

SHELL SEM OUTER AND INNER STRUCTURE AND RISSEOCEAN PHYLOGENY. IV. *RISSEOCEA MEMBRANACEA* (J. ADAMS, 1797) (PROSOBRANCHIA: RISSEOCEA: RISSEOIDEAE)

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ABSTRACT: In the paper the authors give descriptions of the shell SEM structures of *Rissoa membranacea* (J. Adams, 1797): protoconch habitus and microsculpture, teleoconch outer surface macro- and microsculpture, teleoconch inner surface microsculpture and teleoconch sections, perpendicular and parallel to the growth lines. The descriptions are illustrated by 36 photographs. Peculiarities of the described structures are stressed and comparisons between this species and other rissoaceans studied so far are made. The authors suggest some closer relationships with *Truncatella*.

KEY WORDS: protoconch habitus, protoconch microsculpture, teleoconch sculpture, teleoconch sections

Folia Malacologica 5/1993 was originally published as No. 1462 of Scientific Bulletins of University of Mining and Metallurgy, Cracow. This digitalised version was prepared by the Association of Polish Malacologists and first published on-line on December 30th, 2016.

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IV. *Rissoa membranacea* (J. ADAMS, 1797)
(*Prosobranchia: Rissoacea: Rissoidae*)**

1. Introduction

Phylogenetic relationships within the *Rissoacea* (= *Truncatelloidea*), the largest group of the *Neotaenioglossa* (PONDER 1988), were recently studied by numerous authors (e.g. GIUSTI & PEZZOLI 1980, RADOMAN 1983, DAVIS, KUO, HOAGLAND, CHEN, YANG & CHEN 1985, PONDER 1985, 1988 and DAVIS 1989). This especially concern the *Hydrobioidea*. Despite it the problem remains controversial and poorly understood (see FALNIOWSKI 1987, 1989c, PONDER 1985, 1988 and PONDER & WARÉN 1988). This is, in part, due to the insufficient number of characters found in those small, often minute gastropods.

A number of characters quite widely used in the taxonomy of the said group have recently been found hardly applicable to hydrobioid relationships weighting (e.g. DAVIS 1989). The simple shell, remarkably uniform radula, and the convergent evolution of the external and internal structures of all the soft parts, accompanied by the worldwide distribution of the superfamily, render the phylogeny of the group hardly understandable. Owing to the mentioned simplicity and small dimensions of the shells any fossil material is difficult to classify, which makes it hardly possible to study the history of the group.

The above situation clearly justifies any attempt to extend a variety of taxonomically useful characters in the group. The shell structure characters seem especially good, since they can be examined in the fossil materials as well as in the recent ones. While the characters of the proto- and teleoconch outer surface were here and there applied to rissoacean taxonomy (for references see FALNIOWSKI 1989a and 1992), the shell inner structure, to the authors' knowledge, was described only in some rissoacean species by FALNIOWSKI (1989a, 1989c, and 1990a, FALNIOWSKI & SZAROWSKA 1991).

Preliminary results of a study on the SEM structures of the rissoacean shell (FALNIOWSKI 1989b) suggest that these characters are useful in phylogenetic relationships weighting within the *Rissoacea*.

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The present paper is a part of a study of rissocean shell SEM structures (the other parts already published: FALNIOWSKI 1990b and 1992, FALNIOWSKI & SZAROWSKA 1991; see also data on hydrobioids and bythinellids in FALNIOWSKI 1989a, b, c, and 1990a). The authors describe the structures of *Rissoa membranacea* (J. ADAMS, 1797). This rissoid morphology and systematic position are described by FALNIOWSKI (1988 and 1989c).

2. Material and methods

The material was collected in the Bay of Puck (Southern Baltic Sea) in July 1973 and July 1974. A few thousands of specimens were dredged and then fixed in 4% solution of formalin in sea water. The material was stored in 70% ethanol.

The SEM techniques applied were exactly the same as described by FALNIOWSKI (1989a, 1990a). The shells were cleaned in a saturated solution of oxalic acid, then washed for 15 minutes in distilled water, rinsed twice with absolute ethanol, dried, mounted on a holder and coated with gold.

To obtain the shell sections the shells were broken and then etched for 10 - 15 seconds with an n/10 hydrochloric acid solution, and finally continuously washed for 30 minutes, rinsed twice with absolute ethanol, dried and, finally, mounted on a holder and coated with gold. With the exception of Fig. 14, all the sections presented in photographs are etched.

The material was examined by means of a Jeol JSM-35 scanning electron microscope. The characters considered were: protoconch habitus and macro- and microsculpture, teleoconch macro- and microsculpture, shell sections.

3. Results

Protoconch habitus and outer sculpture (Figs 1 - 7)

The protoconch (Figs 1 - 5) is rather broad initially, but the diameter of its initial part is quite variable. The diameter of the first half of the first whorl of the protoconch ranges from 75 μm to 110 μm . The whorl breadth increases rather slowly and regularly. The protoconch is flat (Figs 1 - 4); its suture is rather deep (Figs 1 - 3 and 5). There is no visible border between the protoconch and the teleoconch (Figs 3 and 5). There is no macrosculpture in uncorroded protoconchs (Figs 3, 4 and 6), but their appearance is finely rough.

Higher magnifications show vast and deep caves which are numerous but not necessarily regularly distributed (Fig. 7: in general, they may be practically identical with the ones on the teleoconch outer surface, illustrated in

Figs 10 and 11). The caves are approximately circular, with rounded edges; two or more may be fused together, the surface outside the caves is fine-grained. There are neither net of pores, nor fine pores or depressions. Similar caves, but with sharp edges, are known in *Pseudamnicola*, where they are extremely scarce, and in *Dianella*, where they are accompanied by very small pore-like depressions (FALNIOWSKI 1989b).

Teleoconch surface (Figs 8 - 13 and 36)

In *Rissoa membranacea* the macrosculpture is very poor, the growth lines are hardly visible. The periostracum (Figs 8 - 13) is unusually thick, which is striking in the shell sections (Figs 15 - 20, 24, 29, 32 and 33). This, however, is characteristic of this species and not of the other representatives of the genus *Rissoa* DESMAREST, 1814. Fig. 8 shows a fragment of the body whorl, parietal lip and umbilicus under a low magnification. It is irregularly rough.

Under higher magnifications (Figs 9 - 13) there are neither fine pores nor depressions, only big, irregular and approximately circular caves irregularly arranged, like in *Pseudamnicola* and *Truncatella*, but the caves in *Rissoa* have the edges rounded and not sharp like in the other two genera. In *Dianella* the caves occur together with numerous extremely fine pores, while in *Truncatella* they are very scarce: there are only a few big caves per shell (FALNIOWSKI 1992). The caves may be distributed very densely (Fig. 9: this is, however, a corroded surface), densely (Figs 10 and 11), or may be unnumerous (Figs 12 and 13). They are often fused, two or more together (Figs 10 and 11).

In *Rissoa* the surface of the teleoconch as seen under high magnifications (about 10,000 x or more) is rough, composed of compact grains, like in *Bythiospeum*, *Dianella* and *Truncatella*, and not smooth like in the other studied rissoacean genera.

The inner surface of the teleoconch is shown in Fig. 36. It is composed of short trabeculae and small approximately circular caves. The teleoconch inner surface is often much more differentiated within than between families (FALNIOWSKI 1989a and 1990a) so it will not be considered further in the present paper.

Teleoconch inner structure (Figs 14 - 35)

Sections perpendicular to the growth lines are shown in Figs 14 - 23 and 33, sections parallel to the growth lines, in Figs 24 - 31 and 35, and slanting ones, in Figs 32 and 34. Up to three layers can be distinguished even in an unetched perpendicular section (Fig. 14), but much more information can be obtained from the etched sections (Figs 15 - 35).

Out of the rissoacean species studied, it is only in *Rissoa* that the perpendicular sections (Figs 14 - 23 and 33) reveal the palisade layer to adjoin the extremely thick periostracum (Figs 15 - 20 and 33). There is no layer between the periostracum and the pallisade layer, but the columns of the pallisade layer may not reach the periostracum (Figs 15 - 18). In such cases there is a very thin more compact structure which is adjacent to the periostracum; within the structure the columns are hardly discernible (Figs 20, 21 and 33).

The pallisade layer corresponds to the wide diagonal structures layer of the sections parallel to the growth lines. This pattern of organization, which often covers the main part of the shell sections, seems common for all the *Mesogastropoda* (FALNIOWSKI 1989a). In general, it is very similar in various genera and families. There are some peculiarities of the layer structure within particular genera, but they are accompanied by a wide infrageneric, and even infraspecific variability. Therefore the structure of this layer seems plesiomorphic in general, so it is of little taxonomic importance in detail. In *Rissoa* the pallisade layer is also typically mesogastropod; the columns usually are well discernible (Figs 15 - 18) but sometimes they are not (Figs 20, 21, 33 and 34). The arrangement of the columns is rather irregular, many of the columns branching. The relation of one layer to another is highly variable, so hardly useful in taxonomy (FALNIOWSKI 1989a, b, c, 1990a). However, it must be pointed out that in *Rissoa membranacea* the pallisade layer is relatively unusually thin.

The transition between this layer and the adjoining one is neither as sharp as in *Dianella*, nor rather sharp as in the other genera, excluding one, but there is apparently a transitional layer, like in *Bithynia* (Figs 15 - 17, 20, 21, 33 and 34). The transitional layer is much thinner than the layer of angular structures in bithyniids (FALNIOWSKI 1989 a, c, 1990a) and is composed of moderately long fibres flatly arranged. It may be broader (Figs 21 and 34; especially Fig. 21 shows a similarity between this one and the bithyniid angular structure layer: an alternate arrangement of narrowing and broadening columns) or narrower (Figs 15 - 17).

The layer adjoining the palisade one is the innermost in the majority of the rissoacean genera studied; only in *Pseudamnicola*, *Bithynia* and *Rissoa* (FALNIOWSKI 1989b) there is one more layer, and in *Truncatella* (FALNIOWSKI 1992) there are two more layers. The palisade-adjoining layer in *Rissoa* is composed of flatly arranged fibres (Figs 15 - 17, 21 and 34) like in *Hydrobia* and *Dianella*. The fibres (trabeculae) are long and rather broad, with dentate margins. In etched sections they are separated by moderately big spaces. They run approximately parallelly to the shell surface, so it is not the wide diagonal arrangement that is typical of the majority of the rissoaceans as well as of other mesogastropods.

The next layer is spongy-trabecular in character (Figs 15 - 17, 20, 22, 23, and 33). Its structure suggests that it may be homologous to the corresponding layer in *Truncatella*. The structure of this innermost layer in *Rissoa* is peculiar, usually

it is composed of rather short fibres and big spaces between them which are visible after etching (Figs 15 - 17, and 23); there may also be a small "cavital" spaces (circular in outline) being similar to those of some hydrobioids (Figs 15 - 17, but much more numerous and better visible in Figs 20, 22, and 33). The fibres may be smaller, less elongated (Figs 20, 22, and 33), and within the layer there may be a thin "sublayer" of fine, elongate trabeculae arranged perpendicularly to the shell surface (Fig. 22). The innermost layer is absent in not fully grown shells (Fig. 21); if completely developed, it is thick and well discernible from the adjoining layer.

In the sections parallel to the growth lines (Figs 24 - 31, and 35) the periostracum adjoins a wide diagonal structure layer (Figs 28, 29, and 31). Apart from *Rissoa*, this, however, is to be found only in *Lithoglyphus* and *Bithynia* from among the rissoacean studied so far. There may be, however, a thin compact-grainy layer adjoining the periostracum (Figs 24, 25 and, especially, 27). The wide diagonal structure layer generally shows the same structure in all the genera (families) except *Rissoa*, in which it usually is composed of nearly flat fibres that are approximately perpendicular to the section surface (Figs 24 and 25) but may also be in the form of a typical wide diagonal structure layer (Figs. 28 and 29). Its fibres (trabeculae) are relatively short and broad, well discernible.

Next, there is the thick spongy-fibrous layer (Figs 24, 25, 28 and 29). It consists of fibres running approximately perpendicularly to the section surface, and bears vast spaces, which are visible in etched sections. The layer is often relatively thick.

The last, innermost layer (Figs 24 - 26, 28, 30, and 35) is often spongy in character, homogenous fibrous, with big and irregular spaces. It is composed of irregular, fine-dentate, approximately isodiametric flat plates, which are more or less perpendicular to the shell surface. The innermost layer (Figs 28 and 30) may be similar in appearance to the innermost layer that is seen in the sections parallel to the growth lines in *Bythiospeum* (FALNIOWSKI & SZAROWSKA 1991) but usually (Figs 24, 26, and 35) it is composed of less compact fibres.

4. Discussion

REHFELDT (1968) described two forms in Danish *Rissoa membranacea*, differing in ontogenetic pattern, egg size and protoconch dimensions. Later VERDUIN (1976) widely used protoconch diameter, as indicative of a pelagic or intracapsular veliger in ontogeny, to distinguish rissoid species. JABLONSKI (1986) widely exploited the "shell-apex theory" in inferring evolutionary characteristics of a species, upon a basis of the protoconch habitus.

However, in the *Rissoa membranacea* studied by us the protoconch diameter was continuously variable and just intermediate, situated between the two types given by REHFELDT (80 μm for form with pelagic larva and 120 μm for intracapsular development): it was within the range 75 to 110 μm . Also the habitus of the protoconch does not suggest the possible developmental pattern.

This is in agreement with HADFIELD & STRATHMAN's (1990) observations on trochids, among which they found closely related species with/without a pelagic larva, the protoconchs looking similar in the two types of development. The protoconch habitus, although sometimes useful as a character discriminating some closely related rissoacean species, can hardly be applied to relationships weighting on the family level (FALNIOWSKI 1989a, b, 1990b). This is confirmed by the present study. On the other hand, the protoconch outer surface microsculpture in *Rissoa* is unique for the rissoaceans studied so far.

The outer surface and, in particular, the inner structure of the shell, though being infragenerically variable, differ markedly between genera/families (FALNIOWSKI 1989a, b, c, 1990a, b). The SEM structure characters seem correlated with neither shell size/habitus nor habitat character and thence they hardly seem to be of adaptive significance. Therefore they should rather reflect phylogenetic relationships, although in such simple structures both convergence and reversed evolution may have been quite common. Our knowledge of the shell structure within the *Gastropoda* in general, as well as in rissoaceans, is still far from being sufficient, and the data base shows a strikingly mosaic pattern, which necessitates further studies. Despite of the drawbacks, some preliminary conclusions can be presented.

There are a few characters in the teleoconch outer surface and inner structure which are characteristic of *Rissoa*: (1) the characteristic caves on the outer surface, which only in *Rissoa* are big and with rounded edges, the rough shell surface (also in some other rissoaceans studied); (2) the palisade/wide diagonal structures layer usually adjoining the periostracum; (3) the unusually thin palisade layer (only in *Rissoa*), the transition layer between the palisade layer and the next one (apart from *Rissoa* only in *Bithynia*); (4) the spongy-trabecular layer resembling the one of *Truncatella*; (5) the almost flat arrangement of the wide diagonal structures layer in the parallel sections; (6) the homogene fibrous innermost layer in the parallel sections.

Visible in the sections perpendicular to the growth lines, the intergeneric (interfamiliar) similarities in the structure of the layer following the one that adjoins the palisade layer, are noteworthy. The layer is present in *Bithynia*, *Truncatella* and *Rissoa*; out of the *Hydrobioidea* studied it only has been founded in *Pseudamnicola*. In all the genera it is spongy and looks similar. However, its structure seems diversified and rather not homologous between the genera. Perhaps the spongy-trabecular structures of *Truncatella* (FALNIOWSKI 1992) and *Rissoa*, resembling each other, are homologous, but either the spongy-"grained" structure of *Bithynia* (FALNIOWSKI 1989a, b, c, 1990a) or the spongy-trabecular/compact-grained structure of *Pseudamnicola* (FALNIOWSKI 1989b) rather cannot be homologized. The layer in *Rissoa* is somewhat similar to the one found in *Bythiospeum* (FALNIOWSKI & SZAROWSKA 1991), but the spatial

orientation of the structures is conspicuously different. In *Truncatella*, on the inner side of the spongy layer there again is a layer of massive flat fibres (FALNIOWSKI 1992). Anyway, the possibly homologous and structurally similar layers of spongy-trabecular type are not the only one similarity between *Truncatella* and *Rissoa*.

Although there are some similarities between the described structures of *Rissoa* and *Bythiospeum*, the shell structure of the former is, in general, equally different from all the hydrobioids studied so far. The differences are similarly pronounced between *Rissoa* and *Bithynia* and *Dianella*: once more hydrobioids form a group in which every representative is more similar to the others than to any of the studied non-hydrobioid rissoaceans: *Rissoa*, *Dianella*, *Truncatella* and *Bithynia*. Relatively the most profound similarities are observed between *Rissoa* and *Truncatella*, which in general confirms the preliminary phylogeny given by PONDER (1988). However, there are also some similarities between *Rissoa* and *Bithynia*. A more detailed analysis of rissoacean relationships inferred from the shell structure characters will be given in the future.

5. Acknowledgements

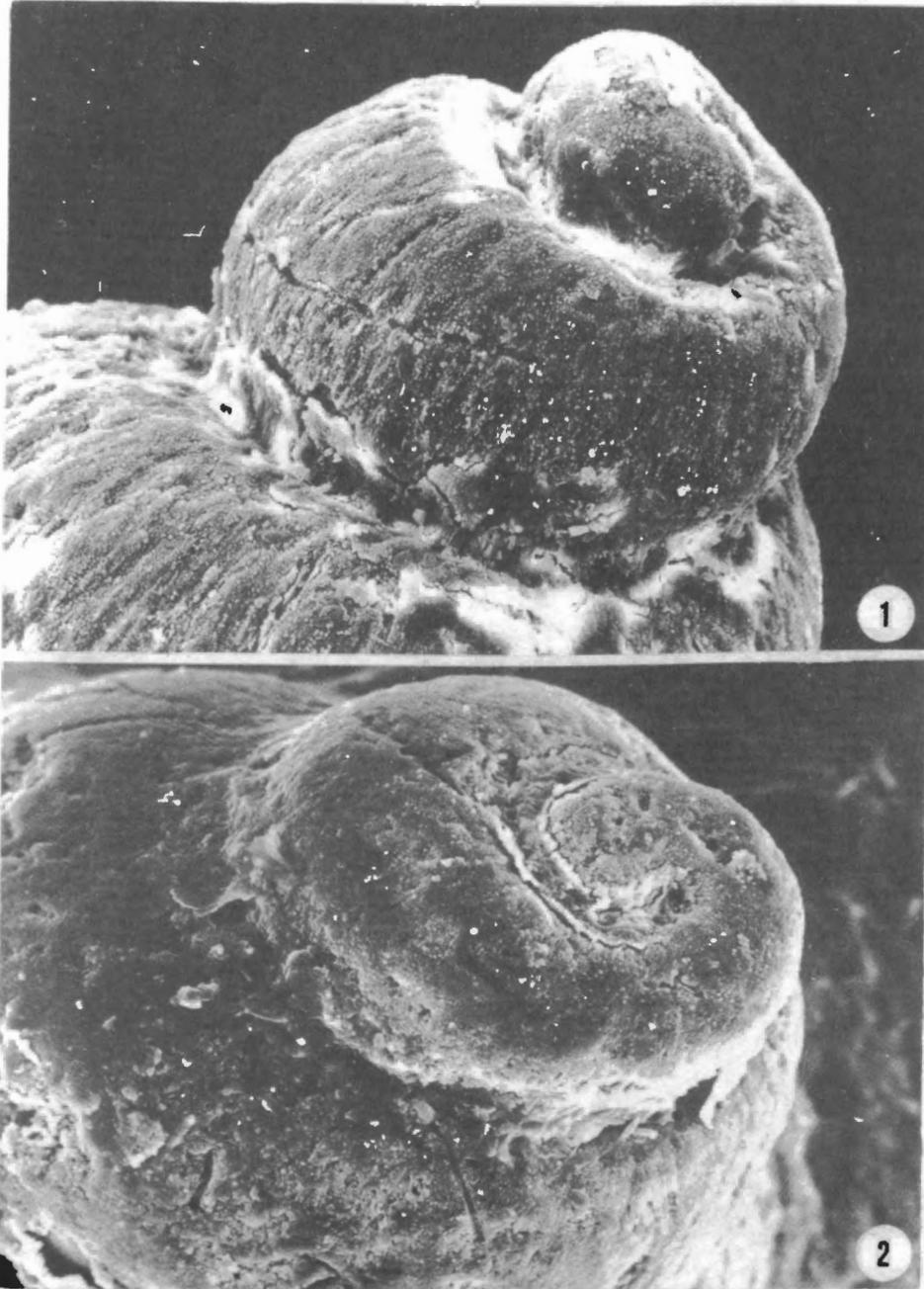
The SEM facilities were provided by the Scanning Microscopy Department of Jagiellonian University. The SEM photographs were done by Mrs Jadwiga Faber, to whom we are grateful. The work was supported by a grant from the Polish Ministry of Education funding the research project: "Variability, speciation and taxonomy of the Polish Prosobranchia".

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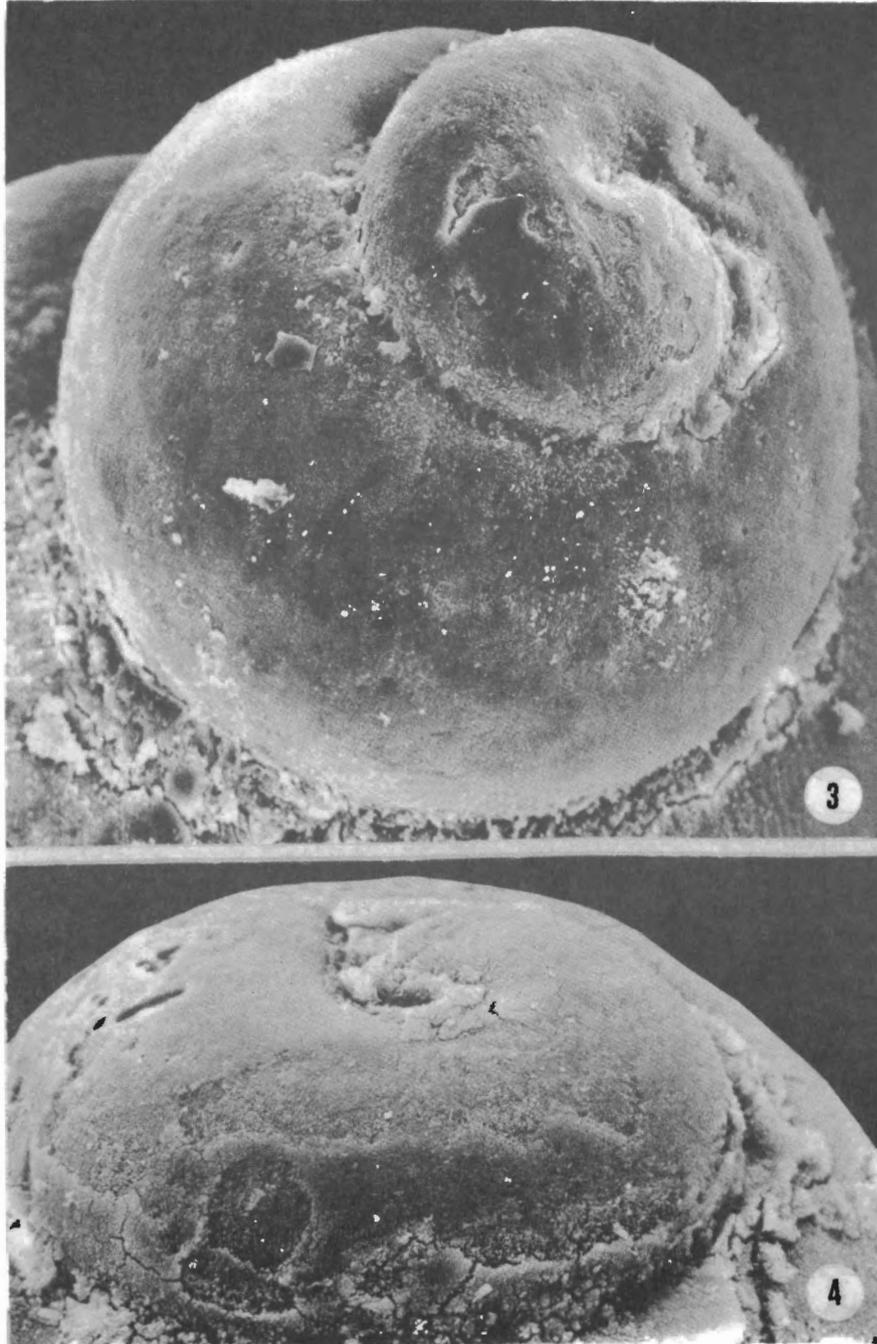
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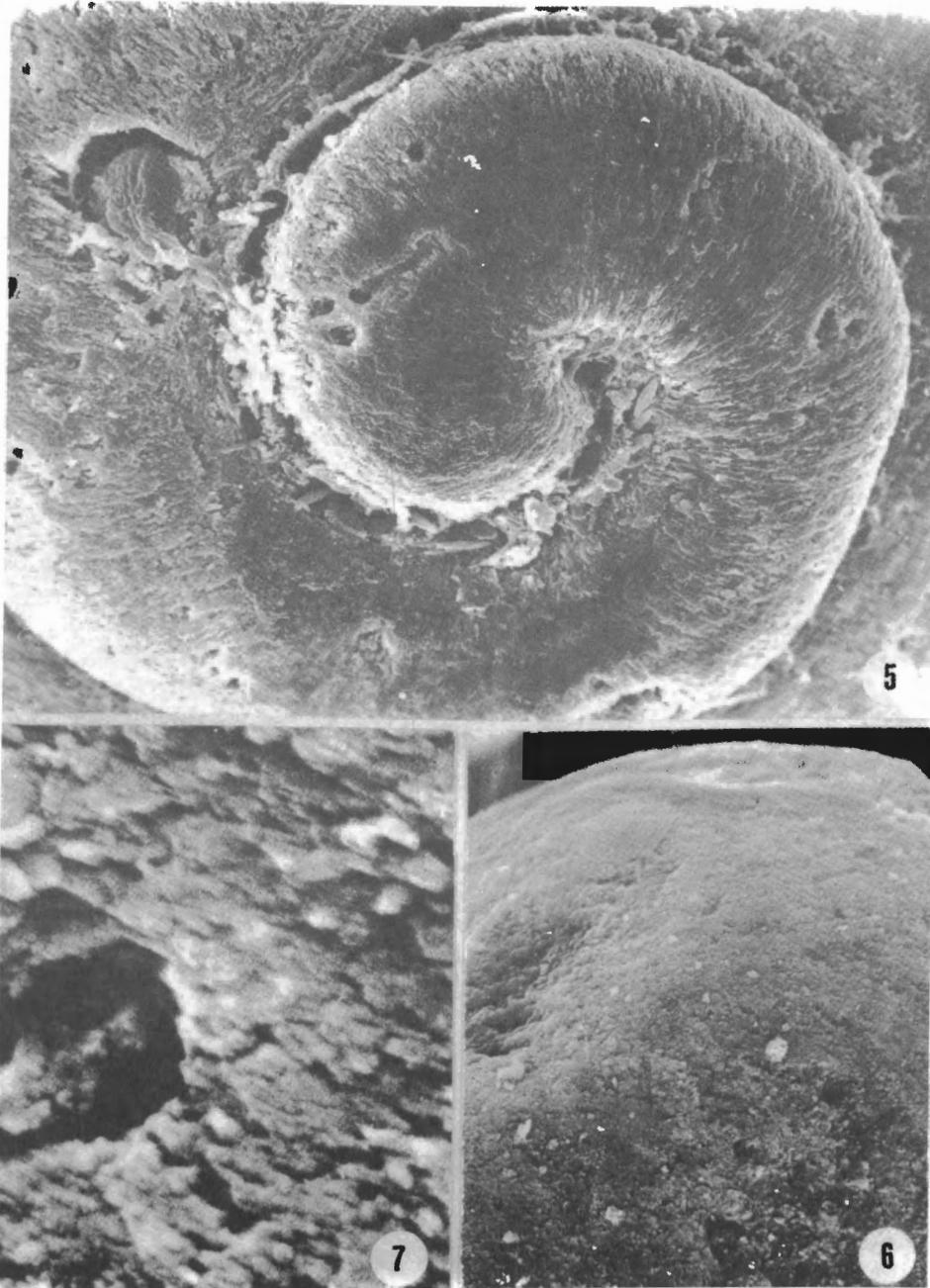
Reviewer: Prof. Stefan Witold Alexandrowicz D. Sc.



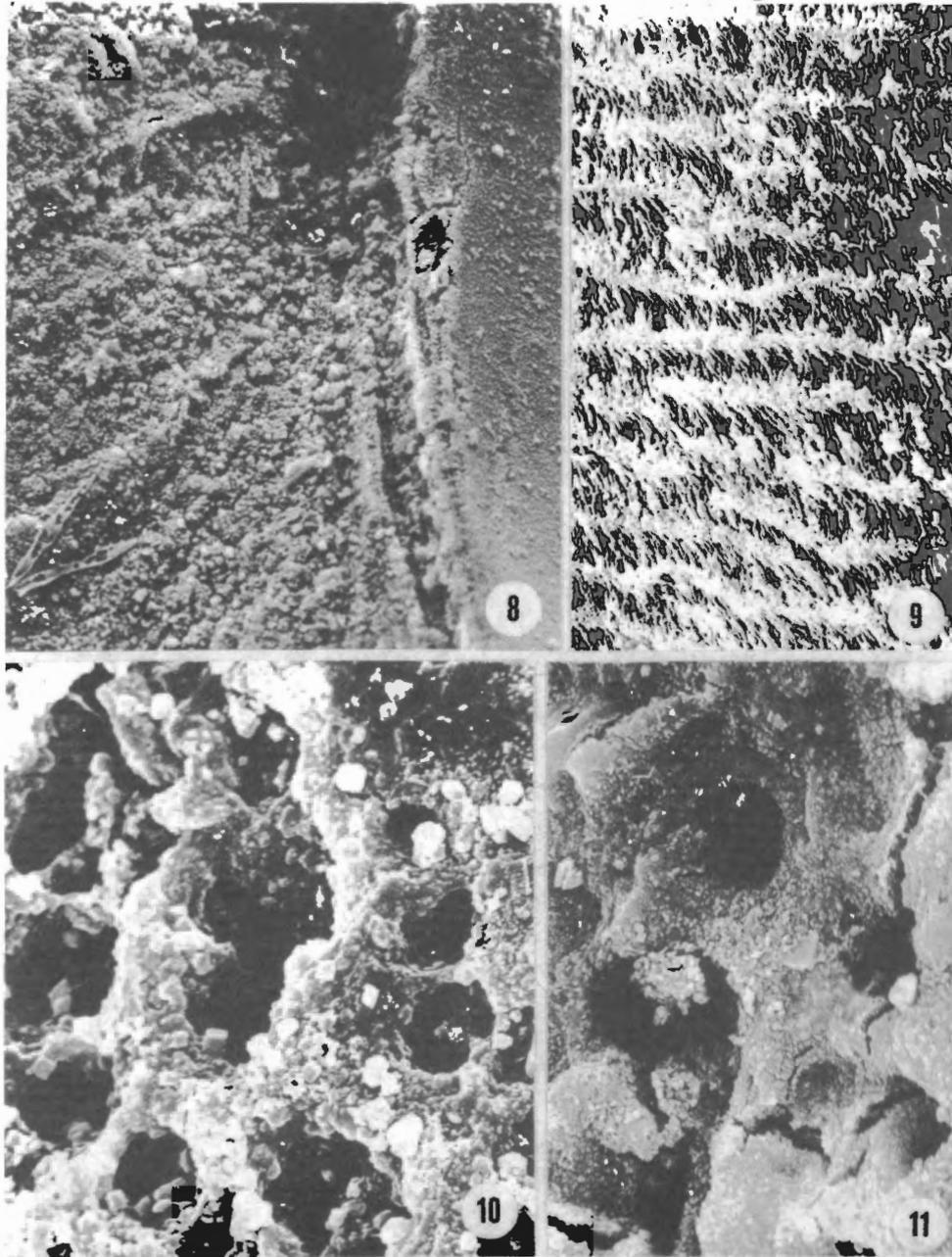
Figs 1 - 2. Protoconchs of *Rissoa membranacea* (200 x)



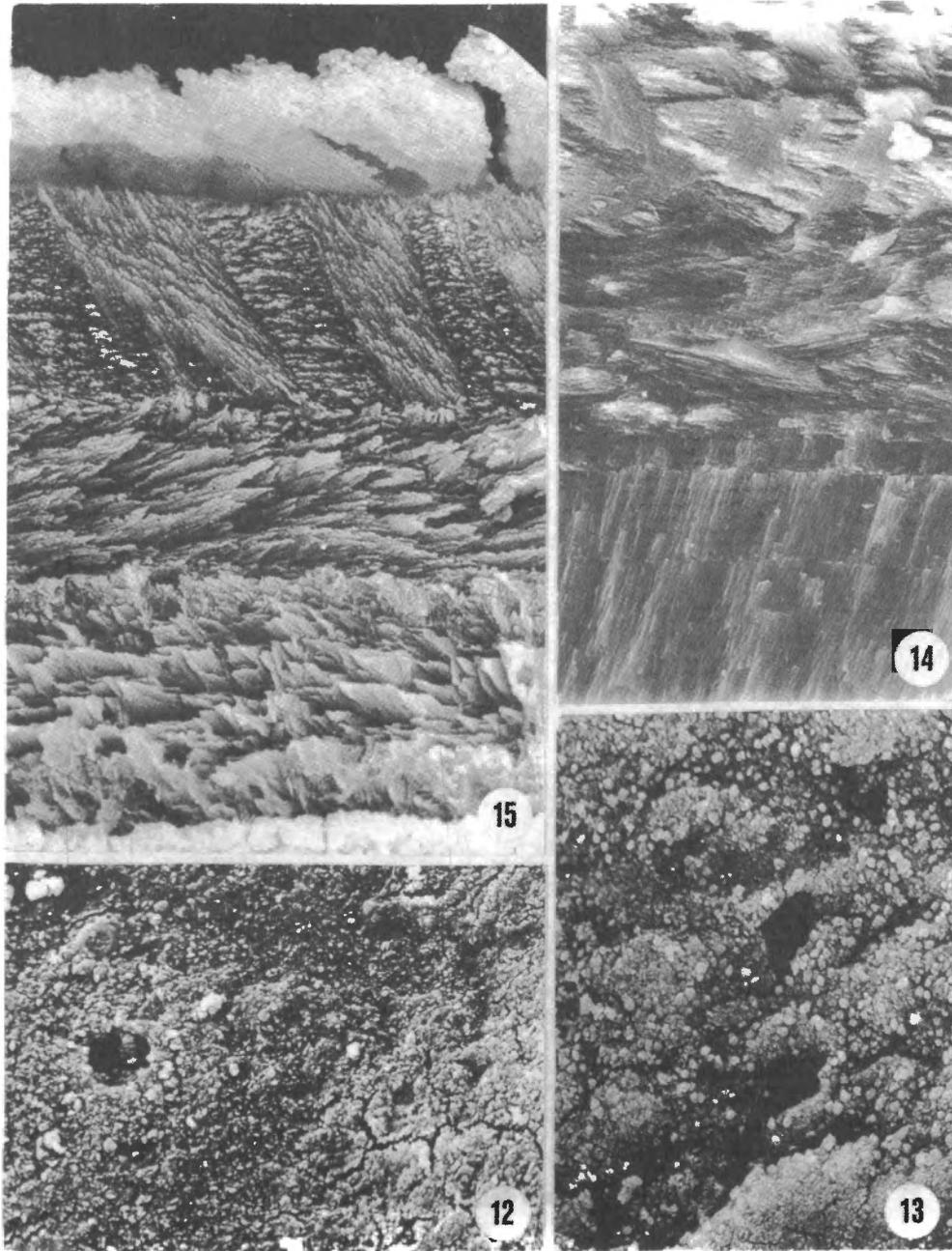
Figs 3 - 4. Protoconchs of *Rissoa membranacea*: (3 - 220 x, 4 - 300 x)



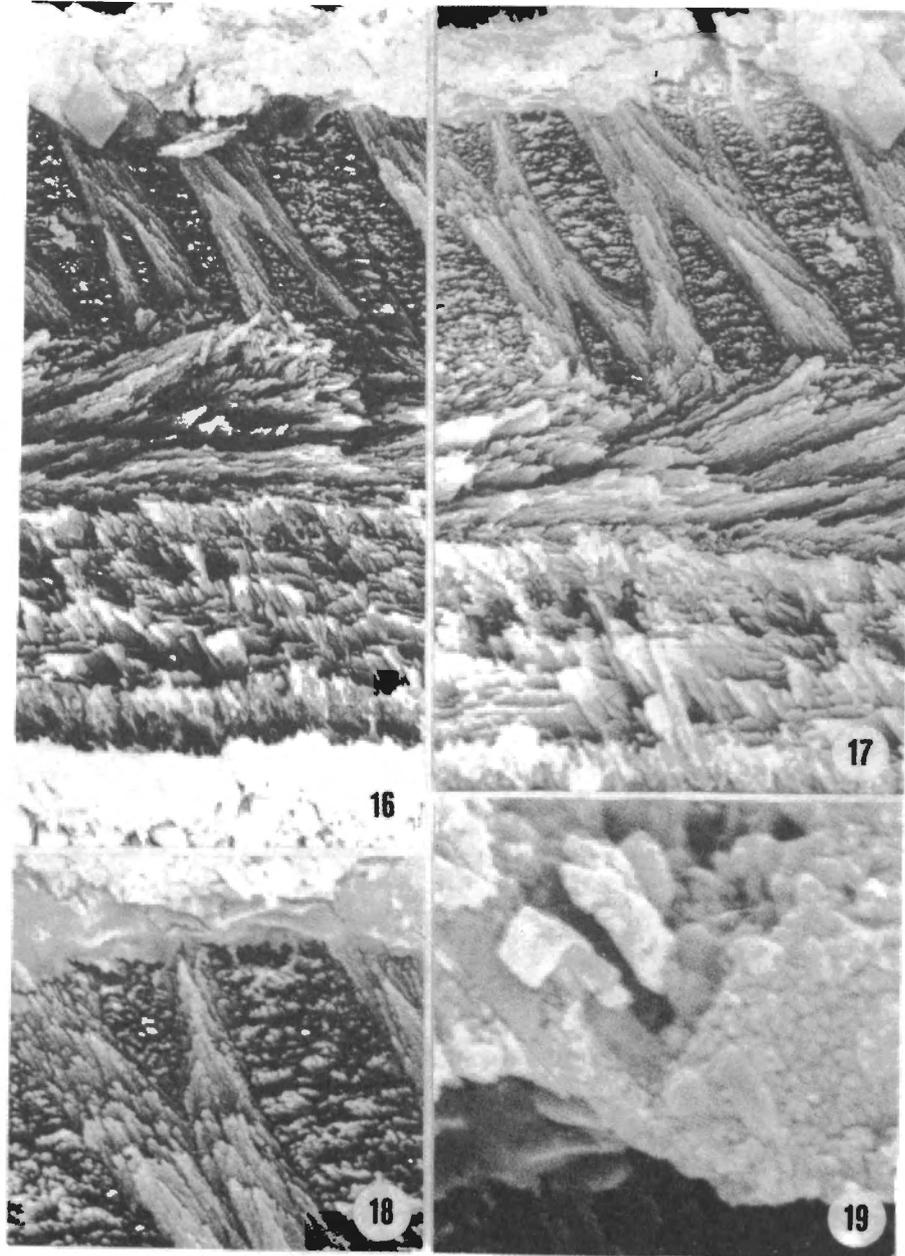
Figs 5 - 7. Protoconchs of *Rissoa membranacea*: 5 - protoconch habitus (360 x); 6 - protoconch outer surface (1,000 x); 7 - protoconch surface, a fragment of 6, with a cave (10,000 x)



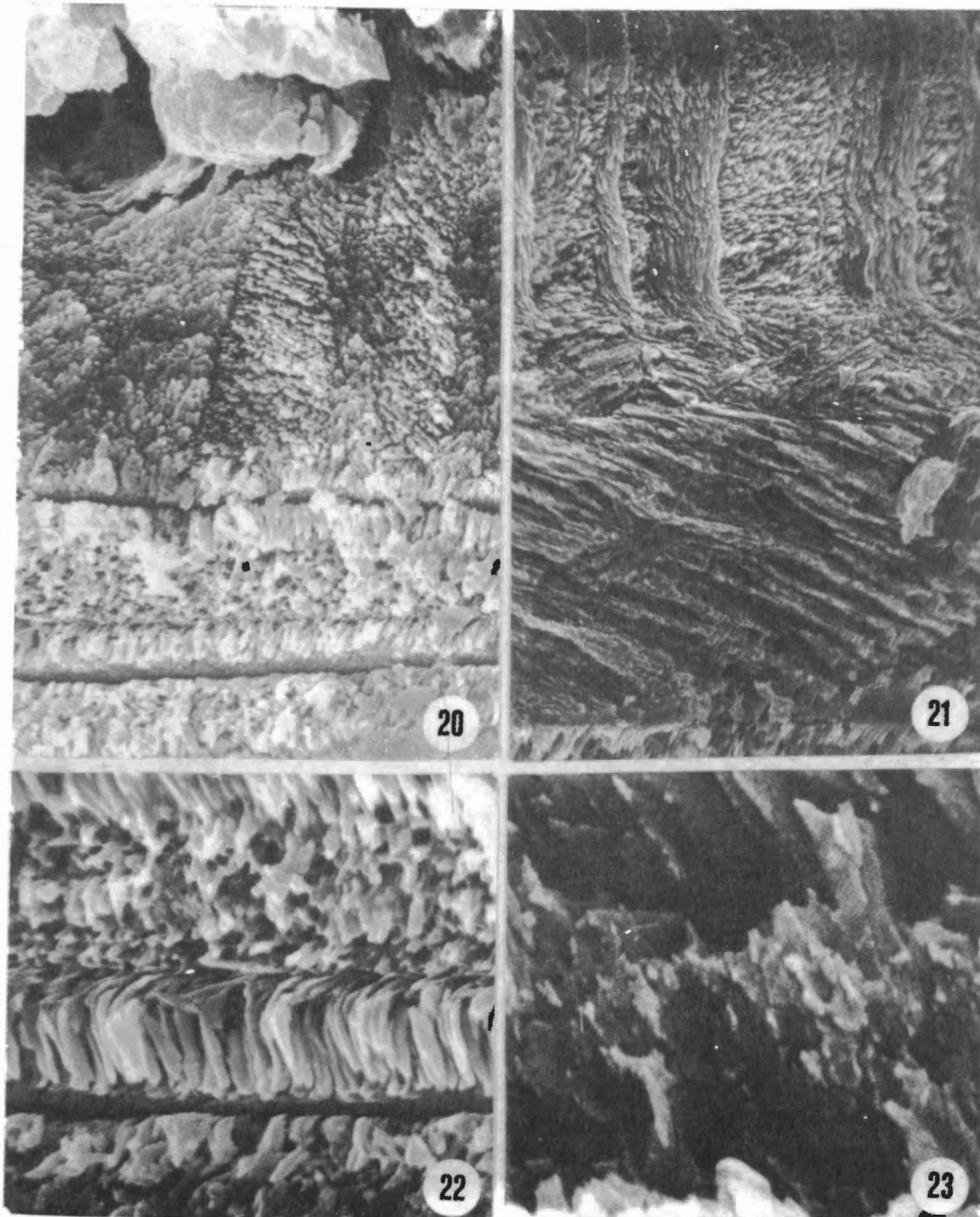
Figs 8 - 11. Teleoconch outer surface of *Rissoa membranacea*: 8 - a fragment of the body whorl, parietal lip and umbilicus (240 x); 9 - body whorl surface (600 x); 10 and 11 - higher magnifications showing caves (10 - 1,200 x, 11 - 1,800 x)



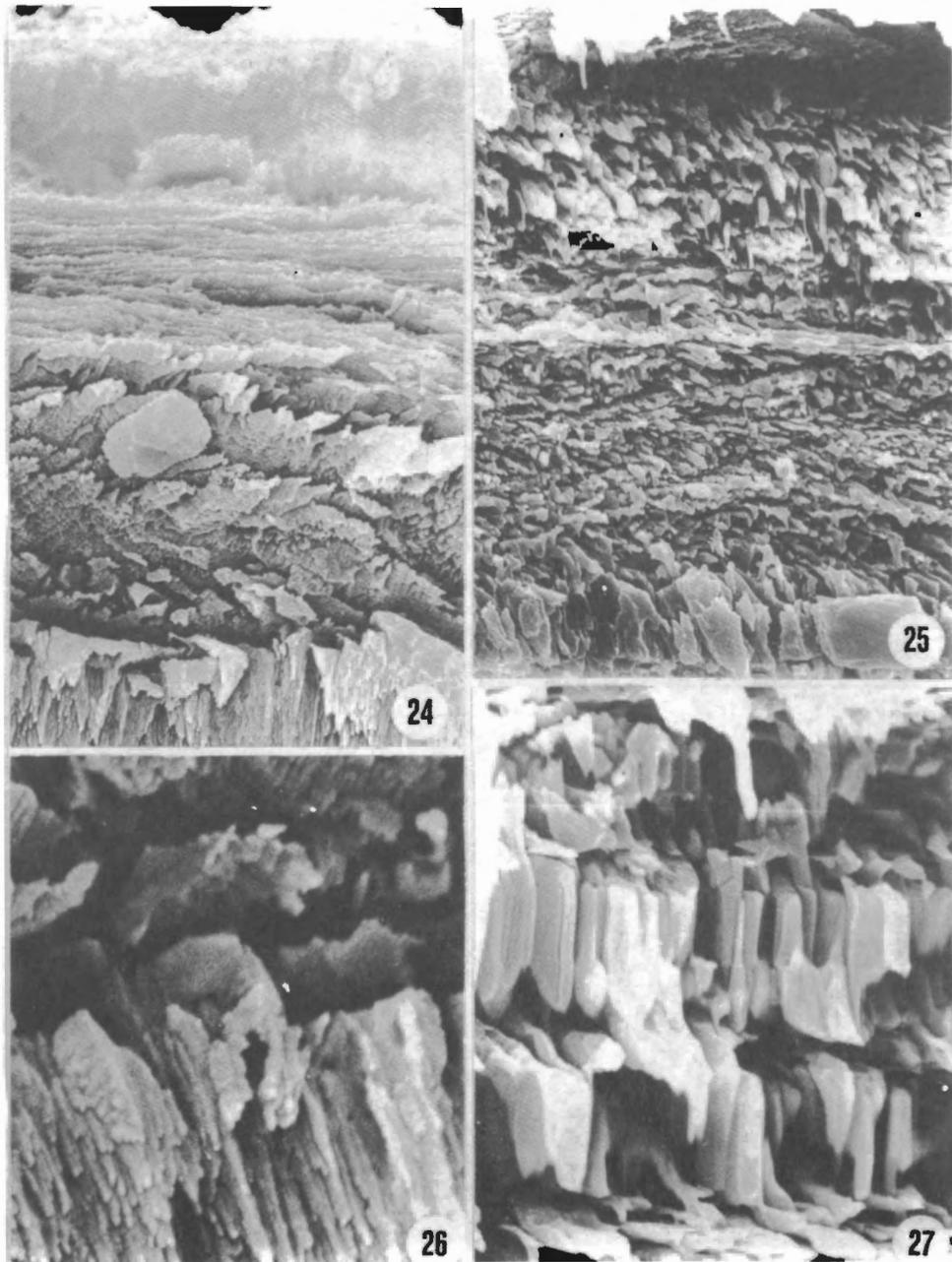
Figs 12 - 15. Teleoconch of *Rissoa membranacea*: 12 and 13 - body whorl surface (12 - 1,200 x, 13 - 1,000 x); 14 and 15 - body whorl sections: 14 - unetched section approximately perpendicular to growth lines, showing rather well discernible three layers (860 x); 15 - etched section perpendicular to growth lines (1,500 x)



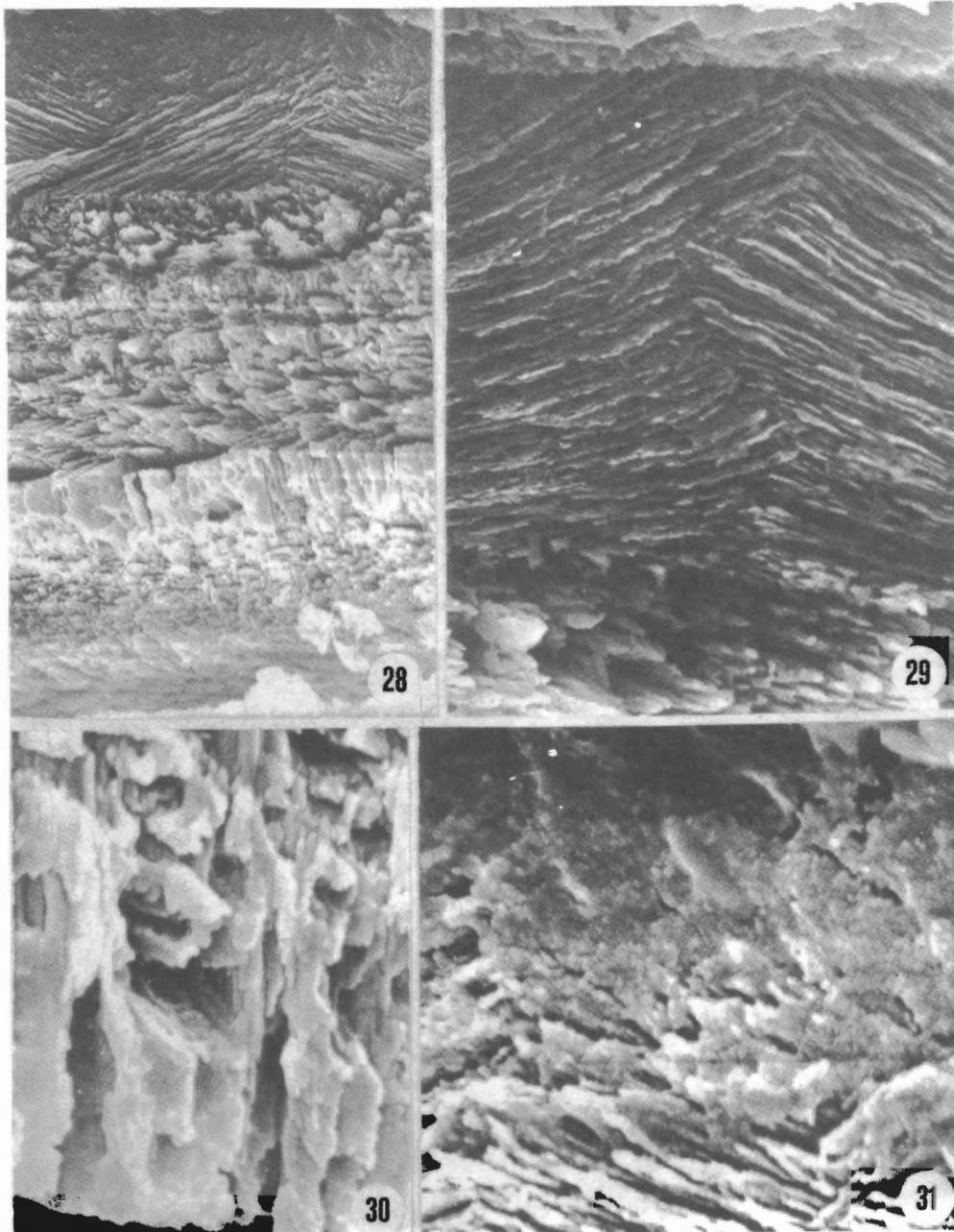
Figs 16 - 19. Teleoconch sections perpendicular to growth lines (16 and 19 - approximately perpendicular) of *Rissoa membranacea*: 16 and 17 - whole sections (16 - 1,300 x, 17 - 1,500 x); 18 and 19 - outermost fragments: 18 - fragment of section 17 (8,000 x), 19 - fragment of section 16 (6,600 x)



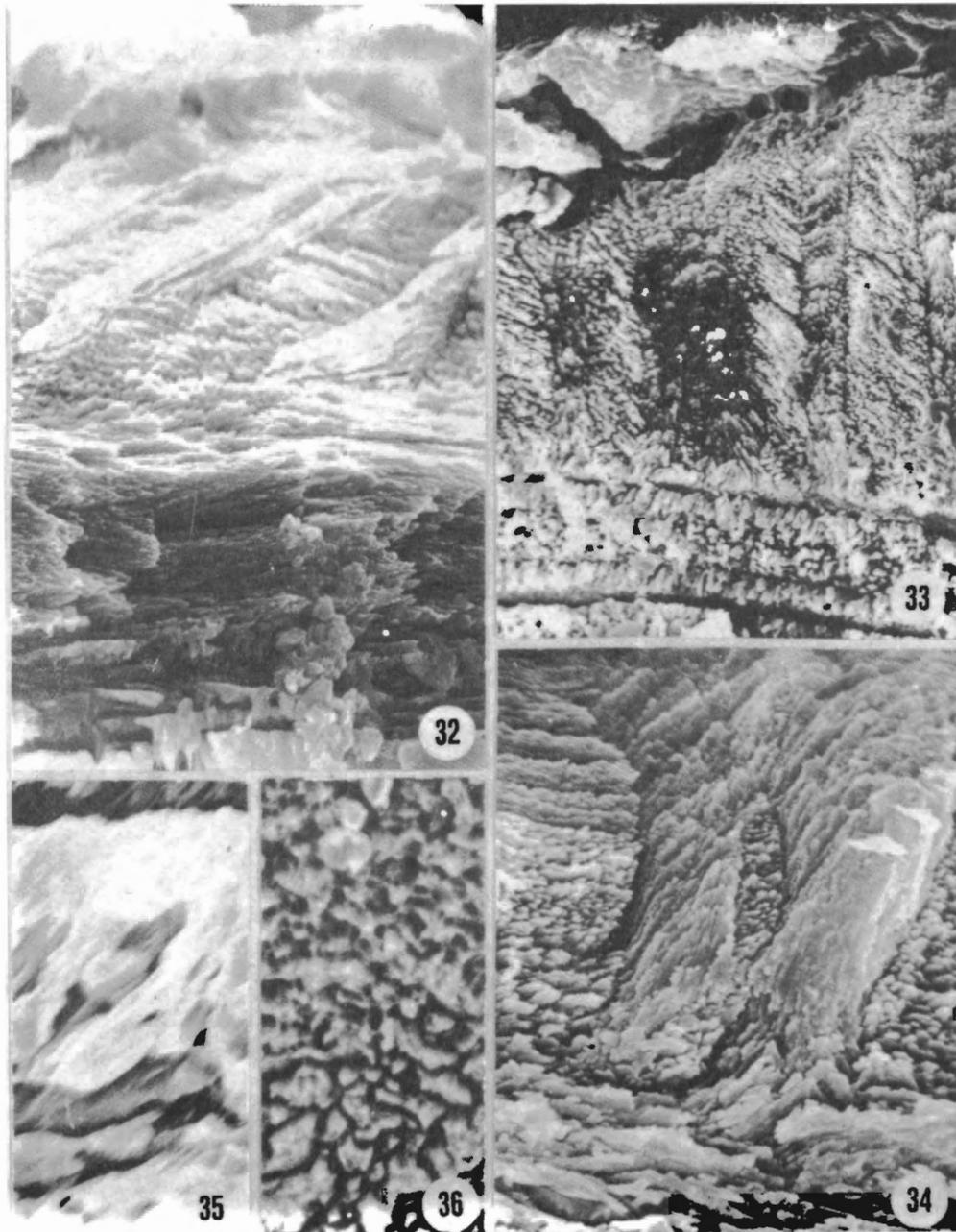
Figs 20 - 23. Teleoconch sections perpendicular to growth lines (20, 22, and 23 - approximately perpendicular) of *Rissoa membranacea*: 20 - 21 - whole sections (20 - 1,800 x, 21 - 1,300 x); 22 and 23 - innermost fragments: 22 - of section 20 (4,000 x), 23 - of section 16 (6,600 x)



Figs 24 - 27. Teleoconch sections parallel to growth lines (24 and 26 - approximately parallel) of *Rissoa membranacea*: 24 and 25 - whole sections (2,000 x); 26 and 27 - fragments (6,000 x): 26 - innermost fragment of section 24, 27 - periostracum-adjointing fragment of section 25



Figs 28 - 31. Teleoconch sections parallel to growth lines (28, 30 and 31 - close to the suture), body whorl, of *Rissoa membranacea*: 28 and 29 - whole sections (28 - 1,200 x, 29 - 3,600 x); 30 and 31 - fragments of section 28 (6,000 x): 30 - innermost fragment, 31 - outermost fragment (periostracum and periostracum adjoining layer)



Figs 32 - 36. Teleoconch of *Rissoa membranacea*: 32 - 35 - sections: 32 - slanting to growth lines (1,600 x), 33 - approximately perpendicular to growth lines (1,300 x), 34 - slanting to growth lines (2,400 x), 35 - innermost layer of section parallel to growth lines (4,800 x); 36 - inner surface of body whorl (4,400 x)