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Shell SEM outer and inner structure and rissoacean phylogeny VII: *Hydrobia ulvae* (PENNANT) (Gastropoda: Prosobranchia: Rissoacea: Hydrobiidae)

With 18 SEM Photographs

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Abstract. Shell structures in *Hydrobia ulvae* (PENNANT, 1777) have been studied by SEM. The protoconch and teleoconch outer surface and shell sections perpendicular and parallel to the growth lines are described and compared with some rissoacean genera studied so far. The authors point out the apparent close relationships between *Hydrobia* and *Bythinella*, *Marstoniopsis* and *Potamopyrgus*, as well as the presence of several primitive character states in *Hydrobia*.

Kurzfassung. **Rasterelektronenmikroskopische Außen- und Innenstruktur der Schale sowie Phylogenie der Rissoacea. VII: *Hydrobia ulvae* (PENNANT) (Gastropoda: Prosobranchia: Rissoacea: Hydrobiidae).** - Die Strukturen der Schale von *Hydrobia ulvae* (PENNANT, 1777) wurden rasterelektronenmikroskopisch untersucht. Die äußere Oberfläche der Protoconcha und der Teleoconcha sowie Schalenschnitte senkrecht und parallel zu den Zuwachslinien werden beschrieben als auch mit bisher untersuchten anderen Genera der Rissoacea verglichen. Die Autoren weisen sowohl auf die anscheinend engen Beziehungen zwischen *Hydrobia* und *Bythinella*, *Marstoniopsis* und *Potamopyrgus* als auch auf das Vorhandensein einiger primitiver Merkmale bei *Hydrobia* hin.

Introduction

The phylogeny of the rissoaceans (= truncatelloideans) is still far from being clearly understood, which one can see when comparing systems proposed by various authors (e.g. GIUSTI & PEZZOLI, 1980; RADOMAN, 1983; FALNIOWSKI, 1987; PONDER, 1988; PONDER & WARÉN, 1988; DAVIS, 1989). FALNIOWSKI (1989a, c, 1990a) has found that shell structures studied by SEM are taxonomically useful, and can be included in the set of characters the phylogeny is based on. The same concerns the rissoaceans (FALNIOWSKI, 1989b). The present study is the seventh part of a description of the rissoacean shell structures (the previous ones: FALNIOWSKI, 1990b, 1992; FALNIOWSKI & SZAROWSKA, 1991; FALNIOWSKI, SZAROWSKA & BĄK, 1993; FALNIOWSKI & SZAROWSKA, 1995a, b). It deals with the structures in *Hydrobia ulvae* (PENNANT, 1777). The morphology descriptions and systematic status of the Baltic *Hydrobia* species are given in FALNIOWSKI (1987).

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Material and methods

The material was collected in Puck Bay (the Southern Baltic Sea) in July 1973 and July 1974. A few thousand specimens were dredged and then fixed in a 4% formalin solution in sea water. The material was stored in 70% ethanol.
The SEM techniques are described by FALNIOWSKI (1989a, 1990a). The shells were cleaned in a saturated solution of oxalic acid, next rinsed for 15 minutes in distiled water, then rinsed twice in absolute ethanol, dried, mounted on a holder and coated with gold.
To obtain shell sections the shells were broken, then etched for 10-15 seconds with n/10 hydrochloric acid solution, and finally continuously washed for 30 minutes, rinsed twice with absolute ethanol, dried, mounted on a holder and coated with gold. The material was examined with a Jeol JSM-35 scanning electron microscope. The characters considered were: protoconch macro- and microsculpture, teleoconch macro- and microsculpture, shell sections.

Results

Protoconch outer sculpture (Figs. 1-2)

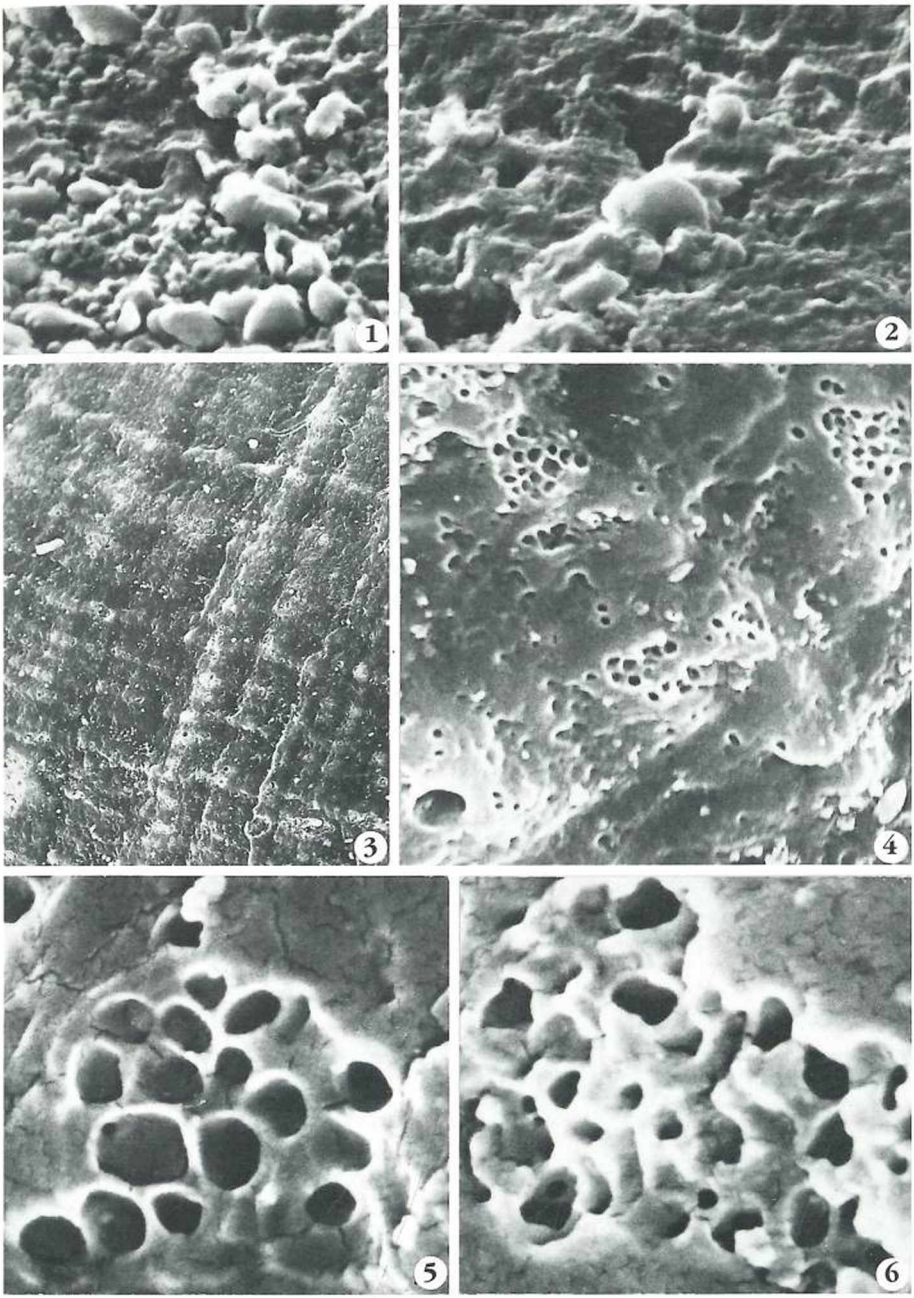
Useful in discriminating some closely related rissoacean species, the protoconch habitus has turned out to have very limited application to relationships weighting. In the Baltic *Hydrobia* the protoconchs nearly always are strongly corroded, so the protoconch habitus of *H. ulvae* is neither illustrated nor described in the present paper. The protoconch microsculpture (Figs. 1-2), although corroded, shows traces of a characteristic net of pores which looks the same as in *Bythinella*. The fine pores, situated entirely within the periostracum, are similar to the ones that occur on the outer surface of the teleoconch.

Teleoconch surface (Figs. 3-8 and 13)

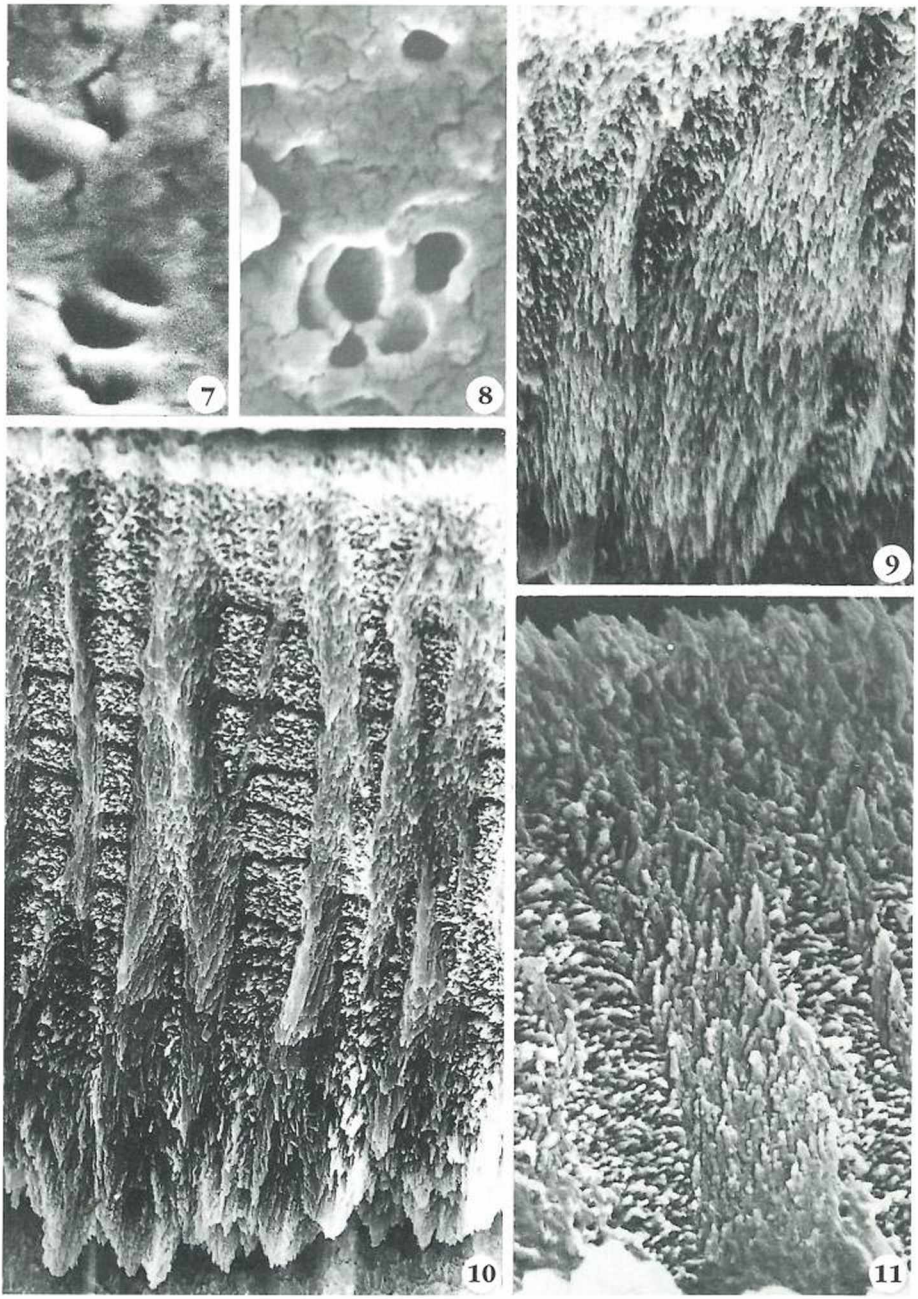
The growth lines, like in all the rissoaceans studied except *Truncatella*, are weak. In *Hydrobia ulvae* they are relatively well discernible (Fig. 3). In the interstices, spiral lines are present, like in *Dianella* and some *Bithynia*. They are not much finer than the growth lines, but much more dense, rather irregularly distributed. The general appearance of the teleoconch surface, as seen under higher magnifications (about 10,000x or more), is not rough like in *Bythiospeum, Dianella, Truncatella* and *Rissoa*, but smooth (Figs. 5-8) like in the other genera studied.
On the outer surface of the teleoconch there is a characteristic net of fine, rather regular pores which are similar to the ones described above of the protoconch surface. They are open at various part of the surface, spotted forming irregular groups (Fig. 4). They look identical with the pores of *Bythinella, Potamopyrgus* and *Bithynia*. Along with the net of pores, a few big pore-like structures may be observed (Fig. 4: bottom left). They seem to be an artifact caused by the cleaning of the shell. The net of pores (Figs. 5-6 and 8) may be accompanied by finer porelets (Fig. 7) which are similar to the „small pores" of *Marstoniopsis* (FALNIOWSKI, 1990b). Thus, the teleoconch surface in *Hydrobia* shows intermediate characters between *Marstoniopsis* and *Bythinella, Potamopyrgus* and *Bithynia*.
The periostracum removed (Fig. 13), the outer surface of the teleoconch reveals moderately long and dentated fibres and rather vast holes. However, the holes neither in size nor in distribution correspond to the pores visible on the outer surface with a periostracum. Therefore, the pores must be limited to the periostracum, as in the other hydrobioid net-of-pores holders.

Teleoconch inner structure (Figs. 9-12 and 14-18)

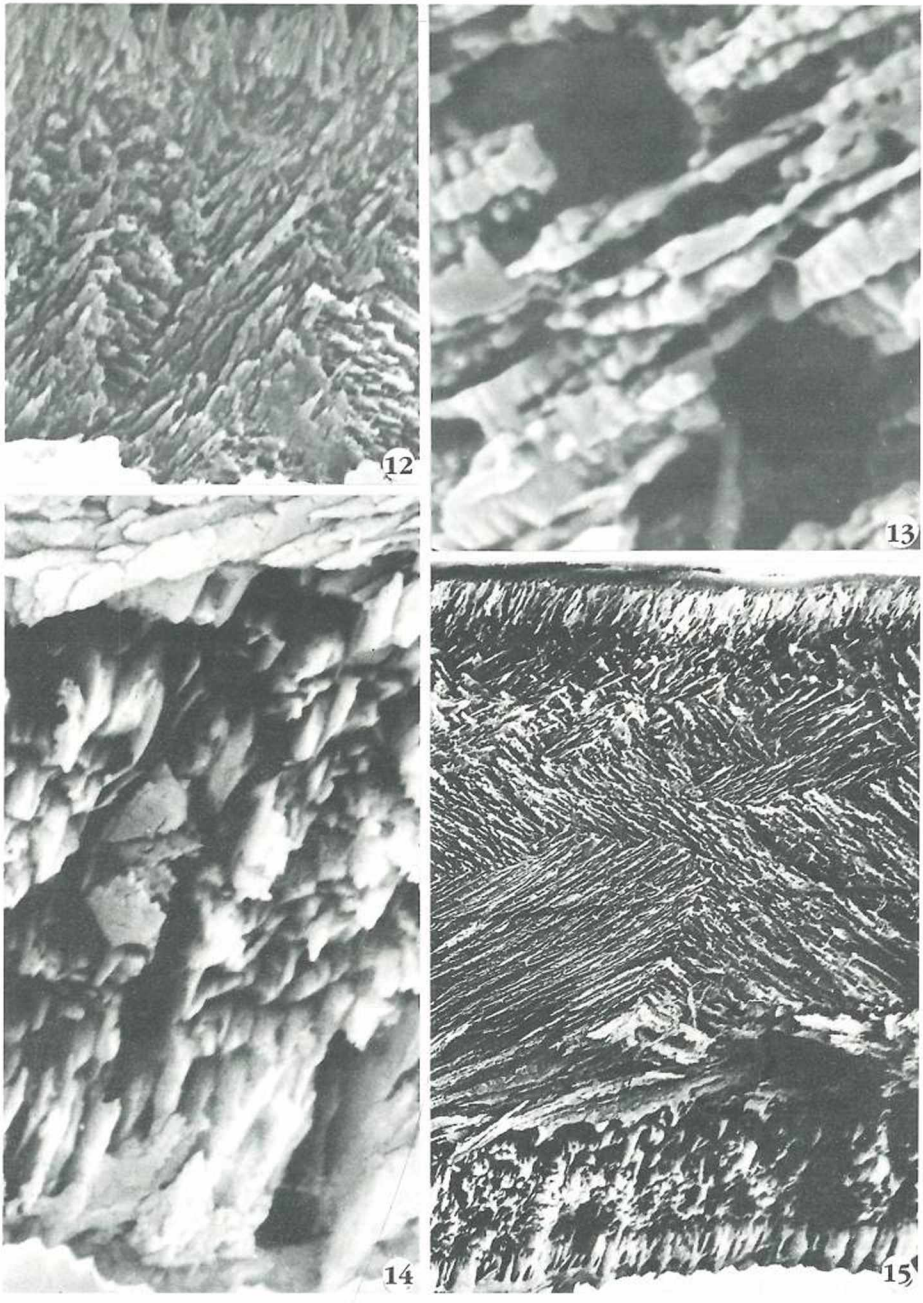
The palisade layer that is visible in sections perpendicular to the growth lines (Figs. 9-11) topographically corresponds to the wide diagonal structure layer that can be discerned in



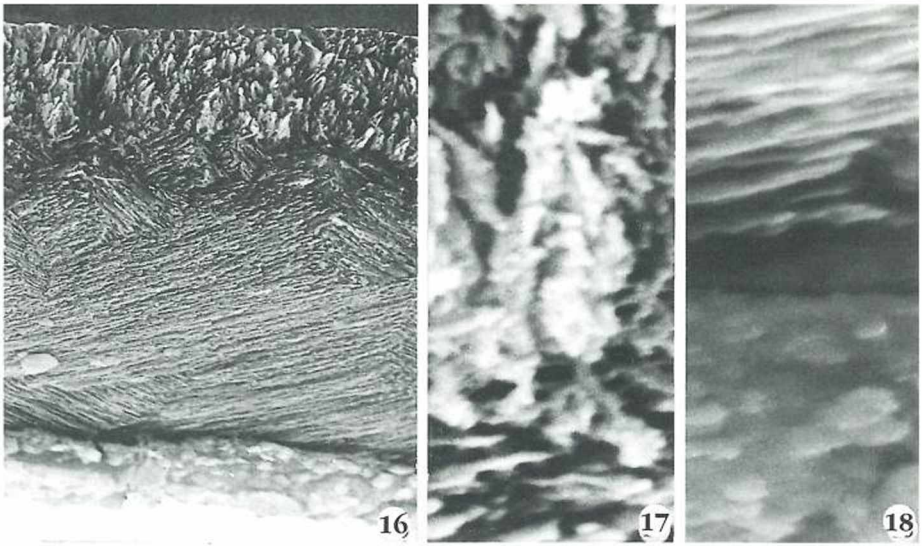
Figs. 1-6: Shell outer surface in *Hydrobia ulvae*: 1-2 - protoconch surface, slightly corroded (10,000x): 1 - artifactual cristals cover bases of pores, 2 - traces of pores better visible; 3-4 - teleoconch (body whorl) surface: 3 - low magnification, growth lines and spiral riblets in interstices well visible (300x); 4 - fragment of 3, with typical net of pores and a big pore-like structure (2,400x); 5-6 - fragments of 4 (10,000x).



Figs. 7-11: Teleoconch (body whorl) structures in *Hydrobia ulvae*: 7-8 - outer surface: 7 - pore-like fine structures, resembling the ones of *Marstoniopsis* (15,000x); 8 - typical net of pores (10,000x); 9-11 - sections perpendicular to growth lines: 9 - with no innermost part (3,000x); 10 - body whorl, close to the suture (1,300x); 11 - approximately perpendicular, periostracum removed (4,400x).



Figs. 12-15: Teleoconch structures in *Hydrobia ulvae*: 12 - outer part of section parallel to the growth lines, periostracum removed (4,400x); 13 - outer surface with no periostracum (6,000x); 14-15 - sections parallel to the growth lines: 14 - innermost fragment of 15 (5,400x); 15 - whole section (1,300x).



Figs. 16-18: Teleoconch sections parallel to the growth lines in *Hydrobia ulvae*: 16 - whole section (1,300x); 17-18 - fragments of 16 (10,000x): 17 - outermost (periostracum adjoining layer), 18 - innermost.

sections parallel to the growth lines (Figs. 12 and 15-16). In all the studied genera the layer is thick or very thick, and makes up the main part of a shell section. The palisade layer is composed of better or worse discernible columns. The columns differ in appearance and characters among genera, and this is accompanied by a wide infrageneric variability. In fact, the layer characters do not seem profitable to taxonomy.

Like in all the rissoaceans studied except *Rissoa*, in the perpendicular sections (Figs. 9-11) the palisade layer does not adjoin the periostracum. There is, in general, a moderately thick layer between the periostracum and the palisade layer. In all the species except *Hydrobia* and *Bythinella*, the layer may be absent. In *Hydrobia* (Figs. 9-11) it is composed of rather long trabeculae (Fig. 11) which are perpendicular to the shell surface (like in *Marstoniopsis, Pseudamnicola, Bithynia, Dianella* and *Truncatella*), or may have a granular appearance (Figs. 9-10) like in *Bythinella, Bythiospeum, Marstoniopsis* and *Lithoglyphus*. The layer may also look compact. In *Hydrobia*, like in *Bythinella* and *Marstoniopsis*, characteristic, cavity-like spaces occur within it (Figs. 9-11). As one can see, the layer structure is widely variable and then hardly useful in relationships weighting, which has been pointed out by FALNIOWSKI (1989b); the cavity-like spaces seem the only taxonomically useful character of the layer. The transition between the palisade layer and the one adjoining it on the shell inner side in *Hydrobia* is smooth (Fig. 10) but does not form a special „transitional" layer. This is a characteristic condition for nearly all the rissoaceans studied.

The layer adjoining the palisade one in *Hydrobia* is the innermost, like in every genera studied except *Pseudamnicola, Bithynia, Rissoa* and *Truncatella*. The palisade-adjoining layer (Fig. 10) in *Hydrobia* is neither of wide diagonal structures like in *Lithoglyphus, Pseudamnicola, Potamopyrgus, Bithynia* and *Truncatella*, nor grained-spongy as in *Bythinella* or *Marstoniopsis*. More or less compact, it is composed of flat fibres, like in *Dianella* and *Rissoa*, and may reveal a structure resembling more or less the ones visible in sections parallel to the growth lines (Fig. 14). Any fine cavity-like spaces like those of *Bythinella, Marstoniopsis* and *Potamopyrgus* cannot be found within the layer.

In shell sections parallel to the growth lines (Figs. 12 and 14-18) the wide diagonal structures layer does not adjoin the periostracum, like in *Lithoglyphus, Bithynia* and *Rissoa*. Instead, in *Hydrobia* there is a moderately thick layer whose structure is far less variable than in the sections perpendicular to the growth lines. Like in *Bythinella* and *Pseudamnicola*, it is composed of long trabeculae perpendicular to the shell surface (Figs. 12 and 15). The layer may be broader (Fig. 16), revealing a more complicated pattern of less elongated trabeculae, still arranged approximately perpendicular to the shell surface (Fig. 17). The layer pattern is characteristic and, apart from some hydrobioids, unequalled. The wide diagonal structures layer shows generally the same structure in all the genera, with the exception of *Rissoa*. The innermost layer in *Hydrobia*, like in *Bythinella, Marstoniopsis, Pseudamnicola* and *Potamopyrgus*, is a one of cylindrical structures (Figs. 14-15). This typically hydrobioid layer (FALNIOWSKI, 1989a and 1990a) is composed of more or less elongated cylinders, perpendicular to the shell surface and better or worse discernible in etched sections. They are, in general, worse discernible than in e.g. *Bythinella*, much fused even in deep-etched sections. The innermost layer may be very compact and nearly homogeneous, even after deep etching (Figs. 16 and 18). The latter concerns thin-walled (younger) shells, and the observed layer may be an artifact (extrapallial fluid crystallization in a killed animal?).

However, in fully developed *Hydrobia* shells, between that layer and the one of wide diagonal structures there is a compact-grained-spongy layer (Figs. 14-15). The layer seems to be formed after having finished the innermost one (a reorganization of an earlier formed layer?). It has to be pointed out that the layer resembles the so-called proper endostracum (FALNIOWSKI, 1989a, c, 1990a) characteristic of *Bithynia* and some valvatids, although does not share the innermost position of the proper endostracum.

Discussion

The net of pores on the protoconch and teleoconch, and the occurrence of small pores of the *Marstoniopsis* type on the latter, are noteworthy. The same concerns the occurrence of cavity-like spaces in the periostracum-adjoining layer of sections perpendicular to the growth lines. All the above character states resemble the pattern characteristic of *Bythinella, Marstoniopsis* and *Potamopyrgus*. On the other hand, the innermost layer of sections perpendicular to the growth lines resembles rather the pattern found in *Dianella* and *Rissoa*, and none of the hydrobioid patterns. The parallel sections seem more interesting from the phylogenetic point of view. The periostracum-adjoining layer is composed of long trabeculae approximately perpendicular to the shell surface, like in *Bythinella* and *Pseudamnicola*. This pattern is not found out of some hydrobioids. The same concerns the innermost cylindrical structures layer which, however, is somewhat modified in *Hydrobia*. On the other hand, there is a peculiar, additional layer between the palisade and innermost ones, resembling much the proper endostracum of *Bithynia* and some valvatids (FALNIOWSKI, 1989a, c, 1990a). In fact, structures of a similar character are also known in *Rissoa* and *Truncatella*.

The layers on the inner side of the shell wall are formed by the mantle far from its edge. It seems that the shell thickening mechanism, working at that region, is more conservative, less modifiable than the one working at the mantle edge. Anyway, in the *Hydrobia* shell a mosaic of typically hydrobioid characters and ones typical of seemingly more primitive mesogastropods is observable. And the latter characters are found in the inner part of the shell sections.

Although a careful phylogenetic analysis based on the shell SEM characters is planned in the future, when the structures description of all the selected rissoaceans is completed, some preliminary conclusions seem obvious. The occurrence of the net of pores places *Hydrobia* closely to *Bythinella* and *Potamopyrgus*, but the pores are known from *Bithynia*

as well. The „small pores" sometimes found in *Hydrobia* confirm the close relationships of *Bythinella, Hydrobia* and *Potamopyrgus* with *Marstoniopsis*. The close relationships among the above four genera seem striking as long as the shell structures are concerned. It is confirmed by the presence of cavity-like spaces in the periostracum-adjoining layer of sections perpendicular to the growth lines, coupled with the characteristic pattern of long trabeculae perpendicular to the shell surface in the same layer visible in sections parallel to the growth lines, as well as the occurrence of the cylindrical structure layer as the innermost one in the latter sections.

All this suggests that there are close relationships between *Hydrobia* and *Bythinella, Marstoniopsis* and *Potamopyrgus*, while less close between *Hydrobia* and *Pseudamnicola*. Nothing can be said about possible relationships between the former genus and *Lithoglyphus*, the shell of which, in spite of being thick-walled, has a much simplified structure. The structures of *Bythiospeum* are much more distinct. The same can be said about the non-hydrobioid rissoaceans studied, which apparently differ from *Hydrobia* more than all the studied hydrobioids do. However, in *Hydrobia* there are a few characters, especially in the innermost part of sections perpendicular to the growth lines, and close to this region in sections parallel to the growth lines, which probably correspond with the ones observed in *Bithynia*, but also in *Truncatella* and *Rissoa*. They seem primitive traits, and probably reflect the position of *Hydrobia* comparatively less advanced than that of *Marstoniopsis* and, especially, *Bythinella* and *Potamopyrgus*.

This in general confirms the rissoaceans relationships, as given by PONDER (1988), but is not in agreement with the recently acknowledged systems of hydrobioids. The close relationships among *Hydrobia, Potamopyrgus* and *Bythinella*, seem noteworthy, yet needing further verification.

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