

A CRITICAL REVIEW OF SOME CHARACTERS WIDELY USED IN THE SYSTEMATICS OF HIGHER TAXA OF FRESHWATER PROSOBRANCHS (GASTROPODA: PROSOBRANCHIA), AND A PROPOSAL OF SOME NEW, ULTRASTRUCTURAL ONES

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ABSTRACT: In the paper the author presents a critical analysis of some characters, widely used in taxonomy of Prosobranchia, as: shell architecture, external morphology of cephalopodium, heart and mantle cavity organisation, ctenidium, osphradium, kidney, radula, digestive system, central nervous system, and male as well as female reproductive organs. The analysis is mainly based on the author's studies on the Polish freshwater prosobranchs. The author points out limitations of usefulness of practically all characters for recognition of the real phyletic relationships between the higher prosobranch taxa. Then the author proposes some new characters based on SEM shell studies: protoconch and teleconch outer surface sculpture, teleconch inner surface sculpture, and structures visible in shell cross-sections. The structures as well as radulae are presented in 84 SEM photographs. The outer and inner surfaces of both the proto- and teleconch turned out to be rather poorly differentiated and more variable within than between families, while the organisation pattern of shell cross-sections seemed characteristic for a given family and then a good character, not less useful in family grouping than good "classic" ones.

KEY WORDS: ctenidium, osphradium, radula, digestive system, central nervous system, reproductive organs, protoconch, teleconch sculpture/inner structure

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**A CRITICAL REVIEW OF SOME CHARACTERS
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Abstract: In the paper the author presents a critical analysis of some characters, widely used in taxonomy of Prosobranchia, as: shell architecture, external morphology of cephalopodium, heart and mantle cavity organisation, ctenidium, osphradium, kidney, radula, digestive system, central nervous system, and male as well as female reproductive organs. The analysis is mainly based on the author's studies on the Polish freshwater prosobranchs. The author points out limitations of usefulness of practically all characters for recognition of the real phyletic relationships between the higher prosobranch taxa. Then the author proposes some new characters based on SEM shell studies: protoconch and teleconch outer surface sculpture, teleconch inner surface sculpture, and structures visible in shell cross-sections. The structures as well as radulae are presented in 84 SEM photographs. The outer and inner surfaces of both the proto- and teleconch turned out to be rather poorly differentiated and more variable within than between families, while the organisation pattern of shell cross-sections seemed characteristic for a given family and then a good character, not less useful in family grouping than good "classic" ones.

I. INTRODUCTION

The gastropod systematics has for a long time been a subject of interest of many malacologists. However, it raises a lot of controversies, contains many vaguenesses and within numerous groups its character is actually provisional, even with regard to the most general pattern of phyletic relationships. This concerns either the species level (I discuss this problem in a separate paper: Falniowski in press a), or the higher systematic units. It is just enough to compare the systems of different authors as: Pelseneer (1906), Thiele (1931), Fretter and Graham (1962), Wilbur and Yonge (1964), Starobogatov (1970), Graham (1971), Götting (1974), Golikov and Starobogatov (1975), Salvini-Plawen (1980) and Haszprunar (1986a, b).



The above picture is most striking within the prosobranchs. There are several reasons for it. To start with, the group is very rich in species (at least about 70,000), widely distributed, highly differentiated, but still poorly known, particularly in respect of the anatomy. Secondly, the parallel evolution commonly observed within the group makes attempts to create the natural system much complicated. Moreover, many groups present the typical mosaic pattern of some characters regarded as primitive together with some others considered to be derived, there being any theoretically possible composition of them.

The situation renders a basic meaning to the estimation of such characters that the systematics could be based on, the more that many of those widely used so far raise serious doubts as to their usefulness. This is the problem the present paper deals with. After a critical discussion on a number of characters, that have been in use so far, I present the results of my attempt to employ the shell structures for the purposes of family and higher groupings.

II. MATERIAL

The present critical review of taxonomical characters has become the basis of revisions of the Polish Prosobranchia, completed by the author (Falniowski 1987a and Falniowski in press b). For reasons beyond the author's control, this is turning up later than the issuing revisions. All the data concerning the shell architecture, soft part morphology and anatomy, this critical review is based upon, are contained in those two papers together with the description of the material and the methods employed. On the contrary, no characteristics of particular families in respect of the outer and inner shell structures have been presented so far, hence it has been necessary to present them in the further chapters of this paper. It must be stressed, that the Polish freshwater Prosobranchia, the analysis deals with, are not the best for the purposes of such a general comparison. Unnumerous species belong to different groups which, being rich in species and differentiated worldwide, are not necessarily closely related by ancestry. It seems, however, that in spite of the patchy character of the data base a comparison of the characters concerning their usefulness proves justified.

The system of the Polish freshwater prosobranchs (Falniowski 1987a, Falniowski in press a and b) has been drawn as follows: order Neritacea: family Neritidae; incertae sedis (probably though not certainly Caenogastropoda: Rath 1986): family Valvatidae; order Caenogastropoda: suborder Architaenioglossa and suborder Rissoacea. Within the Architaenioglossa:

family Viviparidae. Within the Rissoacea: family Bithyniidae (?) and superfamily Hydrobioidea, the latter containing the families: Lithoglyphidae, and Bythinellidae, as well as the genus Potamopyrgus of unknown systematic position (Falniowski 1987a).

Such relationships render the discussion limited to the family level, considering on the one hand the distinctness of the Meritidae as a representative of the Meritacea and on the other hand markedly close relations between the families of the Hydrobioidea.

III. STUDY TECHNIQUES OF THE SHELL STRUCTURES

Shells for the outer surface analysis were cleansed of debris in the saturated water solution of oxalic acid, brushing them with needles and a short-haired brush to accelerate the process, then intensively washed in tap water first, and in distilled water in the end. Next, the shells were washed twice in absolute alcohol and dried. Besides the protoconchs, fragments of the body whorls were chosen for the outer surface structure analysis. The chosen fragments of the shells were stucked to a holder and coated with gold.

The inner shell-surface was studied within the body whorl, too. It was necessary to choose relatively small pieces of shell walls to be stucked so that their whole surface was clinging to a holder (to avoid the electrostatic effect making it impossible to obtain satisfactory photographs). Etching was also necessary (carried out as for cross-sections, see below), as well as examining numerous specimens.

To omit age variability, the inner shell-structure examining was also limited to the body whorls of full-grown shells. Shells were broken up with tweezers, paying attention to the direction of a section in relation to the growth lines of the shell. Sections perpendicular to the growth lines have proved most useful for systematic purposes, while parallel ones were less often employed. Diagonal sections as well as ones being close to the columella were rejected, since they were very difficult to be interpreted. The chosen fragments were usually situated far from the suture, more or less at the middle height of the body whorl.

The properly broken up, chosen pieces of shells were washed in tap water and etched. An unetched cross-section (Fig. 66) is slightly differentiated, bearing little information, and generally similar in all the gastropods studied in the present work. There is no way but etching to show a variety of structures (Figs 67 - 84). The best results were obtained by 10 - 25 seconds of etching in n/10 hydrochloric acid solution. After that a very intensive continuous washing was necessary for not less than 30 mi-

notes, distilled water needed at least in the end. Finally, after rinsing twice in absolute alcohol, the shell pieces properly arranged were stuck to a holder and coated with gold.

IV. REVIEW OF MOST COMMONLY EXPLOITED CHARACTERS

In the present gastropod systematics the tendency is observable to exploit as many characters as possible, attempting to consider the morphology of all structures. This approach aims to find possibly all the morphologic differences, that appear between the taxa under consideration. Those differences are thought to reflect potential phyletic relationships between the taxa.

However, as phenetic as cladistic approach must exploit various structures in a various degree. For instance, Davis and Pons da Silva (1984), distinguishing 32 useful characters in the systematics of the Hydrobiidae s. lato, found not less than 50% of the characters in the structure of the reproductive organs (female: 34%, male 16%), while the shell characters covered only 9%, the head, mantle and foot morphology: 22%, the radula characters: 6%, and the remaining 12% were evenly distributed among the characters of the mantle cavity, stomach nervous system, and eggs (each covering 3%).

1. Shell

The shell, or more precisely its architecture is only exceptionally useful in family groupings (Radoman 1973, Davis 1979, 1980, 1981, Davis and Pons da Silva 1984, Ponder and Yoo 1980, Falniowski 1987a). Additionally, it must be underlined that whereas there may be marked differences in shell architecture between particular families, no shell form exists being unique for only one family. Moreover, numerous gastropods also from among the Polish prosobranchs are distinct with their primitive, conic shells.

This was a family grouping based on shell characters, completed with rough studies of the radula, that the family Hydrobiidae, as understood in the traditional way, resulted from. After more thorough studies that family turned out to be an absolutely artificial assemblage of tiny rissoaceans having mainly such primitive conic shells. The case is just as if the shell (with few exceptions) was "neglected" in the process of radiation. Hence, family groupings are almost entirely based upon the soft part morphology and anatomy.

2. External morphology of soft parts

Family groupings commonly employ the external features as: the proportions of the head (especially snout) and cephalic tentacles, the presence

or absence of the hyperciliation of one of the latter, the proportions and outline of the foot, its possible division into the pro-, meso-, and metapodium, the development stage and possible general pattern of the cephalopodium pigmentation, the number, situation, shape, and development stage of the outlets of the bigger mucous glands of the foot, as well as the occurrence and development stage of the metapodial and pallial tentacles.

The characters mentioned above are not very useful. They are rather uniformly developed, so descriptions of the mentioned structures may be, in fact, identical for a number of families. Additionally, it may be hazardous to draw conclusions on relationships from those characters: for instance, the well developed pallial tentacles forming siphons occur in the Viviparidae, Bithyniidae and Valvatidae, though more thorough studies have proved their origin different in each family.

3. Anatomy

The characters in use are as follows: the general organization of the mantle cavity together with gills and osphradium, the structure of the heart, kidney, radula, alimentary system, central nervous system, and male and female reproductive organs. The mentioned characters are relatively most useful, but of course the degree of the usefulness of particular ones is different.

The heart organization of the Neritidae, representing the separate order Neritacea, distinguishes them from the Polish Prosobranchia. The remaining caenogastropod families are not diversified in respect of the heart structure, thus the character is not useful on the family level. The mantle cavity and gill organization also permits the Neritidae to be distinguished, but the Valvatidae, what is worth of attention, are also distinguishable owing to this character. The gill of the latter is very peculiarly organized and does not seem homologous with the ctenidia of either the Diotocardia or Caenogastropoda (Rath 1986); also the mantle cavity organization in the Valvatidae is unique. However, as it has been mentioned above, the positioning of the Valvatidae within the Caenogastropoda is controversial. As regards the remaining families, the ctenidium and mantle cavity do not show a more conspicuous interfamilial variability.

The size and proportions of the osphradium also happen to be used for family groupings. It must be added, however, that on the one hand no more considerable interfamilial differences are marked in the states of those characters, and on the other hand a strong influence of the environment inhabited by a given gastropod is well expressed. Alternatively, the fine structure of the osphradium seems to reflect well relationships between higher gastropod taxa (Haszprunar 1983).

When considering relationships, either the position of the kidney towards the viscera and pallium or the accompanying structures (e.g. the characteristic big coelomatic sacs of the Neritidae) and the entire kidney structure are used. All the families under consideration are characterized by a bi-armed kidney, one of the arms being thin-walled and originated as an osmoregulatory organ - an adaptation to inhabiting fresh and brackish waters. The thin-walled arm (most developed in the Bithyniidae, while less in the Viviparidae and least in the Valvatidae) usually lies alongside the mantle cavity, but in the Hydrobioidae it fills the spaces between the viscera. The outlet of the arm lies posteriorly, deep in the mantle cavity in the Neritidae and Bithyniidae, whereas in the Viviparidae and Valvatidae it is situated anteriorly, near the mantle edge. The origin of the arm is also variable (Johansson 1950): it is a pallial structure in the Valvatidae, while a renal one in the Bithyniidae. Hence, it is obvious that some characters of the kidney structure may be a useful criterion.

Radula

The radula is one of the earliest considered inner structures, however, one must be reluctant to accept its unlimited usefulness. It is widely acknowledged that the radula, because of its intimate contact with feeding substrates, is easily modified evolutionarily, and that radulae are not conservative in character. It is acknowledged that macroevolution in the Gastropoda was in the way of food specialisation (Cooke 1921, Purchon 1977), though some rather common cases of convergence are known in the radula structure (Solem 1973). The rhipidoglossate radula of the Neritidae (Figs 1 - 3) is quite different, indeed, from the taenioglossate radulae of the other Polish prosobranchs (Figs 4 - 17).

As Hickman (1980) remarked judiciously, it is simple to analyse homology in the case of the primitive rhipidoglossate radulae, but very difficult (if not impossible) in case of the derived taenioglossate radulae, originated as a result of numerous reductions of teeth. The reductions are hardly homologisable and one should be aware that the Taenioglossa radula could have originated many times, in various ways, thus its presence in a certain group of gastropods does not necessarily prove their monophyletic origin.

Hickman (1980) remarked that the observed appearance of the radula has been affected with a number of factors, besides those controlled by its phylogeny and function. Whereas the general organization of the radula and probably the morphology of the basal parts of its teeth reflect the general pattern and are inherited from far ancestors (in this part radiation does not lead to the apparent similarity of the radulae of the ani-

mals which are not related more closely but feed in similar way), a number of the radula characters are determined by other factors that could be divided into six groups: mechanical, ecological, programmatic, maturational, degenerative, and constructional ones.

The mechanical factors are responsible for the modifications that strengthen the radula or improve its functioning, as for instance basal expansion and overlap or interlock to distribute stress that might tear the thin, delicate radular membrane during feeding.

The ecological factors are direct adaptations of the radula to the character of food, what seems neither rapid nor precise. The programmatic ones are associated with disturbances in functioning of odontoblasta, effecting in teeth being untypical, fused, deleted, etc., what repeats in successive transverse rows. Some structures as denticles, knobs, and surface irregularities of some other kind (Fig. 7), may be an effect of the constructional factors, that means determined by poorly known properties of the process of chitin formation. The maturational factors comprise changes newly-formed teeth underwent when moving forward, that is formation and hardening of the teeth. The degenerative ones cover alterations in cusps through usage, in oportunistic species for example resulting in considerable differences between individuals as an effect of their feeding on various food.

There are a lot of examples of the lack of more conspicuous differences in both food character and feeding mode between even not quite closely related families. The case is observed, for instance, in the Viviparidae (Figs 4 - 6) and Bithyniidae (Figs 10 - 11); it is evident that their similar diet did not alter some characters having probably rather phylogenetic but not functional determinants. There are, for example, basal cusps on the dens centralis in the Bithyniidae (Fig. 11), but not in the Viviparidae (Fig. 5). On the contrary, there may be considerable food differences within one family.

On the one hand, the radula cannot be absolutely unadapted to the food character and the mode of feeding (e.g. feeding on algae overgrowing stones demands a considerably stronger radula than feeding on those overgrowing macrophytes), but the tolerance range is fairly wide and one particular food may be eaten by an animal whose radula has the structure belonging to a quite wide diversity interval, especially if the food has no special mechanical properties. On the other hand, most of the structure types of radula are quite universal and, in spite of very few cases of the extremely specific mode of feeding, can fulfil their tasks. The fact that practically none from among the Polish taenioglossate gastropods is narrowly specialised towards the mechanical properties of the food it feeds on, is also important for the problem discussed.

Since cusps are in a direct contact with food, they seem most closely associated with the niche character, so best reflecting adaptive radiation. However, their usefulness is very limited, especially by a considerable variation, also within a species (e.g. Figs 8 and 9).

There being a considerable individual variation and the common taenioglossate pattern the interfamilial differences are small. To consider the rhachis almost solely, as it is often practised, is an additional limit of the taxonomic usefulness of the radula. For example, the spoon-shaped inner marginal teeth of the Valvatidae (Fig. 7) are characteristic of this family.

The radulae of the Bithyniidae (Figs 10 - 11) do not differ more conspicuously from those occurring in the Hydrobioidea (Figs 12 - 17) and show little interfamilial difference. Hence, the radulae are of a limited usefulness at the family level, and their use needs a thorough analysis of the character of the observed differences as well as satisfactory data on their variability

Digestive system

Although similar remarks may in general concern the digestive system, there are some essential differences. For instance, when a gastropod alters its food, searching for soft and easily assimilable substrates, both the radula and digestive system are becoming simplified. The radula, in spite of its simplification and size reduction, maintains some characters resulting from its former organisation, while the simplified digestive systems of various gastropods, originated from variously organised former systems, are generally similar. For instance, the digestive systems of the Viviparidae and Valvatidae are very similar to each other, whereas their radulae differ considerably.

In practise, the characters employed for the purposes of systematics are as follows: the absence or presence of one, two or three jaws, the occurrence and stage of development of the dorsal folds of the mid-oesophagus and oesophageal glands, the proportional length of the intestine and rectum and their arrangement, as well as, especially, numerous details of the stomach organisation, as the presence and stage of the development of the style sac, typhlosoles, gastric shields and caecum-like prominences.

The length of the alimentary canal, especially of the intestine, is much depending on what food is digested. All the gastropods discussed in the paper, particularly the Valvatidae and Viviparidae, have the alimentary canals shortened. The oesophageal glands occur if there is no crystalline style and no sac (Fretter and Graham 1962), what is observed in the Valvatidae and Viviparidae. The crystalline style occurs in the Bithyniidae and Hydrobioidea. Some families of the Hydrobioidea are distinct with their stomachs having the posterior chamber with a fold and posterior prominence (among the discussed gastropods only Potamopyrgus has such a stomach).

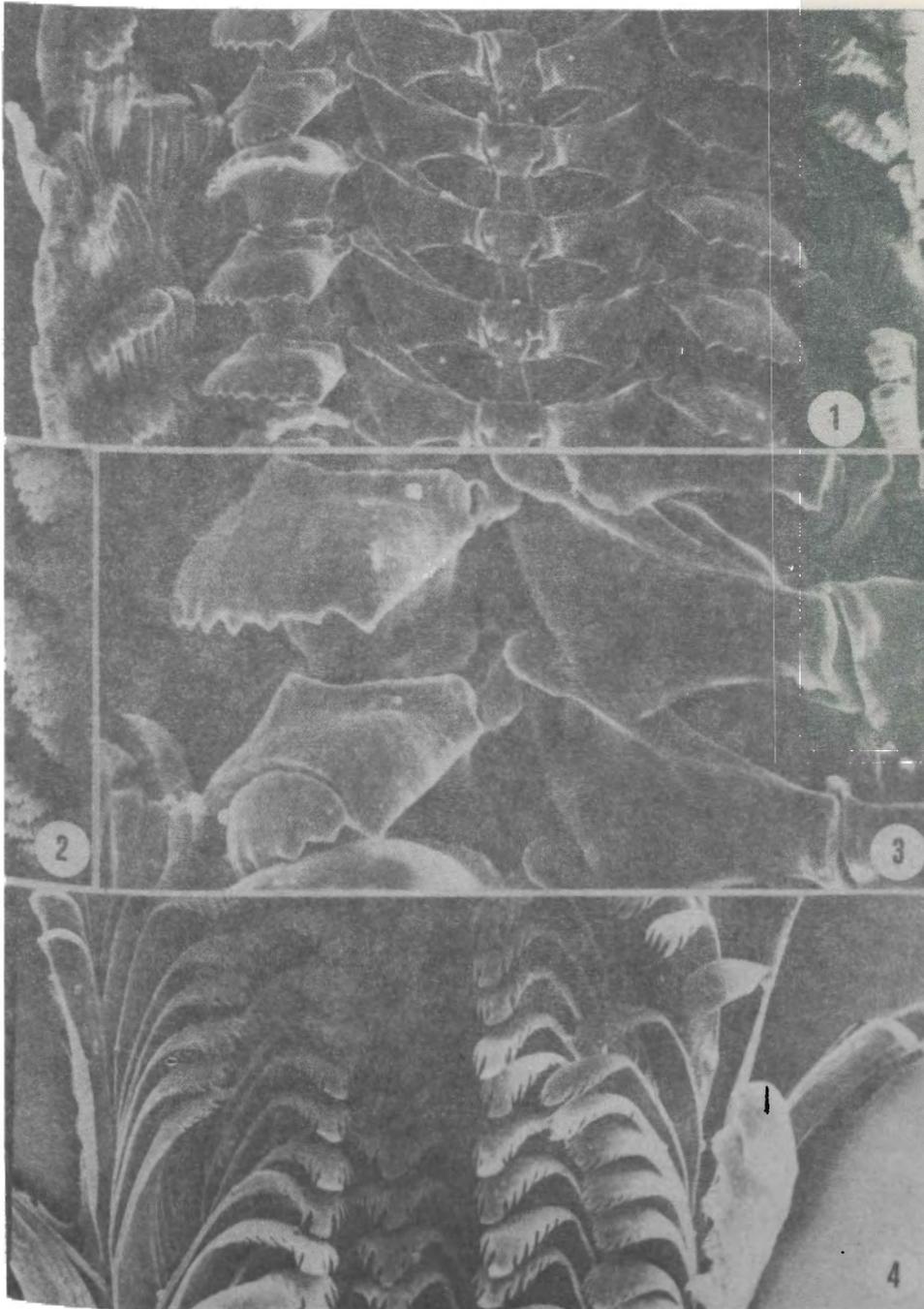


Plate I. Radulae: 1 - 3 - Theodoxus fluviatilis (Linnaeus, 1758) (1 - general view of transverse rows, 180 x; 2 - marginal teeth, 330 x; 3 - lateral teeth, 430 x); 4 - Viviparus viviparus (Linnaeus, 1758), general view of transverse rows, 130 x

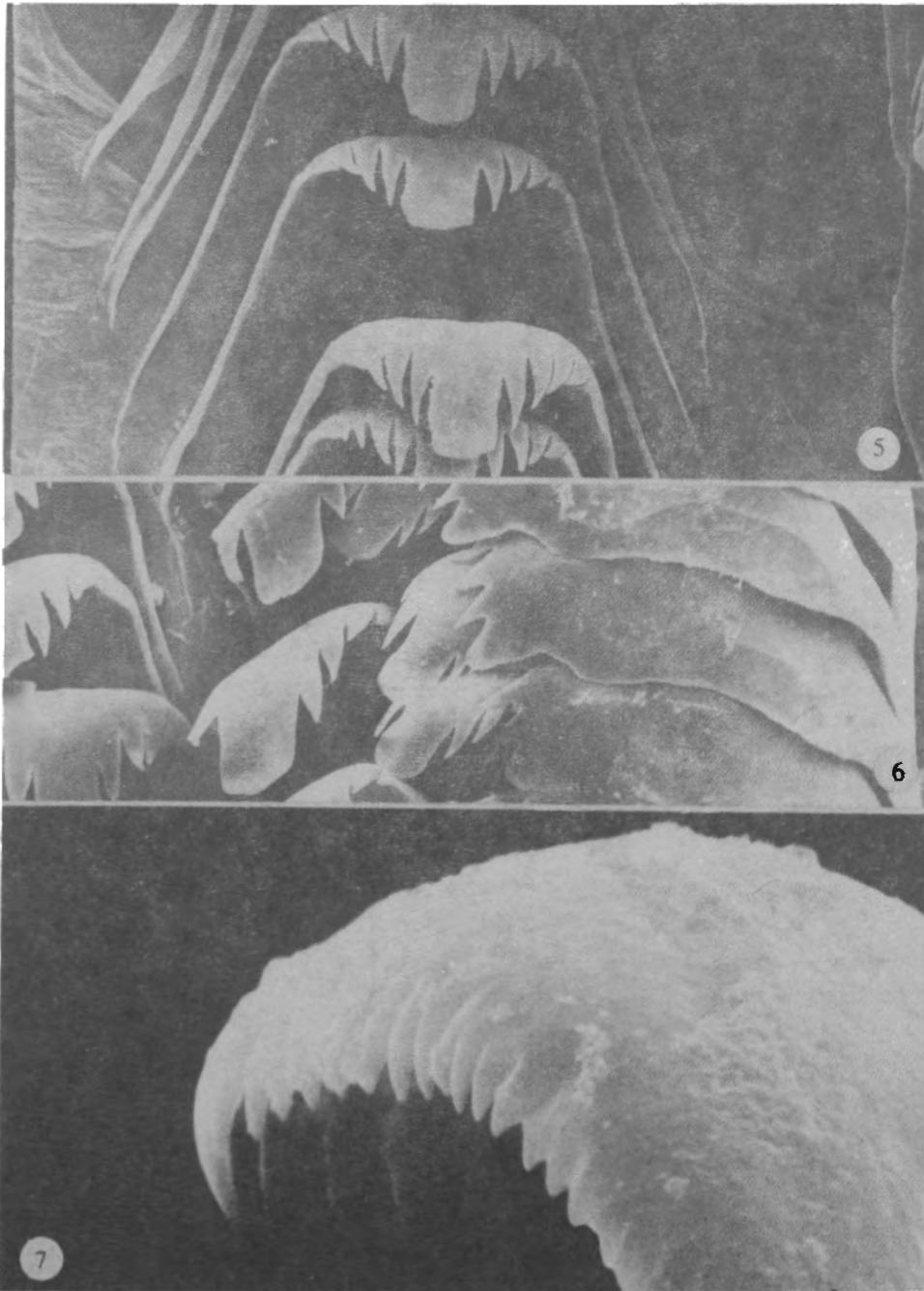


Plate II. Radulae: 5 - Viviparus contectus (Millet, 1813), central teeth, 300 x; 6 - V. viviparus (Linneaus, 1758) fragments of central teeth, lateral and marginal teeth, 300 x; 7 - Valvata pulchella Studer, 1820, distal part of outer marginal tooth, spoon-shaped, 4,400 x

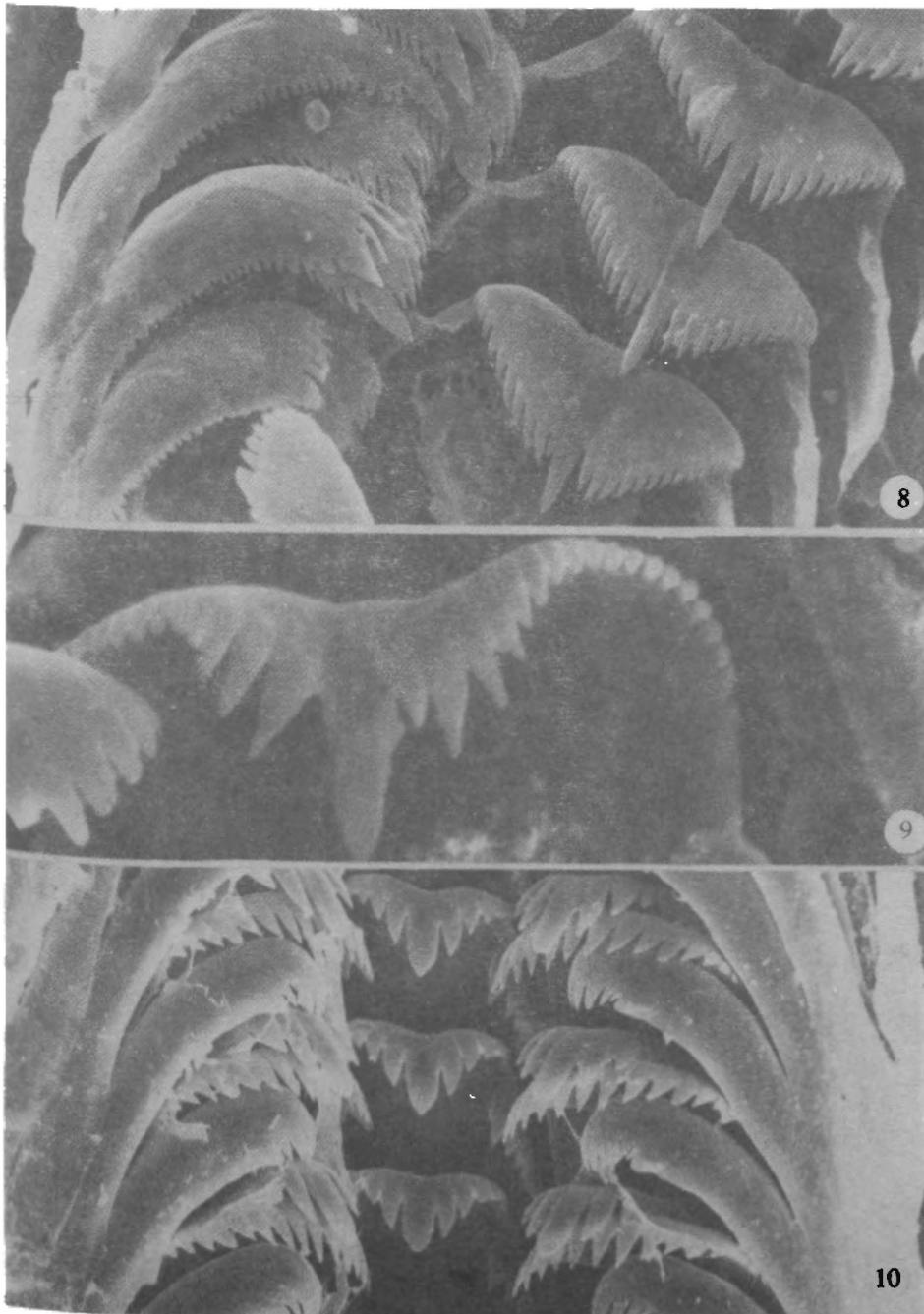


Plate III. Radulae: 8 - 9 - Valvata piscinalis (O. F. Müller, 1774): 8 - general view of half of transverse rows, 600 x; 9 - central tooth, 1,600 x; 10 - Bithynia tentaculata (Linnaeus, 1758), general view of transverse rows, 550 x

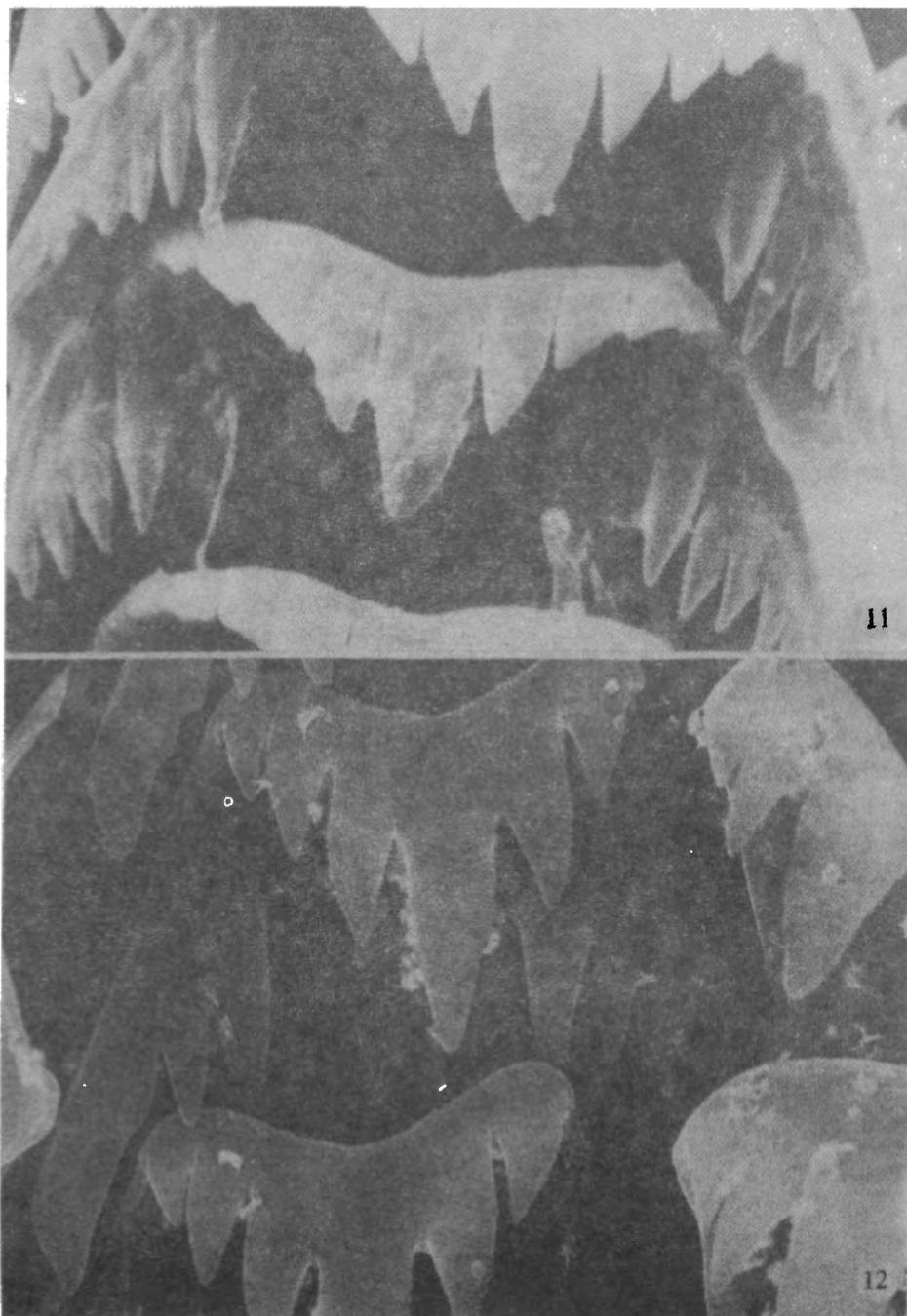


Plate IV. Central teeth of radulae: 11 - Bithynia leachi (Sheppard, 1823), 2,200 x; 12 - Lithoglyphus naticoides C. Pfeiffer, 1828, 1,300 x

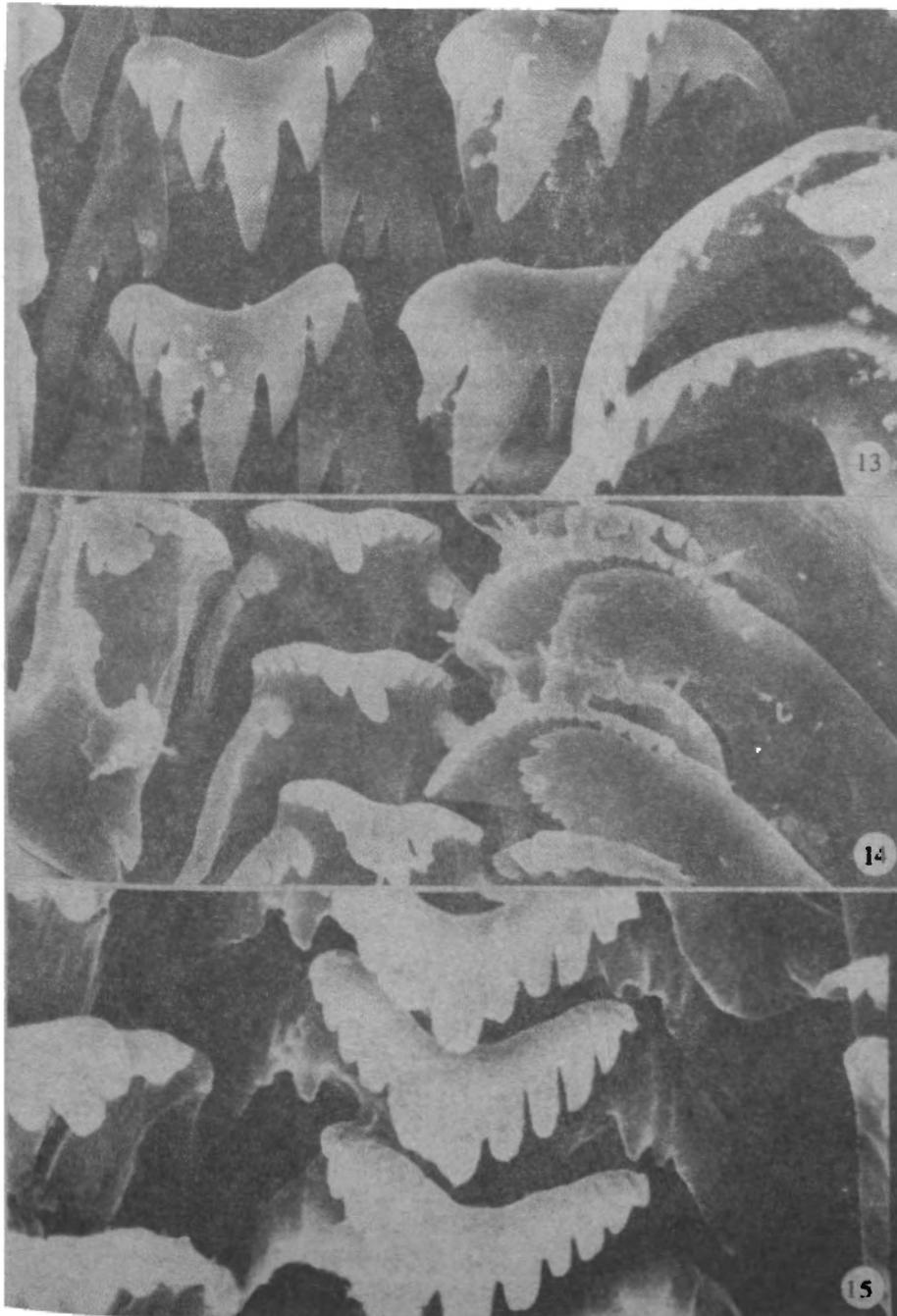


Plate V. Radulae: 13 - Lithoglyphus naticoides C. Pfeiffer, 1828, central, lateral and inner marginal teeth, 780 x; 14 - Marstoniopsis scholtzi (A. Schmidt, 1856), central, lateral and marginal teeth, 1,500 x; 15 - Bythinella richerdzinskii Falniowski, 1980, central teeth, 3,600 x.

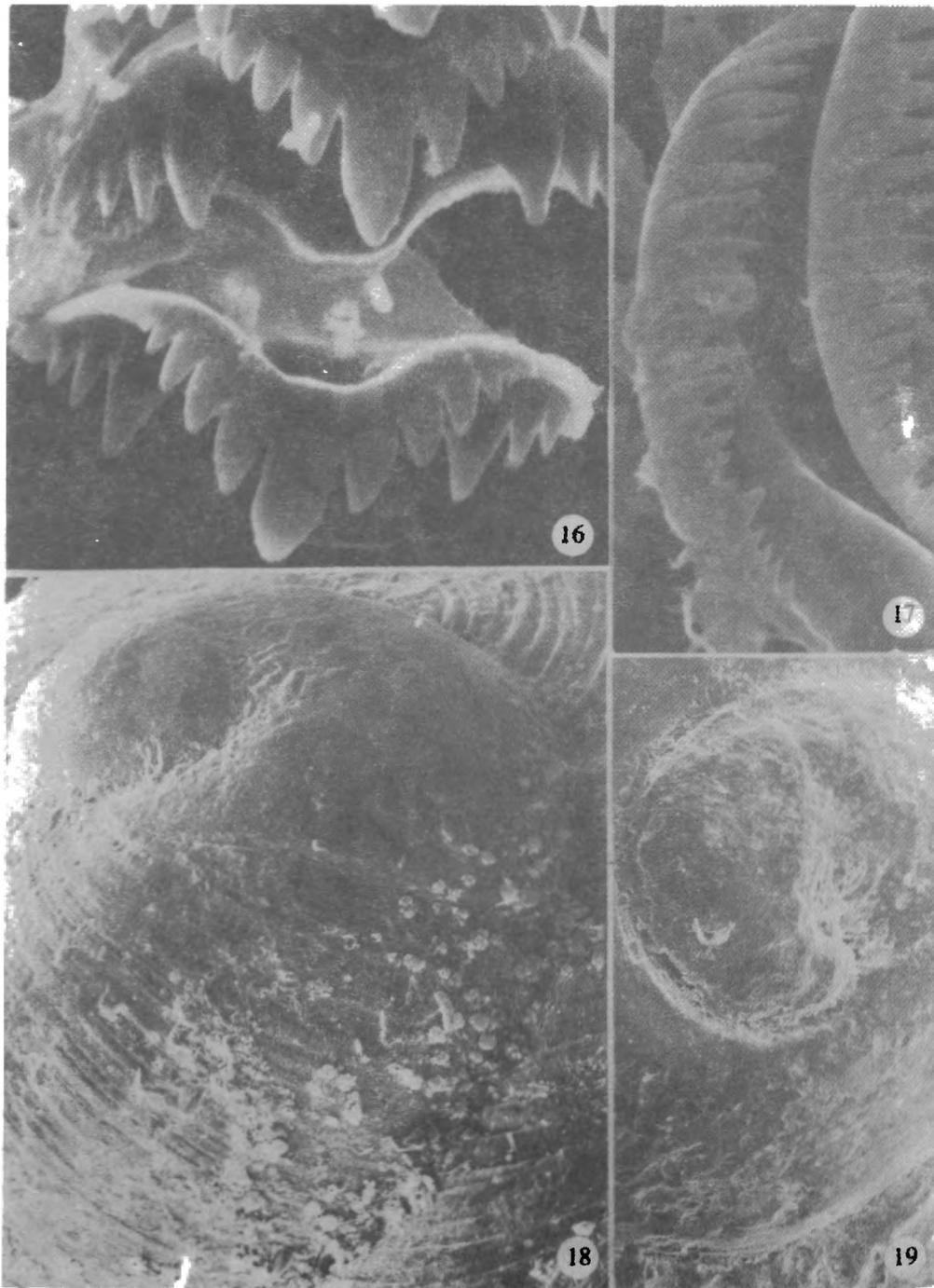


Plate VI. 16 - 17 - radulae of Potamopyrgus jenkinsi (E. A. Smith, 1889):
16 - central teeth, 2,600 x; 17 - distal parts of inner marginal teeth,
2,200 x. 18 - 19 - protoconchs: 18 - Theodoxus fluviatilis (Linnaeus,
1758), 50 x; 19 - Viviparus viviparus (Linnaeus, 1758), 43 x

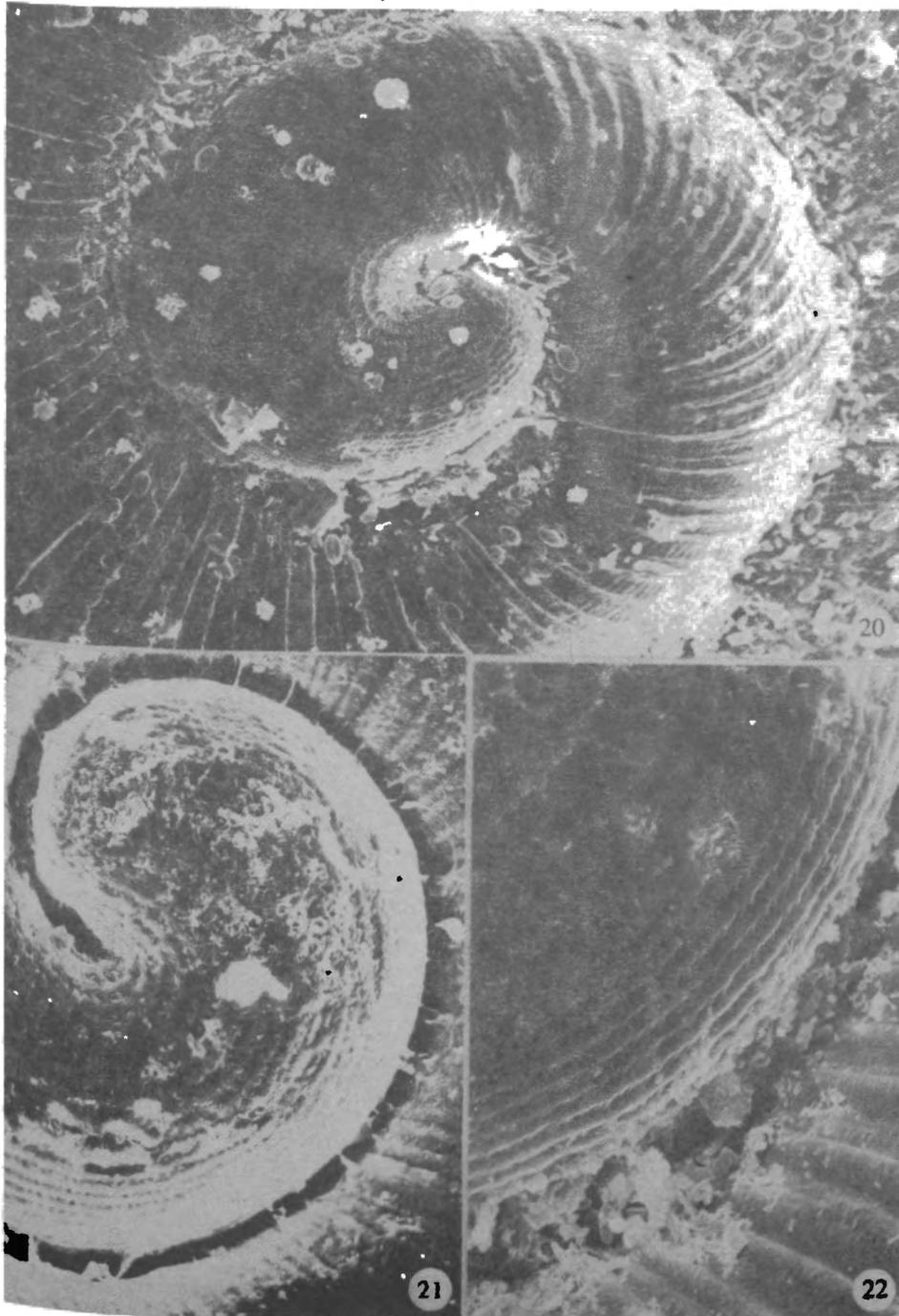


Plate VII. Valvatid protoconchs: 20 - Valvata piscinalis (O. F. Müller, 1774), 100 x; 21 - V. cristata O. F. Müller, 1774, 200 x; 22 - V. piscinalis, comparison of protoconch and teleconch sculptures 390 x

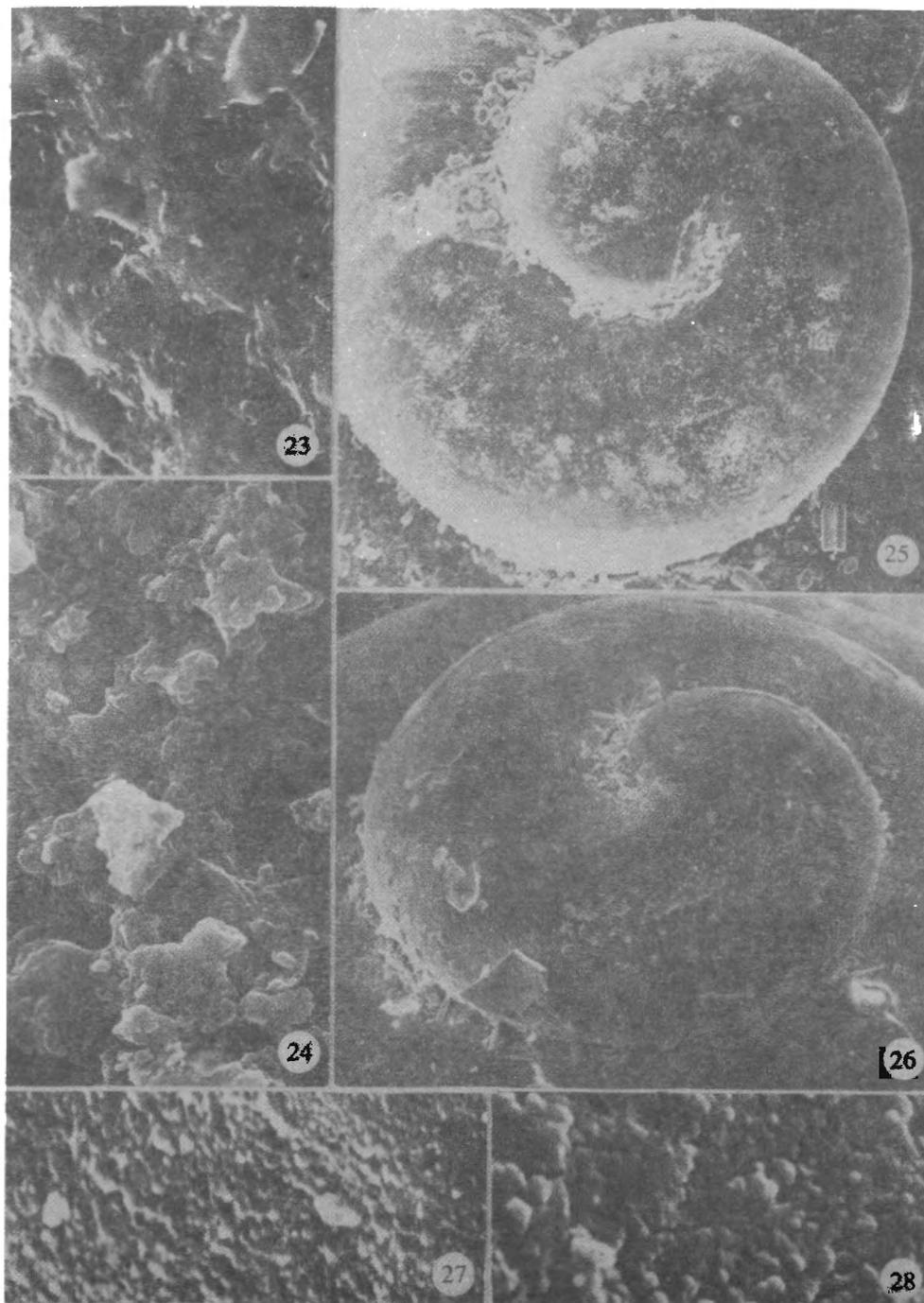


Plate VIII. Protoconchs: 23 - 24 - fragments of sculpture under higher magnification: 23 - Valvata cristata O. F. Müller, 1774, 1,800 x; 24 - V. pulchella Studer, 1820, 2,000 x; 25 - 26 - general view of protoconch: 25 - Bithynia leachi (Sheppard, 1823), 80 x; 26 - B. troscheli (Paasch, 1842), 60 x; 27 - 28 - fragments of sculpture under higher magnification: 27 - Bithynia leachi, 6,500 x; 28 - B. tentaculata (Linnaeus, 1758), 4,700 x

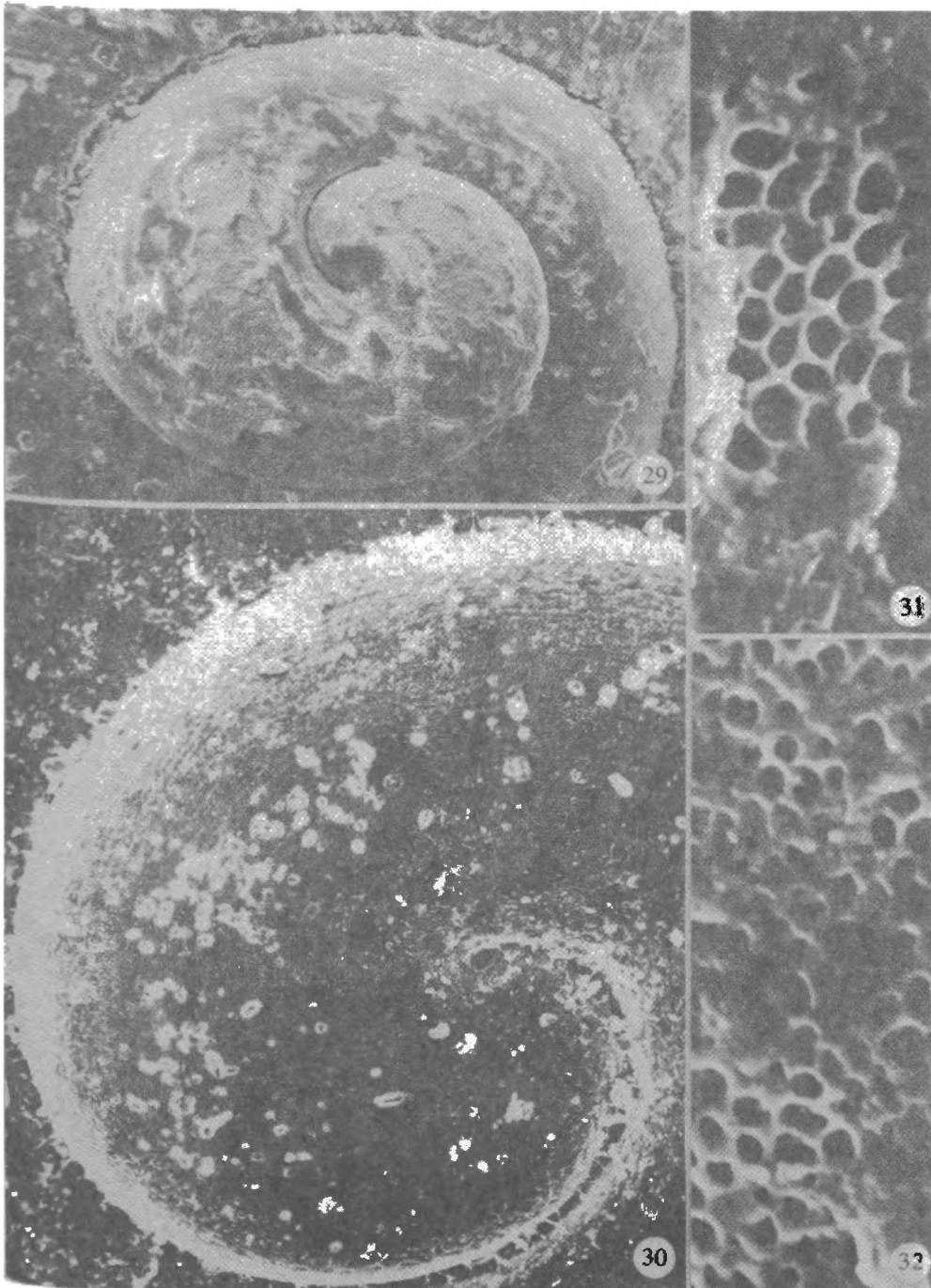


Plate IX. Protoconchs: 29 - 30 - general view: 29 - Lithoglyphus naticoides C. Pfeiffer, 1828, 60 x; 30 - Bythinella micherdzinskii Falniowski, 1980, 200 x; 31 - 32 - B. micherdzinskii, fragments of surface, visible net of open pores, 10,000 x

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Plate X. 33 - 34 - protoconchs: 33 - Bythinella zvjonteki Falniowski, 1986, 150 x; 34 - Potamopyrgus henkinsi (E. A. Smith, 1889), 220 x. 35 - 36 - Theodoxus fluviatilis (Linnaeus, 1758), fragments of sculpture of outer surface of body whorl: 35 - 300 x, 36 - 500 x

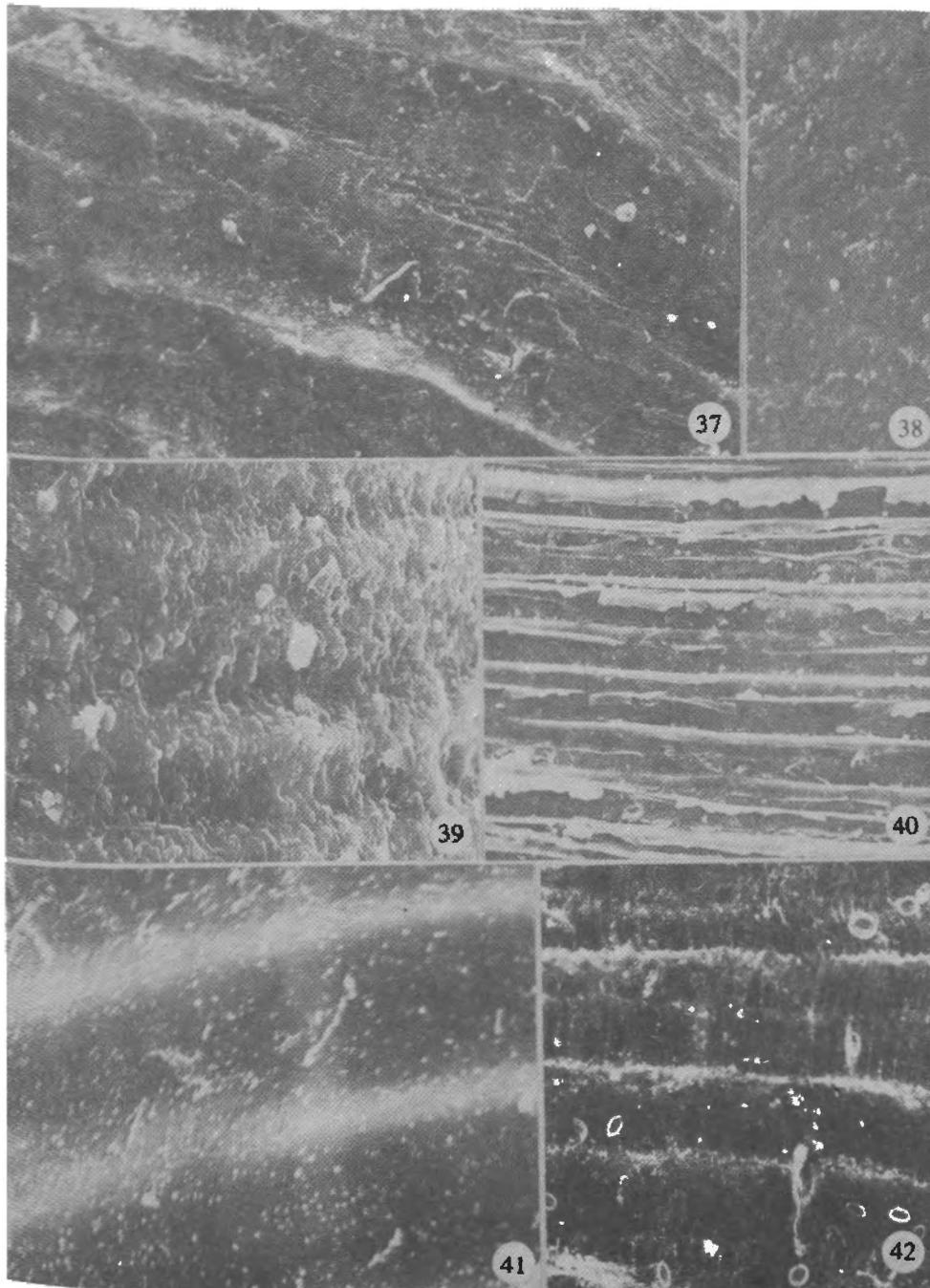


Plate XI. Fragments of sculpture of outer surface of body whorl: 37 - 38 - Viviparus coniectus (Millet, 1813): 37 - 100 x, 38 - 1,000 x; 39 - 42 - Valvata: 39 - V. cristata O. F. Müller, 1774, 1,100 x; 40 - 41 - V. pulchella Studer, 1820: 40 - laminar growth lines, 80 x; 41 - flat and rounded, non-laminar growth lines, 750 x; 42 - V. piscinalis (O. F. Müller, 1774), in interstices visible spiral lines, 100 x

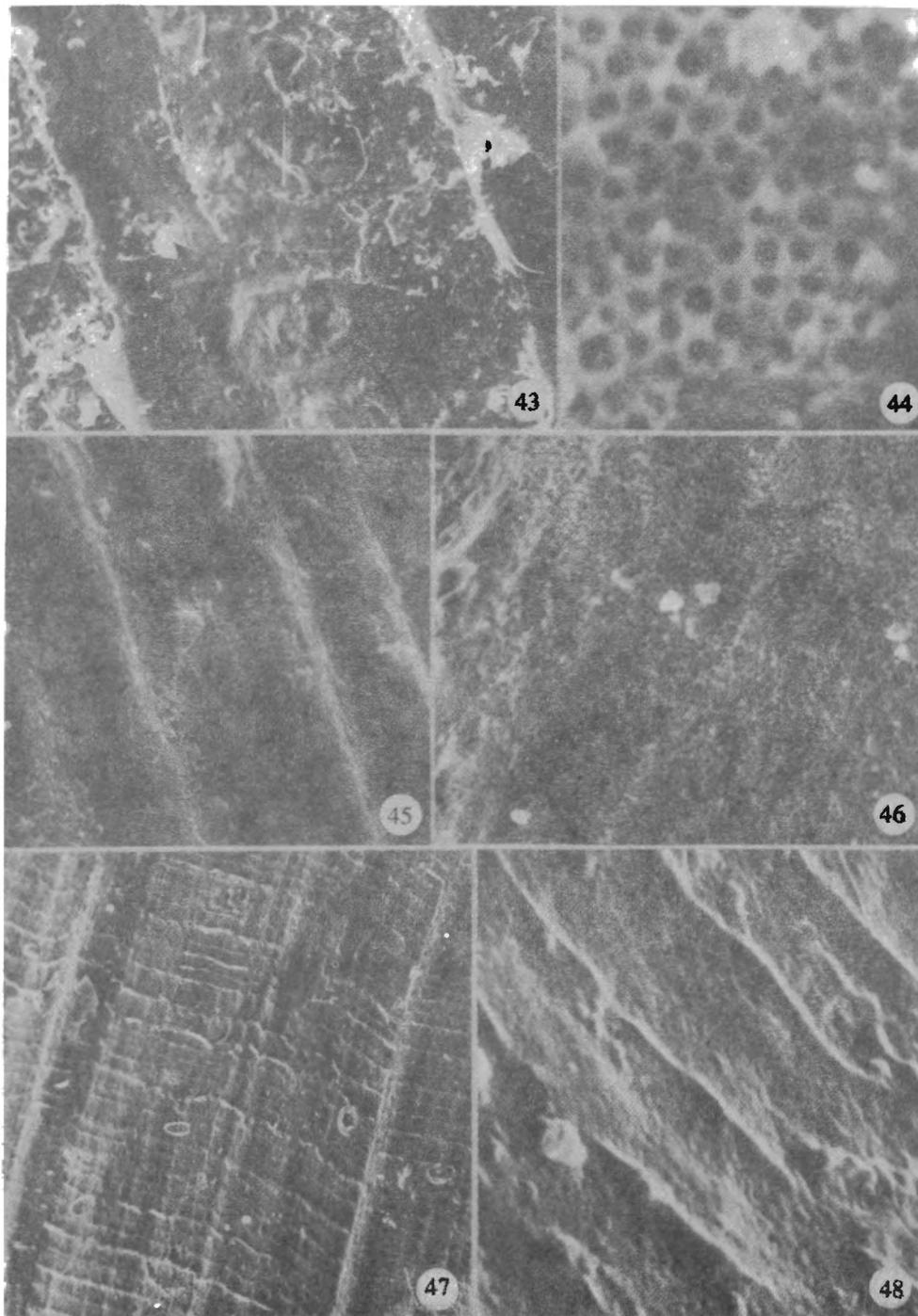


Plate XII. Fragments of sculpture of outer surface of body whorl: 43 - Valvata piscinalis (O. F. Müller, 1774), spiral lines transverse to growth lines, 1,000 x; 44 - 48 - Bithynia: 44 - B. tentaculata (Linnaeus, 1758), pores, 9,000 x; 45 - B. troscheli (Paasch, 1842), 500 x; 46 - 48 - B. leachi (Sheppard, 1823): 46 - fragment with open pores, 2,200 x; 47 - growth lines and transverse spiral lines, 220 x; 48 - spiral lines under higher magnification, 3,000 x

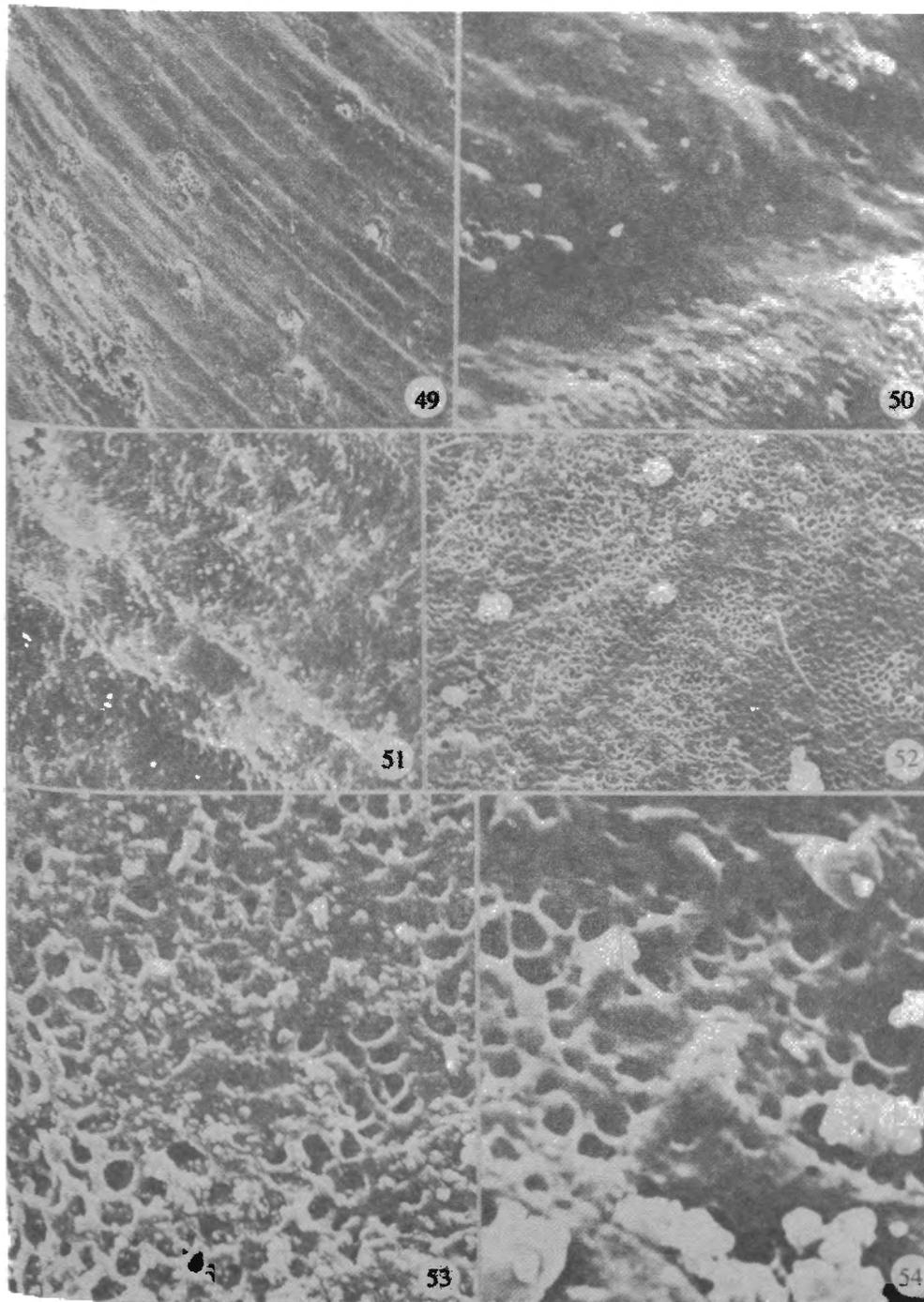


Plate XIII. Fragments of sculpture of outer surface of body whorl: 49 - 50 - Lithoglyphus naticoides C. Pfeiffer, 1828: 49 - 100 x, 50 - 3,000 x; 51 - 54 - Bythinella: 51 - B. micherdzinskii Falniowski, 1980, fragment with covered pores and visible growth line, 2,000 x; 52 - B. zyvionteki Falniowski, 1986, visible numerous pores, 2,000 x; 53 - B. zyvionteki, pores under higher magnification, 6,600 x; 54 - B. micherdzinskii, pores under higher magnification, 10,000 x

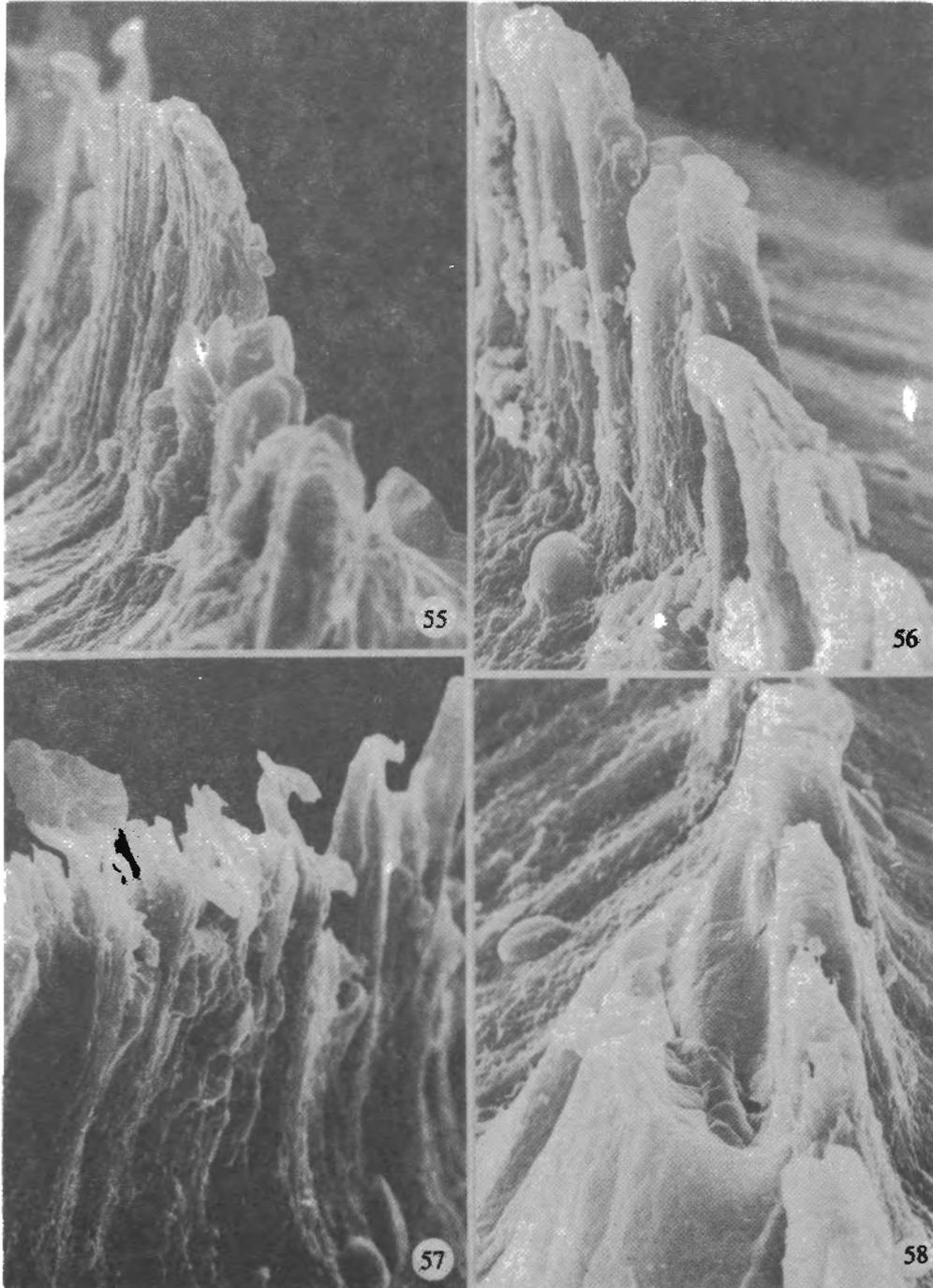


Plate XIV. 55 - 58 - Potamopyrgus ienkinsi (E. A. Smith, 1889) f. carinata Marshall, 1889, fragments of keel in various specimens, 1,000 x

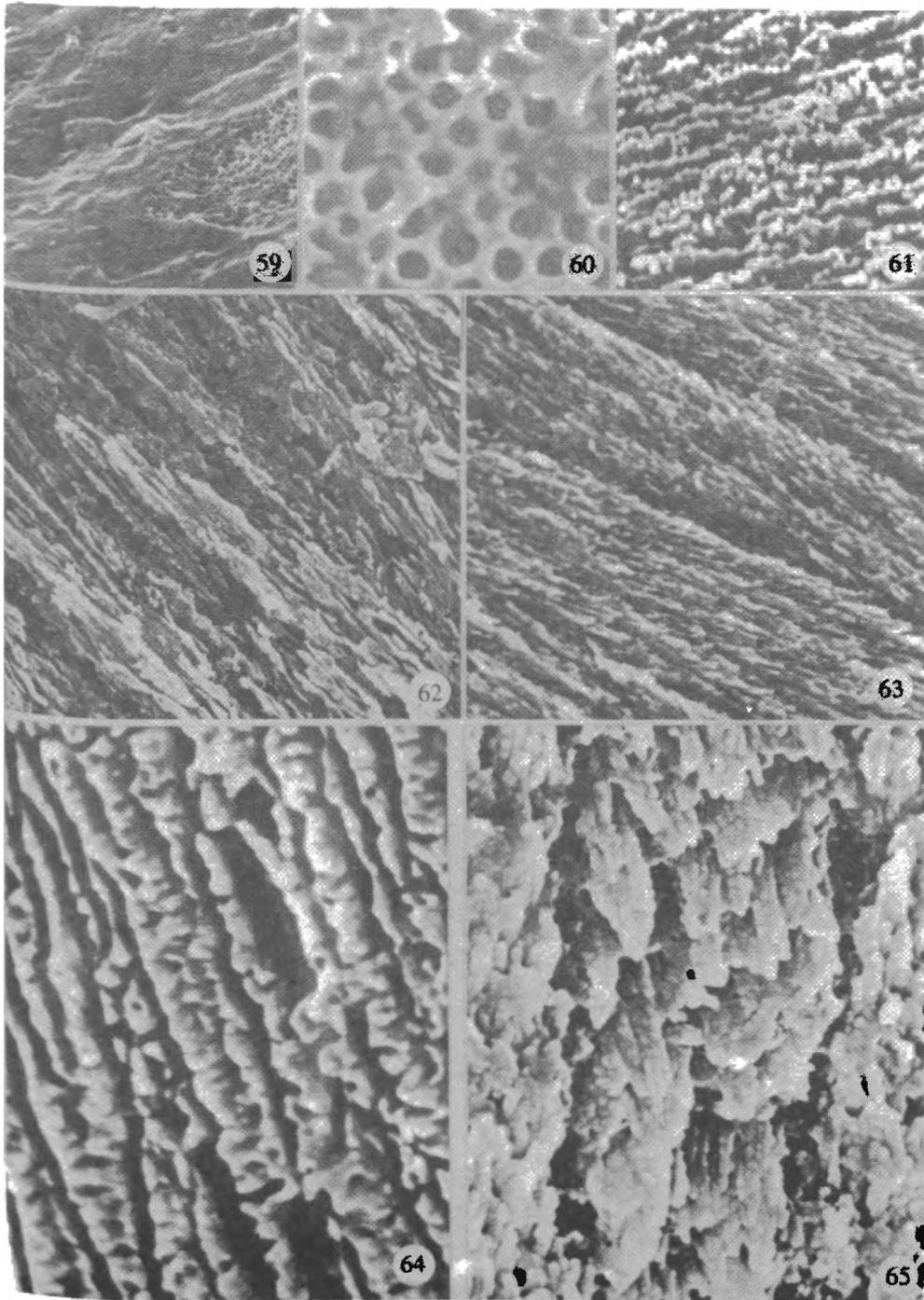


Plate XV. 59 - 60 - Potamopyrgus jenkinsi (E. A. Smith, 1889), fragments of outer surface of body whorl under higher magnification: 59 - in the right part of the photograph group of pores visible, 3,000 x; 60 - pores under higher magnification, 10,000 x. 61 - 65 - fragments of sculpture of inner surface of body whorl, etched: 61 - Potamopyrgus jenkinsi, 6,000 x; 62 - Valvata naticina Menke, 1845, 3,000 x; 63 - Viviparus contectus (Millet, 1813), 2,400 x; 64 - Valvata cristata O. F. Müller, 1774, 10,000 x; 65 - Bythinella micherdzinskii Falniowski, 1980, 6,000 x

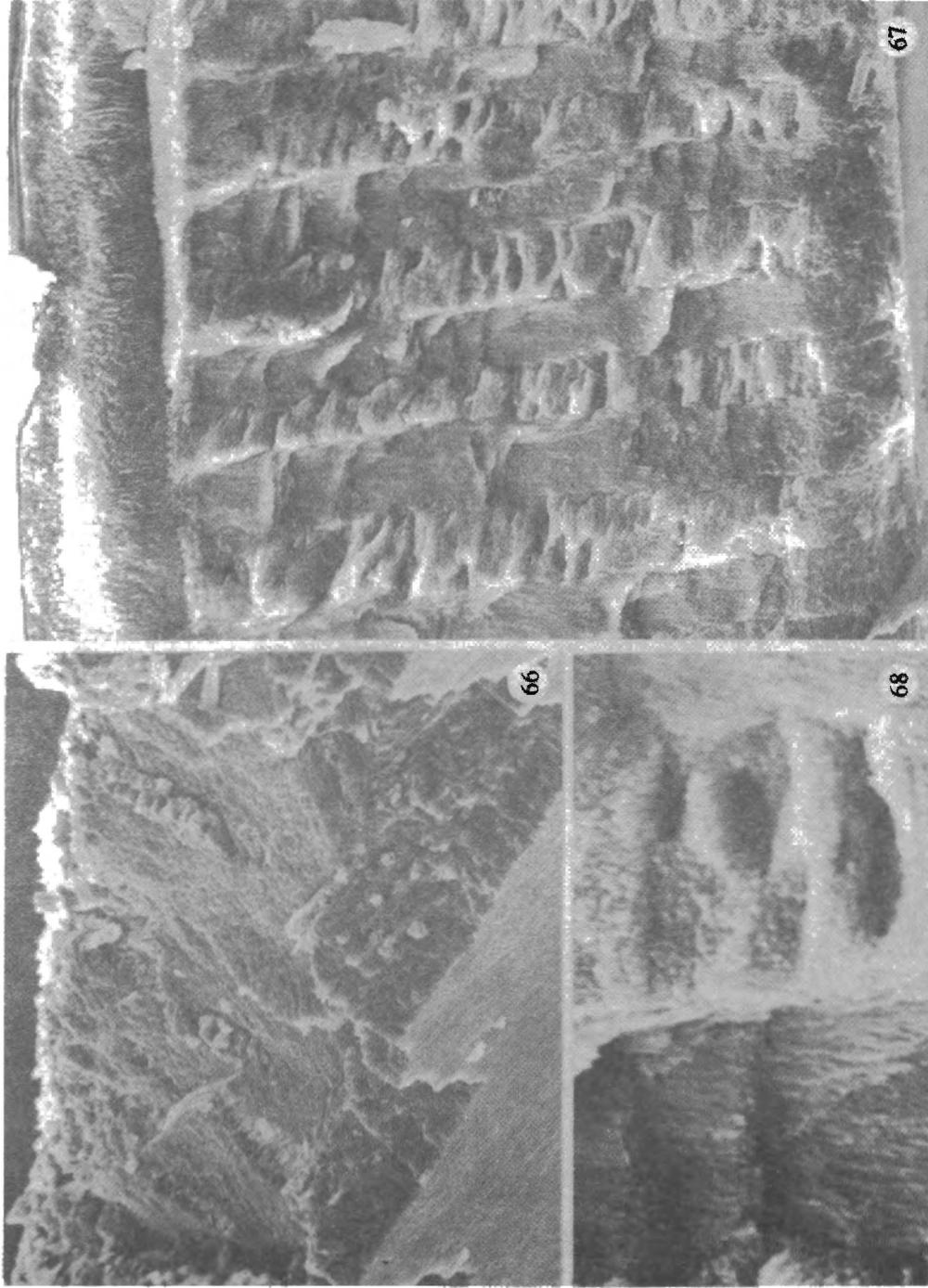


Plate XVI. Cross-sections of body whorl, perpendicular to growth lines: 66 - *Theodoxus fluviatilis* (Linnaeus, 1758), 900 x, unetched; lack of information and simple structure observable here are striking; 67 - 68 - etched, *Theodoxus fluviatilis* (Linnaeus, 1758); 67 - whole section, 360 x, 68 - fragment of columns of *Pectinella leachi* (Sheppard, 1823), 1750 x.

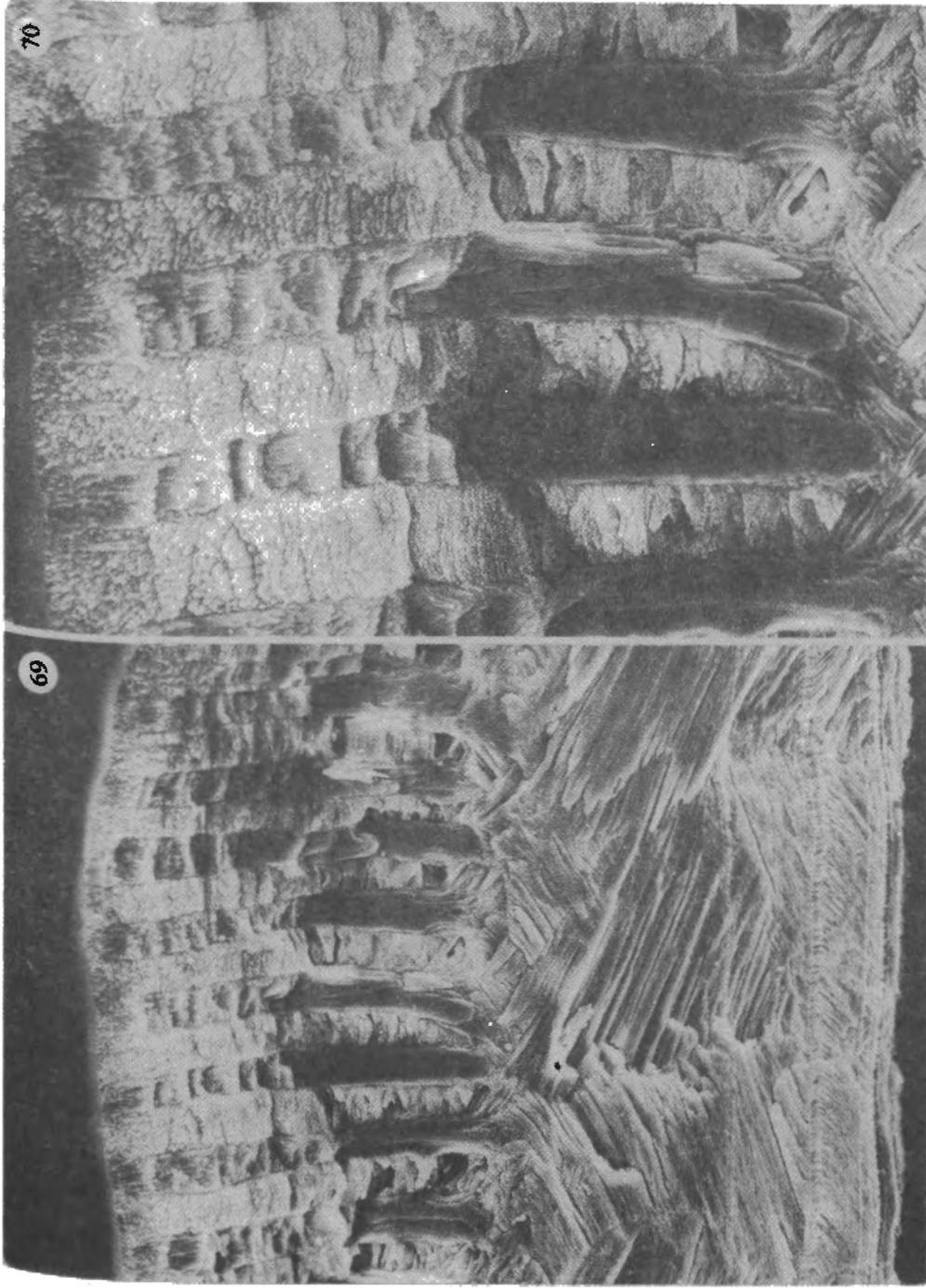


Plate XVII. Cross-section of body whorl of *Viviparus contextus* (Millet, 1813), perpendicular to growth lines, etched: 69 - whole section, 300 x; 70 - fragment of palisade layer under higher magnification, below visible conchioline (?) column envelopes, 650 x

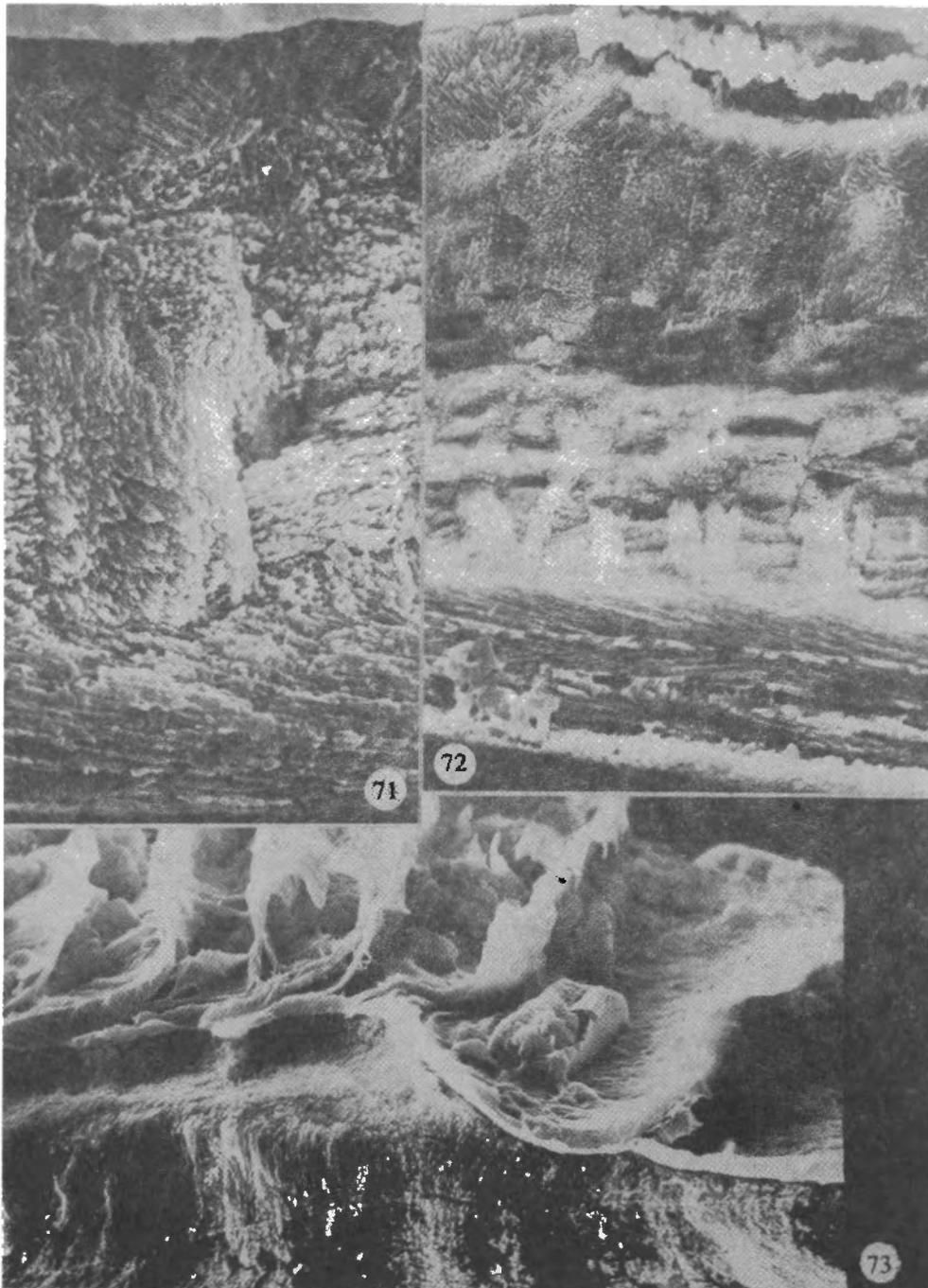


Plate XVIII. Cross-sections of body whorl of Valvata, perpendicular to growth lines, etched: 71 - V. pulchella Studer, 1820, 2,400 x; 72 - V. piscinalis (O. F. Müller, 1774), 600 x; 73 - V. pulchella, fragment of section, in the upper part visible large, laminar growth lines, 650 x

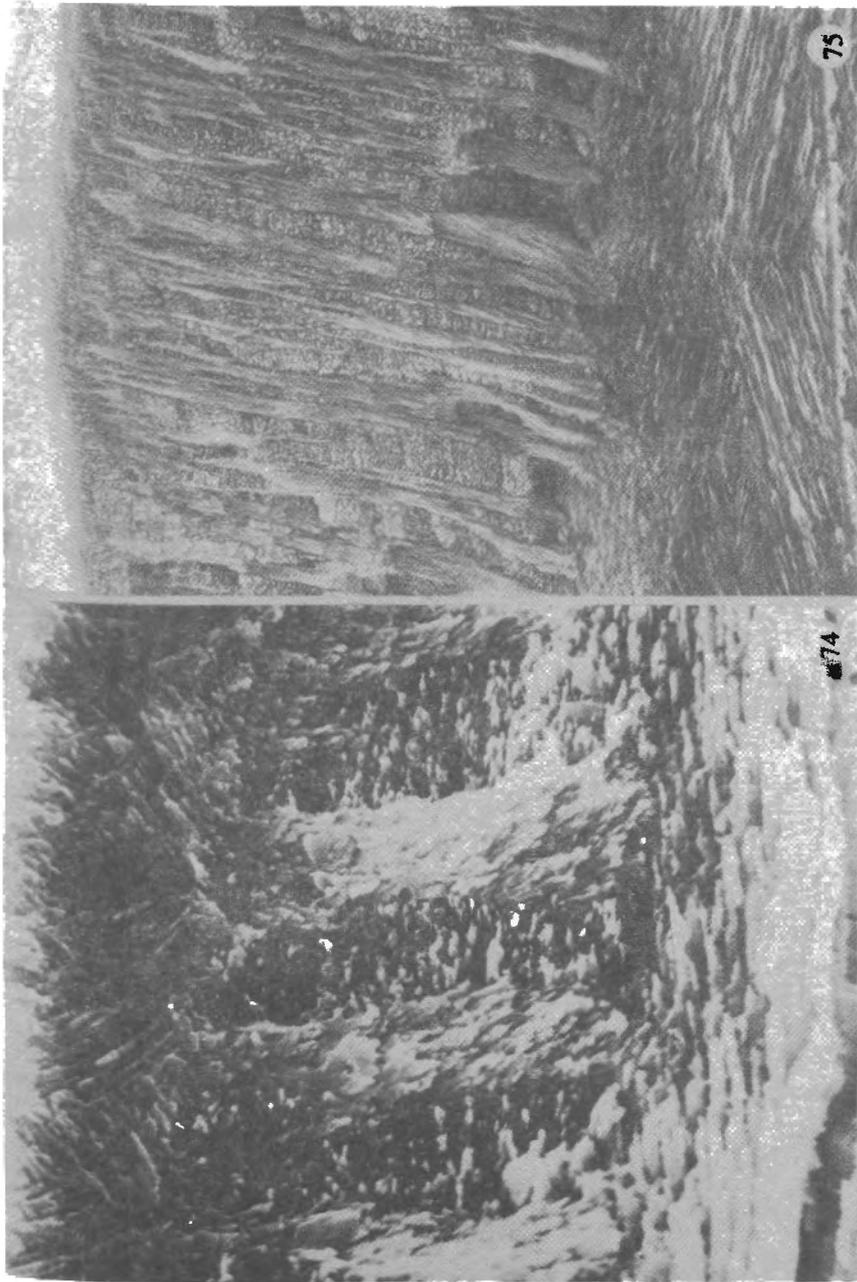


Plate XIX. Cross-sections of body whorl of *Valvata*, perpendicular to growth lines, etched; 74 - *V. cristata* O. F. Müller, 1774, 3,600 x; 75 - *V. naticoides* Menke, 1845, visible columns with conchioline (?) envelopes, 650 x

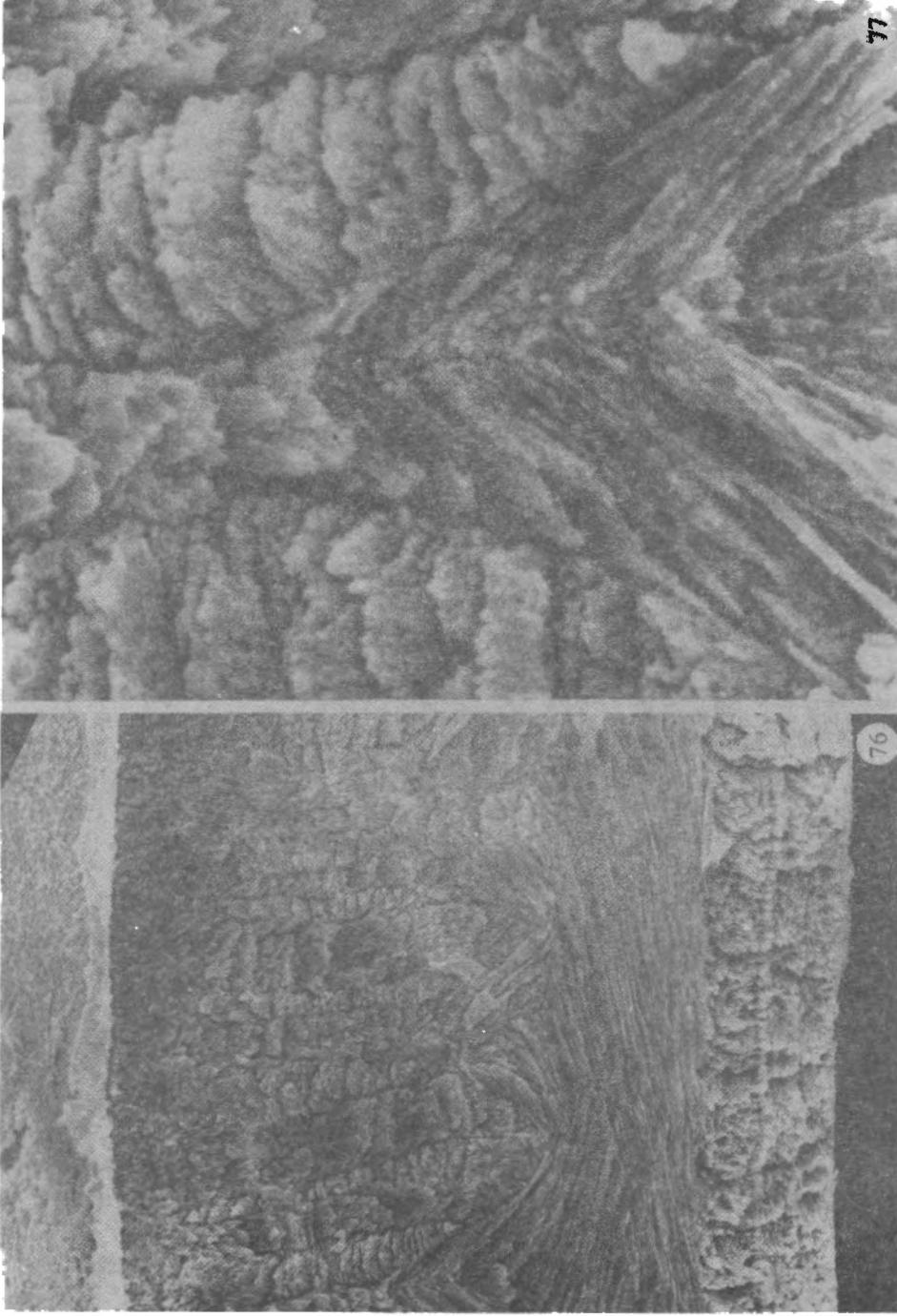


Plate XX. Cross-sections of body whorl of Bithynia tentaculata (Linnaeus, 1758), perpendicular to growth lines, etched: 76 - whole section, 930 x; 77 - fragment of 76 under higher magnification, revealing layer of angular structures, 5,000 x

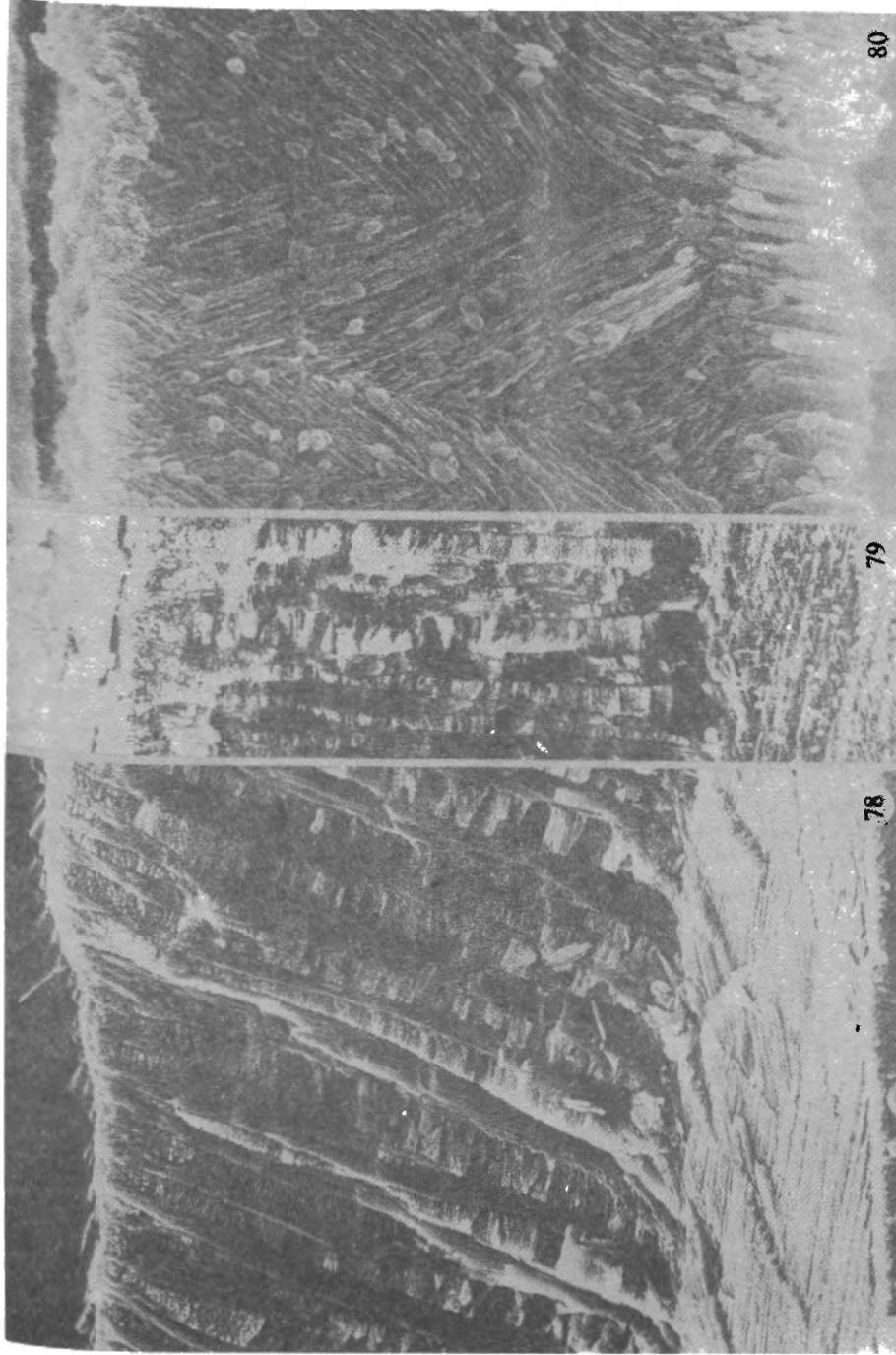


Plate XXI. Cross-sections of body whorl, etched: 78 - 79 - Lithoglyphus naticoides C. Pfeiffer, 1828, perpendicular to growth lines: 78 - 600 x; 79 - 390 x; 80 - Bithynella zvyionteki Falsiowski, 1986, parallel to growth lines, 1,300 x

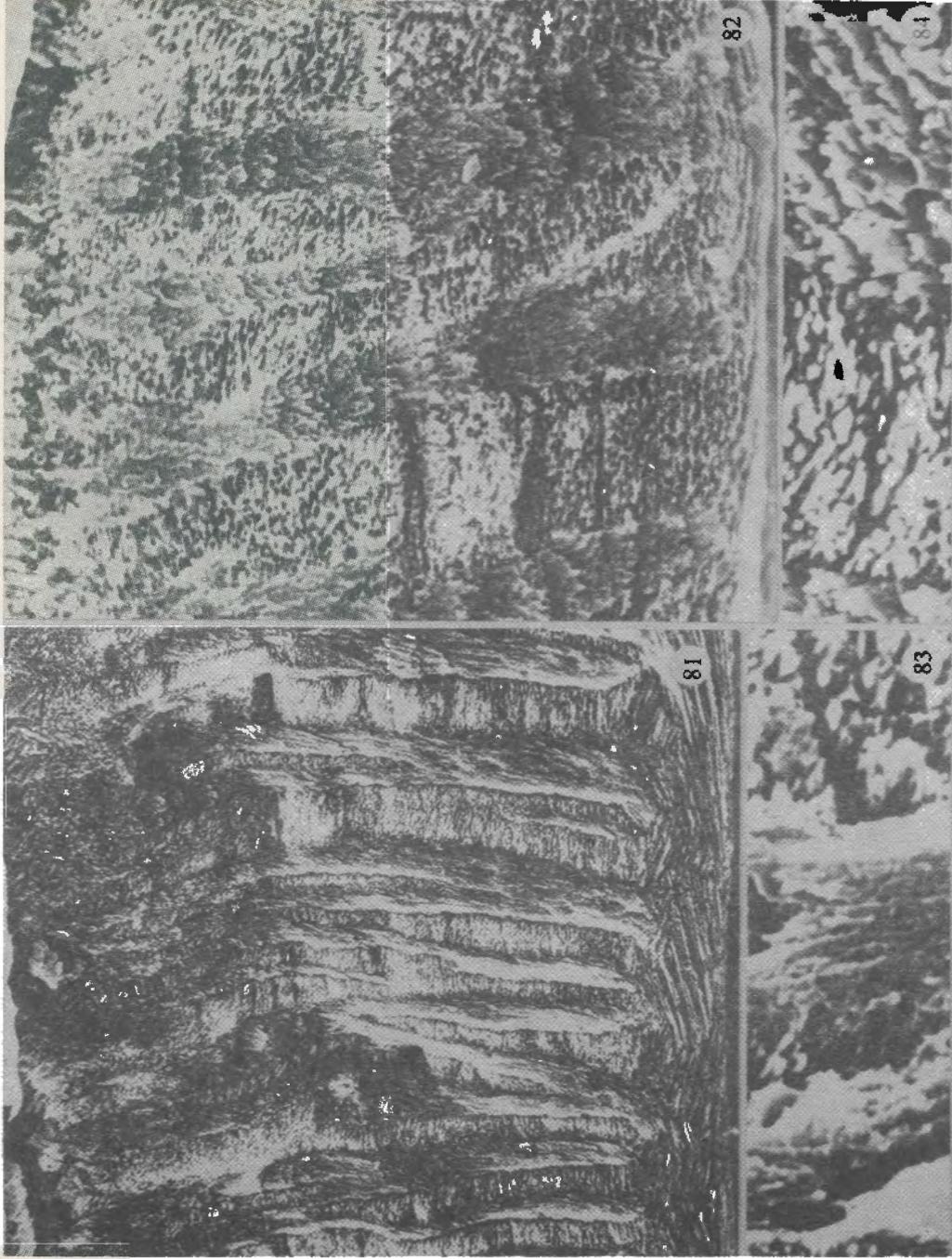


Plate XXII. Cross-sections of body whorl, perpendicular to growth lines, etched: 81 - *Potamopyrgus jenkinsi* (E. A. Smith, 1889), 750 x; 82 - *Bythinella zvyiontseki* Falniowski, 1986, 2,000 x; 83 - 84 - fragments of columns of palliade layer. 83 - *Bythinella zvyiontseki*, 4,000 x; 84 - *Potamopyrgus jenkinsi*, 6,000 x.

In general, the digestive system seems a good character for the determination of relationships within some families, but its usefulness for family grouping is very limited.

Central nervous system

The central nervous system is commonly acknowledged the relatively least variable structure, being the only one whose development shows more, or less constant regularities and consistent tendencies. In the Neritacea it is primitive hypoathroid, in the Viviparidae less primitive dystenoid, whereas derived epiathroid at a various stage of concentration in the others.

Concentration improves the effectiveness of functioning and abilities of the central nervous system, however, no gastropod appears to have made much of the chance of mental evolution which the situation offers. It seems that gastropods have not evolved towards development of the central nervous system and resulting mental abilities. Hence, the most concentrated systems are found not in the highest advanced neogastropods, but rather in small or minute forms at an intermediate stage of the general development. Centralisation is there rather a consequence of the miniaturisation of all structures. Moreover, quite closely related species have the nervous system of a various degree of centralisation (e.g. Davis 1967, Davis and Mazurkiewicz 1985).

Hence, the central nervous system not necessarily reflects either a general stage of evolutionary progress or phyletic relationships, the more that it is not always possible to homologise particular ganglia fusions in various concentrated systems, there being observed common examples of parallel evolution.

Reproductive organs

The list of the anatomic structures being more important for systematics is completed up with the structure of the reproductive organs. The organs have for some time focused the attention of taxonomists dealing with various groups of animals, though in some cases there seem to be no reasons for so much interest. Much diversified the reproductive organs show at the same time not less variation, and also parallel evolution being very common in the Prosobranchia. There are many cases of convergence as, for example, the various origin of the penis or the hermaphrodite organs originated in a number of rather distantly related groups.

Out of the Polish Prosobranchia only the Valvatidae are hermaphrodites, their reproductive organs being unique, so good a character to distinguish the family from the others. With regard to the other families it is necessary to consider the male and female organs separately.

The male reproductive organs have a relatively simple structure, this however being usually much less complex than that of the female ones. The

characters that are employed for systematics are as follows: the presence or absence of the prostate, the structure of the prostate (mainly in what degree it is separated from the vas deferens: numerous tubules clustered around the posterior part of the vas deferens and opening at intervals into it, like in the Bithyniidae, are regarded as primitive, whereas the prostate having one outlet to the vas deferens joining all the tubules, like in the Valvatidae, as derived), the position of the outlet of the pallial section of the vas deferens from the prostate (proximal or distal), as well as the presence or absence of the penis, details of its organisation and the occurrence of the flagellum.

Out of the Polish species the Bithyniidae and Hydrobioidea have the vas deferens forming thickened loops of a glandular function, while the vas deferens of the Viviparidae is short. The flagellum can be found in the Bithyniidae and Bythinellidae, but the other Hydrobioidea, though closely related to the latter are lacking it. The prostate occurs in all the Polish freshwater prosobranchs and has, with a few exceptions, a simple and rather primitive structure. Virtually, all the characters concerning the prostate should be regarded as not very useful for family grouping, since within a single family the prostate may be present or not (e.g. Rissoidae: Ponder 1985, Falniowski 1988a, b).

The details of the structure of the male reproductive organs could thus be useful here and there, but certainly not everywhere on the family level. This is on account of not only the relatively simple structure of the organs, resulting in a low number of potential characters, but also their function being exactly the same in different gastropods and fulfilled apart from even considerable morphologic modifications.

Almost the same remarks refer to the penis. The occurrence of the penis is a derived character, though otherwise it is known that a number of taxa highly specialised in respect of their other characters are penisless, and the lack of penis may often be secondary (Fretter and Graham 1962). All the Polish species have the penis. Also the occurrence of a groove instead of a closed duct inside the penis (the Neritidae have the former one) is regarded as a primitive character, there being similar limitations.

The penis appeared many times in the course of gastropod evolution; it is proved by its origin being pedal as a rule, but sometimes pallial (Bithyniidae) or cephalic (Neritidae, Viviparidae). The situation of the penis inside the right cephalic tentacle is both unusual and characteristic of the Viviparidae. In the other families the penis is bi-armed (Bithyniidae and Bythinellidae) or single. Inside the penis glandular structures can be found; the penis may bear lobes, a distinguishable filament, etc. All the characters, however, seem generally useful on the species, or at most genus level.

The taxonomic usefulness of the female reproductive organs is not far greater. The unique organs of the Neritidae do, indeed, differ apparently from those of the other families, but there are no such striking differences between the remaining families.

A number of the characters distinguished in the organisation of the female reproductive organs cannot be employed for family grouping. For instance, viviparity occurs in all the Viviparidae, but also in single representatives of the Valvatidae and Hydrobioidea; it is always connected with the occurrence of the brood pouch being similarly situated and organised, though in some cases actually non-homologous between the families. Many gastropods have the organs of a simple structure, then their similarity proves not necessarily their actual relationships. The Viviparidae and Bithyniidae are an example.

The presence of specific structures may increase the usefulness of the female reproductive organs, though this is not the rule, the more that it is difficult to indicate any at least moderately constant evolutionary regularities in the structure of the reproductive organs. For example, Radoman (1973) and Giusti and Pezzoli (1980) grouping families within the Hydrobioidea considered the occurrence or lack of the receptaculum seminis, the presence of one or two receptacula, and the occurrence of a secondary receptaculum to be important characters. On the contrary, Davis (1979) and Thompson (1979), regarding the Hydrobioidea as a single family, stated that the above characters are useless on the subfamily level. The more or less apparent separateness of the sperm channel from the oviduct and glands need not reflect a stage of evolutionary progress (Ponder 1985), and raises doubts as a criterion in family grouping (Falniowski 1987a).

Hence, the structure of the female reproductive organs is not necessarily useful on the family level. In addition, one may come to the general conclusion that the closer the taxa considered the more important the structure of the reproductive organs is for systematics, whereas in the case of higher groups less closely related the structure is not a reliable criterion.

V. OUTER AND INNER STRUCTURES OF THE SHELL

The preceding chapter deals with the characters of the soft part morphology and anatomy, which are more important for family grouping. The usefulness of all of them has turned out to be more or less limited, so that even if they are employed altogether no univocal and complete picture of relationships can be obtained. Hence, it seems necessary to find additional characters to support the traditionally employed, "classic" ones.

I attempted the shell structures as such supplementary characters. Positive results of this attempt would be the more valuable, that the shell is the only structure that remains as a fossil. For that reason, the shell structures could make the reconsideration of the systematics of fossil forms easier, what would be of crucial importance for the systematics of recent gastropods.

It must be stressed that the shell structures of the Polish representatives of the prosobranch gastropods have not been studied as yet (except the Viviparidae: Kessel 1933), therefore the characteristics presented here are entirely based on the characters found in the unnumerous species I have studied (all the Polish freshwater prosobranch species), thus further studies may bring numerous supplements. Since SEM turned out to be absolutely not useful for studying the structure of the periostracum, I have limited the description of cross-sections to the calcareous layers.

1. Outer surface of the protoconch

There were attempts at employing this for the purposes of the systematics of the prosobranchs (Binder 1967, Robertson 1971, Ponder and Yoo 1976, Fish and Fish 1977, Thompson 1979, Ponder 1982, 1983a, b, 1984, 1985, 1986, Davis, Mazurkiewicz and Mandracchia 1982, Davis, Kuo, Hoagland, Chen, Yang and Chen 1984, 1985, Davis and Mazurkiewicz 1985, and Bandel 1986).

In most cases a general appearance of the protoconch was described, the magnifications used being low, so little information was obtained. It is worth of attention that Thompson (1979) found the microsculpture of the Nymphophilinae distinct from the remaining Hydrobiidae (Hydrobioidea). Fish and Fish (1977) as well as Ponder (1984 and 1985) found the occurrence of characteristic pores in the Hydrobioidea. Hemistomia (Ponder 1982) has the pores identical with those I have found in some Polish Hydrobioidea, but Potamopyrgus from Lord Howe Island (Ponder 1982) has no pores and the very peculiar structure of its periostracum raises doubts as to its being congeneric with Potamopyrgus jenkinsi (E. A. Smith, 1889) occurring in Europe.

The habitus of the protoconch (Figs 18 - 21, 25 - 26, 29 - 30 and 33 - 34) may be characteristic of a species, but rather not of a family. The well marked, slightly bisinuate protoconch lip in the Neritidae (Fig. 18) is worthy of attention, the other families lacking it. In the Valvatidae the sculpture of the protoconch (Figs 20 -, 21) is sharply different from that of the teleoconch (Fig. 22), whereas in the remaining families the only macroscopic difference between the protoconch and the teleoconch sculptures is that the former is lacking growth lines.

Neritidae - protoconch surface (Fig. 18) smooth, only slightly granular under higher magnification.

Viviparidae - protoconch surface (Fig. 19) fine-grained.

Valvatidae - protoconch surface with a strong complex sculpture (Figs 20 - 22), higher magnifications reveal interspecific differences (Figs 23 - 24).

Bithyniidae - protoconch surface smooth (Figs 25 - 26), higher magnifications reveal a slight granulation (Figs 27 - 28).

Hydrobioidea - protoconch surface granular of identical with the surface of the younger whorls (Figs 29 - 34), interfamilial differences as follows:

- Lithoglyphidae (Fig. 29): smooth
- Bythinellidae (Figs 30 - 33): fine pores entirely within periostracum, the pores open at a greater part of the surface
- Potamopyrgus (Fig. 34): smooth

2. Outer surface of the body whorl

SEM pictures of the teleoconch surface have since recently been used in the gastropod systematics; usually low magnifications are used (Solem 1970, Ponder 1974, 1983a, and Meier-Brook 1983).

Neritidae - growth lines rather well developed, but broad, flat and blunt (Figs 35 - 36), better visible near the suture (Fig. 35), spiral lines in interstices hardly visible (Fig. 36); under higher magnification the surface smooth.

Viviparidae - growth lines hardly visible, blunt (Fig. 37), surface fine-grained under higher magnification (Fig. 38).

Valvatidae - growth lines from hardly visible (Figs 39 and 41 - 42) to very well marked and laminated (Figs 40 and 73), the full variability range even within a single species (Figs 40 - 41); spiral lines sometimes present in interstices (Figs 42 - 43); surface smooth (Figs 41 and 43) or coarse-grained (Fig. 39) under higher magnification.

Bithyniidae - growth lines hardly visible, flat and blunt (Figs 45 and 47), spiral lines in interstices present in some species (Figs 47 - 48); under higher magnification the surface between the growth lines and spiral lines smooth (Fig. 48), or with a net of characteristic pores (Figs 44 and 46) contained within the periostracum and opened on a greater or smaller part of the area.

Hydrobioidea - growth lines hardly visible (Figs 49 and 51), in numerous representatives pores, similar to those in Bithyniidae (Figs 52 - 54 and

59 - 60), open on a greater or smaller part, visible under higher magnification:

- Lithoglyphidae (Figs 49 - 50): open pores absent
- Bythinellidae (Figs 51 - 54): pores open on a greater part of the surface
- Potamopyrgus (Figs 55 - 60): growth lines weak; on the body whorl in numerous specimens an entirely conchioline, spiral keel from hardly to well visible (Figs 55 - 58), being composed of successive growth lines extended into a kind of bristles; open pores (Fig. 60) present, but limited to a small part of the area (Fig. 59).

3. Inner surface of the body whorl

The structure of the inner surface of the shell may be a good diagnostic character on the species level (Falniowski in press a): the process of shell thickening, going on throughout gastropod's life, is under the direct control of the organism of the mollusc, hence the appearance of the formed crystals and their arrangement must be closely connected with the chemistry of the operating enzymes, i.e. also with the enzyme structure.

It seems, therefore, that the structure of the inner surface of the shell should be a good taxonomic character: the molecular level character, yielding generally similar results as electrophoresis.

A practical use of the structure of the inner shell-surface is difficult. The killing of a gastropod stops the process of shell formation, hence a rapid recrystallisation of extrapallial fluid sets in. For that reason, to reveal the crystals formed by the yet living gastropod it is necessary to etch the inner surface mildly and then wash it very intensively, though artifacts, being numerous and hardly distinguishable from non-artificial structures, are actually unavoidable. This necessitates examining numerous specimens of each species. For that reason the examining is tiresome and time-consuming. Hence, I only have managed to obtain satisfying specimens of some from among the species, so only the inner surfaces of those species have been recognised.

The results I have obtained so far prove the usefulness of the inner shell-surface in the systematics on the species level (Falniowski in press a), though its usefulness in higher groupings has got no confirmation.

For instance, the structures of the inner shell-surface of Potamopyrgus jenkinsi (Fig. 61) resemble those of Valvata cristata O. F. Müller, 1774 (Fig. 64) more than those of Bythinella micherdzinskii Falniowski, 1980 (Fig. 65). Secondly, the structures of Valvata naticina Menke, 1845 (Fig. 62) resemble those of Viviparus contectus (Millet, 1813) (Fig. 63) or even those of Bythinella micherdzinskii (Fig. 65) more than the ones typical of Valvata cristata, another representative of the Valvatidae (Fig. 64). The infrafamilial variation may thus be greater than the interfamilial one.

4. Inner structure of the body whorl

The literature on the inner structure of the shell concerns mainly bivalves, but also pulmonates, chitons, and cephalopods (listed in Falniowski in press a and b). Moreover, those studies did not concern the taxonomic aspect, though some reflection of the order separateness in the bivalve shell structure was noticed (Taylor, Kennedy and Hall 1969). Only the paper of Kessel (1933) concerning the Viviparidae as well as the one of Andrews (1935) on the shell repair in the Neritidae dealt with prosobranch species occurring in Poland.

Neritidae - cross-sections perpendicular to the growth lines (Fig. 67: all the photographs of cross-sections, presented in this paper, are so arranged, that the periostracum is in the upward position) under the periostracum reveal two thin layers: the granular layer, and the layer of fine fibres perpendicular to the shell surface. Underneath the two there is an exceptionally broad pallisade layer (Figs 67 - 68) having a very regular structure, consisted of broad, giant columns extended up to the entire inner surface, where the column bases are well visible, even when examined with a stereoscopic microscope. Even the oldest specimens lack any layer corresponding to the endostracum, though the shells are very thick-walled. This shell structure is markedly different from the one observed in both the other Polish prosobranchs and the marine Archaeogastropoda (at least in the species examined so far), what seems to be another argument for the distinctness of the Neritacea.

Viviparidae - cross-sections perpendicular to the growth lines reveal two calcareous layers (Fig. 69). The first one is a pallisade layer (Fig. 70) with markedly distinguishable, very regularly arranged, slim columns of equal length, often having envelopes (Fig. 70: the lower parts of alternate columns). The second one, lying underneath the pallisade layer, is a layer of wide, rather flat, diagonal structures (Fig. 69) of quite compact fibres. There is no layer of the proper endostracum character.

Valvatidae - cross-sections perpendicular to the growth lines (Figs. 71 - 75) reveal up to four calcareous layers. Beneath the periostracum there is a layer of fine diagonal structures (Figs 71 - 72 and 74), being not always well developed (Figs 73 and 75). The pallisade layer has an apparently irregular arrangement, but its columns are nearly always parallel to each other, very poorly distinguishable and lacking envelopes (Figs 71 - 74); V. (Borysthenia) naticina (Fig. 75) differs apparently from this picture. The next layer is composed of big fibres which are slightly shell-surface-slanting and divided by large spaces (Figs 71 - 72 and 74 - 75). The proper endostracum, having a non-fibrous, spongy structure (Figs 72

and 74), is full-developed in older specimens of some species, while in the other species it is more or less reduced or absent (V. naticina: Fig. 75).

Bithyniidae - cross-sections perpendicular to the growth lines (Figs 76 - 77) of a full-developed shell permit five calcareous layers to be distinguished. Underneath the periostracum (Fig. 76) there is a thin layer of more or less perpendicular or slightly section-surface-slanting short lamellae, the structure of this layer being spongy, sometimes developed in the form of fine diagonal structures. The pallisade layer has the columns distinguishable less than those found in the Viviparidae, though better than those observed in a majority of the Valvatidae; the columns are arranged less regularly than in the Viviparidae, the longer lying alternately with shorter ones, and their breadth varies with no regularity (Fig. 76). The next layer comprises angular structures being specific of this family (Fig. 77); every second column of the pallisade layer terminates here with a rather blunt wedge and the others are broadened into diagonal structures (in some species this layer is more or less reduced). Then follows a layer of wide diagonal structures, sometimes having a fibrous-spongy character; the last one is the proper endostracum, being non-fibrous and strongly spongy (Fig. 76); this layer is not always present.

Hydrobioidea - cross-sections perpendicular to the growth lines (Figs 78 - 79 and 81 - 84) reveal three calcareous layers. Beneath the periostracum there is a layer of fine diagonal structures, composed of thick trabeculae arranged at an approximately right or slightly acute angle (Fig. 81); this layer is not always present, instead of there may be a thinner layer of a fine-grained character (Figs 78 - 79 and 82), yet sometimes absent. The pallisade layer shows a very irregular pattern with numerous branchings and the slanting arrangement of the columns (Figs 78 - 79 and 81 - 82), the columns dividing the forked ones being fusiform. Cross-sections parallel to the growth lines show that the next layer is composed of characteristic, elongate cylindrical structures (Fig. 80), whereas cross-sections perpendicular to the growth lines reveal it having either a system of diagonal fibres divided by large spaces (Figs 78 - 79 and 81) or a fibrous-spongy structure (Fig. 82); the last layer is sometimes absent. The distinguishing characters of the particular families are as follows:
 - Lithoglyphidae (Figs 78 - 79): on cross-sections perpendicular to growth lines a very thin granular layer under periostracum, often absent; columns formed of thin and long lamellae often very characteristically arranged (Falniowski in press a); wide diagonal structures of thick fibres, spaces between them large, slit-like only;

- Bythinellidae (Figs 80 and 82 - 83): on cross-sections perpendicular to growth lines (Fig. 82) fine-grained layer with large cavital spaces under periostracum thin, or columns of pallisade layer begin directly beneath periostracum; pallisade layer with columns of a very characteristic different from that of Lithoglyphidae, arrangement of their components (Fig. 83); last layer fibrous-spongy in character, with columns of pallisade layer petering out and with characteristic, fine cavital spaces (Fig. 82);
- Potamopyrgus (Figs 81 and 84): on cross-sections perpendicular to growth lines under periostracum a thin layer of fine diagonal structures with large spaces between thick trabeculae (Fig. 81), sometimes absent; columns of pallisade layer have the typical structure of a majority of Caenogastropoda (Fig. 84); fibrous-spongy layer with large slits and common cavital spaces lying along slits on a cross-section (Fig. 81); sometimes composed of flat lamellae.

VI. CONCLUSIONS

The above description shows that the ultrastructural characters, apart from their considerable variability, can be used in the systematics of the family level. Pictures of the inner structures seem more useful than those of the surfaces which are relatively little differentiated and in most cases rather not helpful for concluding on relationships.

These are only the Valvatidae who have the protoconch of a characteristic sculpture distinguishing the family. The macrosculpture of the teleoconch can only be useful within a family: for instance, spiral lines are characteristic of some species of the Bithyniidae and Valvatidae. In many cases the interfamilial variation of macrosculpture is less wide than infrafamilial one. Microsculpture has turned out to be rather simple and little differentiated, so perhaps except the closely related families of the Hydrobioidea it cannot be employed as a character for family grouping.

The inner shell-surfaces are much diversified, but often more within than between families, thus they cannot be used for systematic purposes on the family level.

Despite a considerable variability of the inner shell-structure, the descriptions referring to various families do not overlap and there are, indeed, a number of constant, specific characters. As the above descriptions suggest, in each case it is necessary to consider the whole section, because the variability intervals of particular layers, determined for each family, may be overlapping.

The immense complexity and variability of cross-sections, especially those perpendicular to the growth lines, provide many data which may be

useful for systematics. The occurrence of the characteristic, non-fibrous and apparently spongy endostracum in the Valvatidae and Bithyniidae is noteworthy, since it may indicate some relationship between these families. The data on the shell structure also confirm the validity of excluding Bithyniidae from Hydrobioidea and, to a certain degree, of dividing the latter into a number of families upon the basis of the anatomic characters used in this case (Radoman 1973 and Falniowski 1987a).

The shell structure of the Neritidae, being completely different from those of the other families, is relatively most simple and regular. Also the Viviparidae, whose primitiveness seems beyond doubt, are characterized by a simple (only two calcareous layers) and very regular shell structure. It seems that all the patterns of organisation found in the studied monotocardian families are derivable from the one typical of the Viviparidae.

The Bithyniidae and Valvatidae have the highest number of layers and a less regular shell structure. The Hydrobioidea, however, being undoubtedly higher advanced are lacking some layers or having them much reduced. So far as comparisons of the shell structures of bithyniid and hydrobioid representatives of different size allow to conclude (Falniowski in press a), this must, at least in part, be connected with the small size of the hydrobioid shell and its resulting thin wall. It is interesting that, contrary to expectation, thinner-walled monotocardian shells generally do not exhibit the miniaturisation of all their structures, but rather the elimination of some of the layers. The Hydrobioidea are also characterised by the greatest irregularity and a high variability of the shell structure.

A comparison of the shell structures of the discussed species seems to lead to the conclusion, that the organisation pattern of the shell inner structures has rather no adaptive significance: shells varying much in structure fulfil the same function in practically the same way. Physico-chemical environmental factors affect the process of shell formation to a certain, sometimes high degree. This, together with genotypic variation, results in the observed picture of a great variability being, however, contained within a given pattern of organisation.

The pattern of the shell organisation determined through an analysis of a rich material seems to indicate well the mono-or polyphyletism of the studied group, as well as its relationships with others and, perhaps, its stage of evolutionary progress. The shell structure seems useful for family grouping not less than good "classic" characters, and may be very helpful for the recognition of the real relationships between various groups of gastropods.

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KRYTYCZNY PRZEGLĄD NIEKTÓRYCH CECH SZEROKO WYKORZYSTYWANYCH W
SYSTEMATYCE WYŻSZYCH JEDNOSTEK SŁODKOWODNYCH PRZODOSKRZELNYCH
(GASTROPODA: PROSOBRANCHIA) I PROPOZYCJA WYKORZYSTANIA PARU
NOWYCH, ULTRASTRUKTURALNYCH

Streszczenie: Autor zwraca uwagę na niejasność i kontrowersyjność systematyki Prosobranchia. W tej sytuacji podstawowego znaczenia nabiera znalezienie cech, na których opierać się może systematyka, cech dobrze odzwierciedlających pokrewieństwa. Praca omawia właśnie cechy stosowane w systematyce szczebla rodziny i rzędu, bazując na danych o polskich słodkowodnych przodoskrzelnych.

Po przedstawieniu przyjętego systemu polskich przodoskrzelnych i metod badań muszli przy użyciu skaningowego mikroskopu elektronowego, autor krytycznie omawia kolejne stosowane cechy.

Wskazuje na bardzo ograniczoną użyteczność architektury muszli i niewiele większą - morfologii zewnętrznej części miękkich. Dalej omówione zostały cechy anatomiczne: plan budowy jamy płaszczowej, budowa skrzel, osphradium, serca, nerki, tarki, przewodu pokarmowego, centralnego układu nerwowego oraz męskich i żeńskich narządów rozrodczych. Wykazana została ograniczona przydatność każdej z tych cech. Dokładniej omówiono tarki, zilustrowane fotografiami (Figs 1 - 17), wskazując na wielość czynników określających ich morfologię, a także na przecenianie użyteczności tej struktury dla systematyki. Podobnie krytycznie oceniono układ pokarmowy i centralny system nerwowy, a także narządy rozrodcze.

W dalszej części pracy przedstawiono pokrój i urzeźbienie protokonchy (Figs 18 - 34), rzeźbę ostatniego zwoju (Figs 35 - 60), wewnętrzną powierzchnię ostatniego zwoju (Figs 61 - 65) oraz budowę przełomów ostatniego zwoju (Figs 66 - 84) dla kolejnych rodzin. Wskazano, że struktury SEM muszli, pomimo znacznej zmienności, nadają się do wykorzystania w systematyce, zwłaszcza struktury wewnętrzne widoczne na przełomach ostatniego zwoju.