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The Functional Morphology of the Cambrian Univalved Mollusks—Helcionellids. 1

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Abstract—The soft-body anatomy of helcionellids is reconstructed on the basis of a morphofunctional analyses of their shells. Evidently, two systems for the internal organization of helcionellids are possible: the first corresponds to that of the gastropodian class; the second, to that of the monoplacophorian.

INTRODUCTION

Intensive study of the Cambrian fauna and stratigraphy during recent decades shows us a diverse biota of this geological period. Mollusks are well represented among the numerous newly described taxa in a variety of groups. As a result, a significant number of scientific papers were devoted to the problems on the morphology and evolution of the Cambrian mollusks, including their systematics (Rozanov *et al.*, 1969; Starobogatov, 1970; Runnegar and Pojeta, 1974; Runnegar and Jell, 1976, 1980; Pojeta and Runnegar, 1976; Yochelson, 1978; Minichev and Starobogatov, 1979; Runnegar, 1981, 1983, 1985; Golikov and Starobogatov, 1988; Missarzhevsky, 1989; Peel, 1991a, 1991b; Geyer, 1994; Bandel, 1997). In spite of numerous studies, the systematics of the phylum especially that of the lower taxa is still uncertain. The view of some specialists on the systematics of the different groups of mollusks or indeed of the whole phylum may vary or even sometimes be contradictory. Generally, it can be explained by the specificity of the paleontological material: the mollusks shells (or often only their internal molds) carry only a small part of the features that are used by zoologists in the systematics of extant mollusks. Paleomalacologists do not have the opportunity to study such structures, as the radula, digestive, excretory and reproductive systematics, etc., which are very important in the systematic of recent organisms. Thus, functional analyses based on shell morphology plays an important role in the study of Cambrian mollusks. By analyzing the different shell structures, it is possible to reconstruct some details of the animals soft body parts and to suggest ecological peculiarities. In this way it is possible to obtain data that may shed light on systematic problems.

Clearly, this may give rise to a number of different points of view on the anatomy of the organisms studied, and consequently, on their systematics. Possibly, the most rational approach in such cases is the choice of those morphofunctional interpretations, which, firstly, are the most simple, and secondly, supported by the

maximum number of analogies and the least number of contradictions with recent animals.

Helcionellids were common elements of the malacofauna in the Early–Middle Cambrian and achieved a rather high taxonomic diversity in comparison with other molluskan groups. The shell morphology of these mollusks and attempts at reconstruction of their internal soft-body parts and gross anatomy are given below.

The mollusks illustrated on Plate 6 come from the Atdabanian–Botomian of the South Australia, the material is housed in the Paleontological Institute, Russian Academy of Sciences, collection no. 4664.

DISCUSSION

Functional Morphology of Internal Folds in Helcionellid Shells

The internal surface on the sub-apical area of the shells of some Cambrian mollusks show peculiar elements resembling distinct longitudinal ridge-like folds. The folds begins from the apical region and extends towards the aperture (Fig. 1). Such folds were first discovered by Robison (1964, pl. 92, figs. 11–17) in the shell of "*Helcionella*" *arguta* Resser, 1939 from the Middle Cambrian of Utah. Latter, the folds were observed by Runnegar and P.A. Jell (1976, pl. 9c, figs. 1–10, pl. 9d, figs. 11–13) in the following helcionellid species from the Middle Cambrian of Australia: *Helcionella terraustralis* Runnegar et Jell, 1976, *Helcionella* *sp.* (pl. 10b, fig. 10), "*Latouchella*" *accordionata*¹ Runnegar and Jell, 1976 (pl. 10c, figs. 1–18), "*L.*" *merino* Runnegar et Jell, 1976 (pl. 9d, figs. 1–10; Peel, 1991a, fig. 23; Peel, 1991b, fig. 12).

¹ The recent restudy of the material on *Latouchella* (Gubanov and Peel, 1998) revealed, that the type species of the genus *L. costata* Cobbold, 1921 is not planispirally coiled, but slightly asymmetrical and can be considered as sinistral. Thus, all planispiral forms previously referred to the genus *Latouchella* should be excluded from it. Hence, in the present paper the species of *Latouchella* are placed arbitrarily in this genus, while the generic name is marked by a comma.

Then Peel (1991a, fig. 13; 1991b, fig. 24) found similar structures among several species of "*Latouchella*" from the Middle Cambrian of Greenland. The number of the folds varied from one to three pairs.

Runnegar and Jell (1976) believed helcionellids to be exogastrically coiled (Fig. 2a) and interpreted these folds as structures, which controlled the water currents entering into the shell through the anterior edge of the aperture. Peel and Geyer (1986) had a contrasting view on helcionellids shell orientation and considered them endogastric (Fig. 2b). According to Peel, the shell apex was directed posteriorly, while the posterior sub-apical part of the last whorl was occupied by the mantle cavity with symmetrically arranged gills. The water currents entered the shell from the lateral flanks and left from the posterior (sub-apical) edge of the aperture. Such a reconstruction was proposed by Peel for all helcionellid-like mollusks and made the basis for establishing the class Helcionelloida Peel, 1991. Followed this type of shell orientation, Peel interpreted the interior folds as structures for the separation of water currents inside the molluskan mantle cavity.

Geyer (1994) did not explain the function of the folds, but reconstructed them within the mantle cavity.

In my view, a functional explanation of these folds as structures for water current regulation inside the mantle cavity is not very likely. Firstly, the folds are very long: they go from the apertural margin almost to the apical region. It is difficult to imagine, that the mantle cavity with separating folds was extended up to the apex of the shell. It seems, that in such a high, narrow cavity effective circulation would be hampered.

Secondly, two pairs of folds of "*L. merino*" (Figs. 1a and 1b) and three pairs of "*Latouchella*" sp. (Figs. 1c and 1d) mean the presence of four-five and six-seven grooves correspondingly. All of these grooves have to transport a reverse water flow (in similarly directed currents the function of the separation folds is uncertain). This kind of water circulation inside the mantle cavity is hard to explain.

I suggest another interpretation for these morphological features of helcionellid shells. These ridge-like longitudinal folds probably served as support and separation of the muscle threads from the soft body parts and attached to the shell in the sub-apical region. Analogous structures are widely distributed among recent gastropods as parietal and columellar folds. The helcionellid folds correlate with the parietal folds of gastropods for the following reasons. Firstly, the sub-apical margin of the helcionellid aperture is analogous (and possibly homologous) to the parietal margin of the gastropod aperture. Secondly, the T-shaped profile of the folds in "*Latouchella merino*" is very similar to the profile of the parietal-columellar fold of some gastropods (families Volutidae, Marginellidae, Mitridae, Costellariidae, etc.). Thirdly, it is noteworthy, that the folds were observed among helcionellids with a rather high shell, which consequently required greater effort and

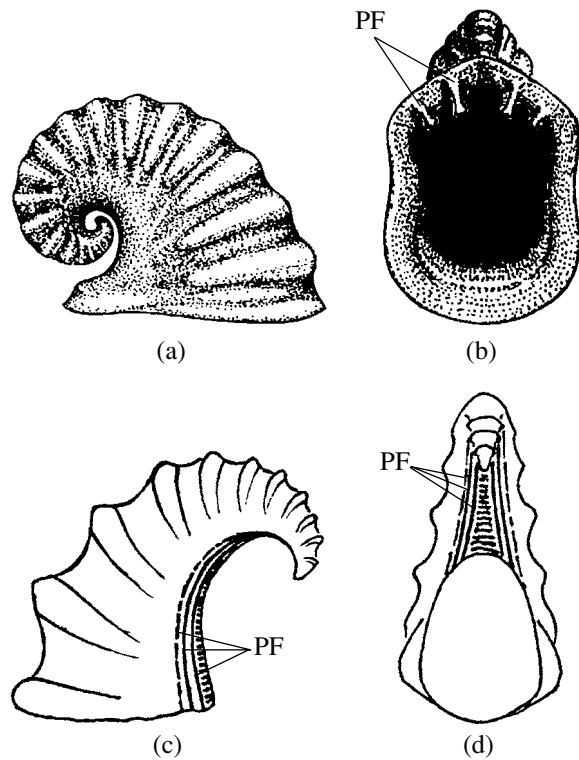


Fig. 1. Shells of "*Latouchella*" with parietal folds: (a) and (b) "*L. merino*" Runnegar et Jell, 1976 (from Peel, 1991b, text-fig. 23): (a) lateral view; (b) view from the aperture; (c) and (d) "*Latouchella*" sp. (from Peel, 1991b, text-figs. 24d–24g): (c) lateral view; (d) view from parietal side. Abbreviation: PF—parietal folds.

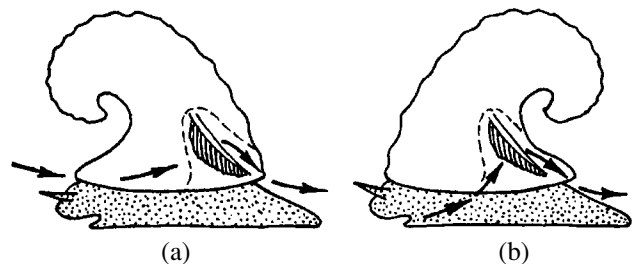


Fig. 2. Reconstruction of "*Latouchella*"-like mollusk: (a) exogastric untorted mollusk closer to monoplacophorans (Runnegar and Pojeta, 1974; Runnegar and Jell, 1976); (b) endogastric untorted mollusks assigned to class Helcionelloida Peel, 1991 (Geyer, 1986, 1994; Peel, 1991b). Arrows show the supposed water currents.

more complex manipulations to maintain balance in comparison with that of lower shells. As it is observed in gastropods, for instance among recent Pupillinoidei (order Limaciformes, subclass Pulmonata) by Shileyko (1984) and Suvorov (1993), the apertural folds serve for shell orientation above the animals foot and increased the efficiency of control of the high-spined shell.

Such a comparison of the shells of the recent land snails with the Cambrian marine mollusks could be jus-

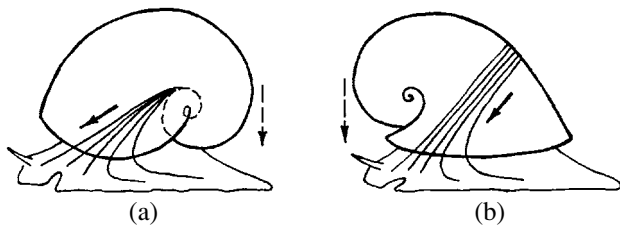


Fig. 3. Character of muscle arrangement in the planispiral shell (after Starobogatov, 1970): (a) the shell is endogastric, muscles attached to the parietal side of the whorl, (b) the shell is exogastric, muscles attached to the peripheral side of the whorl. Dashed arrows show the gravity force of the spire, solid arrows show the compensating force of the muscles.

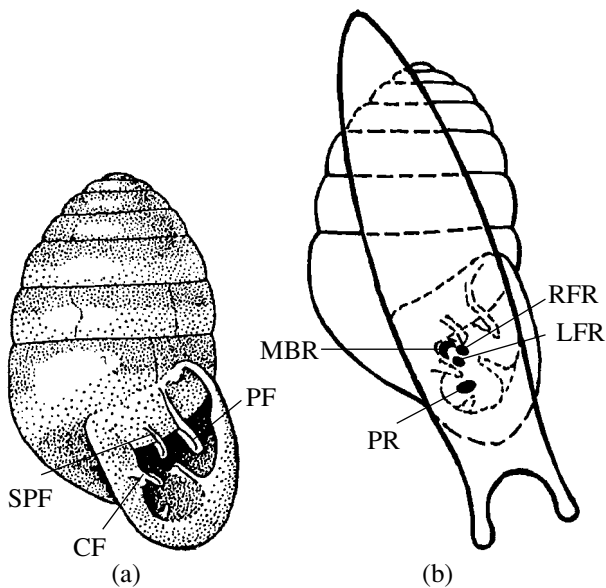


Fig. 4. Arrangement of parietal and columellar folds in the shell of recent land snails (Pulmonata, Limaciformes, Pupilloidei, Orculidae): (a) the shell of *Euxinolauria (Caucasipupa) tenuimarginata* (Pilsbry, 1922) (from Shileyko, 1984), (b) orientation of the *Euxinolauria* shell in respect to the foot-head mass (contours are given schematically) and position of the main branches of the columellar muscle (Suvorov, 1993). Abbreviation: PF—parietal fold, SPF—sub-parietal fold, CF—columellar fold, MBR—mantle buttress retractor, PR—pharynx retractor, RFR—right foot retractor, LFR—left foot retractor.

tified by their similar size and consequently similar shell-controlling mechanics.

Thus, it seems reasonable to suppose, that the main muscles that controlled the helcionellid shell and in cases withdrew the soft body, were separated by the parietal folds and were attached to the parietal wall of the shells.

Interestingly, Peel (1991a, p. 168) noted the morphological similarity of the internal folds of "*Latouchella*" with the columellar folds of gastropods, but refused their analogous function possibly, due to his

assumption, that helcionellids were endogastric but untorted mollusks. Actually, in this case the shell muscles could be reconstructed as attached to the peripheral region of the last whorl (as in monoplacophorans) but not to the parietal side. Consequently, the functional connection of the muscles and parietal folds is obscure.

Scheme of Helcionellid Internal Organization

It is very important to clarify what the shell orientation on the helcionellid body, was, the shell endo- or exogastric? The endogastric shell with posterior orientation of the apex is most likely for several reasons. Firstly, as it is excellently explained by Starobogatov (1970) with bellerophontiform mollusks as an example, the type of orientation of the planispiral shells is correlated with the type of muscle arrangement (Fig. 3). In such shells the center of gravity is not projected to the center of the aperture, so the muscles threads should be obliquely orientated to balance the coils weight. If the shell is endogastric (Fig. 3a) the muscles should be attached to the parietal wall, if it is exogastric (Fig. 3b) the muscles should be attached to the peripheral area of the last whorl. Following this principle, and believing, that helcionellids muscles were attached to the parietal wall, one could suppose, that the mollusks under the discussion have an endogastric shell.

The second, also important observation supporting an endogastric orientation of the helcionellids shell is the position of the parietal folds itself. In recent mollusks the folds are orientated sub-parallel to the sagittal plane of the foot and occur on the posterior (in relation to the movement direction) sector of the aperture (Fig. 4). Hence, the sub-apical margin of the aperture in helcionellid shells bearing such folds could also be considered as posterior (Fig. 5a).

Also it is important to understand, where in the shell the mantle cavity occurs? Obviously, the lateral position of the mantle cavity is doubtful due to the strong lateral compression of the helcionellid shell (Yochelson, 1978). The sub-apical region of different helcionellids is significantly narrower than the opposite side (Plate 6, figs. 2, 5b, 7, 9 and 14), so it is logical to suppose the position of the mantle cavity to be within the wider contra-apical area of the last whorl. In the endogastric orientation of the shell that was assumed above, the mantle cavity should be considered as anterior (Fig. 5a). In such a position it is not pressed by the spire and the work of the muscles attached to the posterior (parietal) side of the last whorl does not interfere with its function.

For the completion of the helcionellid reconstruction we should answer the question: were they torted or not? Evidently, if they were torted, all helcionellids should be assigned to gastropods; if not, they are closer to monoplacophorans. This is the most difficult problem to solve in helcionellid reconstruction since molluskan shells do not have any features, that can unam-

biguously support either a gastropod or monoplacophoran assignment (Haszprunar, 1988). It is commonly considered that the spire orientation and symmetry (or asymmetry) of the shell could indicate the position of the form under discussion within the two mentioned classes of mollusks. But it is not the general case. It is known that shell symmetry is typical not only for monoplacophorans, but also to several gastropods groups (Cyclobranchia, part of Scutibranchia, etc.), while the spirally coiled protoconch of recent monoplacophorans is asymmetrically placed above the cap-shaped teleoconch (Lemche and Wingstrand, 1959, pl. 10, fig. 34, pl. 13, fig. 49). Also, it is generally accepted that the exogastric shell is typical for monoplacophorans, while endogastric shell characterizes gastropods. However, some monoplacophorans (*Hypseloconus* Berkey, 1898; *Kirengella* Rozov, 1968; *Knightoconus* Yochelson, Flower et Webers, 1973) are interpreted as endogastric (for details see Geyer, 1994), while the endogastric nature of Cyclobranchia (=Docoglossa) sometimes arouses doubts (Shileiko, 1977). The pattern of the muscle scars also is not so certain for assignment to the two classes (Harper, Rollins, 1982; Haszprunar, 1988). For example, the symmetrical shell muscles typical for monoplacophorans may be observed among recent gastropods and is apparently only a consequence of their shell symmetry. Moreover, multiple muscle scars believed to be diagnostic for monoplacophorans sometimes occur among recent gastropods (Ponder and Lindberg, 1997).

Generally, the character of the shells muscles is completely controlled by the shell geometry and by functional peculiarities connected with the life-style of mollusks (Wahlman, 1992). So, a diagnostic role of the muscle structure in mollusks for higher systematic ranking is significantly limited (Haszprunar, 1988).

Nevertheless I shall try to resolve the question concerning the torsion of helcionellids. Above we outlined an important proposal that these mollusks possessed an endogastric shell, retractor muscles attached to the parietal wall of the last whorl and a mantle cavity housed in the anterior part of the shell. Such a combination could be observed among recent gastropods. It is accepted that gastropods obtained these features and branched as a separate class after torsion of monoplacophoran-like ancestor, which had an exogastric shell, retractors attached to the peripheral part of the last whorl, and a posteriorly placed mantle cavity. If our assumptions on the helcionellid gross anatomy are correct, these mollusks should be assigned to gastropods, while their scheme of internal organization could be similar to that illustrated on Fig. 5c. Of course, we can not dismiss the possibility of the existence of non-torted mollusks with characteristic features figured above. But in this case we have to alter the traditional understanding of the "pallial assemblage of organs" (Zarenkov, 1989) and exclude the rectum and anus from it, since without torsion they should be placed on the posterior of the animals body while the mantle cav-

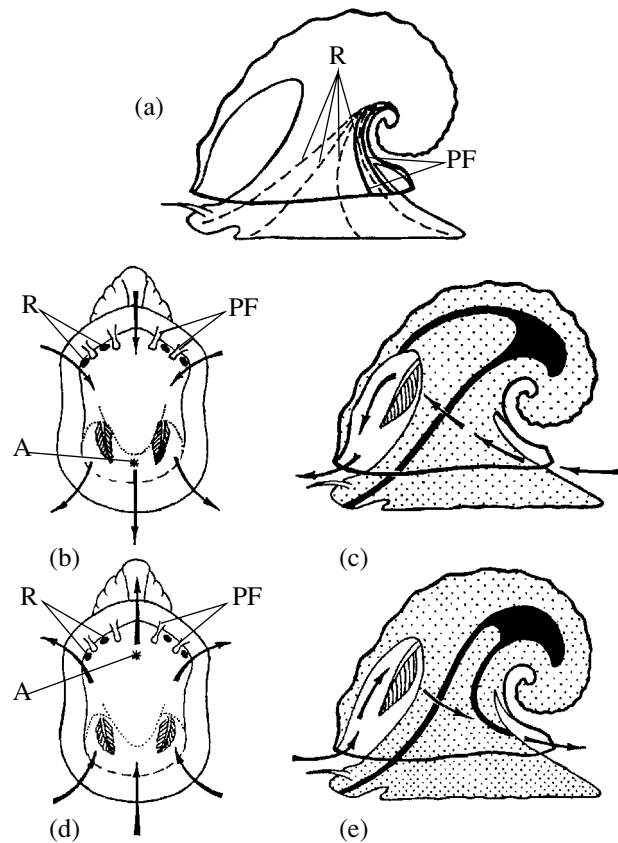
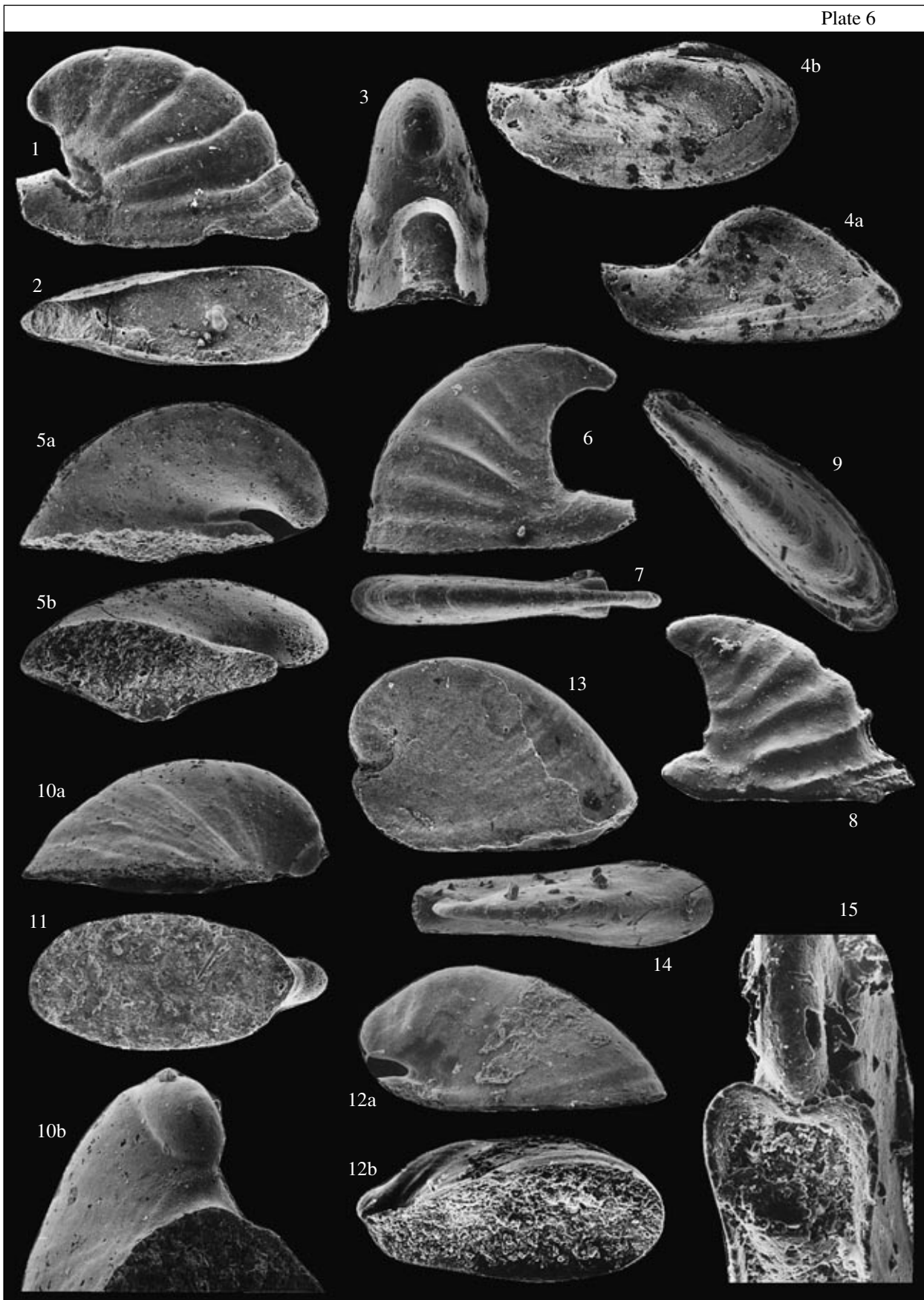


Fig. 5. Alternative reconstructions of "Latouchella": (a) shell orientation in respect to the animal's body and the muscles position, (b) and (c) supposed position of the mantle cavity and water circulation pattern of the torted mollusk, (d) and (e) the same of the untorted mollusk. Abbreviation: PF—parietal folds, R—retractors, A—anus; digestive tract is black, arrows show the supposed water currents.

ity had anterior position. Similar suggestions were already discussed earlier (Yochelson, 1978). For example, consider as the monoplacophoran prototype a mollusk with a cap-shaped shell with a central or sub-central apex and soft body anatomy similar to recent *Neopilina* (posterior anus, paired mantle cavity inside the circum-pedal furrow). If we derive from such a form the exogastric planispiral monoplacophorans (like cytonellids, for instance) on the one hand, and the endogastric helcionellids on the other, we could hypothesize, that the posterior mantle cavity of cytonellids, and the anterior mantle cavity of helcionellids originated as a result of migration of the ancestral lateral mantle cavity to those parts of the shell, that were not subjected to the pressure of the spire. In such a situation the untorted endogastric helcionellids (Fig. 5e) with a posterior anus could have originated.

A difference in the anal position certainly results in a difference in the water circulation pattern inside the mantle cavity between torted (Figs. 5b and 5c) and untorted (Figs. 5d and 5e) helcionellids.



Explanation of Plate 6

All specimens originated from the Atdabanian–Botomian strata of the Stansbury Basin (Yorke Peninsula, South Australia).

Figs. 1–3. *Mackinnonia rostrata*, Zhou et Xiao, 1984: (1) specimen no. 4664/233, internal mold from the right side, $\times 30$ (Horse Gully section, sample no. HG6); (2) specimen no. 4664/244, internal mold from posterior side, $\times 53$ (Horse Gully section, sample no. HG6); (3) specimen no. 4664/272, internal mold from aperture, $\times 66$ (Horse Gully section, sample no. HG6).

Fig. 4. *Helcionellidae* gen. et sp. nov., specimen no. 4664/665, internal mold with preserved fragments of the shell (Horse Gully section, sample no. HG4): (a) right view, $\times 45$, (b) oblique view from the dorsum, $\times 47$.

Fig. 5. *Igorellina* sp., specimen no. 4664/1499, internal mold (Horse Gully section, sample no. HG3): (a) left view, $\times 27$, (b) oblique view from the aperture, $\times 27$.

Figs. 6 and 7. *Stenothecca drepanoidea* (He et Pei in He *et al.*, 1984): (6) specimen no. 4664/1731, internal mold from the left side, $\times 48$ (borehole SYC-101, depth 168.8 m), (7) specimen no. 4664/608, internal mold from the dorsum, $\times 60$ (Horse Gully section, sample no. HG4).

Figs. 8 and 9. *Parailsanella* sp.: (8) specimen no. 4664/1662, internal mold from the dorsum, $\times 42$ (borehole SYC-101, depth 205.6 m), (9) specimen no. 4664/1698, internal mold from the right side, $\times 62$ (borehole SYC-101, depth 197.4 m).

Figs. 10 and 11. *Bemella* sp. 1: (10) specimen no. 4664/1494, internal mold (Horse Gully section, sample no. HG4): (a) from the left, $\times 21$, (b) sub-apical region, $\times 60$; (11) specimen no. 4664/1502, internal mold from the aperture, $\times 50$ (Horse Gully section, sample no. HG3).

Fig. 12. *Bemella* sp. 2, specimen no. 4664/1744, internal mold (borehole SYC-101, depth 135.25 m): (a) right view, $\times 40$, (b) oblique view from the aperture, $\times 40$.

Figs. 13–15. *Anabarella australis* Runnegar in Bengtson *et al.*, 1990: (13) specimen no. 4664/1780, internal mold with preserved fragments of the shell, right view, $\times 48$ (borehole CD-2, depth 32.66 m), (14) specimen no. 4664/1624, internal mold from the dorsum, $\times 60$ (borehole SYC-101, depth 209.0 m), (15) specimen no. 4664/1201, internal mold with preserved fragments of the shell viewed from the spire, $\times 220$ (Horse Gully section, sample no. HG2).

In the case of a posterior anus (Fig. 5d), the inhalant currents enter the mantle cavity from the anterior margin of the aperture, pass the gills, then proceed laterally from the foot, wash the anus and leave the shell through the posterior margin of the aperture. This scheme of water circulation is supported by the condition of an antero-posterior circulation pattern being typically found in recent monoplacophorans (Lemche and Wingstrand, 1959, pl. 15, fig. 57) and recent gastropods from the subclass Cyclobranchia (Barns, 1987, text-fig. 11–10a). Possibly, the posterior and lateral inhalant currents in Patellidae (Zarenkov, 1989, text-figs. 11–a–3 and 11–a–4) are secondary (Haszprunar, 1988) and are caused by the reduction of the primary ctenidia inside the mantle cavity and the origin of the secondary adaptive pallial gills along the circum-pedal furrow. However, even in this case the typical primary current is preserved in the mantle cavity, and the water enters to the shell interior from the left anterior sector of the aperture and exits from the right posterior sector. Also the possibility of a posterior exhalant current could be supported by the presence of a notch (or groove) on the subapical region of some helcionellids (Pl. 6, fig. 3), which is interpreted by some specialists (Geyer, 1986, 1994; Peel, 1991a, 1991b) as the anal sinus.

In the case of the anterior anus position (Fig. 5c), the inhalant currents enter the shell from the posterior edge of the aperture, proceed laterally along the foot, enter the mantle cavity, pass the gills, then wash over the anus and exit from the shell through the anterior apertural margin. This scheme of water circulation is suggested for helcionellids by Golikov and Starobogatov (1988) and modifies their proposal of helcionellid affinity with gastropods, namely with representatives of the subclass Patelliformes, in which some of groups have a similar type of circulation. The possibility of such a

pattern of circulation is supported by the presence of a well developed parietal train in some helcionellids (Pl. 6, figs. 4 and 6) and among sea limpets, members of the patellid group. Parietal train forms a roof-line structure above the posterior part of the foot, which drives the water into the anterior mantle cavity by its ciliary epithelium and/or undulating movements (Golikov and Starobogatov, 1988). The presence of an anterior exhalant current can be supported by the presence of a longitudinal buttress extending along the periphery of the whorl in some helcionellids (*Purella* Missarzhevsky, 1974; *Rozanoviella* Missarzhevsky, 1981; *Gonamella* Valkov et Karlova, 1984). The buttress, probably forming a groove on the shell interior, served as a type of standage water drainage sump in the

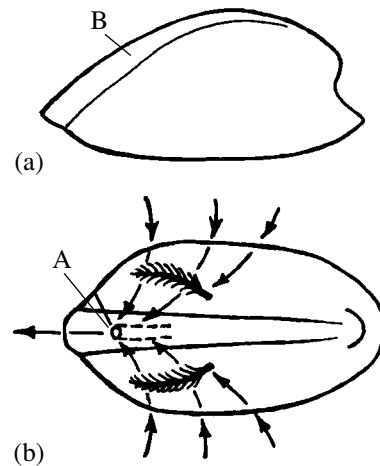


Fig. 6. The supposed water circulation in the shells of helcionellids possessing a peripheral buttress. A—anus, B—buttress.

mantle cavity of the mollusk. It presumably served to accumulate and expel waste water with excrement from the anterior edge of the aperture (Fig. 6).

It is interesting to note that such helcionellids could have been the ancestors of the bellerophonitid branch, since their water circulation pattern only slightly differs from the circulation of the typical bellerophonitid representatives: the postero-lateral currents would have to be transformed into lateral or antero-lateral, and the anterior slit of the aperture would have to originate at the edge of the exhalant buttress.

Besides the evidences mentioned above, some helcionellids, for instance *Anabarella* (Pl. 6, fig. 15), *Xianfengella* (Qian Yi, Bengtson, 1989, pl. 28) and *Protowenella* (Runnegar, Jell, 1976, figs. 6F and 6J), have a spire that descends very low and divides the posterior margin of the aperture on two lateral sectors with consequently two currents. These currents could be most likely interpreted as inhalant (in the case of an opposite function, the correlation of the two lateral exhalant currents and medially placed anus is obscure).

The Shell Muscle System of Helcionellids

It is really surprising that in spite of the extensive material on helcionellids, the position of the retractor muscles is still uncertain. This situation has been much discussed in literature (Runnegar and Pojeta, 1974; Pojeta and Runnegar, 1976; Yochelson, 1978; Peel, 1991b). It is rather strange, that the shells or internal molds of helcionellids, in some cases excellently preserved and even with observable microstructure of shell matter (Runnegar, 1983; Bengtson *et al.*, 1990), lack muscle scars. The latter are commonly preserved in other Cambrian mollusks (pelecypods, bellerophonitids, etc.). I believe that this peculiarity of helcionellids may be explained by the specific position of the zone on the shell interior to which the retractors were attached. As a result of very few coils and the great rate of whorl expansion, the major area of the mold surface is the peripheral wall of the last coil. This is the surface which is commonly studied by specialist searching of the muscle scars (following the analogy with the typical representatives of Monoplacophora). In fact, the peripheral wall of the last whorl lacks the attachment imprints of the retractors, that is also supported by perfectly preserved material from the Early Cambrian of South Australia, which is currently being studied by the author.

There seems to be one reason for this—that the muscles were attached to another area inside the shell, namely to the opposite part of the whorl, the sub-apical surface, or in other words, to the parietal area. This view accords with the suggested reconstruction of “*Latouchella*” (Fig. 5a) and confirms my opinion on the endogastric nature of helcionellids (Fig. 3a).

Generally, it is rather difficult to find the muscle scars on the sub-apical region of the shell: usually this

area is smaller and, rarely preserved compared with the peripheral area (the apical region is often broken off), or even completely closed by the preceding whorl in the case of shells with one or more complete coils. Possibly, the muscle scars have not been found because of these “drawbacks”. However, a few specimens from the Lower Cambrian of South Australia show some interesting structures on the sub-apical surface of the internal molds of the shells (Pl. 6, figs. 10 and 12). They could be interpreted as muscle scars, but this assumption needs further study and corroboration in more taxonomically diverse material.

CONCLUSIONS

Thus, two alternative schemes for the internal organization of helcionellids are possible (Figs. 5c and 5d). If we accept the torted scheme, helcionellids should be assigned to gastropods, possibly closer to the subclass Cyclobranchia, as was suggested by Golikov and Starobogatov (1988). Alternatively reconstruction (Fig. 5d), helcionellids are undoubtedly monoplacophorans,² albeit having a rather specific anatomy (endogastric shell, anterior or antero-lateral mantle cavity). In this case they should be assigned a high systematic rank and may be separated as a subclass, Helcionelliones Peel, 1991 (trans. hic ex Helcionelloida Peel, 1991).

For a specification of the most likely plan of organization of the group under discussion and consequently its systematic position within the molluscan phylum, the functional morphology of enigmatic helcionellids from the genus *Yochelcionella* needs to be studied (Parkhaev, in press).

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² I follow the traditional understanding of Monoplacophora and include in this taxon all univalved untorted mollusks.

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