae by Runnegar & Jell (1980) together with *Anabarella* which Missarzhevsky (1989) placed within the Family Coreospiridae Knight, 1952; Runnegar & Jell (1976) placed *Coreospira* Saito, 1936 within their Helcionellidae! Missarzhevsky (1989) recognised the affinity of *Protowenella* Runnegar & Jell, 1976 with the helcionelloids, endorsed here (see discussion below), while Runnegar & Pojeta (1985) had assigned it to their Order Bellerophontida of the Class Monoplacophora.

No sub-division of the Class Helcionelloida is presented here. It is stressed that a number of the Late Cambrian and Early Ordovician fossils variously re-

ferred to the Monoplacophora and bellerophontiform Mollusca (as both Monoplacophora and Gastropoda, or both) in published literature may be members of the classes Tergomya, Gastropoda and possibly Helcionelloida.

### Functional morphology of the Class Helcionelloida

Morphological features of the shell aperture in the Class Helcionelloida, such as emarginations and the presence in some forms of a snorkel, support the reconstruction of an essentially posterior mantle cavity in an endogastric shell. The mantle cavity was probably located posteriorly, essentially beneath the sub-apical surface. Water currents usually entered the mantle cavity laterally, passing over postero-laterally arranged gills prior to leaving the mantle cavity as a single, median posterior stream (Peel, 1991a; Fig. 12B; see also discussion of size in functional morphological interpretation, above).

The shell in *Helcionella* is low, and ovoid in plan view, reminiscent of tryblidiacean tergomyans such as *Pilina* and *Neopilina*, although these are commonly several times larger. While considered to be endogastric (*contra* the exogastric tergomyans) *Helcionella* may have possessed a mantle cavity extending along the lateral surfaces (Fig. 22).

In strongly coiled and lateral compressed helcionelloids such as *Latouchella*, the mantle cavity was probably concentrated in the posterior portion of the shell in similar fashion to its more restricted distribution in the gastropods and cephalopods, due to life in the narrow cone-like shell. This reduction of the mantle cavity, and possibly also a concomitant reduction in the number of pairs of gills relative to *Helcionella*, probably also occurred in hypseloconellacean tergomyans such as *Hypseloconus* and *Knighthoconus*.

### The mantle cavity in *Latouchella*

Robison (1964) reported longitudinal ridges on the interior of the sub-apical surface of *Latouchella* in silicified specimens from the Middle Cambrian of the western United States. Runnegar & Jell (1976) described similar material in a size range of 1 to 5 mm from the Middle Cambrian of Australia, some of which is described here (Fig. 23).

Phosphatic internal moulds (length 1–2 mm) of *Latouchella* described here from the Middle Cambrian Henson Gletscher of Peary Land, central North Greenland preserve deep grooves on the sub-apical surface, corresponding to the internal ridges of the silicified

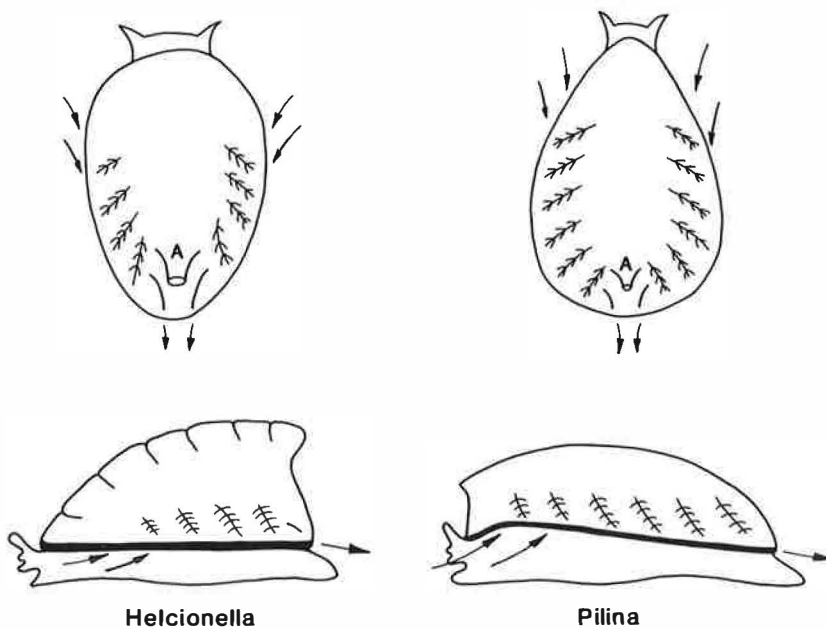


Fig. 22. Reconstructions of the mantle cavity in *Helcionella* and a tryblidiacean tergomyan such as *Pilina*. Both molluscs are drawn in dorsal and lateral views. There is no direct evidence as to the number of pairs of gills present in *Helcionella* but the form of the shell suggests that the mantle cavity may have extended relatively far forward when compared to more strongly coiled helcionelloids such as *Latouchella*. *Pilina* is restored with six pairs of gills; inhalant currents enter the shell antero-laterally by way of pronounced emarginations (cf. Fig. 2D). Thick black line, apertural margin; A, anus.

material (Fig. 24). The grooves are not present at the earliest growth stages, although subsequent deposition of calcium carbonate on the shell interior may have obscured their presence.

The grooves are arranged symmetrically in pairs about the median plane of symmetry (Fig. 24A, D); as few as a single pair and as many as three pairs have been observed. In the latter case, the inner pair originates nearer to the shell apex while the outer pairs commence more distally (Fig. 24D-G), although this may not be a result of simple ontogenetic increase in the number of ridges. The individual ridges responsible for producing the grooves on the shell interior are not necessarily entire but may be periodically interrupted (Fig. 24D-G).

The silicified material from Australia (Fig. 23) shows the ridges terminating just within the aperture; the shape of the structures in cross-section is well-rounded, not acute, with a tendency to be T-shaped (Fig. 23C).

The ridges reflect folds in the overlying soft-tissue of the mantle cavity wall and probably served to separate lateral inhalant water currents from a median exhalant stream. This mantle cavity configuration is similar to that described in the bellerophonacean gastropods *Plectonotus* Clarke, 1899 and *Tritonophon* Öpik, 1953 by Peel (1974; 1984; see also the description of *Knightites* Moore, 1941 by Knight in Moore, 1941 and Knight, 1952). In *Plectonotus* and *Tritonophon*, which range in length from about 1 to 3 cm, conspicuous trilobation of the dorsal area (Fig. 25) reflects separation of the two lateral inhalant currents from the median exhalant cur-

rent (Fig. 26). The degree of trilobation in many large specimens of *Plectonotus* is so great that internal moulds are often marked by deep spiral channels separating the three dorsal lobes (Peel, 1974; Fig. 25).

The mantle cavity within the dorsally trilobed *Plectonotus* and *Tritonophon* probably contains a pair of laterally disposed gills, by analogy with primitive gastropods (Knight, 1952; Peel, 1974, 1977b, 1984; Fig. 26). While the presence of as many as three pairs of ridges in *Latouchella* might conceivably suggest that a corresponding number of pairs of gills was present, the narrowness of the shell, variation in the number of ridges and the presumably restricted size of the mantle cavity argue against this interpretation. It should be noted, however, that multiple gills are sometimes present in the small posterior mantle cavity of polyplacophorans (cf. Smith, 1960; Yonge, 1960).

The silicified specimens of *Latouchella* from Australia show no trace of a median emargination in the apertural margin of the sub-apical surface, although such an emargination is conspicuous in many helcionelloids (Runnegar & Jell, 1976; see also Figs 9-11) and also in the dorsal apertural margin of plectonotiform gastropods (Figs 25, 26).

Silicified specimens of *Latouchella* with well-preserved apertural margins may show shallow lateral emarginations associated with a tendency for the aperture to become keyhole-shaped (Fig. 23C, D, F-H). The lateral impression of the apertural margins producing the narrower waist in this keyhole-shape in apertural

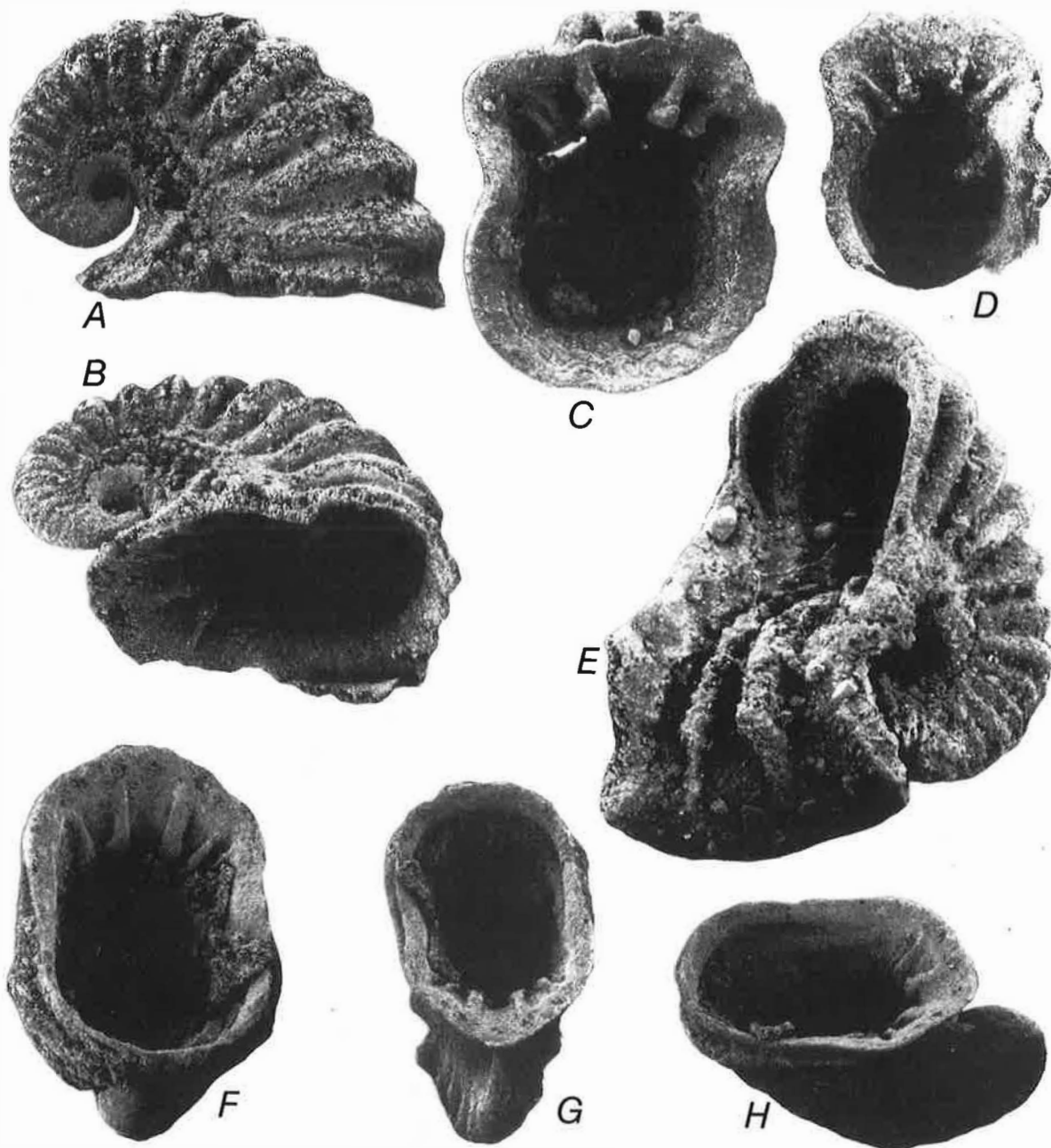


Fig. 23. Internal ridges in the helcionelloid *Latouchella* controlling water currents in the posterior mantle cavity. Silicified replicas of *Latouchella merino* Runnegar & Jell, 1976 from the Middle Cambrian Coonigan Formation, New South Wales, Australia, Australian National University Bulk Collection 10352 (see Runnegar & Jell, 1976, p. 110), showing ridges on the sub-apical wall. A, B, MGUH 19.557 in lateral and aperturo-lateral views showing two pairs of ridges within the aperture. The prominent comarginal rugae on the shell exterior are restricted to the dorso-lateral areas of the shell, leaving the umbilico-lateral areas smooth. The adumbilical termination of the individual comarginal rugae corresponds with the constriction in the aperture producing the key-hole shape seen in C and D,  $\times 10$ . C, MGUH 19.559 in apertural view showing the key-hole shape of the aperture and the bulbous thickening of the crests of the two pairs of ridges on the sub-apical wall,  $\times 10$ . D, MGUH 19.556 in apertural view, as last,  $\times 10$ . E, MGUH 19.558, oblique lateral view of broken specimen showing the ridges on the interior of the sub-apical wall extending deep into the shell interior,  $\times 15$ . F-H, MGUH 19.560 in various apertural views to show the two pairs of internal ridges and the shallow sinus in the lower right of the apertural margin in H,  $\times 7$ .

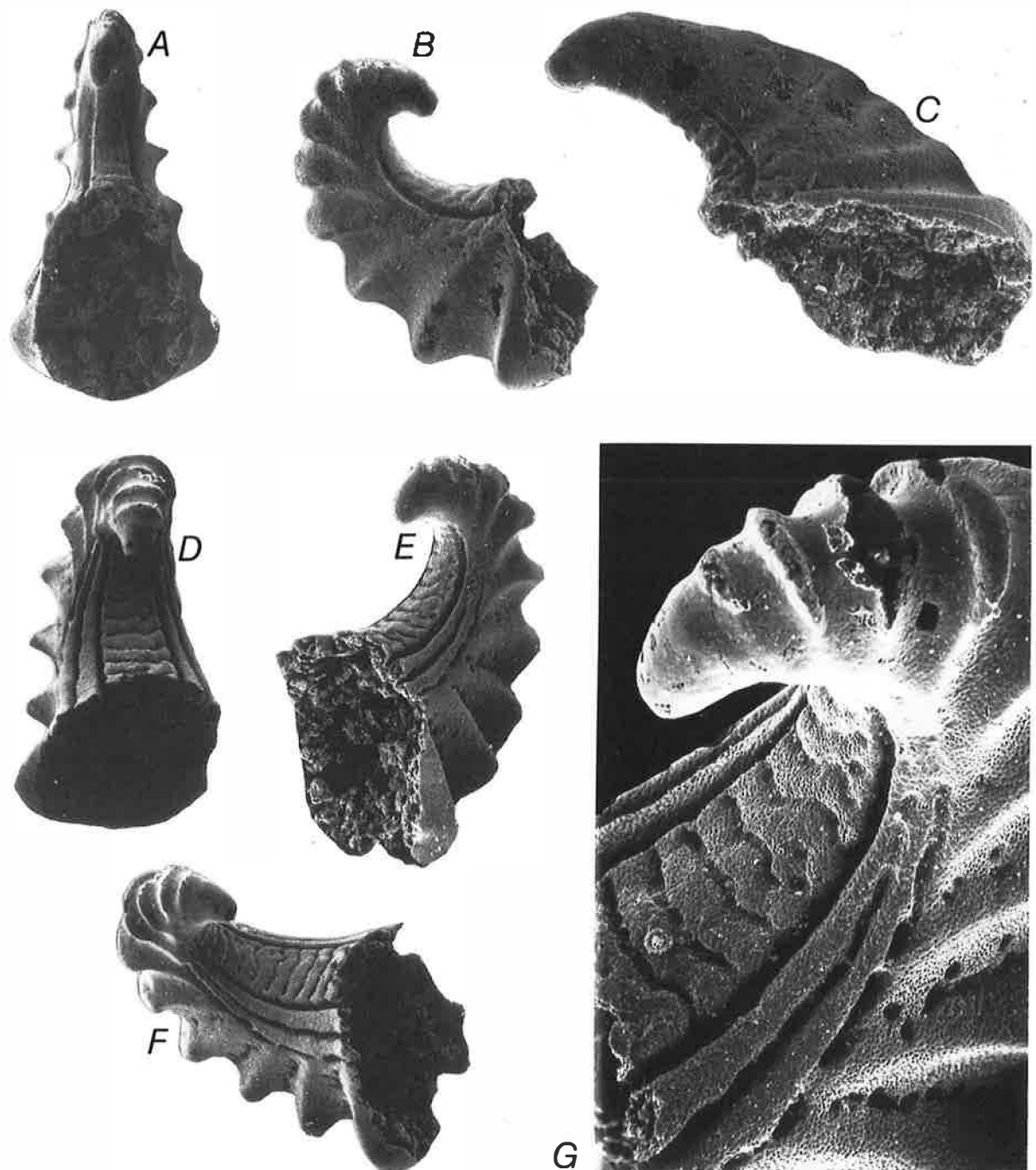
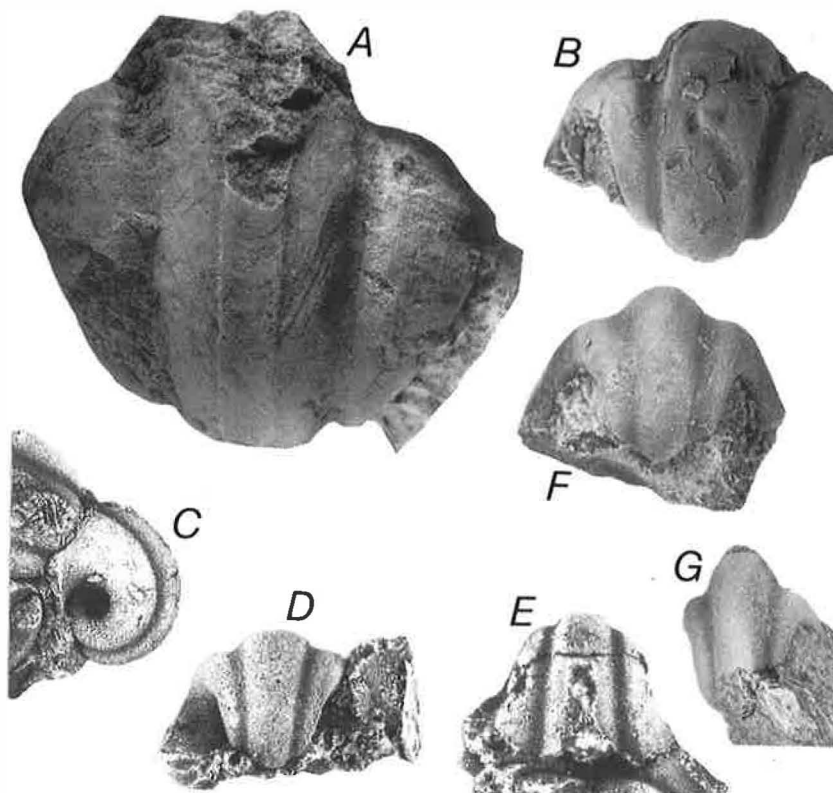


Fig. 24. Internal moulds of the helcionelloid *Latouchella* showing furrows produced by ridges on the shell interior. The ridges control water currents in the posterior mantle cavity. A-G, *Latouchella* spp., late Middle Cambrian, Henson Gletscher Formation, Løndal, Peary Land, central North Greenland, GGU collection 271718, internal moulds. A, B, MGUH 19.562, posterior and oblique lateral views showing a single pair of grooves on the sub-apical surface of the internal mould representing ridges on the shell interior,  $\times 30$ . C, MGUH 19.563, oblique lateral view of a second species of *Latouchella* showing one of a pair of grooves on the internal mould corresponding to a ridge on the shell interior,  $\times 50$ . D-G, MGUH 19.561, oblique posterior views of the sub-apical surface showing three pairs of ridges preserved as furrows in the surface of the internal mould,  $\times 30$ . Note that the outer pair of ridges is discontinuous (G,  $\times 85$ ).



Fig. 25. Silurian plectonotiform bellerophontacean gastropods showing the development of dorsal trilobation as an adaptation to enhance separation of inhalant and exhalant currents within the mantle cavity. A, *Plectonotus boucoti* Peel, 1974 from near Llandeilo, Wales, U.K., NMW 39.180 G14,  $\times 3$ . The medial dorsal selenizone is generated by a short slit representing the point of exit of the exhalant stream; inhalant streams enter the mantle cavity antero-laterally under the flanking folds. B, *Plectonotus boucoti* Peel, 1974, internal mould, Doctors Brook Formation, Nova Scotia, USNM 169590,  $\times 2$ . C-E, *Plectonotus boucoti* Peel, 1974, internal mould, Tonlegee, Cong, Ireland, SM A39164 (C, E) and SM A39165 (D),  $\times 2$ . F, *Tritonophon kivitlonae* Peel, 1974, internal mould, Stonehouse Formation, Nova Scotia, GSC 32782,  $\times 2$ . G, *Tritonophon trilobata* (Sowerby, 1839), internal mould, Moydart Formation, Nova Scotia, USNM 169594,  $\times 3$ .



view corresponds to the sudden termination of the prominent comarginal rugae of the supra-apical surface against the essentially unornamented sub-apical surface, when the shell is viewed laterally (Fig. 23A, B).

The keyhole-shape of the aperture suggests that the mantle cavity was located in the area between the narrow waist and the apertural margin of the sub-apical surface, an interpretation supported by the location of the shallow lateral emarginations at the narrow waist. The keyhole-shape may represent incipient separation of an antero-ventral aperture from the more posteriorly located mantle cavity interpreted elsewhere in this discussion as present in *Yochelcionella*, *Eotebenna* and *Eurekapegma*.

Runnegar & Jell (1976, p. 127) suggested that the ridges on the interior of the sub-apical wall in *Latouchella* formed an anterior inhalant channel in the exogastrically oriented shell. Following the model of Runnegar & Pojeta (1974), this interpretation would require that the inhalant current divided along either side of the body mass as it passed over laterally arranged respiratory surfaces, and that exhalant streams left the mantle cavity along each lateral surface (cf. Pojeta & Runnegar, 1976, fig. 9B; see also Fig. 12A). This orientation

is opposite to that accepted here, where inhalant currents are believed to have entered the endogastric shell laterally or postero-laterally and to have united prior to exhalation as a single median, posterior stream (Fig. 12B).

The internal ridges in *Latouchella* probably reflect mantle cavity folds which helped to separate these lateral inhalant currents from the posterior exhalant stream. Oxygen-rich water entered the mantle cavity along two relatively wide surfaces, achieving maximum supplies for respiration. The force of expulsion of the exhalant current would be increased by the unification of the two lateral inhalant streams, thus carrying oxygen-depleted water away from the shell.

The internal ridges in *Latouchella* can be discussed in terms of a number of other functions, but these are considered unsatisfactory. A possible role as supports for shell muscle attachment is rejected due to the positive relief of the ridges within the shell interior and their persistence to the apertural margin. Muscle scars are usually impressed into the shell and therefore raised on the internal mould (cf. Horny, 1965a; Peel, 1972, 1976, 1977a, 1980a, 1982; see Figs 1, 18D-F, 19). Longitudinal ridges and other structures are often associated with

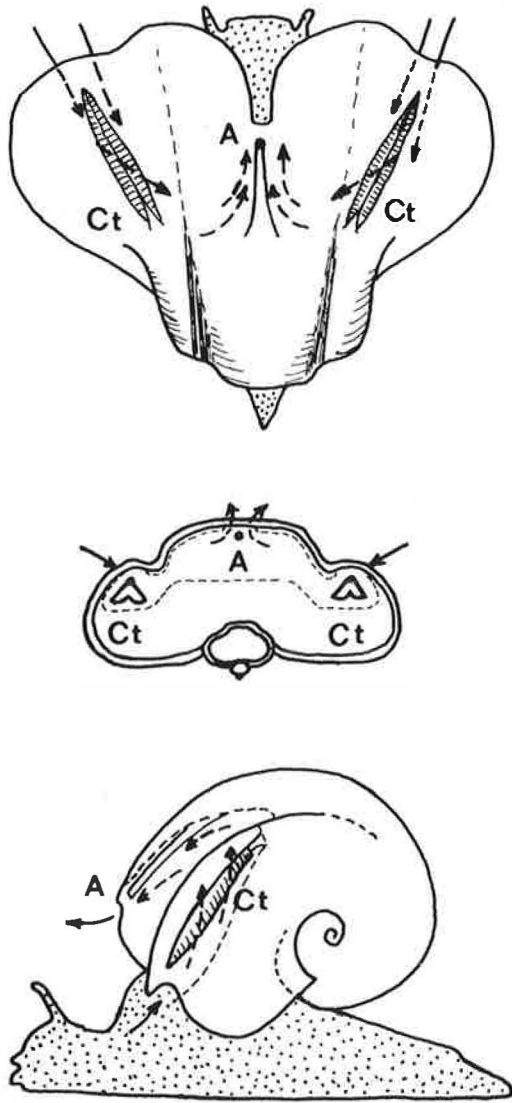


Fig. 26. Reconstruction of the mantle cavity in *Plectonotus boucoti* Peel, 1974, seen in dorsal, transverse and lateral aspects. Water currents entering the shell beneath the flanking lobes pass over the gills (Ct) prior to expulsion through the median dorsal slit. A, anus (after Peel, 1974).

muscle scars in bellerophonts and gastropods (cf. Peel, 1977a, 1982; Fig. 19) but these show little similarity to the prominent internal ridges described here.

An hypothesis that the ridges may have controlled mantle folds in association with retraction of soft parts into the shell is also rejected. On account of the rapid rate of expansion of the shell and the planar aperture suited to clamping against the substrate, there is little reason to suggest that these helcionelloids were capable of substantial retraction into the shell.

Many gastropods develop columellar folds reminiscent of the structures in *Latouchella*. Signor & Kat (1984) reported a high degree of correlation between such folds and the burrowing habit in living high-spired gastropods, enabling the recognition of this mode of life in high-spired gastropods at least as old as Silurian (Peel, 1984). However, there is little in the location of the ridges or the form of the shell in *Latouchella* to suggest that the ridges performed the muscle-control function documented by Signor & Kat (1984).

The shell aperture in some living terrestrial pulmonate gastropods and a number of marine gastropods is constricted by lamellae or palatal folds which are often attributed a defensive function; the folds may also strengthen the outer lip against breakage by predators. The ridges described in *Latouchella* morphologically resemble these apertural lamellae and folds but their distribution on the sub-apical surface is far too restricted to serve the same function.

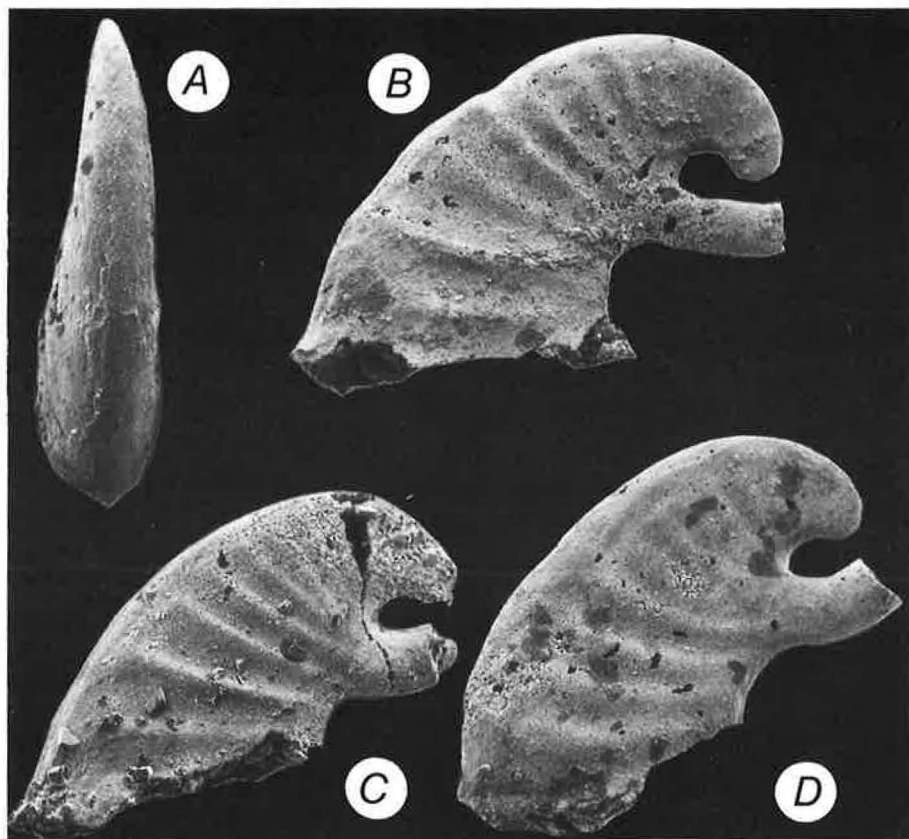
In conclusion, the spiral ridges in *Latouchella* are interpreted as controlling mantle folds associated with increasing mantle cavity efficiency. Their presence on the sub-apical surface of the laterally compressed shells is construed as evidence for a posterior location. Hence, shell coiling is believed to be endogastric.

#### The function of the snorkel in *Yochelcionella*

*Yochelcionella* Runnegar & Pojeta (1974) has been described from Lower and Middle Cambrian strata throughout the world (Berg-Madsen & Peel, 1987; Geyer, 1986; Runnegar & Jell, 1976; Missarzhevsky & Mambetov, 1981; Pei, 1985; Peel, 1988a, 1991a; Runnegar & Pojeta, 1980; Voronova *et al.*, 1987). In Greenland, *Yochelcionella* is abundant in the Paralleldal Formation of latest Early Cambrian age, but it also occurs in the slightly older Henson Gletscher Formation (Peel, 1980b and unpublished observations). Species of *Yochelcionella* vary in form from strongly curved and laterally compressed (such as *Yochelcionella americana* Runnegar & Pojeta, 1980; see also Peel, 1988a and Fig. 27 herein) to tall and slender cones such as *Yochelcionella ostentata* Runnegar & Jell, 1976. The characteristic snorkel is developed on the sub-apical surface in all species.

Pojeta & Runnegar (1976, fig. 9) discussed the function of the snorkel in *Yochelcionella* suggesting four possible reconstructions summarised in Fig. 28. In accordance with their earlier model of molluscan evolution (Runnegar & Pojeta, 1974), they concluded that the shell of *Yochelcionella* was exogastrically coiled with the anterior snorkel serving as a conduit for water entering the mantle cavity (Fig. 28A). The inhalant current

Fig. 27. *Yochelcionella americana* Runnegar & Pojeta, 1980, late Early Cambrian, Forteau Formation, Gros Morne, western Newfoundland, Canada, phosphatic internal moulds. A, dorsal view, GSC 85863,  $\times 45$ . B, GSC 85862 in lateral view showing the prominent snorkel located posteriorly, on the sub-apical surface,  $\times 45$ . C, GSC 85864, as last,  $\times 55$ . D, GSC 85865, as last,  $\times 45$ .



subsequently divided prior to passing over the laterally located respiratory surfaces; exhalant currents left the mantle cavity along each postero-lateral surface. This interpretation was refuted by Yochelson (1978), Geyer (1986), Peel & Yochelson (1987; see also Berg-Madsen & Peel, 1987) and Peel (1991a) who considered that the posteriorly located snorkel in the endogastrically coiled shell contained the exhalant stream from the mantle cavity (Fig. 28B, but see discussion of size in functional morphological interpretations, above).

The mantle cavity in *Yochelcionella* is considered to be mainly restricted to the posterior region of the shell, particularly in those species with relatively narrow, cone-shaped shells. Oxygen-rich water enters the mantle cavity along two relatively wide postero-laterally surfaces, providing maximum supplies for respiration. Unification of the two lateral streams and concentration of the single exhalant current in the narrow snorkel carries oxygen-depleted water away from the shell.

Interpretation of the snorkel as the conduit for the inhalant current, as suggested by Pojeta & Runnegar (Fig. 28A), restricts intake of oxygenated water to a single narrow stream which is diminished further by being divided into streams passing along each side of the

mollusc. Thus, the narrowness of the snorkel in the model of Pojeta & Runnegar (1976) inhibits the supply of oxygenated water to the mantle cavity while this same narrowness in the reconstruction favoured by Peel (1991a) is interpreted as an adaptation to carry oxygen-depleted water away from the mantle cavity.

Some infaunal bivalves employ a narrow siphon for both inhalation and exhalation and this dual function is also ascribed to presumed sessile species of *Yochelcionella* and *Eotebenna*, as discussed below. However, the majority of species of both these taxa appear to be active members of the epifauna. As with modern epifaunal gastropods and some protobranch bivalves, a stream of water through the mantle cavity offers better water supply.

#### Snorkel development in *Eotebenna*

*Eotebenna* was originally described on the basis of two species from the Middle Cambrian of Australia (Runnegar & Jell, 1976). Peel (1989; 1991a) has described a Lower Cambrian species (length about 4 mm) from the Henson Gletscher Formation of Freuchen Land, central North Greenland and a late Middle Cam-

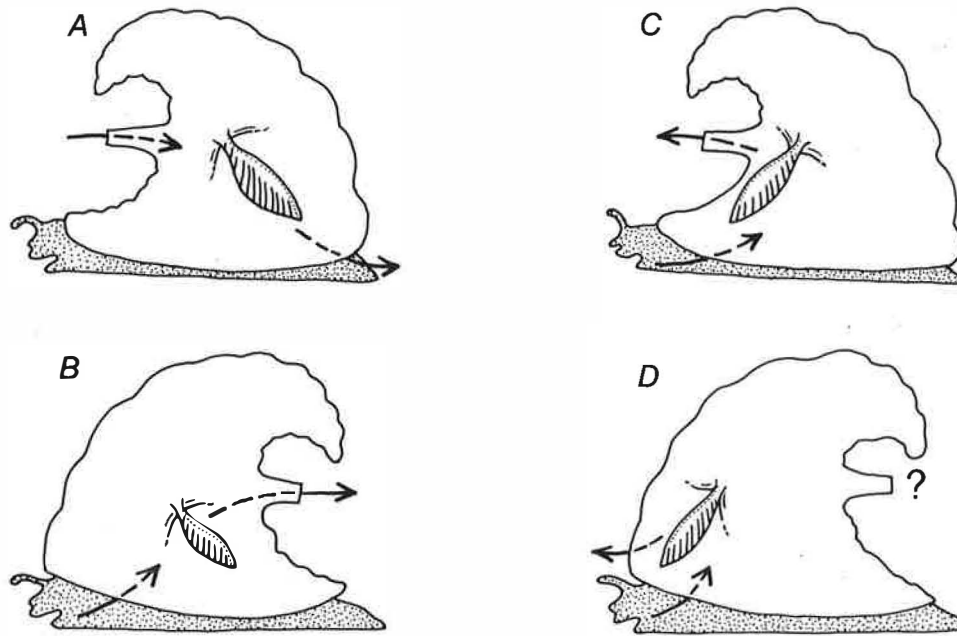


Fig. 28. Possible reconstructions of *Yochelcionella*. A, *Yochelcionella* interpreted as an exogastric untorted mollusc (same shell orientation as *Tergomya*) in which the single inhalant current enters the mantle cavity through the snorkel and divides to pass over the laterally disposed gills prior to postero-lateral exhalation. This is the reconstruction favoured by Runnegar & Pojeta (1974 and subsequent papers) which is rejected here. B, *Yochelcionella* interpreted as an endogastric untorted mollusc (helcioneloid) with water currents entering the mantle cavity laterally and passing over the gills prior to expulsion as a single median stream through the posterior snorkel. This is the reconstruction favoured by Geyer (1986), Peel & Yochelson (1987) and Peel (1991a) and adopted herein. C, *Yochelcionella* interpreted as an exogastric gastropod. Water currents enter the mantle cavity antero-laterally and are exhaled through the anterior snorkel; gastropods, however, are typically endogastric and this restoration is rejected. D, *Yochelcionella* interpreted as an endogastric gastropod. Water currents enter the mantle cavity antero-laterally and are expelled anteriorly; the posterior snorkel has no obvious function in terms of respiration. This interpretation is also rejected here (modified after Pojeta & Runnegar, 1976).

brian species from the Andrarum Limestone of Bornholm, Denmark (Figs 29–31).

Missarzhevsky (1989, pl. 31, fig. 6) assigned to *Eotebenna* an Early Cambrian (Botomian) species from

Central Asia, originally described as *Yochelcionella recta* Missarzhevsky in Missarzhevsky & Mambetov, 1981. The specimen is only illustrated in lateral view, making interpretation difficult. There is at least super-

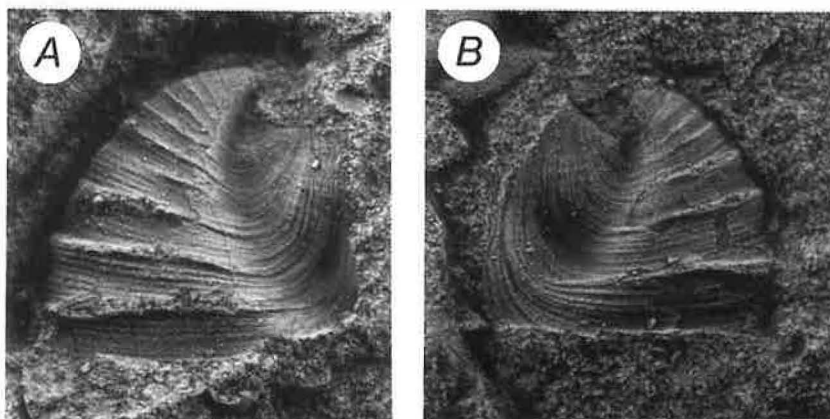


Fig. 29. *Eotebenna arctica* Peel, 1989 from the late Early Cambrian Henson Gletscher Formation, south-east Greenland, central North Greenland, GGU collection 315109,  $\times 10$ . A, MGUH 18.702, lateral view with anterior to left. B, MGUH 18.701, lateral view with anterior to right. Note the prominent sail-like snorkel-fold on the sub-apical surface.

ficial resemblance to *Eotebenna pontifex* Runnegar & Jell, 1976 from the Middle Cambrian of Australia but it is not immediately apparent from the illustration why this unusual species was rejected from *Yochelcionella*.

*Eotebenna* is also characterised by the development of a snorkel but it differs from *Yochelcionella* in that the small perforation at the distal end of the snorkel is usually connected to the shell aperture by a narrow slit. Thus, the snorkel in *Eotebenna* more closely resembles a deep fold in the sub-apical apertural margin rather than a discrete tube, and the genus may be considered as a morphological intermediate between species of *Latouchella* with an apertural fold beneath the apex and *Yochelcionella* (Fig. 11).

The snorkel in *Eotebenna* is considered to lie posteriorly and to contain the exhalant current from the mantle cavity, as in *Yochelcionella*. The shell aperture is antero-ventral; this is also the orientation proposed for the aperture in rostroconchs by Pojeta & Runnegar (1976) and Pojeta (1980; 1987), although their interpretation of *Eotebenna* would place the aperture postero-ventrally.

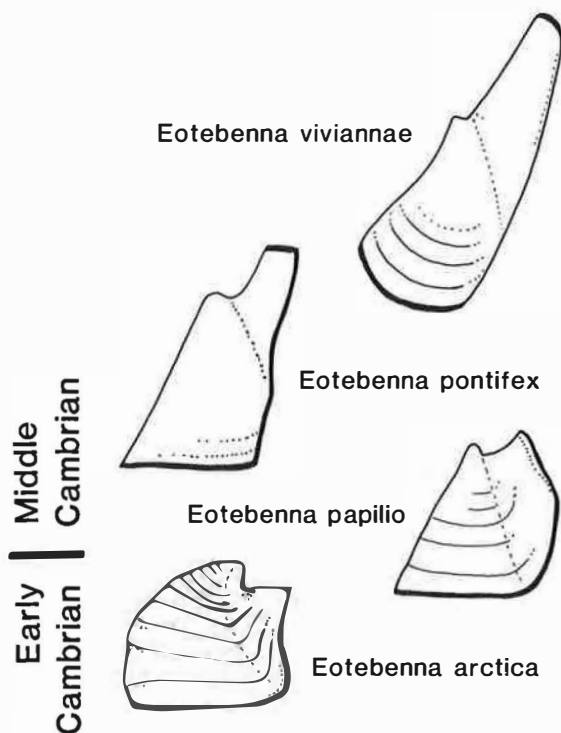


Fig. 30. Morphological series of species of *Eotebenna*. All species are oriented in lateral view with the anterior to the left; thick black lines indicate the extent of shell openings. The series shows progressive elongation of the shell and increasing separation of the snorkel from the principal aperture, interpreted as a response to greater penetration of the bottom sediment.

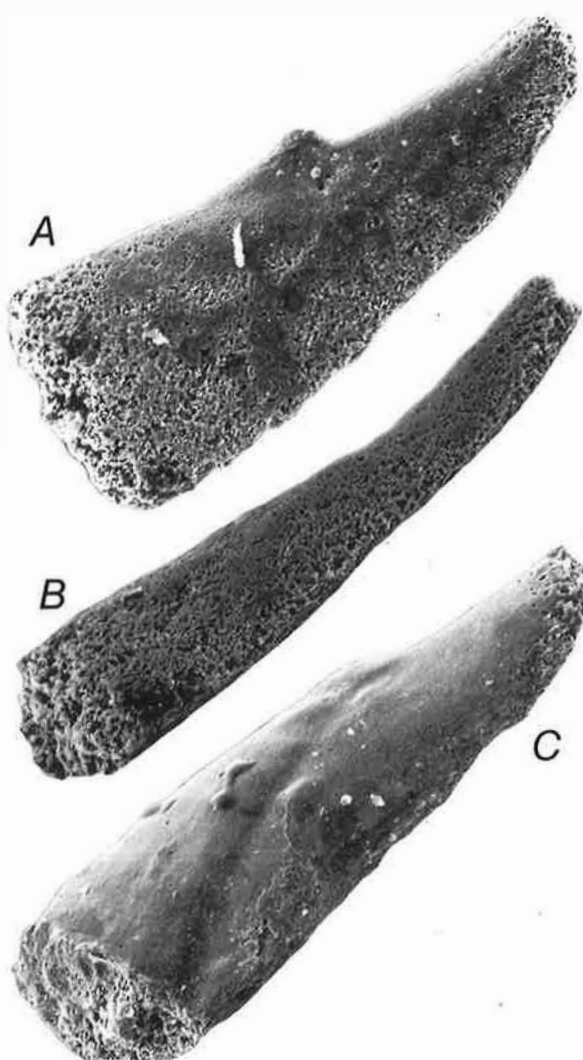


Fig. 31. *Eotebenna viviannae* Peel, 1991, late Middle Cambrian, phosphatic internal moulds from the Andrarum Limestone, Bornholm, Denmark. A, MGUH 19.565 in lateral view with greatly extended snorkel on the sub-apical surface located to the right,  $\times 100$ . B, as last but rotated to show the line of contact between the lateral areas of the shell,  $\times 110$ . C, MGUH 19.566 in slightly oblique lateral view with the greatly extended snorkel (right) delimited by a fold producing a groove on the internal mould, crossing from near the apex to the shell aperture (lower left),  $\times 100$ .

Peel (1991a) recognised a morphological series from *Latouchella* to the late Early Cambrian *Eotebenna arctica* Peel, 1989, through the early Middle Cambrian *E. papilio* Runnegar & Jell, 1976 and the medial Middle Cambrian *E. pontifex* to the late Middle Cambrian *E. viviannae* from Bornholm (Figs 11, 30, 31). The series is characterised by increasing separation of the deepest part of the snorkel-emargination from the aperture,

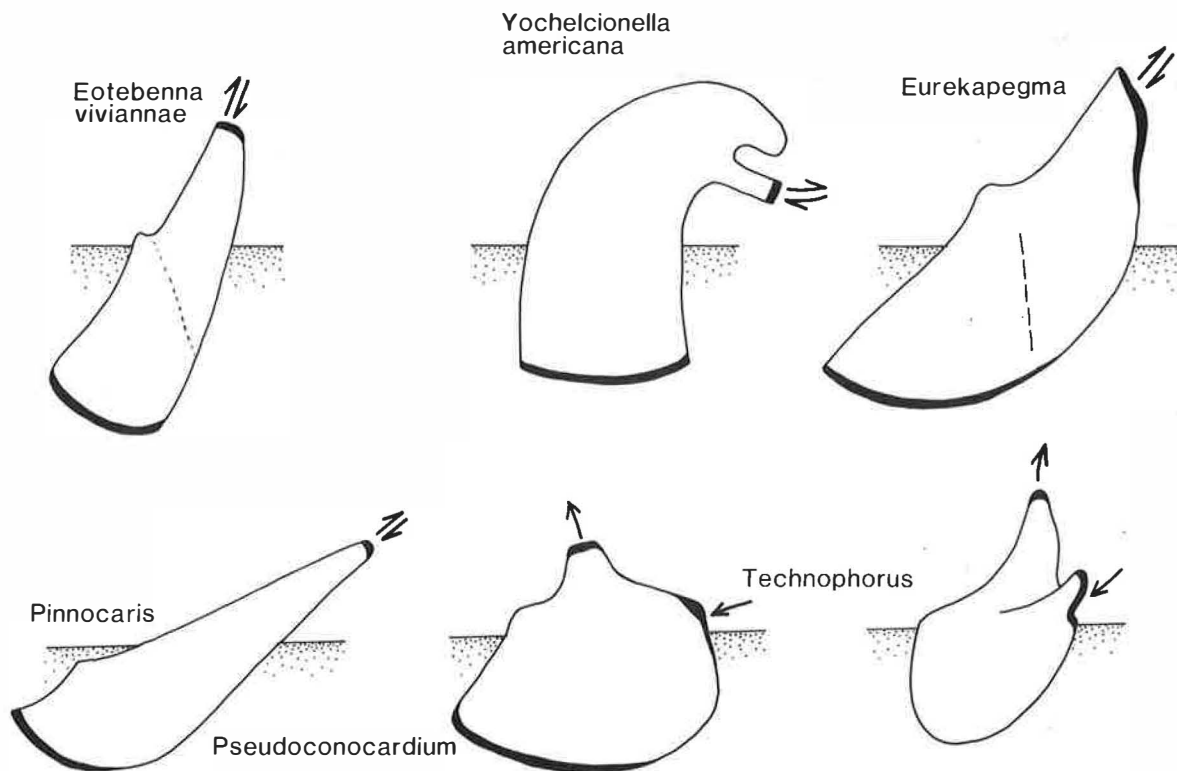


Fig. 32. Reconstructions of the helcionelloids *Yochelcionella americana*, *Eotebenna viviannae* and *Eurekapegma*, and the rostroconchs *Pinnocaris*, *Pseudoconocardium* and *Technophorus*, showing semi-infaunal mode of life. The margins of shell gapes and apertures are indicate by thick black lines, while arrows show inhalant and exhalant water currents. The zygion occurring internally in *Eurekapegma* is illustrated by a broken line. All shells are oriented with anterior to the left. The large shell gape occupied by the foot (except in *Technophorus*) is located antero-ventrally within the sediment, indicating that respiration was accomplished via the postero-dorsal shell opening(s). Rostroconchs after Pojeta & Runnegar (1976).

manifested in elongation of the shell as a result of pronounced allometry, and is interpreted in terms of increasing penetration of the sediment-water interface. However, the anomalous Early Cambrian species from Soviet Central Asia noted above, if an *Eotebenna*, stresses that this series is morphological and not necessarily phylogenetic.

Early species of *Eotebenna* probably lived at the sediment-water interface with only slight penetration, but the late Middle Cambrian forms were largely infaunal, with only the shell posterior protruding from the sediment (Fig. 32). This semi-infaunal mode of life probably caused modification of the circulation pattern of water currents within the mantle from that envisaged in older species of the genus and most species of *Yochelcionella* (cf. Fig. 28B). However, the strongly coiled and laterally compressed *Yochelcionella americana* may be interpreted in a similar manner to these late Middle Cambrian *Eotebenna* (Fig. 32). The snorkel in these species may have served both inhalant and exhalant functions,

as in scaphopods, many bivalves and rostroconchs, since the antero-ventral aperture was presumably buried within the bottom sediment (Fig. 32). Water supply to the mantle cavity could have been achieved with simultaneous inhalation and exhalation through separate siphons, as in bivalves, but it is perhaps more likely that alternating inhalation and exhalation was employed, as in scaphopods (Yonge & Thompson, 1976, p. 232).

When restored in this way, *Eotebenna viviannae* parallels the mode of life inferred for many rostroconchs by Pojeta & Runnegar (1976) and Pojeta (1987; see Fig. 32 and discussion below) where small posterior and rostral openings above the sediment surface (cf. Runnegar & Pojeta, 1976; Pojeta, 1987) probably indicate separation of the inhalant and exhalant streams.

#### The temporary snorkel of *Oelandia*

*Oelandia* was originally described by Westergård (1936) from the Middle Cambrian of Sweden but Peel &

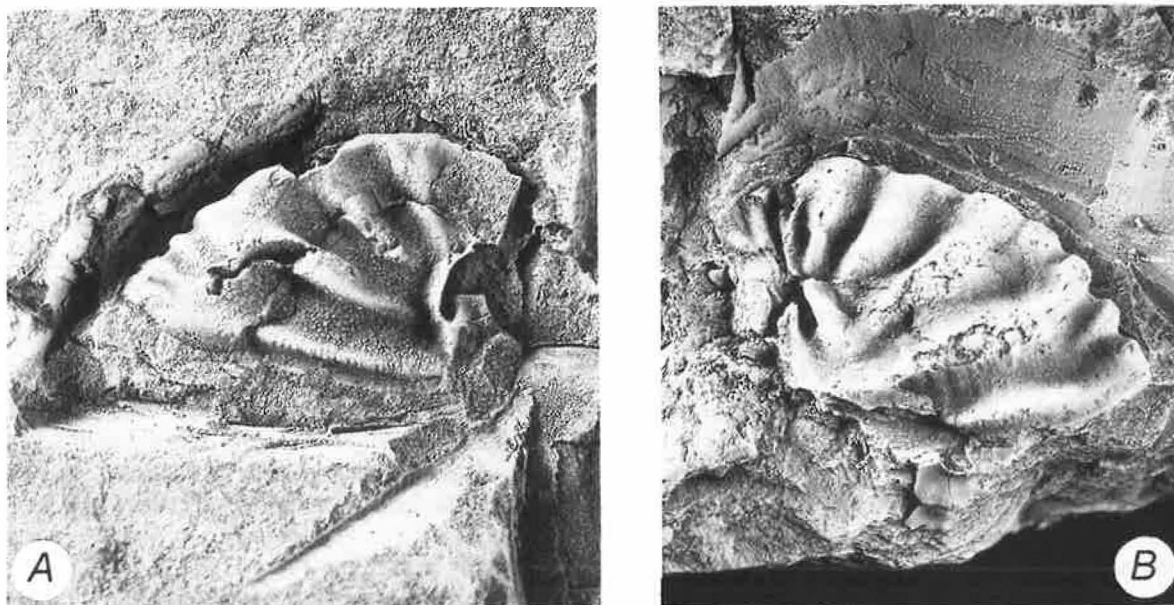


Fig. 33. The helcionelloid *Oelandia pauciplicata* Westergård, 1936, Middle Cambrian, Öland, Sweden, internal moulds in lateral aspect showing the prominent sediment-filled sub-apical snorkel; the apex of the shell is missing in both specimens. A, LO 5757t, with anterior to the left. The flat-topped snorkel is closed distally (top in figure), probably due to its abandonment with subsequent growth,  $\times 6$ . B, LO 57578t, with the anterior to the right,  $\times 6$ .

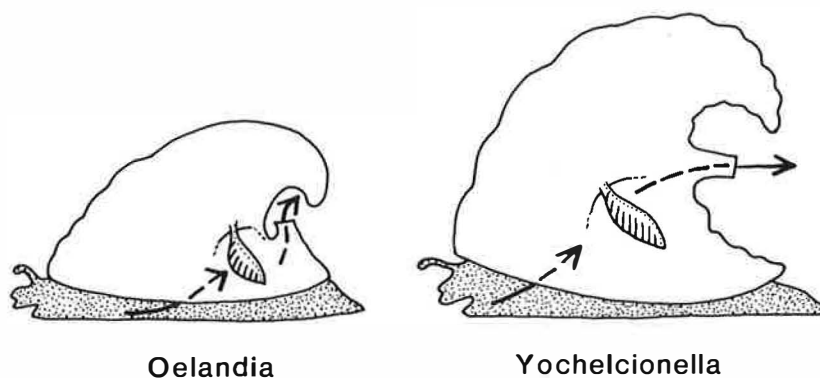
Yochelson (1987) also noted species from China and North Africa (Geyer, 1986; Yu & Ning, 1985). An undescribed occurrence has been noted in collections from the Middle Cambrian of Bohemia made by Mr. P. Slehofer and Dr. L. Marek (Czechoslovakian Academy of Sciences, Prague).

*Oelandia* is unusual among helcionelloids on account of its lack of bilateral symmetry in shell ornamentation. The prominent comarginal plications develop alternately on each lateral area and terminate near the mid-dorsum.

A short tubular structure on the sub-apical wall of new specimens of *Oelandia* from Sweden (Fig. 33) was

compared by Yochelson & Peel (1987) to the snorkel of *Yochelcionella* (Fig. 34). A similar structure was illustrated by Geyer (1986, pl. 3, fig. 37) in *Oelandia comma* (Geyer, 1986) from the Middle Cambrian of North Africa. The tube rises from the plane of the aperture toward the apex and is closed adapically. Peel & Yochelson (1987) suggested that this closure indicated abandonment of the snorkel with increased growth, its function as the locus of the exhalant current from the mantle cavity possibly being taken over by the median fold in the aperture below the apex. The snorkel in *Oelandia* may have developed periodically during ontogeny, as do the spines and anterior siphon of some

Fig. 34. Water currents within the mantle cavity of *Oelandia* and *Yochelcionella*. Inhalant water streams enter the mantle cavity laterally, and pass over the laterally placed gills prior to exhalation through the posterior snorkel in the sub-apical surface.



gastropods, but no preserved material shows more than a single tube.

### Mode of life of *Eurekapegma*

*Eurekapegma* MacKinnon, 1985, a Middle Cambrian helcionelloid from New Zealand (Figs 32, 35), is characterised by extreme lateral compression, apertural margins convex away from the apex when viewed laterally, and by an internal plate (zygion) connecting opposing lateral areas beneath the apex (MacKinnon, 1985). The zygion might be interpreted as a 'pegma-like' structure reminiscent of that characteristic of rostroconchs, but MacKinnon (1985, fig. 6) considered that it supported internal musculature.

MacKinnon (1985) restored *Eurekapegma* as semi-infaunal, with the sub-apical surface within the sediment (Fig. 35A). He considered the sub-apical surface to be anterior, in agreement with the model of Runnegar & Pojeta (1974). However, he proposed that the mantle cavity was located posteriorly, near the supra-apical margin, and not concentric around the margins of the shell aperture as suggested by Pojeta & Runnegar (1976) in *Yochelcionella*.

Peel (1991a) proposed that the zygion partially delimited the mantle cavity in the sub-apical surface and that *Eurekapegma* should be restored with the posterior mantle cavity below the sub-apical surface (Fig. 35B). This is the opposite orientation to that suggested by MacKinnon (1985). The shield-like, convex lateral margins in *Eurekapegma* also suggest a semi-infaunal mode of life, as suggested for some species of *Eotebenna* (Fig.

32). The closeness of the apertural termination of the zygion and the almost conjoined apertural margins indicate that water currents probably entered and left the shell on the sub-apical side of the zygion, in similar fashion to the mantle cavity structure proposed for the late Middle Cambrian *Eotebenna* from Bornholm and many rostroconchs and bivalves in which the larger antero-ventral gape was also buried in the bottom sediment (Fig. 32).

### *Protowenella*, a strongly coiled helcionelloid

*Protowenella* is a small (length about 1–2 mm) bellerophontiform mollusc which was first described from the Middle Cambrian of Australia by Runnegar & Jell (1976) and discussed in detail by Berg-Madsen & Peel (1978) on the basis of material of similar age from Denmark (Fig. 36). *Protowenella* has been described subsequently from strata of Early and Middle Cambrian age from many parts of the world (e.g. Geyer, 1986; MacKinnon, 1985; Missarzhevsky, 1989). In North Greenland, Peel (1979) reported *Protowenella* from the uppermost beds of the Henson Gletscher Formation in Løndal, western Peary Land, in strata of Middle Cambrian age.

The small, globose shell of *Protowenella* is coiled through about one and a half whorls; its shape prompted Runnegar & Jell (1976) and Runnegar & Pojeta (1985) to place it as an intermediate form between the helcionelloids and the bellerophontiform molluscs in their Order Bellerophontida of the Monoplacophora, together with the globose and strongly

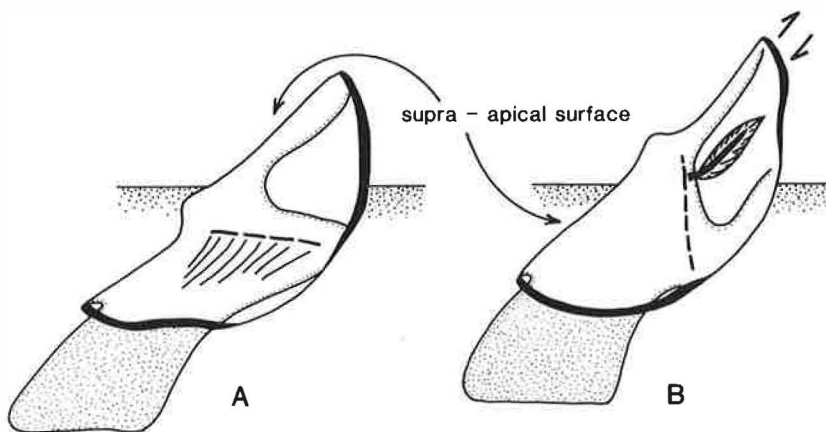
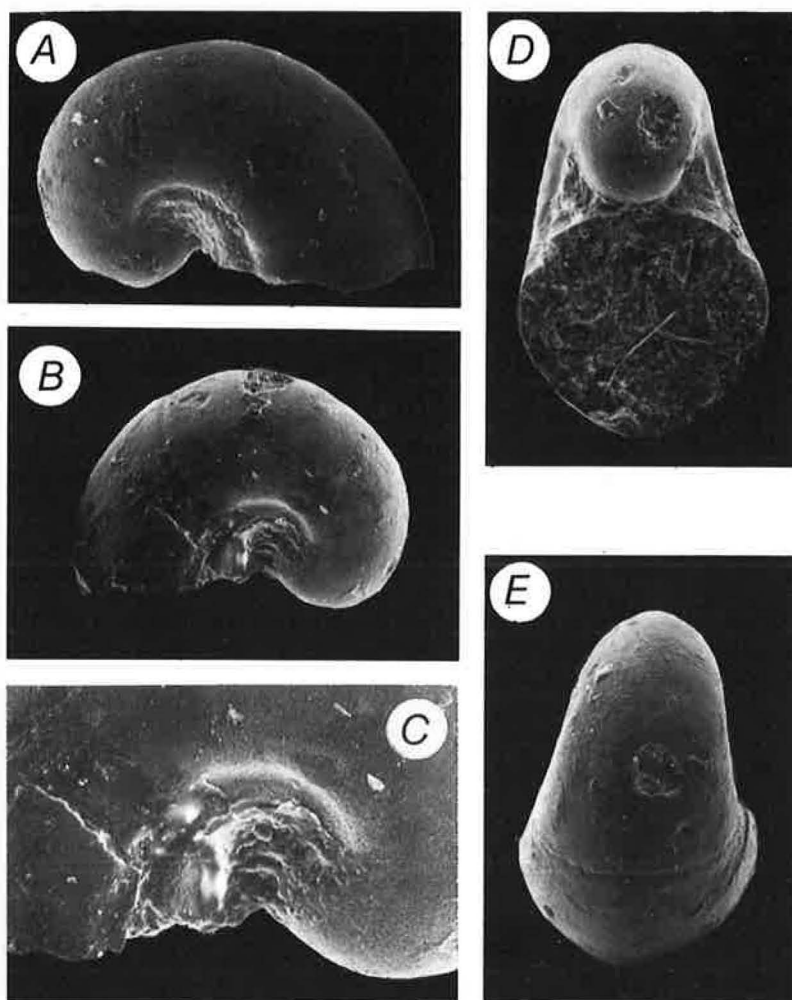


Fig. 35. The mode of life of *Eurekapegma*, from the Middle Cambrian of New Zealand. A, reconstruction of MacKinnon (1985) in which the exogastric shell is oriented with the sub-apical surface within the sediment. The zygion (dashed line) is considered to provide muscle attachment for the foot (stippled) and the postero-dorsal mantle cavity is located beneath the supra-apical surface. B, interpretation favoured here in which the endogastric *Eurekapegma* is oriented with the supra-apical surface within the sediment and with the postero-dorsal mantle cavity below the sub-apical surface. Shell gapes are indicated by thick black lines while arrows indicate inhalant and exhalant water currents.



Fig. 36. *Protowenella flemingi* Runnegar & Jell, 1976, the late Middle Cambrian, Kalby Clay, Bornholm, Denmark; MGUH 13.991, internal mould. A, B, lateral views with anterior to right and left, respectively, showing the prominent circumbilical fold,  $\times 65$  and  $\times 55$ . C, as B, showing detail of circumbilical channel,  $\times 110$ . D, apertural view with posterior at top and anterior at base, showing the prominent circumbilical folds,  $\times 85$ . E, slightly oblique antero-dorsal view showing traces of transverse ornamentation,  $\times 65$ .



coiled *Multifariites*, an action strongly criticised by Missarzhevsky (1989).

Berg-Madsen & Peel (1978) rejected the idea that all bellerophontiform molluscs were untorted monoplacophorans. They considered many to be torted, and therefore gastropods. However, functional interpretation of umbilico-lateral emarginations suggested that *Protowenella* was untorted and Berg-Madsen & Peel (1978) consequently assigned it to the Monoplacophora.

*Protowenella* was assigned to the Class Helcionelloida by Peel (1991a), following abandonment of the Class Monoplacophora. The transfer confirmed the independent conclusion of Missarzhevsky (1989) that *Protowenella* was related to the Helcionellidae. Missarzhevsky placed the genus in a Family Khairkhaniidae Missarzhevsky, 1989, although his concept of the suprafamilial taxon (to which he gave the name Order Eomonoplacophora) as exogastrically coiled is rejected here (see discussion above).

The lateral emarginations in *Protowenella* which Berg-Madsen & Peel (1978) interpreted as marking inhalant water currents are considered comparable to the emarginations noted above in *Latouchella*, although they are located more deeply within the umbilici on account of the increased inflation of the whorls. *Protowenella* is thus considered to be endogastric and not exogastric as earlier suggested by Runnegar & Jell (1976), Berg-Madsen & Peel (1978) and Missarzhevsky (1989). The functional interpretation by Berg-Madsen & Peel (1978) of *Protowenella* as an exogastric tergomyan related to *Multifariites* remains feasible, but general morphology, the similarity to other helcionelloid taxa and geological age strongly support interpretation of *Protowenella* as an endogastric helcionelloid.

Danish and Australian specimens assigned to *Protowenella* can be compared closely to *Perssuakiella* described from the latest Middle Cambrian Holm Dal Formation (Tavsens Iskappe Group) of central North

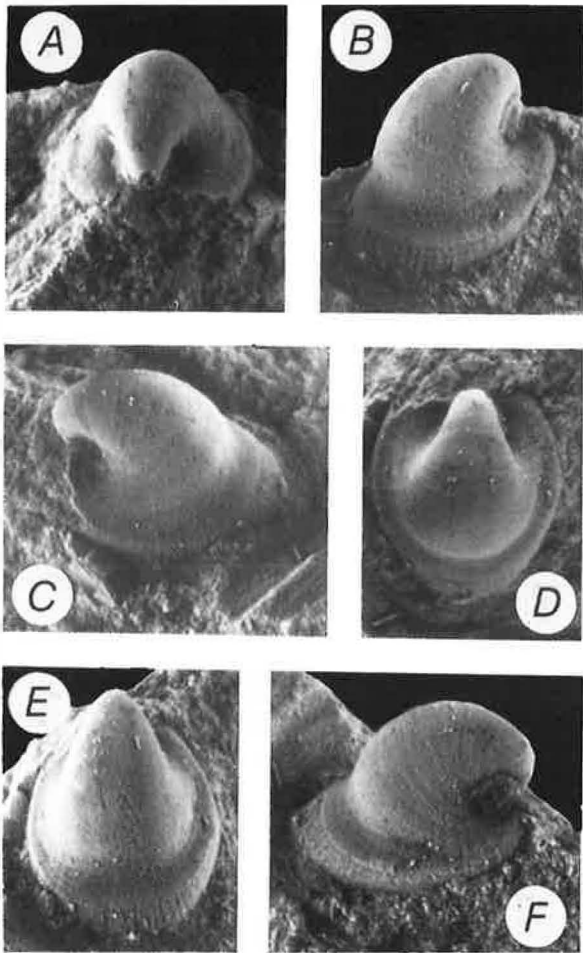


Fig. 37. The helcionelloid *Perssuakiella troelseni* Peel, 1988, late Middle Cambrian, Holm Dal Formation, Gustav Holm Dal, Peary Land, central North Greenland, MGUH 18.687 from GGU collection 225537, holotype,  $\times 15$ . A, oblique posterior view. B, C, F, oblique lateral views showing the similarity to *Protowenella* prior to the expanded aperture. D, dorsal view with posterior uppermost in the photograph. E, oblique dorsal view.

Greenland by Peel (1988b; see Fig. 37). *Perssuakiella* differs from *Protowenella* in developing an expanded aperture during the final growth stage, in which feature it resembles the early growth stages of *Helcionella*. *Protowenella*-like morphologies can thus be expected to result from preservation of the early growth stages of different helcionelloids.

*Tichkaella hamata* Geyer, 1986 from the Middle Cambrian of Morocco (Geyer, 1986, pl. 4, fig. 52c) has similar folds on the sub-apical wall to those described in *Protowenella* and these also may be interpreted as the loci of inhalant currents. *Tichkaella* resembles *Protowenella* in terms of its convex dorsal profile but is more loosely coiled.

## Helcionelloids and rostroconchs

Runnegar & Pojeta (1974) proposed that members of the Class Rostroconchia were derived from helcionelloids and themselves gave rise to the Class Bivalvia (Fig. 5). An anterior apex and coiling toward the rear are a unifying theme within the concept of the Sub-phylum Diasoma. Thus, Runnegar & Pojeta (1974) homologised helcionelloids with the exogastric tryblidiacean tergomyans, in similar orientation to the majority of bivalves. Rostroconchs, considered to be the only extinct molluscan class by Runnegar & Pojeta (1974), formed an intermediate link between helcionelloids and bivalves and were assumed to have had a similar original orientation. Pojeta & Runnegar (1976), Pojeta *et al.* (1977), Runnegar (1978) and Pojeta (1985; 1987) give detailed accounts of rostroconch morphology and evolution.

### Rostroconch orientation

A tubular extension of the shell reminiscent of the helcionelloid snorkel is present in many rostroconchs (Fig. 32). By analogy with scaphopods and bivalves Runnegar & Pojeta (1974) interpreted this rostrum as lying posteriorly and serving a respiratory function. In contrast, Runnegar & Pojeta considered that the snorkel of *Yochelcionella* and *Eotebenna* performed a similar function, but they located it anteriorly (Fig. 28A, see discussion above).

Similar morphological adaptations to those evident in advanced species of *Eotebenna* (e.g. *Eotebenna vivianae* from Bornholm) are present in several rostroconchs and these are also interpreted as having lived partially infaunally (Fig. 32). However, the model of Runnegar

& Pojeta (1974) requires that the posterior protrudes from the sediment in rostroconchs while the anterior protrudes in *Eotebenna* (see Fig. 35 and discussion of *Eurekapegma*, above).

Runnegar & Pojeta (1974) noted that many rostroconchs have a large gape which they interpreted as antero-ventral by comparison with living bivalves. A smaller posterior gape often occurs at the tip of the rostrum (Fig. 32). Similar gapes are present in *Eotebenna viviannae* but the model of Runnegar & Pojeta requires that the larger gape is postero-ventral and the smaller opening at the tip of the snorkel is antero-dorsal; this is the opposite orientation to that which they proposed for rostroconchs.

Following the recognition of the endogastric form in helcionelloids, the large gape and the small snorkel opening of *Eotebenna viviannae* are now interpreted in the same manner as the corresponding structures in rostroconchs (Fig. 32). Hence, the snorkel of *Eotebenna* and the rostrum of rostroconchs are both considered to lie at the posterior, while the large gape through which the foot gained contact with the sediment is placed antero-ventrally in both rostroconchs and the helcionelloid genus. As a consequence, similar modes of life can be inferred for *Eotebenna viviannae* and many rostroconchs on the basis of homologous functional adaptations (Fig. 32).

### Pegma-like structures

Rostroconchs are characterised by the presence of a pegma, a transverse strengthening bar located near the apex. Its appearance in the diasome lineage delimits members of the class from the ancestral helcionelloids (cf. Pojeta, 1985, p. 302; see Fig. 5). By reference to the common supposedly posterior extension of the rostroconch shell, Runnegar & Pojeta (1974) proposed that the pegma lay anterior to the apex.

A number of helcionelloids preserve structures on the sub-apical surface of the shell interpreted by Runnegar & Pojeta as 'pegma-like'. Comparison of these structures with the pegma of rostroconchs is a major element in the interpretation of the sub-apical surface of helcionelloids as anterior in the model of Runnegar & Pojeta (1974). However, the supposed homology between many of these structures and the rostroconch pegma is not convincing or is the subject of debate (MacKinnon, 1985; Peel, 1991a).

MacKinnon (1985) considered the supposed pegma in the Lower Cambrian *Heraultipegma*, the oldest rostroconch of Runnegar & Pojeta (Fig. 5), to be produced by phosphatisation around the margin of the sub-apical surface leaving an impression of the shell edge. Kerber

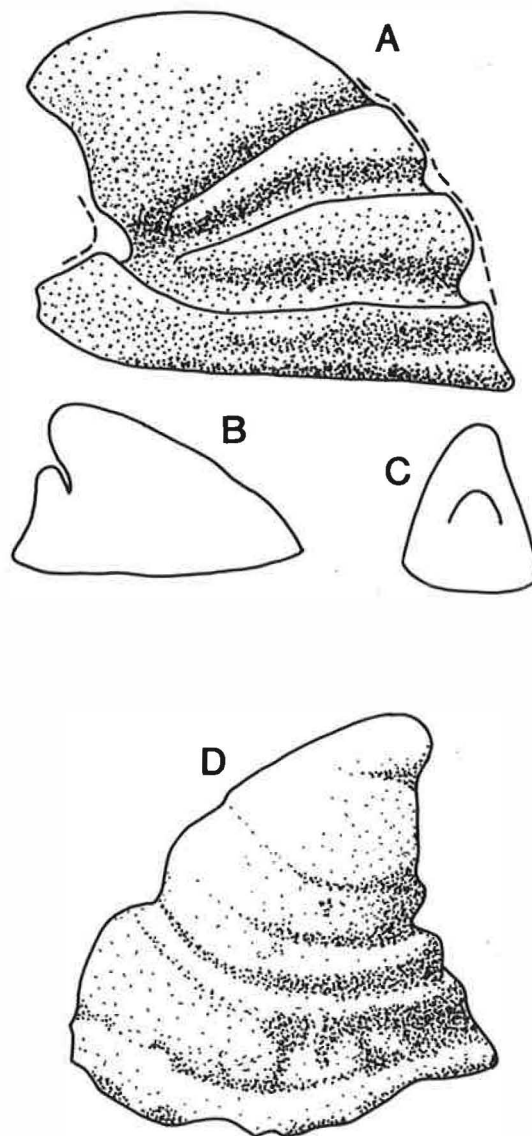


Fig. 38. Pegma-like structures in *Mackinnonia*, *Enigmaconus* and *Parailsanella*. A, lateral view of internal mould of *Mackinnonia davidi* Runnegar in Bengtson *et al.*, 1990 from the Lower Cambrian of South Australia showing prominent constrictions produced by varix-like thickening on the shell interior. The pegma-like notch below the apex represents part of a continuous comarginal thickening of the shell interior. The original outline of the shell exterior surface is represented by a broken line,  $\times 42$  (drawn from Runnegar, 1985, fig. 1A). B, C, *Enigmaconus parvus* MacKinnon, 1985 from the Middle Cambrian of New Zealand; sketches based on the holotype, a largely exfoliated internal mould, illustrated by MacKinnon (1985) showing the pegma-like notch in lateral and posterior views,  $\times 40$ . D, *Parailsanella acris* Zhegallo, 1987 from the Lower Cambrian of the MacKenzie Mountains, Canada; sketch based on the holotype internal mould illustrated by Voronova *et al.* (1987, pl. 22, fig. 1),  $\times 12$ .

(1988) went further, however, and followed Cobbold (1935) and Müller (1975) in considering *Heraultipegma* to be an arthropod and not a mollusc. He synonymised *Heraultipegma* with *Watsonella* Grabau, 1900, a step supported by Landing (1989), who nevertheless followed Runnegar & Pojeta (1976) in considering *Watsonella* to be a rostroconch.

Peel (1991a) noted that sudden changes in growth parameters on the sub-apical surface of helcionelloids can produce deep notches in this surface reminiscent of the rostroconch pegma. Such a notch is visible in the internal mould of a species of *Anabarella* from the Lower Cambrian of Australia illustrated by Runnegar (1983, fig. 4A) and Runnegar & Pojeta (1985, fig. 20A; Fig. 11 herein). The species was described as *Anabarella argus* Runnegar in Bengtson *et al.* (1990, fig. 164H-N). A similar structure was illustrated by Geyer (1986, pl. 3, figs 35-42) in *Oelandia comma* from the Middle Cambrian of Spain.

A less deeply incised notch more closely comparable to that in other helcionelloids is present in *Anabarella simesi* MacKinnon, 1985 from the Middle Cambrian of New Zealand (MacKinnon, 1985, fig. 3a, b). The notch in the Australian species reflects the development of a sub-apical exhalant emargination in this unusually strongly coiled and laterally compressed form. As such, it can be compared with similar apertural folds developed in *Eotebenna arctica* (Figs 11, 29, 30) and *Oelandia pauciplicata* (Fig. 33).

Runnegar (1985, fig. 1A-E) illustrated an internal mould from the Lower Cambrian of South Australia as *Latouchella?* n. sp. with pronounced constrictions produced by varix-like thickenings of the shell interior. The specimen was referred to *Mackinnonia davidi* n. gen. and n. sp. by Runnegar in Bengtson *et al.* (1990, fig. 159). A deep cleft below the apex resembles the impression of a pegma when the shell is viewed laterally (Fig. 38A). However, the cleft and all the deep channels in

the surface of the internal mould are produced by thickenings of the shell interior (the outer surface is smooth) which are continuous around the shell and can not be compared to the rostroconch pegma. Similar specimens occur in the lower member of the Aftenstjernesø Formation (Brønlund Fjord Group, Early Cambrian) of Peary Land, North Greenland (J. S. Peel, unpublished information). *Leptostega? corrugata* Runnegar in Bengtson *et al.* (1990, fig. 160A-G), also from the Lower Cambrian of Australia, shows similar channels on the internal mould probably representing thickenings of the shell interior.

*Paraisanella* Zhegallo in Voronova *et al.*, 1987, from the Lower Cambrian of the MacKenzie Mountains of Canada, preserves similar structures on the internal mould, interpreted as constrictions on the shell interior (Fig. 38D).

A more convincing pegma-like structure on the sub-apical surface is present in *Enigmaconus* MacKinnon, 1985, from the Middle Cambrian of New Zealand (Fig. 38B, C). *Enigmaconus*, however, has a relatively broad, cone-shaped shell quite different in morphology from the strongly laterally compressed shell of early rostroconchs, making any proposed functional equivalence between the respective transverse bars tenuous. In addition, the pegma-like structure in *Enigmaconus* is interpreted as posterior, lying on the sub-apical surface, while the pegma of rostroconchs lies anterior to the apex.

*Merismoconcha* Yu, 1979 preserves transverse furrows on the broadly convex, apparently supra-apical surface of internal moulds which may resemble a pegma-like structure (cf. Kerber, 1988, fig. 19). Kerber (1988) relegated the supposed Class Merismoconchia to a family within the helcionelloids, but the status of this group of problematic Lower Cambrian fossils remains unresolved (cf. Qian & Bengtson, 1989; Yu, 1989, 1990).

## Origin of the cephalopods

More than a century ago, Schmidt (1888) described a small Lower Cambrian fossil, *Volborthella*, as the oldest cephalopod. The claims of this and the closely related genus *Salterella* Billings, 1861 (Fig. 39) to cephalopod ancestry have been restated subsequently by many geologists and biologists. In the context of Greenland geology, Poulsen (1927, 1932, 1958) described species of *Salterella* from the Lower Cambrian Wulff River Formation of Inglefield Land, North-West Greenland stating

his belief in their cephalopod affinities (cf. Yochelson & Peel, 1980; Peel & Yochelson, 1982).

It is now widely accepted that *Salterella*, *Volborthella* and related genera are neither cephalopods nor molluscs, but belong to a new phylum to which Yochelson (1977) gave the name Agmata. Fossil agmatans are widespread in Lower Cambrian strata and possess coniform shells containing laminated deposits bearing only a superficial resemblance to the camerate shells of the

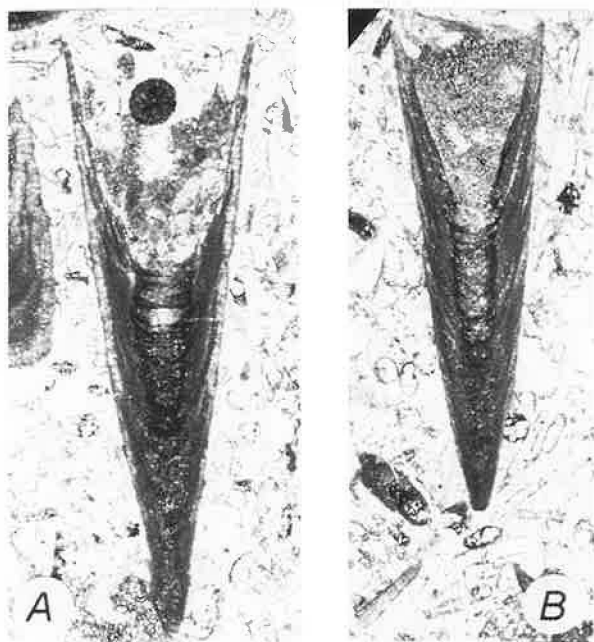


Fig. 39. *Salterella maccullochi* (Murchison, 1859) from the Lower Cambrian Hyolithus Creek Formation, Kap Weber, North-East Greenland,  $\times 10$ . Transverse longitudinal sections through the agmatan conch showing the internal lamination and central canal interpreted by some earlier workers as the cephalopod camerae and siphuncle. A, MGUH 15.918; B, MGUH 15.920.

cephalopods (Yochelson 1970, 1981; Fritz & Yochelson, 1988). A single well documented occurrence of the agmatan genus *Ellisell* Peel & Berg-Madsen, 1988, from the Middle Cambrian of Bornholm, Denmark, represents the youngest record of the phylum (Peel & Berg-Madsen, 1988).

While agmatans are no longer considered to be closely related to the earliest cephalopods, no consensus has emerged subsequently to explain the origin of the first undoubted cephalopods in the Late Cambrian. The most favoured hypothesis is that cephalopods were derived from tall hypseloconellacean monoplacophorans (here placed within the Order Hypseloconida of the Class Tergomya) with internal septation, by the subsequent acquisition of a siphuncle (Yochelson *et al.*, 1973; see also Webers & Yochelson, 1989); it can be termed the *Knighthoconus* hypothesis after the hypseloconellacean genus used as a model for the ancestral tergomyan (Fig. 40).

The *Knighthoconus* hypothesis is not without opponents and these mainly base their objections on the need for the siphuncle in the model proposed by Yochelson *et al.* (1973) to somehow 'penetrate' the se-

quence of imperforate septae characteristic of *Knighthoconus* (cf. Chen & Teichert, 1983; Teichert, 1988; Wade, 1988).

Dzik (1981) suggested that cephalopods were derived from slender, planktonic monoplacophorans which were possibly related to the circothecid hyoliths (Fig. 40). Jell (1978) derived the cephalopods from *Yochelcionella*, developing the siphuncle from the characteristic snorkel (Fig. 40); this hypothesis was subsequently supported by Pojeta (1980; 1987).

Kobayashi (1987) proposed that cephalopods were descended from monoplacophoran molluscs, and he recognised a series from septate *Helcionella* through Middle Cambrian forms tentatively assigned by Runnegar & Jell (1976) to the Ordovician genus *Pollicina* Holzapfel, 1895. Peel (1991a) independently speculated that cephalopods may have been derived from basically endogastric helcionelloids rather than hypseloconellacean tergomyans such as *Knighthoconus* (Fig. 41). He stressed the fundamental difference in coiling between the Tergomya and the Helcionelloida, the whole question of direction of coiling having been overlooked by Kobayashi (1987).

#### The *Knighthoconus* hypothesis

Yochelson *et al.* (1973) derived the first cephalopods from tall monoplacophoran molluscs with septate early growth stages, by the subsequent development of a siphuncle. They postulated that a strand of tissue may have retained contact with the earliest portion of the shell as the main body mass migrated anteriorly with growth, and that septa may have formed astride this remnant of tissue which subsequently developed into a siphuncle. Their model was based on the Late Cambrian *Knighthoconus* Yochelson, Flower & Webers, 1973 in which the apparently endogastric shell bears some morphological similarity to the earliest cephalopod *Plectronoceras* Ulrich & Foerste, 1933, described from the Late Cambrian of China (Fig. 40). *Knighthoconus* is a member of the group of supposedly untorted molluscs which Stinchcomb (1986) placed in the Superfamily Hypseloconellacea (Fig. 42); members of this superfamily form the basis of the tergomyan Order Hypseloconida. *Knighthoconus* is distinguished from the nominate genus *Hypseloconus* Berkeley, 1898 mainly on account of its abundant internal septae.

Muscle scars in *Hypseloconus* were compared by Stinchcomb (1980) with similar muscle scar patterns in tryblidiacean tergomyans such as *Pilina* (Fig. 1), suggesting that *Hypseloconus* was indeed endogastric, as deduced by Yochelson *et al.* (1973). Tergomyans are exogastrically coiled, however, and any phylogenetic

Fig. 40. Some theories concerning the origin of the earliest cephalopods (*Plectronoceras*). A, Dzik (1981) suggested that cephalopods were derived from slender, planktonic monoplacophorous molluscs currently classified among the circothecid hyoliths. B, Yochelson *et al.* (1973) derived cephalopods from endogastric hypseloconellacean *Tergomya* such as *Knightoconus*. C, Runnegar & Jell (1976) considered that tall, slender, secondarily endogastric species of *Yochelcionella* gave rise to endogastric hypseloconellaceans such as *Knightoconus* which, following Yochelson *et al.*, were ancestral to the cephalopods. The theory that cephalopods were derived from endogastric helcionelloids is illustrated in Fig. 41. D, Jell (1978) and Pojeta (1980, 1987) proposed that tall, slender and secondarily endogastric species of *Yochelcionella* (such as *Y. ostentata*) gave rise to cephalopods by conversion of the snorkel into a siphuncle.

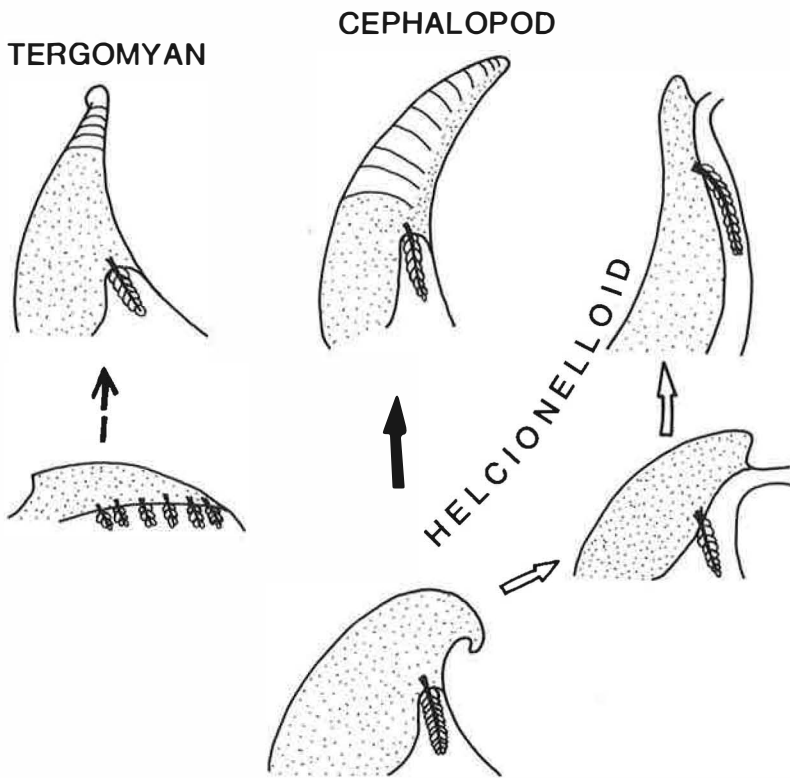
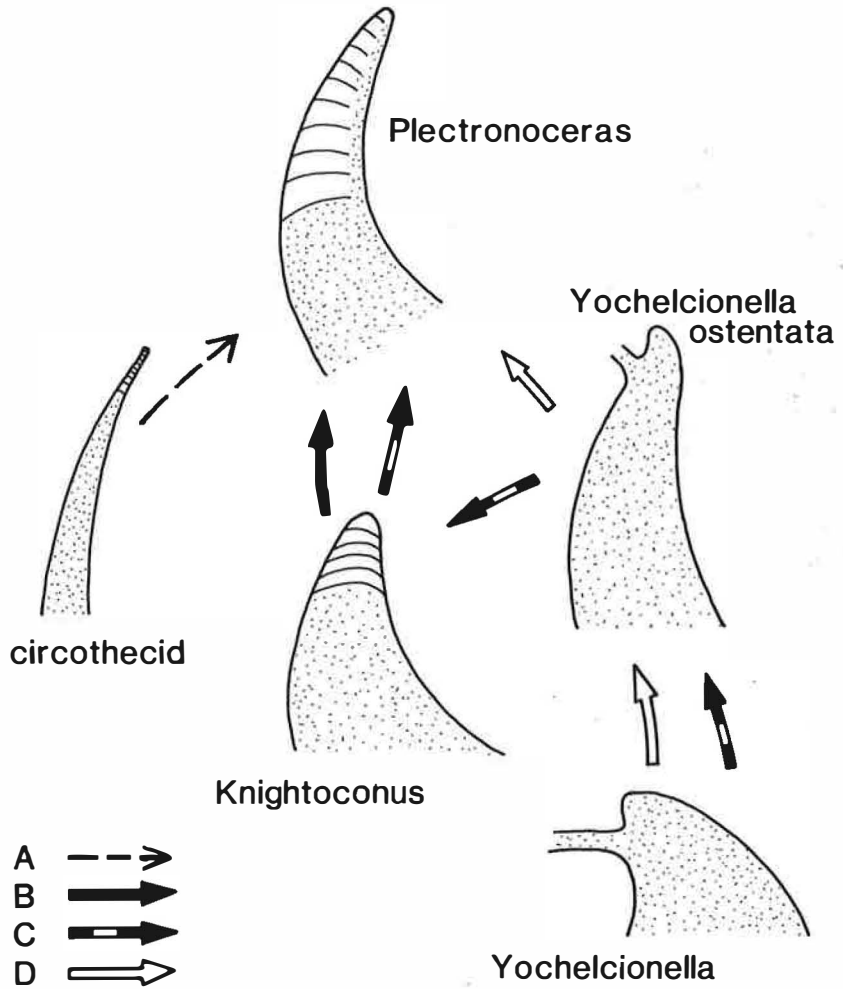


Fig. 41. Derivation of endogastric cephalopods from endogastric helcionelloids compared with the evolution of morphologically similar shell forms within the *Tergomya* and the helcionelloid *Yochelcionella*. All specimens are similarly orientated, with anterior to the left and posterior to the right. The mantle cavity and gills are illustrated schematically.

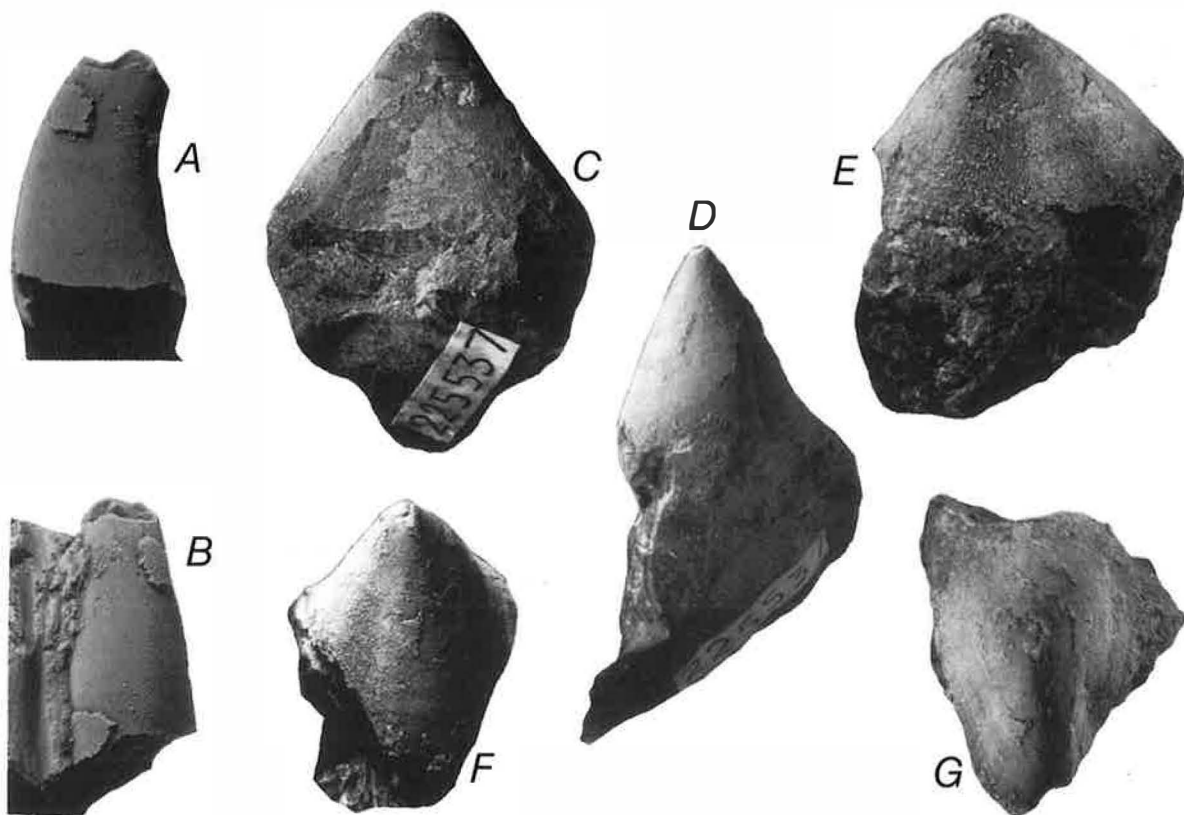


Fig. 42. Hypseloconellid tergomyans from the late Middle Cambrian Holm Dal Formation, Peary Land, central North Greenland. A, B, internal mould of early growth stages of *Hypseloconus* sp. in which the apex and the more widely expanded late growth stages are missing, MGUH 18.689 from GGU collection 225529,  $\times 5$ ; A, lateral view; B, anterior view. C-G, undetermined hypseloconellacean sp., MGUH 18.691 from GGU collection 225537,  $\times 2$ ; C, lateral view with slightly concave sub-apical surface to right; D, anterior view; E, F, oblique lateral views showing trilobed fold in supra-apical surface; G, apical view with supra-apical surface at bottom.

relationship between them and the apparently endogastric hypseloconellaceans would require a fundamental change in direction of coiling. This discrepancy was resolved by Webers & Yochelson (1989, fig. 2; see also Webers *et al.*, in press) who described the early growth stages of *Knighthoconus*, clearly demonstrating their exogastric form. *Knighthoconus* changed its direction of coiling during ontogeny to become endogastric in the adult, thus acquiring a pseudo-endogastric shell-form similar to that of *Plectonoceras* (Fig. 41).

Chen & Teichert (1983) and Teichert (1988) rejected the theory of Yochelson *et al.* (1973) that cephalopods were derived from septate *Knighthoconus* stating that it is the siphuncle and not the presence of septa which characterises the Cephalopoda (a statement which Yochelson *et al.*, 1973 did not deny). Septa may be expected in any relatively narrow conical shell in which the animal abandons the narrow early part of the shell

and they are developed in a variety of molluscs, including gastropods, helcionelloids and tergomyans. As noted above, the presence of septa in circothecid hyoliths prompted Dzik (1981) to suggest that slender, planktonic monoplacophorans currently placed within this group may have given rise to the Cephalopoda (Fig. 40).

Chen & Teichert (1983) are undoubtedly correct in their belief concerning the relative importance of the siphuncle and septation in the definition of cephalopods, although the role of septation (or the ability to produce septa) must not be too readily dismissed.

It is the combination of septa and siphuncle which provides the flotation mechanism which was so successfully exploited in cephalopods in the Late Cambrian. More correctly, it is the acquisition of calcareous septa in association with the siphuncle that has allowed recognition of the mechanism of cephalopod flotation in the

fossil record. A flotation mechanism involving soft tissue alone would leave little trace within the early fossil record (cf. Salvini-Plawen, 1981).

Harper & Rollins (1982) rejected the model of Yochelson *et al.* (1973) considering *Knichtoconus* to be a cyclomyan and not an untorted tergomyan (in the sense of Horny, 1965a, b). They believed the Cyclomya to be gastropods; acceptance of the theory of Yochelson *et al.* (1973) consequently would have required derivation of the untorted cephalopods from the torted Gastropoda and not from some untorted mollusc. This clearly unacceptable derivation of cephalopods from presumed gastropods is avoided here since *Knichtoconus* is interpreted as a specialised tergomyan and not a gastropod; hence it is untorted.

### Pseudo-endogastric and pseudo-exogastric

In reviewing the origin of cephalopods, Runnegar & Jell (1976, p. 125) speculated that *Hypseloconus* was able to develop a tall cone because of its endogastric coiling. They considered that endogastric coiling "must have been the most important single character for the production of the Cephalopoda, for it would allow for the development of buoyancy tanks above the body mass". They anticipated the description of the ontogenetic change in the direction of coiling of *Knichtoconus* by Webers & Yochelson (1989) and Webers *et al.* (in press), noting how *Yochelcionella ostentata* from the Middle Cambrian of Australia changed its direction of coiling during ontogeny to acquire a tall shell (Fig. 40). Runnegar & Jell (1976) suggested that the change in shell curvature resulted from a need to elevate the snorkel and that the curvature was retained in *Hypseloconus* and *Knichtoconus* after the snorkel was lost.

It is implicit in this argument that Runnegar & Jell considered *Hypseloconus* and *Knichtoconus* to be derived from *Yochelcionella*. However, in the present paper the former two genera are referred to the Class Tergomya while *Yochelcionella* is assigned to the Class Helcionelloida (cf. Peel, 1991a).

The restoration of *Yochelcionella ostentata* proposed by Runnegar & Jell (1976) shows coiling to be originally exogastric and subsequently endogastric; the resultant pseudo-endogastric shell form is thus directly analogous to *Hypseloconus* and *Knichtoconus* (Fig. 40). *Y. ostentata* is now interpreted as endogastric in its earlier growth stages, however, with exogastric coiling being developed in its adult stage. Thus, the shell in *Y. ostentata* is pseudo-exogastric and not pseudo-endogastric (Fig. 41), while the hypseloconellacean *Knichtoconus* is pseudo-endogastric.

Following the previously mentioned arguments ex-

pressed by Runnegar & Jell (1976) concerning buoyancy, both pseudo-exogastric and pseudo-endogastric shell forms permit the acquisition of tall and slender cones with a potential for the development of buoyancy above the body mass. This result is also achieved without ontogenetic reversal of coiling direction in straight cones or in shells with a low spiral angle (e.g., *Obtusococonus* Yu, 1979, see also '*Helcionella*' *buttsi* Resser, 1938; Fig. 11). The development of an orthocone aperture in a straight cone maintains the centre of gravity in a central position above the aperture. Similarly, the development of an opisthocone apertural margin would place the centre of gravity in a similar position in exogastric or endogastric shells with a low spiral angle.

The earliest cephalopods are endogastrically coiled or straight but it is not known if the spectrum of growth forms they represent results from isometric or allometric growth, or from examples of both.

From the point of view of shell coiling, the endogastric shell-form of *Plectronoceras*, the oldest cephalopod, could have been derived equally from the allometrically coiled, pseudo-endogastric tergomyans such as *Knichtoconus* or from an isometrically coiled helcionelloid which decreased the tightness of coiling of the endogastric shell (Fig. 41), although derivation from a third as yet unrecognised source must not be ruled out. In the first two cases, the deep and narrow, posteriorly located mantle cavity may have contributed to the differentiation of the tissue strand which ultimately developed into the relatively wide siphuncle of the earliest cephalopods. However, as noted by Wade (1988), the siphuncle itself is not developed from the mantle cavity but from the general molluscan cape. The location of the snorkel in *Yochelcionella ostentata* and morphologically similar species of *Eotebenna* indicates that the mantle cavity extended almost to the apex; a similar configuration was probably present in some hypseloconellaceans (Fig. 41) and represents a logical trend to obtain the maximum separation of inhalant shell currents from the exhalant stream. The progressive adapertural deposition of septa around the adapical termination of a mantle fold to close off the early growth stages of a slender shell when most of the body mass had migrated adaperturally might thus produce the forerunner to the siphuncle.

### The *Yochelcionella* hypothesis

While slender species of *Yochelcionella* such as *Y. ostentata* may offer an important analogy to the 'pre-cephalopod' in terms of shell coiling, as discussed in the previous section, it is unlikely that they were direct



ancestors of cephalopods as proposed by Jell (1978) and Pojeta (1980, 1987 and Fig. 40 herein).

The reconstruction of *Y. ostentata* favoured by Pojeta & Runnegar (1976) involves a mantle cavity developed all around the shell aperture with anterior snorkel and laterally disposed gills (Fig. 22A). The development of the snorkel into a siphuncle would place the siphuncle on the opposite side of the shell to that seen in *Plectronoceras*, the earliest cephalopod, while much of the rest of the mantle cavity would be postero-laterally disposed.

Differentiation of the most adapical part of the elongate mantle cavity into a siphuncle in the reconstruction of *Y. ostentata* favoured here would locate the siphuncle beneath the convex surface (in lateral view) and not beneath the concave surface, as is the case in *Plectronoceras* (Fig. 41).

### The helcionelloid hypothesis

Kobayashi (1987) derived cephalopods from septate *Helcionella* by way of tall Middle Cambrian shells tentatively (but incorrectly) referred to *Pollicina* by Runnegar & Jell (1976); the same authors also referred grossly similar shells to two species of *Stenotheca* Hicks, 1872, indicating that tall shells were developed in several lineages during the Middle Cambrian.

Kobayashi considered *Helcionella* to be a monoplacophoran. He appears to have accepted the presence of endogastric coiling in *Helcionella*, following the orientation proposed by Knight *et al.* (1960) who, however, considered *Helcionella* to be a gastropod and monoplacophorans to be exogastric. Kobayashi (1987) made no reference to the differentiation of this assumed endogastric coiling from the undoubted exogastric coiling of the *Tergomya*; neither did he discuss the relationship between *Helcionella* and the *Tergomya*.

The new Class Helcionelloida proposed by Peel (1991a) is characterised by endogastric coiling, as distinct from the exogastric coiling of the Class *Tergomya*. Unaware of Kobayashi's earlier paper, Peel considered the helcionelloids to be possible ancestors of the earliest cephalopods on account of their common endogastric coiling (Fig. 41). In contrast to Kobayashi (1987), Peel

(1991a) clearly delimited the relationships of the basic coiling patterns in the major taxa which are fundamental to this hypothesis.

The first cephalopods differentiated into a variety of endogastric and exogastric forms which vary from straight to shallowly curved and tightly coiled (Chen & Teichert, 1983). However, the dominance of endogastric shells in the earliest fossil record of the class suggests derivation of cephalopods from an endogastric ancestor. Thus, derivation of cephalopods from the endogastric helcionelloids offers a viable alternative to the belief that cephalopods originated from pseudo-endogastric hypseloconidan members of the generally exogastric *Tergomya* as proposed by Yochelson *et al.* (1973; cf. Peel, 1991a). As noted above, and as also proposed by Yochelson *et al.* (1973), progressive adapertural deposition of septa across a tissue strand connecting the body mass to the apex may have eventually resulted in the establishment of a siphuncle.

Helcionelloids are typical of Lower and Middle Cambrian strata while the first cephalopod, *Plectronoceras*, is of Late Cambrian (late Franconian) age (Chen & Teichert, 1983). Hypseloconids, favoured by Yochelson *et al.* (1973) and Webers & Yochelson (1989) as the stem group for cephalopods, characterise latest Middle Cambrian and younger strata; helcionelloids and hypseloconids are rarely found together, although one such rare occurrence is within the late Middle Cambrian Holm Dal Formation of Peary Land, central North Greenland (Peel, 1988b).

The tall cones of *Yochelcionella ostentata* and similar species, *Knighthoconous* and other hypseloconids, and the earliest cephalopods represent broadly similar morphological adaptations to possibly analogous environments. Slender species of *Yochelcionella* are known from Lower and Middle Cambrian strata and rarely exceed 5 mm in height. The hypseloconids appear in the latest Middle Cambrian (cf. Peel, 1988b) and their massive shells may be ten times larger than *Yochelcionella* and most helcionelloids. The first *Plectronoceras* from the Upper Cambrian are less than 1 cm tall (Yochelson *et al.*, 1973). The variety in shell form both between and within these major taxa suggests that they followed more than one mode of life.

## Diasoma and Cyrtosoma

The model of molluscan evolution presented by Runnegar & Pojeta (1974) and subsequently presented in more detailed form by Pojeta & Runnegar (1976, fig. 14) and Runnegar (1983, fig. 1) refers the univalved and bivalved molluscs (the Conchifera of Salvini-Plawen, 1980, 1981, 1985) to the Sub-phyla Diasoma and Cyrtosoma (Fig. 5 and discussion above). Diasomes have univalved (Classes Rostroconchia and Scaphopoda) or bivalved shells (Class Bivalvia) and are characterised by an essentially straight gut. The shell is usually univalved in cyrtosomes and the gut is bent into a U-shape or twisted by torsion. Runnegar & Pojeta (1974) referred the gastropods, cephalopods and the Class Monoplacophora of their broad usage to the Cyrtosoma.

Approximately equivalent terms to Diasoma and Cyrtosoma employed in neontological circles, but based on other morphological criteria, include Ancyropoda and Loboconcha (for Diasoma) and Rhacopoda and Visceroconcha (for Cyrtosoma; see Lauterbach, 1983a; Salvini-Plawen, 1985; Haszprunar, 1988).

Helcionelloids, interpreted as exogastric monoplacophoran cyrtosomes derived from the tryblidiid lineage, were considered by Runnegar & Pojeta (1974) to be the ancestors of the Diasoma, indicating that the cyrtosomes are ancestral to the diasomes (Runnegar & Pojeta, 1985, p. 25). The present re-interpretation of helcionelloids as endogastric inevitably promotes re-examination of this model; the relationship between the Tergomya and the Helcionelloida is discussed in a later section.

### The polyphyletic Diasoma

Peel (1991a) accepted the derivation of the rostronchs from the helcionelloids proposed by Runnegar & Pojeta (1974). He considered rostroconchs to be originally endogastric, however, in similar fashion to helcionelloids, and not exogastric as proposed by Runnegar & Pojeta (1974, and later references).

Derivation of rostroconchs from endogastric helcionelloids allows similar structures in both groups to be interpreted as performing the same function, in the same orientation (Fig. 32), while still generally accepting the rostroconch morphological and functional analyses described by Runnegar & Pojeta (1974) and Pojeta & Runnegar (1976).

Peel (1991a) accepted the interpretation of the Bivalvia as basically exogastric, as suggested by Runnegar & Pojeta (1974). He therefore concluded that the Sub-phylum Diasoma of Runnegar & Pojeta consists of two

distinct, but parallel lineages, with Rostroconchs (and subsequently the scaphopods) evolved from an endogastric helcionelloid ancestor. Hence, Diasoma is not maintained as a monophyletic group since bivalves are presumed to be descendants of an exogastric tergomyan mollusc (cf. Salvini-Plawen, 1985; Stasek, 1972), and not of the endogastric helcionelloids. Haszprunar (1988, p. 403) restated earlier opinions that the bivalve ancestor may have had a more restricted mantle cavity than that of known tryblidiid tergomyans in which the multiple gills are serially arranged. Thus, the peripodial mantle cavity of bivalves with a single pair of gills might be an early molluscan character rather than a secondary simplification from a serial respiratory system. Wingstrand (1985), however, found evidence for serially arranged muscle and gills in early bivalves.

Runnegar & Pojeta (1985) pointed out that muscle scars are not known in helcionelloids (but see discussion of *Scenella* sp. undet. below) or the earliest supposed rostroconch of their model (*Watsonella crosbyi* Grabau, 1900, = *Heraultipegma varensalense* (Cobbold, 1935), according to Landing, 1989). By analogy to early rostroconchs they suggested that muscles in helcionelloids were concentrated anteriorly and posteriorly of the apex, with a single muscle field in each area crossing the dorsal mid-line from one side of the shell to the other (see Pojeta & Runnegar, 1976, figs 1, 3). Runnegar & Pojeta (1985, p. 41) further noted that true adductor muscle scars are absent from rostroconchs (with the possible exception of *Eopteria* Billings, 1865) and that acquisition of these muscles is associated with the "critical event in the origin of the Bivalvia...the appearance of two shell valves with an intervening ligament".

Subsequently, Runnegar & Pojeta (1985) deduced from the lateral asymmetry of *Watsonella* (cf. *Heraultipegma* in Fig. 5), where the supposedly posterior (in their interpretation) supra-apical surface is relatively enlarged, that the posterior adductor muscle scar in the first bivalves should be larger than the anterior adductor scar. In this light, they argue that the large posterior adductor muscle scars of the Early Cambrian bivalves *Fordilla* Barrande, 1881 and *Pojetaia* Jell, 1980 are not unexpected.

Following the present interpretation of helcionelloids, the larger muscle attachment area in many rostroconchs (and helcionelloids, if they show a similar musculature but see *Scenella* sp. undet. below) is anterior and not posterior, as in *Pojetaia* and *Fordilla*, thus weakening the similarity proposed by Runnegar & Pojeta (1985). However, in view of the differences in

location between the transdorsal muscle scars in rostroconchs (and possibly helcionelloids) and the separate adductor scars of *Pojetaia* and *Fordilla*, and associated differences in shell morphology, it is unlikely that the proposed (but here rejected) analogy had any phylogenetic significance. Extant bivalves develop adductor muscle scars of different sizes depending on the relative proportions of the anterior and posterior regions of the shell (cf. Allen, 1985).

As a group of largely infaunal or semi-infaunal molluscs Rostroconchs (Cambrian–Permian) are analogous to the Bivalvia (Cambrian–Recent). However, they were outlived by the bivalves which became increasingly abundant during the post-Palaeozoic. The third class referred to the Diasoma by Runnegar & Pojeta (1974), the Class Scaphopoda, may represent a specialised remnant of the helcionelloid-rostroconch lineage. Scaphopods (?Middle Ordovician–Recent, cf. Pojeta & Runnegar, 1979) were probably derived from rostroconchs since helcionelloids are essentially confined to the Early and Middle Cambrian.

#### Status of the Sub-phylum Cyrtosoma

The Sub-phylum Cyrtosoma was proposed by Runnegar & Pojeta (1974) to include the classes Gastropoda

and Cephalopoda, together with a broadly defined Class Monoplacophora (Fig. 5). According to Wingstrand (1985), the 'Monoplacophora' forms a stem-group to the conchiferan molluscs and should be removed from the Cyrtosoma, refuting the opinion of Runnegar & Pojeta (1985) that the cyrtosomes were the ancestors of the diasomes. The Tryblidiida is a sister group to the other Conchifera in the scheme of Salvini-Plawen (1985, fig. 42; see also Lauterbach, 1983a, b, who used the term Neopilinida). However, the remaining Cephalopoda and Gastropoda were considered to form a monophyletic group by Wingstrand, as were the diasomes (Fig. 43).

Wingstrand's concept of the Monoplacophora was essentially identical to the Order Tryblidiida of the Class Tergomya of the present usage, although Runnegar & Pojeta (1974) employed a much wider definition of the Monoplacophora, including representatives of a number of other molluscan classes. Wingstrand (1985, p. 54) noted, however, that "the real troubles come when the pattern of side branches from a tryblidian-like stem is discussed ... No wonder ... that details are missing on this point in most phylogenetical diagrams." His own diagram (Fig. 43) is no exception, although this is readily understood when consideration is given to the host of imperfectly known, but supposedly molluscan lineages

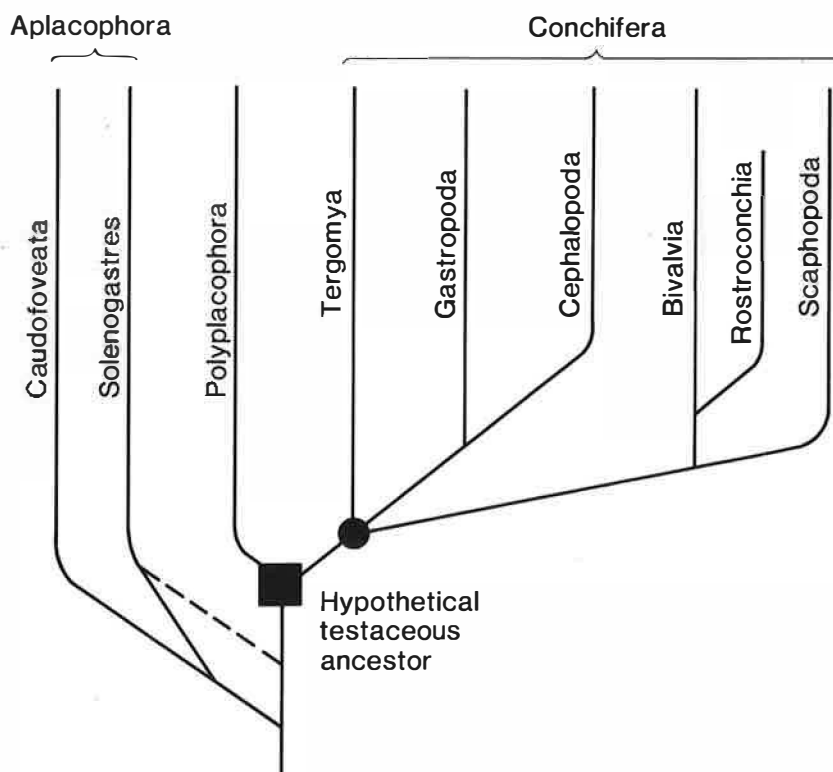


Fig. 43. Evolution of molluscan classes expressed through a diagram simplified from Wingstrand (1985). The Class Tergomya is substituted for Tryblidiida.

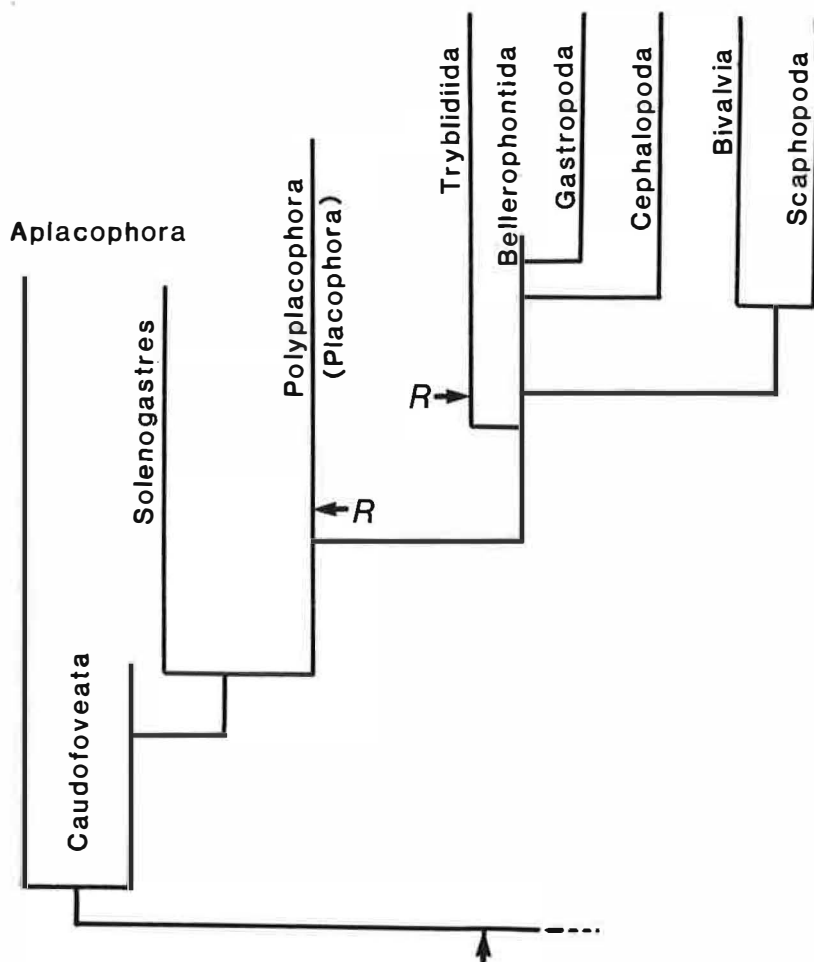


Fig. 44. Molluscan relationships according to Salvini-Plawen (1985, fig. 42). The diagram is modified and simplified, with removal of supposed seven-valved polyplacophorans (see discussion in text). Repetition of gills (R) is considered to have occurred independently in the polyplacophoran and tryblidiid (= tryblidiid tergomyan) branches.

present in Lower and Middle Cambrian strata (cf. Runnegar & Jell, 1976; Yu, 1987; Missarzhevsky, 1989; Qian & Bengtson, 1989; Bengtson *et al.*, 1990).

Failure to accept the Monoplacophora of Runnegar & Pojeta (1974) as a single phylogenetic entity naturally promotes inspection of the integrity of the original Subphylum Cyrtosoma. Any doubts would be reinforced by acceptance of the hypothesis concerning derivation of cephalopods from endogastric helcionelloids, since gastropods were probably derived from exogastric tergomyan-like untorted molluscs resembling the cyrtoneiid *Tergomya* (for an alternative view see Haszprunar, 1988). Derivation of gastropods by torsion in endogastric helcionelloids would produce an exogastric shell and not the familiar endogastric coil of the Gastropoda.

Some morphological similarities between gastropods and cephalopods, such as the posteriorly restricted mantle cavity and the frequently tightly coiled endogastric shell, could in part represent convergence resulting from life within a narrow cone and, as such, are also seen in some helcionelloids. The posterior mantle cavity, however, may also represent an early molluscan feature and its lateral distribution with serial gills in tryblidiid tergomyans would therefore represent a derived condition following the thesis of Salvini-Plawen (1985, fig. 42; see Fig. 44).

In view of the abandonment of *Diasoma* and the uncertainty surrounding its application, *Cyrtosoma* is not employed herein in the classification of the Phylum Mollusca.

## Ancestral conchiferans

A recurring theme in discussions of early molluscan evolution involves the serial distribution of gills and other structures (Salvini-Plawen, 1985; Wingstrand, 1985; Haszprunar, 1988; see also Yochelson 1978, 1979; Runnegar & Pojeta, 1985). Is the serial repetition of gills present in polyplacophorans and tryblidiid tergomyans a primary character (cf. Wingstrand, 1985), or is it derived from an ancestral condition in which only a few gills are located posteriorly (Salvini-Plawen, 1985)? Complications, inevitably, must be expected since secondary multiplication or reduction of gills and muscle scars may have taken place in response to changes in shell morphologies as molluscs diversified and adapted to their environments. Some measure of the magnitude of these adaptations is indicated by the gill structure of present day gastropod limpets. Fissurellids have a symmetrical pair of bipectinate gills representing the primitive archaeogastropod condition. Acmaeids have only a single gill but may develop secondary gills in the mantle groove around the foot. Both gills are lost in patellids where respiration is accomplished entirely by a series of secondary gills. Limpetoid mesogastropods and neogastropods normally have a single monopectinate gill on the left-hand side of the mantle cavity, while opisthobranch limpets have a single posterior gill. Pulmonate limpets lack gills but the vascularised mantle cavity is thrown into folds resembling gills (Branch, 1985).

The model of Salvini-Plawen (1980, 1981, 1985) and others involves two episodes of acquisition of serially repeated gills, one with advancement from the aplacophoran level to the polyplacophoran (= Placophora) level, and the second after differentiation of the tryblidiid lineage from the early Conchifera (Fig. 44). Subsequent derivation of the remaining Conchifera maintains a low number of gills with concentration of the mantle cavity in a posterior position (gastropods and cephalopods) or acquisition of a peripodial mantle cavity containing a single pair of gills (bivalves). This model contrasts with that of Wingstrand (1985) and others where the paired muscle scars and gills of tryblidiid tergomyans and polyplacophorans represent a primary molluscan condition (Fig. 43). Thus, according to Runnegar & Pojeta (1985), helcionelloids are derived from a tergomyan-like ancestor by reduction in the number of gills; the Diasoma, being derived in their model from helcionelloids (Fig. 5), must also be considered to have undergone reduction in the number of gills during their evolutionary history. Interestingly, Wingstrand (1985) recognised clear evidence of serial gills and muscle scars in early bivalves which might appear anomalous if these

were derived from helcionelloids with a reduced number of gills as required by Runnegar & Pojeta (1974).

Fossil tryblidiid Tergomya show some variation in the number of pairs of muscle scars (Knight & Yochelson, 1960). The fossil record may also provide evidence of secondary reduction of gills within the Tergomya where the morphological series from tryblidiids (with multiple muscle scars and gills, cf. *Pilina*, Figs 1, 15A) to cyrtoneidids (Figs 15D, 18D-F) involves reduction in the number of pairs of muscle scars and (presumably) gills due to the development of a tightly coiled shell. The model of Salvini-Plawen (1985), however, would argue that possession of only a few gills was an original molluscan feature in at least some cyrtoneidids; in this model the Bellerophonitida were considered to be untorted (i.e. cyrtoneidid tergomyans) molluscs ancestral to the gastropods.

A similar trend in muscle and gill reduction is also well known in gastropods. On a cautionary note, however, it should be remembered that muscle scars are known in very few fossil univalve molluscs and critical evidence concerning their relationships is wanting or highly speculative. Similarly, as pointed out by Wingstrand (1985), it is series of muscle scars that are preserved in fossils and not series of gills.

By analogy with cyrtoneidid tergomyans and gastropods, laterally compressed and strongly coiled helcionelloids probably had few gills (perhaps only a single pair). This interpretation is possibly strengthened by the small size of helcionelloids (Runnegar & Pojeta, 1985), although the general small size of Early Cambrian molluscs noted by these authors presumably also applies to the supposedly ancestral tergomyans. The interpreted paucity in the number of gills in helcionelloids is common to the present model, where the mantle cavity is considered to lie posteriorly in an endogastrically coiled shell (cf. Fig. 12B), and to the reconstruction of Runnegar & Pojeta (1974), where an anterior mantle cavity lies within an exogastric shell (Fig. 12A). The problem is to decide if this condition is an early molluscan feature (cf. the model of Salvini-Plawen, 1985 which did not make reference to helcionelloids and other problematic Cambrian molluscs) or a derived character resulting from reduction in the number of gills after descent from tryblidiid-like Tergomya, as supposed by Runnegar & Pojeta (1974) and by Wingstrand (1985, although he also did not refer to helcionelloids directly). The issue is central to elucidating the relationship between the Classes Helcionelloida and the Tergomya and focuses attention on the possible occurrence of both

taxa in the earliest fossil record. The relationship between the two classes can only be elucidated from fossil material by reference to muscle scars and functional morphological assumptions, such as the restricted space available within tall, narrow, shells. As noted above in the discussion of the cyclomyan and tergomyan condition within the Class Tergomya, distribution and variation in muscle scar patterns is also closely related to changes in the coiling parameters of the coiled shell.

### Helcionelloid muscle scars

Undoubted muscle scars are not reported from typical helcionelloids, a feature which prompted Missarzhevsky (1989) to suggest that shell muscles were initially attached into an epithelial layer, with direct attachment to the shell being a later evolutionary development. Missarzhevsky's (1989) idea merits further investigation. Runnegar (1985 and in Bengtson *et al.*, 1990) demonstrated a variety of microscopic structures on phosphatic internal moulds of helcionelloids, many of which replicate the crystal structure of the shell interior. Other structures, e.g. the fine pitting in the internal mould of *Latouchella* illustrated here as Fig. 24G (see also MacKinnon, 1985, fig. 1R), are less readily interpreted in this manner. Missarzhevsky's (1989) suggestion served as the basis for his establishment of an Order Eomonoplacophora for the taxa here placed within the Class Helcionelloida but the term is not employed here (see discussion above).

Runnegar & Pojeta (1985) supported their theory concerning the derivation of helcionelloids from a tryblidiid-like ancestor by reference to *Scenella* sp. undet. of Rasetti (1974), a Middle Cambrian cap-shaped form from British Columbia in which 6 pairs of muscle scars are preserved (Fig. 45). The muscle scars were held to indicate the anatomy of *Neopilina*, although *Scenella* was referred to the Superfamily Helcionellacea in their classification of Cambrian molluscs. As noted elsewhere, the relationship between Rasetti's specimens and the Early Cambrian type species of *Scenella* is not certain and some authors have even suggested that *Scenella* is not a mollusc (Yochelson & Gil-Cid, 1984). Relationship of *Scenella* sp. undet. to the helcionelloids rather than to the tergomyans is preferred, however, suggesting that helcionelloids showing at least this relatively widely expanded morphology may also have had serially arranged muscle scars and gills (cf. Fig. 22). Supporters of the theory of Salvini-Plawen might argue that these multiple muscle scars in *Scenella* sp. undet. represent a secondary proliferation or that helcionelloids are derived from the tryblidiid lineage after the

development of serial gills and muscle scars characteristic of that group.

Rasetti (1954, plate 12, fig. 5; see Runnegar & Pojeta, 1985, fig. 11 and Fig. 45 herein) noted that the apex in his specimens of *Scenella* sp. undet. was excentric and he assumed that it was displaced to the anterior, following Knight (1952). His reconstruction of *Scenella* is therefore as a tergomyan. Rasetti noted that the pairs of scars were located mainly laterally to, and posterior of, this presumed anterior apex and he related the absence of scars from the sub-apical surface to the presence of the head. The scars are not of uniform size and display slight asymmetry in their distribution (similar asymmetry has been described in *Pilina* by Peel, 1977a).

Following the current reconstruction of helcionelloids as endogastric molluscs, the apex in *Scenella* sp. undet. is considered to lie posteriorly. Hence, the absence of scars from the sub-apical region probably does not reflect the position of the head, as suggested by Rasetti (1954), but the location of the mantle cavity.

The uncertainty concerning the systematic position of *Scenella* sp. undet., its relatively young geological age

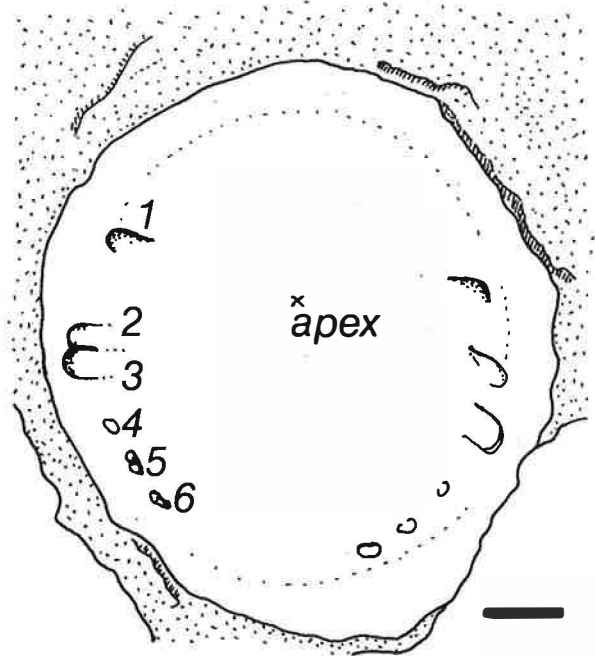


Fig. 45. *Scenella* sp. undet. of Rasetti (1954, pl. 12, fig. 5). Sketch of USNM 123374, Mt. Whyte Formation, Middle Cambrian, British Columbia, Canada, showing the excentric apex and the paired muscle scars. Rasetti interpreted the apex as anterior, restoring the specimen as a tergomyan, but the apex is here considered to be posterior and *Scenella* sp. undet. is interpreted as an unusually expanded helcionelloid. Bar is 2 mm.

(for a helcionelloid), its specialised morphology when compared to other members of the class, and the lack of confirming evidence of musculature from other helcionelloid taxa make *Scenella* sp. undet. an unreliable indicator of helcionelloid morphology. On the basis of the available evidence, however, it must be tentatively concluded that at least some helcionelloids possessed a serial arrangement of muscle scars and gills, although this need not be analogous with the condition in tryblidiid Tergomya.

### The earliest Cambrian molluscs

Runnegar & Pojeta (1985) pointed to the occurrence of cap-shaped, limpet-like, shells in the earliest Cambrian of China (cf. Qian & Bengtson, 1989) which they interpreted as primitive monoplacophorans similar to tryblidiid tergomyans such as *Neopilina*. These supposedly exogastric limpets were considered to represent a separate calcification event from that which produced the eight-valved polyplacophoran shell (fossils of which are first known from the Late Cambrian) and were not the result of some kind of 'morphological fusion' of a series of ancestral polyplacophoran-like valves into a single shell as otherwise has been postulated (Haszprunar, 1988, p. 402, seems to have misinterpreted this statement in claiming that Runnegar & Pojeta proposed derivation of polyplacophorans from monoplacophoran ancestors). The Meishucun limpets were interpreted by reference to *Scenella* sp. undet. of Rasetti (1954; see also Runnegar & Pojeta, 1985, fig. 11) in which the preserved multiple pairs of muscle scars were considered to indicate the anatomy of *Neopilina* (Fig. 45). As noted above, Runnegar & Pojeta (1985) derived helcionelloids from tryblidiid tergomyans by secondary reduction of the serially arranged gills, muscle scars and other organs, regarding the helcionelloids as the exogastric probable ancestor of the other shelled molluscs.

Inspection of the Meishucun limpet-like shells figured by Qian & Bengtson (1989) fails to produce morphologies which can be closely compared to either *Scenella* sp. undet. of Rasetti or to tryblidiid tergomyans. The most conspicuous elements in the Meishucun molluscan fauna are shells with a scaly or granular surface sculpture, and a variety of coiled shells.

### Scaly and granular shells

This group includes specimens 1–2 mm in length which are referred to *Purella* Missarzhevsky, 1974, *Xiadongoconus* Yu, 1979 and *Canopoconus* Jiang, 1982. As the shell sculpture implies, these shells are characterised by surface textures suggestive of formation by the co-

alescence of spicules and a similar process has been invoked by Bengtson (1990) to explain the formation of the anterior and posterior shells in articulated halkieriids described from the Lower Cambrian of Greenland by Conway Morris & Peel (1990; see Peel, 1991b, fig. 2). The Meishucun shells are similar to the halkieriid plates but can not be referred conclusively to a comparable scleritome. The resemblance to tergomyans is superficial and not convincing. In particular, *Xiadongoconus* preserves an unusual sub-apical fold or extension of the aperture which is more suggestive of a sclerite within a scleritome than of a single univalved molluscan shell.

Other cap-shaped forms from Meishucun, such as *Ocruranus* Liu, 1979 *Eohalobia* Jiang, 1982 and *Yunnano-pleura* Yu, 1987, may also represent elements within as yet unrecognised scleritomes, and have little to recommend them as tergomyans or even monoplacophorous molluscs. Some of these, together with co-occurring paracarinachitids, form the basis of the ill-conceived 'Meishucunian polyplacophorans' of Yu (1987, 1989, 1990; Haszprunar, 1988, p. 402), admirably rejected by Qian & Bengtson (1989; see Peel, 1991b).

### Helcionelliform shells

The second group of Meishucunian coiled shells includes apparent helcionelloids (length up to 2.5 mm) tentatively referred to *Bemella* Missarzhevsky, 1969 and an unusual shell (length up to 2.6 mm) called *Xianfengella* He & Yang, 1982, with similar planispiral coiling but showing a tendency to develop apertural angulations at the lateral margins of the sub-apical surface in some specimens (cf. Qian & Bengtson, 1989, fig. 78). In a speculative interpretation, these angulations may represent the locus of inhalant currents to a posterior mantle cavity located sub-apically; this would be in accordance with reconstruction as a helcionelloid since the apertural margin is also excavated to form a possible exhalant sinus beneath the apex. In other respects, however, *Xianfengella* resembles some members of the Class Stenothecoida but Qian & Bengtson (1989) were unable to support earlier claims that the genus was bivalved.

The most striking coiled shell from Meishucun is *Archaeospira* Yu, 1979 represented by three species (length up to about 2.8 mm), although Qian & Bengtson (1989) point out that species which they tentatively referred to *Bemella* are closely similar. *Archaeospira* shows a similar degree of coiling and the same coarse comarginal ornamentation as *Latouchella korobkovi* (Vostokova, 1962), from the earliest Cambrian of the Soviet Union, but appears to be distinguished from this

species (and other helcionelloids) by being anisometrically coiled. In standard orientation for a gastropod (which *Archaeospira* is not), with the aperture facing the viewer and the apex uppermost, *Archaeospira* is seen to be sinistrally coiled.

In all shell features apart from this anisometric coiling, *Archaeospira* is typically helcionelloid. The asymmetry can be interpreted, in similar fashion to the asymmetry in pelagiellids (cf. Runnegar & Pojeta, 1985, fig. 16B; see also Linsley & Kier, 1984), as slight torsion or reorientation of the shell in an essentially untorted mollusc. Pelagiellids are restored by these authors as exogastrically coiled, with the apex anterior, in accordance with their model for tergomyans and helcionelloids. *Archaeospira*, interpreted here as an endogastric helcionelloid, would have the apex located posteriorly. Its anisometric coiling allows formation of a sinus immediately adjacent to the coil (cf. Qian & Bengtson, 1989, fig. 73) and can be viewed as an adaptation to allow the tightly coiled shell to develop an essentially posterior emargination in the otherwise tangential aperture, with minimal interference from the earlier coiled portion of the shell. The relatively great width of the sinus suggests that its purpose was not solely related to improving mantle cavity structure (cf. the broad emargination in some sinuitid gastropods resulting from the development of lateral shield-like extensions to the aperture, Figs 18, 20). As in many pelagiellids, the great rate of whorl expansion produces a shell in which slight asymmetry in coiling has only a small effect on shell balance.

In summary, while helcionelloids are well represented in the earliest Cambrian Meishucun fauna, there are no cap-shaped shells which can be assigned to the Tergomya or considered to be their close ancestors with any degree of confidence. The scaly-ornamented *Purella* and *Canopoconus* have bilaterally symmetrical, slightly coiled, relatively high shells showing some similarity to helcionelloids and with a sub-apical emargination which might also support this assignment. It remains to be established, however, whether or not these shells are the univalved shells of molluscs.

Of course, earliest Cambrian molluscs and mollusc-like fossils are neither restricted to Meishucun nor to China. Several decades of research in the Soviet Union provided the classic studies of early Cambrian fossils (e.g., Rozanov *et al.*, 1969, translated as Raaben, 1981), most recently synthesised by Missarzhevsky (1989). A greater variety of shells is present than at Meishucun, with primitive bivalves, pelagiellids and coiled gastropod-like forms such as *Aldanella* Vostokova, 1962. Helcionelloids are conspicuous. As in the Meishucun faunas described by Qian & Bengtson (1989), convincing tergomyans are absent, but the relationships of many taxa are problematic.

Early Cambrian faunas from South Australia described by Bengtson *et al.* (1990) include a variety of helcionelloids, pelagiellids and onychochilids. Several internal moulds are assigned to *Proplina?* spp., a tryblidiid tergomyan genus, but the figured example shows little to commend this identification.

### Direction of coiling

Elucidation of the relationship between tergomyans and helcionelloids requires assessment of the importance assigned to differences in coiling direction in early molluscan evolution. As noted above, the Tergomya show considerable variation in the relationship between shell form and the pattern of muscle scars, with regard to the tergomyan and cyclomyan conditions (Figs 15–17), but exogastric coiling is clearly evident in almost all cases, including the pseudo-endogastric Hypseloconida. Within the gastropods, undoubtedly the most diverse molluscan group, endogastric coiling of the shell is also a persistent feature throughout their geological record. Features to suggest that some helcionelloids were not endogastric have not been observed and the form of shell coiling within the group as a whole appears to be uniform. Simple shells without apertural structures obviously yield little direct evidence of orientation, but this comment can be addressed to the shells of tergomyan and gastropod limpets with equal force and to most fossil shells without living relatives. Thus, the endogastrically coiled shell of the helcionelloids is believed to represent a fundamental feature of the class, representing a major difference from the exogastric shell of the Tergomya. Interestingly, the individual conical valves of early polyplacophorans show endogastric coiling, with the apex located posteriorly (cf. Runnegar *et al.*, 1979; Rolfe, 1981).

Interpretations of early mollusc groups such as the Pelagiellida and Onychochilida tend to assume exogastric coiling on account of their development within the conceptual framework that all molluscs of the 'monoplacophoran-grade' were exogastric (cf. Linsley & Kier, 1984; Runnegar & Pojeta, 1985). This assumption requires re-assessment in the light of the description of the helcionelloids as endogastric. The tight coiling of the pelagiellids implies only few gills, probably only a single pair, as interpreted in helcionelloids. This strong coiling, their presumed gill structure and early geological appearance promote the idea that pelagiellids may be closely related to the helcionelloids, and therefore endogastric, or represent a parallel development to the Helcionelloida. The circum-apertural structures interpreted as muscle scars by MacKinnon (1985, fig. 10) show some similarity to the folds in the sub-apical surface in *Protowenella* (Fig. 36).



The multi-whorled, earliest Cambrian, *Aldanella*, variously interpreted as a pelagiellid, the first gastropod (or both), a paragastropod or not even a mollusc, may also represent a branch from this early stock (cf. Yochelson, 1978, 1979; Linsley & Kier, 1984; Runnegar & Pojeta, 1985; Missarzhevsky, 1989). Ignoring the seductive, but probably fallacious, resemblance to younger gastropods, there is little in the shell form of *Aldanella* to preclude helcionelloid affinity. Coincidentally, the interpretations of *Aldanella* as gastropod or helcionelloid share endogastric coiling of the shell, although torsion is assumed to have taken place in the former but not in the latter.

## Discussion

The sparse evidence available from the Middle Cambrian *Scenella* sp. undet. suggests that at least some helcionelloids possessed a series of muscle scars and gills. Helcionelloids are conspicuous already from the earliest Cambrian and, following arguments inherent in the model of Salvini-Plawen (1985) concerning the secondary acquisition of multiple paired muscle scars in tryblidiid tergomyans, the paired muscle scars in *Scenella* sp. undet. might be an adaptation to the widely expanded shell form. This would involve at least three episodes of serialisation of muscle scars within early

molluscan phylogeny, namely in connection with the origin of the polyplacophorans, the tryblidiid tergomyans and the helcionelloids, unless these groups are related in a manner not foreseen by the model.

A more parsimonious approach would be to follow the thesis of Wingstrand (1985) and others that the serially arranged gills and muscle scars are a fundamental molluscan feature. In this case, secondary reduction in the number of gills becomes a feature of all the other molluscan groups. This theme forms the basis for a graphical representation of the relationships of the mollusc groups discussed in this paper (Fig. 46).

Unfortunately, from the point of view of this representation and Wingstrand's thesis, there is currently scant fossil evidence to support the idea that tryblidiid-like tergomyans with serially arranged muscles and gills were present in the Early Cambrian, as might be expected if they were ancestral to helcionelloids. Helcionelloids are conspicuous in collections of this age and there is a general absence of other cap-shaped shells which might be ancestral to the Tergomya and Helcionelloida. The limitations of the fossil record are legend, of course, but Wingstrand (1985) has rightly pointed out the necessity of rooting phylogenetic discussions in fossil material, rather than solely in the extract of the more than 500 000 000 years of molluscan evolution represented by the anatomy of the living fauna.



Fig. 46. A graphical representation of the relationship of mollusc groups. The central theme is that molluscs show some degree of original serial distribution of muscles, gills and other organs which is often subsequently lost or reduced. This serialisation, however, may have not been as fully expressed as in tryblidiid Tergomya and Polyplacophora. Halkieriids are interpreted as possible early molluscs, representing a parallel (or ancestral?) lineage to the Polyplacophora. Helcionelloida form an early endogastric branch (N) from which Rostroconchia, Scaphopoda and possibly Cephalopoda were derived. Pelagiellida and Onychochilida parallel the helcionelloid branch or may be derived from the helcionelloid lineage if interpreted as endogastric. Stenothecoida and Bivalvia represent unrelated adaptations to the bivalve form, paralleling the trend seen within the endogastric Rostroconchia; the relationship of the Stenothecoida to other molluscan groups is unclear, as is its presumed originally exogastric coiling (X).

Helcionelloids dominate the Early and Middle Cambrian with tergomyans first becoming conspicuous near the Middle Cambrian – Late Cambrian boundary, with the incoming of the Hypseloconida. Thus, the fossil record arguably promotes the idea that helcionelloids are ancestral to the Tergomya, or that they represent an early offshoot from the ancestral line leading to the Tergomya. Pelagiellids and onychochilids similarly may represent branches from this line. Supporters of the Salvini-Plawen model can cite this as evidence for the secondary acquisition of serial muscle scars and gills in tergomyans if it is accepted that only few gills are originally present in early helcionelloids (although see discussion of *Scenella* sp. undet. above) and pelagiellids; it is not unlikely that tryblidiid tergomyans, like gastropod limpets, modified their internal anatomy, including muscles and gills, in response to the limpetoid shell form. However, the change may be an increase in the degree of serialisation rather than the development of serialisation from an ancestor without serially arranged gills and muscle scars.

Applying the same geological measure, polyplacophorans should also be a relatively late development in molluscan evolution, a point of view lacking support in both the models of Salvini-Plawen (1985) and Wingstrand (1985), although favoured by Yochelson (1978, 1979). The recent description of the articulated halkieriid scleritome (Conway Morris & Peel, 1990; Peel, 1991b) provides a potential solution to this quandary if a role can be allocated to halkieriids in early molluscan evolution (Fig. 46). However, some of the problems associated with the lack of agreement between the various models and the fossil record can be resolved if formation of the dorsal shell by fusion of spicules occurred later in the tergomyan lineage than in the helcionelloid branch, in the same way that the Polyplacophora and possibly the halkieriids (cf. Bengtson, 1990; Peel, 1991b) may also represent separate calcification events (cf. Runnegar & Pojeta, 1985). This would imply that shell development in the Conchifera, widely considered to be a unifying character, took place on more than one occasion.

Early molluscan evolution, viewed in a palaeontological context, is more complex than the models expressed by Wingstrand (1985) and Salvini-Plawen (1985), although it must be stressed that their respective points of view lie in studies of molluscan groups which have survived to the present. Almost 30 years ago, Yochelson (1963; see also 1978, 1979) expressed the point of view that a radiation of molluscs in the Early Cambrian was eclipsed by more advanced forms such as the cephalopods and bivalves evolving near the Cambrian–Ordo-

vician boundary. Placement of the tryblidiid tergomyans (as Monoplacophora) within this second group clearly indicated that these were not considered to be the basic molluscan stock. It is this apparently late appearance (or calcification?) of both tryblidiid tergomyans and polyplacophorans (and also cephalopods and undisputed gastropods) in the fossil record, in this second burst of molluscan evolution, that currently causes difficulties for the models of Wingstrand (1985) and Salvini-Plawen (1985). The passing decades since Yochelson's paper in 1963 have seen a great increase in our knowledge of especially Early Cambrian molluscs and attempts such as those of Runnegar & Pojeta (1974) and Yu (1989, 1990) to extend familiar molluscan classes, such as the gastropods, bivalves, tergomyans and polyplacophorans, back through the Cambrian to these early times. So far, these efforts have met with varying degrees of success in an ancient world where the 'comfortable' molluscan morphologies of present seas comprise a minority in a spectrum of unfamiliar shapes and forms. Most of the early experiments, such as the helcionelloids discussed here, the pelagiellids and the stenotheccidans, were short lived, scarcely surviving the Cambrian, although other problematic lineages such as the Rostroconchia, Onychochilida and the Hyolitha survived through most or all of the Palaeozoic (the Hyolitha may or may not be molluscs, see discussion by Runnegar *et al.*, 1975; Marek & Yochelson, 1976; Sysoyev, 1984). As is often the case (cf. Bengtson, 1991; Ramsköld & Hou, 1991), new information from early Cambrian fossil groups creates initial confusion, generates opposing standpoints and requires digestion before it can be assimilated ultimately into a larger vista of evolving life. The study of early molluscs is no exception, but this is both the enigma and the fascination of the Cambrian.

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Institutions are denoted by the following abbreviations cited in the text: GGU, Geological Survey of Greenland, Copenhagen, Denmark; GSC, Geological Survey of Canada, Ottawa, Canada; LO, Palaeontological type collections of the University of Lund, Sweden. MMH and MGUH, Geological Museum, University of Copenhagen, Denmark; NMW, National Museum of Wales, Cardiff, Wales, U.K.; OUM, Oxford University Museum, U.K.; P2 L, Department of Palaeontology,

National Museum of Prague, Czechoslovakia; SM, Sedgwick Museum, Cambridge, U.K.; YPM, Yale Peabody Museum, New Haven, Conn., U.S.A.; USNM, U.S. National Museum of Natural History, Washington D.C., U.S.A.; their staffs are acknowledged for the loan of specimens in their care.

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## References

- Aksarina, N. A. 1968: [New data on the geology and guide fossils of western Siberia] 3, 77–86. Tomsk: Univ. Tomsk, [in Russian].
- Allen, J. A. 1985: The recent Bivalvia: their form and function. In Trueman, E. R. & Clarke, M. R. (ed.) *The Mollusca 10. Evolution*, 337–403. Orlando: Academic Press.
- Bengtson, S. 1990: The solution to a jigsaw puzzle. *Nature* **345**, 765–766.
- Bengtson, S. 1991: Oddballs from the Cambrian start to get even. *Nature*, **351**, 184–185.
- Bengtson, S., Conway Morris, S., Cooper, B. J., Jell, P. A. & Runnegar, B. N. 1990: Early Cambrian fossils from South Australia. *Mem. Australas. Assoc. Palaeontol.* **9**, 364 pp.
- Berg-Madsen, V. 1987: *Tuarangia* from Bornholm (Denmark) and similarities in Baltoscandian and Australasian late Middle Cambrian faunas. *Alcheringa* **11**, 245–259.
- Berg-Madsen, V., & Peel, J. S. 1978: Middle Cambrian monoplacophorans from Bornholm and Australia, and the systematic position of the bellerophonitiform molluscs. *Lethaia* **11**, 113–125.
- Berg-Madsen, V., & Peel, J. S. 1987: *Yochelcionella* (Mollusca) from the late Middle Cambrian of Bornholm, Denmark. *Bull. Geol. Soc. Denmark* **36**, 259–261.
- Branch, G. M. 1985: Limpets: evolution and adaptation. In Trueman, E. R. & Clarke, M. R. (ed.) *The Mollusca 10. Evolution*, 187–220. Orlando: Academic Press.
- Brasier, M. D. 1975: An outline history of seagrass communities. *Palaeontology* **18**, 681–702.
- Chen Jun-Yuan & Teichert, C. 1983: Cambrian cephalopods. *Geology* **11**, 647–650.
- Cobbold, E. S. 1935: Cambrian faunas from Hérault, France. *Ann. Mag. Nat. Hist.* **16**, 25–49.
- Conway Morris, S. & Peel, J. S. 1990: Articulated halkieriids from the Lower Cambrian of north Greenland. *Nature* **345**, 802–805.
- Doguzhaeva, L. A. 1981: [Sinus in cap-shaped monoplacophorans]. *Doklady Akad. Nauk SSSR* 1981, 208–211. [in Russian].
- Dzik, J. 1981: Origin of the Cephalopoda. *Acta Palaeont. Pol.* **26**, 161–191.
- Dzik, J. 1991: Is fossil evidence consistent with traditional views of the early metazoan phylogeny? In Simonetta, A. M. & Conway Morris, S. (ed.) *The early evolution of Metazoa and the significance of problematic taxa*. 47–56. Cambridge: Cambridge Univ. Press and Univ. Camerino.
- Fritz, W. H. & Yochelson, E. L. 1988: The status of *Salterella* as a Lower Cambrian index fossil. *Can. J. Earth Sci.* **25**, 403–416.
- Geyer, G. 1986: Mittelkambrische Mollusken aus Marokko und Spanien. *Senckenbergiana lethaea* **67**, 55–118.
- Harper, J. A. & Rollins, H. B. 1982: Recognition of Monoplacophora and Gastropoda in the fossil record: a functional morphological look at the bellerophonit controversy. *Proc. III N. Am. Paleont. Conv.* **1**, 227–232.
- Haszprunar, G. 1988: On the origin and evolution of major gastropod groups, with special reference to the Streptoneura. *Jour. Molluscan Stud.* **54**, 367–441.
- Horny, R. J. 1963a: On the systematic position of cyrtoneuloids (Mollusca). *Časopis národ. Mus. Praze* **132**, 90–94.
- Horny, R. J. 1963b: Lower Palaeozoic Monoplacophora and patellid Gastropoda (Mollusca) of Bohemia. *Sbor. Ústred. Úst. Geol.* **38**, 7–83.
- Horny, R. J. 1963c: New finds of Silurian Drahomirinae (Monoplacophora) in Bohemia and notes on their ontogeny and bionomy. *Čas. národ. Mus. Praze* **132**, 79–89.
- Horny, R. J. 1965a: *Cyrtolites* Conrad, 1838 and its position among the Monoplacophora (Mollusca). *Sbor. národ. Mus. Praze* **21**, 2, 57–70.
- Horny, R. J. 1965b: On the systematic position of *Cyrtolites* Conrad, 1838 (Mollusca). *Čas. národ. Mus. Praze* **134**, 8–10.
- Horny, R. J. 1970: Muscle scars and outer shell sculpture of *Retipilina* Horny (Mollusca, Monoplacophora). *Čas. národ. Mus. Praze* **137**, 9–16.
- Horny, R. J. 1990: Muscle scars in Sinuites (Strangulites) (Mollusca) from the Ordovician of Bohemia. *Čas. národ. Mus. Praze* **155** (for 1986), 109–118.
- Horny, R. J. in press a: Shell morphology and muscle scars of *Sinuitopsis neglecta* Perner (Mollusca, Monoplacophora). *Čas. národ. Mus. Praze*.
- Horny, R. J. in press b: Muscle scars in Sinuites (Mollusca, Gastropoda) from the Lower Ordovician of Bohemia. *Čas. národ. Mus. Praze*.
- Jell, P. A. 1978: *Mollusca. McGraw Hill yearbook science and technology*, 1976, 269–271. New York: McGraw Hill.
- Kerber, M. 1988: Mikrofossilien aus Unterkambrischen Gesteinen der Montagne Noire, Frankreich. *Palaeontographica A* **202**, 127–203.
- Knight, J. B. 1947: Bellerophonit muscle scars. *Jour. Paleont.* **21**, 264–267.
- Knight, J. B. 1952: Primitive fossil gastropods and their bearing on gastropod classification. *Smithson. Misc. Colls* **114**, 13, 1–55.
- Knight, J. B., & Yochelson, E. L. 1960: Monoplacophora. In Moore, R. C. (ed.) *Treatise on Invertebrate Paleontology, 1, Mollusca 1*, 177–184. Lawrence: Univ. Kansas Press and Geol. Soc. Am.
- Knight, J. B., Cox, L. R., Keen, A. M., Batten, R. L., Yochelson, E. L. & Robertson, R. 1960: Systematic descriptions. In Moore, R. C. (ed.) *Treatise on Invertebrate Paleontology, 1, Mollusca 1*, 1169–1310. Lawrence: Univ. Kansas Press and Geol. Soc. Am.
- Kobayashi, T. 1987: The ancestry of the Cephalopoda. *Proc. Japan Acad.* **63**, ser. B, 135–138.

- Koken, E. & Perner, L. 1925: Die Gastropoden des baltischen Untersilurs. *Mém. Acad. Sci. Russie, Leningrad* **37**, 1–326.
- Krasilova, I. N. 1987: The oldest representatives of the bivalve mollusks. *Paleont. Jour.* **1987**, **4**, 21–26.
- Landing, E. 1989: Paleocology and distribution of the Early Cambrian rostroconch *Watsonella crosbyi* Grabau. *Jour. Paleont.* **63**, 566–573.
- Lauterbach, K. E. 1983a: Gedanken zur Entstehung der mehrfach paarigen Exkretionsorgane von *Neopilina* (Mollusca, Conchifera). *Zeitschr. zool. Syst. & Evolutionsforsch.* **21**, 38–52.
- Lauterbach, K. E. 1983b: Erörterungen zur Stammesgeschichte der Mollusca, insbesondere der Conchifera. *Zeitschr. zool. Syst. & Evolutionsforsch.* **21**, 201–216.
- Lemche, H. 1957: A new living deep-sea mollusc of the Cambro-Devonian Class Monoplacophora. *Nature* **179**, 413–416.
- Lemche, H. & Wingstrand, K. G. 1959: The anatomy of *Neopilina galathea* Lemche, 1957. *Galathea Rept* **3**, 9–71.
- Lindström, G. 1884: On the Silurian Gastropoda and Pteropoda of Gotland. *K. svenska Vetenskaps Akad. Handl.* **19**, 250 pp.
- Linsley, R. M. 1977: Some 'laws' of gastropod shell form. *Paleobiology* **3**, 196–206.
- Linsley, R. M. 1978: Shell form and evolution of the gastropods. *Amer. Sci.* **66**, 432–441.
- Linsley, R. M. & Kier, W. M. 1984: The Paragastropoda: a proposal for a new class of Paleozoic Mollusca. *Malacologia* **25**, 241–254.
- Linsley, R. M. & Peel, J. S. 1983: Gonad pouches in a new clam-like monoplacophoran from the Silurian of Sweden. *Lethaia* **16**, 273–280.
- MacKinnon, D. I. 1982: *Tuarangia paparua* n. gen. and n. sp., a late Middle Cambrian pelecypod from New Zealand. *Jour. Paleont.* **56**, 589–598.
- MacKinnon, D. I. 1985: New Zealand late Middle Cambrian molluscs and the origin of Rostroconchia and Bivalvia. *Alcheringa* **9**, 65–81.
- Marek, L. & Yochelson, E. L. 1976: Aspects of the biology of the Hyolitha (Mollusca). *Lethaia* **9**, 65–82.
- Missarzhevsky, V. V. 1989: [Oldest skeletal fossils and stratigraphy of Precambrian and Cambrian boundary beds]. *Trudy Ordena Trydov. Kras. Zhameni geol. Inst. Akad. Nauk SSSR* **443**, 237 pp. [in Russian].
- Missarzhevsky, V. V. & Mambetov, A. J. 1981: [Stratigraphy and fauna of Cambrian and Precambrian boundary beds of Maly Karatau]. *Trudy Ordena Trydov. Kras. Zhameni geol. Inst. Akad. Nauk SSSR* **326**, 92 pp. [in Russian].
- Moore, R. C. 1941: Upper Pennsylvanian gastropods from Kansas. *Bull. Kansas geol. Surv.* **38**, 121–163.
- Morton, J. E. 1979: *Molluscs* (5th edition). London: Hutchinson, 264 pp.
- Müller, K. J. 1975: 'Heraultia' varenalensis COBBOLD (Crustacea) aus dem unteren Kambrium, der älteste Fall von Geschlechtsdimorphismus. *Paläont. Zeitschr.* **49**, 168–180.
- Peel, J. S. 1972: Observations on some Lower Palaeozoic tremantiform Bellerophontacea (Gastropoda) from North America. *Palaentology* **15**, 412–422.
- Peel, J. S. 1974: Systematics, ontogeny and functional morphology of Silurian trilobed bellerophontacean gastropods. *Bull. geol. Soc. Denmark* **23**, 231–264.
- Peel, J. S. 1976: Musculature and systematic position of *Megalomphala taenia* (Bellerophontacea, Gastropoda) from the Silurian of Gotland. *Bull. geol. Soc. Denmark* **25**, 49–55.
- Peel, J. S. 1977a: Relationship and internal structure of a new *Pilina* (Monoplacophora) from the Late Ordovician of Oklahoma. *Jour. Paleont.* **51**, 116–122.
- Peel, J. S. 1977b: Systematics and palaeontology of the Silurian gastropods of the Arisaig Group, Nova Scotia. *Biol. Skr. Dansk Videnskabs. Selsk.* **21**(2), 89 pp.
- Peel, J. S. 1978: Faunal succession and mode of life of Silurian gastropods in the Arisaig Group, Nova Scotia. *Palaentology* **21**, 285–306.
- Peel, J. S. 1979: *Protowenella* (Mollusca) from the Cambrian of Greenland. *Rapp. Grønlands geol. Unders.* **91**, 92 only.
- Peel, J. S. 1980a: A new Silurian retractile monoplacophoran and the origin of the gastropods. *Proc. Geol. Assoc.* **91**, 91–97.
- Peel, J. S. 1980b: Yochelcionellids from the Early and Late Cambrian of North Greenland. *Rapp. Grønlands geol. Unders.* **101**, 44 only.
- Peel, J. S. 1982: Muscle scars in *Bellerophon reticostatus* (Mollusca) from the Carboniferous of Ireland. *Jour. Paleont.* **56**, 1307–1310.
- Peel, J. S. 1984: Autecology of Silurian gastropods and monoplacophorans. *Spec. Pap. Palaeontology* **32**, 165–182.
- Peel, J. S. 1987: Class Gastropoda. In Boardman, R. S., Cheetham, A. H. & Rowell, A. J. (ed.) *Fossil Invertebrates*, 304–329. Palo Alto, Oxford, London: Blackwell Scientific Publications.
- Peel, J. S. 1988a: *Yochelcionella americana* (Mollusca) from the Lower Cambrian of Newfoundland. *Can. J. Earth Sci.* **24**, 2328–2330.
- Peel, J. S. 1988b: Molluscs of the Holm Dal Formation (late Middle Cambrian), central North Greenland. *Meddr Grønland Geosci.* **20**, 145–168.
- Peel, J. S. 1989: A Lower Cambrian *Eotebenna* (Mollusca) from Arctic North America. *Can. J. Earth Sci.* **26**, 1501–1503.
- Peel, J. S. 1990a: Morphology and systematic position of *Tryblidium Canadense* Whiteaves, 1884 (Mollusca) from the Silurian of North America. *Bull. geol. Soc. Denmark* **38**, 43–51.
- Peel, J. S. 1990b: Studying the early history of life in Greenland. *Rapp. Grønlands geol. Unders.* **148**, 54–56.
- Peel, J. S. 1991a: Functional morphology of the Class Helcionelloida nov., and the early evolution of the Mollusca. In Simonetta, A. & Conway Morris, S. (ed.) *The early evolution of Metazoa and the significance of problematic taxa*, 157–177. Cambridge: Cambridge Univ. Press and Univ. Camerino.
- Peel, J. S. 1991b: Introduction. Articulated halkieriids and microchitons. *Bull. Grønlands geol. Unders.* **161** (this volume).
- Peel, J. S. 1991c: Salpingostomatiform and related bellerophontacean gastropods from Greenland and the Baltic region. *Bull. Grønlands geol. Unders.* **161** (this volume).

- Peel, J. S. & Berg-Madsen, V. 1988: A new salterellid (Phylum Agmata) from the upper Middle Cambrian of Denmark. *Bull. geol. Soc. Denmark* **37**, 75–82.
- Peel, J. S. & Yochelson, E. L. 1982: A review of *Salterella* (Phylum Agmata) from the Lower Cambrian in Greenland and Mexico. *Rapp. Grønlands geol. Unders.* **108**, 31–39.
- Peel, J. S. & Yochelson, E. L. 1987: New information on *Oelandia* (Mollusca) from the Middle Cambrian of Sweden. *Bull. geol. Soc. Denmark* **36**, 263–273.
- Pei Fang 1985: First discovery of *Yochelcionella* from the Lower Cambrian of China and its significance. *Acta Micropalaeont. Sinica* **2**, 395–400.
- Pojeta, J., Jr. 1980: Molluscan phylogeny. *Tulane Studies in Geol. Paleont.* **16**, 55–80.
- Pojeta, J., Jr. 1987: Class Rostroconchia. In Boardman, R. S., Cheetham, A. H. & Rowell, A. J. (ed.) *Fossil invertebrates*, 358–380. Palo Alto, Oxford, London: Blackwell Scientific Publications.
- Pojeta, J., Jr. & Runnegar, B. 1976: The paleontology of rostroconch molluscs and the early history of the Phylum Mollusca. [*U. S.*] *geol. Surv. Prof. Pap.* **968**, 88 pp.
- Pojeta, J., Jr. & Runnegar, B. 1979: *Rhytidentalium kentuckyensis*, a new genus and species of Ordovician scaphopod, and the early history of scaphopod mollusks. *Jour. Paleont.* **53**, 530–541.
- Pojeta, J., Jr., Gilbert-Tomlinson, J. & Shergold, J. H. 1977: Cambrian and Ordovician rostroconch molluscs from northern Australia. *Bull. Bur. Mines Min. Res., Geol. Geophys. (Austr.)* **171**, 1–54.
- Poulsen, C. 1927: The Cambrian, Ozarkian and Canadian faunas of Northwest Greenland. *Meddr Grønland* **70**(1), 2, 233–343.
- Poulsen, C. 1932: The Lower Cambrian faunas of East Greenland. *Meddr Grønland* **87**(6), 66 pp.
- Poulsen, C. 1958: Contribution to the palaeontology of the Lower Cambrian Wulff River Formation. *Meddr Grønland* **162**(2), 25 pp.
- Qian Yi & Bengtson, S. 1989: Palaeontology and biostratigraphy of the Early Cambrian Meishucunian Stage in Yunnan Province, South China. *Fossils and Strata* **24**, 156 pp.
- Raaben, M. E. (ed.) 1981: *The Tommotian Stage and the Cambrian lower boundary problem*, 359 pp. New Delhi: Amerind Publ. Co. [English translation of Rozanov *et al.*, 1969].
- Ramsköld, L. & Hou Xianguang 1991: New early Cambrian animal and onychophoran affinities of enigmatic metazoans. *Nature* **351**, 225–228.
- Rasetti, F. 1954: Internal shell structures in the Middle Cambrian gastropod *Scenella* and the problematic genus *Stenothecoides*. *Jour. Paleont.* **28**, 59–66.
- Robison, R. A. 1964: Late Middle Cambrian faunas from western Utah. *Jour. Paleont.* **38**, 510–566.
- Rolfe, W. D. I. 1981: *Septemchiton* – a misnomer. *Jour. Paleont.* **55**, 675–678.
- Rollins, H. B. 1969: The taxonomic position of *Cyrtionella mitella* (Hall) (Mollusca, Monoplacophora). *Jour. Paleont.* **43**, 136–140.
- Rollins, H. B. & Batten, R. L. 1968: A sinus-bearing monoplacophoran and its role in the classification of primitive molluscs. *Paleont.* **11**, 132–140.
- Rozanov, A. Yu., Missarzhevsky, V. V., Volkova, N. A., Voronova, L. G., Krylov, I. N., Keller, B. M., Korolyuk, I. K., Lenzion, K., Michniak, R., Pykhova, N. G. & Sidorov, A. D. 1969: [The Tommotian Stage and the problem of the lower boundary of the Cambrian]. *Trudy Geologicheskogo Inst. Akad. Nauk SSSR* **296**, 380 pp. [in Russian., see Raaben (1981) for the English translation].
- Rozov, S. N. 1968: A new genus of Late Cambrian mollusks of the Class Monoplacophora (southern part of the Siberian platform). *Doklady Akad. Nauk SSSR* **183**, 214–217. [translated from Novy rod pozdnemebriyskikh mollyuskov iz klassa monoplakofor (yuzhnaya chast' Sibirskoy platformy). *Doklady Akad. Nauk SSSR* **183**, 1427–1430].
- Rozov, S. N. 1969: Morphology and terminology of Monoplacophora. *Paleont. Jour.* 1969, **4**, 548–551.
- Rozov, S. N. 1975: A new order of the Monoplacophora. *Paleont. Jour.* 1975, **1**, 39–43.
- Runnegar, B. 1978: Origin and evolution of the Class Rostroconchia. *Phil. Trans. R. Soc. London* **B 284**, 319–333.
- Runnegar, B. 1981: Muscle scars, shell form and torsion in Cambrian and Ordovician univalved molluscs. *Lethaia* **14**, 311–322.
- Runnegar, B. 1983: Molluscan phylogeny revisited. *Mem. Assoc. Australas. Palaeont.* **1**, 121–144.
- Runnegar, B. 1985: Shell microstructure of Cambrian molluscs replicated by phosphate. *Alcheringa* **9**, 245–257.
- Runnegar, B., & Jell, P. A. 1976: Australian Middle Cambrian molluscs and their bearing on early molluscan evolution. *Alcheringa* **1**, 109–138.
- Runnegar, B., & Jell, P. A. 1980: Australian Middle Cambrian molluscs: corrections and additions. *Alcheringa* **4**, 111–113.
- Runnegar, B., & Pojeta, J., Jr. 1974: Molluscan phylogeny: the paleontological viewpoint. *Science* **186**, 311–317.
- Runnegar, B., & Pojeta, J., Jr. 1980: The monoplacophoran mollusk *Yochelcionella* identified from the Lower Cambrian of Pennsylvania. *Jour. Paleont.* **54**, 635–636.
- Runnegar, B., & Pojeta, J., Jr. 1985: Origin and diversification of the Mollusca. In Trueman, E. R. & Clarke, M. R. (ed.) *The Mollusca 10, Evolution*, 1–57. Orlando: Academic Press.
- Runnegar, B., Pojeta, J., Morris, N. J., Taylor, J. D. & McClung, G. 1975: Biology of the Mollusca. *Lethaia* **8**, 181–191.
- Runnegar, B., Pojeta, J., Taylor, M. E. & Collins, D. 1979: New species of the Cambrian and Ordovician chitons *Matthevia* and *Chelodes* from Wisconsin and Queensland: evidence for the early history of polyplacophoran mollusks. *Jour. Paleont.* **53**, 1374–1394.
- Salvini-Plawen, L. von 1980: A reconsideration of systematics in Mollusca (phylogeny and higher classification). *Malacologia* **19**, 247–278.
- Salvini-Plawen, L. von 1981: On the origin and evolution of the Mollusca. *Origine dei grandi Phyla dei Metazoi, Atti dei Convegni Lincei, Accad. Naz. dei Lincei* **49**, 235–293.

- Salvini-Plawen, L. von 1985: Early evolution and the primitive groups. In Trueman, E. R. & Clarke, M. R. (ed.) *The Mollusca 10, Evolution*, 59–150. Orlando: Academic Press.
- Schmidt, F. 1888: Über ein neuentdeckte unterkambrische Fauna. *Mém. Acad. Sci., St. Petersbourg*, 7 ser. **36**, 1–29.
- Signor, P. W., & Kat, P. W. 1984: Functional significance of columellar folds in turritelliform gastropods. *Jour. Paleont.* **58**, 210–216.
- Smith, A. G. 1960: Amphineura. In Moore, R. C. (ed.) *Treatise on Invertebrate Paleontology, I, Mollusca 1*, 141–176. Lawrence: Univ. Kansas Press and Geol. Soc. Amer.
- Stanley, S. M. 1975: Adaptive themes in the evolution of Bivalvia (Mollusca). *Ann. Rev. Earth Planet. Sci.* **3**, 361–385.
- Starobogatov, Ya. I. 1970: Systematics of Early Paleozoic Monoplacophora. *Paleont. Jour.* **1970**, **3**, 293–302.
- Stasek, C. R. 1972: The molluscan framework. In Florkin, M. & Scheer, B. T. (ed.) *Chemical Zoology*, 1–44. New York: Academic Press.
- Stinchcomb, B. L. 1980: New information on Late Cambrian Monoplacophora *Hypseloconus* and *Shelbyoceras* (Mollusca). *Jour. Paleont.* **54**, 45–49.
- Stinchcomb, B. L. 1986: New Monoplacophora (Mollusca) from Late Cambrian and Early Ordovician of Missouri. *Jour. Paleont.* **60**, 606–626.
- Stinchcomb, B. L. & Echols, D. J. 1966: Missouri Upper Cambrian Monoplacophora previously considered cephalopods. *Jour. Paleont.* **40**, 647–654.
- Swedmark, B. 1968: The biology of interstitial mollusca. *Symp. Zool. Soc. London* **22**, 135–149.
- Sysoyev, V. A. 1984: The morphology and systematic position of the hyoliths. *Paleont. Jour.* **1984**, **2**, 1–10.
- Teichert, C. 1988: Main features of cephalopod evolution. In Clarke, M. R. & Trueman, E. R. (ed.) *The Mollusca 12, Palaeontology and neontology of cephalopods*, 11–75. Orlando: Academic Press.
- Vermeij, G. J. 1975: Evolution and distribution of left-handed and planispiral coiling in snails. *Nature* **254**, 419–420.
- Vermeij, G. J. & Dudley, E. C. 1985: Distribution of adaptations: a comparison between the functional shell morphology of freshwater and marine pelecypods. In Trueman, E. R. & Clarke, M. R. (ed.) *The Mollusca 10, Evolution*, 461–478. Orlando: Academic Press.
- Voronova, L. G., Drosdova, N. A., Esakova, N. B., Zhegallo, E. A., Zhuravlev, A. Yu., Rozanov, A. Yu., Sayutina, T. A. & Ushatinskaya, G. T. 1987: [Lower Cambrian fossils of the MacKenzie Mountains (Canada)]. *Trudy Paleont. Inst. Akad. Nauk SSSR* **224**, 88 pp. [in Russian].
- Wade, M. 1988: Nautiloids and their descendants: cephalopod classification in 1986. *Mem. New Mexico Bur. Mines Min. Res.* **44**, 15–25.
- Warmke, G. L. & Almodovar, L. R. 1963: Some associations of marine molluscs and algae in Puerto Rico. *Malacologia* **1**, 163–177.
- Webers, G. F. & Yochelson, E. L. 1989: Late Cambrian molluscan faunas and the origin of the Cephalopoda. In Crame, J. A. (ed.) *Origins and evolution of the Antarctic biota. Spec. Publ. geol. Soc. London* **47**, 29–42.
- Webers, G. F., Pojeta, J., Jr., & Yochelson, E. L. in press: Cambrian Mollusca from the Minaret Formation, Ellsworth Mountains, West Antarctica. In Webers, G. F., Craddock C. & Spletstoeser, J. (ed.) *The geology and paleontology of the Ellsworth Mountains, west Antarctica. Mem. geol. Soc. Amer.* **170**.
- Wenz, W. 1940: Ursprung und frühe Stammesgeschichte der Gastropoden. *Arch. Molluskenk.* **72**, 1–10.
- Westergård, A. H. 1936: *Paradoxides oelandicus* beds of Öland with the account of a diamond boring through the Cambrian at Mossberga. *Sver. geol. Unders. C*, **394**, 66 pp.
- Wingstrand, K. G. 1985: On the anatomy and relationships of Recent Monoplacophora. *Galathaea Rept* **16**, 7–94.
- Yochelson, E. L. 1963: Problems of the early history of the Mollusca. *Proc. XVI Internat. Congr. Zool. Washington D.C.* **2**, 187 only.
- Yochelson, E. L. 1967: Quo vadis, *Bellerophon*? In Teichert, C. & Yochelson, E. L. (ed.) *Essays in paleontology and stratigraphy*, 141–161. Lawrence: Univ. Kansas Press.
- Yochelson, E. L. 1968: Stenothecoida, a proposed new class of Cambrian Mollusca. *Abstr. Internat. Paleont. Union, Prague, Czechoslovakia*, 34 only.
- Yochelson, E. L. 1969: Stenothecoida, a proposed new class of Cambrian Mollusca. *Lethaia* **2**, 49–62.
- Yochelson, E. L. 1970: The Early Cambrian fossil *Salterella conulata* Clark in eastern North America. [U.S.] *Geol. Surv. Prof. Pap.* **683-B**, B1–10.
- Yochelson, E. L. 1977: Agmata, a proposed extinct phylum of Early Cambrian age. *Jour. Paleont.* **51**, 437–454.
- Yochelson, E. L. 1978: An alternative approach to the interpretation of the phylogeny of ancient mollusks. *Malacologia* **17**, 165–191.
- Yochelson, E. L. 1979: Early radiation of Mollusca and mollusc-like groups. In House, M. R. (ed.) *The origin of the major invertebrate groups*, 323–358. New York: Academic Press.
- Yochelson, E. L. 1981: A survey of *Salterella* (Phylum Agmata). *U.S. Geol. Survey Open-file Report* **81-743**, 244–248.
- Yochelson, E. L. 1988: A new genus of Patellacea (Gastropoda) from the Middle Ordovician of Utah: the oldest known example of the superfamily. *Mem. New Mexico Bur. Mines Min. Res.* **44**, 195–200.
- Yochelson, E. L. & Gil-Cid, D. 1984: Reevaluation of the systematic position of *Scenella*. *Lethaia* **17**, 331–340.
- Yochelson, E. L. & Nuelle, L. M. 1985: *Strepsodiscus* (Gastropoda) in the Late Cambrian of Missouri. *Jour. Paleont.* **59**, 733–740.
- Yochelson, E. L. & Peel, J. S. 1980: Early Cambrian *Salterella* from North-west Greenland. *Rapp. Grønlands geol. Unders.* **101**, 29–36.
- Yochelson, E. L. & Stanley, G. D. 1981: An early Ordovician patelliform gastropod, *Palaeophacmaea*, reinterpreted as a coelenterate. *Lethaia* **15**, 323–330.
- Yochelson, E. L., Flower, R. H., & Webers, G. F. 1973: The bearing of the new Late Cambrian monoplacophoran genus *Knighthoconus* upon the origin of the Cephalopoda. *Lethaia* **6**, 275–310.
- Yonge, C. M. 1960: General characters of Mollusca. In Moore,

- R. C. (ed.) *Treatise on Invertebrate Paleontology I, Mollusca I*, I3-I36, Lawrence: Univ. Kansas Press and Geol. Soc. Amer.
- Yonge, C. M., & Thompson, T. E. 1976: *Living marine Molluscs*. London: Collins, 288 pp.
- Yu Wen 1987: Yangtze micromolluscan fauna in Yangtze Region of China, with notes on Precambrian-Cambrian boundary. *Stratigraphy and palaeontology of systematic boundaries in China. Precambrian-Cambrian Boundary (1)*, 19-344. Nanjing: Nanjing Univ. Publ. House.
- Yu Wen 1989: Did the shelled mollusks evolve from univalved to multivalved forms or vice versa? *Developments in Geoscience. Contribution to 28th International Geological Congress, 1989, Washington D. C., U.S.A.*, 235-244. Chinese Acad. Sci., Beijing: Science Press.
- Yu Wen 1990: The first radiation of shelled molluscs. *Palaeontologia cathayana* 5, 139-170.
- Yu Wen & Ning Hui 1985: Two Cambrian monoplacophorans from Borohore, Xinjiang. *Acta Palaeont. Sin.* 24, 47-50.