

ANATOMICAL CHARACTERS AND SEM STRUCTURE OF RADULA AND SHELL IN THE SPECIES-LEVEL TAXONOMY OF FRESHWATER PROSOBRANCHS (MOLLUSCA: GASTROPODA: PROSOBRANCHIA) COMPARATIVE USEFULNESS STUDY

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ABSTRACT: The paper, based on 15 prosobranch species inhabiting freshwater habitats in Poland, is devoted to a comparative analysis of the usefulness of several taxonomical characters. Such commonly used characters as: shell “macrocharacters”, operculum, soft part external morphology and pigmentation, ctenidium and osphradium, male and female reproductive organs and penis have already been described in detail in earlier papers of the author: in this paper they are essentially characterized and illustrated for comparative purposes. The paper presents descriptions of SEM structures of the radula, protoconch habitus and outer surface, teleoconch outer and inner surfaces and teleoconch inner structure visible on sections parallel and perpendicular to the growth lines of the shell, for all the 15 species. The descriptions are illustrated with 336 SEM micrographs. Then, all the characters are discussed considering their taxonomical usefulness. It is pointed out that all the characters show a more or less restricted usefulness. On the other hand, the SEM shell structural characters prove not less useful in taxonomy than “good” conventionally used ones. In Appendix II the author has described concisely the general organization of the shell of the studied prosobranchs.

KEY WORDS: shell, operculum, soft part, morphology, pigmentation, ctenidium, osphradium, reproductive organs, radula, protoconch sculpture, teleoconch sculpture/inner structure

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Anatomical characters and SEM structure
of radula and shell in the species-level taxonomy
of freshwater prosobranchs
(Mollusca: Gastropoda: Prosobranchia):
a comparative usefulness study

ABSTRACT

The paper, based on 15 prosobranch species inhabiting freshwater habitats in Poland, is devoted to a comparative analysis of the usefulness of several taxonomical characters. Such commonly used characters as: shell "macrocharacters", operculum, soft part external morphology and pigmentation, ctenidium and osphradium, male and female reproductive organs and penis have already been described in detail in earlier papers of the author; in this paper they are essentially characterized and illustrated for comparative purposes. The paper presents descriptions of SEM structures of the radula, protoconch habitus and outer surface, teleoconch outer and inner surfaces and teleoconch inner structure visible on sections parallel and perpendicular to the growth lines of the shell, for all the 15 species. The descriptions are illustrated with 336 SEM micrographs. Then, all the characters are discussed considering their taxonomical usefulness. It is pointed out that all the characters show a more or less restricted usefulness. On the other hand, the SEM shell structural characters prove not less useful in taxonomy than "good" conventionally used ones. In Appendix II the author has described concisely the general organization of the shell of the studied prosobranchs.

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I. INTRODUCTION

The *Prosobranchia* are a large group of predominantly marine gastropods, only few freshwater taxa being included that belong to various and often distantly related groups which are, in general, marine. This makes it quite difficult to study the taxonomical usefulness of their characters. On the other hand, this being a group of a highly diversified morphology and, thence, taxonomically useful characters, it is possible to analyse a wide variety of characters, which seems worth of attention.

The aim of the paper is to analyse some of the characters which are most often used in the prosobranch taxonomy at the species level, and to propose some new ultrastructural ones. The critical review of the taxonomical characters presented in this paper has constituted the basis for revision of the Polish *Prosobranchia*, completed by the author (FALNIOWSKI 1987 and 1989a). For reasons beyond the author's control this is turning up later than the issuing revisions. Characters applicable to the systematics of higher taxa have been discussed elsewhere (FALNIOWSKI 1989b).

The gastropod systematics of the species level has for a long time been a subject of interest of many malacologists, but it still raises a lot of controversies, and within numerous groups is actually provisional. Species is practically defined in many ways, and it is to be pointed out that this vagueness of the species as such is a source of serious problems. The biological concept of species (e.g. MAYR 1969 and 1970) can hardly be applied, since the serious lack of information on many aspects of the biology of prosobranch species is just a rule. Hence, the taxonomy is still based mainly on the sole morphology. Moreover, morphological data are incomplete, or even fragmentary. So, the careful character weighting is of supreme importance.

The study is based on the prosobranchs inhabiting freshwater in Poland. 15 species only, which come from a relatively small area, make it impossible to obtain results which could be accepted as a rule. Hence the present results are preliminary. It seems, however, that in spite of the patchy character of the data base a comparison of the characters, considering their usefulness, proves justified.

All the presented data concerning the shell architecture, as well as soft part external morphology and anatomy, are based on my previous papers (FALNIOWSKI 1987 and 1989a). Data of major importance for discussion are cited here and illustrated with figures. SEM structures of radulae and shell are shown in detail. Some SEM data illustrated with some micrographs have already been presented in my earlier papers (FALNIOWSKI 1989a and b). However, the majority of the presented material has not been published yet.

II. GENERAL REMARKS

1. History of studies

Anatomical research

The anatomical studies on gastropods, the task of which was to find anatomically useful characters at the species level, were started in the beginning of the XXth century (e.g. ROSZKOWSKI 1914). Such studies concerning prosobranchs were started much later than those dealing with pulmonates, and were devoted mainly to minute representatives of the *Rissoacea* (e.g. BOETERS 1973, 1981, GIUSTI & PEZZOLI 1977, 1982, HERSHLER & DAVIS 1980, DAVIS 1981, DAVIS, MAZURKIEWICZ & MANDRACCHIA 1982, PONDER 1984, 1985, 1986, VARGA 1984, DAVIS & MAZURKIEWICZ 1985, FALNIOWSKI 1987 and 1989a),

Radular studies

The radula was the first internal structure considered by malacologists, hence data on its habitus in particular species are numerous in the literature. On the contrary, papers describing in detail the radula structure, function and development in the ontogeny are relatively unnumerous. The prosobranch radular characters are described, though not necessarily with an appropriate accuracy and criticism, in most papers concerning the *Prosobranchia*.

Because of its thickness, the radula is actually an inconvenient object of light microscope study. Hence many descriptions based on this technique are unexact or even erroneous, the latter case being not as accidental as one could expect. Although the light microscope may be useful in radular studies, for instance when determining species, studying radula ontogeny, or describing the variability of cusp number, only the scanning electron microscope (SEM) is applicable to detailed examinations of the radula structure, and thus to the full recognition of radular characters.

There are numerous papers describing SEM images of the radula, out of which the ones of RUNHAM & THORNTON (1967), THOMPSON & HINTON (1968), ALDRICH, BARBER & EMERSON (1971: *Cephalopoda*), SOLEM (1972, 1973), THOMPSON & BEBBINGTON (1973), JUNGBLUTH & PORSTENDORFER (1975), PONDER & YOO (1976), GIUSTI & PEZZOLI (1977, 1982), PLOEGER & BREURE (1977), and PONDER (1982a, b, 1983a, b, 1985, 1986) can be cited as examples.

Protoconch surface

There were some attempts to employ the outer surface of the protoconch for the purpose of the taxonomy of both the prosobranchs (BINDER 1967, ROBERTSON 1971, HADZIŠČE, PATTERSON, BURCH & LO VERDE 1976, PONDER & YOO 1976, FISH & FISH 1977, THOMPSON 1979, DAVIS, MAZURKIEWICZ & MANDRACCHIA 1982, PONDER 1982b, 1983a,

b, 1984, 1985, 1986, MARSHALL 1983, DAVIS, KUO, HOAGLAND, CHEN, YANG & CHEN 1984, 1985, DAVIS & MAZURKIEWICZ 1985, BANDEL 1986, and DAVIS, GUO, HOAGLAND, ZHENG, YANG & ZHOU 1986) and pulmonates (e.g. COPPOIS & DE VOS 1986 and RIEDEL 1987). Apart from BINDER (1967) all of them applied SEM (REM). Especially noteworthy is a fundamental paper of BANDEL (1982) describing both the outer and inner structures, and the formation of the protoconchs of the *Conchilera*, in this mainly the *Prosobranchia*.

In the studies cited above the general appearance of the protoconch was commonly described, the magnifications used being low, so little information was obtained. It is worth of attention that BINDER (1967) pointed out interspecific differences in the *Valvata*: also clearly distinct and characteristic sculpture patterns of the protoconch outer surface were shown for several valvatid and hydrobioid species by HADZISCE, PATTERSON, BURCH & LO VERDE (1976). THOMPSON (1979) found the microsculpture of the *Nymphophilinae* distinct from the remaining *Hydrobiidae* (= *Hydrobioidea* in this paper). FISH & FISH (1977) as well as PONDER (1982b and 1985) recorded the occurrence of characteristic pores in the *Hydrobioidea*.

Teleoconch surface

The teleoconch inner surface has not been described so far. The outer surface has been used since recently in the gastropod systematics; usually low magnifications are applied (e.g. SOLEM 1970, PONDER 1974, 1983a, PONDER & YOO 1980, MARSHALL 1983, MEIER-BROOK 1983, COPPOIS & DE VOS 1986, DAVIS, GUO, HOAGLAND, ZHENG, YANG & ZHOU 1986, and RIEDEL 1987).

Teleoconch inner structure

The literature on the inner structure of the shell concerns mainly bivalves and pulmonates (especially *Helicidae*), but also opisthobranchs, cephalopods and chitons, sometimes also prosobranchs (e.g. BØGGILD 1930, ABOLINS-KROGIS 1958, KADO 1960, KOBAYASHI 1964, MUTVEI 1964, MACLINTOK 1967, TAYLOR, KENNEDY & HALL 1969, WISE 1970, SALEUDDIN 1971, GREGOIRE 1972, RAMPAL 1973, BANDEL 1977a, b, 1981, HAAS 1977, 1982, POPOV 1977, WALLER 1980, POULICEK & KREUSCH 1983, ALEMANY 1986, BAXTER & JONES 1986, POULICEK & VOSS-FOUCARD 1986 and DULLO & BANDEL 1988).

In this respect the *Prosobranchia* seem the least known group of molluscs. Moreover, the papers cited above, except those of TAYLOR, KENNEDY & HALL (1969) and POPOV (1977), do not consider the taxonomical aspect. Numerous data on various prosobranchs are given by BANDEL (1977a, b, 1979a, b and 1981). However, even the latter papers do not deal with the species-level taxonomy. Only the paper of KESSEL (1933) concerning the *Viviparidae* as well as the one of ANDREWS (1935) on the shell repair in the *Neritidae* include some information on the shell structure of prosobranchs occurring also in Poland.

From among numerous papers dealing with the problem of the shell formation the ones of VILLEPOIX (1892), MANIGAULT (1933, 1939), BEVELANDER & BENZER (1948), WAGGE

(1951), MCGEE-RUSSEL (1954), WILBUR & YONGE (1964), HALEY & GIBSON (1971), UOZUMI & TOGO (1975), JONES & SALEUDDIN (1978), UOZUMI & SUZUKI (1979), FALNIOWSKI (1980), WILBUR & SALEUDDIN (1983) and EYSTER & MORSE (1984) can be cited as examples.

2. Material and methods

An annotated systematical list of the studied species is given in Appendix I. The material was collected during five years from numerous localities in all regions of Poland. Some additional material was collected in Hungary, Romania and Bulgaria. The author used common techniques of sampling and sorting. Specimens were fixed with 70% ethanol or 4% formalin; contrary to commonly acknowledged opinions, the latter proved much more suitable for the prosobranch fixation, especially for studying anatomy. A more detailed description of the material and techniques applied to its collection and of the methods used for the anatomical study is given in FALNIOWSKI (1987 and 1989a).

The techniques applied to the shell SEM study were exactly the same as described in my earlier paper (FALNIOWSKI 1989b). The preparation of the radula for SEM is quite difficult. Method of PLOEGER & BREURE (1977) could not be applied for technical reasons. Hence I had to introduce a new method. In minute gastropods the radula was mechanically removed. It was therefore not quite free of soft tissues, but at the same time there was no danger of losing it when boiling. In bigger gastropods the buccal mass was boiled in 10% KOH solution. The cleaned and washed radula was passed to absolute ethanol which was then changed twice.

The radula submerged in a drop of absolute ethanol was placed on a microscope glass cover slip. Within a thin layer of ethanol it was stretched and properly arranged with the use of thin needles, and then covered with another cover slip; the upper cover slip was tightened with a load of 2...5 g. Then the radula was allowed to dry between the cover slips. When dry, the radula was taken away from the cover slips. Sometimes it was impossible to disjunct a radula from a cover slip: in such cases the cover slip was broken to obtain the smallest piece still holding the whole radula, and then the piece of glass was mounted similarly as a separated radula.

The radulae were mounted on heavy aluminium foil discs whose diameter equalled the diameter of a holder. The foil discs let the holder be free for another preparation without the destruction of the used-up one which could still be ready for another examination, if necessary. The radulae were mounted with an adhesive tape, or with Master Compact glue. The mounting was difficult and troublesome, and had to be carried out under a binocular, since the radulae had to be arranged with their upper sides upwards, unlike for the light microscope where it is not obligatory. The mounted preparations were coated with gold.

Shells for the SEM study of the outer surfaces were cleaned with saturated oxalic acid solution for about 15...25 minutes, 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 ethanol and dried. Selected fragments of the shells were stuck to an aluminium disc or directly to a holder and coated with gold.

The shell inner surface was studied within the body whorl. It was necessary to choose relatively small pieces of shell walls to be stuck 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 obtain shell sections, shells were broken up with tweezers, attention being paid to the direction of a section in relation to the growth lines. For the selection of broken pieces see Appendices II and III. Properly broken up, the chosen pieces were washed in tap water and etched. There is no way but etching to show a variety of structures (see Appendix II). The best results were obtained by 10...25 seconds of etching with n/10 hydrochloric acid solution. After that a very intensive continuous washing was necessary for not less than 30 minutes, distilled water needed at least in the end. Finally, after rinsing twice in absolute ethanol, properly arranged shell pieces were stuck to a holder and coated with gold.

The SEM research was carried out using a Jeol JSM-35 Scanning Electron Microscope. The magnifications applied ranged from 20 to 5,000 times, and in some cases to about 12,000...16,000 times. Such specimens could not be satisfactorily photographed at higher magnifications, so the latter were rarely used. The voltage applied ranged from 15 to 35 kV.

III. SYSTEMATIC DESCRIPTION OF THE STUDIED SEM STRUCTURES

1. Radula

Theodoxus fluviatilis (Figs. 1 - 7)

The radula of the rhipidoglossate type, fulfilling the general formula:

$$\infty m + 5l + c + 5l + \infty m.$$

The first and fourth lateral teeth of *T. fluviatilis* are big and massive, the second and third ones between them being small and knob-like; the fifth lateral tooth resembles the marginal teeth but is more massive, hence the formula for the species is as follows (FALNIOWSKI 1989b: the dominants underlined):

$$\infty m + 1l + \underline{1l} + 2l + \underline{1l} + c + \underline{1l} + 2l + \underline{1l} + 1l + \infty m$$

The rhipidoglossate radula seems primitive and traditionally was regarded as basic for all the other, "derived" gastropod radulae (e. g. FRETTER & GRAHAM 1962), although recently (e. g. HASZPRUNAR 1988) the stereoglossate radula of the *Dacrydissa* has been acknowledged more primitive, and probably characteristic for the gastropod archetype. On the other hand, its structure is connected with the adaptation of the gastropod to feeding on algae scraped from rocks (PURCHON 1977). The multicuspid marginal teeth scrape the food which is shifted by the large lateral teeth to the buccal cavity.

On account of this function the rhachidian tooth (Fig. 5) is small and rather smooth, widened in the anterior part, blunt edges appearing on the margins. The structure of the central tooth makes it possible for the radula to bend freely along its axis of symmetry. The proportions of the central tooth are variable (Figs. 1 - 3).

The first lateral tooth (Fig. 5) is the largest one in the radula; it is axe-blade-shaped and shows variable proportions (Figs. 1 - 5). It is well set on the basic membrane; along its anterior edge a blunt fold is observable: this widens laterally and its probable function is shifting food. Both the second and third lateral teeth are strongly reduced, minute, knob-shaped (more or less elongated), and hardly visible (Fig. 7; also Figs. 1 - 5). The fourth lateral tooth (Figs. 4 and 6) is smaller but more sturdy, and has its anterior region terminated with a strong and cuspid edge

which probably also helps to scrape food. A large number of uniform marginal teeth (Figs. 1 - 3 and 6 - 7) have numerous but rather fine and blunt cusps. The marginal teeth are very thin, delicate, style-shaped (Fig. 7).

Viviparus conlectus (Figs. 8 and 13 - 16)

The radula of the species, as well as of all the others described below, is typically taenioglossate, fulfilling the formula:

$$3 + c + 3,$$

or more precisely:

$$2m + 1l + c + 1l + 2m$$

The central tooth (Fig. 8) is solid with a large trough-like base having its lateral margins bent upwards, and with no basal cusps. In the rhachis the central cusp is large, blunt, almost rectangular (Figs. 8 and 14 - 16). On its both sides about five cusps can be observed, being usually sharp, triangular, and diminishing regularly towards the sides.

The lateral tooth (Figs. 13 - 16) has also a wide, trough-shaped base; the tooth-plate is bent upwards and backwards but not twisted to the straight basis of the tooth. The plate is asymmetrical; about eight to ten cusps, usually sharp and slender, are arranged on two sides of a larger, blunt, more or less rectangular cusp which is similar as in the central tooth.

The marginal teeth (Figs. 13 - 14) have narrower bases twisted to the plates. The cusps of the inner marginal tooth appear on both the terminal and lateral margins of the plate; the single rectangular cusp is much smaller than in the lateral tooth; laterally about four to five cusps occur. On the outer marginal tooth about seven cusps, all of them sharp, are present only on the terminal margin of the plate; the rectangular one is absent.

Viviparus viviparus (Figs. 9 - 12)

SEM photographs reveal only slight differences in radular characters between *V. viviparus* and *V. conlectus*. In *V. viviparus* the cusps of all the teeth are more slender, they are also longer; the lateral teeth are broader than in *V. conlectus* (Figs. 9 - 12). However, these slightly marked differences are not always observable.

Valvata piscinalis (Figs. 17 - 25)

The radula shows a very characteristic pattern (Figs. 17 - 18) that differs strikingly from the ones found in the non-valvatid prosobranchs. Its variability is also remarkable: the number of cusps on particular teeth and the teeth shape are much varied even within one radula, asymmetry being commonly observed in the rhachis.

The central tooth (Figs. 17 - 21 and 25) has a large base with prominent lateral elongations at its proximal part, and a large tooth-plate which is triangular (the triangle proportions highly variable: Figs. 17 - 18 and 25) or reduced to sole cusps and knobs (Figs. 20 - 21). The basal cusps are absent. The central cusp is large (at least twice longer than the two adjoining lateral ones), slim and sharp. The remaining cusps are long, sharp, dagger-shaped (Figs. 17 - 19 and 25), laterally often in the form of blunt oval knobs (Figs. 20 - 22). The most frequent formulae of the dens centralis (to simplicise, the common asymmetry is omitted) are as follows: 13 - 1 - 13, 12 - 1 - 12, 15 - 1 - 15, 16 - 1 - 16, 17 - 1 - 17, and 19 - 1 - 19.

The base of the lateral tooth (Figs. 17 - 18 and 22) is slightly arched in the region close to the plate; the plate bends slanting to the long axis of the base. The plate (Fig. 22) is asymmetrical, with one long cusp (more than twice longer than any other one on its sides) which is often massive but not always sharp (Figs. 17 - 18); the remaining cusps are slim, narrow, dagger-like and long. The most frequent formulae: 8 - 1 - 6, 7 - 1 - 8, 7 - 1 - 9, 6 - 1 - 11, 7 - 1 - 17, and 16 - 1 - 14.

The two marginal teeth (Figs. 17 - 18 and 22 - 25) show both the same organization pattern: the base is proximally extended triangularly on one side (Fig. 25), the rest of the base being arched, spoon-shaped (Fig. 24); no tooth-plate can be distinguished. The teeth are laterally strongly bent; cusps are visible on both sides along the terminal half of a tooth (Figs. 18 and 23 - 25). The cusps are narrow, fairly long, dagger-like, always sharp, about 30...about 50 per tooth. The largest ones occur at the distal end of the tooth (Figs. 18 and 22 - 24), laterally they gradually diminish with the growing distance from the end of the tooth, but even the smallest ones are sharp. A smooth, cusplless section may occur between the small cusps.

Valvata putchella (Figs. 26 - 35)

The radula, if compared with that of *V. piscinalis*, shows such conspicuous differences in organization pattern between particular teeth that it suggests different modes of feeding. According to the biological concept of species (MAYR 1969 and 1970) this confirms the separateness of the two species.

All the teeth (Figs. 26 - 35) have the tooth-plates hardly distinguishable: the margin is bent and cut into cusps and knobs. The dens centralis (Figs. 26 and 30) is similar in shape to that of *V. piscinalis* and has no basal cusps either. Its anterior margin has a sinus (Figs. 26 and 35); the large central cusp that is very characteristic of *V. piscinalis* is lacking in *V. putchella*: sometimes the central section of the anterior margin is smooth, cusplless (Fig. 26). The cusps (Figs. 26 and 30) are always in the form of fine cylinders terminating as blunt cones. There are 16...28 cusps on the rhachis.

The lateral tooth (Figs. 27, 31 and 35) is completely different from the one described for *V. piscinalis*. The basis is massive, short, neither arched nor twisted but quite straight (Fig. 31), proximally with triangular outgrowths: the terminal and lateral ones (situated on the side closer to the marginal teeth). About 20...25 blunt, cylindrical, fine knobs occur along the terminal and inner (closer to the dens centralis) tooth edges (Figs. 27, 31 and 35). On the terminal edge the knob

size practically does not change (Fig. 5), while on the inner margin the knobs gradually diminish with the growing distance from the distal edge.

The marginal teeth are diversified (Figs. 27 - 29 and 31 - 34). The habitus of the inner ones resembles the one being characteristic of the lateral tooth of *V. piscinalis*. The plate is slanting to the base and asymmetrical, having one bigger cusp and several smaller ones on its both sides (Figs. 29, 31 and 33 - 34). The most frequent formulae are as follows: 6 - 1 - 9, 11 - 1 - 4, 9 - 1 - 8, and 9 - 1 - 7. The cusps are rather big and sharp, but not dagger-like, rather triangular, sometimes blunt. The outer marginal teeth are spoon-shaped, similar as in *V. piscinalis* (Figs. 29 and 32; see also Fig. 7 in FALNIOWSKI 1989b). The cusps are less numerous (about 25...45), shorter and less sharp than in *V. piscinalis*. Some of them are quite broad and short, trapezoid.

Similarly as in *V. piscinalis* the radula is very variable; even in one radula the successive rows differ in cusp shape and number.

Vahata cristata and *V. naticina*

The radulae have not been studied because the material was not sufficient to provide readable SEM photographs.

Bithynia tentaculata (Figs. 36 - 42)

On the central tooth of the *Bithynidae* (Figs. 38 - 39, 41 - 42, 44 - 45, 47 and 49 - 50), similarly as in all the Polish *Hydrabiidae* (Figs. 52, 54 - 55, 62 - 63, 65 - 66, 68 - 69 and 73 - 75) there are basal cusps. However, SEM photographs show their different arrangement in these two groups. In the *Bithynidae* the basal cusps lie along the lateral margins of the tooth base, while in the *Hydrabiidae* their bases are arranged more or less parallelly to the tooth plate (anterior edge of the rhachis). In *B. tentaculata* the rhachis (Figs. 36 - 42) has a broad and solid base. It fulfils the following formulae:

$$\begin{array}{cccc} \underline{4-1-4} & \text{or } \underline{3-1-3} & \text{or } \underline{4-1-4} & \text{or } \underline{5-1-5} \\ 6-6 & 7-7 & 5-5 & 5-5 \end{array}$$

The central cusp on the plate is big, often blunt, whereas the other cusps (both those of the plate and the basal ones) are usually sharp (Figs. 36, 38 - 39 and 41 - 42).

The lateral tooth (Figs. 36 and 39 - 42) is similar in organization pattern as in the *Viviparidae*, fulfilling the formulae: 2 - 1 - 4 or 2 - 1 - 3 or 3 - 1 - 4. The predominance of the biggest cusp is not so much expressed in length, however, the cusp is very broad and has a rounded tip, the other cusps being sharper.

The inner marginal tooth (Figs. 36 - 37, 39 - 40 and 42) with a long base is arcuately bent close to the tooth-plate which is slanting to the base and bears about 15 slender, rather big, dagger-like but not always sharp cusps along its edge. The outer marginal tooth (Figs. 36 - 37, 39 and 41 - 42) has no markedly distinguishable plate. About 12 rather big and sharp cusps

surround the terminal section of the tooth. The radula is widely variable, which is not always mentioned in the literature (e.g. BERRY 1943).

Bithynia leachi (Figs. 43 - 48)

The radula is very similar to that described for *B. tentaculata*. The dens centralls (Figs. 44 - 45 and 47 - 48) most often fulfils the same formula as in most specimens of *B. tentaculata*:

$$\frac{4-1-4}{6-6}$$

yet the following formulae are not rare:

$$\frac{3-1-3}{6-6} \text{ and } \frac{5-1-6}{6-6}$$

The latter formulae exceed the variability range of the formerly described species. The same concerns the lateral teeth (Figs. 43 - 46 and 48) whose formulae are: 2 - 1 - 3 or 3 - 1 - 3 or 4 - 1 - 3.

The inner marginal tooth (Figs. 43 - 46 and 48) has 13...18 (most often 15...17) cusps, while in *B. tentaculata* the type number is about 15. The outer marginal teeth (Figs. 43 - 46 and 48) have about 10 cusps each (about 12 cusps in *B. tentaculata*). The cusps are bigger and more slender than in *B. tentaculata*.

The radula variability range, similarly as in *B. tentaculata*, is markedly wide, hence the presented interspecific differences are of statistical character and do not always occur. The variability ranges of the two species are overlapping. This concerns especially the cusp number.

Bithynia troscheli (Figs. 49 - 50)

The radula variability range of the species is contained within the ranges given for *B. tentaculata* and *B. leachi*.

Bythinella micherdzinskii (Figs. 51 - 58)

The radula is typical hydrobioid (DAVIS 1966, 1979, RADOMAN 1973, 1976, GIUSTI & PEZZOLI 1980). The dens centralls (Figs. 51 - 55) shows a rather wide variability (compare Figs. 54 and 55). It fulfils the following formulae:

$$\frac{6-1-6}{2-2} \text{ or } \frac{5-1-5}{2-2} \text{ or } \frac{5-1-5}{2-2}$$

The asymmetry of the rhachis is frequently noted. The denominator of the formula, describing the basal cusps, may also be in the form: $2 - 2(3)$ or $2(3) - 2(3)^*$. The central cusp of the tooth-plate, being not conspicuously bigger than the two adjoining lateral ones, is rather short, narrow and not massive, and has a rounded tip (Figs. 54 - 55). The lateral cusps are long, with rounded tips and nearly parallel edges; they diminish rather slowly with their growing distance from the central cusp.

The lateral tooth (Figs. 51 - 53 and 56 - 57) fulfils the formulae: $3 - 1 - 4$ or $3 - 1 - 5$ or $2(3) - 1 - 5$. The biggest cusp is not markedly bigger than the adjoining two, sometimes it may be difficult to recognize it as the biggest (Figs. 52 and 56). All the cusps are similar as on the dens centralls: slowly diminishing, rather big and long, having nearly parallel edges and rounded tips.

The inner marginal tooth (Figs. 51 - 53 and 56 - 57) has 19...21 cusps similar in shape to those of the lateral tooth, but smaller, rather broad and having rounded tips. The outer marginal tooth (Figs. 51, 56 and 58) bears about 23 cusps limited to the terminal edge and to the short terminal section of the lateral edge. The cusps are always blunt, often knob-like, and always minute (Fig. 58).

Bythinella zyzioneteki (Figs. 59 - 62)

The dens centralls (Figs. 59 - 60 and 62) fulfils the formulae:

$$\frac{5 - 1 - 5}{3 - 3} \text{ or } \frac{5 - 1 - 5}{2(3) - 2(3)}$$

Asymmetry has not been observed and the variability of the cusp number is very restricted. The central cusp is markedly bigger than in *B. micherdzinskii*: it is nearly twice longer and about twice broader than the laterally adjoining cusps. The size of the cusps on both sides of the central cusp diminishes more rapidly than in *B. micherdzinskii*. They are proportionally shorter, more conspicuously triangular and usually sharper than in that species, though having broad bases and rounded tips (compare Figs. 62 and 54).

On the lateral tooth (Figs. 59 - 60) the dominance of the biggest cusp is marked better than in *B. micherdzinskii*; however, the cusp is always markedly broader (Figs. 59 - 60) but not necessarily longer (Fig. 59) than the adjoining cusps on the tooth. It is oval with a somewhat sharpened tip, the other cusps being triangular and having usually sharp (Fig. 60) but sometimes blunt (Fig. 59) tips, the latter perhaps through usage. The formulae of the studied teeth are: $3 - 1 - 3$, $3 - 1 - 4$, and $3 - 1 - 5$.

The inner marginal tooth (Figs. 59 - 61) bears about 17...25 cusps which are longer and sharper than in *B. micherdzinskii*. They are narrow, dagger-shaped, quite triangular and sharp-tipped (Figs. 60 - 61), although sometimes more or less blunt (Fig. 59), which is perhaps through usage. The outer marginal tooth (Fig. 60) has about 25 cusps being longer, more slender and

*Here and in other radular formulae the parentheses indicate a not fully developed cusp; 2(3) means here: two fully developed cusps accompanied with a third, hardly marked one.

sharper than in *B. micherdzinski*. The cusps are long, dagger-shaped and sharp. The variability of the radula is not conspicuous.

Marstoniopsis scholtzi (Figs. 63 - 66)

The radula was described by JOHANSEN (1918), KRULL (1936), VAN REGTEREN ALTENA (1936) and GIUSTI & PEZZOLI (1980). The radulae of the studied specimens are presented in my earlier paper (FALNIOWSKI 1983a). The dens centralis (Figs. 63 and 65 - 66) fulfils the formula:

$$\frac{5-1-5}{3-3}$$

So, the number of the basal cusps is higher than given in the literature (1 or 1 - 2). The basal cusps with rounded tips are more conspicuous than in both described here *Bythinella* species. The tooth-plate, only part of it being cusps, is triangular, and has a well marked sinus on its anterior edge. The cusps diminish regularly with their distance from the central cusp which moderately dominates. All the cusps on the plate are moderately elongated, rather broad, and have rounded tips (Figs. 65 - 66).

The lateral tooth (Figs. 63 - 65) accords to the formulae: 1 - 1 - 4 or 2 - 1 - 3, which renders it contained within the range given in the literature. The biggest cusp on the tooth hardly dominates in size, all the cusps being short and broad with blunt, rounded or even truncate tips.

The inner marginal tooth (Figs. 63 - 64) with about 28 cusps (according to the literature: about 20) little varied in size: only the very marginal cusps are somewhat smaller than the others. All the cusps are narrow, dagger-shaped, but have the tips rounded. The outer marginal tooth (Fig. 63) bears about 30 cusps situated as in *Bythinella*. In a particular tooth the cusp dimensions are almost constant, the cusps being in the form of small, blunt knobs. The radula is slightly variable.

Lithoglyphus naticoides (Figs. 67 - 72)

The radula of the species is very characteristic: showing all the basic hydrobioid characters, it is remarkable for both the extreme reduction of cusp number per tooth and the extremely large dimensions of all the cusps (Figs. 67 - 72).

The dens centralis (Figs. 67 - 72) is characterised by its long base (along the axis of the radula), hence the basal cusps are situated rather far from the tooth-plate (Figs. 68 - 69). The unsatisfactory development of a marginal cusp on one side is the reason for the commonly observed asymmetry of the dens centralis (Fig. 68 is an example). Apart from the asymmetry, the following formulae of the rhachis have been found:

$$\frac{3(4)-1-3(4)}{3-3} \text{ or } \frac{3-1-3}{3-3} \text{ or } \frac{2(3)-1-2(3)}{3-3}$$

The denominators of the formulae, describing the basal cusps, may also be in the form: 4 - 4 or 4 - 3 or 2 - 3. The basal cusps (Figs. 68 - 72) being usually somewhat more sharp than the ones on the plate are often dagger-shaped. All the rhachis cusps are in the form of slender, long, sharply terminated and distinctly separated triangles; the central cusp of the plate is not less than twice longer than the adjoining lateral ones.

The lateral tooth (Figs. 67 - 68 and 70 - 72) fulfils the formulae: 2 - 1 - 4 or 2 - 1 - 3 or 2 - 1 - 2. The extremely prominent and strongly elongated dominant cusp is triangular and sharp, the other cusps being similar in shape but evidently smaller.

The inner marginal tooth (Figs. 67 and 69 - 72) has 5...9 prominent and slender cusps with sharp tips. They are also distinctly separated; the biggest ones are situated in the terminal part of the tooth. The outer marginal tooth (Figs. 67, 70 and 72) is very characteristic in its large, prominent cusps. The cusps, 7...9 per tooth, are massive, spherical triangle in shape. The variability of the radula, apart from the mentioned asymmetry of the dens centralis, is rather restricted.

Potamopyrgus jenkinsi (Figs. 73 - 81)

The radula is moderately variable. The formula of the dens centralis is, as illustrated by Figs. 73 and 75):

$$\frac{4(5) - 1 - 4(5)}{3(4) - 3(4)}$$

However, as is shown in Fig. 74, there may be also:

$$\frac{3(4) - 1 - 3(4)}{1 - 1}$$

The rhachis presented in Fig. 74, having only one basal cusp on each side, is very peculiar. Neither MUUS (1967) and NORDSIECK (1972) nor GIUSTI & PEZZOLI (1984), the latter using also SEM micrographs, observed less than two basal cusps on both sides of the rhachis (usually 2...3...4 were given in the literature). However, such a peculiar dens centralis I have found in only one specimen. The central cusp of the tooth-plate is rather prominent, about twice longer than the adjoining lateral ones, but has the same proportions as the other cusps on the plate, which are well marked, rather broad and quite long, with rounded tips. The basal cusps are more triangular and often sharper than the cusps of the plate.

The lateral tooth (Figs. 76 - 78) fulfils the formula: 2 - 1 - 3. The broad oval and blunt dominant cusp (Figs. 77 - 78) is about twice longer than the adjoining ones. The other cusps are rather triangular, less broad and more or less sharp (Fig. 76).

The inner marginal tooth (Figs. 77 - 78) bears unnumerous (about 10), distinct, round-tipped cusps (Fig. 80) being triangular and broad, and diminishing abruptly towards the margins of the tooth-plate. The outer marginal tooth (Figs. 77 - 79) has about 25 cusps situated along the terminal edge and a lateral one (Fig. 79). The cusps on the lateral edge are similar to those of the

inner marginal tooth, but more fine and slender, while the ones on the terminal edge are very characteristic (Fig. 81) in their having form of long and narrow filaments slowly diminishing in breadth.

2. Protoconch habitus and outer surface

Theodoxus fluviatilis (Fig. 82)

The protoconch comprising 1 1/2 whorls constitutes a greater part of the small protruded spire (Fig. 82). Initially narrow, the whorl breadth grows rapidly. The protoconch lip is well marked on the shell surface; it is slightly bisinuate and extended close to the suture. The surface is rough but without any regular sculpture.

Viviparus cortectus (Fig. 83)

The protoconch is initially rather broad; the whorl breadth increases slowly. There is no visible border between the proto- and teleoconch (Fig. 83). The protoconch surface has no regular sculpture, and is often corroded. Sometimes there is only a delicate spiral sculpture along the whorls.

Viviparus viviparus (Fig. 84)

The protoconch is similar as in *V. cortectus*; the only difference being in habitus: initially narrower, the whorl breadth increases more rapidly than in the former species (compare Figs. 83 and 84). It is frequently corroded and has no regular sculpture.

Valvata piscinalis (Figs. 85 - 89 and 98)

In this species, as well as in the other Polish valvatid gastropods, the protoconch sculpture is conspicuous and even macroscopically different from the teleoconch sculpture (Fig. 85). The growth lines are rather well marked on the teleoconch surface while absent on the protoconch, hence the border between the proto- and teleoconch is quite well marked. However, the characteristic protoconch sculpture vanishes gradually outside the protoconch, just in the initial part of the teleoconch (Figs. 86 - 89).

The protoconch comprises about 1 1/2 whorls that broaden slowly and regularly. The protoconch is initially broad (Figs. 86 - 87 and 89) but may be narrow (Fig. 88). In the *V. antiqua* SOWERBY, 1852 (Figs. 87 - 88) and in the typical form (Figs. 86 and 89) the protoconch shows the same range of variability.

The protoconch microsculpture (Fig. 98) is regular and very characteristic in being composed of spiral, parallelly arranged strips densely juncted with arcuately concave, poorly marked bridges

which are perpendicular to the strips. The surface of both the strips and bridges, as well as of the hollows between them, is regularly granular (Fig 98).

It is noteworthy that the sculpture pattern, as well as protoconch habitus described above for *V. piscinalis* are actually identical with the ones described and illustrated by HADZISCE, PATTERSON, BURCH & LO VERDE (1976) for the Pleistocene fossil shell of *V. humeralis* (SAY). The similarity is as pronounced as to acknowledge that the two above taxa belong to the same species.

Valvata pulchella (Figs. 90 - 94 and 100 - 101)

The protoconch habitus (Figs. 90 - 91) is very similar as in *V. piscinalis*: it is always initially broad. The macrosculpture is also similar as in the former species, but being restricted only to the protoconch surface it vanishes sharply at the rather well marked protoconch lip (Fig. 91). The surface of the calcareous layers, visible after removing the periostracum, is shown in Figs. 92 - 93.

The microsculpture (Figs. 94 and 100 - 101) is completely different from the one described for *V. piscinalis*: it is composed of relatively large, coarse and often irregularly juncted, flat grains (Figs. 94 and 100), and deep irregular pores (Fig. 101), scattered on the surface with no regularity (Fig. 100).

Valvata cristata (Figs. 95 - 96 and 99)

The protoconch habitus (Figs. 95 - 96) is contained within the variability range described for *V. piscinalis*, which does not confirm the differences given by BINDER (1967). The protoconch, initially broad or very broad, slowly increases in whorl breadth and only slightly protrudes over the teleoconch. The border between the proto- and teleoconch is often well marked (Fig. 95), but sometimes a vestigial protoconch-type sculpture is observable also on the surface of the initial part of the teleoconch (Fig. 96). Macroscopically the protoconch sculpture resembles the one described for *V. piscinalis*.

The microsculpture (Fig. 99), visible under higher magnifications, differs markedly from the microsculptures of both *V. piscinalis* (Fig. 98) and *V. pulchella* (Fig. 100), although if at all, it resembles the former species. If compared with *V. piscinalis*, the microsculpture of *V. cristata* (Fig. 99) is less regular, with the spiral strips broader and lower, arched and without sharp edges; the bridges between the strips are very poorly marked, vestigial and irregularly arranged, the surface of all the sculpture elements being very slightly granular.

Valvata naticina (Figs. 97 and 102 - 103)

The protoconch habitus (Fig. 97) contains within the range of variability described for *V. piscinalis*, which does not confirm the data of BINDER (1967). The sculpture is macroscopically somewhat similar as in other valvatids, spiral in character (Fig. 97), although

under higher magnifications (Figs. 102 – 103) it appears completely different from any other Polish valvatid species.

The microsculpture is composed of spirally arranged, nearly parallel lines of pits. The pits are irregular in outline and sometimes juncted (Fig. 102; sometimes nearly all pits are juncted, hence there are irregular continuous lines as seen in Fig. 103: this surface character, however, seems caused with corrosion). The pit surface is fibrous, the surface between the pits being smooth, non-granular.

Bithynia tentaculata (Figs. 104 – 105)

The protoconch (Fig. 104) is initially broad; the whorl breadth increases slowly and regularly; the border between the proto- and teleoconch is blurred and just invisible. There is no macrosculpture: under lower magnifications the protoconch appears smooth (Fig. 104). Under high magnifications (Fig. 105) the surface is coarse-grained (irregular grains) with numerous branched furrows running in irregular zigzags.

Bithynia leachi (Figs. 106 – 107 and 111)

The protoconch macroscopically (Fig. 106) shows the same character states as in *B. tentaculata*, but its microsculpture (Fig. 107) is quite different: very fine-grained with no furrows. The crystals of the calcareous layer, visible when the periostracum is removed, are shown in Fig. 111.

Bithynia troscheli (Figs. 108 and 109 – 110)

Macroscopically (Figs. 109 – 110) the protoconch is practically identical as in the two former bithynid species, but its microsculpture (Fig. 108) is distinct: smooth, with no grains, but with numerous branched furrows running similarly as in *B. tentaculata* and having a various width.

Bythinella micherdzinstii (Figs. 112 – 115)

The protoconch (Figs. 112 – 113) is initially narrow, the whorl breadth grows first rapidly and abruptly, then rather slowly and regularly. The border between the proto- and teleoconch is blurred and just invisible. Macroscopically a very delicate spiral sculpture (Fig. 112), often hardly visible (Fig. 113), can be observed together with numerous fine pits of corrosion which is common in the species.

The microsculpture (Figs. 114 – 115) is composed of a quite smooth surface and numerous groups of pores unevenly but densely distributed on the surface. These typically hydrobioid pores (PONDER 1982b, 1985, and FALNIOWSKI 1989b) are very characteristic, regular in outline and all contained within the periostracum, hence no trace of them can be observed in the calcareous layers when shell cross-sections are analysed. Their appearance is probably due to the specific

structure of the periostracum which is common in many hydrobioid and bithyniid gastropods, however, the proportion of open pores which are the pores visible on the surface varies with species. In *B. micherdzinskii* the proportion is high.

Bythinella zyzionteki (Figs. 116 - 119)

The protoconch habitus (Figs. 116 - 118) does not differ from the one described for *B. micherdzinskii*. The only difference is in spiral sculpture, this being better visible here than in that species, in some specimens even quite conspicuous (Fig. 118). The microsculpture (Fig. 119) is composed of pores identical with those in *B. micherdzinskii*, though more of them being open.

Marstoniopsis scholtzi

All the available specimens of the species had the shells with strongly corroded protoconchs, so that it was impossible to study their protoconch surfaces.

Lithoglyphus naticoides (Figs. 120 - 122)

The protoconch habitus (Figs. 121 - 122) is similar as in *Bythinella*: initially narrow, the whorl breadth grows first rapidly and abruptly, then rather slowly and regularly. The border between the proto- and teleoconch is also blurred and invisible. The corrosion of the protoconch is common and intensive (Figs. 121 - 122). The protoconch periostracum surface is smooth under both low and high magnifications. The protoconch surface at places without the periostracum (Fig. 120) is granular.

Potamopyrgus jenkinsi (Figs. 123 - 124)

The protoconch habitus (Figs. 123 - 124) is very characteristic. Initially very narrow, the whorl grows in breadth bilaterally, first rapidly and abruptly (Fig. 123), then regularly, slowly and unilaterally as in the other described species. Out of the gastropods described in the paper this is the only one showing the bilateral growth. The border between the proto- and teleoconch is blurred and just invisible. Macroscopically the protoconch surface looks smooth, without any sculpture, while under high magnifications it appears fine-grained.

3. Teleoconch outer surface

Theodoxus murvialis (Figs. 125 - 129)

The teleoconch sculpture (Figs. 25 - 127) is composed of low, wide and rounded growth lines having no edges (Fig. 126) and being better developed close to the suture (Fig. 125). A delicate

and hardly visible spiral sculpture can often be observed on both the growth lines and interstices (Fig. 126). Under higher magnifications (Fig. 127) the surface of all the sculpture elements is quite smooth, non-granular. The lip surface (Figs. 128 - 129), having delicate irregular striation (Fig. 128), is fine-grained under higher magnifications (Fig. 129).

Viviparus coriectus (Figs. 130 - 132)

The teleoconch macrosculpture (Fig. 130) is composed only of growth lines. They are widely distributed, not straight but bent or arched, varied in height (although they are never conspicuous). At cross sections the growth lines reveal their triangular outline. Under higher magnifications (Figs. 131 - 132) the surface is regularly granular.

Viviparus viviparus (Figs. 133 - 134)

The macrosculpture is identical as in *V. coriectus*. Under higher magnifications (Fig. 33) the surface shows as well the same fine-granular character as in *V. coriectus* (compare Figs. 131 - 132 with 133). A high magnification of the grains is shown in Fig. 134.

Valvata pischnalis (Figs. 135 - 142)

The macrosculpture (Figs. 135 - 139 and 142) is composed of widely distributed and weak growth lines whose appearance shows a rather wide variability. The lines are usually poorly marked but sharp (Figs. 136 and 138 - 139), their cross section resembling a spherical triangle. Sometimes they are broader but flat, in the form of slightly convex strips without sharp edges (Figs. 135 and 137), or even very broad and flat (Fig. 142).

All SEM photographs of well cleaned surfaces show numerous and regularly arranged fine spiral riblets (Figs. 138 - 142). Minute but well marked, much more delicate than the growth lines, the riblets are perpendicular to them. Under higher magnifications (Figs. 140 - 141) the surface between the growth lines and spiral riblets is quite smooth, non-grained.

The sculpture of *V. pischnalis antiqua* (Figs. 135 - 139) when compared with the one of the typical form (Figs. 140 - 142) shows no significant difference. In general, the growth lines variability is wider in *V. antiqua*: close to the apex the lines often look as shown in Fig. 135, while on the body whorl they are sometimes extremely poorly marked (Fig. 136). The spiral riblets are somewhat better marked in *V. antiqua*. However, the macrosculpture variability ranges of the two forms are practically the same, the microsculpture showing exactly the same picture in both taxa.

Valvata pulchella (Figs. 143 - 146)

The conspicuous, strongly marked growth lines are one of the basic diagnostical macroscopic characters of the shell of *V. pulchella*. However, already low SEM magnifications (Figs. 143 and 145) show the striking variability of the growth lines habitus. The presented photographs show

two extreme cases of the continuous variability range. One extreme are the growth lines in the form of thin and high lamellae (Fig. 143) perpendicular to the shell surface. They are often bent (Fig. 144) and have lacinated edges. The opposite extreme of the variability range are the wide and low growth lines, quite weakly marked (Figs. 145 - 46). However, the non-laminar growth lines are rare within the continuous variability range. No kind of the spiral sculpture is present. The surface at interstices is smooth with minute pits (Fig. 148), or slightly granular (Fig. 144).

Valvata cristata (Figs. 147 - 149)

The teleoconch macrosculpture is similar as in the *V. pulchella* with non-laminar growth lines shown in Fig. 145. No spiral sculpture can be observed and the flatly arched growth lines are relatively broader and more densely arranged (Fig. 147) than in *V. pulchella*. The microsculpture, the same on both the growth lines and interstices (Figs. 147 - 149), is completely different from those of the other valvatid species. It is well marked and quite regular, fibrous-granular with no pits.

Valvata naticina (Figs. 150 - 152)

The teleoconch sculpture, especially in the upper part of the spire, is often quite identical with that of the protoconch (Fig. 150). The macrosculpture is very hardly marked; there is no spiral sculpture, the growth lines are closely arranged, in the form of delicate convexities. The microsculpture (Fig. 151) is delicate, fine-grained-fibrous, rather regular and very poorly marked. The surface with no periostracum is shown in Fig. 152.

Bythynia tentaculata Figs. 153 - 155 and 158)

The teleoconch macrosculpture is composed of loosely distributed, wide and low growth lines rounded, with no sharp edges. Under higher magnifications (Figs. 153 - 154) the surface appears very fine-fibrous-grained here and there (Fig. 154) if the pores are covered, but the greater part of the surface is composed of a dense net of open pores (Fig. 53), covered here and there with small crystals being probably an artifact caused with cleaning the shell in oxalic acid. The pores (Figs. 155 and 158), regular and contained entirely within the periostracum, are similar as described for the protoconch of *Bythynella*.

Bythynia leachi (Figs. 157 and 159 - 167)

The macrosculpture (Fig. 159) is composed of similar growth lines as in *B. tentaculata*, being combined with spiral riblets. The riblets (Figs. 157 and 160 - 162) are numerous and dense, regularly arranged, delicate but sharply marked.

Under high magnifications (Figs. 157, 162 and 165) the surface between the growth lines and spiral riblets shows more or less a slight granular character. The shape and diameter of the

grains, if they are well marked (Fig. 157), indicate that each of them covers a pore lying over a very thin outermost layer of the periostracum. The pores are identical as in *B. tentaculata*, though they are rarely open (Figs. 163 – 164) while in *B. tentaculata* almost all of them are open or at most covered with sediment. The arrangement of the pores seems more dense in *B. leachi* than in *B. tentaculata*.

The appearance of the teleoconch outer surface with no periostracum (Figs. 166 – 167) proves that the pores do not pass into the calcareous layers, since no trace of them can be seen when the periostracum is removed.

Bithynia troscheli (Figs. 156 and 168 – 171)

The teleoconch macrosculpture (Figs. 168 – 169) is similar as in *B. tentaculata* in being composed of loosely distributed, wide and low growth lines rounded, with no sharp edges, and in lacking any sculpture of the spiral type.

Under higher magnifications (Figs. 158 and 170) there are visible fine and delicately marked grains covering the pores which are similar in character to those in *B. tentaculata* and *B. leachi*. However, in this species they are more fine and nearly always covered. The surface with the periostracum removed is shown in Fig. 171.

Bythinella micherdzinski (Figs. 172 – 175)

The teleoconch macrosculpture is composed of sole growth lines densely distributed and very slightly marked, in the form of wide and smooth, fine convexities. Higher magnifications (Figs. 172 – 173) show a net of pores, the latter however being more often covered than open. The pores (Figs. 174 – 175) are quite similar as in the *Bithynidae*. Occurring only within the periostracum, they seem somehow less regular and uniform than in *Bithynia*. They are irregularly scattered in groups on the surface which apart from them is rather smooth.

The outer lip even under a magnification of 13,000 x is smooth, besides only very fine irregularities.

Bythinella zvirinteki (Figs. 176 – 180)

The macrosculpture is similar as in *B. micherdzinski*, but the growth lines are not so weakly marked as in that species, and better visible (Figs. 176 – 177), although still fine. The pores (Figs. 178 – 179) are open (Figs. 176 – 178) within a greater part of the surface than in the previously described *Bythinella* species. They are well marked even if covered (Fig. 179), their shape and diameter being identical as in *B. micherdzinski*.

The lip surface, composed of compact crystals little variable in size (Fig. 80), is completely different from that of *B. micherdzinski*.

Marstoniopsis scholzi (Figs. 181 - 182)

The teleoconch outer sculpture variability has not been studied because the available material was insufficient. In a few specimens studied the macrosculpture (Fig. 181) was composed of growth lines in the form of fine and delicate, loosely distributed faults running not quite straight. Some sections of the lines were less visible. Higher magnifications showed no pores but a slightly fine-grained surface. A fragment of the surface with the periostracum removed is shown in Fig. 182.

Lithoglyphus naticoides (Figs. 183 - 188)

The macrosculpture (Fig. 184) is composed of relatively dense, well marked but narrow and low, quite fine growth lines, sometimes combined with a hardly developed spiral sculpture which is usually absent. The macrosculpture of a specimen from the Danube river, shown in Fig. 183, is somewhat different. However, this specimen may not be conspecific with *L. naticoides* from Poland, though according to the revision of BOLE (1981) it also belongs to this species.

Under higher magnifications (Fig. 185) the surface of the periostracum is almost smooth with fine irregularities, or slightly granular; the pores are never observed. The periostracum is thin so that the growth lines are well marked also on the surface of the crystalline layer (Fig. 186). It is also delicate: there are often quite big surfaces with the periostracum peeled off (Fig. 186). Fig. 187 shows a high magnification of such a surface lacking periostracum. The lip surface composed of regular compact crystals is shown in Fig. 188.

Potamopyrgus jenkinsi (Figs. 189 - 199)

The species is famous for its considerable shell sculpture variability (see FALNIOWSKI 1987). Besides the most common smooth-shelled *L. ecarinata* JENKINS, 1889, there is the frequently occurring *L. carinata* MARSHALL, 1889 characterized by a more or less prominent spiral keel running from the third whorl closely and parallelly to the suture. In *L. aculeata* OVERTON, 1905, on the younger whorls besides or instead of the keel there are well marked individual spines (bristles); the form however was found in Poland as a single empty and incomplete shell², so the structures of that form were not studied since no sufficient material was available.

The entirely concholine keel produced by a small and blunt appendix of the mantle edge (FRETTER & GRAHAM 1962) shows a wide variability (Figs. 189 - 194): from a slightly marked hump with no sharp edges (Fig. 189), or triangular growth-line widenings (outgrowths) arranged in a line (Fig. 194), to a row of long, prominent, more or less separate spines (Figs. 190 - 193) each of them being an outgrowth of a successive growth line. The spines are varied in size and proportions, with the tips blunt (Figs. 190 - 191) or more or less sharp (Figs. 192 - 193), often irregular (Fig. 193).

² This shell is pictured on the title page of this volume of the journal.

Apart from the keel, the macrosculpture is also variable (Figs. 195 and 197). The growth lines are relatively dense, always convex and without sharp margins (Fig. 195), but varied in width and height. Besides them there may occur spiral riblets (Figs. 195 and 197).

In *L. ecarinata* the growth lines are usually low and broad while the spiral riblets well marked. This, however, falls within the variability range of the keeled form.

Under higher magnifications (Figs. 196 - 198) the surface is never granular but quite smooth (Figs. 197 - 198) or fibrous (Fig. 196). The damage of the outermost layer of the periostracum occurs rarely, so only small spots covered with typically hydrobioid pores are observable (Figs. 197 and 198). The net of pores (Fig. 199) seems more regular than in *Bythinella*.

4. Teleoconch inner surface

The structure of the inner surface of the teleoconch seems a good diagnostic character on the species level, since the process of shell thickening, which proceeds throughout gastropod's life, is under the direct control of the organism of the animal, hence the appearance and arrangement of the formed crystals have to be closely connected with the chemistry of the operating enzymes, which means also with the enzyme structure. It seems, therefore, that the structures observable on the inner surface of the shell should be a good taxonomic character on the molecular level.

It is quite difficult to use the shell inner surface structure characters in practice. Killing a gastropod stops the process of shell formation and causes a rapid recrystallization of extrapallial fluid. For that reason, to reveal the crystals formed by a still living mollusc, it is necessary to etch the inner surface gently and then wash it very intensively. Though numerous artifacts, being hardly distinguishable from non-artificial structures, are actually unavoidable.

Another source of technical problems connected with the inner surface studies is various stages of the process of shell formation: although the growth in thickness of the shell is life-lasting, it does not occur continuously and with the same intensity, but is rather a cyclic phenomenon. Moreover, besides etched surfaces, also non-etched but well cleaned ones should be considered, if possible.

All the facts listed above make the examination of numerous specimens of each species inevitable. For that reason such a study must be tiresome and time-consuming. Hence, I only have managed to obtain as satisfactory as quite univocal results for the *Valvatidae* and *Hydrobiidae*, so only these gastropod structures are described below.

Valvata piscinalis (Figs. 200 - 201)

The unetched inner surface of the teleoconch (Fig. 200) is granular, with fine cracks and fine crystals scattered rather densely on the surface and being probably artifacts. The etched surface (Fig. 201) shows its granular-fibrous character, with the grains fine and irregular and the fibrousness marked slightly. In both forms: *L. yppica* and *L. antiqua*, the inner surface structure is identical.

Valvata pulchella (Figs. 202 - 205)

The unetched inner surface (Fig. 202) does not resemble the one described for *V. piscinalis*. It is densely covered with very fine pores of various outline and diameter, combined with loosely and irregularly arranged cracks being somewhat shorter and wider than in *V. piscinalis*. The etched inner surface (Figs. 203 - 205) also differs from that of *V. piscinalis*. It is fibrous with deep furrows between slightly folded fibres (Figs. 203 and 205) which are fused from place to place and show a very characteristic appearance under higher magnifications (Fig. 204). The furrows are mostly straight.

Valvata cristata (Figs. 206 - 207)

The etched inner surface of the teleoconch (Figs. 206 - 207) is fibrous similarly as in *V. pulchella*. However, under higher magnifications (Fig. 207) the appearance of the fibres is markedly different from that of the *V. pulchella* shown in Fig. 204. The fibres have well marked and often strong transverse folds on both their surface and margins (Fig. 207). Most fibres converge at acute angles (Fig. 206). Between the deep longitudinal furrows which often also converge at acute angles there are others: the parallel ones being shallower and the perpendicular ones being deep but short.

Valvata naticina (Figs. 208 - 209)

The etched inner surface is completely different from the one characteristic of the other Polish valvatid species. It shows a laminar character (Figs. 208 - 209) in being composed of irregularly shaped and arranged laminae. The laminae are fine, rather short and with ragged margins, and approximately parallel to one another.

Bythinella micherdzinski (Fig. 210)

The etched inner surface (Fig. 210) is composed of regularly arranged plates which are irregular in shape, variable in size and have dentate margins. The plates are arranged in groups varied in shape, separated with quite deep and conspicuous furrows. The plates' surface is granular; fine pores irregularly and loosely arranged can be seen on it.

Bythinella zywionteki (Fig. 211)

The etched teleoconch inner surface (Fig. 211), as in *B. micherdzinski*, shows a regular pattern of irregular plates. The plates, varied in size and with dentate margins, are arranged in groups separated with deeper and more conspicuous furrows. However, the plates differ in shape from those described for *B. micherdzinski*. In *B. zywionteki* all the elements are conspicuously finer, and no pores are observable.

Marstoniopsis scholtzi (Fig. 212)

Owing to the mentioned lack of material it was impossible to study the shell structures of the species more extensively. The only satisfying photographs obtained were of the unetched inner surface. The unetched surface (Fig. 212) is evidently fine-grained. Here and there rhomboid crystals occur on it, being probably an artifact.

Lithoglyphus naticoides (Figs. 213 - 214)

The unetched inner surface (Fig. 214) is composed of compact fine grains combined with more loosely arranged and bigger prismatic crystals of aragonite. The etched surface (Fig. 213) is spongy-fibrous, composed of short and irregularly arranged fibres and very small spaces between them.

Potamopyrgus jenkinsi (Fig. 215)

The teleoconch inner surface, when etched (Fig. 215) shows a fibrous character, revealing rather short fibres, approximately parallelly arranged and separated with deep furrows being usually wider than the fibres. The fibres seem composed of single grains arranged in lines.

5. Teleoconch inner structure

Theodoxus fluviatilis (Figs. 216 and 222 - 225)

From among the Polish prosobranchs this species has the shell structure markedly distinct, which additionally proves the distinctness of the *Meritacea* when compared with the *Caenogastropoda* s.lato (FALNIOWSKI 1989a and b). The most striking characters are the shell thickness and the massiveness of the inner structure elements whose majority are visible already under a dissecting microscope. The shell structure is quite simple, little complex. There is nothing that can be identified with the endostracum, while the ecto- and mesostracum show the organization pattern being very regular and poor in elements.

The shell sections, both perpendicular (Figs. 216 and 222 - 223) or parallel (Figs. 224 - 225) to the growth lines always reveal two quite well distinguishable crystalline layers under a rather thick periostracum. The layer close to the periostracum, sometimes called ectostracum (see Appendix II), is here markedly thinner than the mesostracum. It is composed of fine fibrous crystalline structures arranged approximately perpendicularly to the shell surface (Fig. 216). There is a very thin and quite smooth transition from this layer to the mesostracum (Figs. 216, 222 and 224 - 225): this is a very thin layer showing a granular character. The mesostracum looks completely

different at the sections perpendicular than at the ones parallel to the growth lines (compare Figs. 216 and 222 with 224 - 225).

At the shell sections perpendicular to the growth lines (Figs. 216 and 222) the mesostracum is composed of columns, so it can be called a pallasade layer. The thin transitional layer mentioned above diverges here into columns showing the same "granular" character, which alternate with columns looking fibrous. The SEM micrograph analysis shows that the two kinds of columns are, in fact, fibrous and differ only in the spatial orientation of fibres. The seemingly granular columns are composed of fibres running perpendicularly to the section surface (Fig. 223), while the "fibrous" columns are composed of the same fibres, but running approximately parallelly to the section surface (perpendicularly to the shell surface).

The columns (Figs. 216 and 222) run parallelly to one another and perpendicularly to the shell surface and reach the inner surface of the shell. They are rather thick and well marked, straight, never crossing one another or branching. The groves and folds visible in micrographs, which are perpendicular to the long axis of a column and divide it into sections, are probably partly an effect of the cyclic thickness growth of the shell.

The columns are observable at the sections perpendicular to the growth lines, while no trace of similar structures can be found at the ones parallel to the growth lines (Figs. 224 - 225). The latter always reveal wide diagonal structures that are crystalline structures composed of well visible, long, diagonally arranged fibres.

Viviparus costectus (Figs. 217 - 218 and 226 - 230)

The shell structure of the *Viviparidae*, unlike those of the other species the paper deals with, was studied earlier (KESSEL 1933: he gave also a review of the preceding literature). In all the studies I know the research was carried out with the use of the technique of polished microsections examined under a light microscope, often using polarized-light images. Such analyses, many of them very detailed and thorough, were in general devoted to a three-dimensional model of the shell structure and did not pay attention to taxonomically useful characters.

Although the model presented by KESSEL (1933) is much detailed and convincing, my results do not confirm it fully. This may be, in part, an effect of different techniques applied: I have used SEM images which are seemingly three-dimensional and have a high depth of field, while KESSEL had to design the model with the use of series of thin sections; the latter method solely, in my opinion, can never provide a reliable picture of a three-dimensional structure.

Moreover, KESSEL found three calcareous layers under the periostracum, the intermediate one being a pallasade layer, while I have always observed only two layers: the columns of the pallasade one reached the periostracum (Figs. 217 and 230), although they were slightly marked at the outermost zone of the layer, adjoining the periostracum. At the sections parallel to the growth lines (Figs. 228 - 229) I have never observed such columns as those described by KESSEL; at such sections I found only very slightly marked structures resembling columns but they were not situated in the region indicated by KESSEL.

Under the relatively rather thick periostracum (Figs. 217, 226 and 228 - 230) there are very thick, mostly calcareous structures whose homology and nomenclature seem controversial. At the sections perpendicular to the growth lines they are divided into two parallel layers: the pallsade layer and the wide diagonal one. Theoretically, the former could be determined as a mesostracum, while the latter reaching the inner surface of the shell - as an endostracum. However, according to the data of KESSEL and, partly, of my own, such a nomenclature seems not justified.

Most differences between the two layers are due to the different spatial orientation of the same structures. Moreover, the calcareous layer shows a continuous character and the whole of it is probably formed in the same way, through a continuous process. Hence, probably the proper name for the entire crystalline structure should be "mesostracum". For practical reasons I propose the name "false endostracum" for the shell inner layer showing a characteristic pattern of wide diagonal structures, while the name "proper endostracum" I use for the inner layer whose usually spongy, neither granular nor fibrous structure is discontinuous with the other layers. The proper endostracum occurs in many species described in the paper, but never in the *Vinparidae*.

The thickness proportion between the pallsade layer and false endostracum shows a wide variability (Figs. 217, 226 - 227 and 230). The columns of the pallsade layer (Figs. 217 - 218, 226 - 227 and 230) are always parallel to one another and perpendicular to the shell surface; they never cross one another nor branch, with an exception of the regions close to the columella (Fig. 226). All the columns are slender - much more slender than in *Theodorus fluvialis*. All of them show a fibrous structure, with the alternate direction of the fibres of the successive columns (Figs. 218 and 230). Sometimes the columns are hardly discernible (Fig. 230), and sometimes better marked (Fig. 227); in extreme cases there are two conspicuously distinct alternate categories of columns (Figs. 217 - 218). The narrower columns are smooth in the sections adjoining to the false endostracum (Fig. 218), having there probably a conchiotine macro-envelope. On each column, transverse lines (growth lines?) are observable.

The false endostracum is composed of long fibres forming wide diagonal structures (Figs. 217, 227 and 230). The angles between the alternately directed fibres are flat, obtuse. After longer, deep etching the layer shows vast spaces between the relatively broad and massive fibres (Fig. 227).

The sections parallel to the growth lines (Figs. 228 - 229) also differ from those described for *Theodorus fluvialis*. Under the periostracum there are visible short and narrow column-like structures, hardly discernible and becoming wider with the growing distance from the periostracum. The whole remaining part of the sections comprises regularly arranged successive layers of long fibres slanting to the shell surface; the whole layer shows a diagonal pattern of organization.

Vinparus vinparus (Figs. 231 - 236)

When compared with *V. conlectus*, the shell structure is similar, showing only slight differences. Sections perpendicular to the growth lines (Figs. 231 and 233 - 237) display a wide

variability of the thickness proportion between the pallsade layer and wide diagonal structure layer. The column proportions are quite variable, too. In this species I have never observed a smooth conchioline macro-envelopes of columns, which is common in *V. corlectus* (see Figs. 217 - 218).

A high magnification of deeply-etched preparations (Fig. 238) has revealed a spongy character of the wider columns; the proportions of both organic and mineral compounds are high in the columns, the trabeculae running almost perpendicularly to the section surface. The transverse (growth?) lines on the "spongy" columns are sharply marked, stronger than in *V. corlectus*; while on the other columns they are hardly visible or even absent (Fig. 233): this also exceeds the variability range described for *V. corlectus*.

The false endostracum (Fig. 234, also 321 and 235 - 237) is very similar as in *V. corlectus*, but the fibres are thinner and more slightly marked (Fig. 234). Within the layer, lines being parallel to the shell surface can often be seen (Figs. 231, 234 and 237). Similar lines may sporadically be recognized at sections of *V. corlectus* (Fig. 217), but they are never marked so strongly.

The picture observed at the sections parallel to the growth lines (Fig. 232) is similar as in *V. corlectus*, but in *V. vimparus* the layer of column-like fine structures is strongly reduced (just vestigial) and hardly discernible.

Valvata piscinalis (Figs. 239 - 246)

At the sections perpendicular to the growth lines (Figs. 239 - 241) of a fully developed shell five layers can be distinguished. The first layer is the periostracum. The second one, adjoining to the periostracum, shows a fine-diagonal pattern of organization (Figs. 239 - 241). It is composed of short but relatively broad and distinctly marked fibres arranged diagonally; the layer thickness varies within a quite wide range, although it is always thinner than the next, pallsade layer.

The columns of the pallsade layer are usually slender, variable in width and rather irregularly arranged, but never crossing or branching. The columns have no conchioline macro-envelopes. They are slightly (Fig. 239) or even hardly (Figs. 240 - 241) distinguishable.

All the columns have a granular appearance, since all the fibres forming them cut the section surface at a quite high value of angle; each column contains the fibres directed at a somewhat different angle than the fibres of the two adjoining ones, and successive columns show the alternate direction of fibres. This is why the columns are observed and why they are varied in discernibility: if the angles between the long axis of the column fibres and the section surface were the same for all columns, no columns would be observable. In *V. piscinalis* some columns may show a tegular arrangement of successive fibres (Fig. 241). On all the columns there are rather well marked, transverse (growth?) lines. There is no smooth transition to the next layer, the columns terminate abruptly.

The false endostracum is much varied in thickness, from quite thin (Fig. 240), to as thick as the pallsade layer (Fig. 239); the thickness depends probably on shell age (shell growth stage). The layer organization is of wide diagonal structure type, however, it is very flat, i.e. the fibres run nearly parallelly to the shell surface (Figs. 240 - 241), or at very low values of the angles between

them and the surface (Fig. 239.) The deep etching results in vast spaces within the layer: this indicates high proportions of both organic and inorganic compounds. This renders the layer similar to the spongy proper endostracum.

The innermost, fifth layer is very often absent and occurs only at the sections of the thick, fully developed shells of old specimens. It is the proper endostracum (Figs. 240, 243 and 244) being spongy with vast spaces visible even after a quite not deep etching. It is neither granular nor fibrous but rather irregular, sharply discontinuous with the false endostracum. No similar structure is observable in *Theodoxus* or *Viviparus*.

The picture at the sections parallel to the growth lines (Figs. 242 - 246) is much less complicated. Under the periostracum there is a rather thin layer of short, well marked fibres running perpendicularly to the shell surface; the layer seems more or less granular. Next, there is the thickest layer: wide diagonal with long and quite distinctly separated fibres (Figs. 242 - 246). Within the layer, at the side of the periostracum, there are often hardly visible pallisade-like structures (Figs. 242 - 244). The remaining layer is a proper endostracum (Figs. 242 - 244, best visible in Fig. 244) which is thin and often absent, looking very similar as at the sections perpendicular to the growth lines.

The shell inner structure of *V. antiqua* is exactly the same as in the typical form.

Valvata pulchella (Figs. 247 - 256)

The teleoconch inner structure is very similar as in *V. piscinalis*. The picture of the sections parallel to the growth lines (Figs. 255 - 256) is practically identical with the one in *V. piscinalis*: the proper endostracum often constitutes the innermost, thin and spongy layer (Fig. 256).

The sections perpendicular to the growth lines (Figs. 247 - 254) reveal some character states which are different from the ones described above for *V. piscinalis*. The outermost calcareous layer adjoining the periostracum (Figs. 249 - 250 and 253 - 254), as in that species, is composed of short fibres forming a fine diagonal structure pattern, however, its thickness is not constant within the same shell (section) but is higher under a rib, and lower under an interstice (Figs. 247 - 248). In some specimens the layer is practically absent (Fig. 251) and the columns begin extremely closely to the periostracum.

The number of columns between the successive ribs is not constant (Figs. 247 - 248), a few columns occurring always between each pair of ribs. The columns of the pallisade layer are usually even less discernible than in *V. piscinalis* (Figs. 249 - 254) and their pattern is more irregular; the transverse lines (Fig. 251) on them are better visible, being often in the form of narrow but deep slits.

The wide diagonal false endostracum is not as sharply demarcated from the pallisade layer as in *V. piscinalis* (Figs. 249 - 250 and 252 - 254), a thin transitional zone being distinguishable. In comparison with *V. piscinalis*, in *V. pulchella* the fibres are evidently laminar, flat and broad, their shape being irregular and margins jagged (Figs. 250, 252 and 254). After deep etching the spaces between the laminae are wider than in *V. piscinalis*. The proper endostracum occurs less often, and if so, it is less developed than in that species.

Valvata cristata (Figs. 257 – 263)

In this species, the most striking feature of the teleoconch inner structure is the occurrence of vast spaces between fibres, which is visible at the etched sections (Figs. 257 – 263) within all layers. The relatively less marked spaces are observable at the sections parallel to the growth lines (Figs. 257 and 262), this however does not concern the zone adjoining directly the periostracum, where the spaces are extremely large.

Apart from the spaces, the sections parallel to the growth lines resemble the ones described for both the valvatid species described above, but the fibres, sometimes massive and very well marked (Fig. 257), are always better discernible (Fig. 262) than in *V. piscinalis* and *V. pulchella*. The spongy proper endostracum is never present in *V. cristata*.

The fine diagonal structures constituting a rather thick layer directly under the periostracum are broad, massive, moderately long and conspicuously separated with spaces. The columns of the pallisade layer (Figs. 258 – 261 and 263) are very variable in this species. Sometimes they are completely indiscernible (Fig. 261), often poorly marked (Figs. 258 and 260), but may also be distinctly marked (Figs. 259 and 263). However, they are in general less marked than in both *V. piscinalis* and *V. pulchella*. The fibres within the columns are very well discernible, flat with undulate margins (Fig. 260). The transverse (growth?) lines on the columns are always absent in *V. pulchella*.

The false endostracum shows a very flat wide diagonal pattern (Figs. 258 – 261). This layer is always relatively thick when compared with both the valvatid species described above. The vast spaces between the loosely arranged fibres render the layer similar to the proper endostracum which also has a spongy character. The fibres in the layer are laminar, broad, massive and long.

Valvata naticina (Figs. 264 – 272)

The teleoconch inner structure differs markedly from the one described for the other valvatid species under consideration. However, it contains within the general characteristic pattern of the family.

At the sections perpendicular to the growth lines (Figs. 264 – 267 and 270 – 272) there is a fine diagonal structure layer directly under the periostracum. The layer is composed of poorly discernible, very fine, thin fibres and is less regular than in the other valvatid species (e.g. see Figs. 266 and 272, also Figs. 265 and 270 – 271). The layer is also thinner than in those species; sometimes it is almost completely absent (Figs. 264 and 267).

The pallisade layer (Figs. 264 – 268 and 270 – 272) is very thick. The columns are narrow and slender, much better discernible than in the other Polish valvatid species, the borders of successive columns being quite strongly marked as distinct lines. The alternate pattern of fibres (Fig. 268) in the successive columns is sometimes in the form of fibres that are perpendicular/parallel to the section surface (Fig. 264); sometimes the direction of the fibres is almost the same in the neighbouring columns (Fig. 267) so the columns are hardly visible, but usually the angle is moderately differentiated (Figs. 265 – 266, 268 and 270 – 272). The spaces between the fibres within the columns are of a medium size.

The pallsade layer pattern is little regular. Usually no alternate arrangement of wider and narrower columns is observed, the column breadth varying between particular columns (Figs. 264 - 268 and 270 - 272). Many of the columns are branched (Fig. 264 is a good example; also Figs. 265 - 266, 270 and 272). Apart from the "normal" columns of full size there are also the shorter ones being usually not longer than half of the "normal" column; the shorter columns are numerous within the zone adjoining the false endostracum (Figs. 265 - 266, 270 and 272), but it is not only there they occur (Fig. 271).

The transition to the next layer is rather sharp, not continuous: the columns terminate abruptly (Figs. 265 - 266 and 270 - 272); the transitional zone is narrow and hardly discernible (Fig. 264). The false endostracum (Figs. 264 - 267 and 270 - 272) is moderately thick, the wide diagonal structures being much flat, composed of long and quite slim trabecular fibres. The fibres are rather sharply marked, the spaces between them being moderately large (Figs. 264, 266 - 267, 270 and 272). The spongy proper endostracum is always absent in *V. naticina*.

At the sections parallel to the growth lines (Fig. 269) directly under the periostracum there is a slightly marked, moderately thick layer; at the sections perpendicular to the growth lines this layer shows a pattern of fine diagonal structures, while at the sections parallel to the growth lines (Fig. 269) it appears to consist of hardly marked, fine pallsade structures. All the remaining part of the shell section is filled by a thick layer having a wide diagonal structure pattern. The pattern is flat, composed of easily discernible, quite long and slender fibres.

Bilhyia tentaculata (Figs. 219 - 220, 273 and 275 - 280)

From among the gastropods under consideration, the *Bilhyiidae* show the most complicated pattern of shell inner structure. The sections perpendicular to the growth lines (Figs. 219 and 275 - 280) of the fully developed shell of the adult gastropod reveal up to six layers.

Directly under the periostracum there is a moderately thick (sometimes just absent: Figs. 278 - 279) layer composed of short laminae, all of them approximately perpendicular or slanting to the shell surface (Figs. 219, 275 - 276 and 280). At the etched sections, the laminae are visibly separated with moderately large spaces. The layer may be replaced by a typical fine diagonal structure (Fig. 277).

The third, pallsade layer (Figs. 219 and 275 - 280) is composed of relatively short and broad laminae having ragged margins and a slightly grained surface (Fig. 273). The columns are, in general, better discernible than in the *Valvatidae* but worse discernible than in the *Viviparidae*. This character is rather variable in *B. tentaculata*, the columns being from quite well (Figs. 219 and 275 - 276) to slightly (Figs. 277 and 279 - 280), or even hardly (Fig. 278) visible. The layer pattern is also moderately regular: less regular than in *Viviparus* but more than in *Valvata*.

Outside the region close to the columella (Fig. 276) the columns usually do not branch. However, their thickness is variable within the same section, showing just no regularity, and they do not run straight (they are bent several times or arched: Figs. 278 - 280 are an example). In the region close to the columella, besides the columns of the typical appearance there are often the

others being rather smooth and composed of hardly marked longitudinal fibres which are parallel to the section surface (Fig. 276).

The fourth one is the specific bithynid layer of angular structures (Fig. 220) which is often rather thick and well developed (Figs. 219 and 275), but sometimes reduced. The layer constitutes a smooth transition from the palisade layer to the layer of wide diagonal structures (false endostracum). The alternate pattern of narrowing and broadening columns (Figs. 219 - 220 and 275) fills up the layer. Thinning gradually, the former columns terminate there, while the latter ones are continuous with the wide diagonal structures of the false endostracum, just constituting the tops of the successive triangles, however, after leaving the layer the fibres direction becomes less slanting to the shell surface. It must be noted that the thickness of the angular structure layer is not constant, since within the same section the tips of the narrowing columns are situated at a various distance from the beginning of the columns (Figs. 219 and 275).

The fifth layer is a false endostracum (Figs. 219, 275 - 278 and 280) composed of wide diagonal, flat structures whose fibres are quite well marked and easily discernible. This layer is moderately thick.

The remaining sixth layer is (not always present) a proper endostracum (Figs. 219, 275 and 279). The proper endostracum is spongy, especially after deep etching, neither granular nor fibrous, almost irregular in pattern. It is similar as in some valvatid species, however, being more common and better developed in *B. tentaculata*.

The shell sections parallel to the growth lines present a much more simple structure: under the periostracum there is a very thick and quite uniform wide diagonal layer reaching the proper endostracum if the latter is present; the proper endostracum appearance at the sections parallel to the growth lines is identical with that at the ones perpendicular to the growth lines.

In general, the not fully developed shells of younger gastropods do not bear all the layers (Figs. 276 and 278 - 280). Hence the last-formed layer, i.e. the proper endostracum, is most often lacking. However, this is not a rule: in numerous shells, directly beneath the palisade layer there is only a thin or very thin layer (Figs. 276 and 278 - 280) showing a mixed character, i.e. bearing close resemblance to both the false and proper endostracum. Within the layer, one can distinguish the fibres whose arrangement is typical of the false endostracum (wide diagonal pattern) but accompanied with vast, irregular spaces as in the proper endostracum (Figs. 276, 278 and 280). Moreover, in some specimens this is simply a typical proper endostracum which contacts with the palisade layer (Fig. 279). The above phenomena indicate that the process of shell formation cannot always be described by a model that assumes the successive covering of the earlier set layers with the new ones, without any, even at least a partial, reconstruction of the former layer.

Bithynia leachi (Figs. 281 - 286)

The structures visible at the sections parallel to the growth lines (Figs. 285 - 286) are exactly the same as those of *B. tentaculata*. On the inner side of a very thick wide diagonal layer often a

spongy proper endostracum can be observed. It is organized identically as in *B. tentaculata*, although never as thick as it may be found in that species.

The sections perpendicular to the growth lines (Figs. 281 - 284) are, in general, similar as in *B. tentaculata*. Some distinct character states, however, can be found. In *B. leachi* the layer situated directly under the periostracum (Fig. 282) is thinner (Figs. 283 - 284), sometimes just absent (Fig. 281) and then the columns become quite distinct directly under the periostracum.

The columns, similarly as in *B. tentaculata*, are more (Fig. 282) or less (Figs. 283 - 284) discernible, but sometimes may be more discernible than in that species (Fig. 281). The columns are usually more slender and more regularly arranged in *B. leachi*. The angular-structure layer (Figs. 281 and 284) is proportionally thinner than in *B. tentaculata*, because the columns become broaden/narrow more rapidly (at more obtuse angles).

The wide diagonal layer is often absent and never as thick as it is sometimes in *B. tentaculata*. The proper endostracum is often absent, or forms a very thin layer of the same spongy character as the one in *B. tentaculata*.

Bilhyria troscheli (Figs. 274 and 287 - 292)

The shell inner structure generally resembles the ones described for the other two bilhyinid species, though some distinct character states can be observed.

The angular structure layer, being fully developed in *B. tentaculata* and thinner but well visible in *B. leachi*, in *B. troscheli* is almost always completely absent (Figs. 287 - 290). At the sections perpendicular to the growth lines the columns may be hardly discernible (Figs. 288 and 290), but may also be sharply marked (Figs. 287 and 289), and then the pallisade layer shows an alternate pattern of broader and narrower columns. The latter columns are often very slender and have the surface seemingly covered with long, scale-like arranged plates which are irregular in shape (Fig. 274: a conchioline macro-envelope?).

The proper endostracum (Figs. 287 and 289, also Fig. 291; no satisfactorily etched section is presented since the material was too scarce to obtain any) is nearly always present, being usually thick in the shells of old molluscs, while the wide diagonal false endostracum is most often absent.

At the sections both parallel (Fig. 291) or slanting (Fig. 292) to the growth lines, the fibres are very well marked and show a conspicuous granular character (especially Fig. 292).

Bythinella micherdzinski (Figs. 293 - 298)

The shell structure, owing to probably the tiny size and extremely thin walls of the shell, is much simplified when compared to the shells of the species described above. Moreover, the inner structure pattern is strikingly less regular. The simplicity and irregularity are visible especially at the sections perpendicular to the growth lines.

The teleoconch sections perpendicular to the growth lines (Figs. 293 - 295) are characterized by a relatively very thick pallisade layer that covers almost all the section breadth. Directly under the periostracum (Fig. 295) there is a thin fine-grained layer. It is always present, quite constant

in thickness (Figs. 293 - 295) and composed of rather fine grains. The grains are plate-like, irregular in shape, from nearly equilateral to more or less elongated (then the long axis is directed perpendicularly to the shell surface) and with ragged margins. Apart from rather well marked spaces between the grains, there are also fine "cavital" spaces being irregular in shape and arrangement (Fig. 295). In *B. micherdzinski* the cavital spaces are rather hardly discernible within this layer.

The next one is a pallsade layer whose columns are poorly discernible (Figs. 293 - 295), the column pattern being very irregular, just chaotic: the columns are varied in width and length, many of them terminating far from the border of the layer, branching or even crossing one another (especially Fig. 294). The columns are composed of irregular, elongated laminae with ragged margins (Fig. 295). The laminae of the successive columns are alternately arranged (almost parallel/perpendicular to the section surface).

Sometimes the columns reach the inner surface of the shell. If not, there is a gradual transition to the innermost layer which is always thin. Within the latter layer the columns gradually disappear. The layer is grained-spongy (Figs. 293 - 294). It contains numerous but slightly discernible and fine spaces of the cavital type. Apart from the cavital spaces, the sponginess of the layer is slightly marked.

At the sections parallel to the growth lines (Figs. 296 - 298) under the periostracum there is always a rather thick layer composed of short and massive fibres running perpendicularly to the shell surface and separated with moderately large spaces which are visible at etched sections. The fibres are variable in shape, more or less elongated (Figs. 296 - 297); the relative thickness of the layer is variable, as well.

The next layer of wide diagonal structures is the thickest. At etched sections it seems composed of very well discernible, long fibres and quite large spaces. The fibres are arranged at an angle of 90° approximately. The innermost layer being always thin (Figs. 296 and 298) is composed of compact grains (sometimes is grained-fibrous). Even a deep etching have not resulted in revealing spaces within this layer.

Bythinella zynianteki (Figs. 221 and 299 - 305)

The teleoconch inner structure bears close resemblance to the one of *B. micherdzinski* described above, some differences however being observable.

At the sections perpendicular to the growth lines (Figs. 299 - 303) directly under the periostracum there is also a fine-grained layer. It seems more variable in thickness and grain shape than in *B. micherdzinski* (compare Figs. 299 - 303 with Figs. 293 - 295). In some specimens it is almost absent (Fig. 303, also 299), while in some others relatively thick (Figs. 300 - 302). The grains of the layer may be approximately equilateral (Fig. 299) or even strongly elongated (Fig. 301), showing a continuous variability between the two extrema (Figs. 300 and 302 - 303). At the etched sections, the spaces between the grains may be somewhat bigger than in *B. micherdzinski*. This concerns especially the cavital spaces (Fig. 299 especially, but

also Figs. 300 - 303) which in this species are often much more conspicuous than in *B. micherdzinskii*

The next, pallsade layer (Figs. 299 - 303 and 305) looks generally similar in character to that in *B. micherdzinskii*, although is slightly less regular, and has the columns usually better discernible than in that species. The columns often branch (Figs. 299 - 300 and 303), cross one another, numerous of them terminating far from the layer borders, but in general the pattern is not as chaotic as in *B. micherdzinskii*

Quite commonly, the layer is much diversified (Fig. 303), there being a pattern of thinner, often branching and seemingly quite smooth columns alternate with wider columns usually not branching and seemingly rough. High magnifications (Fig. 306) show the characteristic pattern of the columns. The wider "rough" ones are composed of laminae being approximately perpendicular to the section surface, and numerous, irregularly oval pores between them (the pores are always much more fine than in the other layers). The narrower "smooth" columns (Fig. 306) are composed of tegularly arranged fine laminae running almost parallelly to both the section surface and long axis of the columns. The laminae are rather long, narrow and ragged-edged.

The columns may reach the inner surface of the shell (Figs. 301 and 303). If not, there is a similar smooth transition to the innermost layer, as in *B. micherdzinskii* (Figs. 299 and 302). The latter layer is similar as in *B. micherdzinskii*, having numerous fine cavital spaces being slightly better discernible than in that species.

When compared with *B. micherdzinskii*, the sections parallel (Figs. 221 and 304) are much more distinct than the ones perpendicular to the growth lines. The layer adjoining the periostracum is thinner than in *B. micherdzinskii* and even at the deep-etched sections has the spaces hardly marked. The thick layer of wide diagonal structures shows considerably larger spaces between better marked fibres. Moreover, the fibre angles within the layer are much more acute than in *B. micherdzinskii*

On the inner side of the shell there is a characteristic layer of cylindrical structures (Fig. 221). The layer was found nowhere else besides the *Hydrabiidae*. It is composed of large, more or less cylindrical, elongated trabeculae which are compact and arranged perpendicularly to the shell surface. The lack of this layer in *B. micherdzinskii* can be explained by its reduction, since the shell wall of that species is much more thinner and more translucent than in *B. zvonitoki*

Marstoniopsis schaltzi (Fig. 306)

Owing to the insufficiency of the available material of the species, only the sections parallel to the growth lines (Fig. 306) are discussed here. In general, they are quite similar as in *Bythinella*.

Apart from the innermost layer, in all layers the spaces visible at the etched sections are large, especially within the layer adjoining the periostracum. Directly under the periostracum there is a rather thick, somewhat thicker than in *Bythinella*, fine-grained layer composed of irregular but in general slightly elongated grains. The next one is a thick layer of wide diagonal structures, composed of large and conspicuous, deckle-edged fibres; the wide diagonal structure is more flat than that described in *Bythinella*.

Even at the deep-etched sections the innermost layer is strikingly compact. The layer resembles the cylindrical structure layer of *Bythinella zvirionteki*; however, its more compact and less regular cylinders are hardly discernible (compare Figs. 221 and 306).

Lithophyphus naticoides (Figs. 307 - 315)

At the sections perpendicular to the growth lines (Figs. 312 - 315) the outermost layer adjoining the periostracum is very thin (Figs. 312 - 313) or almost absent (Figs. 314 - 315) and then the columns of the pallisade layer run directly from the periostracum. The layer is fine-grained with moderately big spaces. The cavital spaces are unnumerous and hardly discernible within it (Figs. 312 - 313).

The pallisade layer consists of columns that are much more discernible than in *Bythinella*, though being better (Figs. 312 and 314 - 315) or worse (Fig. 313) marked. The pattern of the layer is much less irregular than in *Bythinella*. In some cases, especially close to the columella (Fig. 314) some columns are branching, but most of them are straight and full-length. A pattern of alternate wider and narrower columns is often observed. The transverse (growth?) lines on the columns are common, variously developed.

Under high magnifications (Figs. 307 - 311) the columns of the pallisade layer show a various, often characteristic pattern of the elements they consist of. At the etched sections (Figs. 307 - 308) the pattern often resembles that described for *Bythinella zvirionteki* (Fig. 308; compare with Fig. 305), but no pores are visible on "rough" columns and the appearance and arrangement of laminae are somewhat different. The not rare pattern shown in Fig. 307 is completely different. The laminae of the columns of both types are parallel to the section surface, though still perpendicular to one another. The columns of one kind are composed of quite irregular but elongated laminae with ragged margins, running towards the column long axis, while the columns of the other kind consist of laminae which are completely irregular in both size and outline, having ragged margins and being transversely arranged in a column.

A completely different picture is visible at the non-etched sections (Figs. 309 - 311). The sections of the pallisade layer reveal alternately arranged, "smooth" and "rough" columns (Fig. 309). The "smooth" columns show a uniform and regular sculpture of dense, short and broad fibre-like elements (Fig. 310) being probably the edges of deeper-situated plates. The "rough" columns consist of quite well separated groups of numerous fine plates which are almost equilateral, have rounded corners and edges, and are perpendicular or slanting to the section surface (Figs. 309 and 311).

The innermost layer (Figs. 312 - 314) shows no gradual transition from the pallisade layer: unlike in *Bythinella*, the border between the layers is sharp. The layer pattern of the wide diagonal structure type is very flat. The layer is quite thick, composed of moderately discernible, long and thin fibres. Within the layer there are slit-like spaces being common for all the gastropods studied, but no spaces of the cavital type are observed.

The sections parallel to the growth lines are typically hydroblold, though showing no grained layer directly under the periostracum: the wide diagonal structures are in direct contact with the

periostracum. Even at the deep-etched sections the spaces within the wide diagonal structures are fine, so that the structure is rather compact. The sections are extremely simplified when compared with the other hydrobioid shells.

Potamopyrgus jenkinsi (Figs. 316 - 325)

The teleoconch sections perpendicular to the growth lines (Figs. 316, 318 - 320 and 324 - 325) show a pattern being more regular than in *Bythinella*, but less regular than in *Lithoglyphus*.

Directly under the periostracum there is a moderately thick (Figs. 316, 318, 320 and 324 - 325), sometimes nearly absent (Fig. 319) layer of fine diagonal structures, which distinguishes *P. jenkinsi* from the other hydrobioid gastropods under consideration. The layer is composed of rather thin and moderately long trabeculae varied in size and proportions: from short and stout (Figs. 316, 320 and 324) to quite long and slender (Figs. 318 and 325). The angle of the structure is not much obtuse, approaching the right angle.

The trabeculae are rather well discernible, because the spaces between them are moderately big. There are also rather scarce, fine and hardly discernible spaces of the cavital type (Figs. 316 and 324); if present, they are more conspicuous than in *Lithoglyphus*, but less than in *Bythinella*, *B. zvonkovi* in particular.

The pallisade layer (Figs. 316, 318 - 320 and 324 - 325) is characterized by a pattern being also less regular than in *Lithoglyphus*, but more regular than in *Bythinella*. Its columns may be from slightly (Figs. 316, 318 and 325) to quite markedly (Figs. 319 - 320 and 324) discernible. The pattern of alternate wider and narrower columns is often observable (Fig. 324 is an example). All the columns are slim or very slim, although their width varies within a quite wide range. Within the layer, on the side opposite to the periostracum, there are commonly observable junctions of two or three columns into one (Figs. 319 - 320 and 324).

The columns are often composed of short and broad plates which are irregular in shape and have ragged margins (Fig. 317). The transverse (growth?) lines on the columns are more or less developed, though often absent.

The innermost layer may be absent (Figs. 319 - 320) and then the columns of the pallisade layer reach the inner surface of the shell. If present (which is common) it shows a pattern of very flat wide diagonal structures, similar as in *Lithoglyphus*, but not as in *Bythinella*. The layer is rather thin and there is no gradual transition, but a sharp border between this and the pallisade layer (Figs. 316, 318 and 324 - 325).

The layer is composed of either quite long and rather thin fibres with ragged margins (Figs. 316 and 324) or much broader flat laminae (Figs. 318 and 325). Apart from typical silt-like spaces being quite large and similar as in *Lithoglyphus*, cavital spaces are observable within the layer (Figs. 324 - 325). They are situated mostly on the silt spaces, so that they constitute the broadenings of the latter. The cavital spaces are larger in *Potamopyrgus* than in the *Bythinella* species described above, but at many sections they are hardly visible (Figs. 316 and 318).

The sections parallel to the growth lines (Figs. 321 - 323) are typically hydrobioid, resembling the ones of *Bythinella* and *Marsstoniopsis* described above. Directly under the periostracum

there is a grained layer composed of irregular grains which are very slightly elongated (Figs. 321 - 323). The thickness of the layer is variable, being usually, though not always (Fig. 323), moderate (Figs. 321 - 322). The thickest layer is that of quite flat diagonal structures. At the etched sections it is composed of massive and conspicuous, not too slender fibres (Figs. 321 - 322 especially) and large spaces between them.

The innermost layer is composed of slightly elongated cylindrical structures which are compact and little discernible even after a deep etching (Fig. 322). Sometimes the layer is granular in character (Figs. 321 and 323), the grains being quite coarse. The innermost layer always has a compact structure lacking spaces or having them very slightly marked.

IV. CHARACTERS IN THE PROSOBRANCH TAXONOMY OF THE SPECIES LEVEL - A COMPARATIVE ANALYSIS

1. Introductory remarks

The taxonomy of the species level must consider all observable differences between species. Although morphology does not necessarily provide decisive characters for species distinction, and furthermore there are no theoretical bases for the assumption that speciation is best reflected in morphology, these are the morphologic characters which most often are the only ones available for a taxonomist. The above statement especially concerns all poorly known animals, all the prosobranch species under consideration being included.

In such a situation a taxonomist must consider all available morphologic characters, paying attention also to small and not constant differences. At this point I cannot emphasize too strongly that under absolutely no circumstances should one, even very striking and stable interspecific difference, be considered as more valuable for species distinction than a number of various characters showing interspecific differences in their states, even if the variability is high and the character states overlap interspecifically. Another point, which is in fact not as commonly accepted and obvious as it might be supposed, is that the Linnean model in which "systematics = identification" cannot be in force any longer. Theoretically, this needs no discussion. Practically - the Linnean idea is still affecting the gastropod systematics.

Though already ROSZKOWSKI (1914) demonstrated that the species-level taxonomy of gastropods was often just impossible if not based on anatomy, there are still numerous papers that deal with the species-level taxonomy and are based on the shell alone (e.g. ANGELOV 1959, 1976 and PINTER 1968a, b). Several papers deal with the species-level taxonomy, basing on the shell (shell sculpture SEMs being included) and radula (e.g. PONDER & YOO 1976, 1980, MARSHALL 1983, and PONDER 1983a, b and 1984). Shell characters are rather commonly supported with some anatomical ones. If so, the latter may be used occasionally (e.g. RADOMAN 1966, 1973, 1976, 1977 and 1983) or as a rule (e.g. BOETERS 1973, 1981, GIUSTI & PEZZOLI 1977, 1980, 1982, GIUSTI 1979, PEZZOLI & GIUSTI 1980, PONDER 1982b and BANK & BUTOT 1984).

The phenetic taxonomy, no matter whether we do accept its theoretical background or not, is noteworthy since it pays attention to all observable differences, thus taking into consideration a number of characters many of which have been previously simply neglected.

For example, a phenetic analysis of six species of *Tomichia* (*Pomatiopsidae*: DAVIS 1981) showed interspecific differences in the states of 25 characters, 44% of the characters concerning the shell, 20% the radula, 16% the female reproductive organs, 8% the central nervous system, 8% the gill lamellae, and 4% the relative body size. In another paper on *Hydrabia* (HERSHLER & DAVIS 1980) 11 differences between *H. lotteri* MORRISON, 1954 and *H. truncata* VANATTA, 1924 were found, 27% of them concerning shell characters, 55% the medial and distal sections of the male reproductive organs, 9% the gill lamellae, and 9% the mantle morphology.

In a paper on *Stenothyra* (DAVIS, GUO, HOAGLAND, ZHENG, YANG & ZHOU 1986) from among 10 useful characters 40% concerned the radula, 30% the female reproductive organs, 10% the male reproductive organs, and 20% the ctenidium/osphradium complex. Another example might be a paper on *Ethalia* (DAVIS, KUO, HOAGLAND, CHEN, YANG & CHEN 1985). From among 22 characters distinguishing four species 45% were shell characters, 32% radular ones, 9% and 5% features of the female and male reproductive organs respectively, and 9% consisted characters of the external pigmentation of the soft parts.

The above examples may be a good illustration of the fact that there is no general rule as to the more or less universal usefulness of particular characters.

2. Shell "macrocharacters"

To the taxonomy of the species level, shell biometrical characters are commonly applied (e.g. DAVIS et al. cited above, RADOMAN 1976, PONDER 1982b). Such characters, though often clearly confirming species distinctness, are little convenient since they are of statistical character. Moreover, the species distinctness indicated by the characters especially needs confirmation by an analysis of other character states.

The shell "macrocharacters" which are actually useful and convenient for a taxonomist must fulfill the conditions listed below (which in the case of the studied gastropods are, in general, not fulfilled).

(1) Variability must not be continuous within more than one species, or if not, at most intermediate forms should be positively rare. This is not true for the *Viviparidae* (Figs. 338a - d and 339a - e, especially Fig. 339c - d: intermediates), and even more for the *Valvatidae* (Figs. 339f - g, 340a - j and 341a - b). The continuous variability is especially common between *Valvata piscinalis* and *V. pulchella* (Figs. 340a - g). As far as *Bithynia tentaculata* (Fig. 342a) and *B. leachi* (Figs. 341c and 342e) are concerned, the shell variability consists within two markedly separated ranges. *B. truschelli*, however, fills the gap in the variability, showing just a continuous range from a typical *B. tentaculata* to a typical *B. leachi* (Figs. 341d - e and 342a - d). In particular the specimen shown in Fig. 342b displays a variety of intermediate characters.

The *Hydrabioidae* are also, if not to tell especially, characterized by a continuous interspecific variability. As far as the shells of *Potamopyrgus jenkinsi* (Figs. 343a - d) and *Marstoniopsis schaltzi* (Fig. 343e) are concerned, the shell characters are usually, though not always, quite distinct (compare Figs. 343e and 343d). However, the variability within *Bythinella* (Figs. 343f - g

and 344a - b) as well as *Hydrabis* (FALNIOWSKI 1987) is actually continuous, the species distinctness being marked only statistically.

(2) Age variability must be clearly distinguishable from the variability of adults. This is not true for *Bithyniidae*, since the differences between *Bithynia leachi* (Figs. 341c and 342e) and *B. troscheli* (Figs. 341d - e and 342c - d) often concern only the shell dimensions, hence young specimens of the two species cannot be identified.

(3) Sexual dimorphism must not be included into diagnostic characters. This aspect of variability is poorly known in prosobranchs. Usually it is not well marked, although when all interspecific differences are not striking such slight differences between the sexes may be an important source of taxonomic problems. Observations of DAVIS (DAVIS et al., see above) and of my own (FALNIOWSKI 1987) point out that sexual dimorphism is not uniformly marked in prosobranchs, which means that the character states distinguishing one sex in some species may characterize the other sex in some others. This additionally raises the possibility of taxonomic problems connected with sexual dimorphism, so long as the sole shell is concerned.

(4) In polymorphic species, all their forms must be known, and their specific placements must be undebatable. This condition is probably still far from being fulfilled, and phyletic relationships between such shell forms cannot be explained on the sole basis of shell characters.

(5) Interspecific differences are the best if they concern the characters and their states that can be easily and clearly described. The countable characters (e.g. number of ribs, riblets, spines), as well as the ones whose states are clearly binar (yes/not) are the best example. Unfortunately, none from among the gastropods considered in the paper show such characters. Their shells (Figs. 337 - 344b) with an exception of *Theodoxus fluviatilis* (Figs. 337a - f) and *Valvata cristata* (Figs. 339g and 341b) represent the most common, primitive mesogastropod type, and exhibit hardly any such conspicuous feature.

The whorl number depends much on gastropod age and hence is a little useful character. The whorl convexity as well as suture depth seem rather strongly correlated with sexual dimorphism, and this along with continuous variability determine the limits of the usefulness of these characters. Nevertheless, they are sometimes useful in distinguishing species. For example, these character states are different in bithyniids (*Bithynia tentaculata* - *B. leachi* and *B. troscheli*; Figs. 341c - e and 342a - e) as well as in hydrobioids (*Potamopyrgus jenkinsi* - *Marstoniopsis scholtzi*; Figs. 343a - e), or viviparids (*Viviparus costectus* - *V. viviparus*; Figs. 338a and 338c). Also the angle between the suture and columella may be of use in some cases (e.g. *Bythinella*; FALNIOWSKI 1987).

The aperture is, in general, the most variable shell region. In prosobranchs, however, despite its variability it reveals some useful distinctive characters which are especially: its outline (e.g. *Bithynia*; Figs. 341c - e and 342a - e), more or less close application to the body whorl (e.g. *Potamopyrgus jenkinsi*; Figs. 343a - d, when compared with the other hydrobioids having generally similar shells), the angle on its left upper side, being strongly or weakly marked (e.g. the *Viviparidae*; Figs. 338a and 338c, and 339a - e; *Valvata naticina*; Fig. 340j compared with the other *Valvata* species: Figs. 339f - g and 340a - g), and the peristome/lip development.

Similarly, the umbilicus may sometimes be even the best (*Viviparus*: Figs. 338b and 338d) or one of the best (*Bithynia*: Figs. 341c - e and 342a - e) diagnostic characters. In the *Valvatidae* (Figs. 340i and 341a - b) it may be rather narrow or so wide that the successive whorls are visible within it; the character is there interspecifically variable and so, a good one. On the other hand, in numerous gastropods (e.g. *Hydrobia*: FALNIOWSKI 1987) the umbilicus may be covered by a parietal lip in adults, while uncovered in younger specimens.

The colouring of a clean and uncorroded shell may be useful, though not in many cases. The *Viviparidae* (Figs. 338a, 338c and 339a - e) differ from the other Polish prosobranchs in their unique green or greenbrownish, striped shell. The colour pattern of *Theodoxus fluviatilis* (Figs. 337b - f), although markedly variable, differs this species strikingly from the others. Apart from the above species, all the other Polish freshwater prosobranchs show a quite uniform colouring. *Potamopyrgus jenkinsi* seems the most variable in this aspect.

Shell opacity proves of little use in the species-level taxonomy of the gastropods under consideration. The shell macrosculpture which can be studied by means of the conventional light microscope is generally poor within the studied gastropods. These are the valvatids which are the only group having the macrosculpture both well developed and interspecifically variable while intraspecifically quite constant (Figs. 339f - g, 340a - j and 341a - b). In *Potamopyrgus jenkinsi* (Fig. 343c) the apparent keel is commonly observed but this character seems of little significance for taxonomy.

All the above remarks lead to the conclusion that the usefulness of the shell "macrocharacters" in species distinction is very limited. The characters are, moreover, hardly applicable to the estimation of phyletic relationships. In such a situation, the strictly conchological concept of interspecific differences between closely related species, represented for example by RADOMAN (1976), cannot be accepted. Apart from essential doubts connected with the biological reality of the taxa defined in this way, even the sole identification of such taxa is problematic and incomparable when more than one taxonomist is involved. On the other hand, it is impossible to distinguish between the species and forms of one polymorphic or only continuously but widely variable species. Hence, a "careful and thorough" taxonomist could theoretically describe an infinite number of "species" that were, in reality, only nomina.

3. Operculum

The operculum is rather commonly used in the taxonomy of the species level (e.g. PONDER & YOO 1976, PONDER 1982b, 1983a, b and MARSHALL 1983), although its simple structure delimits the number of potential characters to a few, and the variability is as high as in the case of the shell "macrocharacters". In valvatids, for example, the opercula (Figs. 344c - e) differ interspecifically in hardly any character but their dimensions. Slight differences between species can also be observed in the whorl growth of those spiral opercula. Similar remarks concern the opercula of hydrobioids.

The concentric opercula of viviparids (Figs. 344f - g) show only slight interspecific differences in upper angle, the latter being better marked in *Viviparus coniectus*. The operculum of *Bithynia tentaculata*, although intraspecifically variable (Figs. 345a - d), is markedly different from those of *B. irascheli* (Figs. 346a - b) and *B. leachi* (Figs. 346c - e). However, the differences between *B. irascheli* and *B. leachi* are expressed in hardly any character but size.

The operculum of *Theodoxus fluviatilis* (Figs. 346f - g) is apparently distinct and unique within the Polish *Prosobranchia*, but its character states may be useful in the taxonomy of not the species but much higher level.

4. Soft part external morphology

The external morphology of soft parts is rather commonly used in the taxonomy of the species level (e.g. FRETTER & GRAHAM 1962, MUUS 1963, 1967, REHFELDT 1968, BOETERS 1973, 1981, GIUSTI & PEZZOLI 1977, 1980, 1982, GIUSTI 1979, HERSHLER & DAVIS 1980, PEZZOLI & GIUSTI 1980, PONDER 1982b, 1983a, b, BANK & BUTOT 1984, DAVIS, KUO, HOAGLAND, CHEN, YANG & CHEN 1985 and FALNIOWSKI 1987 and 1989a).

However, within the prosobranchs considered herein the soft part external morphology is rather simple and uniform, and then consequently poor in characters, especially if closely related taxa are concerned as it is in the case of the taxonomy of the species level. The head and foot shape and proportions, the body-to-shell-size proportion, the shape and proportions of the cephalic tentacles, the occurrence and appearance of the metapodial and/or pallial tentacle, the gland outlets, as well as the colour and/or pigmentation of the cephalopodium and/or mantle with the rest of the visceral hump, can be listed as the most commonly applied characters.

Within the gastropods considered herein, the above characters show rather uniform states, there being very slight interspecific differences. The relatively most useful prove head habitus and/or pigmentation (Figs. 347A - J, 348A - G and 349A - F). It must be stressed, however, that on one hand the head habitus of fixed specimens shows a striking variability of the artifact type, while on the other hand the head pigmentation is, in general, widely variable within a species. Hence the characters, though are useful for species discrimination, can hardly be used in species determination. The latter, however, is not a general rule: *Hydraticus* may be an example (FALNIOWSKI 1986 and 1987).

The unique habitus of the very slightly pigmented heads of *Theodoxus fluviatilis* shown in Figs. 347A - B is typically neritacean, so it cannot be considered a character state discriminating the species. The viviparids (Figs. 347C - D) are characteristic in their massive snouts as well as tentacles. Out of the latter, the right one that in males contains the penis is cylindrical and enormously massive (Fig. 347D). Their very strong, dark and "grainy" pigmentation is also very characteristic. On the other hand, the head character states of the viviparids are constant within the family and show none interspecific difference.

The heads in the valvatids (Figs. 347E - H) show quite well marked interspecific differences in both habitus and pigmentation pattern. The tentacles of *Valvata naticina* (Fig. 347G) are flat and

broad, gradually narrowing towards the tips, which is characteristic of this species alone. The snout is most intensively pigmented in *V. pulchella* (Fig. 347F), less intensively in *V. piscinalis* (Fig. 347E), while almost unpigmented in *V. cristata* (Fig. 347H).

Interspecific differences in the proportions and pigmentation of the bithyniid head (Figs. 347I - J and 348A - D) are also observable, but they are slightly marked and the variability within the genus *Bithynia* is continuous. Nevertheless, the characters are of some use in species discrimination within the genus.

The hydrobioids, as a rule, differ interspecifically in the head pigmentation pattern whose intraspecific variability, on the contrary, is wide (see FALNIOWSKI 1986 and 1987). The figures (Figs. 348E - G and 349A - F) illustrate the pigmentation patterns of the *Hydrobioidae* species considered in the present paper. At this point, it must be underlined that the pigmentation pattern and/or intensity show sexual dimorphism; in the *Rissoacea (=Truncatelloidea)* the pigmentation may often be more intensive in females (FALNIOWSKI 1987, 1988a and b).

5. Ctenidium and osphradium

The unique bipectinate gill of the *Valvatidae* (Fig. 364A), being apparently not homologous with the ctenidium of the other prosobranchs (RATH 1986, HASZPRUNAR 1988), shows constant character states within all the *Valvata* species, hence cannot be used for species discrimination. All the other Polish prosobranchs except *Theodoxus* have the typical mesogastropod ctenidium and osphradium (Fig. 350).

In the taxonomy of the species level such characters as the ctenidial lamellae number and their shape and proportions, as well as the shape and proportions of the entire ctenidium, the proportional dimensions of the osphradium/ctenidium complex, and the ctenidium shape, are rather commonly applied (e.g. BOETERS 1873, GIUSTI & PEZZOLI 1977, 1980, 1982, GIUSTI 1979, HERSHLER & DAVIS 1980, PEZZOLI & GIUSTI 1980, DAVIS 1981, BANK & BUTOT 1984, DAVIS, GUO, HOAGLAND, ZHENG, YANG & ZHOU 1986 and FALNIOWSKI 1987).

In *Bythinella*, an analysis of numerous osphradia indicated their high intraspecific variation along with slight interspecific differences in shape and appearance (FALNIOWSKI 1987). So, this is one more statistically expressed character being of some help in species discrimination. Similar remarks concern the ctenidium/osphradium size proportions, as well as the proportions and size of the ctenidium itself and of its lamellae.

The number of ctenidium lamellae is rather a popular character among malacologists. It is, however, far more variable and less applicable to taxonomy than it is usually acknowledged. I counted the ctenidium lamellae in numerous specimens of all the Polish prosobranchs (FALNIOWSKI 1987, 1988a, b and 1989a) and in many cases I did not find any, even at least statistically marked difference between close species. The number varies with age and gastropod size, as well as with habitat type and population. It seems that the interspecific differences given in the literature might have been due to too small numbers of the specimens studied.

6. Male reproductive organs

The relatively simple organization of the male reproductive organs (excluding the penis discussed in detail in the next chapter) restricts the number of potentially distinctive characters. This, along with the usually high variation of all glandular structures being of physiological and/or artifact origin, are the reasons why the usefulness of the male reproductive organs in taxonomy is very limited. The male reproductive organs of the *Viviparidae*, as well as the male section of the hermaphrodite reproductive organs of the *Vahvatiidae*, are characterized by a wide intraspecific variability along with quite simple structure and the lack of interspecific diversity, so they are a good example of the organs that are completely useless in the taxonomy of the species level.

Within the congeneric species (e.g. *Stenothyra*) the prostate may occur in some species and not occur in the others (DAVIS, GUO, HOAGLAND, ZHENG, YANG & ZHOU 1986). Similarly, the situation of the vas deferens outlet from the prostate may show infrageneric differences (HERSHLER & DAVIS 1980, FALNIOWSKI 1987) or the dimensions and shape of the prostate may be quite constant intraspecifically, while variable interspecifically (HERSHLER & DAVIS 1980, PONDER 1982b). Such phenomena, however, have not been found in the gastropods the present study deals with. In numerous species, the vas deferens before reaching the prostate is more or less coiled (Fig. 351); this character is very variable and may hardly be applied to species discrimination.

In the *Bithyniidae* (Figs. 341 and 354) as well as *Bythinellidae* (Figs. 352 - 353) the male reproductive organs contain a flagellum. In *Bithynia*, the value of the flagellum-to-penis length proportion (the penis measured along its curvature, from the base to the tip of the right arm containing the vas deferens) has proved the only anatomical character to allow for species discrimination. The value was: 5.0...5.9 for *B. tentaculata*, 2.5...3.25 for *B. leachi* (Fig. 354), and about 4.3 for *B. troschelii* (Fig. 351; FALNIOWSKI 1989a). Similarly, in *Bythinella* (Figs. 352 - 353) the flagellum proportional length and thickness, and the visibility of the canal inside it are of some use in discriminating species (FALNIOWSKI 1987).

7. Penis

From among the soft part characters this is the one most often used and almost all the publications cited above deal with its habitus and structure. Nevertheless, the universal usefulness of this structure raises doubts. Firstly, the penis being simply the terminal part of the vas deferens and running along the centre of the cephalic tentacle, as in the *Viviparidae*, can hardly be considered: the viviparid penes are completely uniform within the family. Secondly, the very high variability of the penis must be acknowledged as a general rule. Examples of the bithynid penis variability (Figs. 355A - I) may be an illustration of the above statement.

The penis dimensions as well as proportions, along with its habitus (including all "lobes", "appendages", etc.) vary with age, season, animal physiologic condition and several other factors.

Moreover, the fixation of an animal, even if after narcotisation, is a source of numerous artifacts. Hence, one should be very careful when applying the penial characters to taxonomy.

The situation is well illustrated in my earlier paper (FALNIEWSKI 1987): the bythinellid species discrimination is based on penial characters as ones of the best, though the wide variability described makes often the species determination impossible if a sufficiently high number of specimens are unavailable. However, the bythinellid species considered in the present paper differ markedly in penial character states (Figs. 358 - 360).

One more point is that the penis is the more useful for taxonomy the more penial characters can be distinguished. In practice, the latter means: the more complicated is the organ. So, the simple penes of *Valvata* (Fig. 356) as well as of *Lithoglyphus* (Fig. 357) actually cannot be considered for the purposes of taxonomy.

Besides the "external" penial characters discussed, there are some "internal" ones, as the visibility of the canals and how they run inside the penis (in loops, zigzags, etc.) or the occurrence, area and situation of glandular structures. All the internal characters are useful in some cases (e.g. MUUS 1963, HERSHLER & DAVIS 1980, FALNIEWSKI 1987) although their usefulness is obviously not less restricted than in the case of the "external" ones. Moreover, some of the internal penial structures, especially the glandular ones, are not necessarily observable if a material is fixed simply with formalin or ethanol, such material being often the only one available.

8. Female reproductive organs

Since their structure is commonly much more complicated than the one of the male reproductive organs, the number of potential characters within the female reproductive organs is high. On the other hand, similar remarks as those concerning the male reproductive organs can be presented on their variability. Although interspecific differences may sometimes occur in ovary dimensions (DAVIS 1981), usually only the characters of the pallial (and renal, if the homology is correctly recognized) region of the organs are applicable.

The organization of the female organs of *Viviparus* (Fig. 361) is quite simple, nevertheless the organs' structure contains the only two anatomic characters observed discriminating species (Figs. 362A - B). In *V. cunctus* (Fig. 362A) the duct of the receptaculum seminis while leaving the receptaculum is usually narrow, whereas in *V. viviparus* (Fig. 362B) it is strongly (rather strongly) widened; in the duct section parallel to the receptaculum there is commonly (not always) a widening in *V. cunctus* (Fig. 362A), but never in *V. viviparus* (Fig. 362B).

Even within one genus there may be viviparous (more precisely: ovoviviparous) as well as oviparous species. Viviparity results in the absence of the nidamental gland along with the presence of the brood pouch. Both the characters are easily observable. Such organs characterise *Valvata naticina* (Fig. 364A), *Potamopyrgus jenkinsi* (Fig. 371A), and both the *Viviparus* species (Fig. 361). It should be stressed however, that the modifications accompanying viviparity, though often (not always: e.g. *Viviparus*) useful as a character discriminating species, do

not necessarily indicate relationships since they are similar in different and often distantly related groups. Hence, the character can hardly be applied in higher classification.

The female section of the hermaphrodite reproductive organs of the *Valvatidae* (Figs. 363 - 368) shows interspecific differences in the habitus and situation of the fertilization chamber - bursa copulatrix section. In *Valvata piscinalis* (Fig. 363A) the section is in the form of two sacs (Figs. 363B and 365A - B) while in the other *Valvata* species this is a single sac (Figs. 364B, 366A - B and 367 - 368). In *V. pulchella* (Figs. 366A - B) the sac lying on the ventral side of the glandular complex, far from the complex margin (Fig. 366C), is dorsally invisible, while in *V. cristata* (Fig. 367) it lies more distally, being protruded outwards the margin of the glandular complex, thus is partly visible dorsally. In *V. naticina*, the single sac (Fig. 364B) is somehow differently located (Fig. 368) than in *V. pulchella* and *V. cristata*. Hence in *Valvata*, the accessory sperm pouches occurrence and situation prove a decisive character in species discrimination.

The female reproductive organs' characters are often considered in the taxonomy of minute rissoaceans (=truncatelloids). Especially, the renal oviduct (called so by HERSHLER & DAVIS 1980, although the homology of this section is still not quite clear), receptaculum seminis, bursa copulatrix and pallial oviduct characters are commonly used in taxonomy (e.g. RADOMAN 1966, 1973, 1976, 1977, BOETERS 1970, 1981, GIUSTI & PEZZOLI 1977, 1980, 1982, GIUSTI 1979, PEZZOLI & GIUSTI 1980, PONDER 1982b, BANK & BUTOT 1984, DAVIS, GUO, HOAGLAND, ZHENG, YANG & ZHOU 1986, and FALNIOWSKI 1987).

The above characters prove rather useful in discriminating species within the Polish rissoacean hydrobioids. In *Potamopyrgus jenkinsi*, the female reproductive organs (Fig. 369A) along with the adaptations to viviparity mentioned above exhibit a characteristic arrangement of the receptaculum seminis against the bursa copulatrix (Figs. 369A - B): the duct of the bursa always crosses the receptaculum. A bursa copulatrix submersed in the tissue of the albuminoid gland (Fig. 370A) is typical of *Lithoglyphus naticoides*, but also of the other *Lithoglyphus* species. On the other hand, the characteristic arrangement of the loop of the oviduct in relation to the receptaculum and bursa (Figs. 370A - B) seems typical of *L. naticoides* alone.

The loop of the oviduct - receptaculum seminis - bursa copulatrix section of the bythinellid female reproductive organs (Fig. 371) proves one of the most basic characters to discriminate species within the family. Such characters as the bursa shape and proportions, its duct distinctness, the proportional length and width of the duct, as well as the shape and proportional dimensions of the receptaculum, I have found interspecifically diversified. On the contrary, these character states are strikingly variable intraspecifically, the variability being continuous within the family and, moreover, the differences between species being slight (see Figs. 372A - L). Hence, as I have already pointed out (FALNIOWSKI 1987), even a simple determination demands studying several specimens to find the range of most commonly observed variability.

Coming to conclusion, a number of female reproductive organs characters may be, and actually are, applied in taxonomy on the species level. However, those characters are often highly variable. Hence, a careful analysis of numerous specimens is always unavoidable, before any character can be accepted as being valid for particular species distinction.

9. Radular characters

Although the radula is almost the earliest considered inner structure, and its characters have for a long time been very commonly exploited in taxonomy, there are numerous restrictions of the taxonomical usefulness of the radular characters. Almost all my remarks on radular characters in the taxonomy of higher taxa (FALNIOWSKI 1989b) are in force for the taxonomy of the species level as well.

Apart from the typically rhipidoglossate radula of *Theodoxus fluviatilis* that is very distantly related with the other Polish prosobranchs, all the other radulae are typically taenioglossate. Hence, the latter are quite similar so that their characters must be potentially far less useful in taxonomy than the ones of the strikingly diverse radulae of some gastropod groups (e.g. *Triphoridae*: MARSHALL 1983). A slight diversity along with high intraspecific variation is just a rule within the taenioglossate gastropods (e.g. PONDER & YOO 1976, DAVIS 1981, PONDER 1982b, 1983a, b, 1984, DAVIS, KUO, HOAGLAND CHEN, YANG & CHEN 1985, DAVIS, GUO, HOAGLAND, ZHENG, YANG & ZHOU 1986 and FALNIOWSKI 1989a and b).

In many papers dealing with taxonomy, especially the earlier ones, only the central tooth is described. Such descriptions, moreover, are usually based on a single/a few specimens. Such an attitude, to my knowledge, cannot be accepted, especially if one takes into account such examples as Fig. 74 compared with Figs. 73 and 75: the rhachis of *Potamopyrgus jenkinsi* shown there has one pair of basal cusps, while usually (the latter all the literature confirms) there are three to four pairs.

The radular characters include the formulae of all teeth, as well as the habitus of all teeth and their cusps; also the length of the radula, the total number of rows, the number of rows in the formative stage, and the position of the tip of the radular sac in relation to the buccal mass are sometimes employed as characters (e.g. DAVIS 1981, PONDER 1983a and DAVIS et al. cited above in this chapter). All the above characters, however, are nearly always continuously variable within a group of closely related species, and interspecific differences, if present, are marked only statistically. In particular, this concerns the tooth formulae. The cusp habitus seems, though not always, somewhat more useful in species discrimination.

From among the gastropods under consideration, the two valvatid species studied are the only example of sharp interspecific differences between congeneric (?) species. The radula of *Viviparus viviparus* hardly differs from the one of *V. cortectus*. There are slight differences in cusp number and habitus that can be observed between the *Bithynia* species along with a continuous variability within the genus.

As concerns both the central and lateral cusps, the variability ranges of the studied hydrobioid species are overlapping. On the other hand, the marginal teeth prove more useful in the taxonomy of the species level. In several cases of even closely related species, I have found interspecific differences in both formulae and cusp habitus. Similar phenomenon I have observed in the *Lymnaeidae* (FALNIOWSKI 1983b). This seems the more important that the marginal teeth are often omitted in radulae descriptions.

10. Protoconch habitus and outer surface

SEM images of the protoconch surface are occasionally used in discriminating species (e.g. PONDER & YOO 1976, PONDER 1982b and 1983a and b) but in some gastropod groups they are a basic criterion (MARSHALL 1983). Among the gastropods under consideration I have found the protoconch habitus to be distinctive only in the case of some hydrobioid species.

The protoconch surface is a good character distinguishing species in the *Valvatidae* and *Elithynidae*. In the others, its simple and variable appearance provides no characters that could be of use for the taxonomy of the species level.

11. Teleoconch outer surface

Some authors have already used this in the taxonomy of the species level (e.g. PONDER & YOO 1976, PONDER 1982b, 1983a, b and MARSHALL 1983). With the exception of the *Viviparidae* species, in all the gastropods studied the teleoconch outer surface displays such character states that are rather constant infraspecifically, while quite diverse interspecifically, the differences being more or less sharp.

The *Elithynidae* species differ between each other in the proportion of covered/uncovered pores on the surface, as well as in the occurrence of the spiral riblets and, to some degree, in growth lines appearance. Similar differences concerning mostly the pores are observable between the species of the *Hydrobiidae*. Among the *Valvatidae* species, differences are better marked and concern both the macrosculpture being more variable, and the microsculpture. The latter is in valvatids characterized by a relative infraspecific stability along with interspecific diversity. In the valvatid species there are no pores; the surface consists of a fibrous structure looking differently in various species.

Among the studied gastropods, the occurrence of distinct interspecific differences in teleoconch outer surface sculpture (the microsculpture in particular) seems unquestionable. Hence, the sculpture characters are commonly useful in the taxonomy of the species level, for they are helpful in species discrimination. On the other hand, their usefulness in the estimation of relationships seems the more restricted the more distant gastropods are concerned. In the quite closely related *Valvata* species, the outer surface characters confirm the placement of *V. natica* into the separate subgenus *Barysthenia* LINDHOLM, 1913, since this species differs from all the other valvatid species more than the latter do between each other.

The teleoconch outer surface characters can also be used in determining species, but with similar restrictions as for conventional diagnostic characters.

12. Teleoconch inner surface

As it has been explained in the systematic part, the inner sculpture of the teleoconch may be expected to be a good, useful character in the species-level taxonomy, for in each species it presents a characteristic, unique pattern. The results obtained so far confirm this hypothesis.

13. Teleoconch inner structure

The present state of the knowledge of the shell inner structure in the studied group makes any more precise character weighting impossible: it is difficult to judge whether a structural character, when compared with others, is more or less useful in species distinction. It is evident that the thickness proportions between the shell layers are widely intraspecifically variable, hence they can hardly be applied to taxonomy. All the other characters seem, to the present knowledge, similarly applicable.

Despite the patchy character of the data base, it seems that every species, practically, has its specific shell structure characterizing only this particular species. As I point it out many times in the systematic part, the variability of the shell structure is wide and covers actually all its characters. Moreover, the variability is not correlated between the layers. So, a taxonomist must consider the structure of all layers.

The interspecific differences most often concern such characters as: the number of layers, the pattern of a particularly situated layer, the size of spaces visible at etched sections, the shape and, to a lesser degree, the arrangement of the fibres (lamellae) of the columns of the pallsade layer, the discernibility and arrangement of the columns of the pallsade layer, the angle between the fibres of successive columns, the angle between the fibres of diagonal structures, and the sharp/smooth transition between layers.

The shell structure characters, like the characters of other kinds, are in some cases more, whereas in some others less useful in the taxonomy of the species level. This means that some closely related species differ in shell structure less than some other ones similarly closely related. Like in family grouping (FALNIOWSKI 1989b) the characters seem useful for relationships weighting, but their applying to species identification may be in many cases rather difficult because of the mentioned variability. However, a determination based on the structural characters is usually possible, with the restrictions of certainty rather not heavier than in the case of conventionally used "classic" characters.

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APPENDIX I

Annotated systematical list of the studied species (after FALNIOWSKI 1987 and 1989a)

Order *Meritacea*

WILBUR & YONGE (1964) proposed an order rank for this group, although perhaps to accept a suborder placement within the *Archaeogastropoda* is more justified. Anyway, some characters of the *Meritacea* seem to indicate their position as nearly the highest within the *Archaeogastropoda*, while the other - as a very primitive and ancestral group, although advanced in some characters.

Family *Meritidae*

1. *Theodoxus fluviatilis* (LINNAEUS, 1758)

Order *Caenogastropoda*

Suborder *Architaenioglossa*

Some authors (e. g. HASZPRUNAR 1988) include this suborder in *Archaeogastropoda*, which seems debatable.

Family *Viviparidae*

(species nomenclature after WATSON 1955 and FORCART 1960)

2. *Viviparus cortectus* (MILLET, 1813)
3. *Viviparus viviparus* (LINNAEUS, 1758)

Incertae sedis: *Valvatoidea*

Systematic position of these gastropods showing several unique characters is not quite clear, and their position within the *Caenogastropoda* is questioned (RATH 1986 and FALNIOWSKI 1989 a and b). HASZPRUNAR (1988) acknowledged the superfamily *Valvatoidea* as the only representative of the suborder *Ectabranchia*, not belonging to the *Caenogastropoda*.

Family *Valvatidae*

4. *Valvata (Valvata) pischalis* (O. F. Müller, 1774)
5. *Valvata (Valvata) pulchella* Studer, 1820

6. *Valvata (Valvata) cristata* O. F. Müller, 1774
7. *Valvata (Borysthenia) naticina* Menke, 1845

Incertae sedis: *Bithyniidae*

Probably rather primitive rissoaceans, this however is not certain (FALNIOWSKI 1989a). PONDER (1988) considered the family as undoubtedly belonging to the *Rissoacea* (= *Truncatelloidea*).

8. *Bithynia tentaculata* (LINNAEUS, 1758)
9. *Bithynia leachi* (SHEPPARD, 1823)
10. *Bithynia troscheli* (PAASCH, 1842)

The species has been so far classified as a form of *B. leachi* BEER & MAKEEVA (1973) dealt with the question whether it is or not a distinct species, but came to no conclusion. *B. troscheli* differs from the typical form of *B. leachi* in its having a larger and slightly different shell, in ecology (e.g. it is tolerant to moderate salinity) and in parasitofauna (BEER & MAKEEVA 1973). According to data on the anatomy as well as on the shell (FALNIOWSKI 1989a) *B. troscheli* does not differ from *B. leachi* less than the latter species from *B. tentaculata*, and is probably of a hybrid origin (*B. tentaculata* x *B. leachi*). Hence, either one or three species should be distinguished within the Polish *Bithyniidae*. According to the biological concept of species (MAYR 1969 and 1970) the latter alternative seems more justified.

**Order *Rissoacea* [= superfamily *Truncatelloidea*:
PONDER (1988)]**

Superfamily *Hydrabioides*

[phyletic relationships acknowledged after RADOMAN (1973), GIUSTI & PEZZOLI 1980 and FALNIOWSKI 1987]

Family *Bythinellidae*

Genus *Bythinella* Moquin-Tandon, 1855

Out of the six Polish *Bythinella* species (FALNIOWSKI 1987) only two have been studied:

11. *Bythinella micherdzinski* FALNIOWSKI, 1980
12. *Bythinella zywionteli* FALNIOWSKI, 1986

Genus *Marstoniopsis* VAN REGTEREN ALTENA, 1936

13. *Marstoniopsis scholtzi* (A. Schmidt, 1856)

Family *Lithoglyphidae*

14. *Lithoglyphus naticoides* C. Pfeiffer, 1828

Incertae sedis: genus *Potamopyrgus* Stimpson, 1865

As I pointed out (FALNOWSKI 1987), the systematic position of *Potamopyrgus* is still unrecognisable.

15. *Potamopyrgus jenkinsi* (E. A. SMITH, 1889) f. A WARWICK, 1952

The only form of the taxon that occurs in Poland, being probably a distinct species not identical with *P. jenkinsi* s. str. (WARWICK 1952), still nondescribed by WARWICK.

APPENDIX II

General organization of the shell (Figs 326 - 336 and 373 - 374)

Within the gastropod shell four layers are commonly distinguished: periostracum, ectostracum, mesostracum, and endostracum (Fig. 373: PE, EKT, MES and ERZ+EW respectively), sometimes yet another one being added, called hypostracum*. However, it must be stressed that this scholar model seems doubtful, especially when the distinctness of the meso- and endostracum is concerned. This was already partly discussed in the systematic part (*Viviparidae*). Moreover, in many cases layers easily discernible at sections perpendicular to the growth lines are not homologisable with any layer visible at section parallel to the growth lines: two layers at a perpendicular section are visible as undoubtedly one at a parallel one.

The almost entirely conchioline periostracum is the thinnest and outermost layer. SEM images show its homogenous character, since its sections are smooth even under high magnifications, although light microscope (KESSEL 1944) as well as transmission electron microscope (TEM: KNIPRATH 1972 and JONES & SALEUDDIN 1978) images indicate that the structure of the periostracum is quite complicated.

The periostracum thickness is highly variable depending on species as well as on habitat condition (FRETTER & GRAHAM 1962). Owing to its function which is to protect the adjoining calcareous layers against corrosion, the periostracum, as a rule, is thickest in the shells of freshwater gastropods, thinner in marine molluscs, while in terrestrial snails it is often completely absent. In the gastropods under consideration the periostracum is moderately thick. The thin periostracum may be the reason for a common intensive corrosion in some species. The chemical composition of conchioline is neither strictly determined nor constant. It varies even within one shell (BEEDHAM 1958). The conchioline is composed of proteins and polysaccharides (BEVELANDER & BENZER 1948).

Under the periostracum there are calcareous layers (Figs 373 - 374) whose thickness is much greater than that of the periostracum. One of their compounds is also conchioline, though it occurs in a very small proportion and the layers are predominantly inorganic - calcareous - composed mainly of calcium carbonate. According to the most common model, directly under the periostracum there is a prismatic layer, composed of calcite and often characterized by a palisade pattern; next there is the layer composed of aragonitic crystals which are arranged more or less parallelly to the shell surface. In many *Archaeogastropoda* (e.g. *Trochus*, *Turbo* and

*It has to be stressed here that in the studied gastropods, neither the *Caenogastropoda* nor the *Meritinae*, there is no nacreous, aragonite layer, in gastropods characteristic of the *Archaeogastropoda* (not all of them), forming there conspicuously marked endostracum.

Monodonta) this layer may be very thick and is then called mother-of-pearl (nacre), because of its blue or blue-green refulgence depending upon the refraction of light by this innermost layer.

The real structure patterns in the shells described in this paper differ much from the scheme given above, and have been described in detail in the systematic part. In the Appendix only some general remarks are given.

The interactions between the organic and inorganic compounds of the shell are very complicated and not satisfactorily understood yet. The conchioline is much more resistant to chemical factors of environment, while the calcium carbonate is more resistant to mechanic load; it has an especially high crushing strength, but its both tensile and bending strength increase while this and the conchioline are appropriately arranged. A decrease in the inorganic compound proportion in the shell causes a decrease in the shell weight. This may be profitous in some circumstances, e.g. in terrestrial habitats.

The organic matrix model of both the formation and structure of the shell as well as of all other mineralized biological structures has been widely and commonly acknowledged recently (e.g. WILBUR 1960, 1980, WILBUR & YONGE 1964, SALEUDDIN 1971, TOWE 1972, WATABE 1974, 1981, UOZUMI & TOGO 1975, IWATA 1978, MUTVEI 1978, 1979, UOZUMI & SUZUKI 1979, WATABE & DUNKELBERGER 1979, BEVELANDER & NAKAHARA 1980, KOBAYASHI 1980, CRENSHAW 1982, WILBUR & SALEUDDIN 1983, EYSTER & MORSE 1984 and MIKHAILOV 1987).

It was stressed already by WILBUR (1960) that the conditions of the deposition of crystals in the process of shell formation are specific. However, some peculiar forms of crystals are not specific for only calcified biological structures. For example, long lamellar crystals commonly observed in the shell result from the crystal growth in both the natural and laboratory process of crystallization (BUCKLEY 1951).

All crystals within the gastropod shell are well defined, since they are surrounded by intercrystalline organic (conchioline) matrix. The mineral crystalline material fills organic envelopes. The envelopes are in general very fine, thin-walled and delicate. However, in some cases there may be also some more solid ones called macro-envelopes in this paper (e. g. observed surrounding the columns of the palisade layer in *Vinparus*).

The shell sections obtained by breaking, independently on section orientation, provide little information on the shell structure; the sections of the protoconch (Fig. 330) and of the teleoconch (Figs. 331 - 336) look similar. They enable to distinguish the innermost spongy proper endostracum layer, if present (Fig. 331), and sometimes also some characteristically looking crystals (Fig. 336). Often the general arrangement of the crystalline structures (Figs 330 - 331 and 333 - 334), as well as the elements of which they are composed (Figs 332 and 335) can be observed at such sections. The transverse section of the columella (Fig. 328) is characteristic and shows a different structure than those of the other shell regions.

The acid etching of sections, if carried out gently dissolves calcium carbonate without affecting conchioline envelopes, results in preparations whose SEM images provide much more information on the shell structure (Figs 216 - 308, 312 - 327 and 329). Hence, these are almost only the etched sections the present descriptions are based upon. Moreover, for each species in the

paper are described the structures of the body whorl as seen far from both the suture and columella, and nearly 360° from the mouth.

Close to the columella (e.g. Fig. 326) the structure is strikingly more compact and irregular, the columns of the pallisade layer often branch, etc. The columella (Fig. 327) as well as suture (Fig. 329) show a characteristic structure pattern.

The aim of the present work is not to create a three-dimensional model of the shell structure, which would need a study of another kind and by use of other methods, but only to describe all the structures that can be seen at sections perpendicular and parallel (Fig. 374F) to the growth lines in every species, pointing out interspecific differences. It must be added that in many cases described the knowledge of the structures observable at sections oriented in only two directions being perpendicular to each other is not sufficient for the complete and clear understanding of the spatial arrangement of all the shell elements.

The nomenclature of different types of structures within the shell, acknowledged particularly for both bivalves (e.g. KOBAYASHI 1964, WATABE 1965, TAYLOR, KENNEDY & HALL 1969, POPOV 1977 and WALLER 1980) or pulmonates (e. g. SALEUDDIN 1971), or even for some prosobranchs (e.g. BANDEL 1977a, b, 1979b and 1981) (the latter rather distantly related with the ones described in the present paper, anyway), in my opinion seems unacceptable (as inadequate) in the case of the gastropods under consideration. Indeed, the majority (if not just all) of their shell structures can be classified as various patterns of the general type called in the literature "crossed-lamellar" (e.g. BANDEL 1979a), rather commonly occurring in various groups of the *Carchitera*. On the other hand, in detail these structures are completely different in character, hence to describe their variety adopting, despite their distinctness, the nomenclature introduced for quite different structures, I have acknowledged unjustified and resulting in nomenclature chaos. Hence I use my own terminology.

At sections perpendicular to the growth lines (Fig. 373) there is (sometimes absent) a thin to moderately thick layer situated directly under the periostracum (EKT in Fig. 373). The structure of the layer is variable: it may be composed of long and thin fibres perpendicular to the shell surface, combined with fine grains (Fig. 373: f and g), of larger grains more or less elongated (if more elongated, they are perpendicular to the shell surface) and separated with larger or smaller spaces visible at etched sections (Fig. 373: e), or of fine diagonal structures containing more or less conspicuous spaces (Fig. 373: b, c and d).

Next there is a pallisade layer (MES in Fig. 373), which is nearly always the thickest layer within the shell. It is composed of columns which are more or less discernible and whose arrangement is more or less regular. The column structure may be various. A variety of columns have been described in the systematic part and their scheme is presented in Fig. 373: h.

The next layer is false endostracum (the nomenclature has been explained in the systematic part: *Miparus*; ERZ in Fig. 373). The layer shows usually a wide diagonal structure pattern (Fig. 373: i and j). The fibres of the layer are widely varied in length and width, the size variation being also noticeable among spaces visible at etched sections. Also the angle between successive groups of numerous fibres (lamellae) parallel to one another varies within the layer, ranging from

quite acute to nearly 180°. A particular case of wide diagonal structures (Fig. 373: k) is the extremely flat pattern composed of fibres nearly parallel to the shell surface.

The innermost layer (EW in Fig. 373) is proper endostracum (the nomenclature explained in the systematic part: *Viviparus*) which is neither fibrous nor granular but spongy (Fig. 373: l). The proper endostracum occurs only in the shells of older specimens of some species. The proper endostracum is often thin or very thin; in caenogastropod (including the *Valvatidae*) shells it is often completely absent, and always absent in *Theodorus*.

The picture at sections parallel to the growth lines (Figs 374A - E) is much less complicated. Directly under the periostracum there is a moderately thick to thin layer being more or less discernible, whose structure may be various. At etched sections it often has large spaces. It may be granular (Fig. 374: e) with the grains various in size and shape; the grains are often arranged perpendicularly to the shell surface (Fig. 374: a). The outermost layer pattern is often more or less palisade in character (Fig. 374: b; c and d), though the columns are always far smaller and worse marked than those of the palisade layer seen at sections perpendicular to the growth lines.

The thickest layer (Fig. 374: f, g, h, i and j) is fibrous, the fibres (lamellae) varying in length and width, and being separated with spaces variable in size. It shows a wide diagonal structure pattern in which it is very similar to the false endostracum layer seen at sections perpendicular to the growth lines.

The diagonal structure may be arranged at various angles (Fig. 374: f, g and h), similarly as in the false endostracum; there may be also a very flat and long-fibrous pattern (Fig. 374: i and j); then the diagonal arrangement of the fibres of successive layers parallel to both the growth lines and section surface is markedly visible.

The wide diagonal structure layer often (in many species always) reaches the inner surface of the shell. If not, the innermost layer may be the proper endostracum (Fig. 374: k) which then is neither fibrous nor granular but irregularly and strongly spongy, looking exactly the same as at sections perpendicular to the growth lines.

In hydrobioids the innermost layer is often a compact layer of cylindrical structures (Fig. 374: l), showing only very small spaces even if observed at deep-etched sections. The inner surface of the shell may be covered with a thin layer of compact and completely flatly arranged fibres typical of wide diagonal structures, but with practically no spaces visible at deep-etched sections (Fig. 374: m). Alternatively, the innermost layer may be composed of grains which are neither as big nor as regular as the cylindrical structures of the *Hydrobioides*.

The orientation of sections is shown in Fig. 374F, and the nomenclature of the teleoconch outer surface structures - in Fig. 374G - L.

APPENDIX III

Notes on the variability of shell ultrastructures and possible artifacts

1. Shell surface

The shell outer surface was cleaned chemically and mechanically. In some species the cleaned surfaces were compared with the uncleaned ones. It was established that the possibility of artifacts of the outer surfaces of the proto- and teleoconch, which would have been difficult to identify, was negligible. Greater parts of uncleaned surfaces were covered with deposits/diatoms, only some areas being free of them. The sculpture of the deposit-free surfaces was identical with that of cleaned shells. The periostracum was sometimes ruptured by cleaning, or small amounts of oxalates or other precipitates formed in the process of chemical cleaning covered some fragments of the surface. Such artifacts, however, were always easily recognisable as such.

In general, the variability of the outer surface sculpture is quite limited. 10...15 specimens of each species (with the exception of *Marstoniopsis scholtzi* out of which only a few specimens were available) from all habitat types were examined, and this seemed enough to deal with the whole variability ranges of the structures. Although this is not the subject of my paper, I would like to note that no distinct relation was found between the habitat conditions and shell sculpture.

It proved necessary to study a greater number of hydrobioid shells to find the proportion of covered/uncovered pores, which is often a species-level taxonomic character being statistically expressed. I always examined the whole shell surface. The teleoconch surface photographs, however, usually show the sculpture of the body whorl alone. This region of the shell is, in general, the least corroded one.

The variability of the teleoconch inner surface is much greater, which is due to various stages of growth at the moment the animal was killed, to the recrystallization of extrapallial fluid, as well as to the conditions of etching, which must have been not exactly the same for all the specimens, and to some other technical reasons. This has been discussed in the systematic part.

2. Shell sections

I observed a great variability of shell sections, particularly of those perpendicular to the growth lines, which produced more information. Based on preliminary observations, the following limits were set to reduce the sources of observed variability:

(1) observations were limited to the body whorl, far from both the suture and columella (see Appendix II and Fig. 374F), and from the mouth, and only to adult specimen shells to eliminate age variability;

(2) the unetched sections were used only occasionally, since they were similar to the etched ones but poor in information (see Appendix II);

(3) all the sections used were etched with HCl, since EDTA etching proved too rapid and vehement in that it affected conchioline envelopes, resulting in poor-quality preparations;

(4) only the sections which were flat and regular, and exactly perpendicular/parallel to the growth lines (with a few exceptions: see the systematic part) were taken into consideration (Fig. 374F): the orientation of a section was always carefully checked during the SEM examination of a specimen.

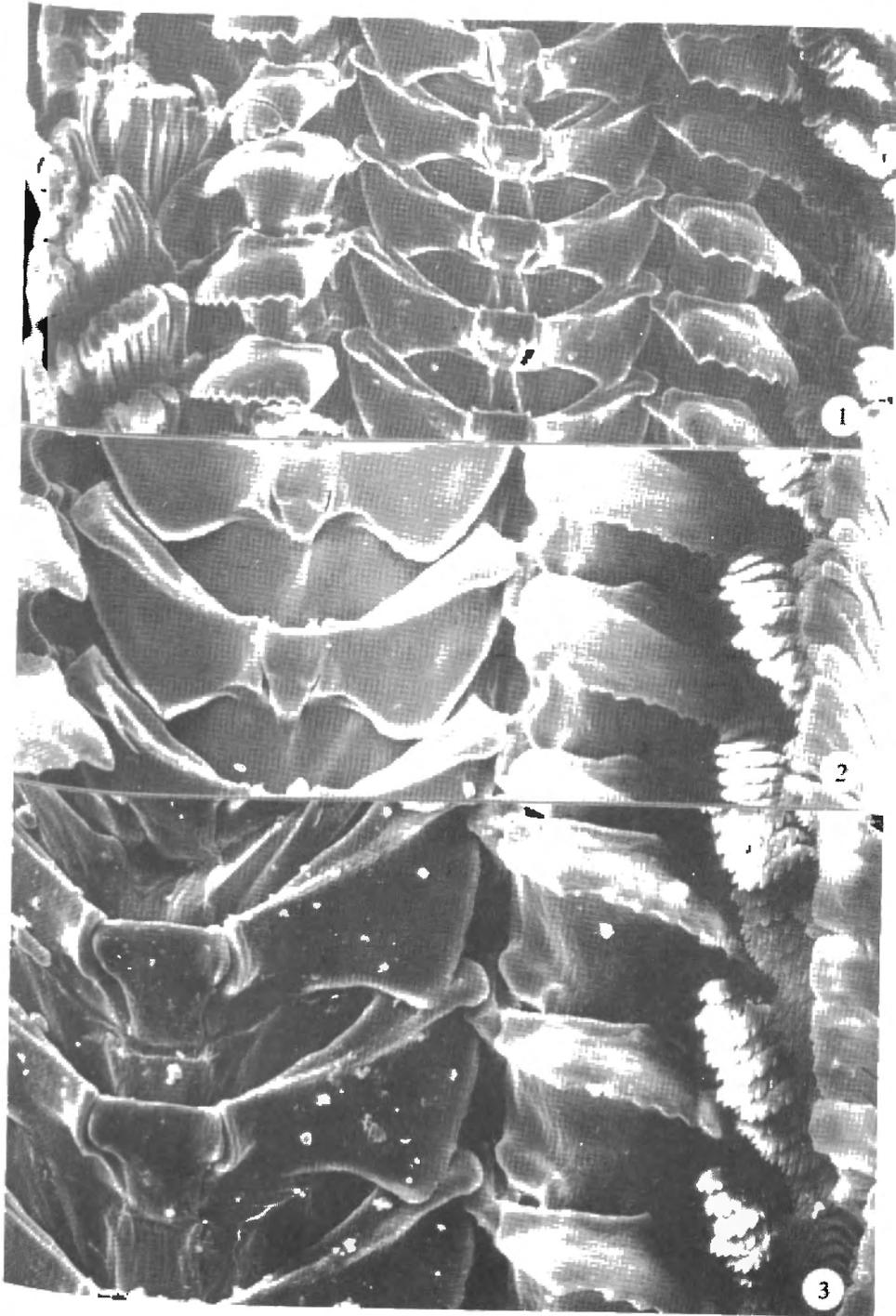
Quite thick deposits of recrystallized calcium carbonate or small agglomerations of crystals often appeared at sections; their identification, however, was not difficult.

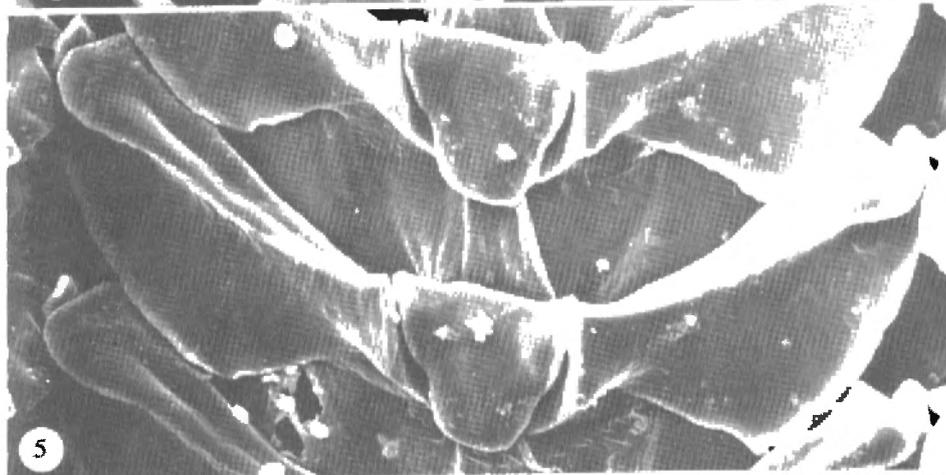
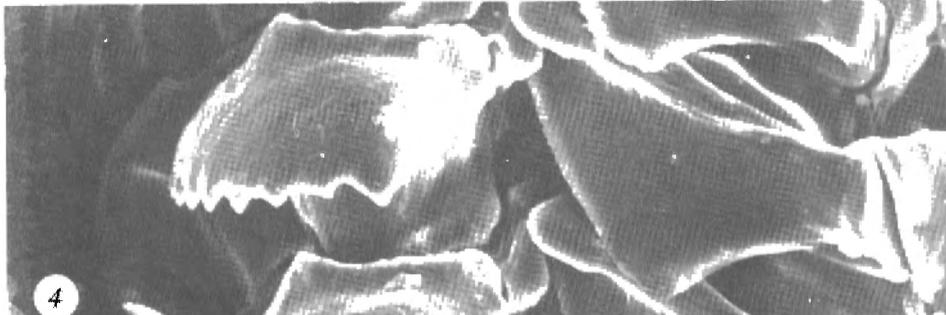
It was clearly observable that the intrapopulation variability was greater than that caused by habitat conditions; it means that the differences occurring between the populations from the habitats of various types were slightly marked, while the variation within each population was high. It is probable, however, that this is not a strict rule, and does not concern extreme conditions (a pronounced calcium deficit may be an example). Anyway, I did not examine such specimens. Further studies on the problem are necessary, but they are outside the scope of the paper. The variability of each structure within each species is discussed in the systematic part.

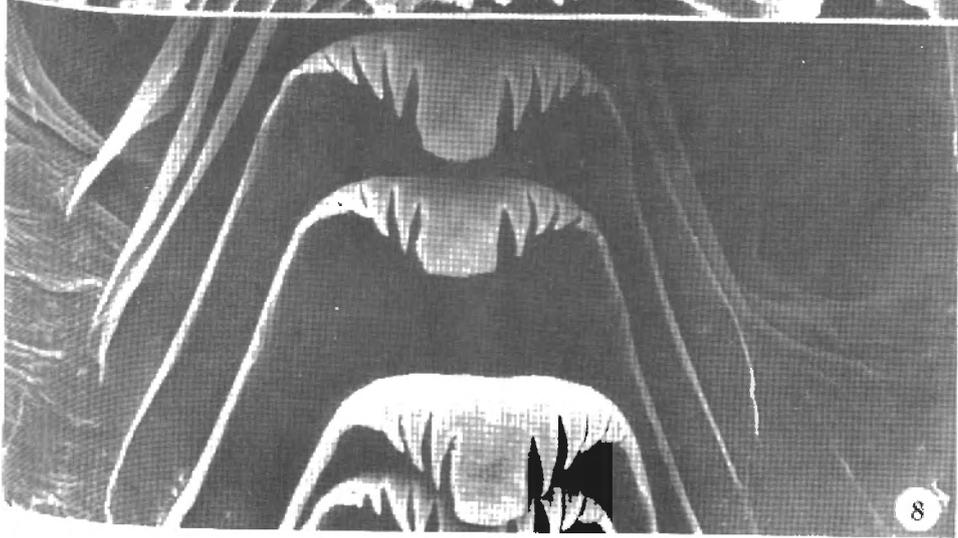
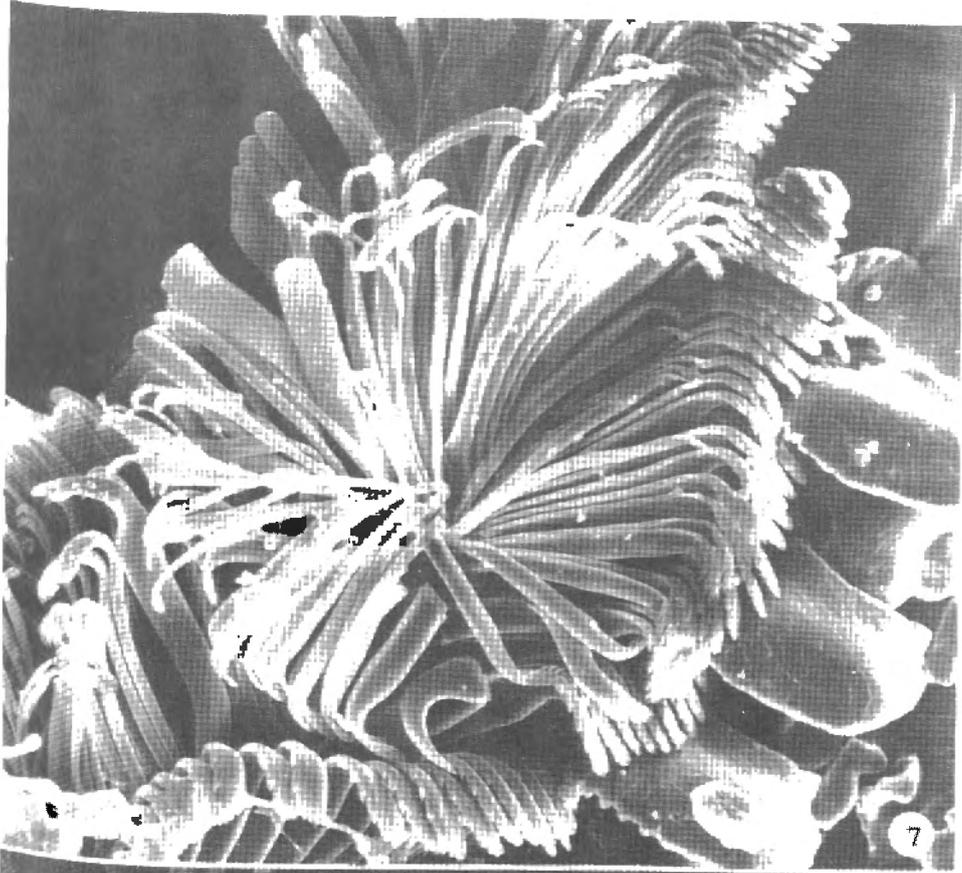
APPENDIX IV

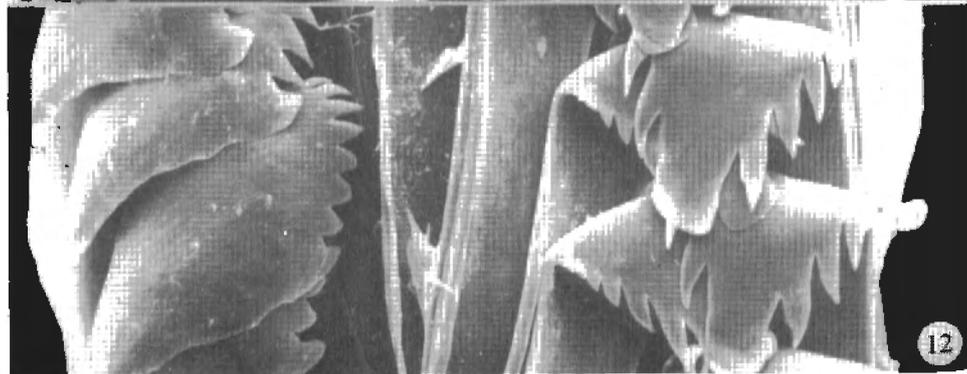
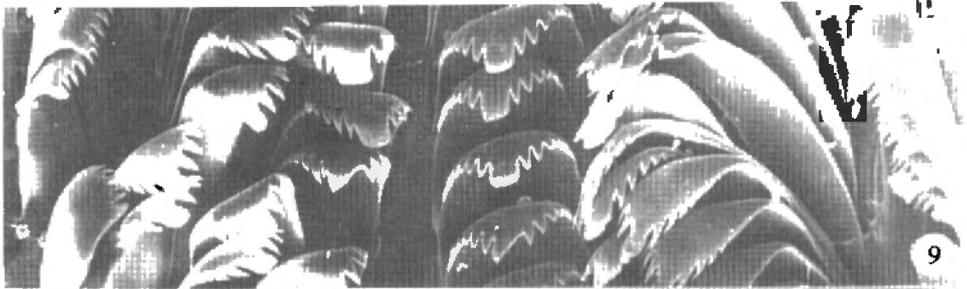
Abbreviations used in figures showing anatomy

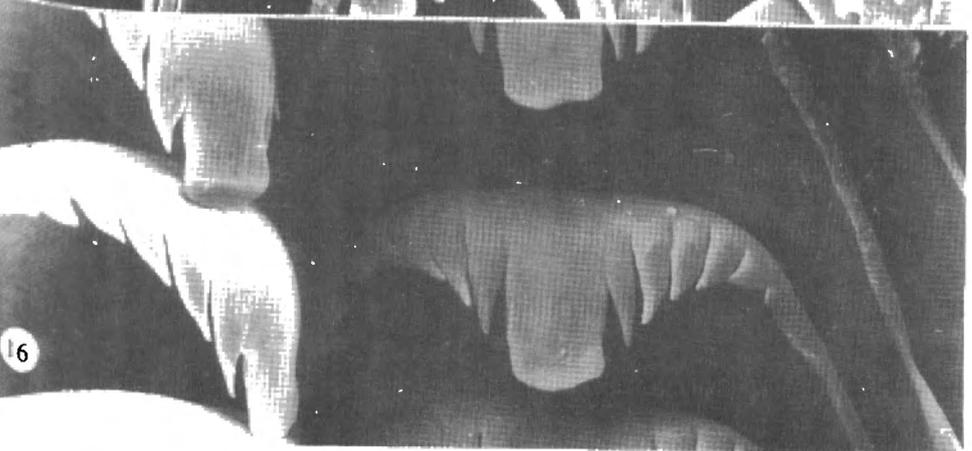
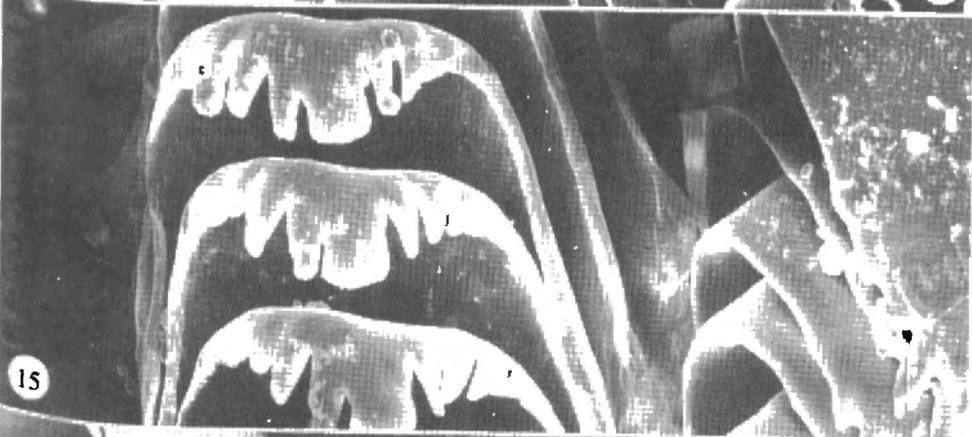
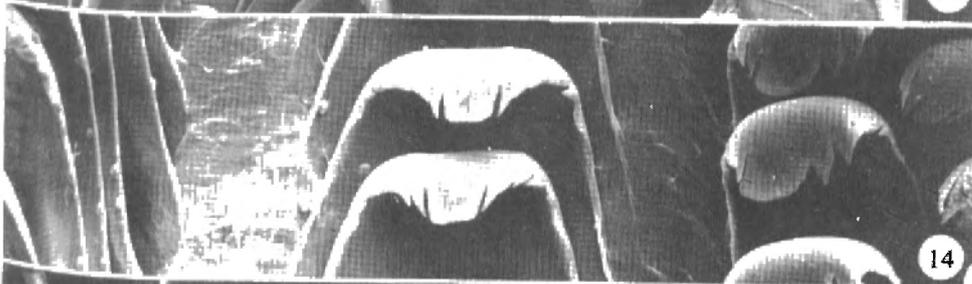
bic - bursa copulatrix, *bip* - brood pouch, *cbc* - canalis bursae copulatrix (duct of bursa), *cl* - ctenidium (gill, not necessarily homologous with the original molluscan ctenidium), *dgp* - ductus gono-pericardialis (gono-pericardial duct), *dth* - ductus haemaphroditicus (hermaphrodite duct), *emb* - embryo, *fch* - fertilization chamber, *fl* - flagellum (penial gland), *ga* - glandula albuminoidea (albuminoid gland), *gm* - glandula mucosae (mucosid gland), *gn* - glandula nidamentalis (nidamental gland), *gp* - gonoporus, *hp* - hepato-pancreas (digestive gland), *as* - asphradium, *ov* - oviductus (oviduct), *ova* - ovarium (ovary), *p* - penispc - pallial cavity, *por* - pallial section of oviduct, *pr* - prostata (prostate), *rec* - rectum, *ror* -renal section of oviduct, *rs* - receptaculum seminis (seminal receptacle), *rsd* - ductus receptaculæ seminis (duct of seminal receptacle), *te* - testis, *v* - vagina, *vd* - vas deferens.

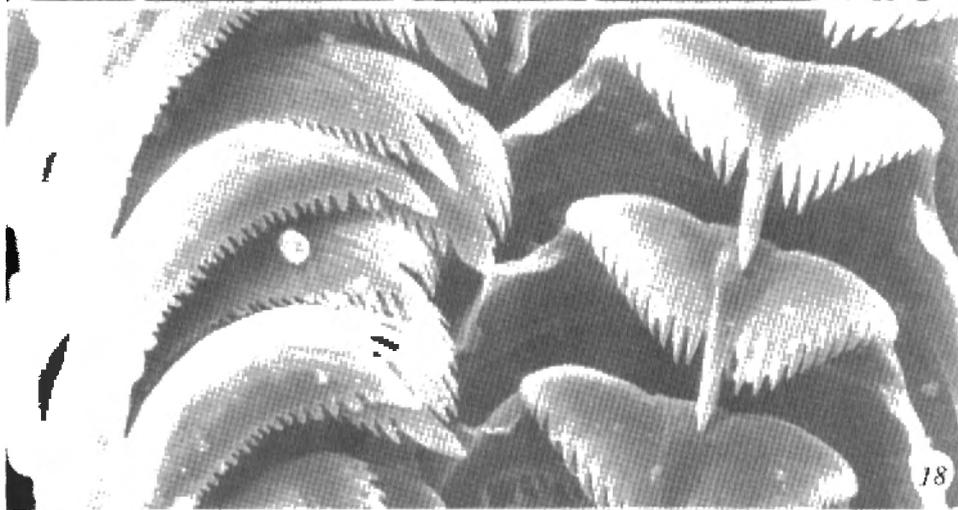
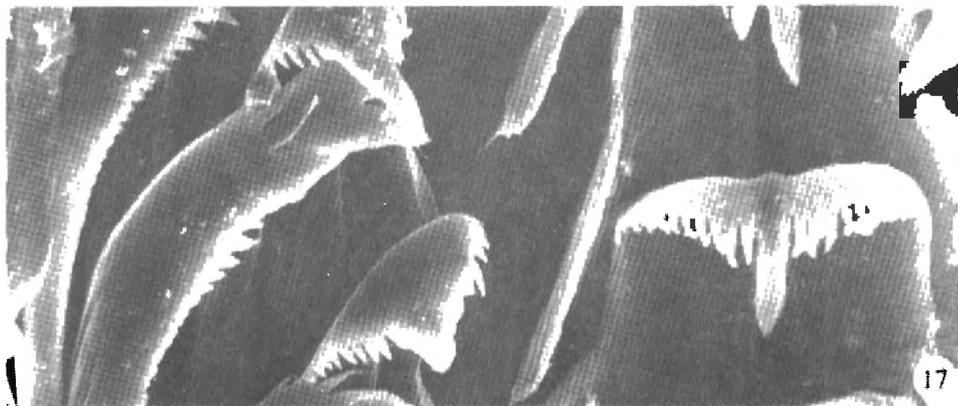






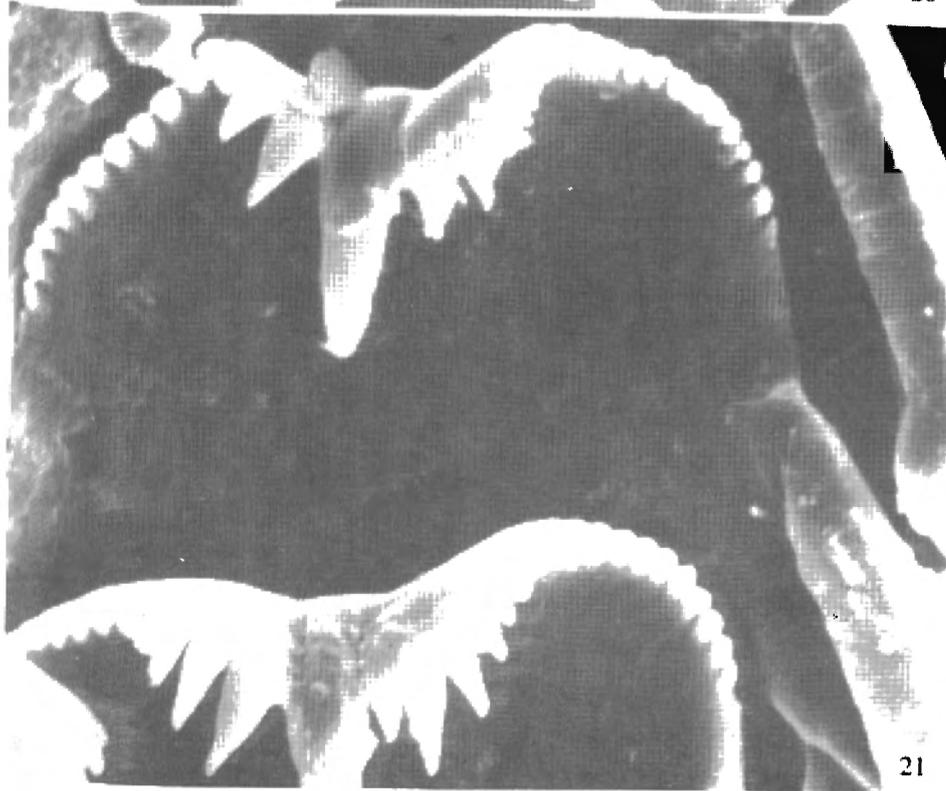




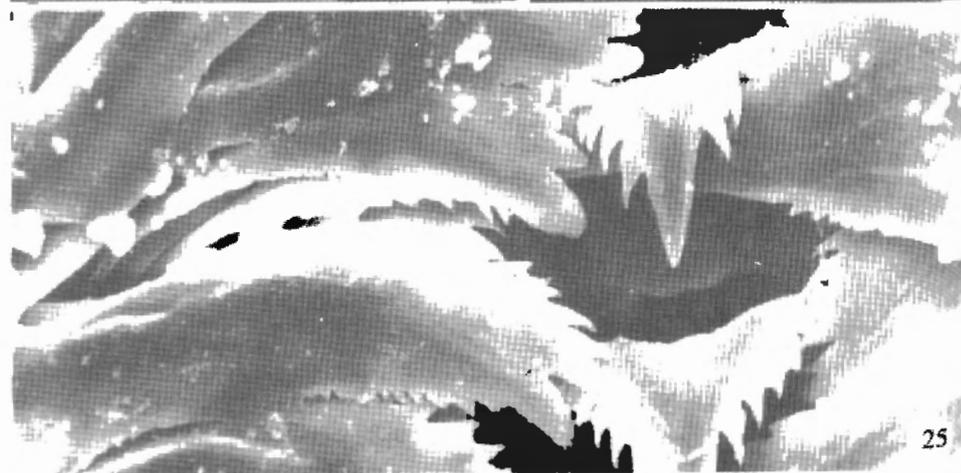
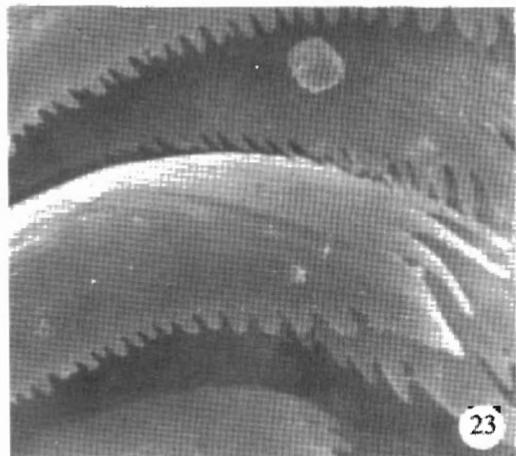


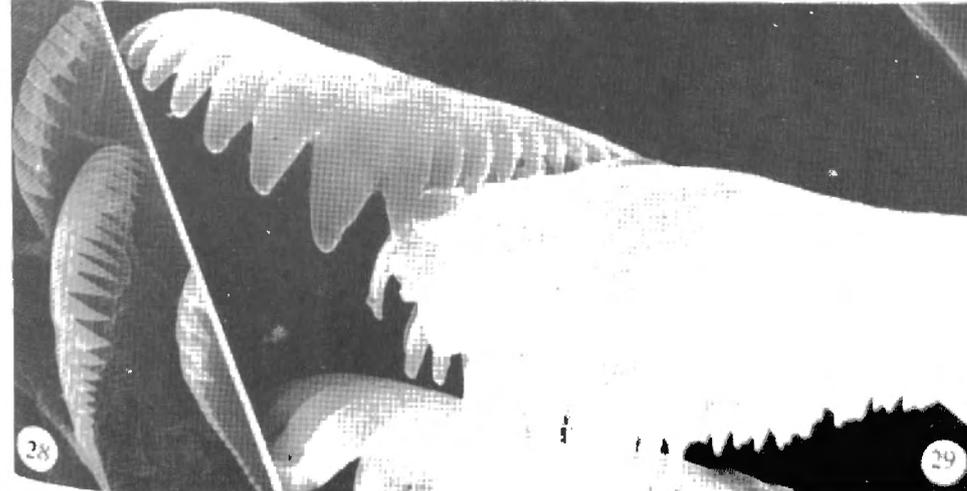
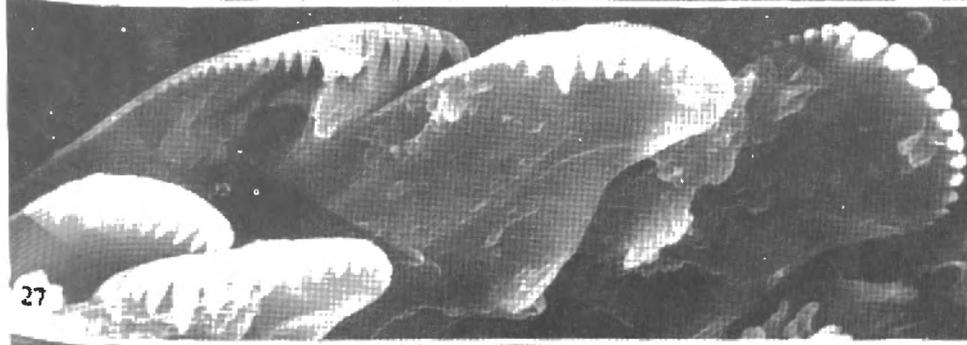
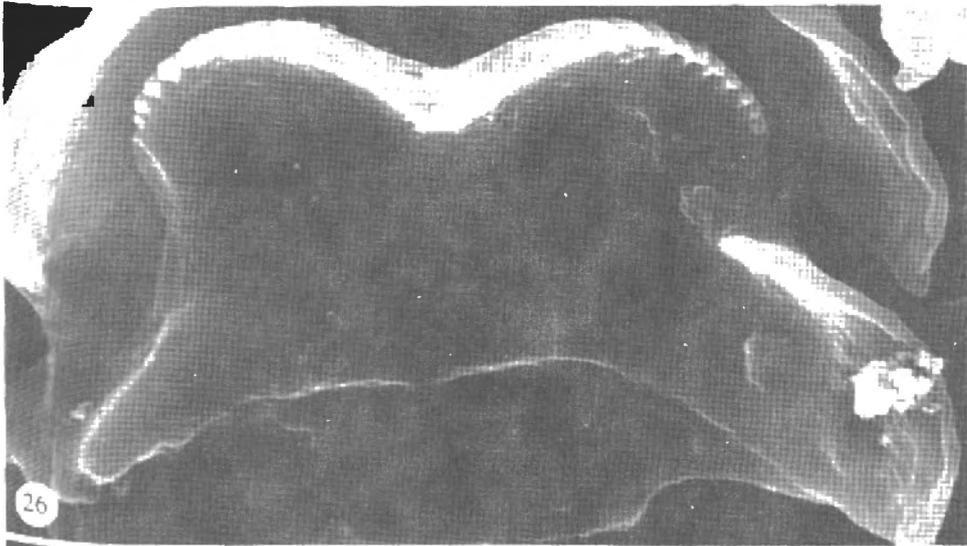


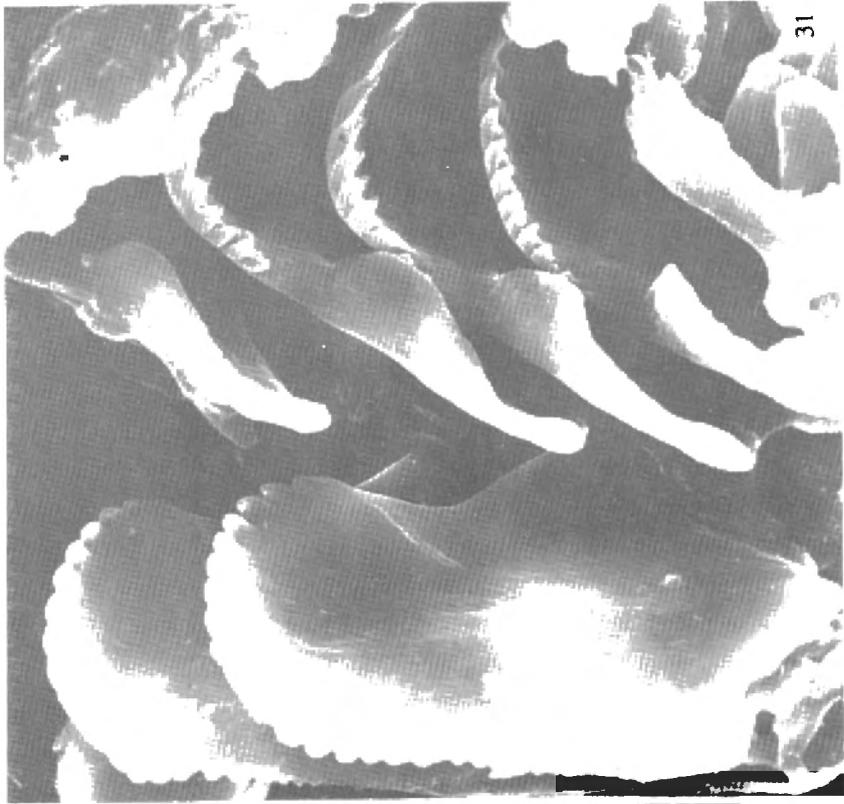
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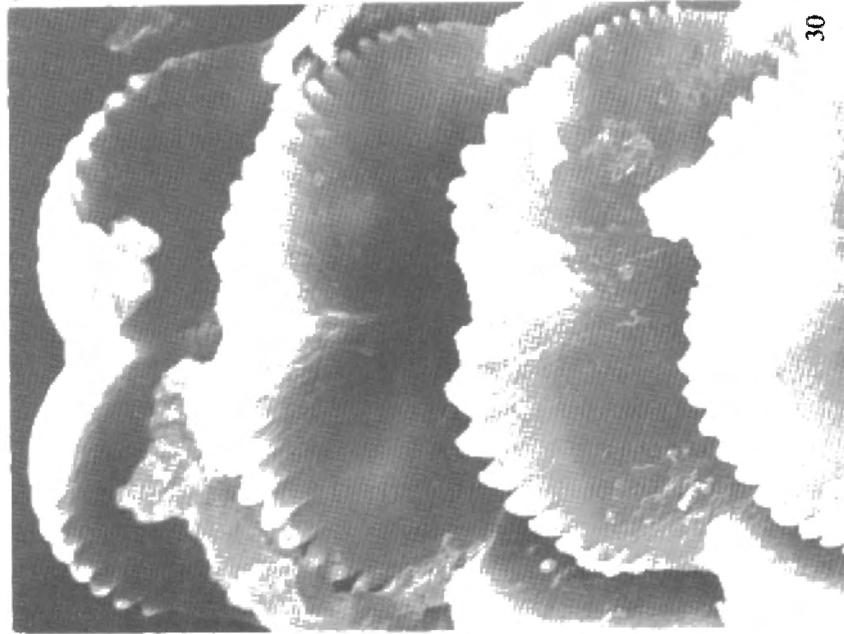
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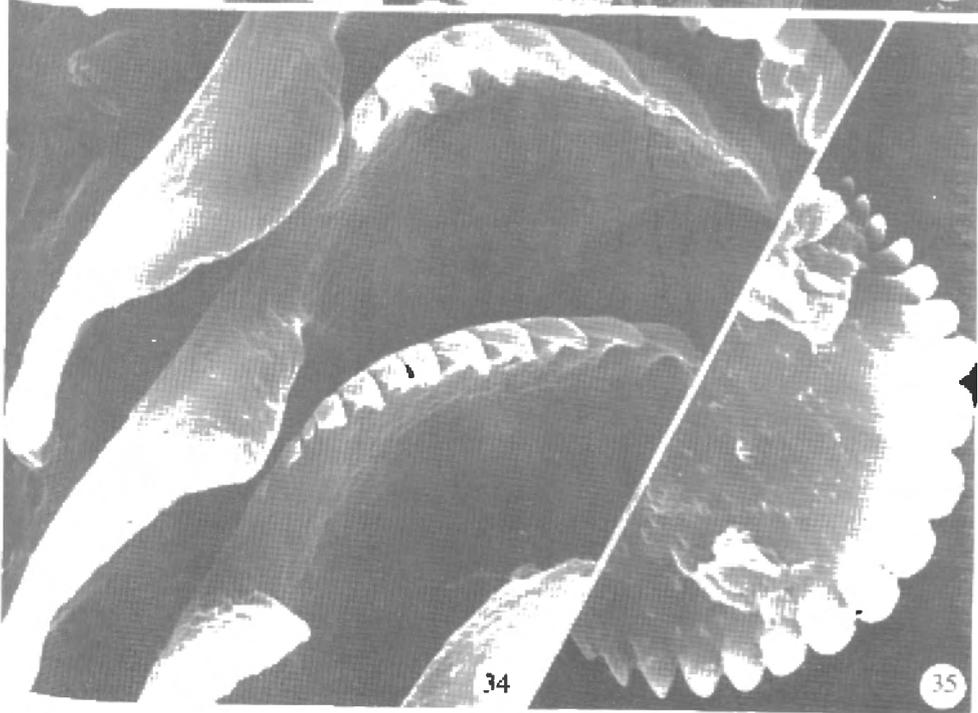
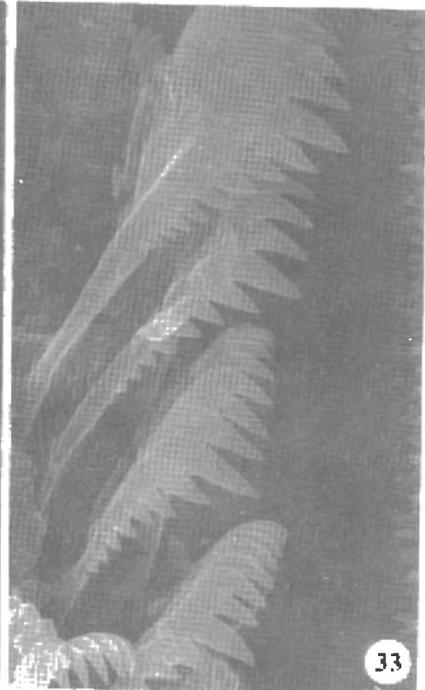
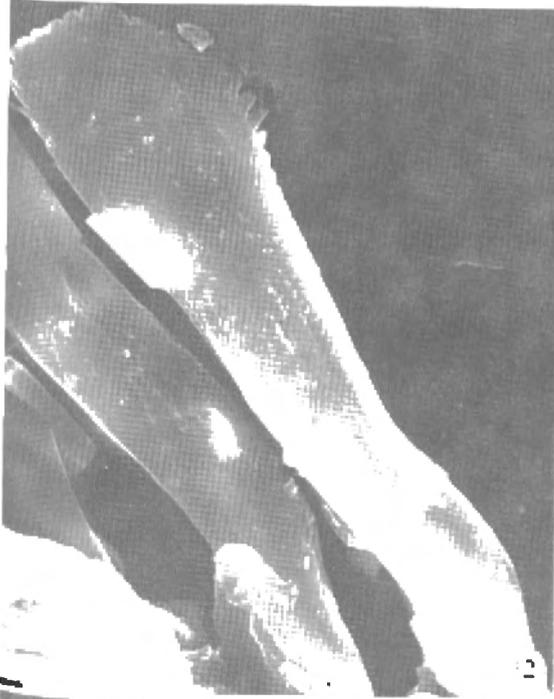


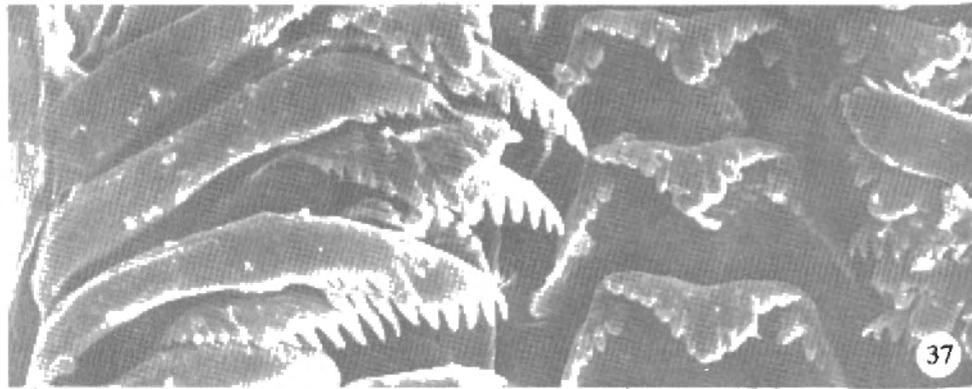
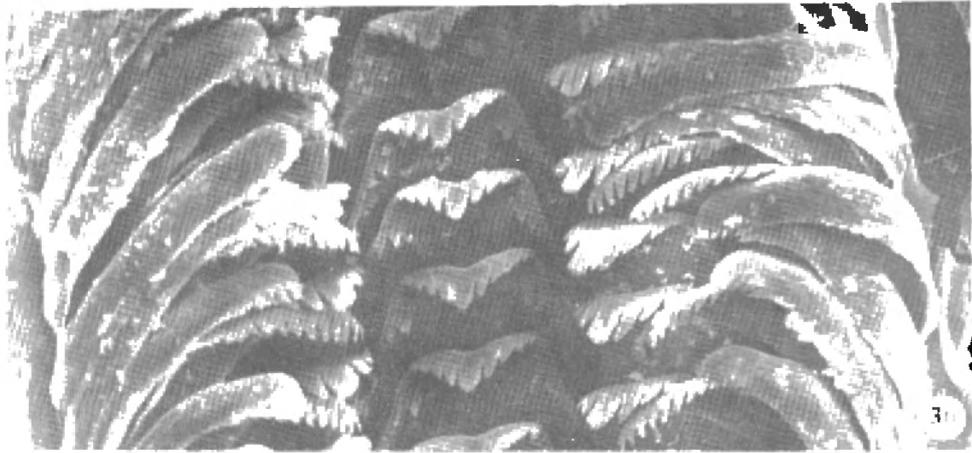


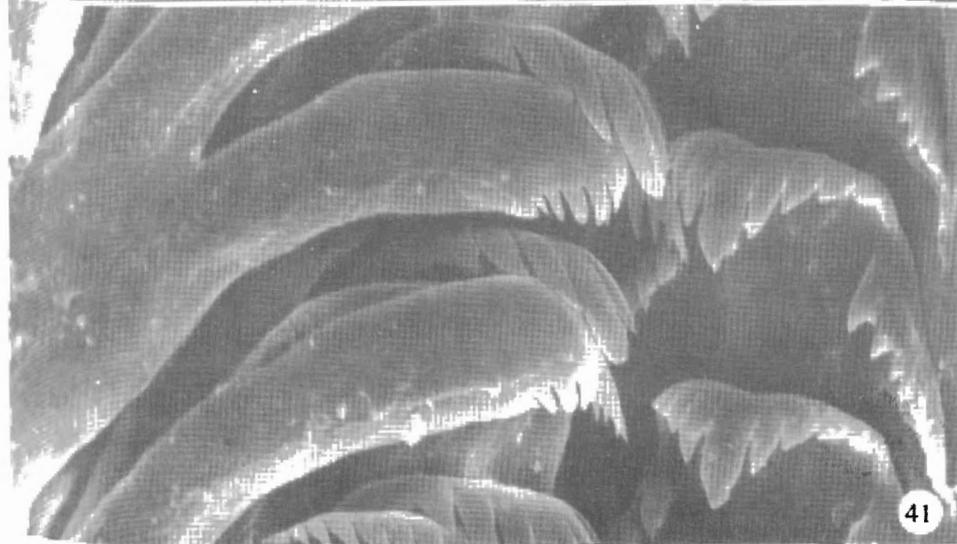
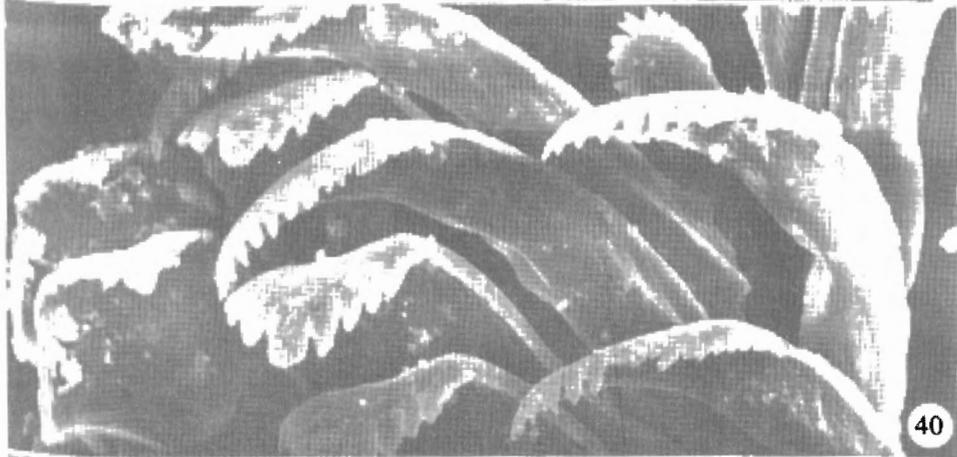
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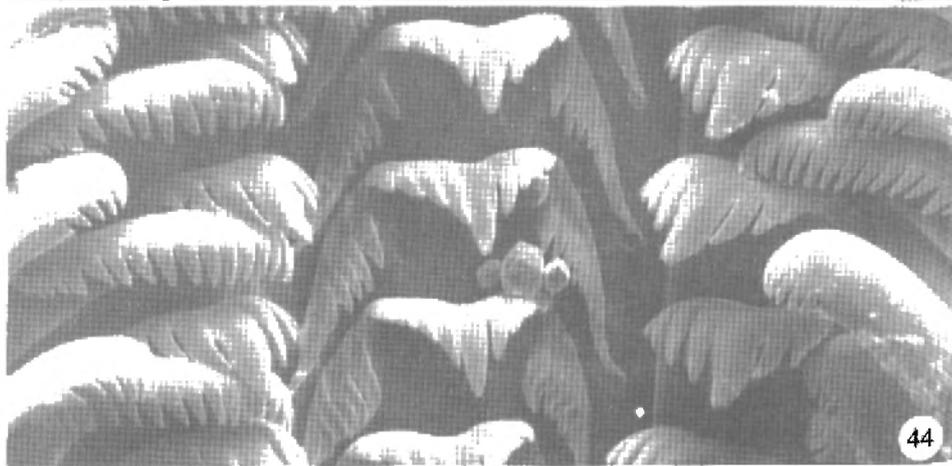
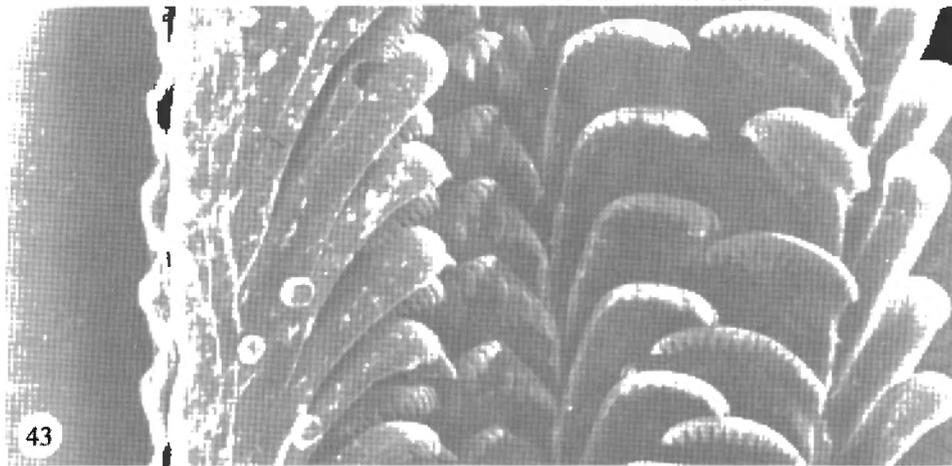
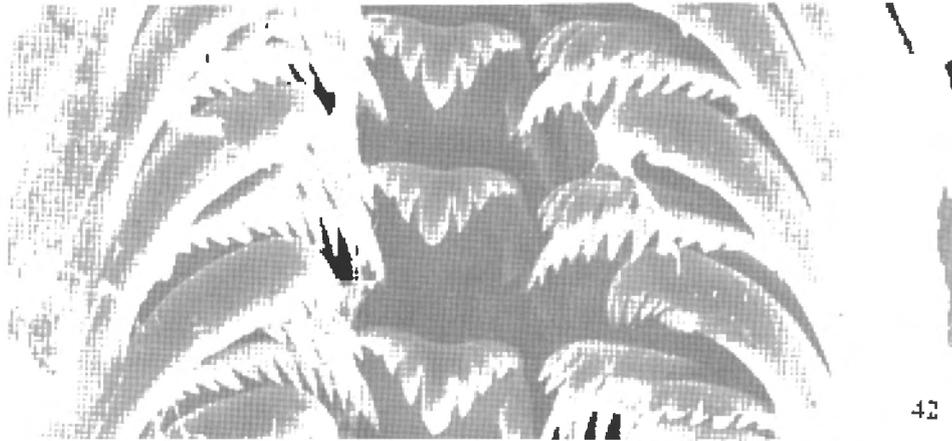
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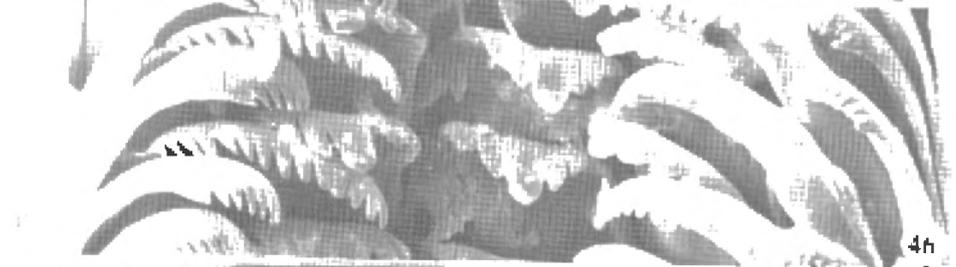


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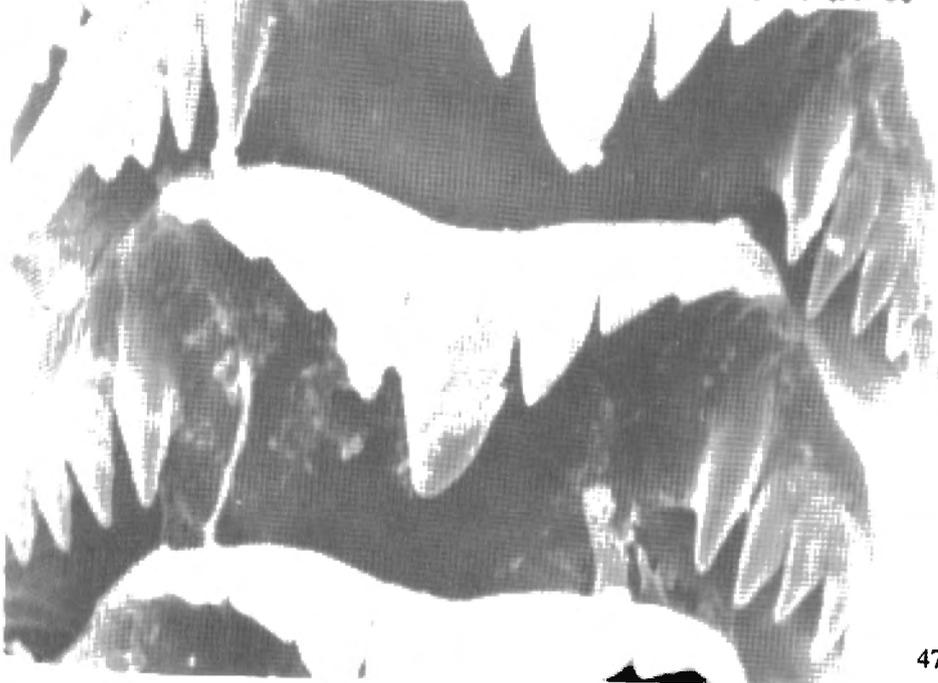




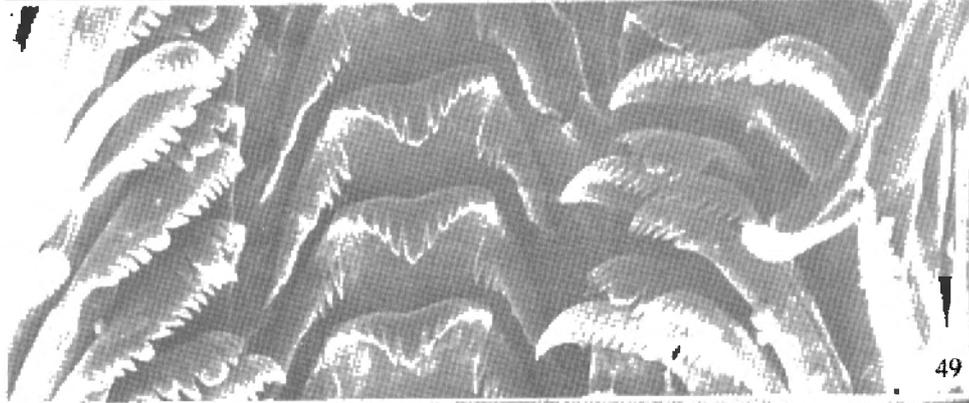
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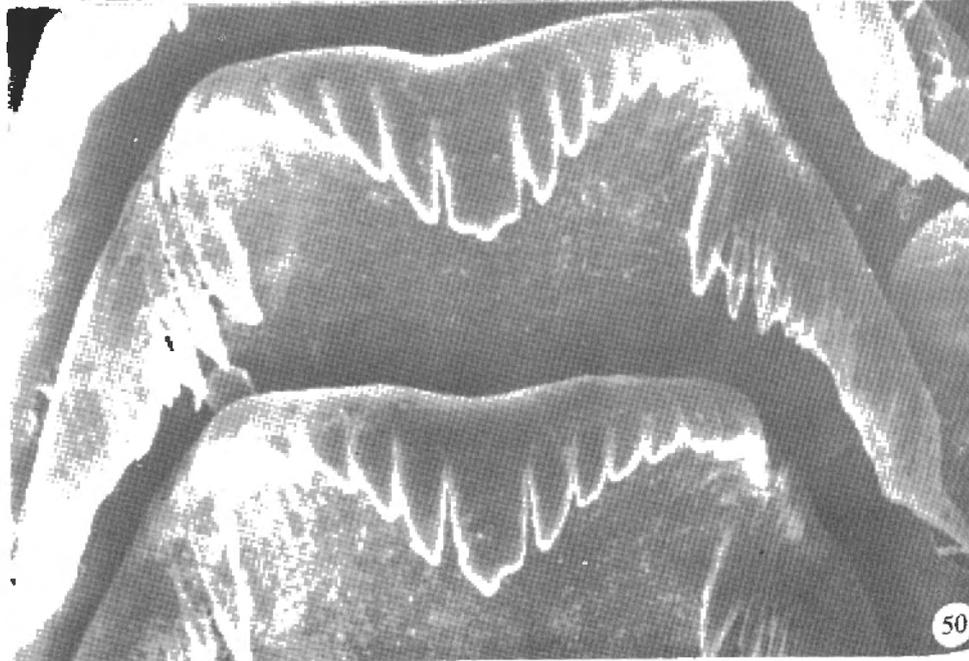
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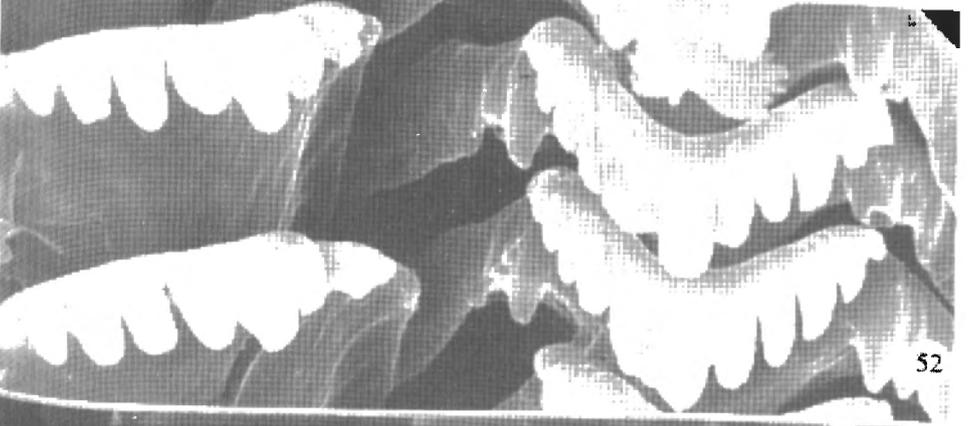


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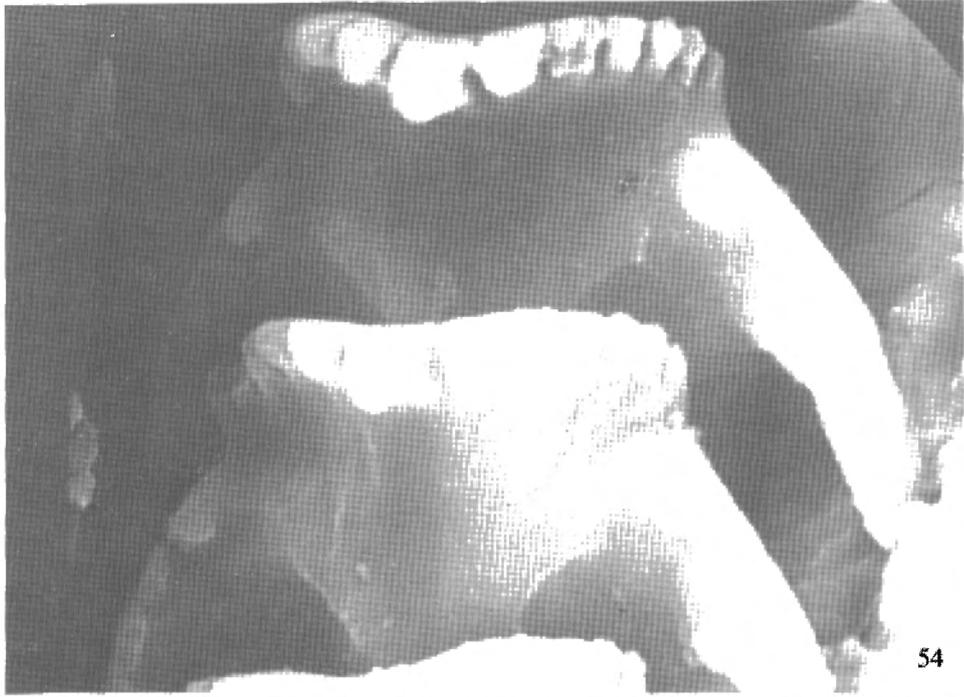
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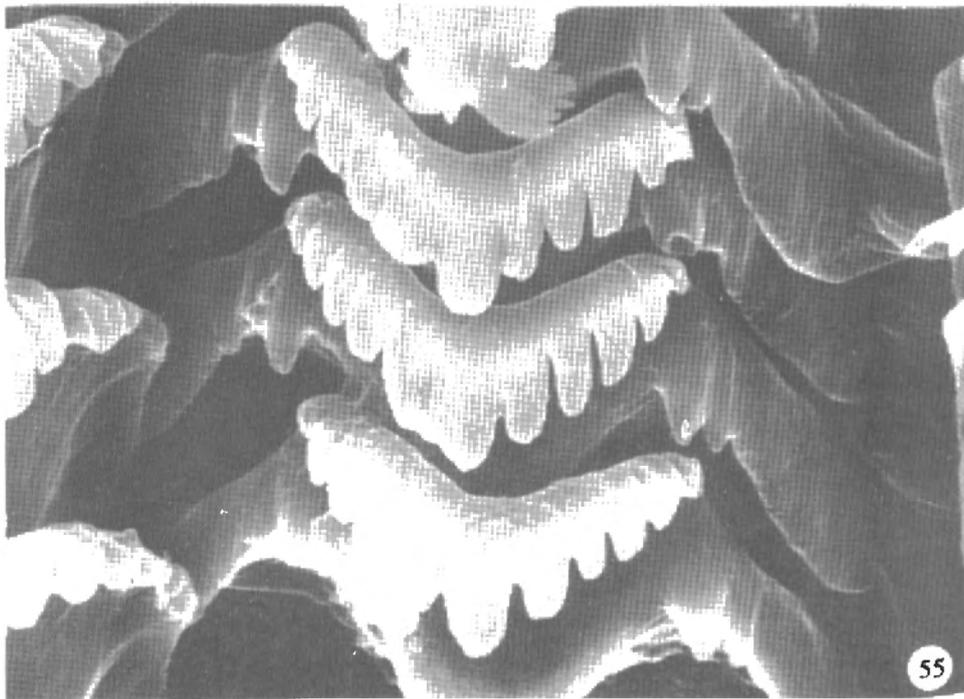
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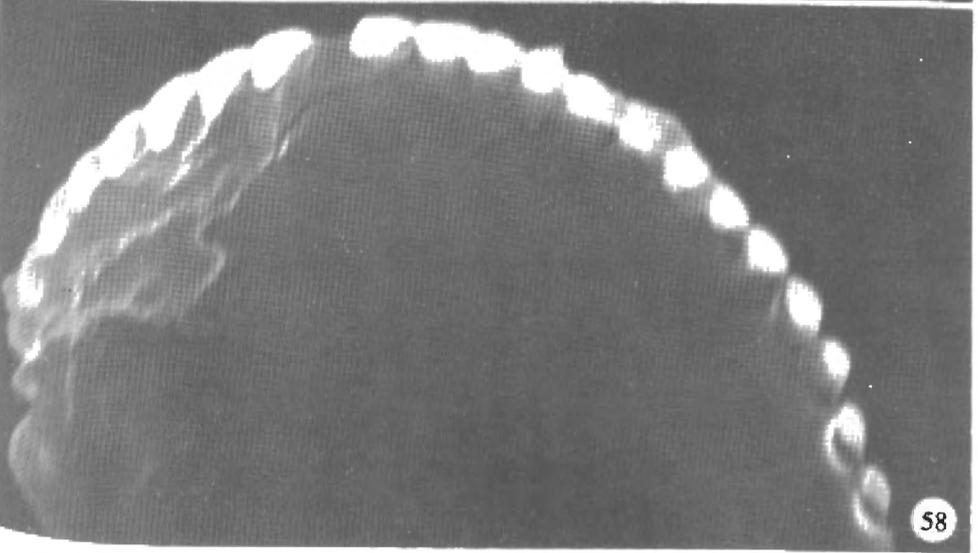
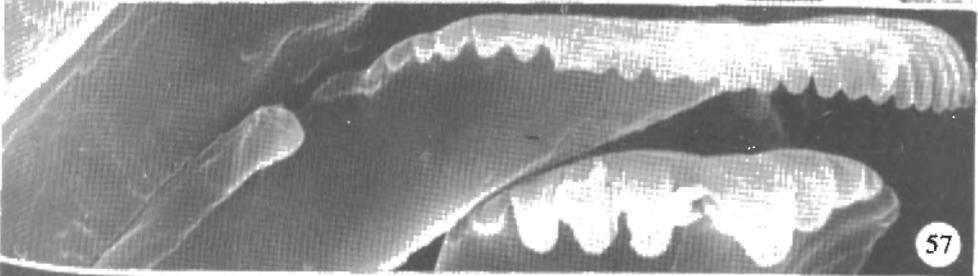
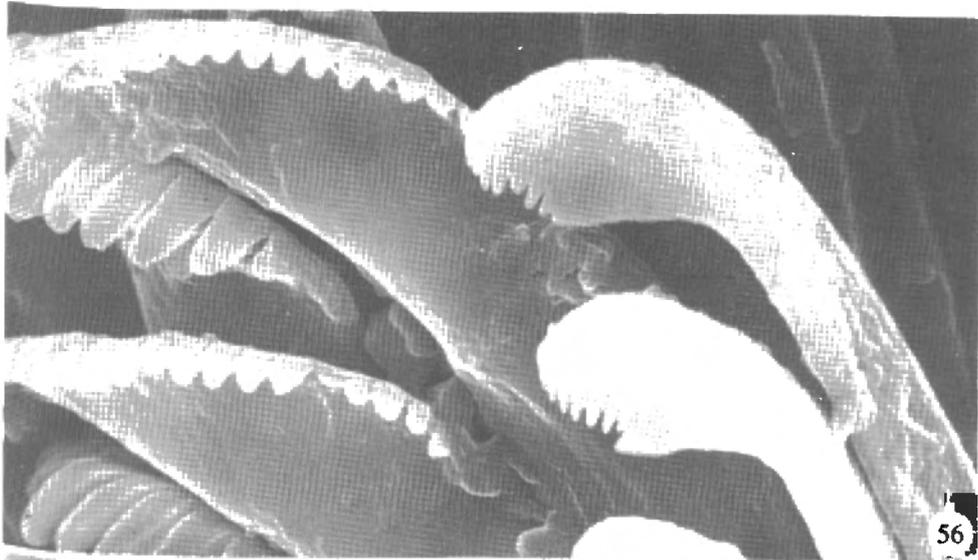
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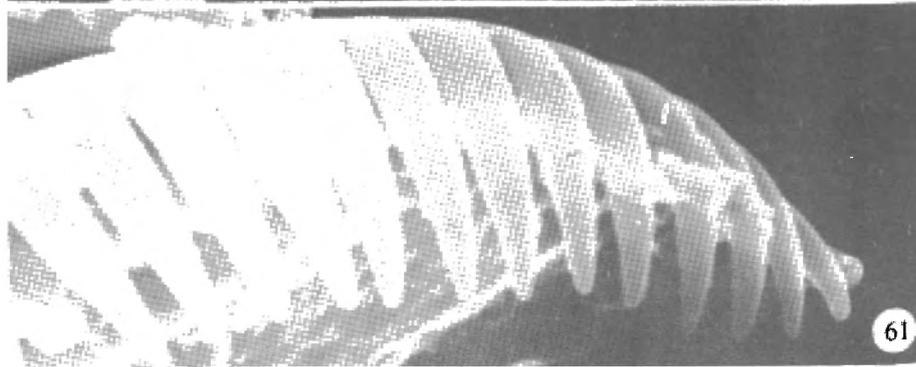
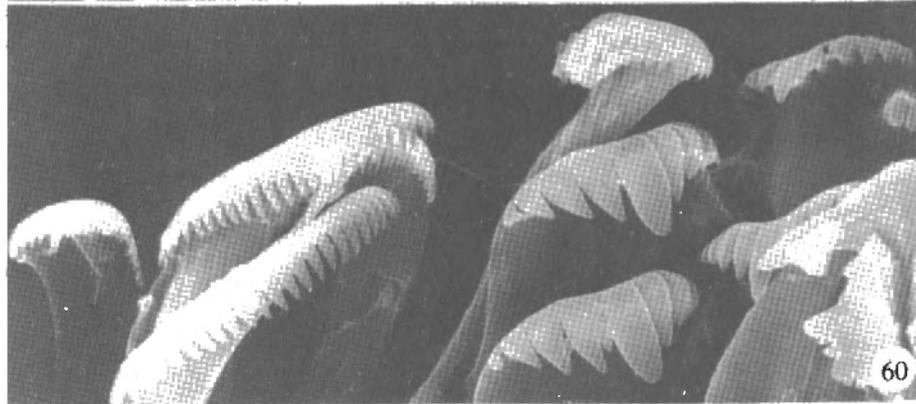
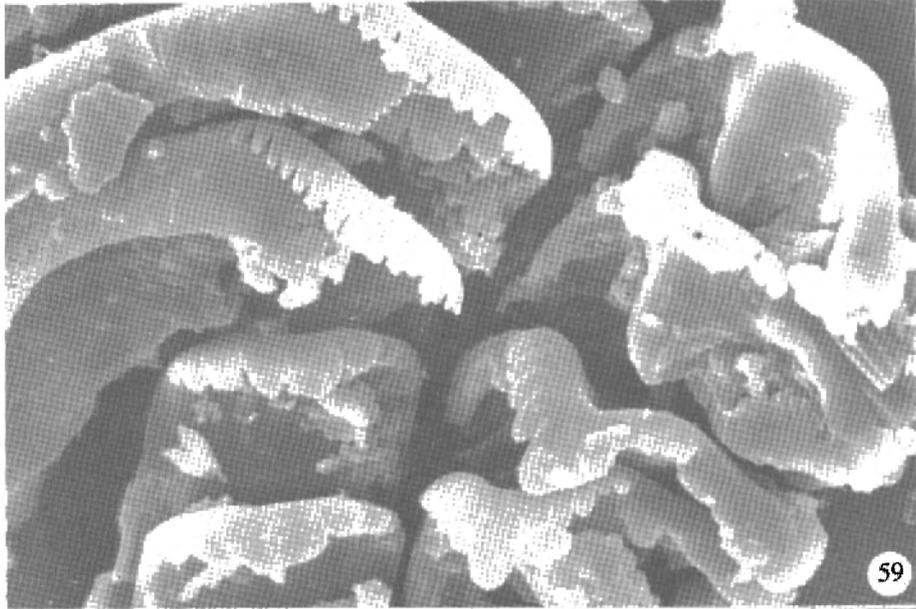


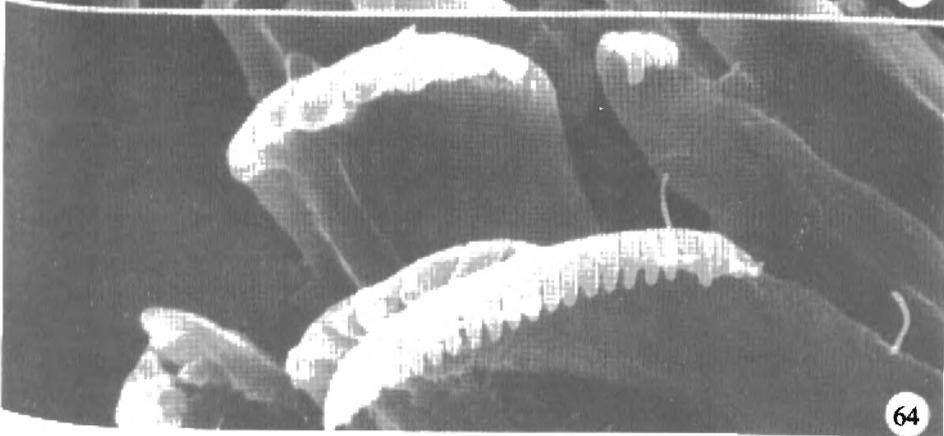
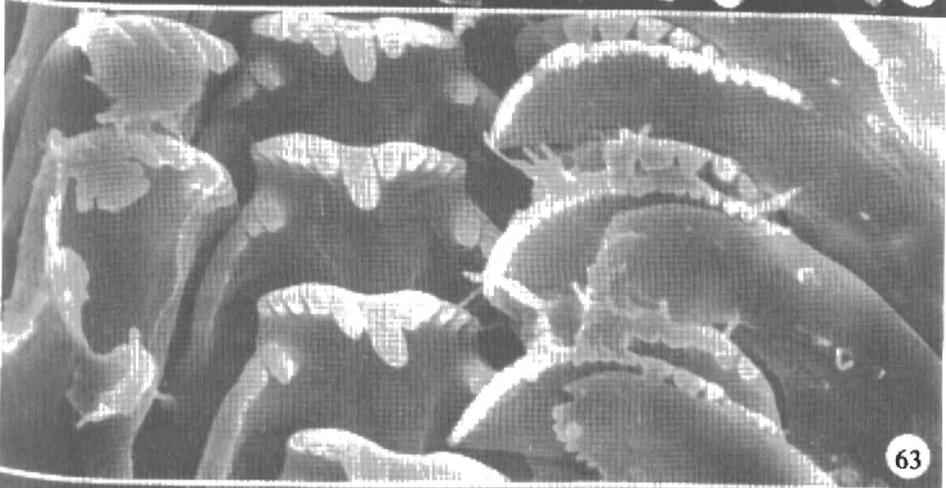
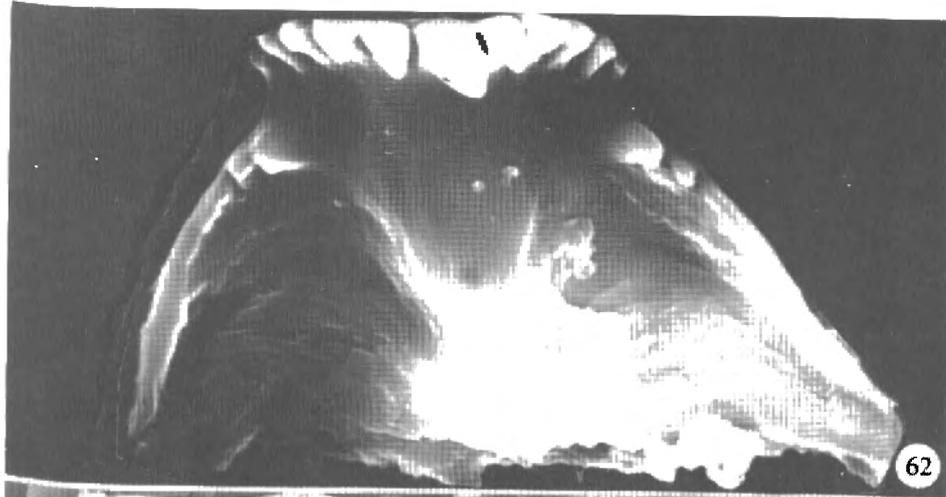
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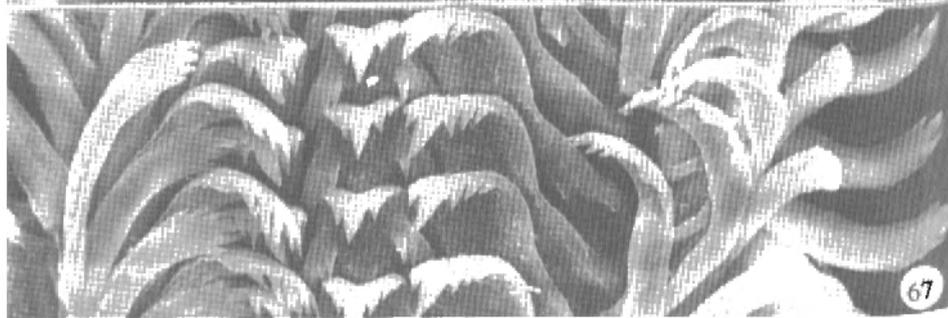
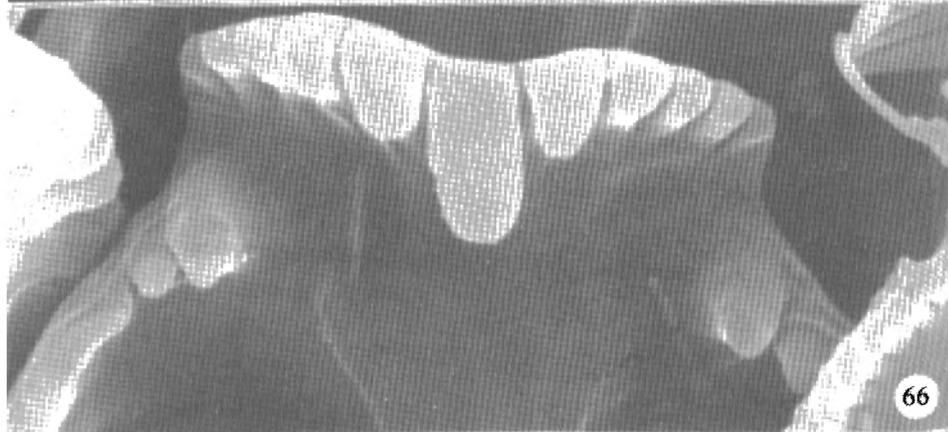
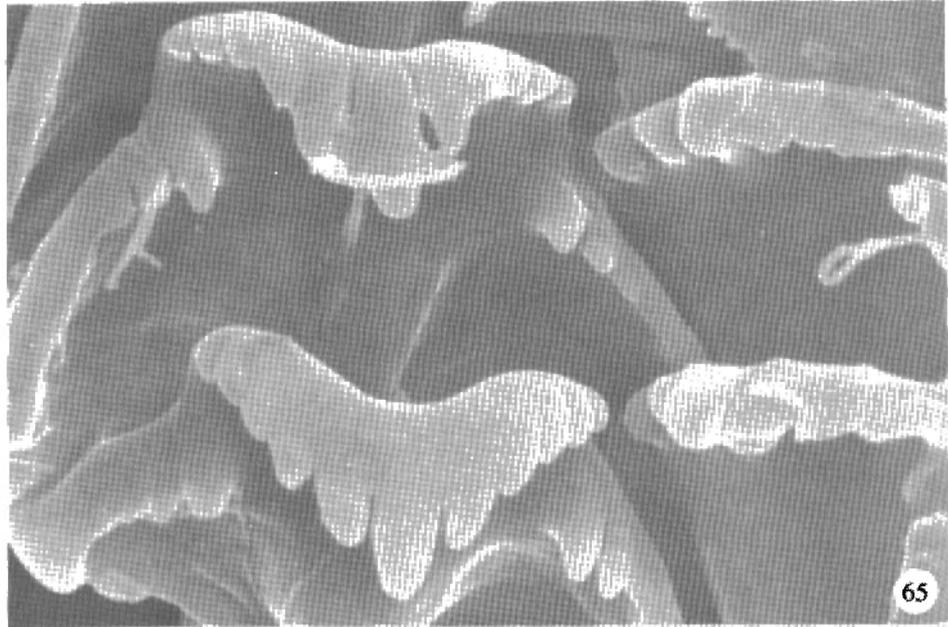


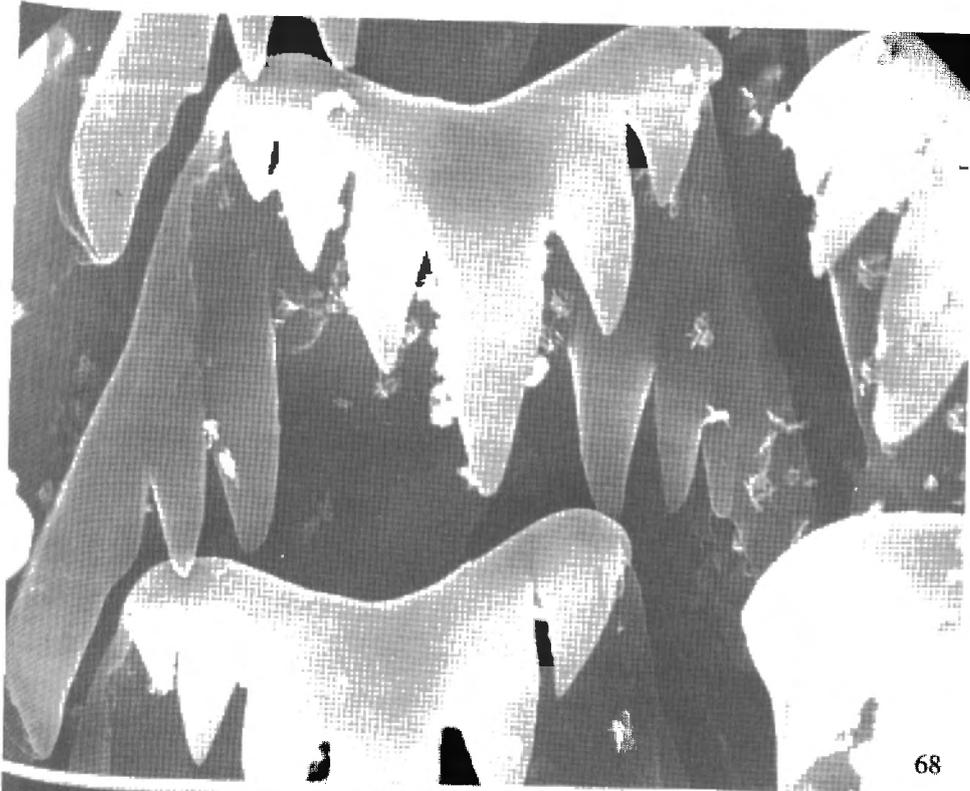
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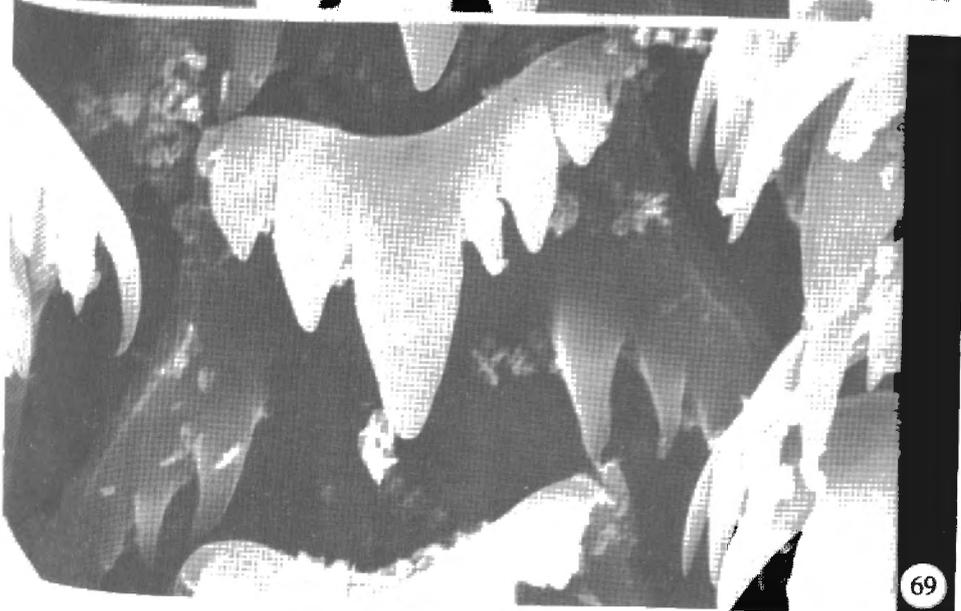




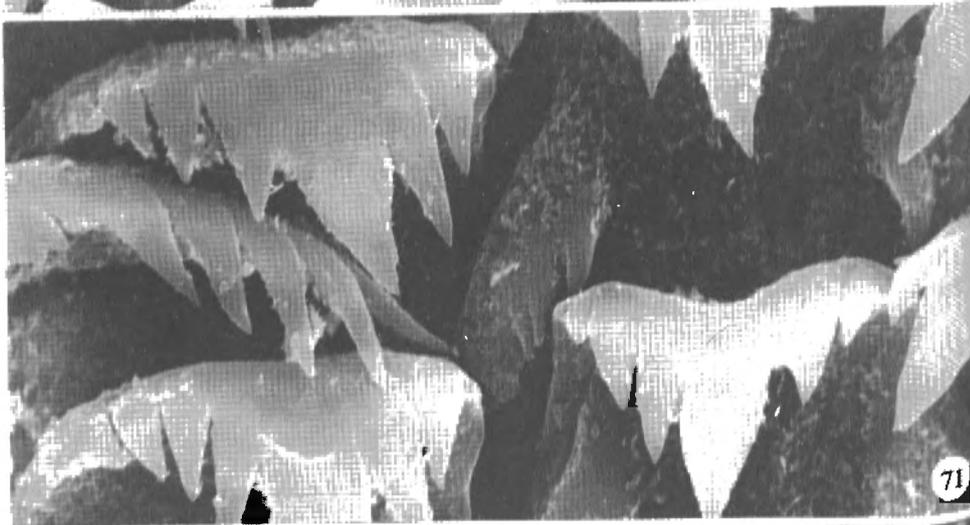
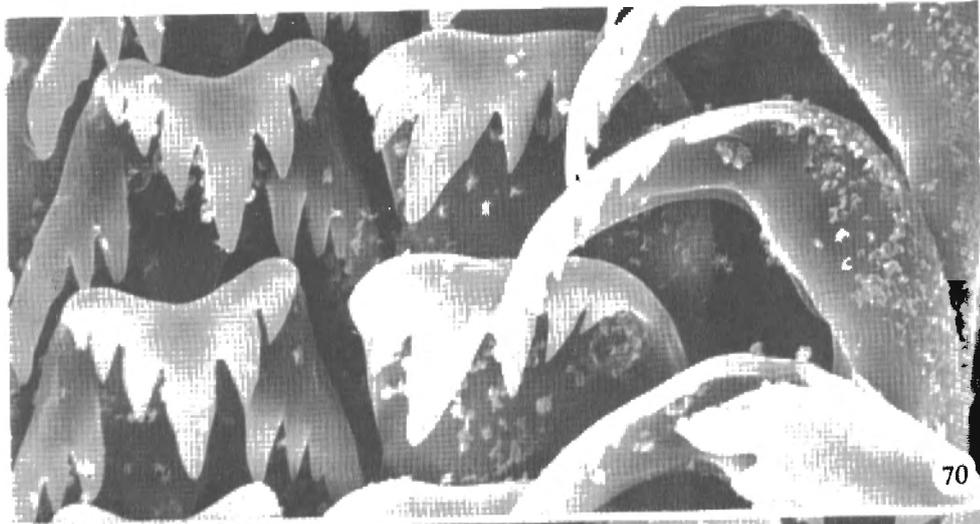


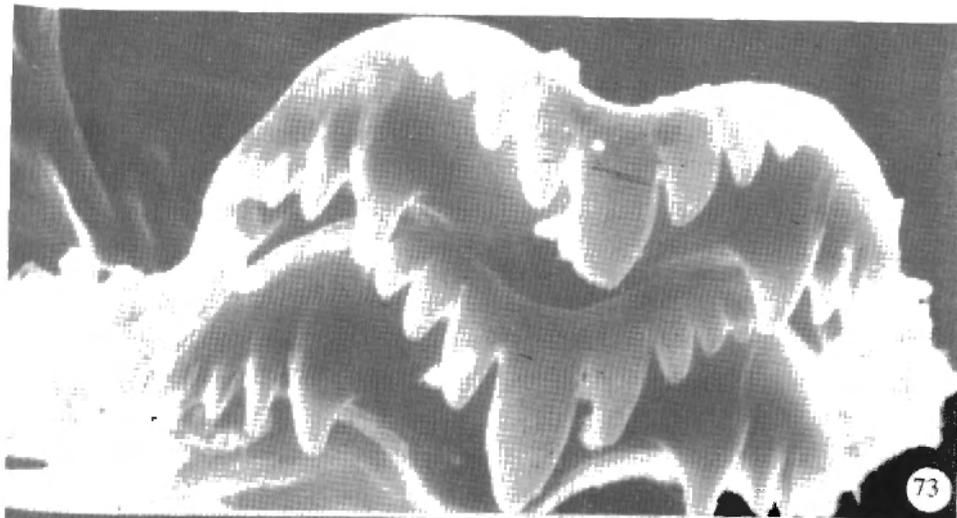


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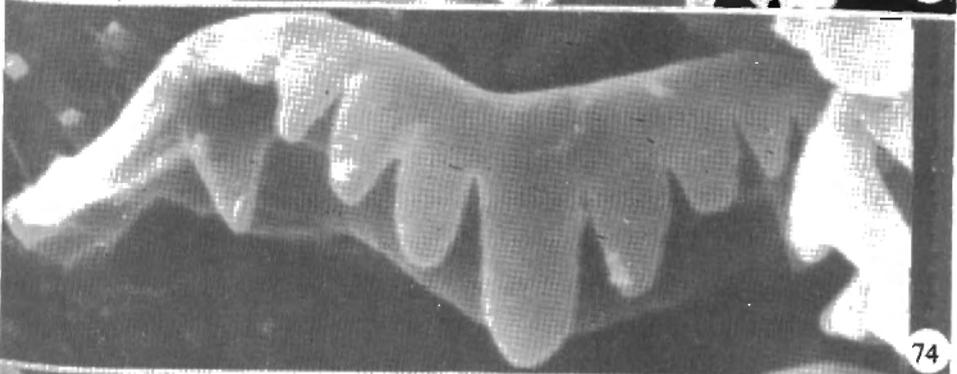


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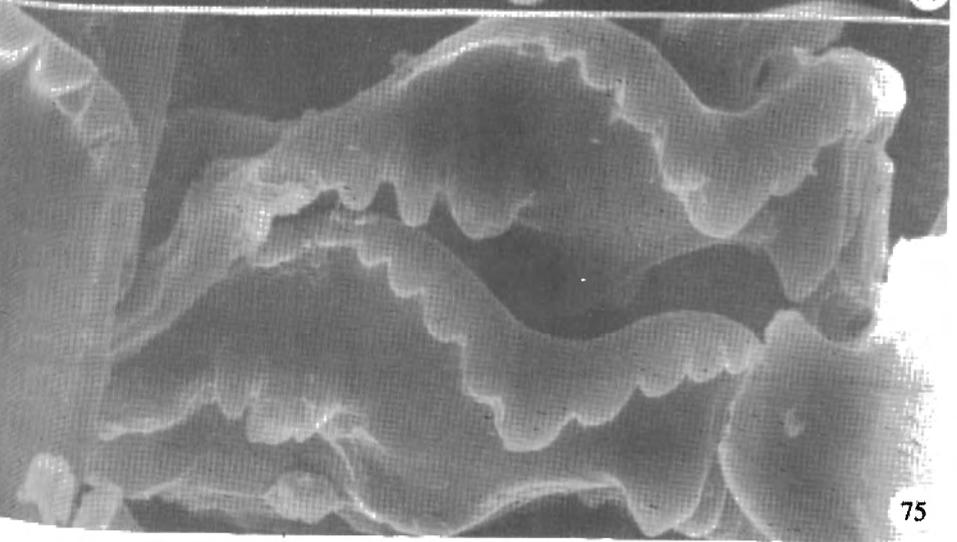




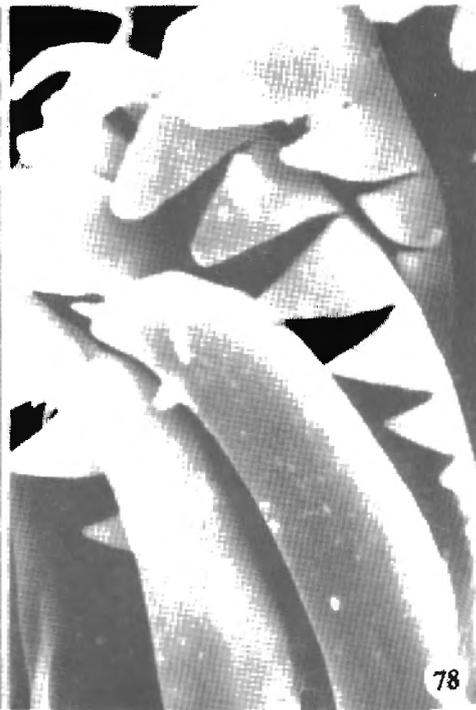
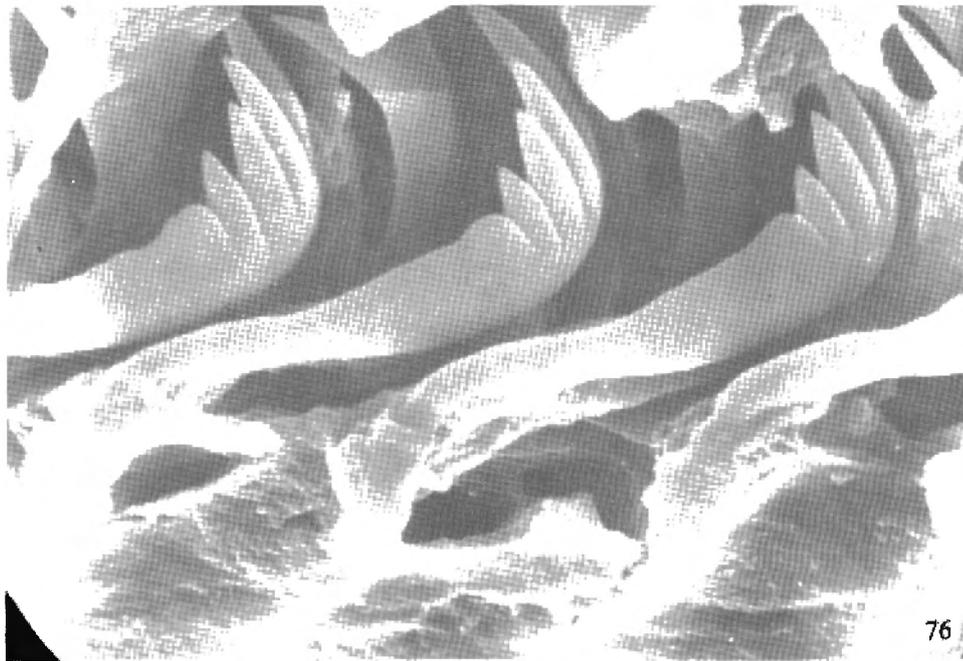
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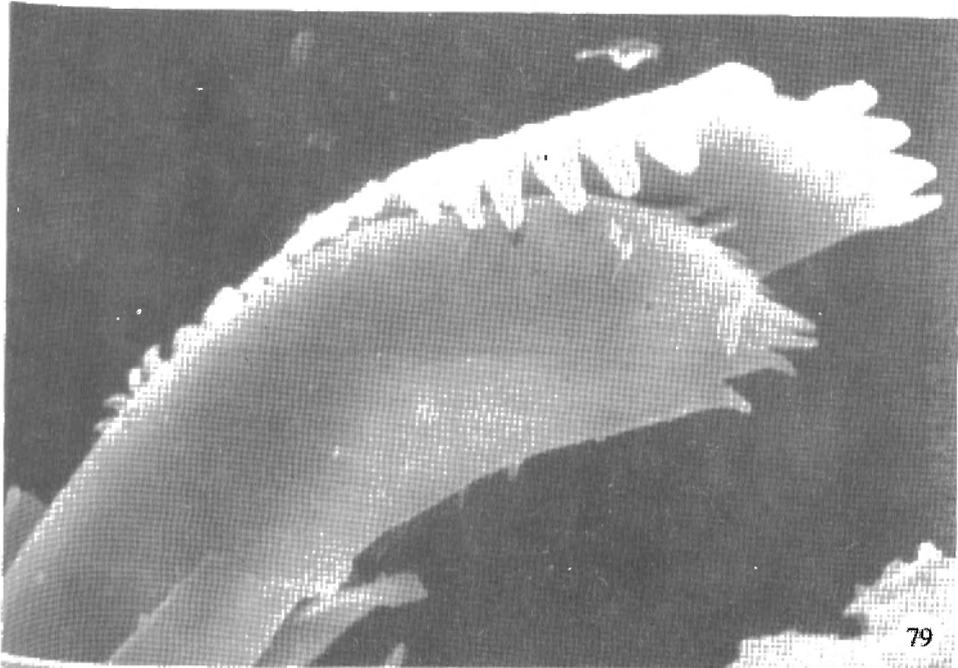


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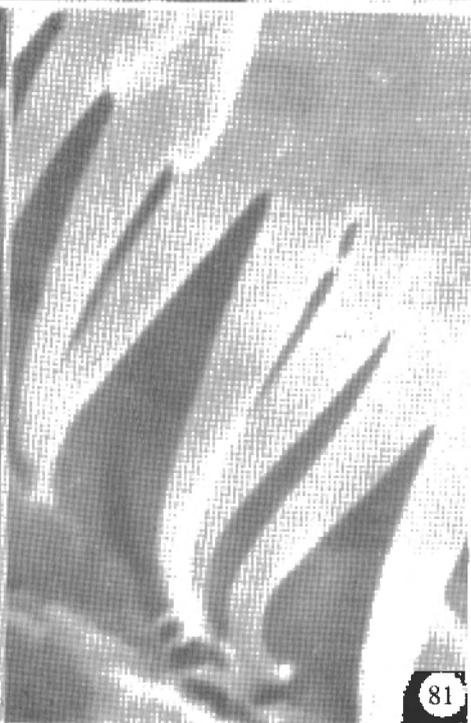




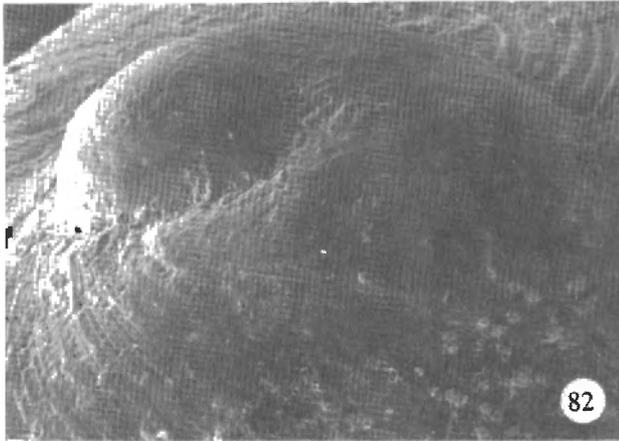
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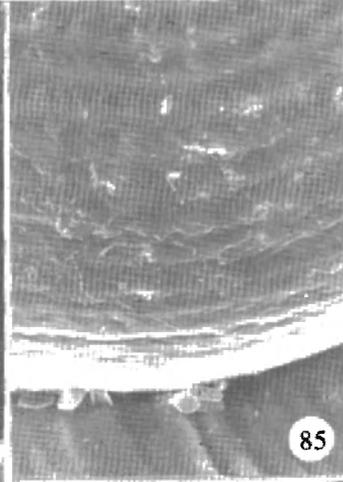
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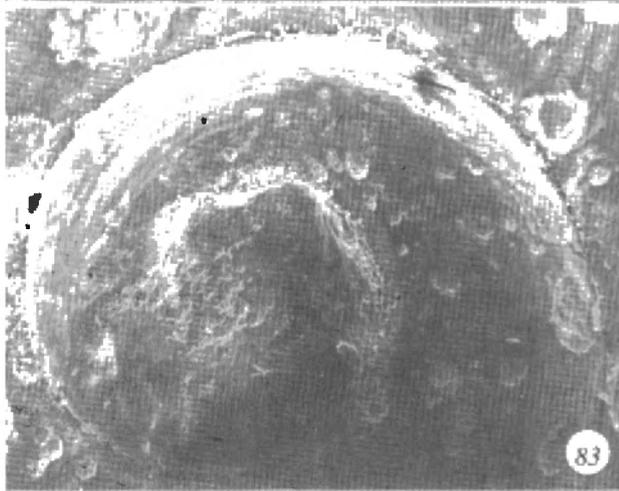
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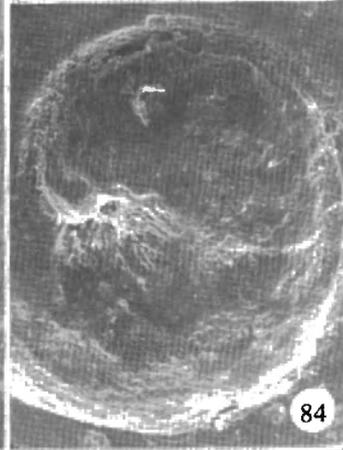
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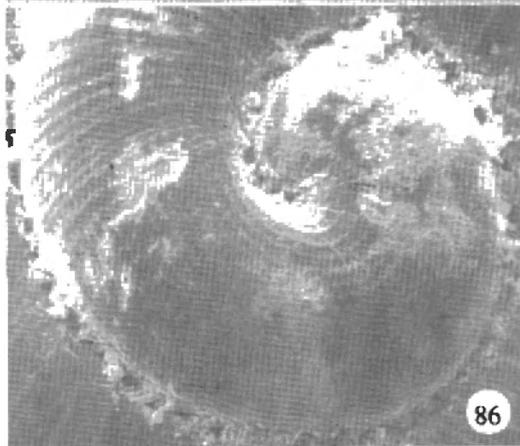
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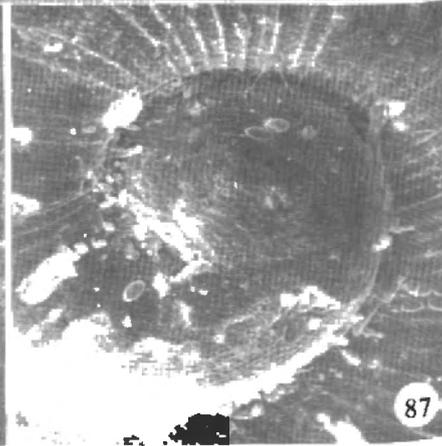
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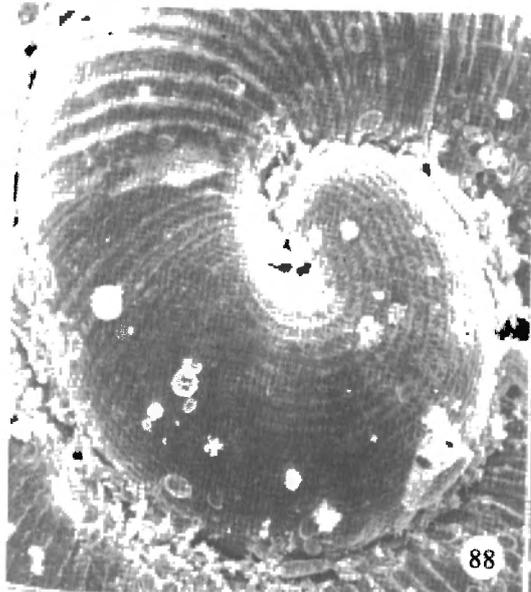
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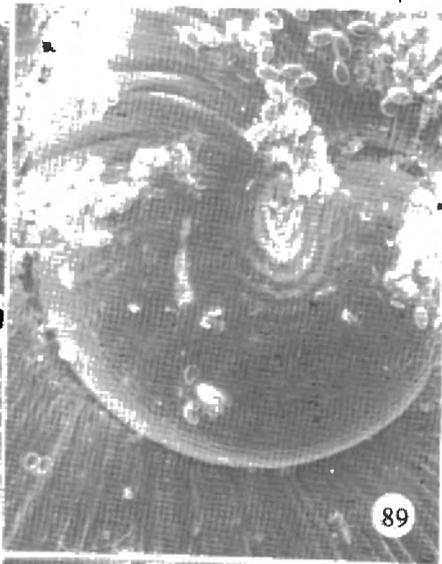
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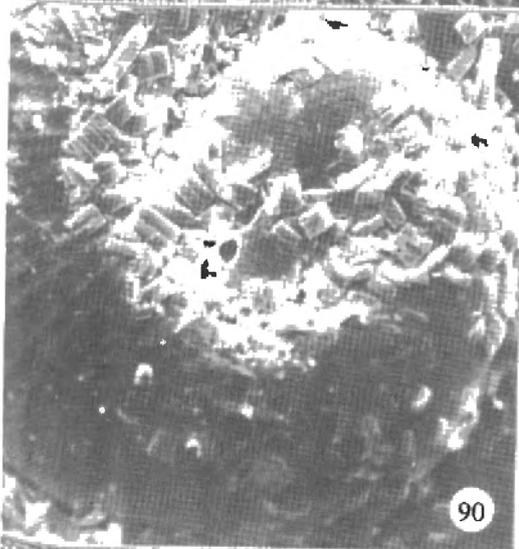
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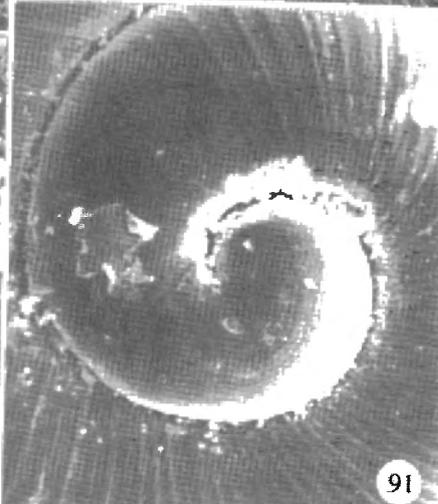
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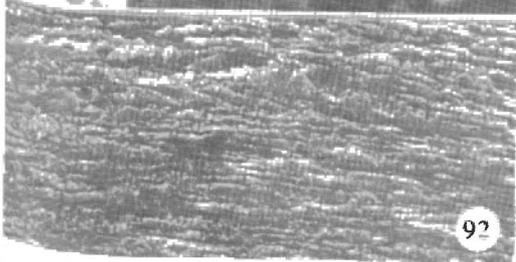
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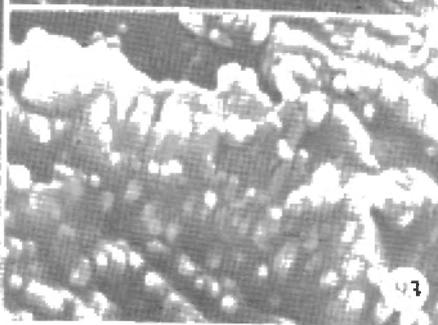
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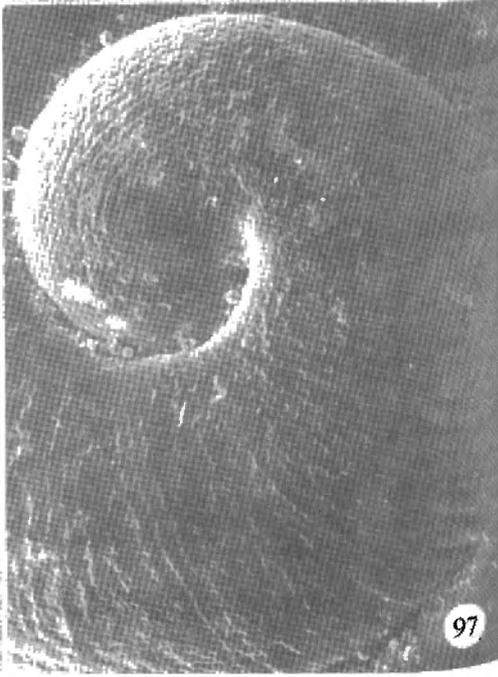
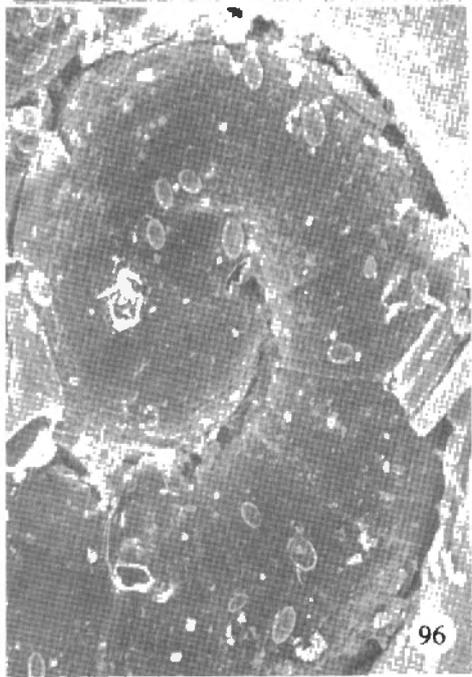
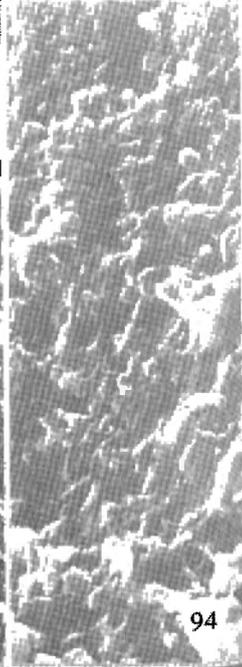
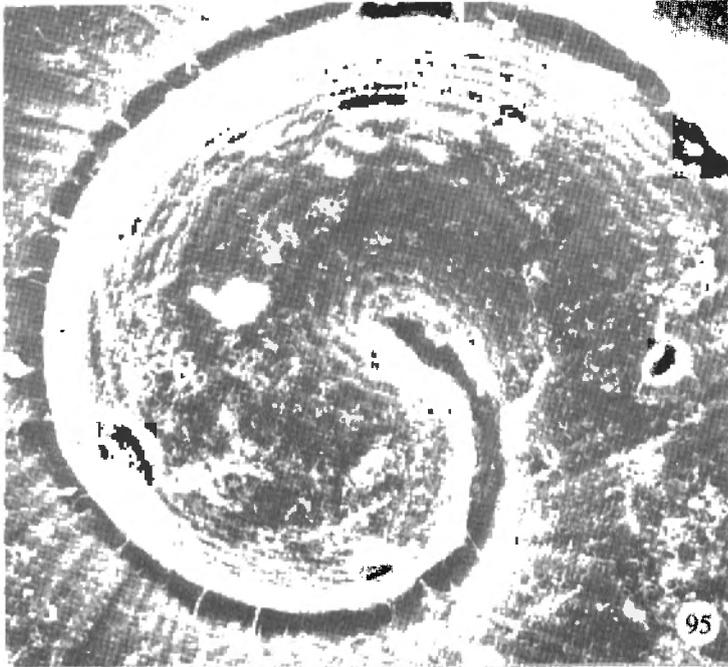
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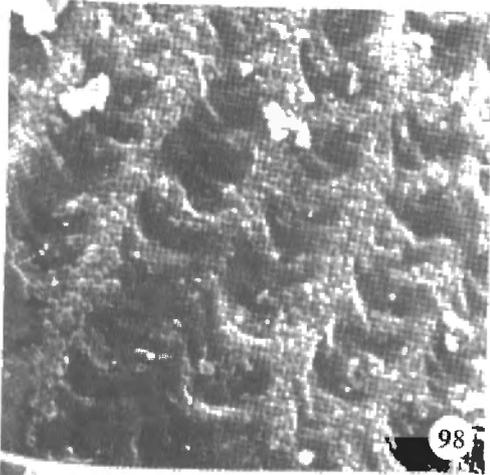


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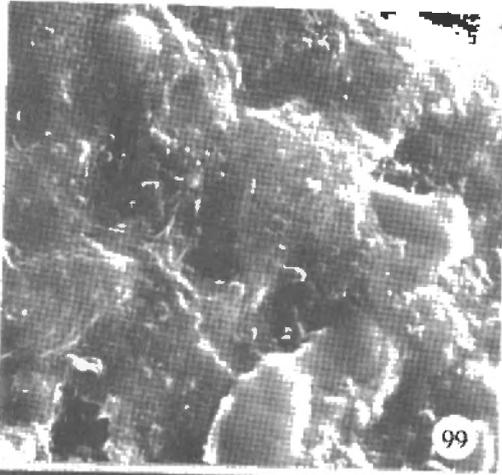


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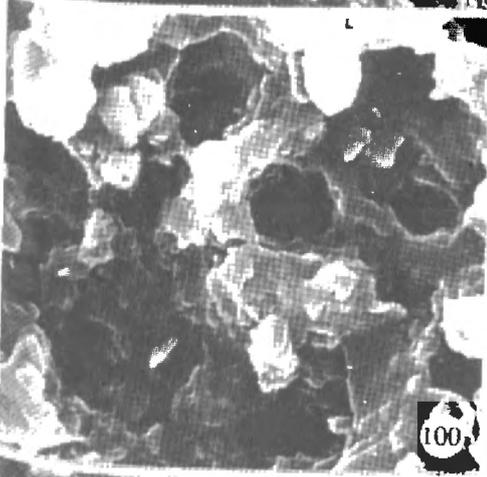




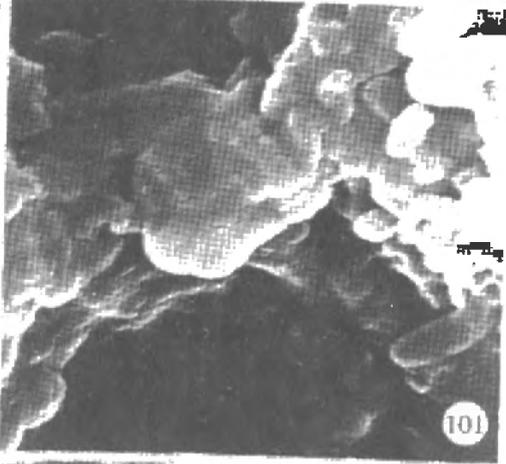
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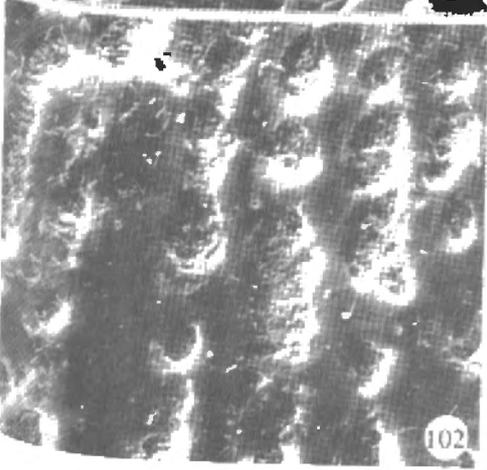
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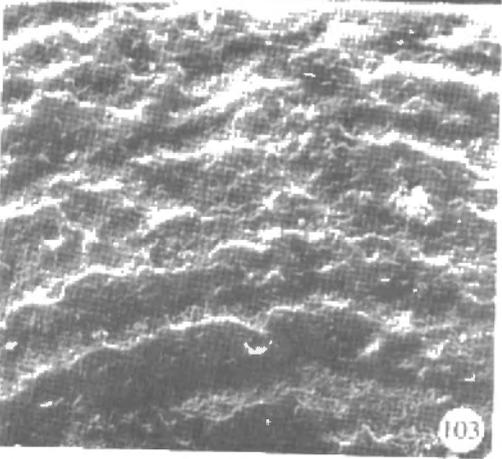
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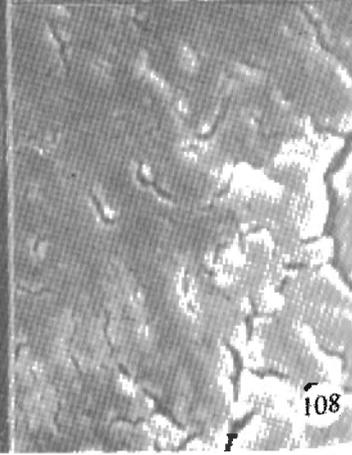
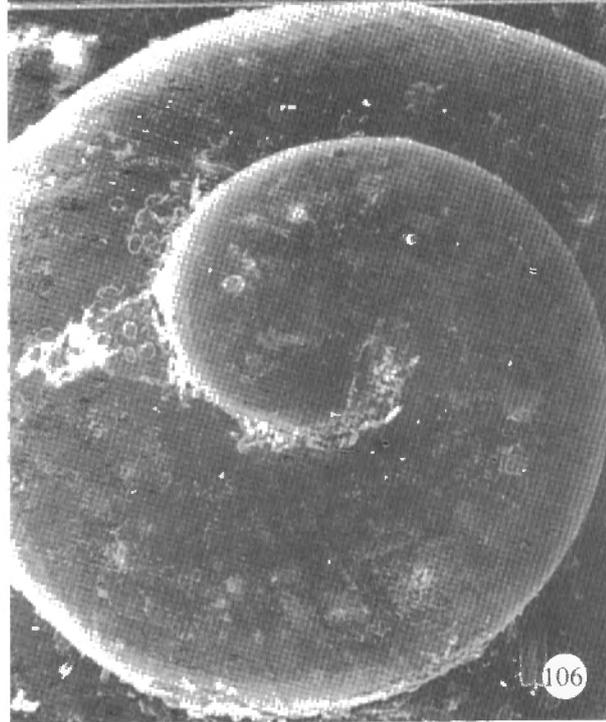
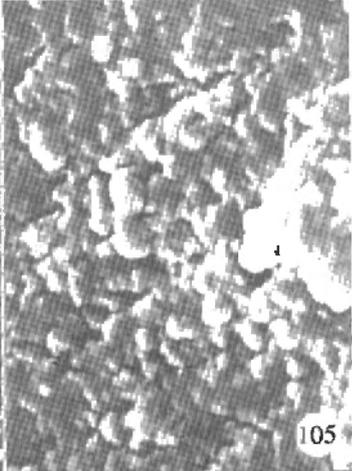
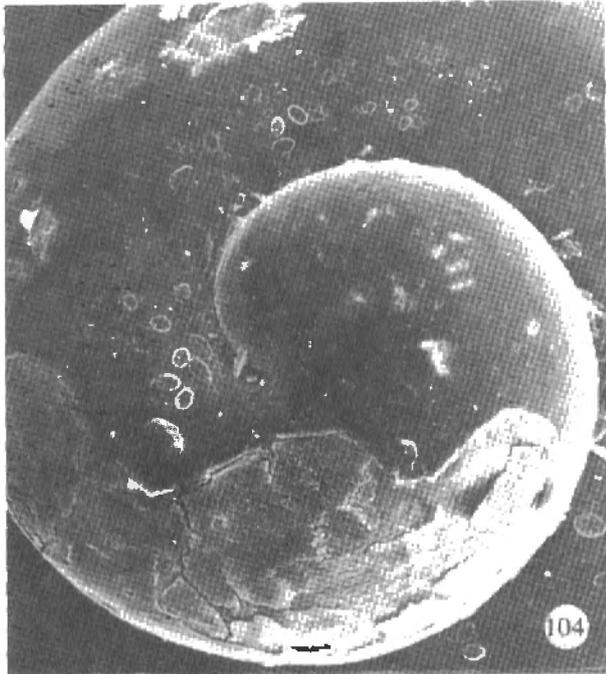
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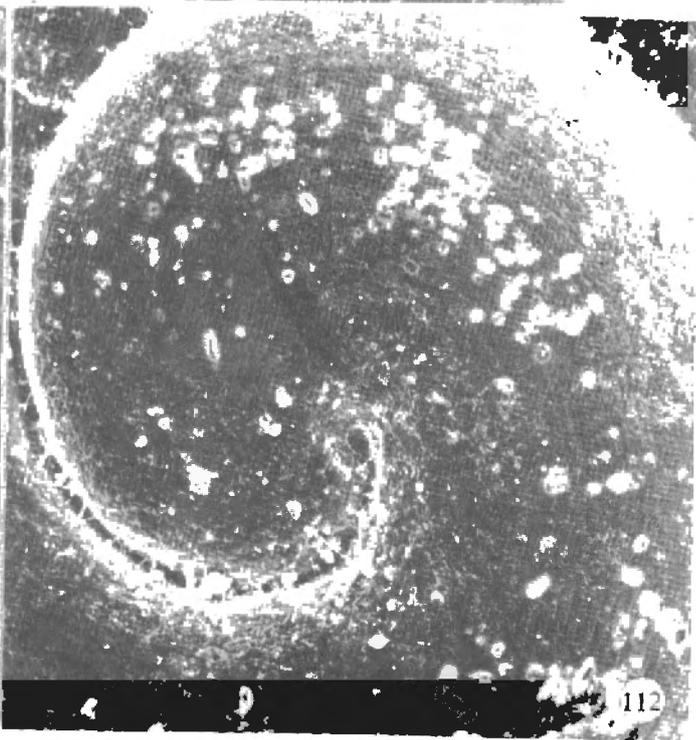
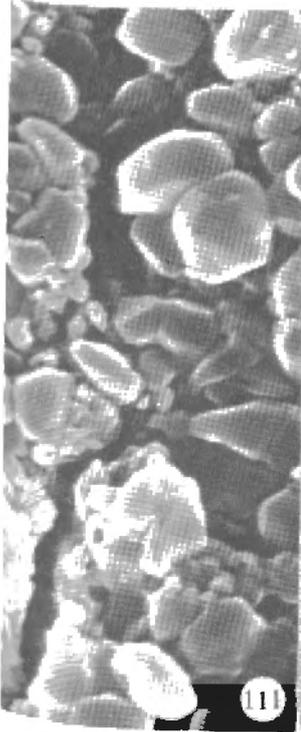
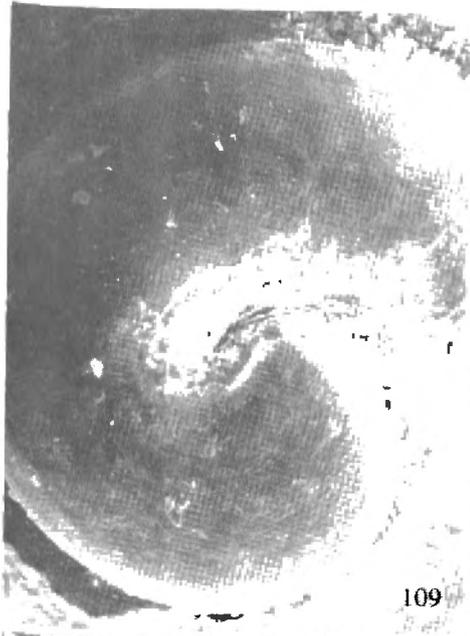


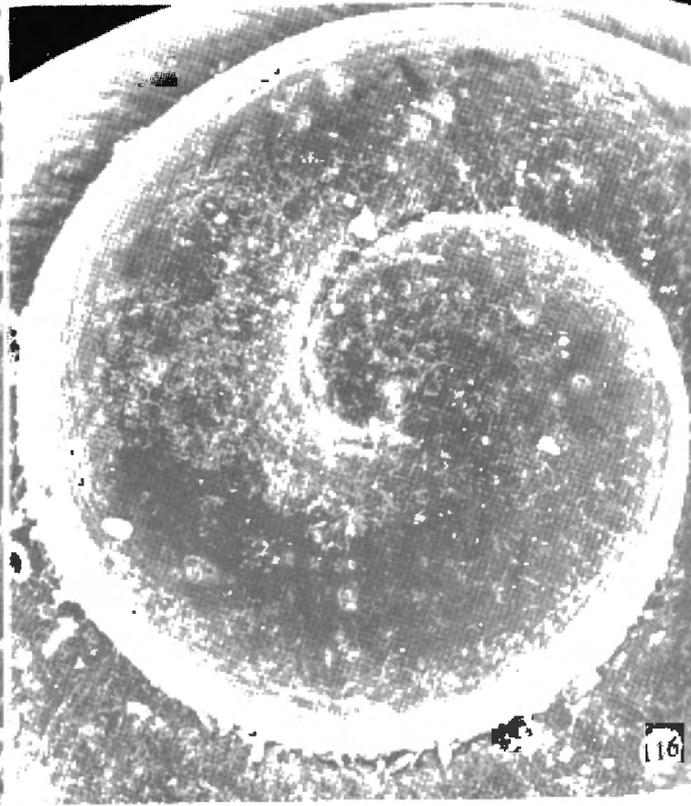
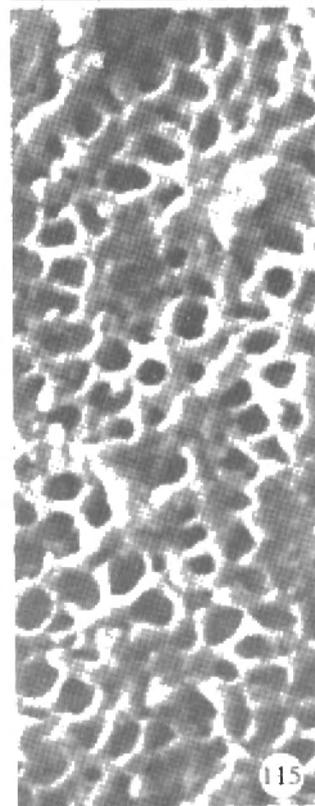
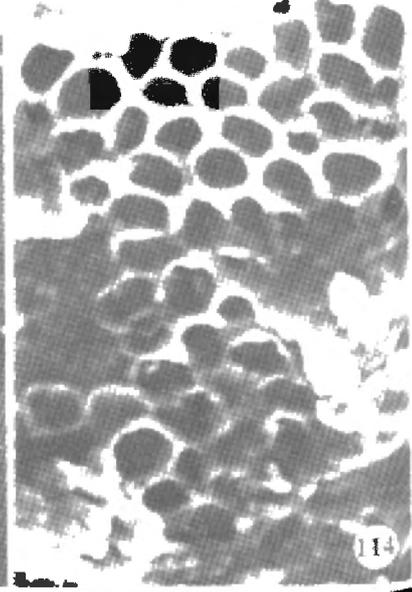
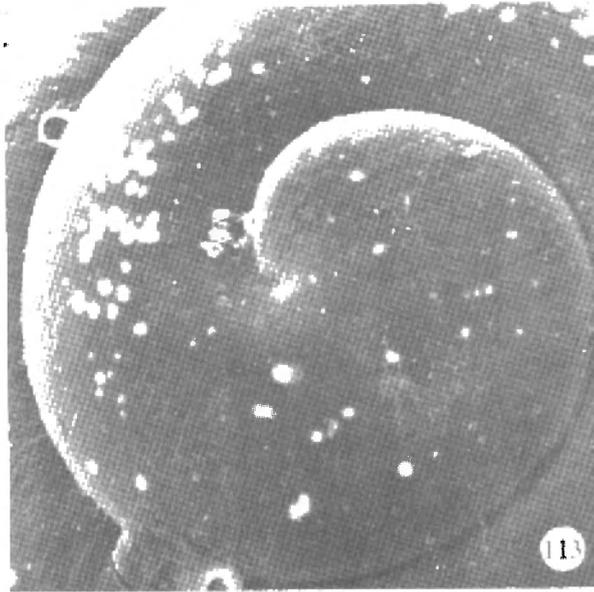
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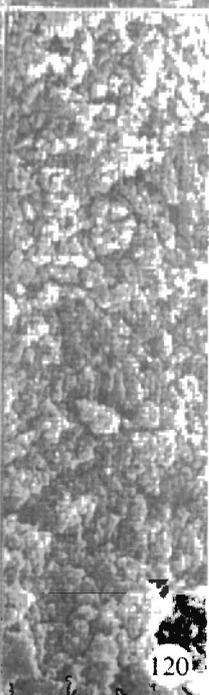
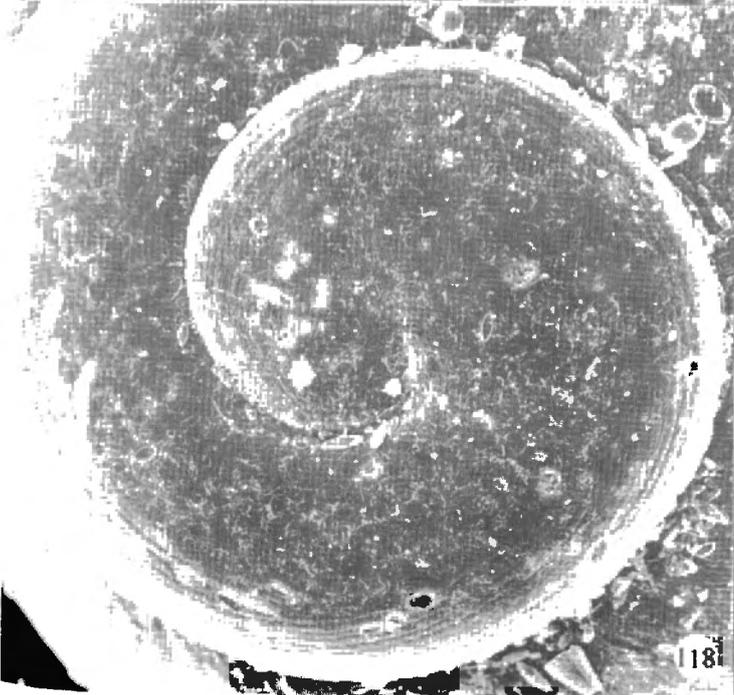
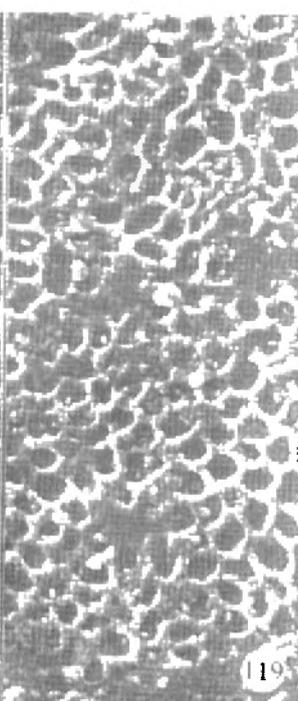
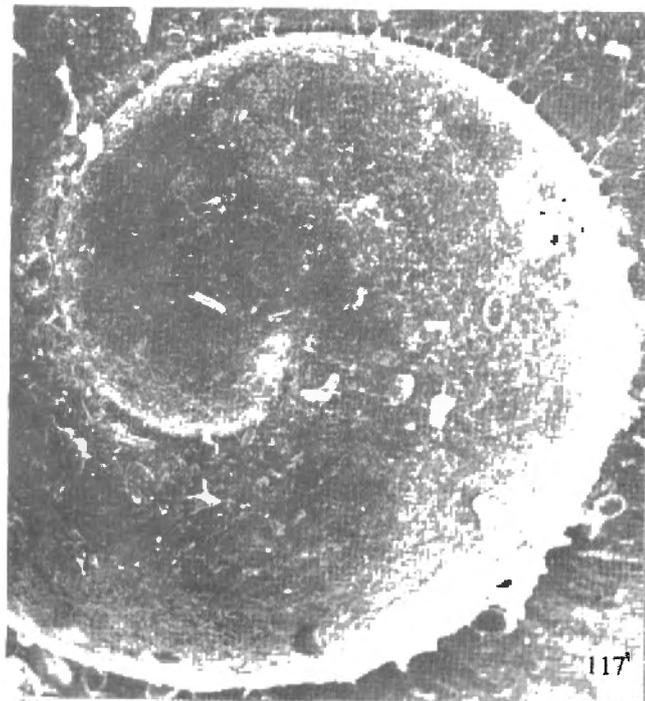


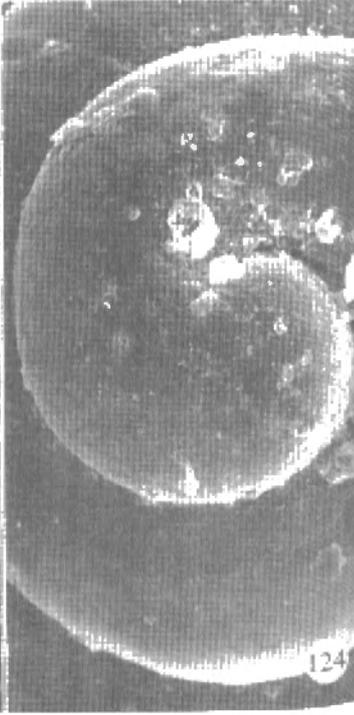
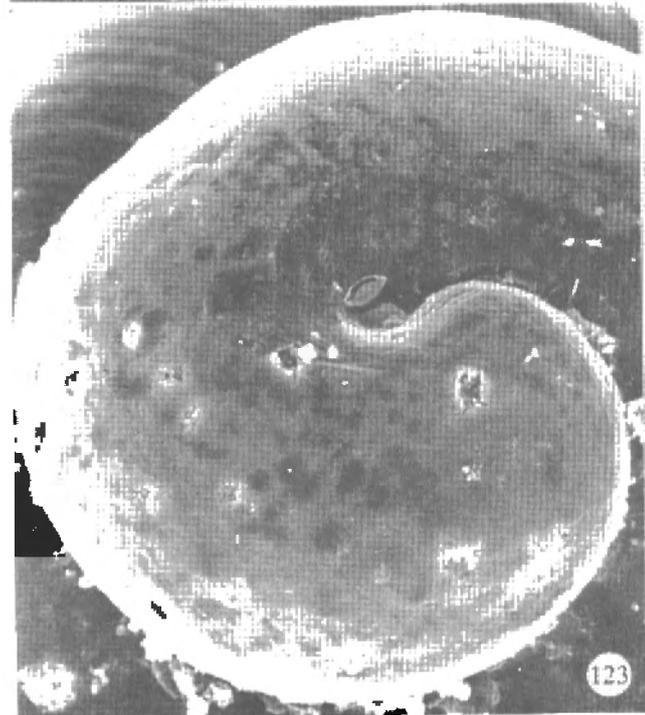
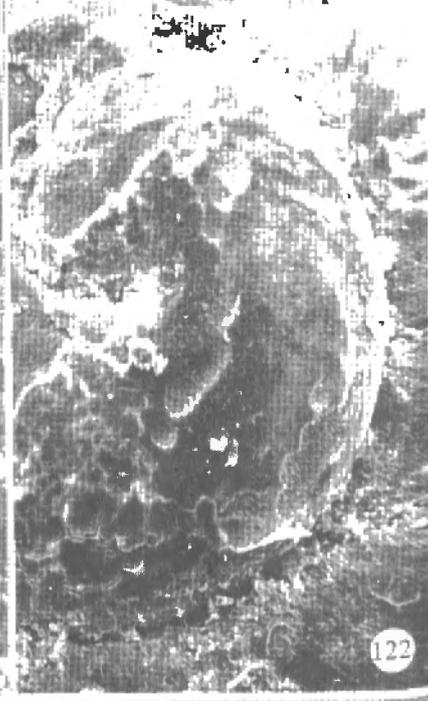
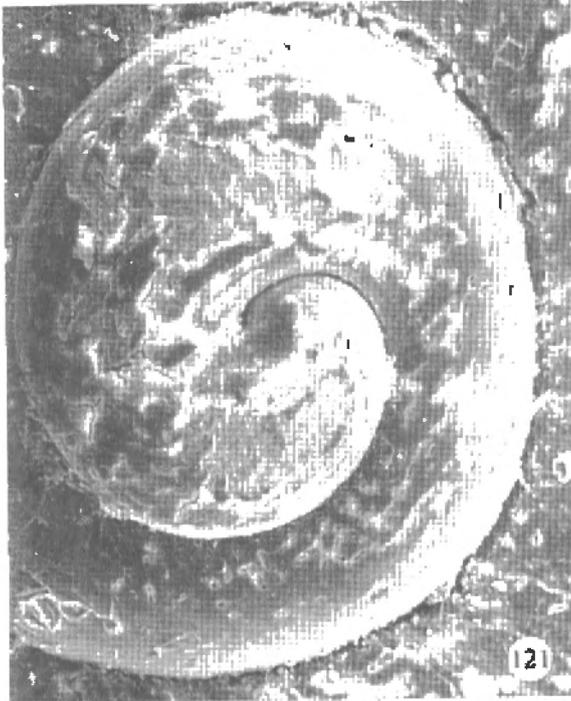
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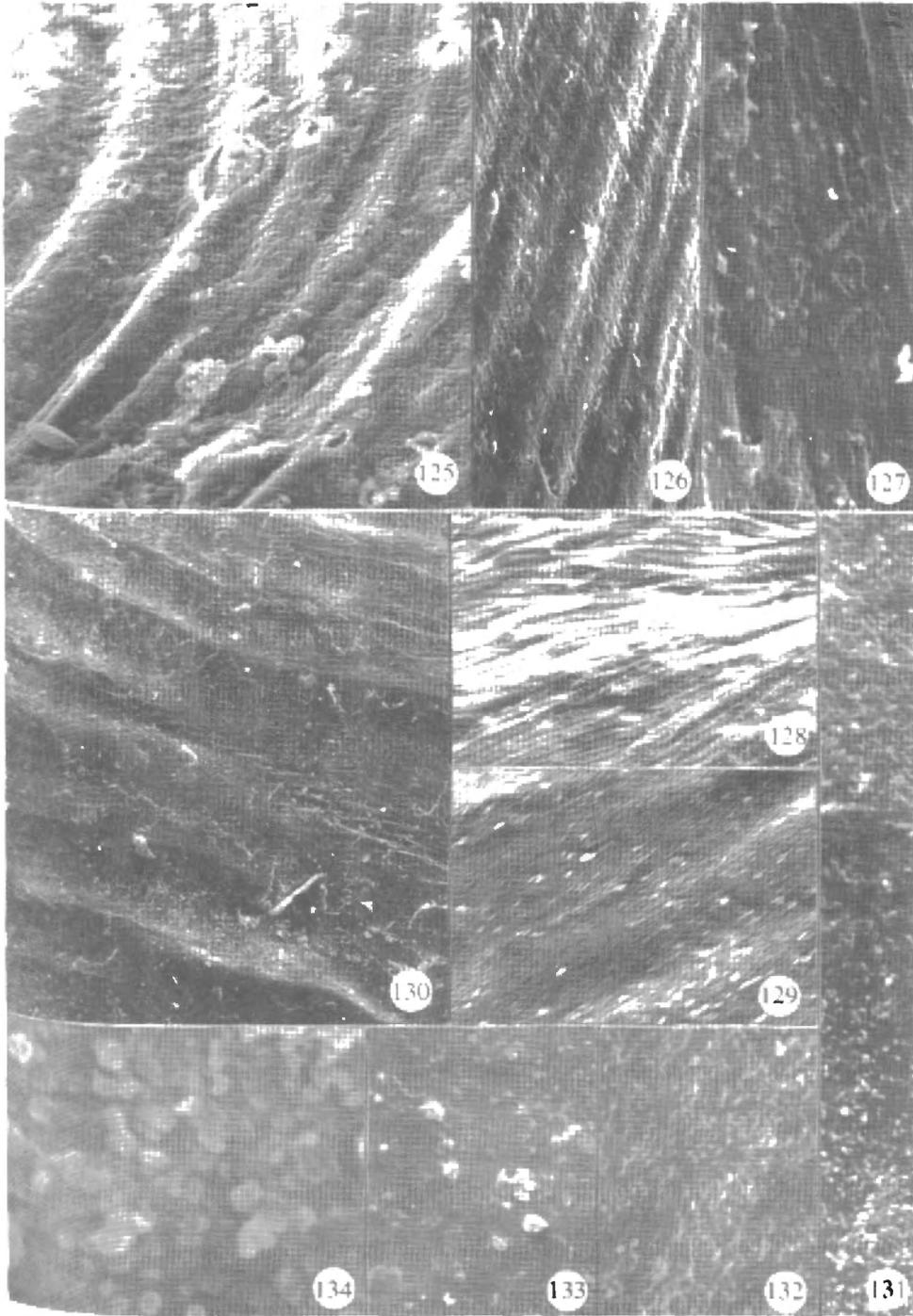


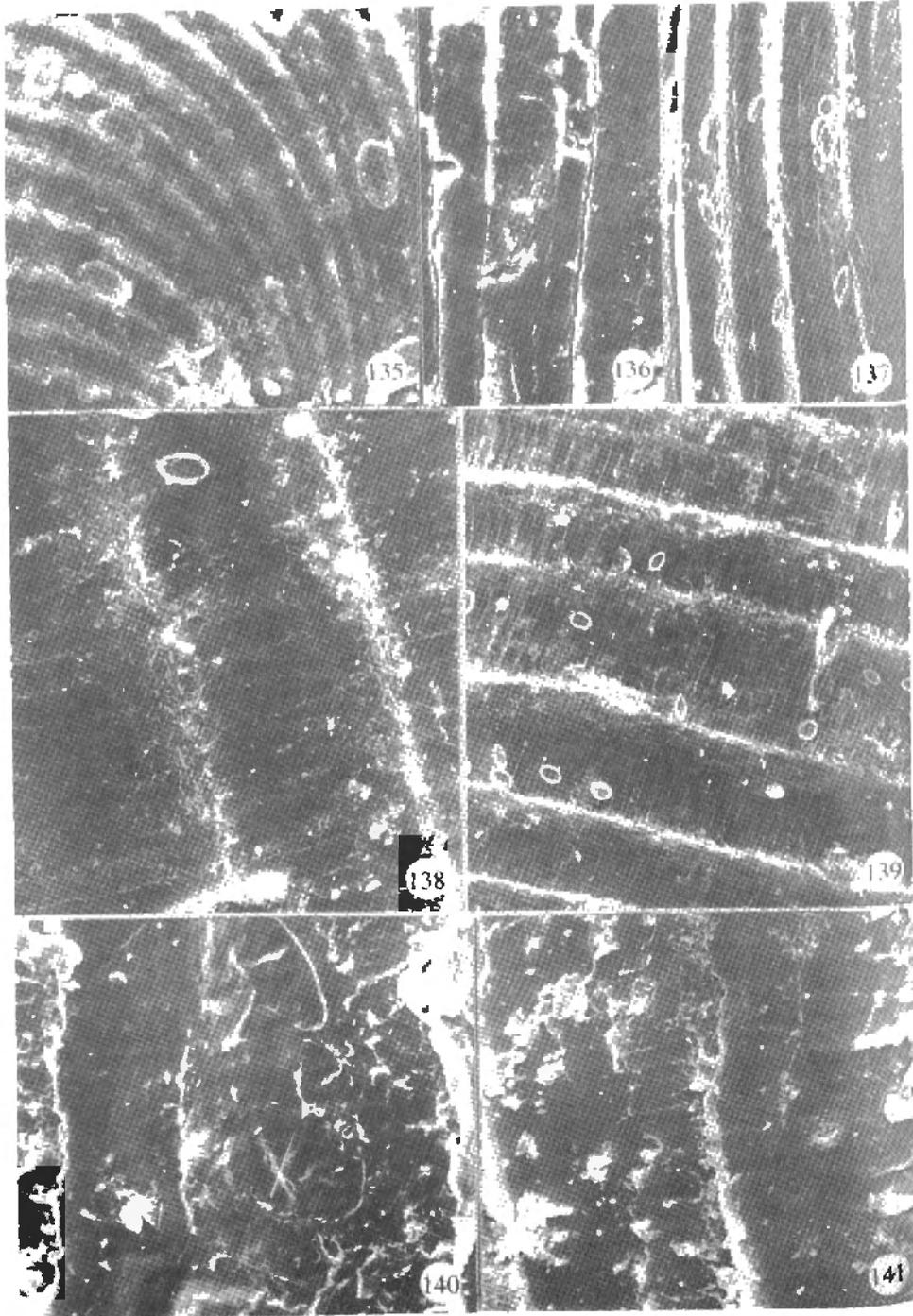


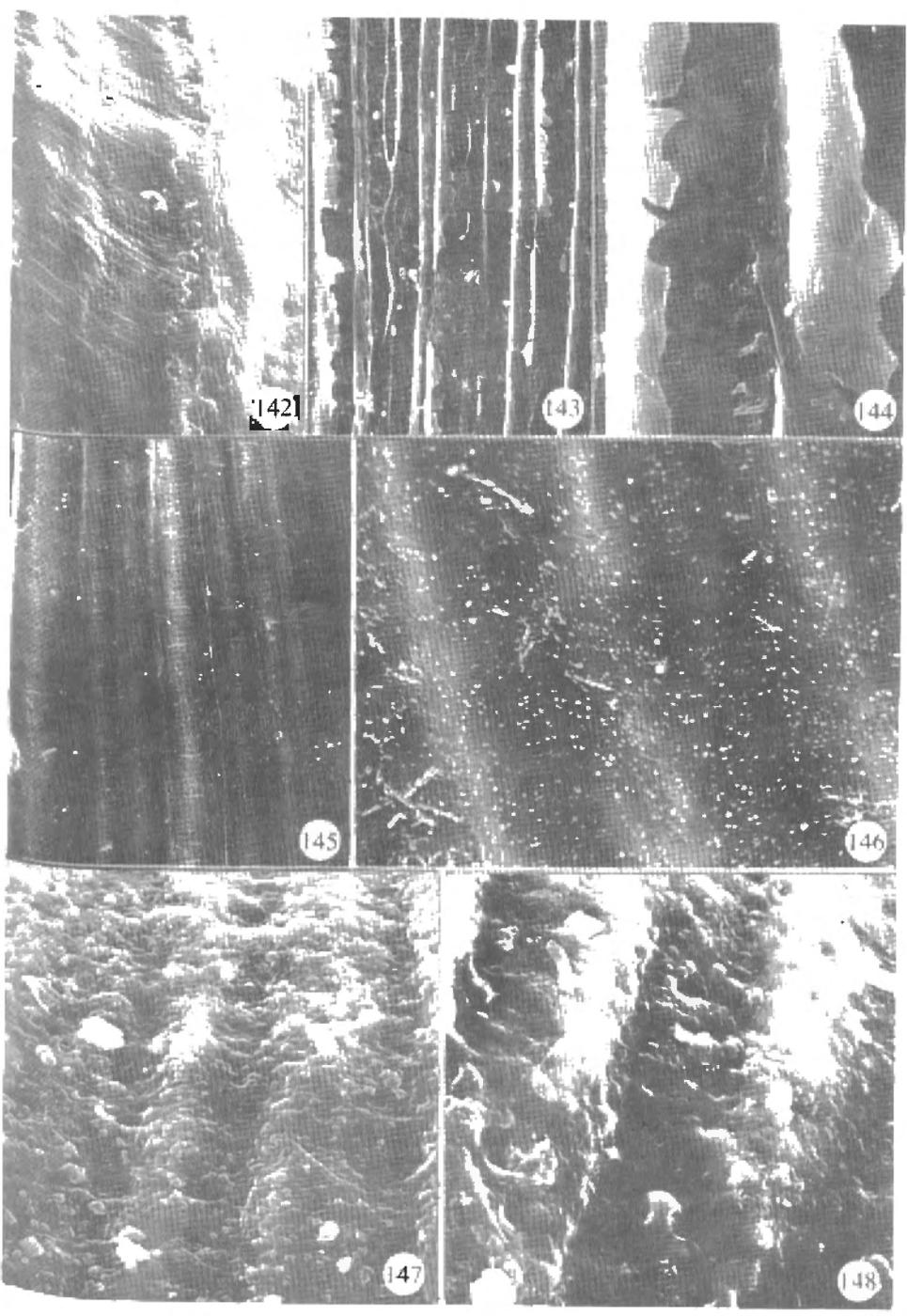


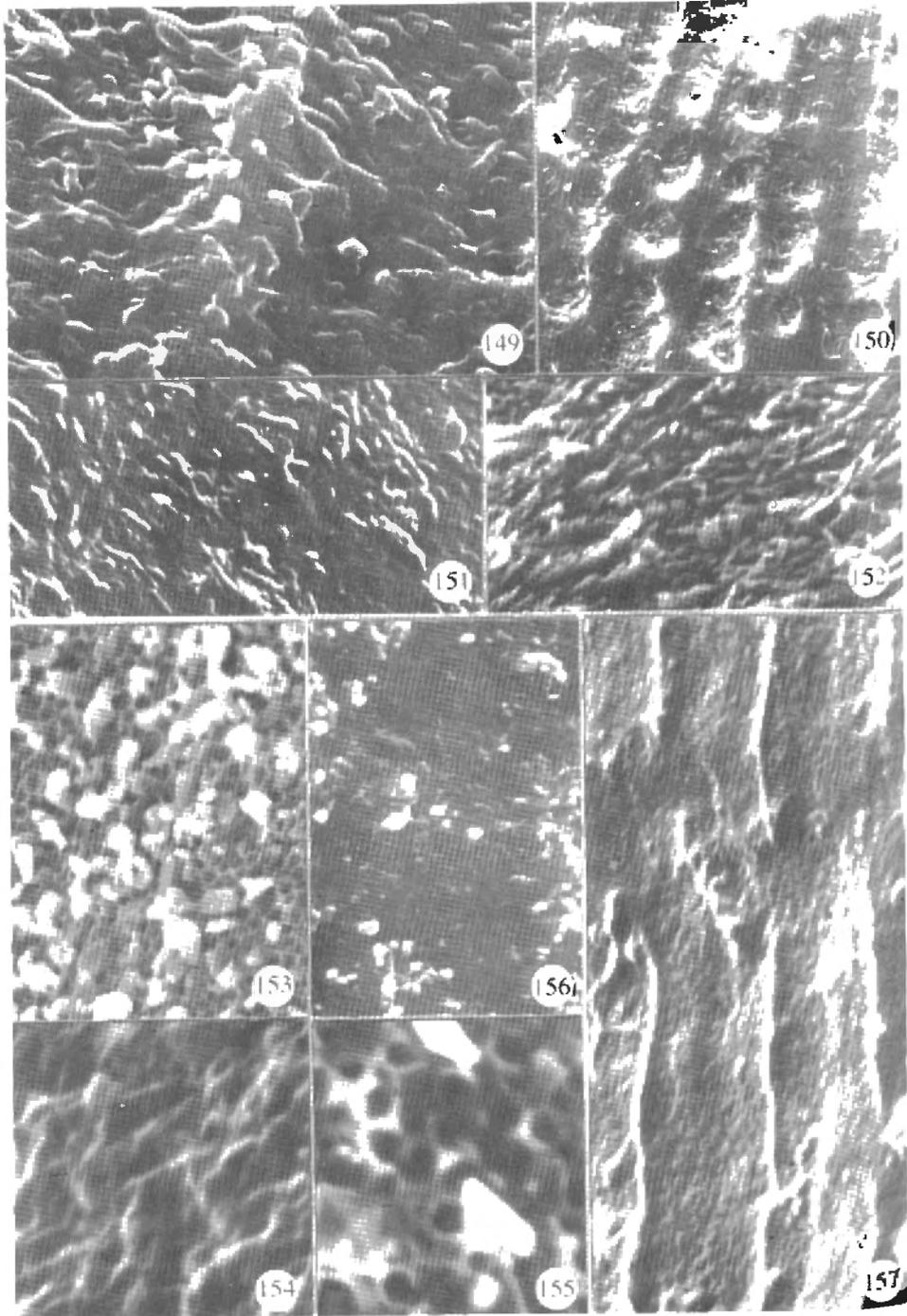


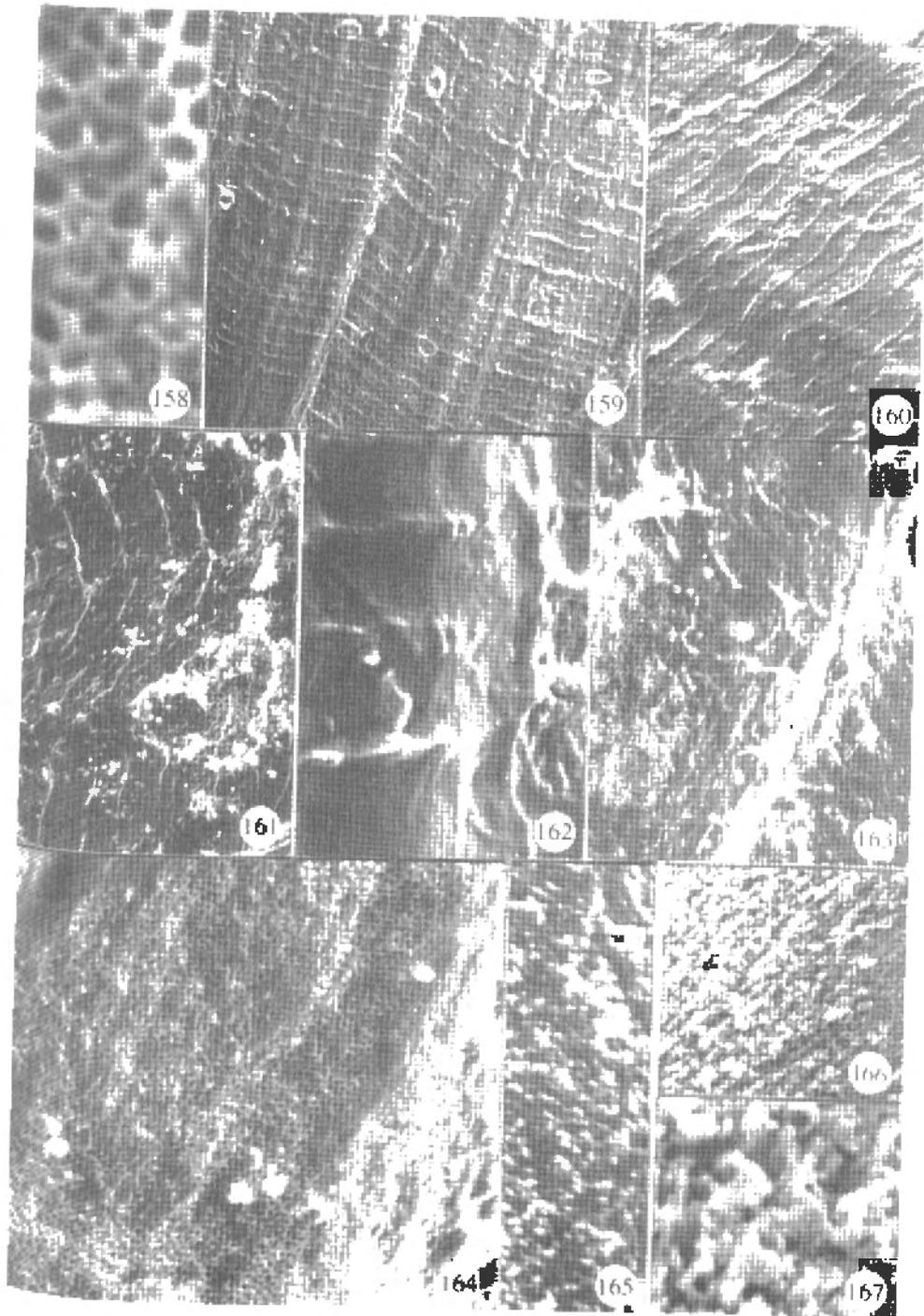


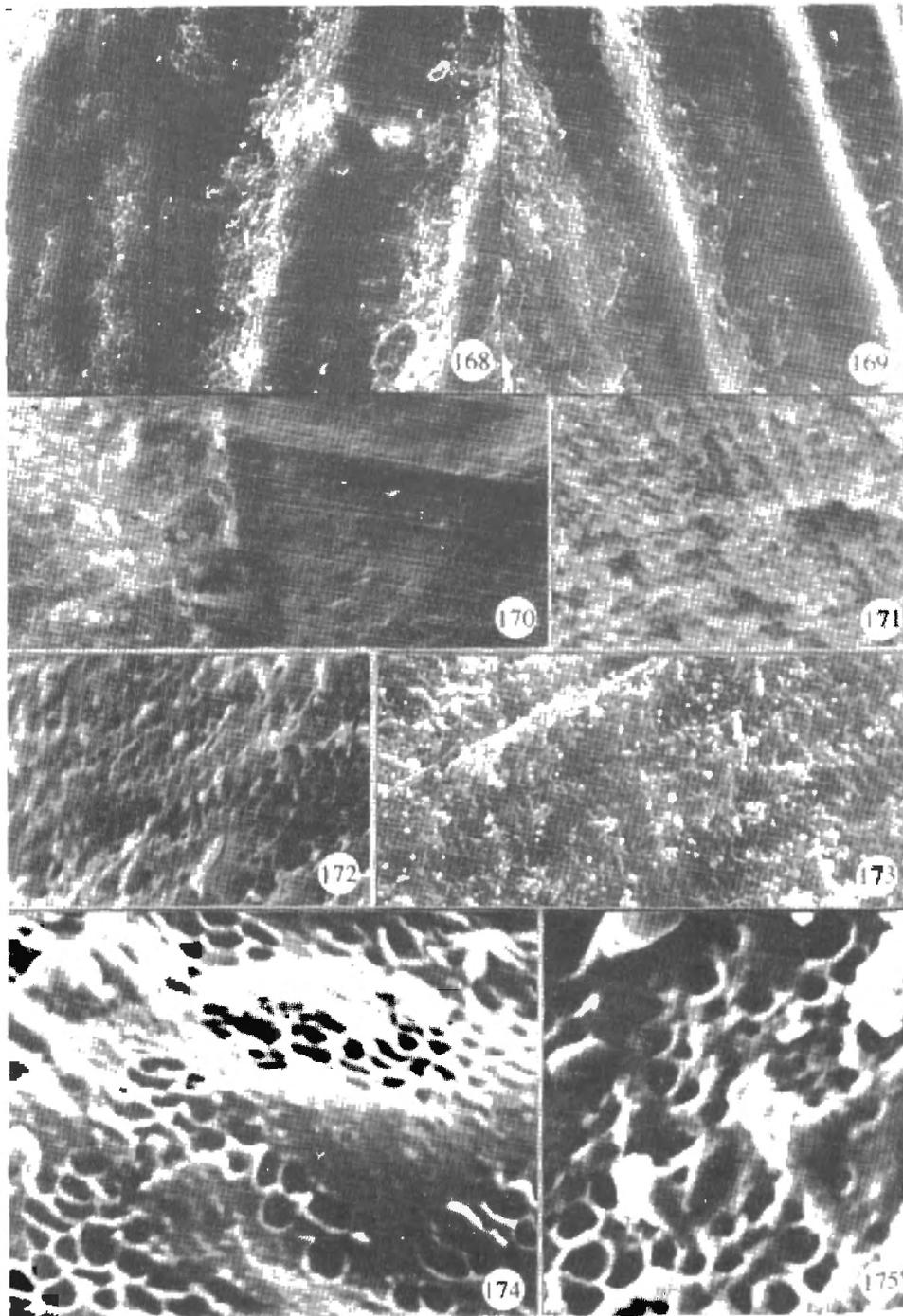


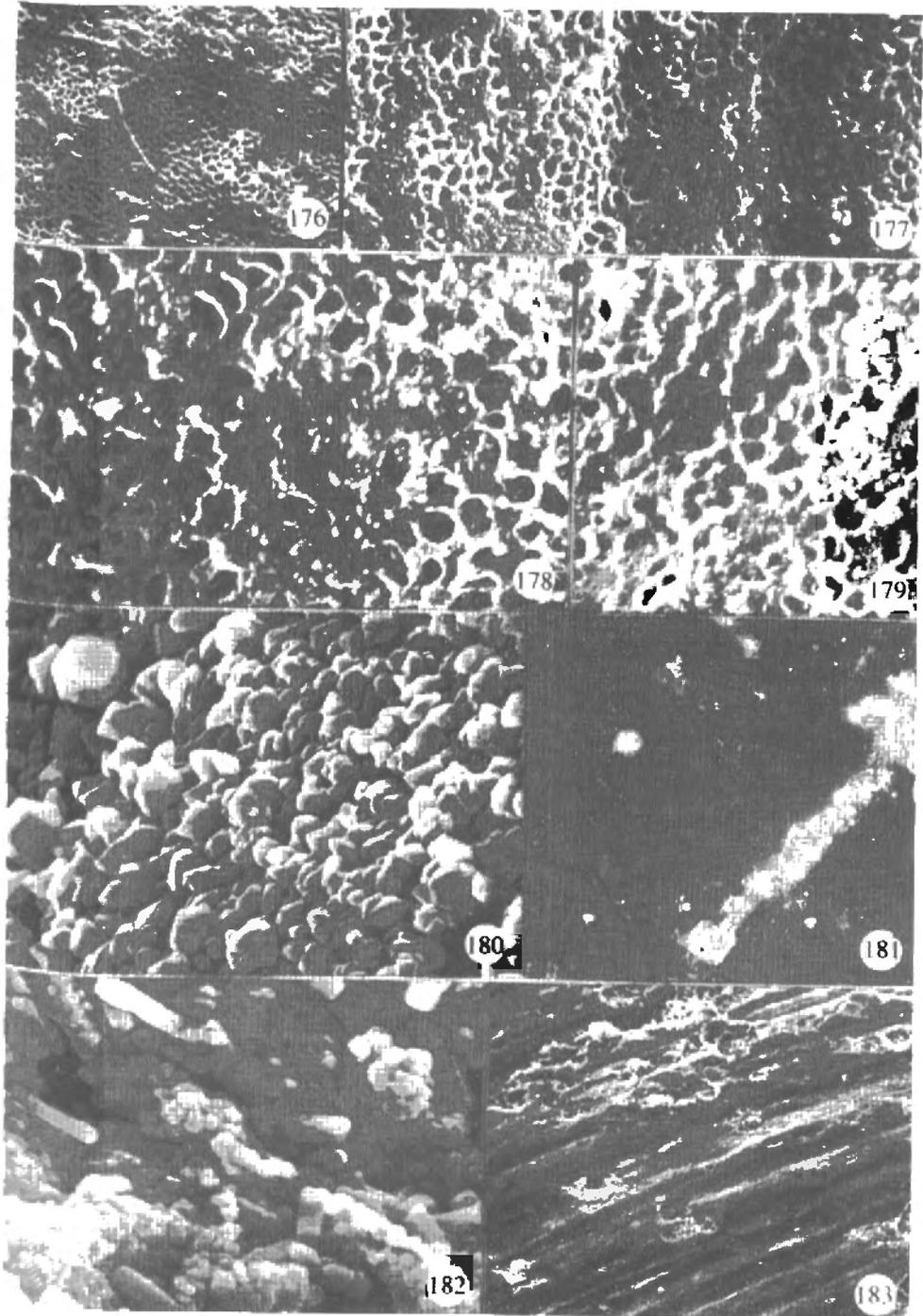


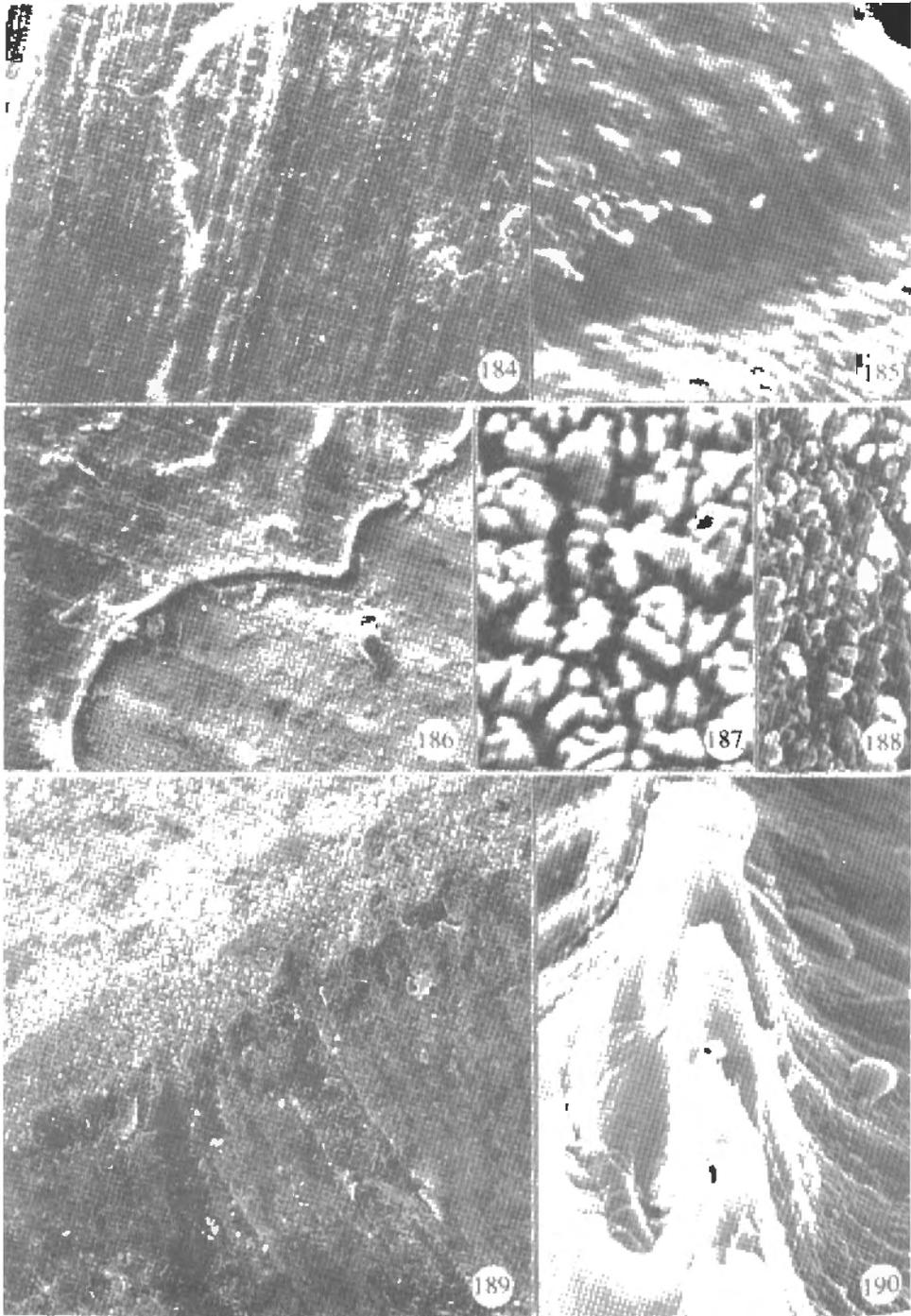


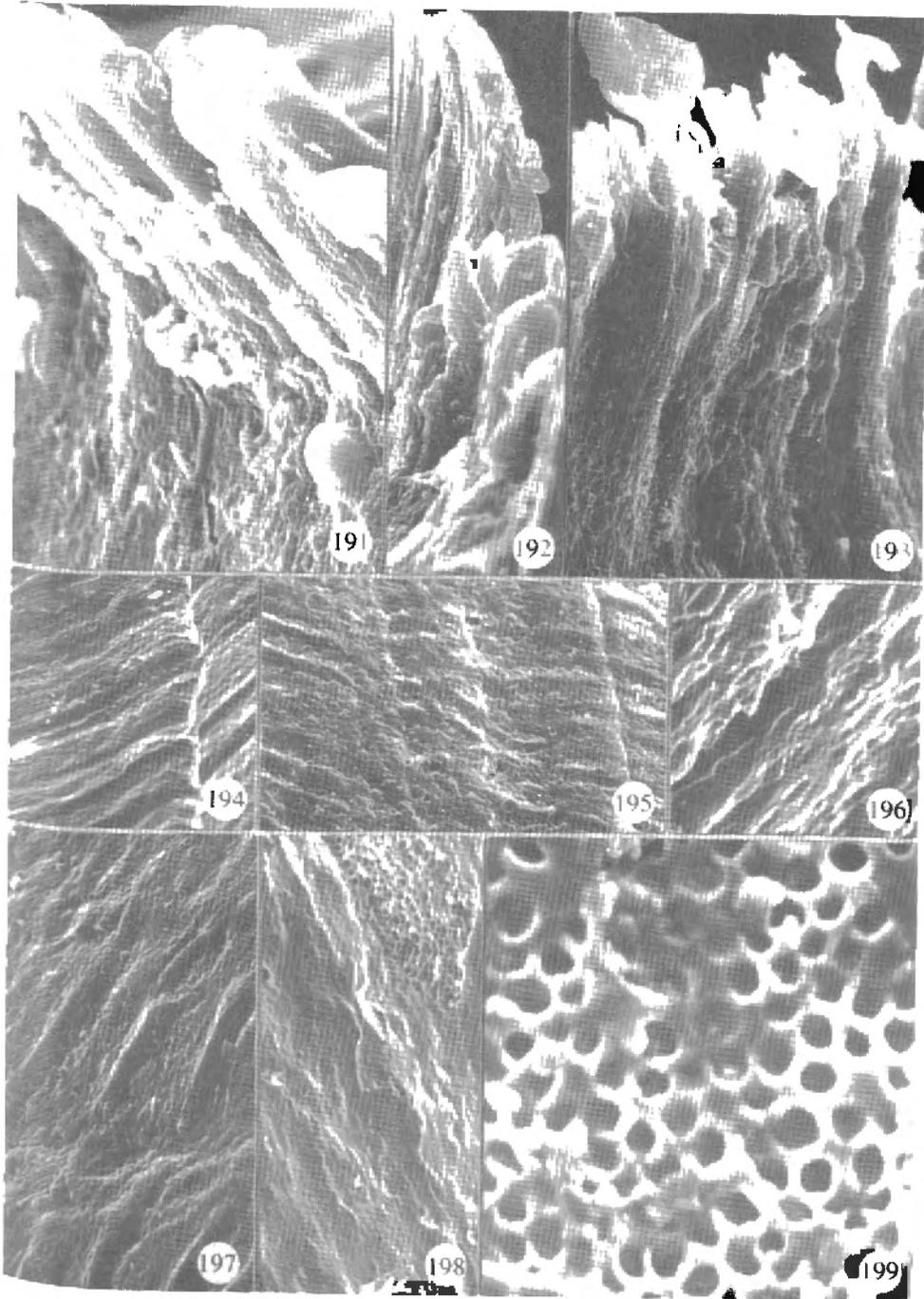


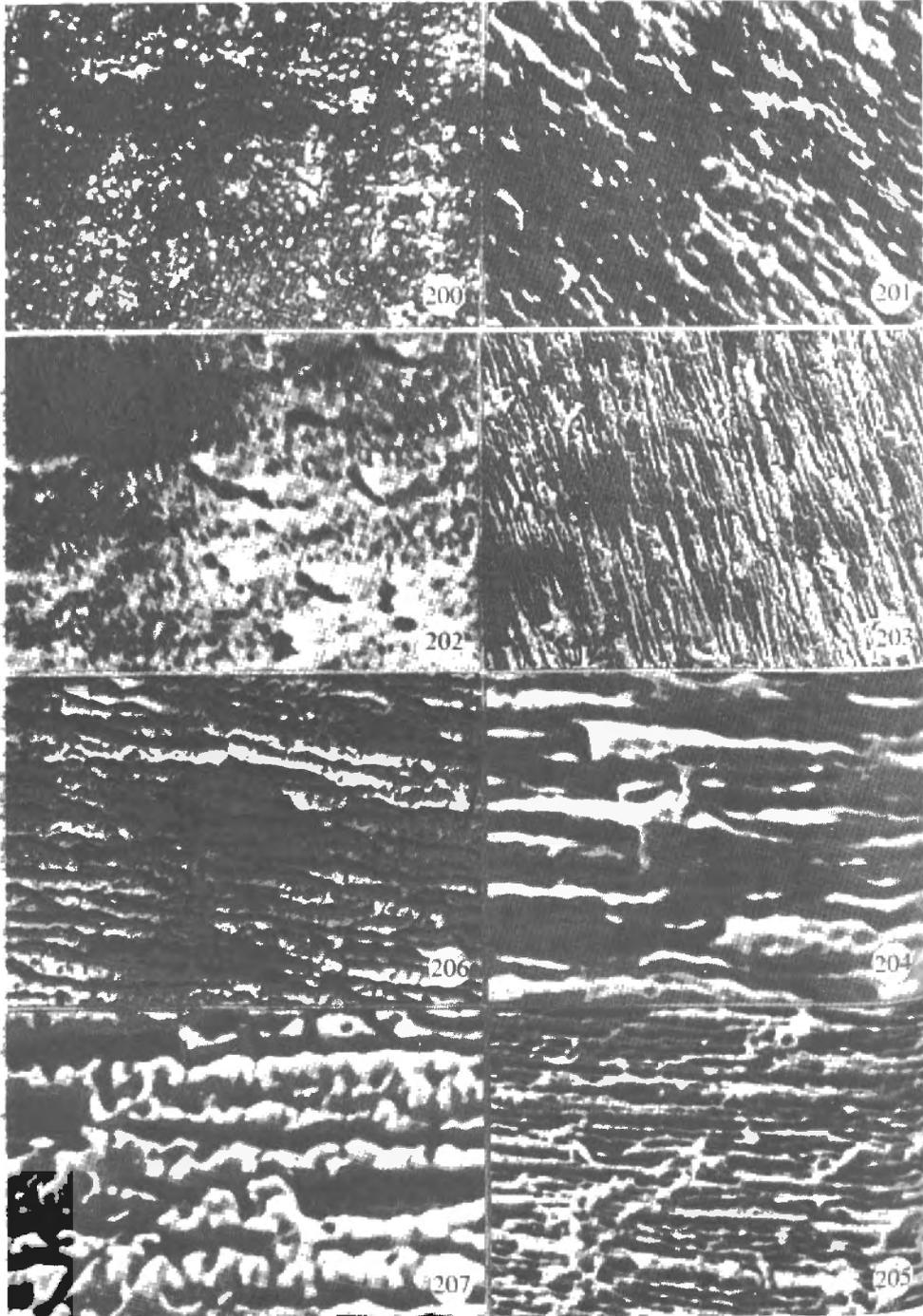


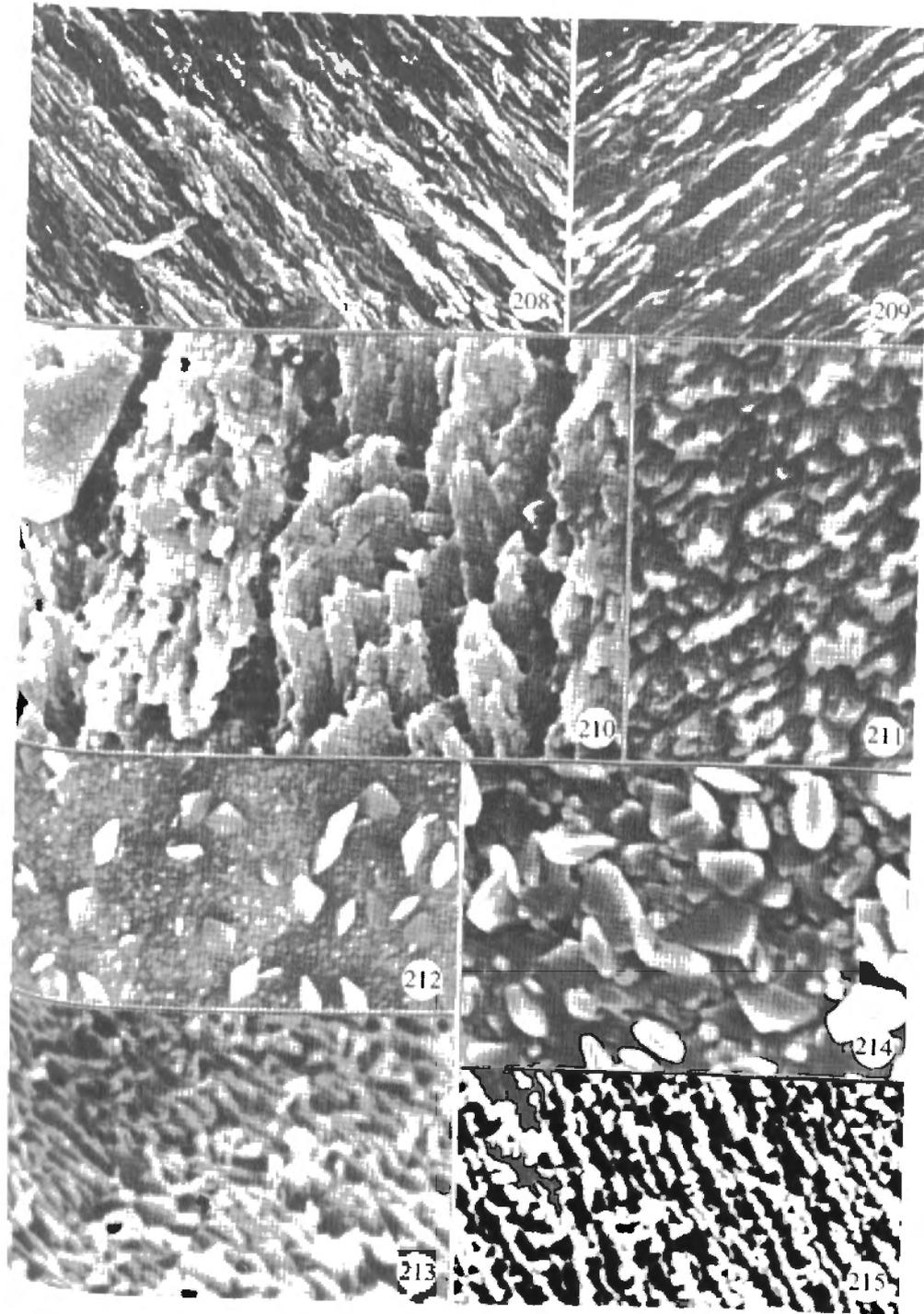


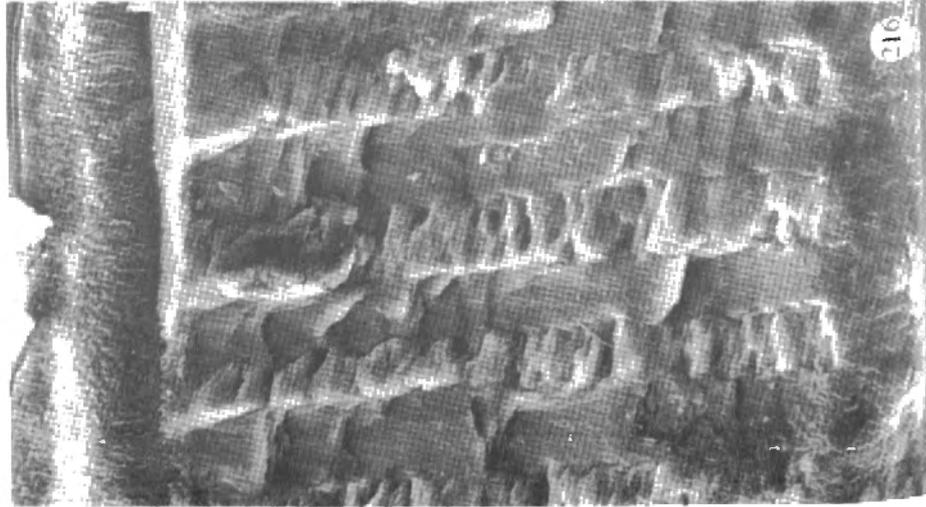
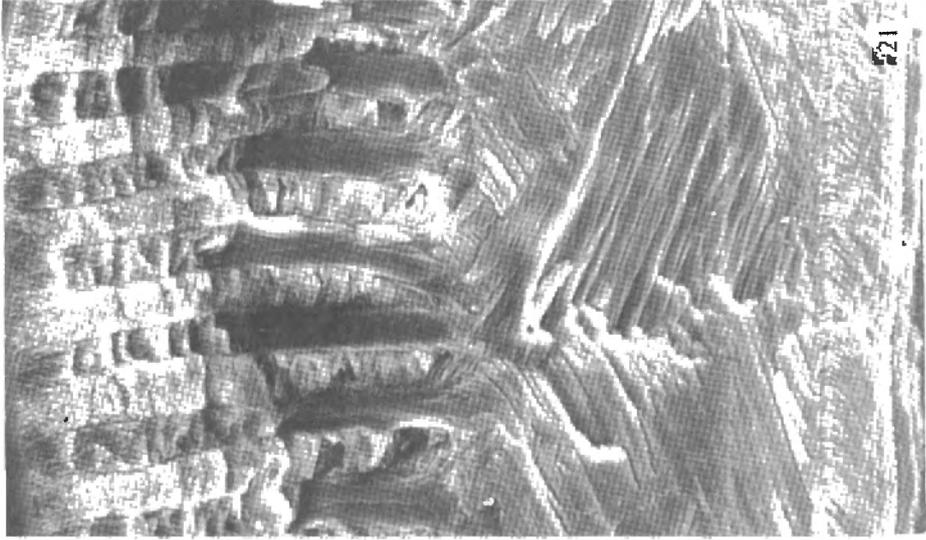


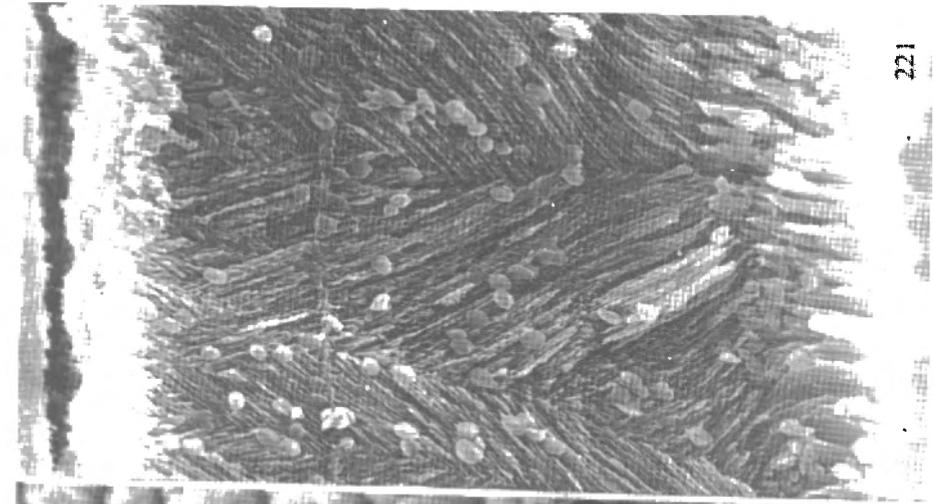




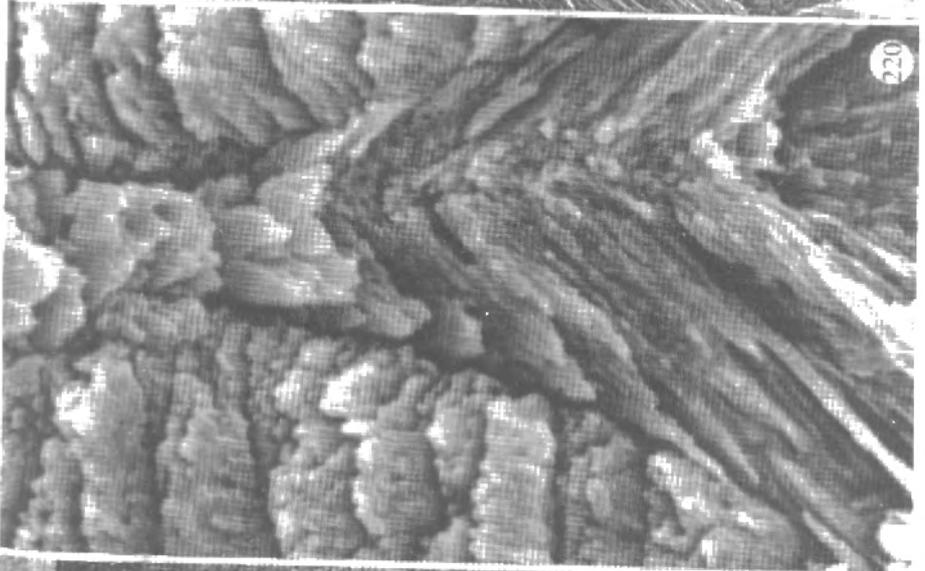








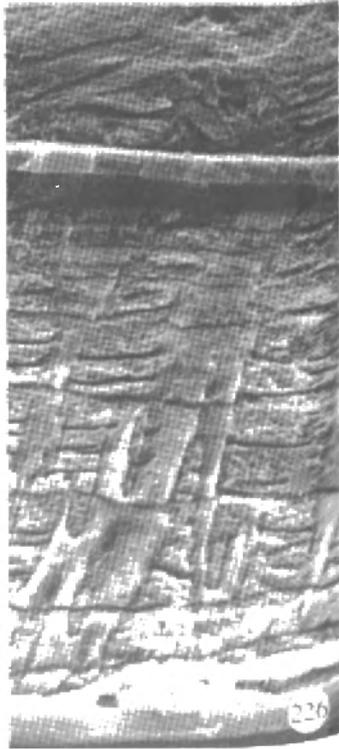
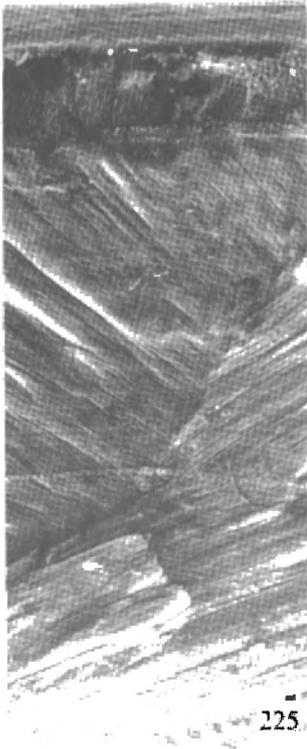
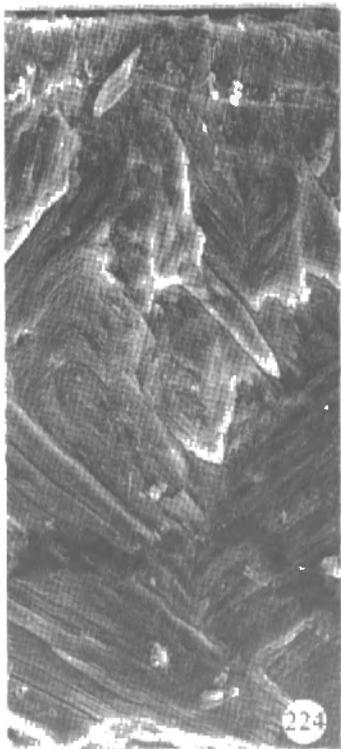
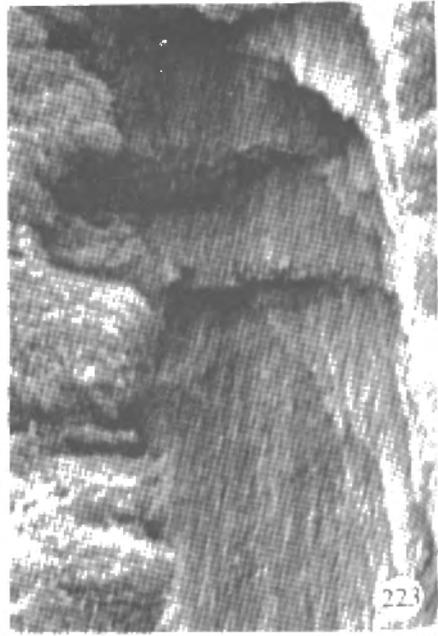
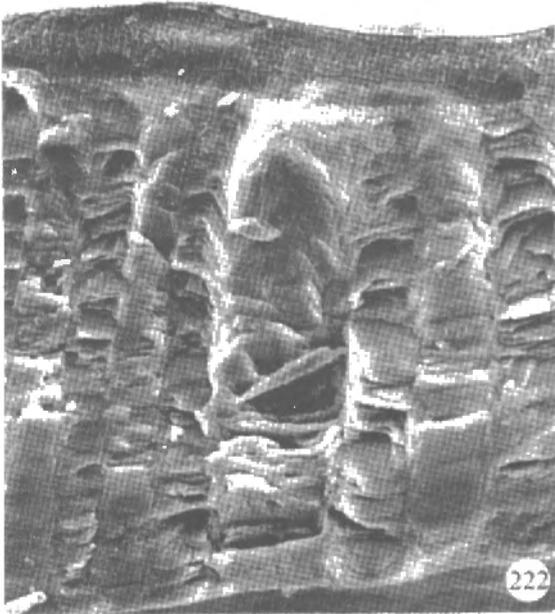
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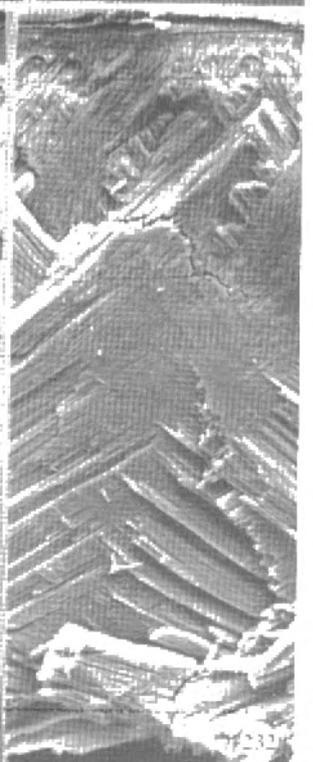
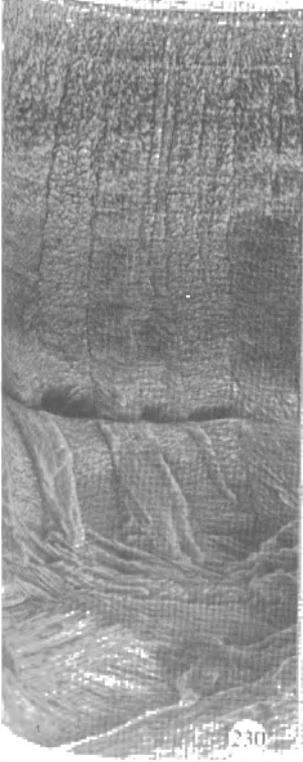
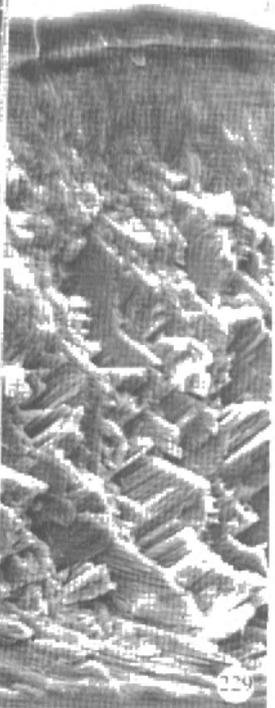
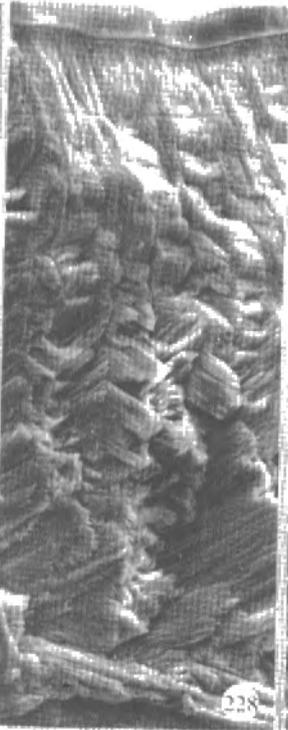
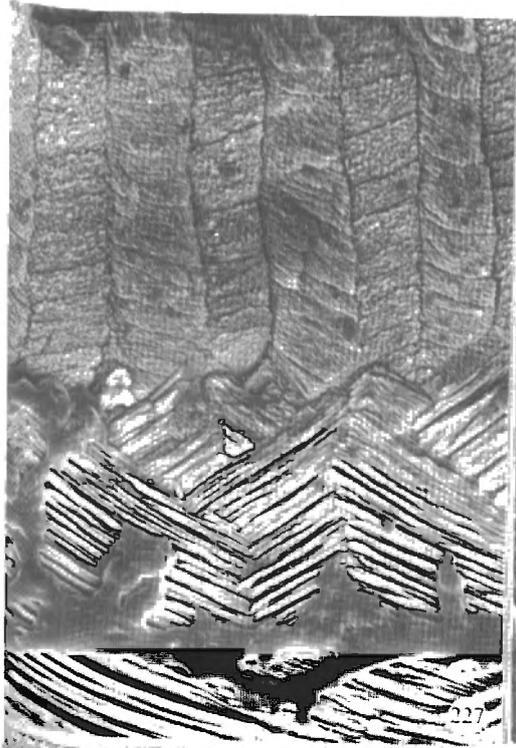


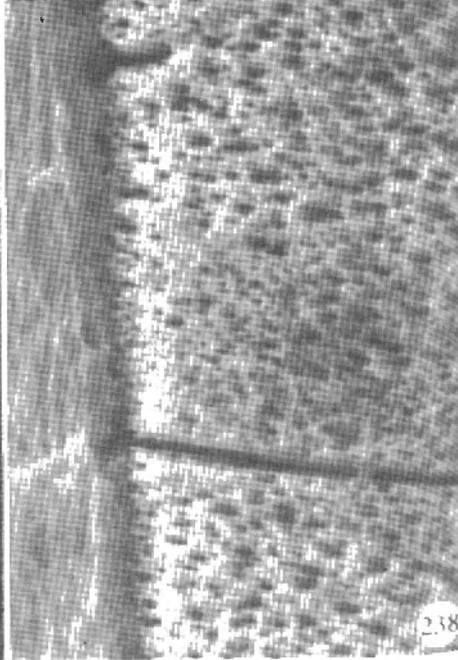
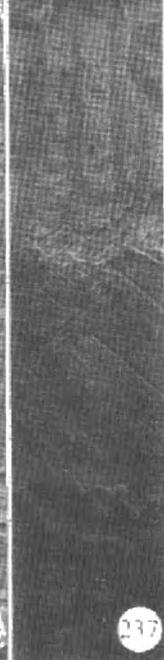
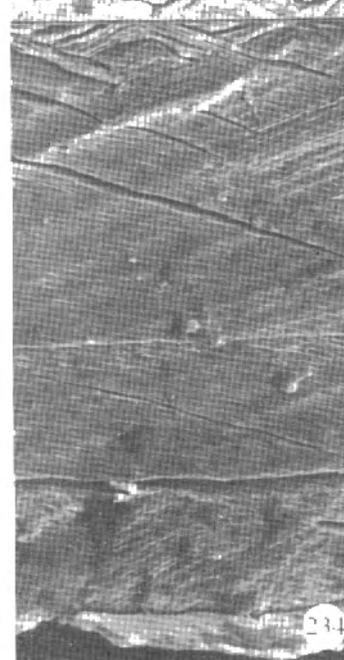
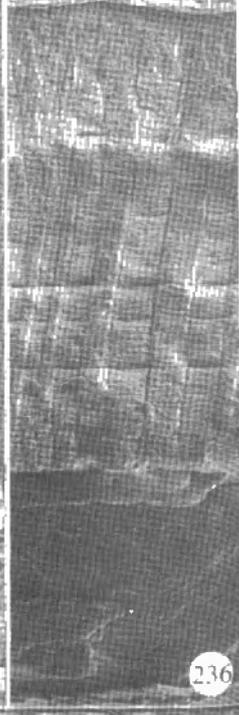
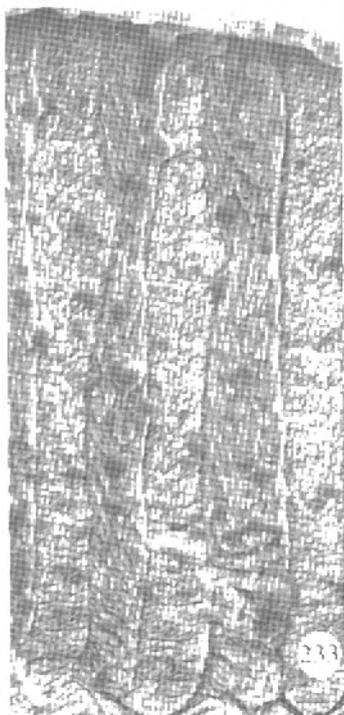
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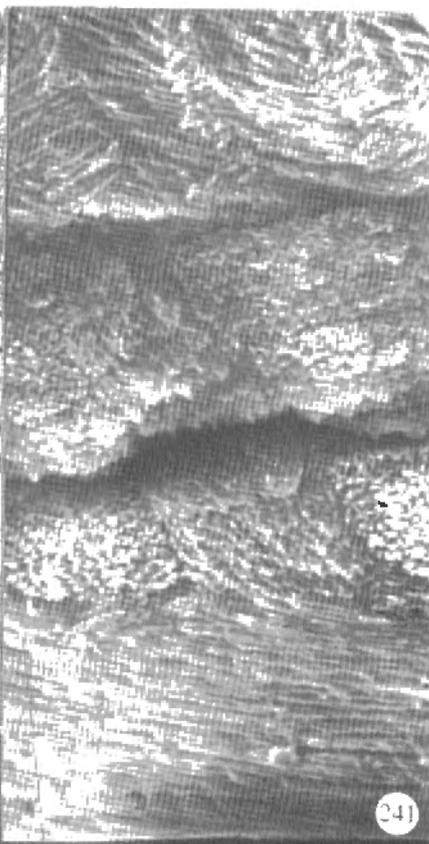




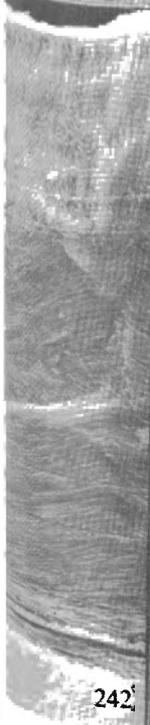
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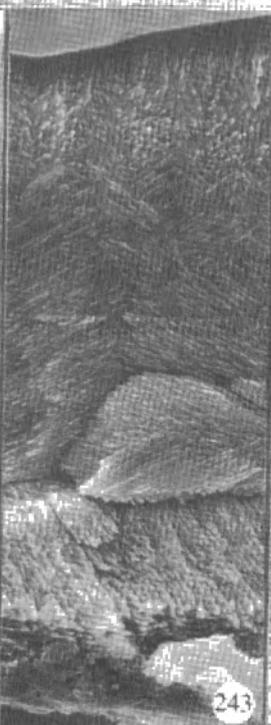
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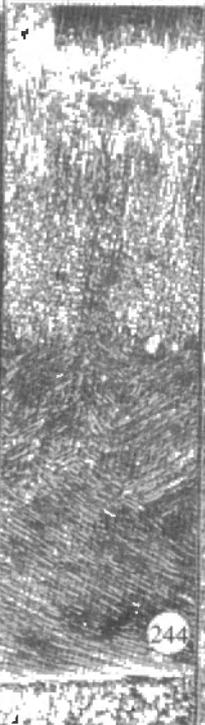
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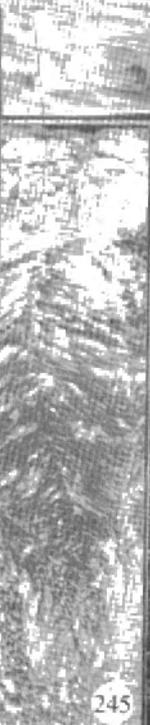
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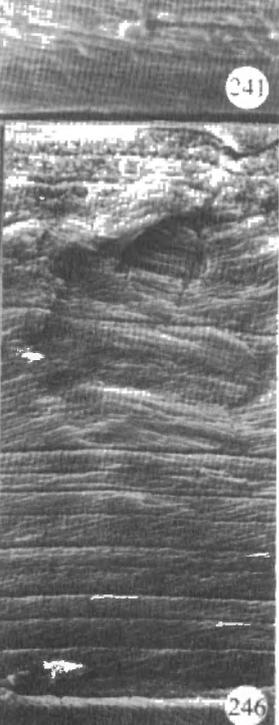
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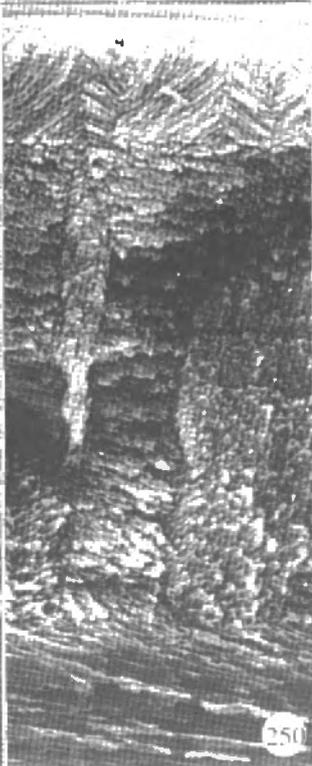
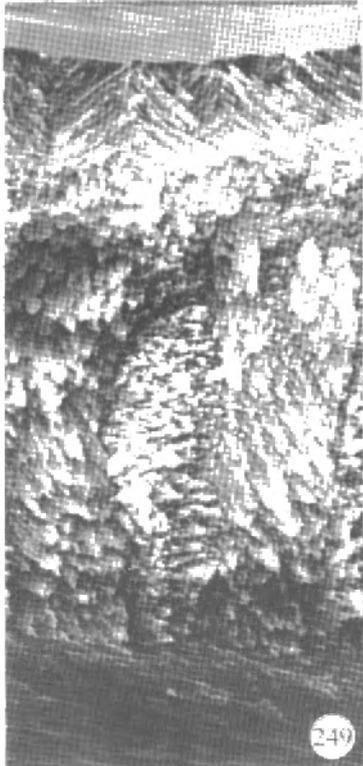
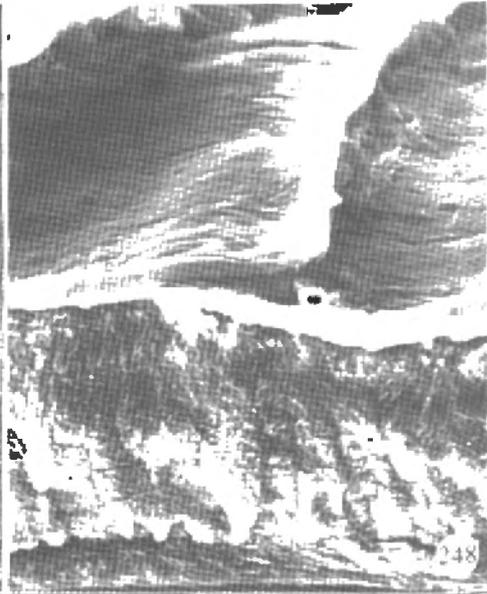
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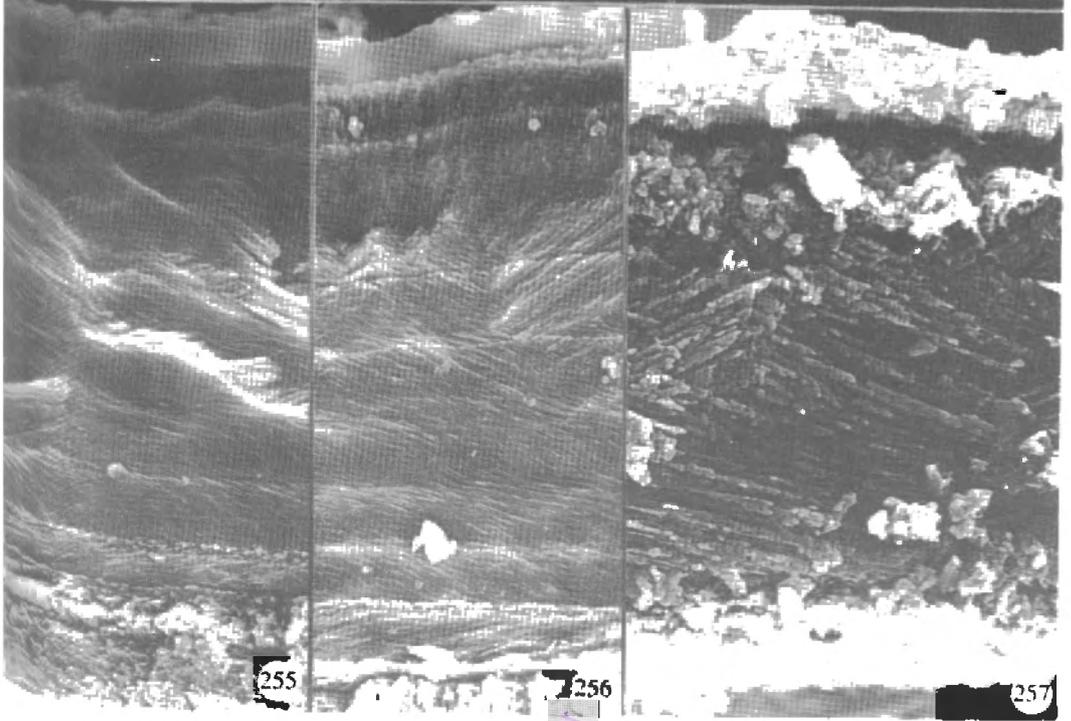
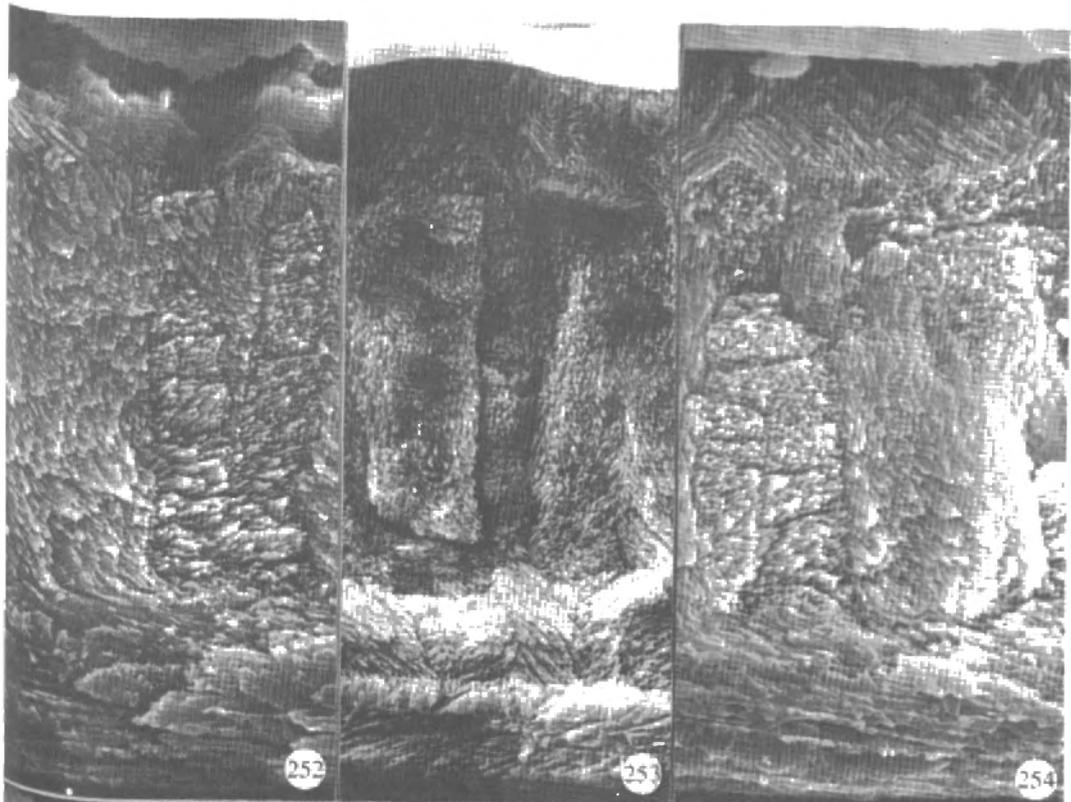


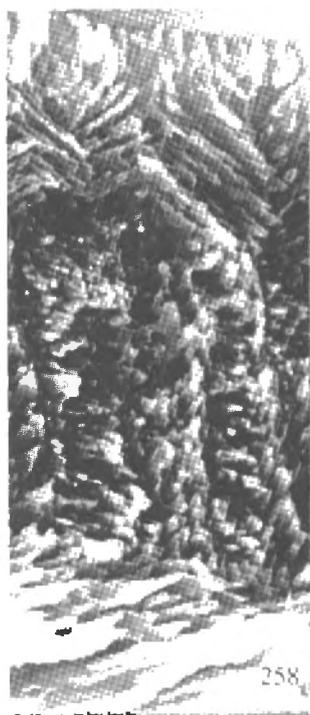
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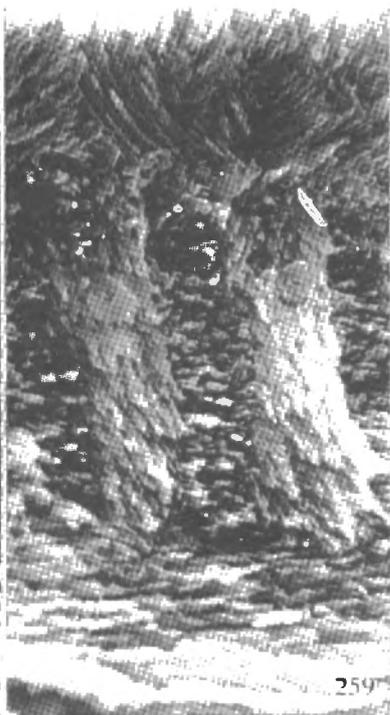
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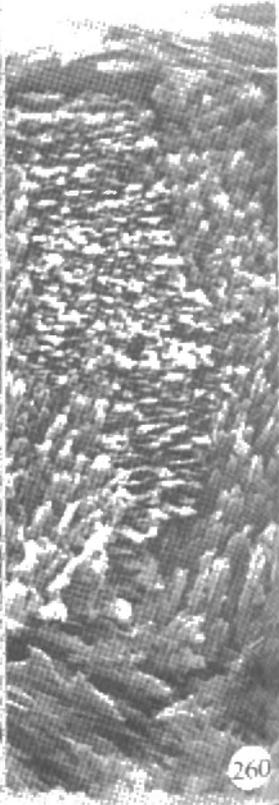




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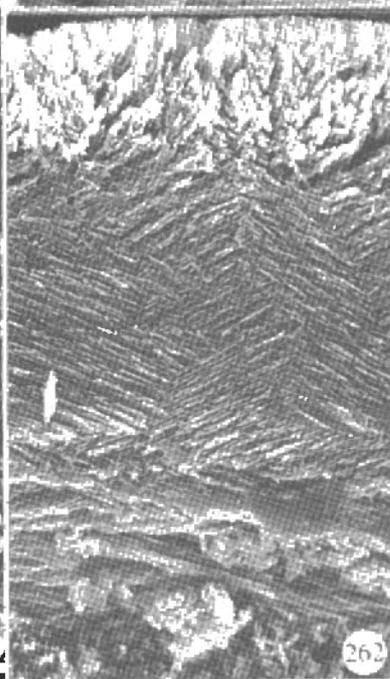
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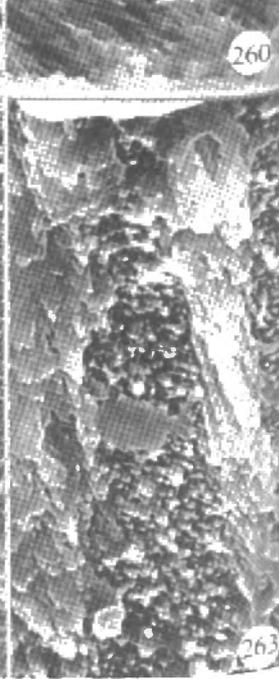
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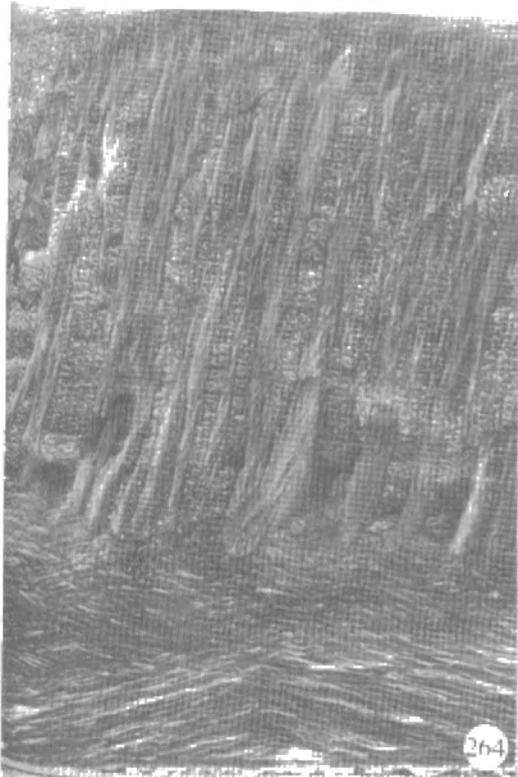
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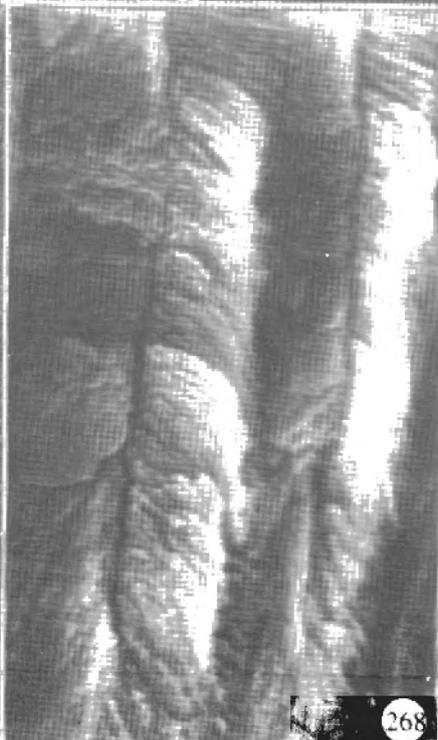
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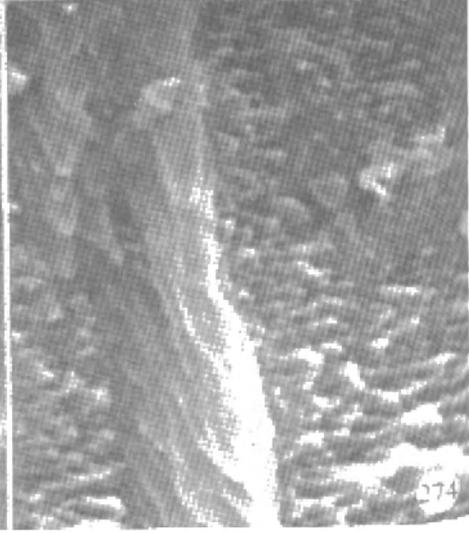
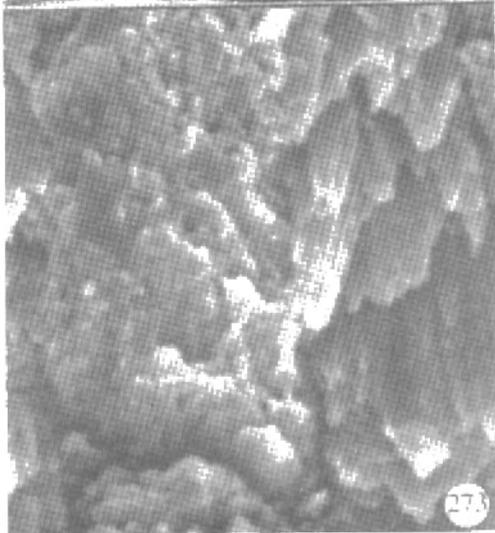
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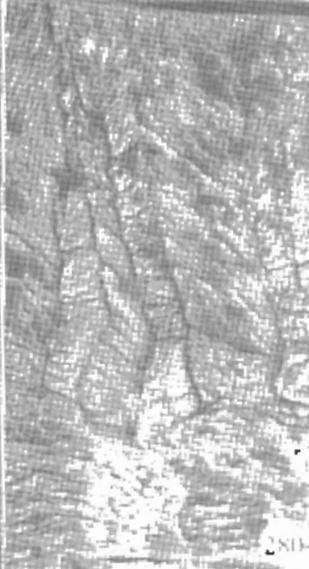
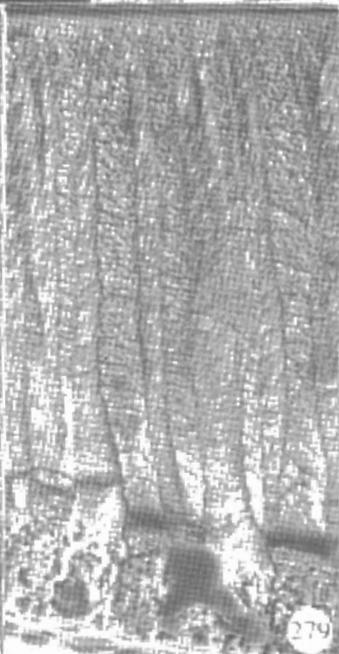
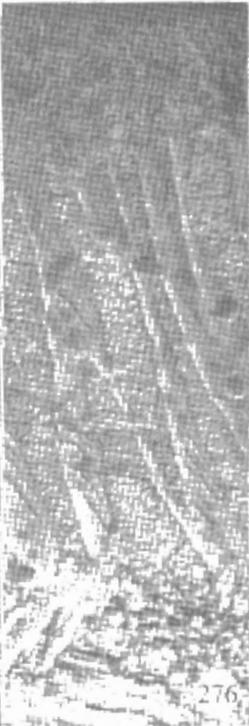


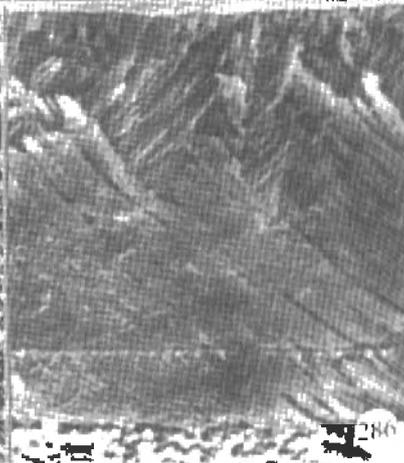
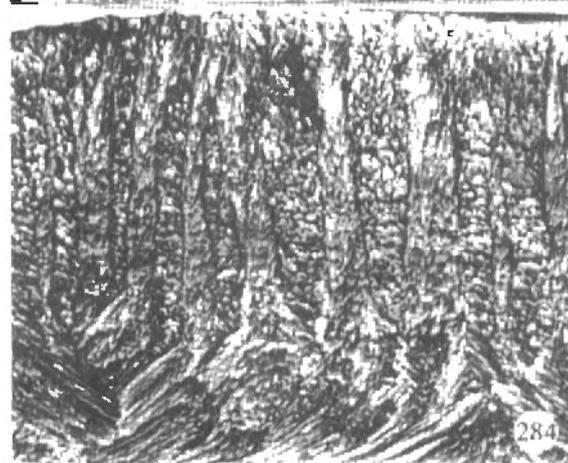
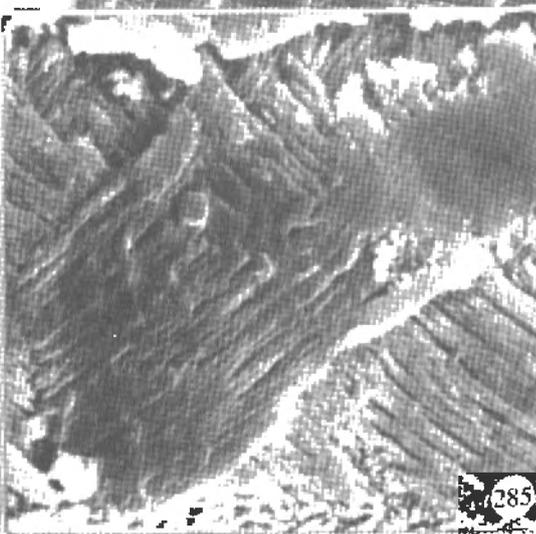
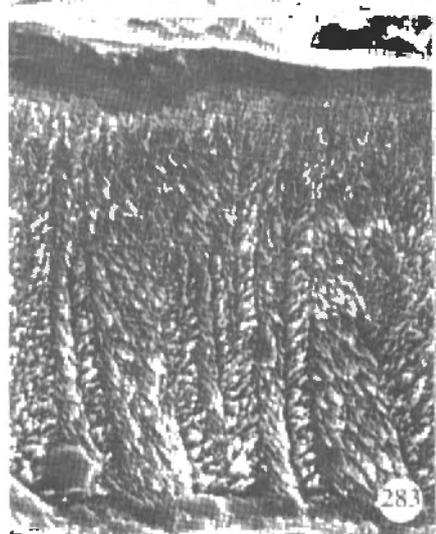
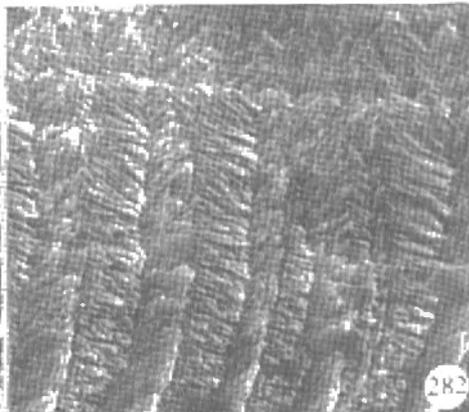
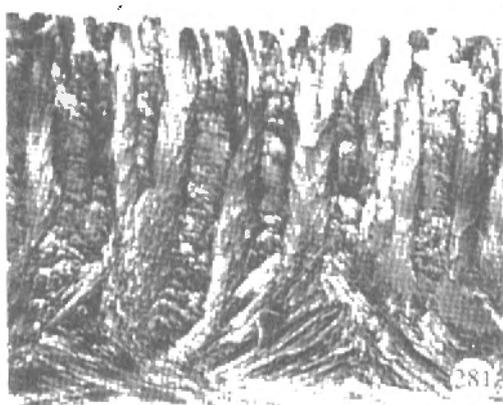
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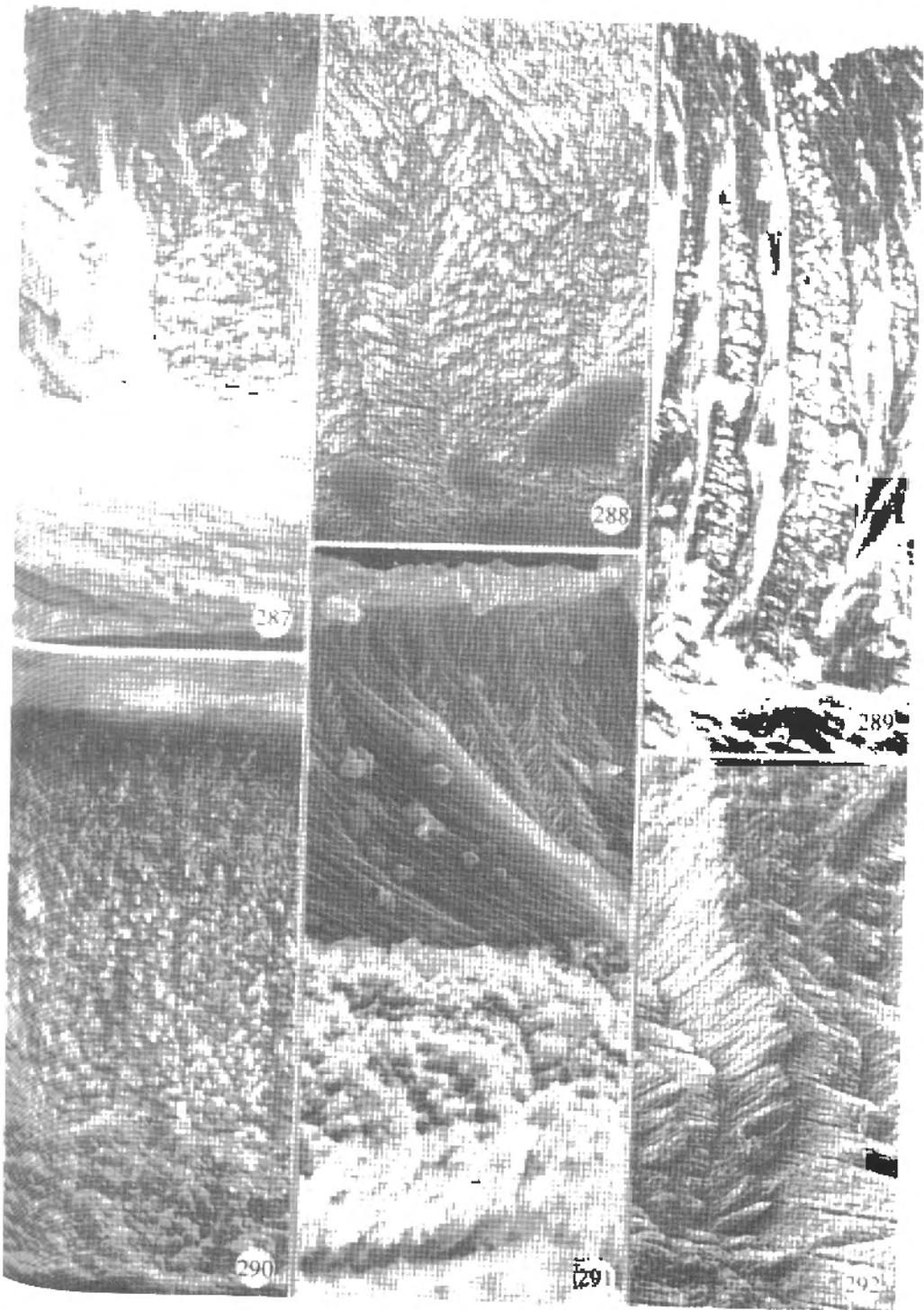


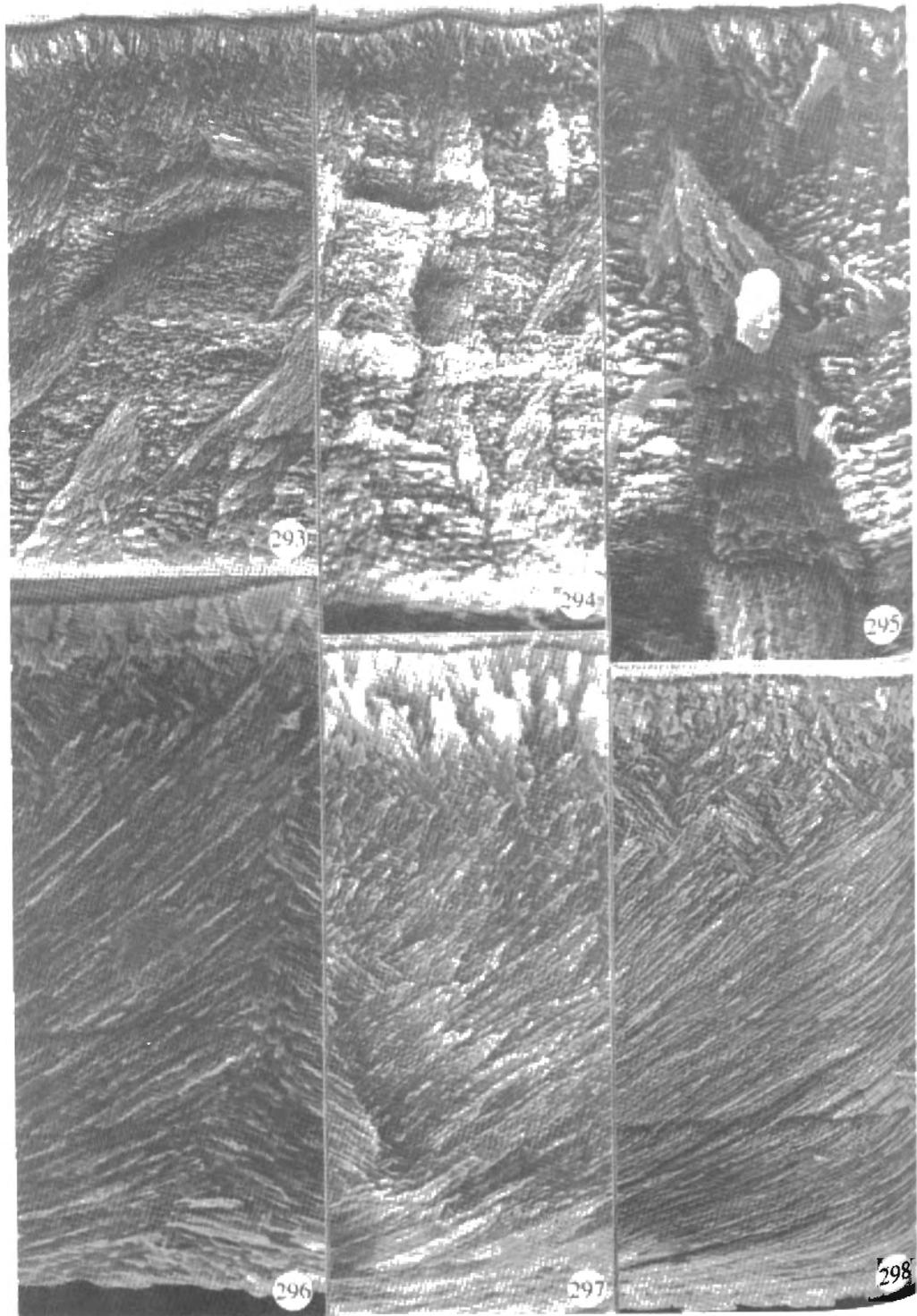
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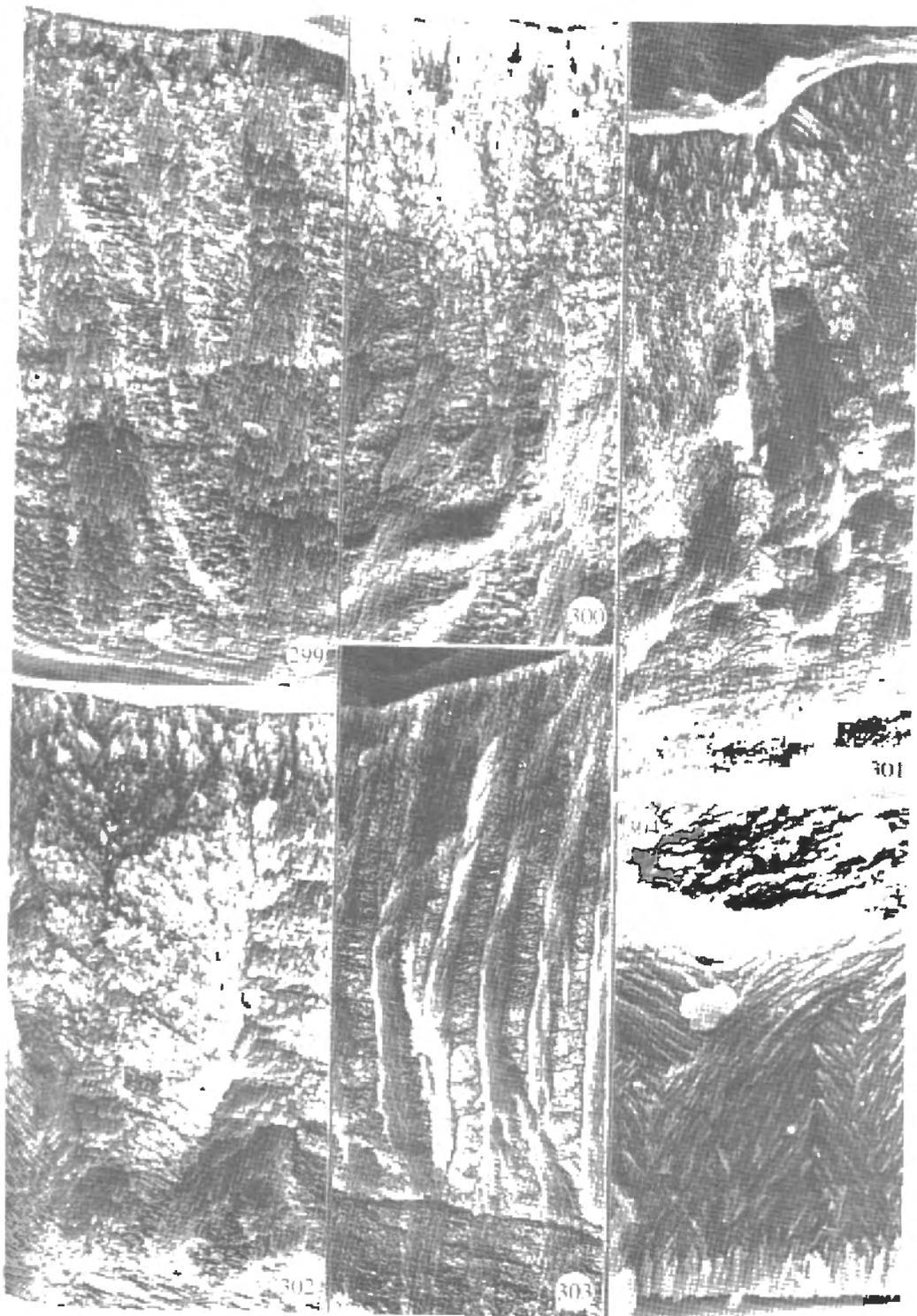


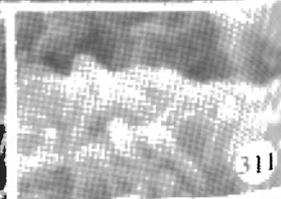
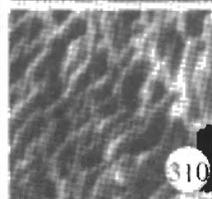
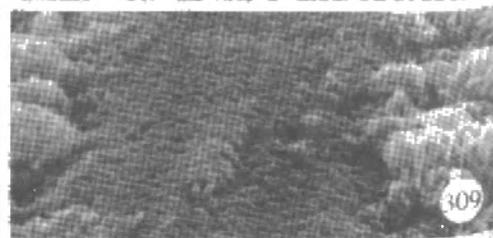
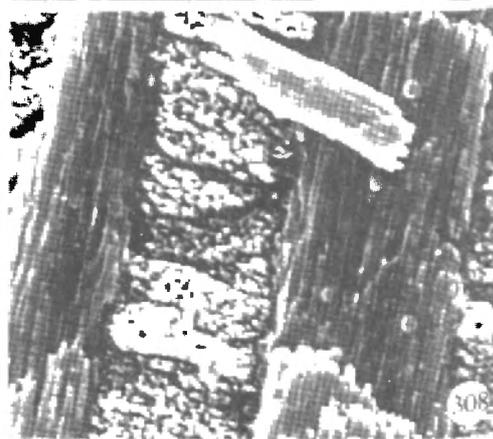
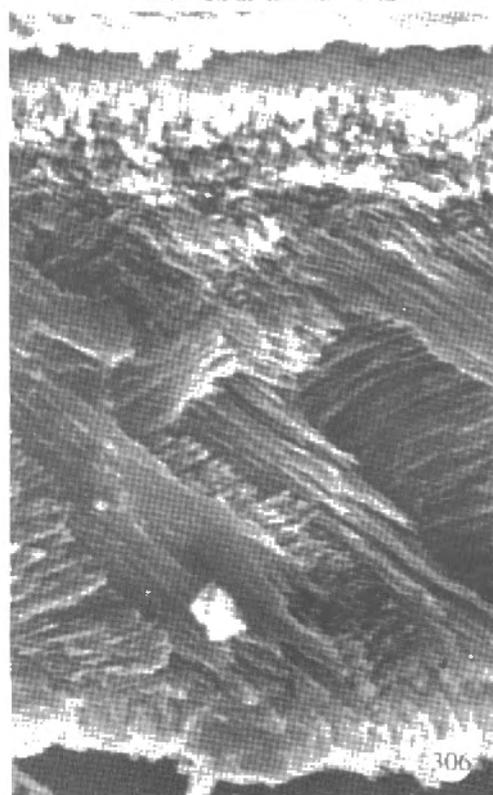
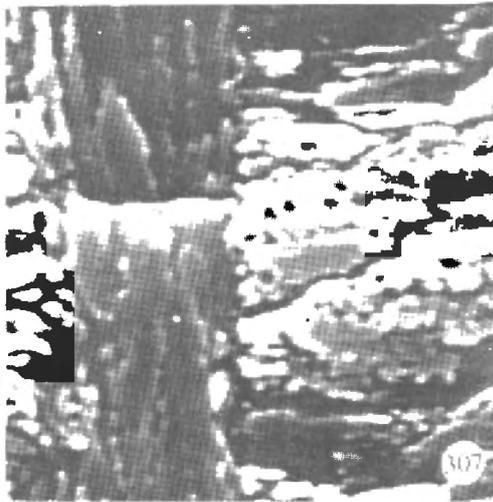










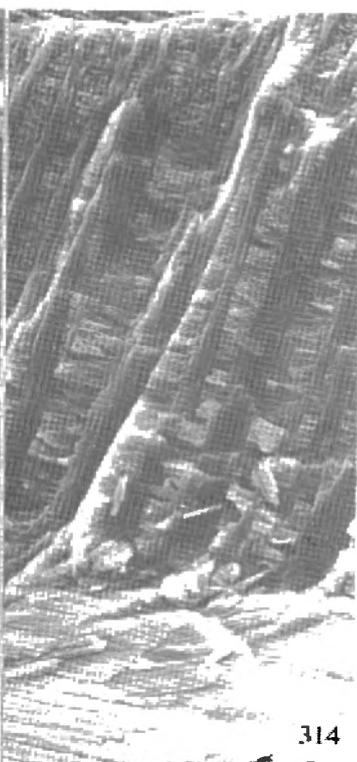




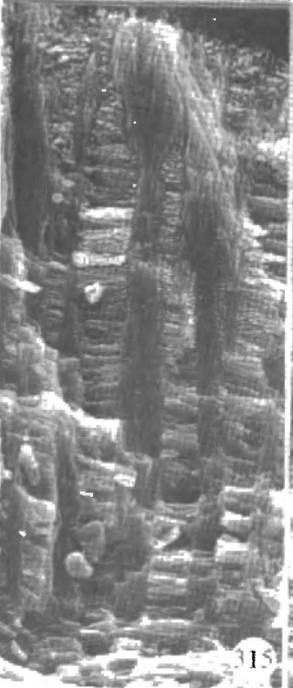
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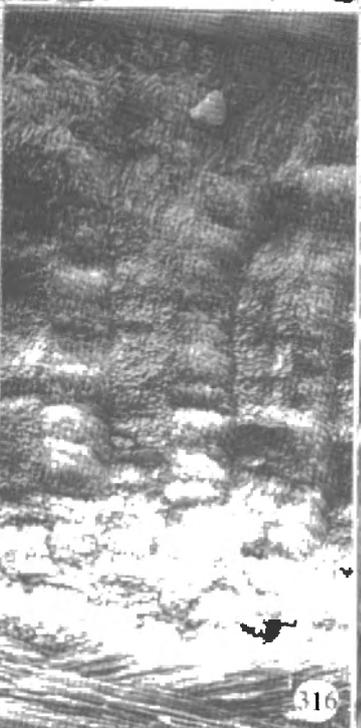
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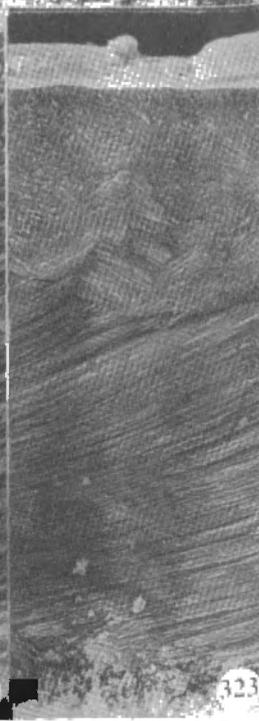
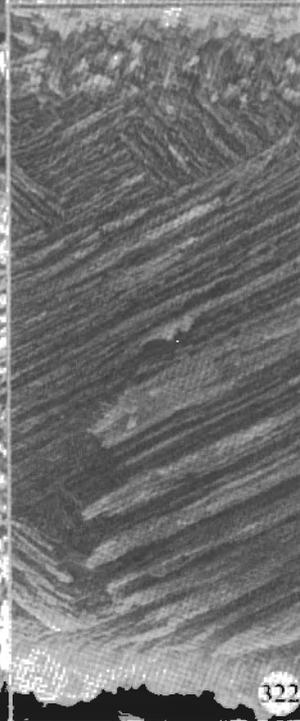
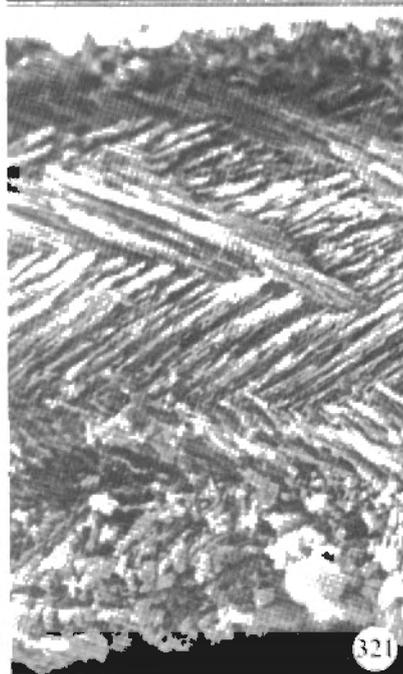
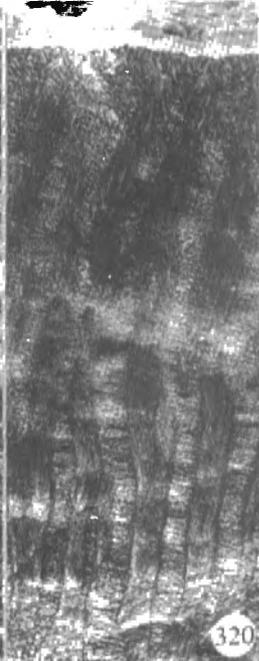
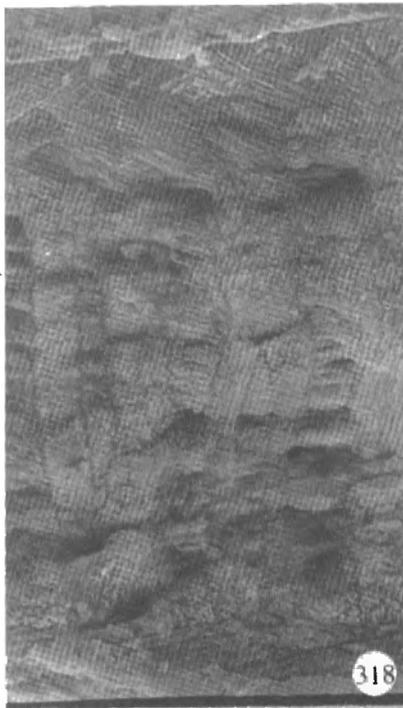
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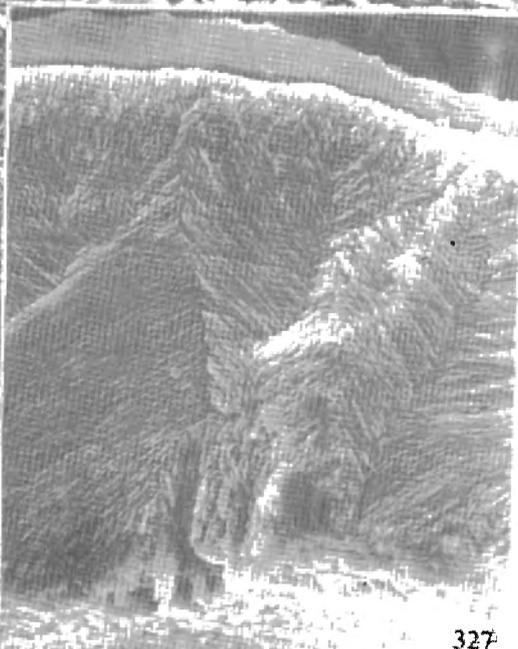
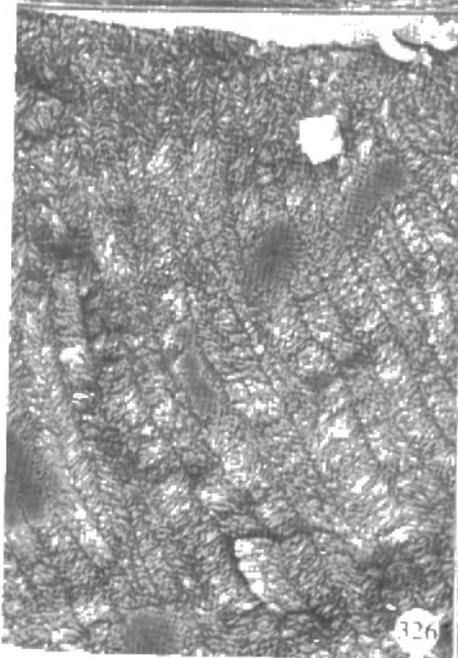
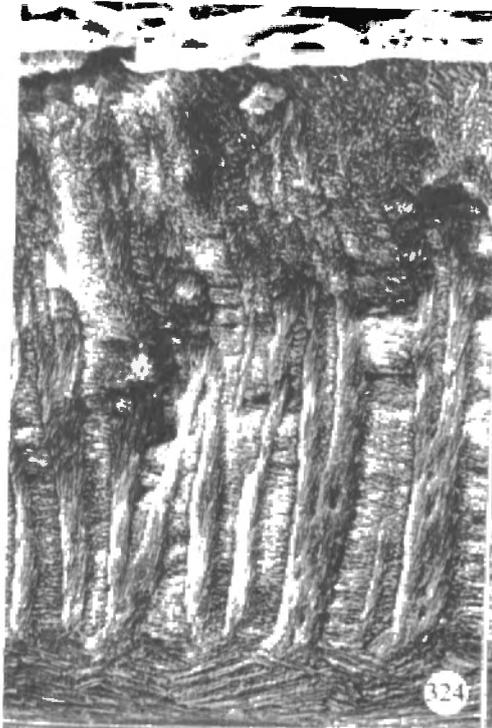


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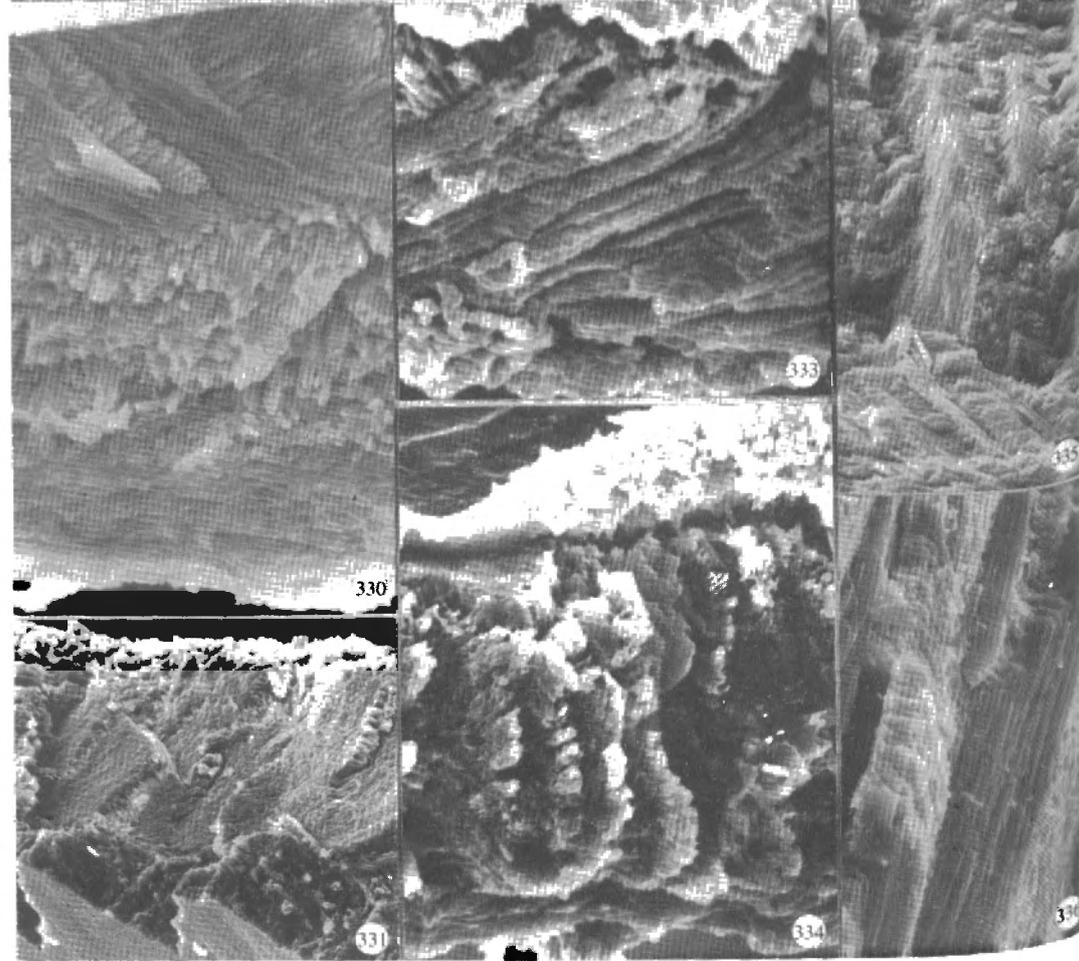
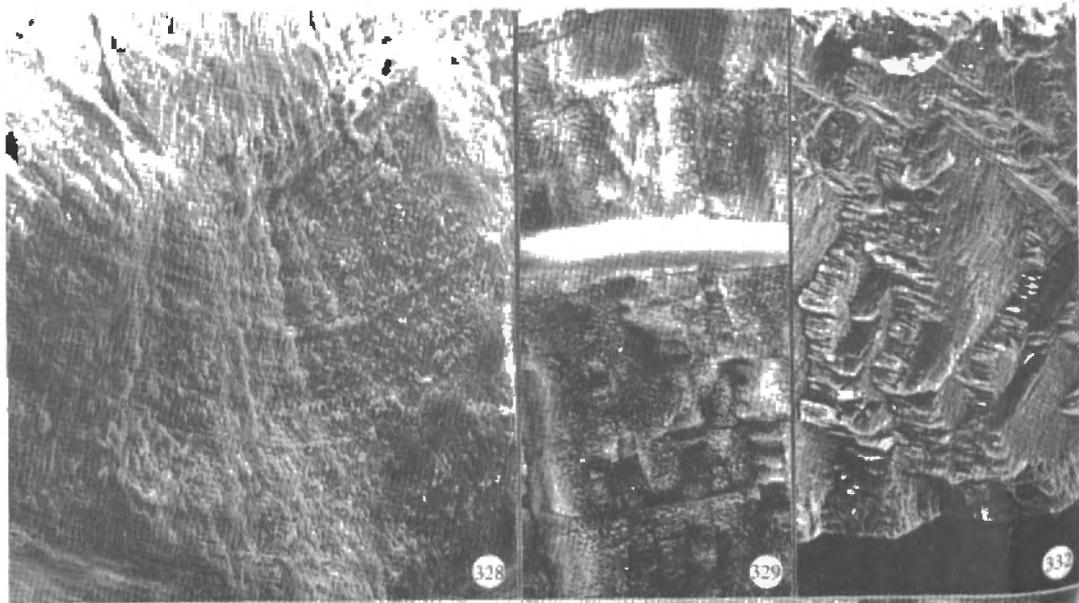


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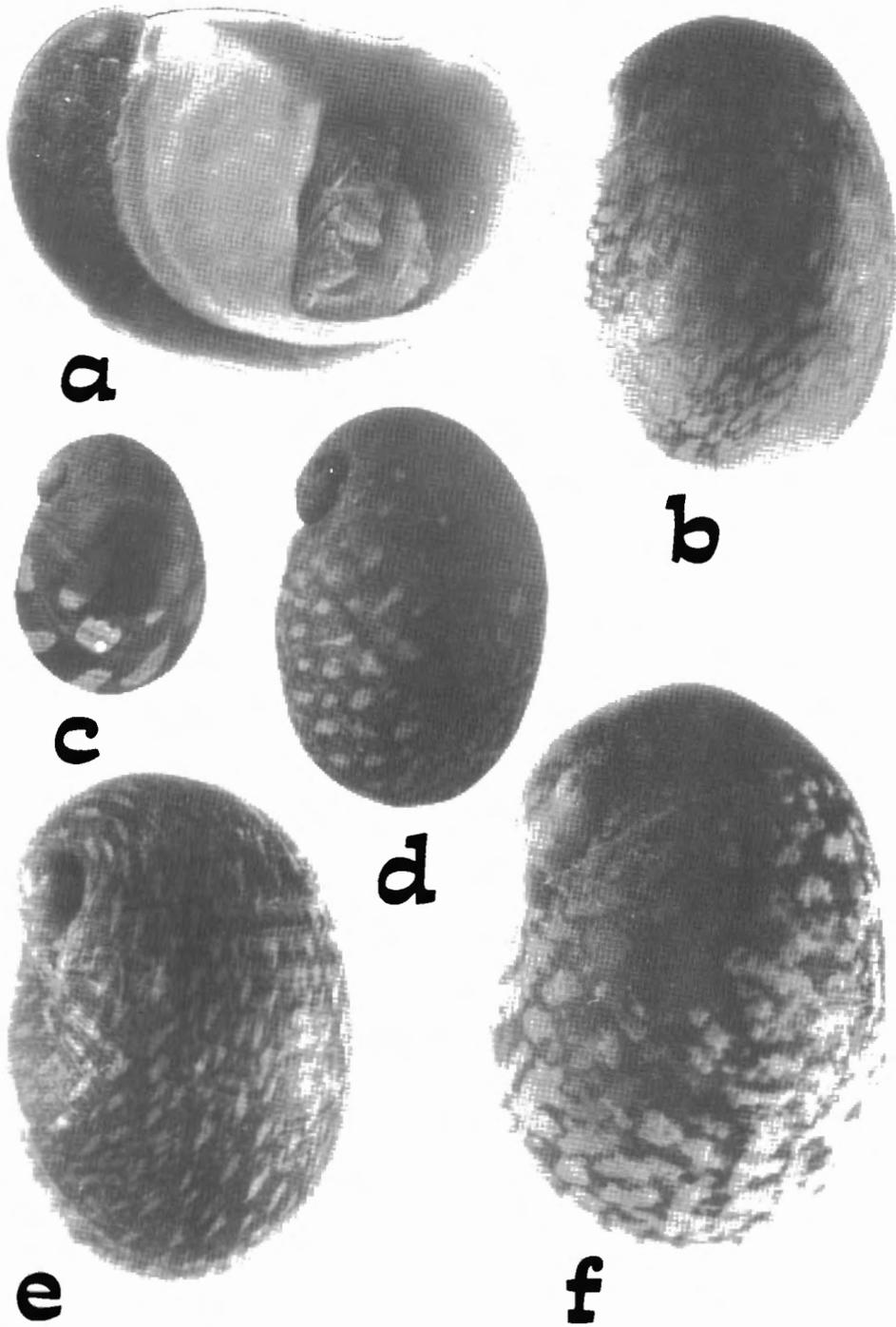


Fig. 337

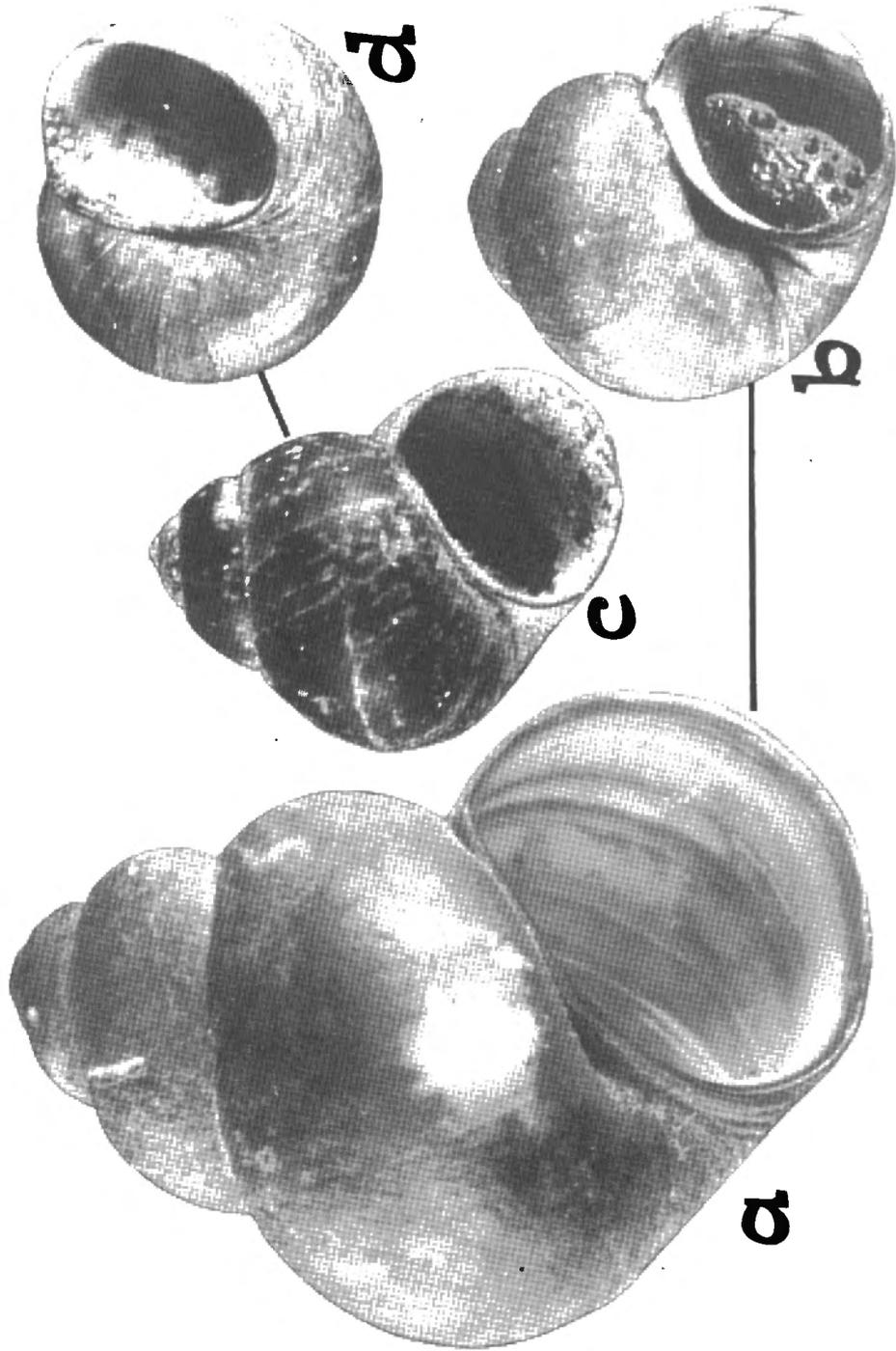


Fig. 338

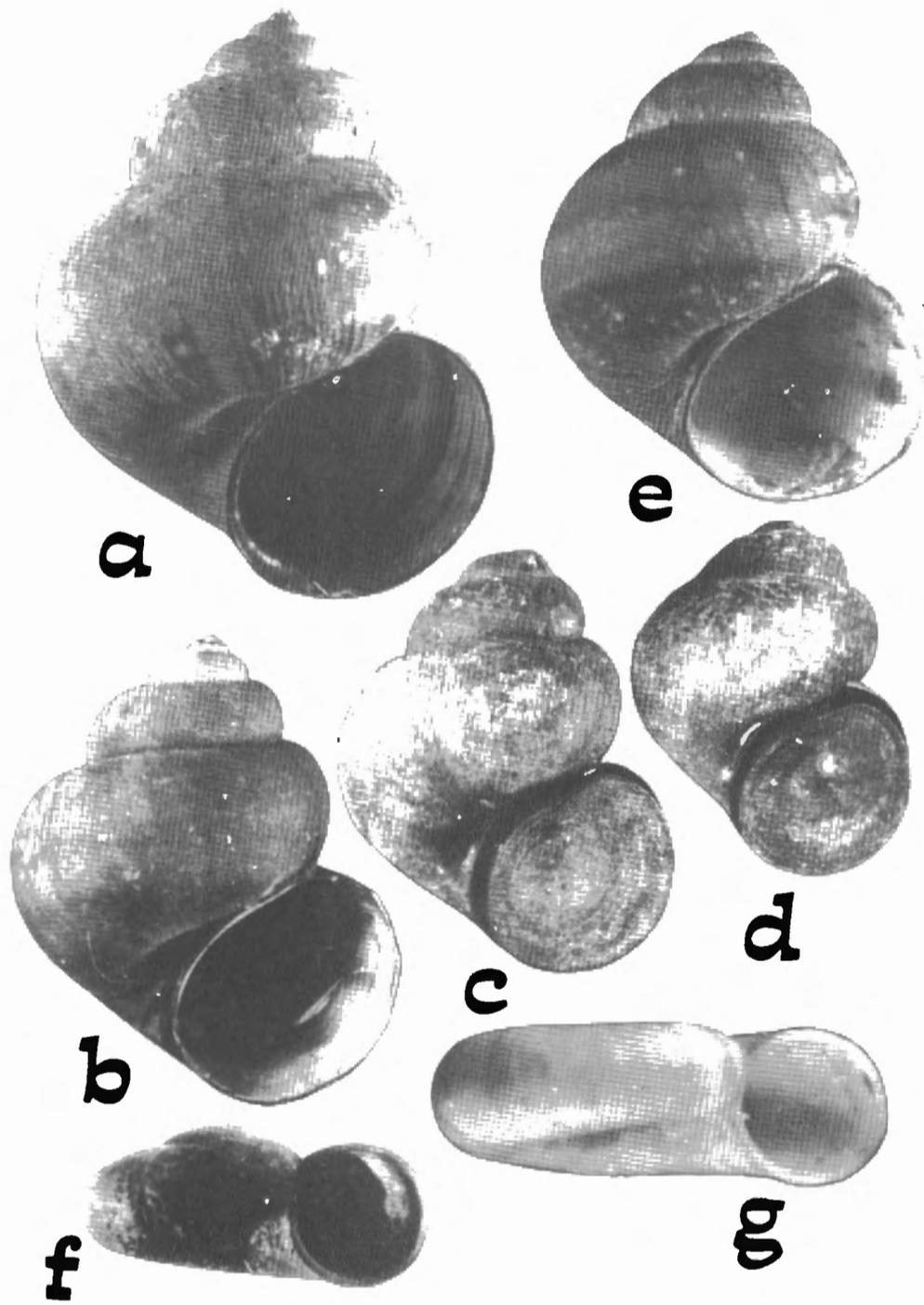


Fig. 399

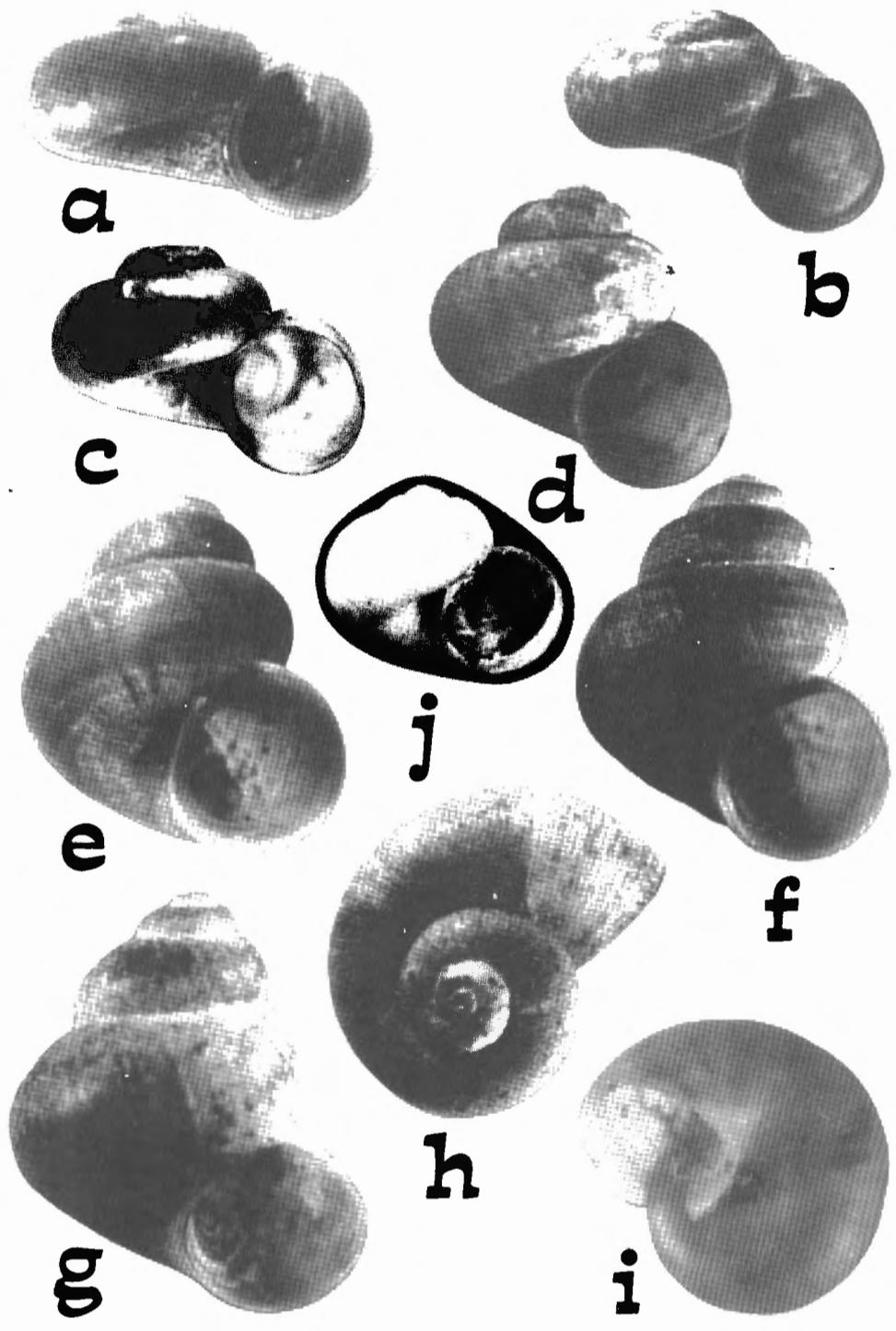


Fig. 340

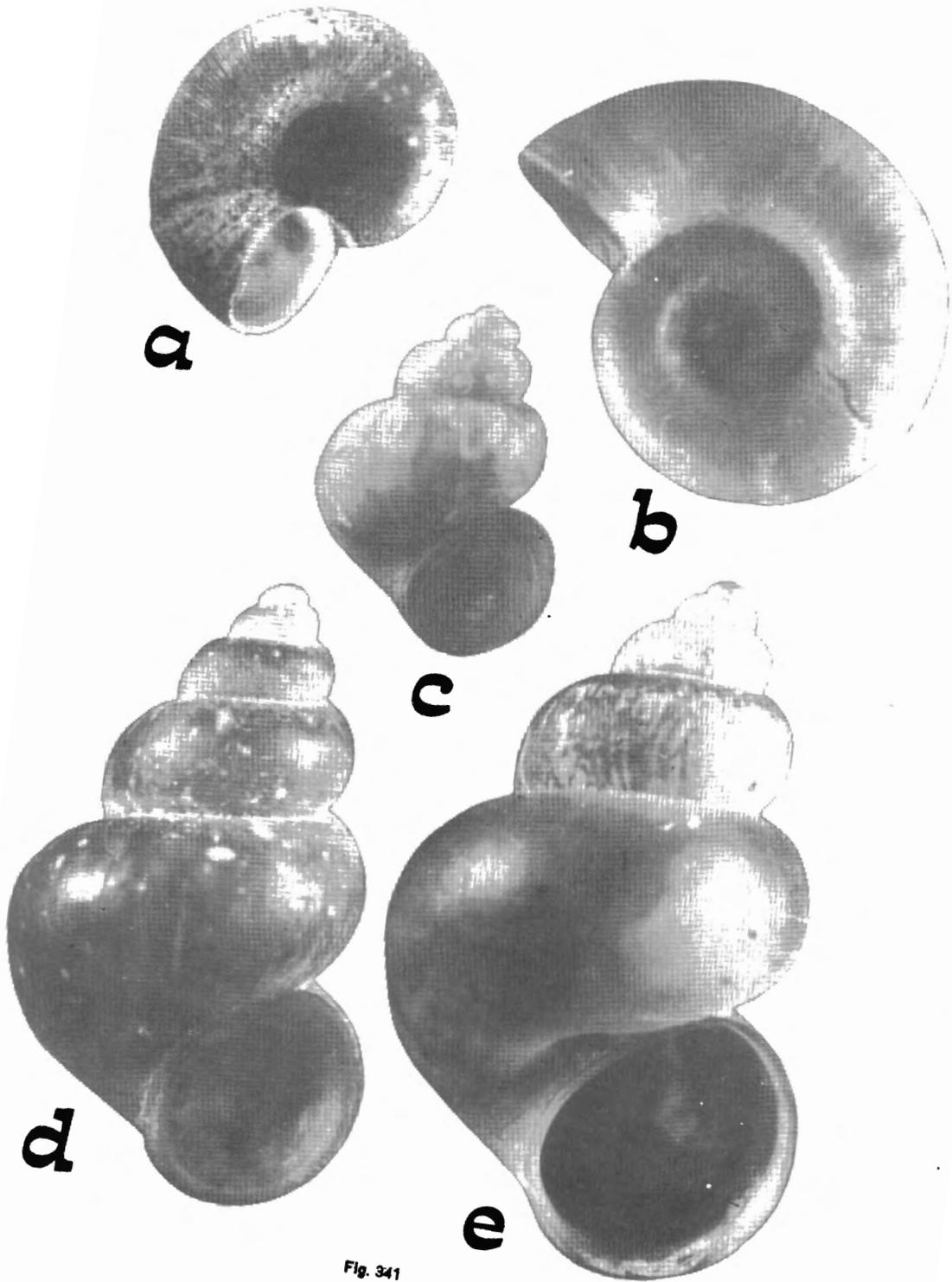


Fig. 341

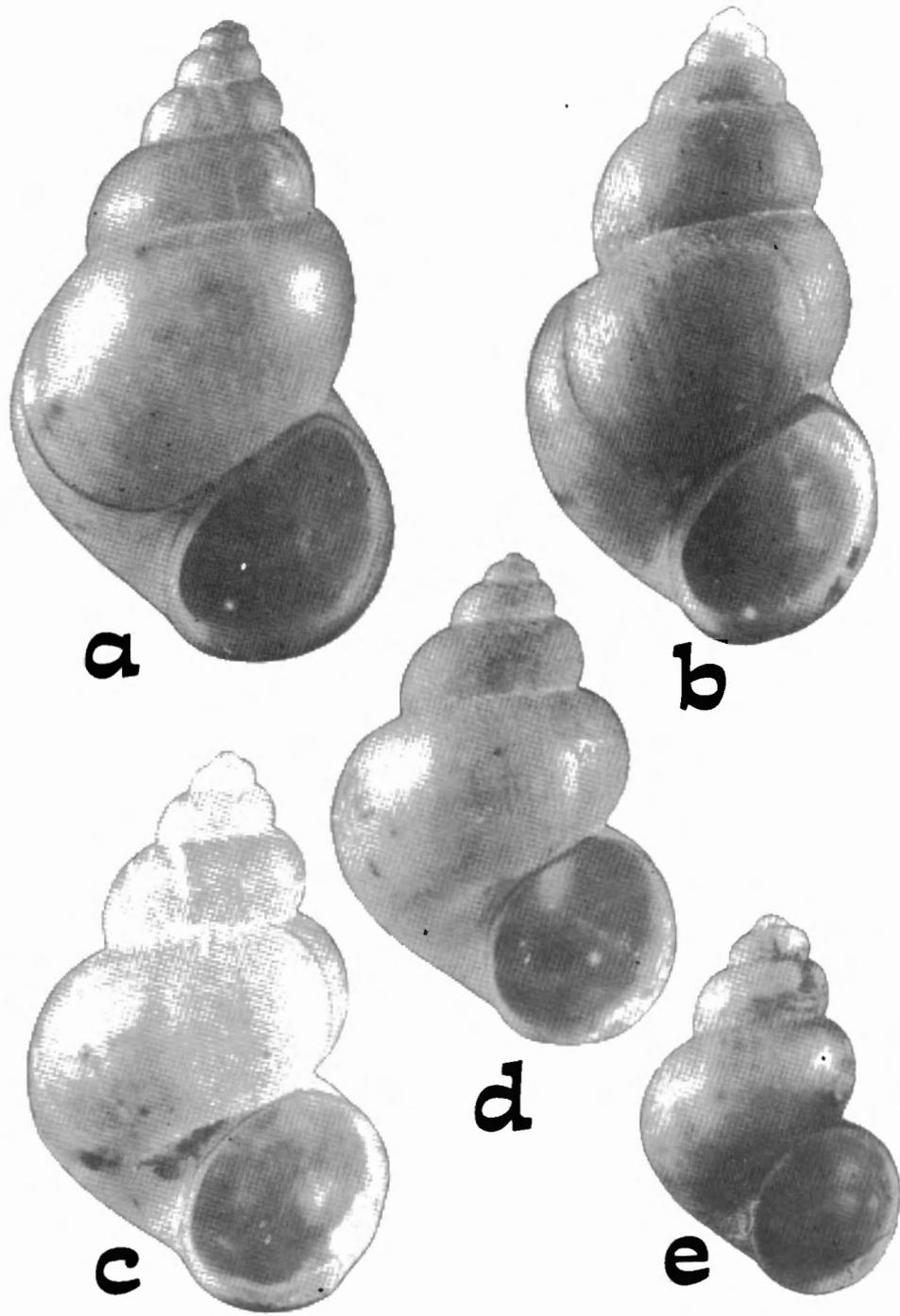


Fig. 342

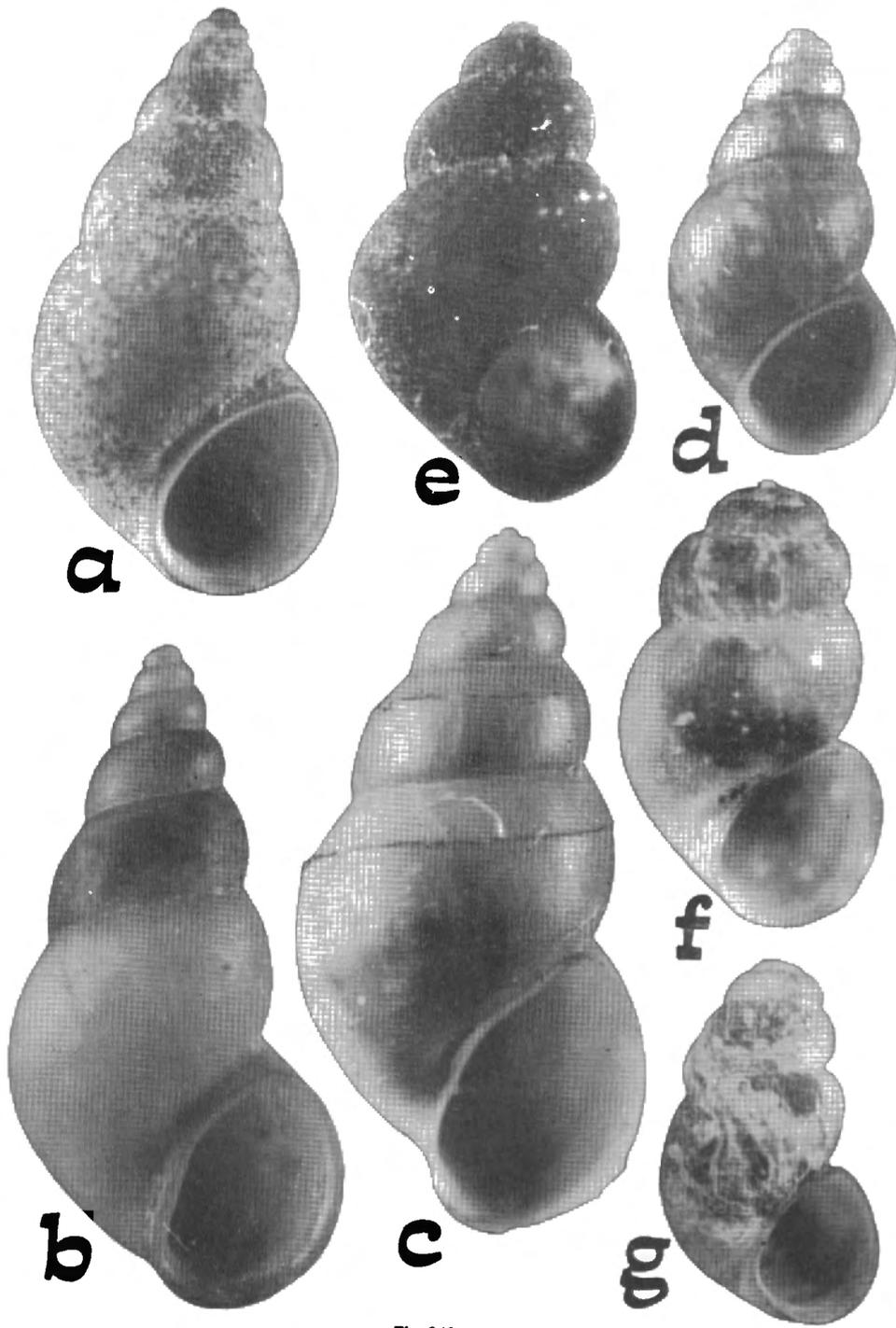


Fig. 343

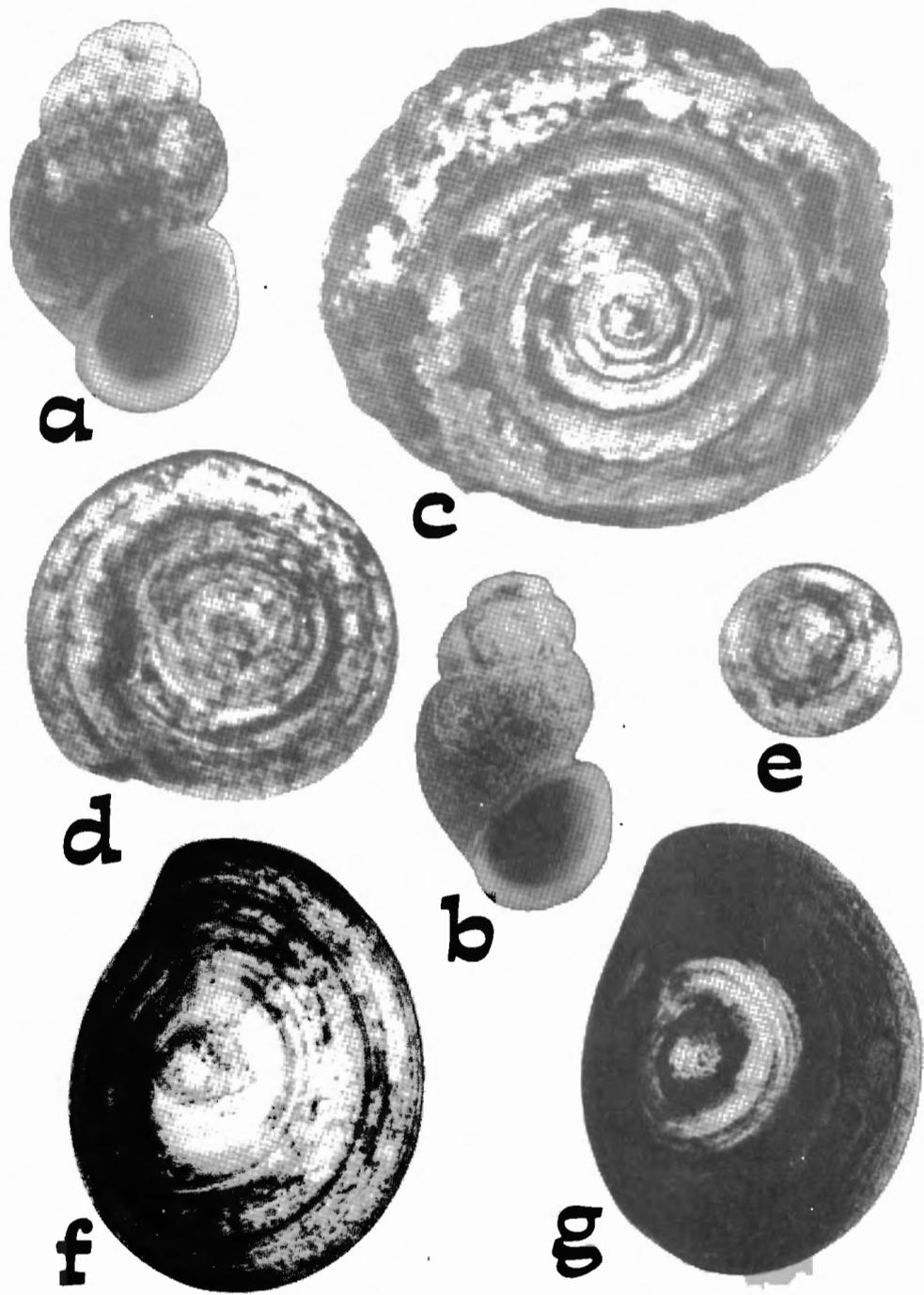


Fig. 344



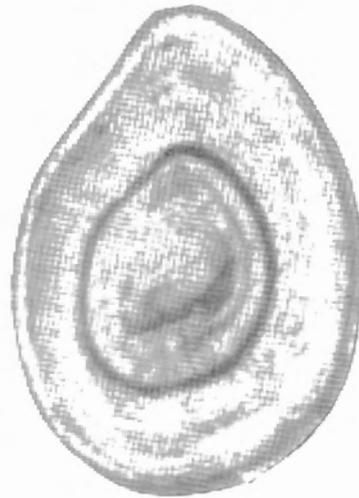
a



b



c



d

Fig. 945

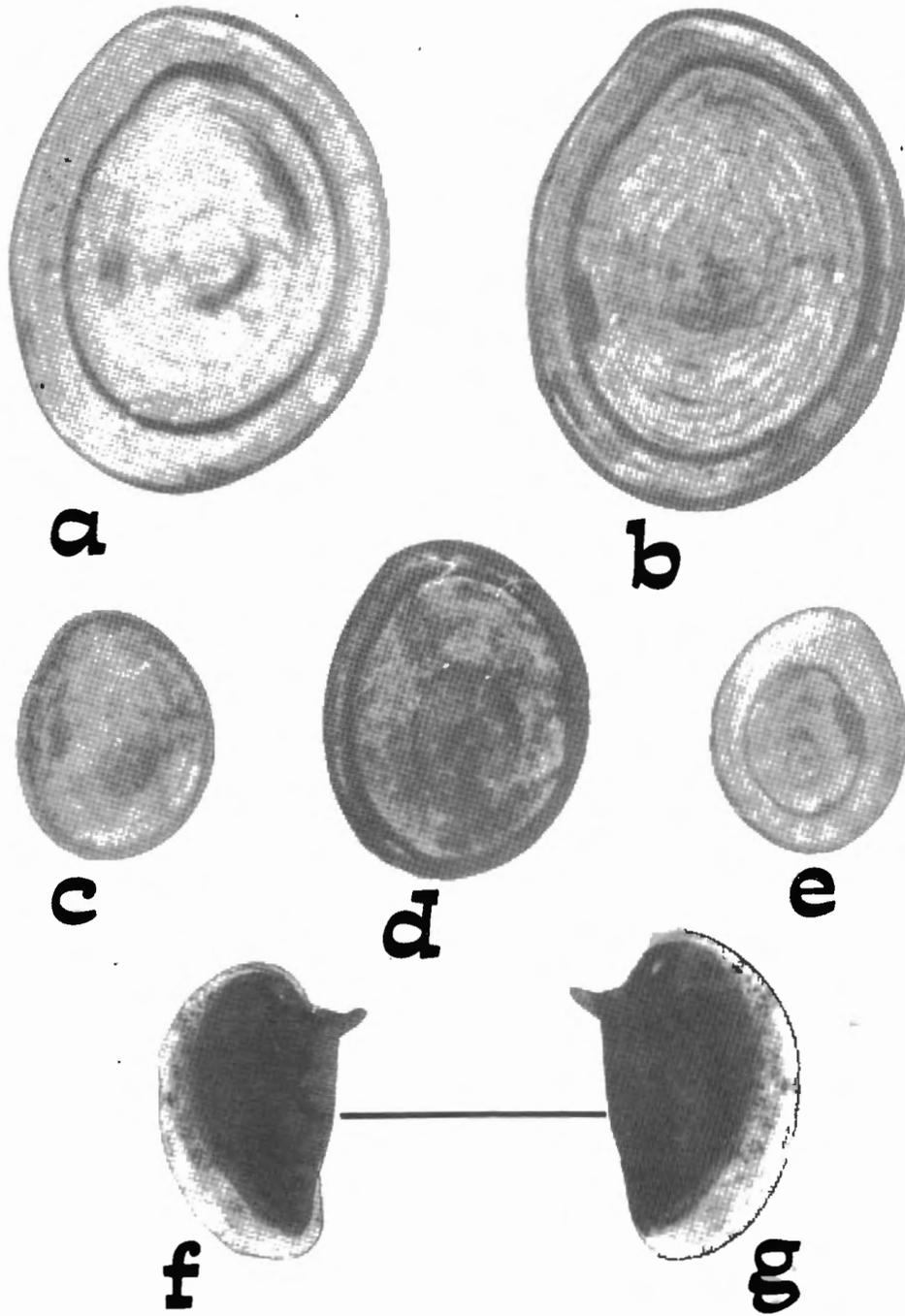


Fig. 346

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- Figs. 4 - 6. Radulae of *Theodoxus fluviatilis*: 4 - lateral teeth (550 x), 5 - central and innermost lateral teeth (650 x), 6 - outermost lateral and marginal teeth (600 x)
- Figs. 7 - 8. Radulae: 7 - *Theodoxus fluviatilis*, marginal teeth, artificially arranged to show their habitus (320 x); 8 - *Viviparus conlectus*, central teeth (300 x)
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Figs. 216 - 218. Shell sections perpendicular to growth lines, to show shell general organization: 216 - *Theodoxus fluviatilis* (360 x); 217 - 218 - *Viviparus contractus*: 217 - whole section (300 x), 218 - columns of pallisade layer (650 x)

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Figs. 227 - 232. Shell sections of *Viviparus*: 227 - 230 - *V. contractus*: 227 and 230 - perpendicular to growth lines (227 - 600 x, 230 - 430 x), 228 - 229 - parallel to growth lines (228 - 300 x, 229 - 240 x); 231 - 232 - *V. viviparus*: 231 - perpendicular to growth lines (220 x), 232 - parallel to growth lines (180 x)

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Figs. 252 - 257. Shell sections of *Valvata*: 252 - 256 - *V. pulchella*: 252 - 254 - perpendicular to growth lines (252 - 2,400 x, 253 - 1,300 x, 254 - 2,400 x), 255 - 256 - parallel to growth lines (1,000 x); 257 - *V. cristata*, parallel to growth lines (3,200 x)

Figs. 258 - 263. Shell sections of *Valvata cristata*: 258 - 261 - perpendicular to growth lines (258 - 5,400 x, 259 - 3,800 x, 260 - 4,400 x, 261 - 3,600 x); 262 - parallel to growth lines (1,300 x); 263 - approximately perpendicular to growth lines, a fragment (3,000 x)

Figs. 264 - 269. Shell sections of *Valvata naticina*: 264 - 268 - perpendicular to growth lines: 264 - 267 - whole sections (264 - 650 x, 265 - 550 x, 266 - 650 x, 267 - 550 x), 268 - a fragment of columns of pallisade layer (2,700 x); 269 - parallel to growth lines (1,000 x)

Figs. 270 - 274. Shell sections perpendicular to growth lines: 270 - 272 - *Valvata naticina* (270 - 271 - 650 x, 272 - 470 x); 273 - 274 - fragments of columns of pallisade layer of *Bithynia*: 273 - *B. tentaculata* (5,000 x), 274 - *B. bruchii* (5,000 x)

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Figs. 287 - 292. Shell sections of *Bithynia troscheli*: 287 - 290 - perpendicular to growth lines (287 - 2,400 x, 288 - 1,600 x, 289 - 900 x, 290 - 2,000 x), 291 - parallel to growth lines (1,300 x), 292 - slanting to growth lines (750 x)

Figs. 293 - 298. Shell sections of *Bythinella micherdzinskii*: 293 - 295 - perpendicular to growth lines: 293 - 294 - whole sections (293 - 1,600 x, 294 - 1,500 x), 295 - a fragment of the outer side (3,600 x); 296 - 298 - parallel to growth lines (296 - 3,200 x, 297 - 4,000 x, 298 - 2,600 x)

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Figs. 312 - 317. Shell sections perpendicular to growth lines (317 - a fragment of pallisade layer, 315 - sole pallisade layer): 312 - 315 - *Lithoglyphus naticoides* (312 - 390 x, 313 - 360 x, 314 - 600 x, 315 - 1,000 x), 316 - 317 - *Potamopyrgus jenkinsi* (316 - 1,300 x, 317 - 10,000 x)

Figs. 318 - 323. Shell sections of *Potamopyrgus jenkinsi*: 318 - 320 - perpendicular to growth lines (318 - 1,000 x, 319 - 600 x, 320 - 500 x), 321 - 323 - parallel to growth lines (321 - 2,000 x, 322 - 1,600 x, 323 - 780 x)

Figs. 324 - 327. Shell sections: 324 - 325 - *Potamopyrgus jenkinsi*, perpendicular to growth lines (324 - 750 x, 325 - 1,000 x); 326 - *P. jenkinsi*, close to columella (600 x); 327 - *Bythinella zywionteki*, columella (660 x)

Figs. 328 - 336. Shell sections, to show shell general organization (329 - etched, others - unetched): 328 - transverse section of columella, *Bithynia troscheli* (160 x); 329 - suture, perpendicular to growth lines, to show the walls of two successive whorls, *Valvata pulchella* (670 x); 330 - protoconch, close to columella, *Bithynia troscheli* (1,330 x); 331 - 336 - teleoconch: 331 - 334 - *B. leachi* (331 - 600 x, 332 - 400 x, 333 - 2,200 x, 334 - 1,500 x), 335 - 336 - *B. tentaculata* (335 - 400 x; 336 - a fragment of mesostracum, 1,300 x)

Fig. 337. *Theodoxus fluviatilis* from some Polish localities: a - shell, apertural aspect; b - f - variability of shell colouring

Fig. 338. Comparison between the shells of two Polish viviparids: a - b - *Viviparus contectus* (a - giant *V. hungaricus* HAZAY, 1881, from the River Drwinka), c - d - *V. viviparus*; a and c - shell habitus, b and d - umbilicus

Fig. 339. a - e - shells of *Viviparus* from some Polish localities: a - b - typical *V. contectus*, c - d - *V. contectus* showing intermediate shell characters (*V. contectus* - *V. viviparus*), e - *V. viviparus*; f - g - comparison between two *Valvata* shells: f - *V. pulchella*, g - *V. cristata*

Fig. 340. Shells of *Valvata*: a - g - continuous variability between *V. pulchella*, *V. piscinalis* f. *typica* and *V. piscinalis* f. *antiqua*: a - *V. pulchella*, b - c - intermediates, d - *V. piscinalis* f. *typica*, e - g - *V. piscinalis* f. *antiqua*; h - i - *V. piscinalis*: h - apical aspect, to show sculpture; i - umbilicus; j - *V. naticina*, to compare with *V. piscinalis*

Fig. 341. a - b - comparison between the umbilicus of *Valvata pulchella* (a) and *V. cristata* (b), not to scale; c - e - shells of *Bithynia*: c - *B. leachi*, d - e - *B. troscheli*

Fig. 342. Continuous variability within Polish *Bithynia*: a - *B. tentaculata*, b - *B. troscheli* showing intermediate characters (*B. troscheli* - *B. tentaculata*), c - d - typical *B. troscheli*, e - *B. leachi*

Fig. 343. Shells of some Polish *Hydrobioidae*: a - d - *Potamopyrgus jenkinsi*, e - *Marstoniopsis scholtzi*; f - *Bythinella micherdzinskii*, g - *B. zywionteki*; not to scale

Fig. 344. a - b - shells of *Bythinella*: a - *B. zywionteki*, b - *B. micherdzinskii*; c - g - opercula: c - e - *Valvata*: c - *V. piscinalis*, d - *V. pulchella*, e - *V. cristata*; f - g - *Viviparus*: f - *V. contectus*, g - *V. viviparus*

Fig. 345. Opercula: a - d - operculum variability in *Bithynia tentaculata* from various localities

Fig. 346. Opercula: a - b - *Bithynia troscheli*, c - e - *B. leachi*, f - g - *Theodoxus fluviatilis* (e and g - inner side)

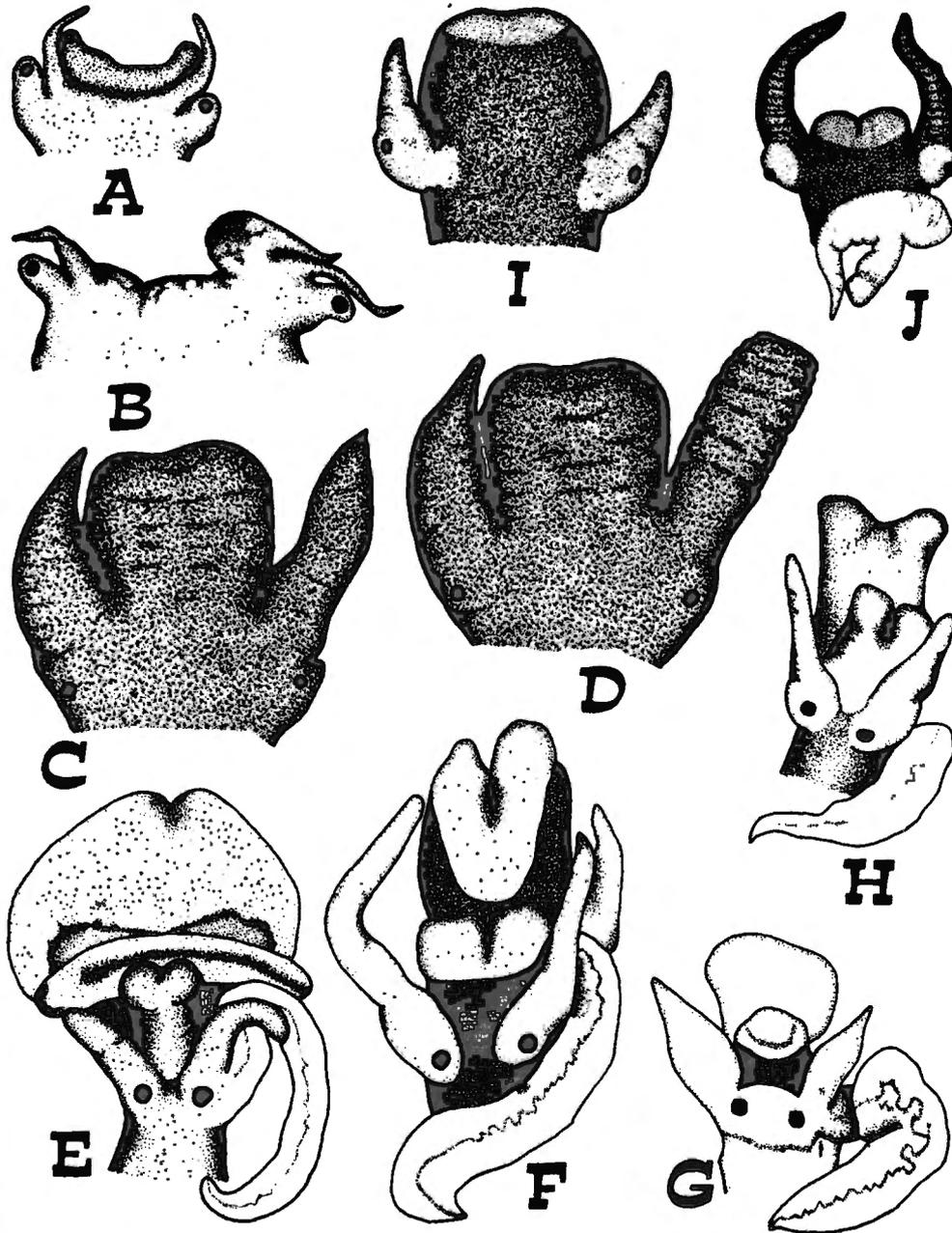


Fig. 347. Head habitus and pigmentation pattern: A - B - *Theodorus flaviventris* (A - female, B - male); C - D - *Viniparus corticosus* (C - female, D - male); E - H - *Valvata*: E - *V. piscinalis*, F - *V. pulchella*, G - *V. medicus*, H - *V. cristata*; I - J - *Blitomyia leachi* (I - female, J - male); not to scale. All the figures after FALNIEWSKI (1982a).

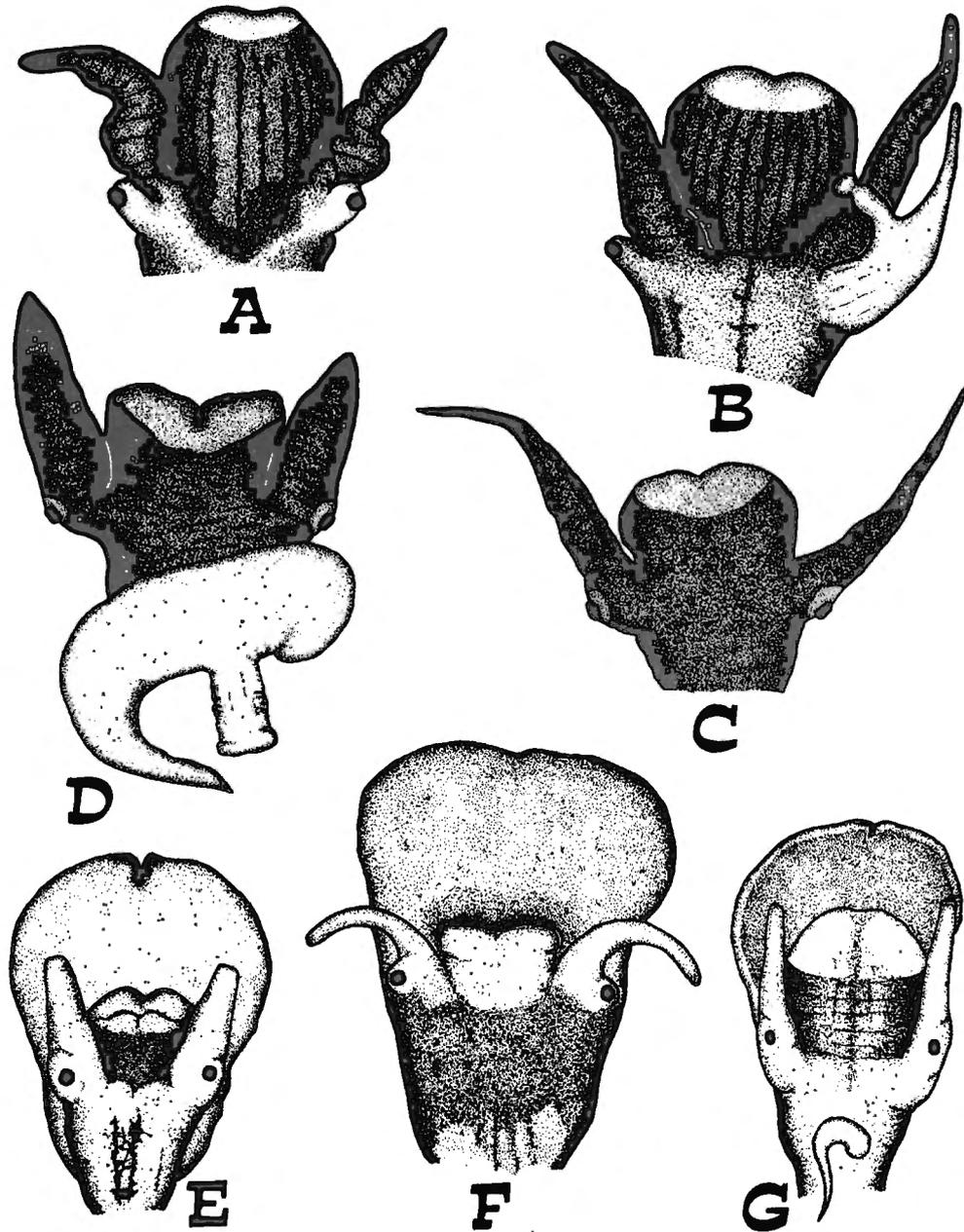


Fig. 348. Head habitus and pigmentation pattern: A - D - *Eithynia* (after FALNIOWSKI 1989a): A - B - *E. lentaculata* (A - female, B - male), C - D - *E. treschali* (C - female, D - male); E - G - hydrobioids (after FALNIOWSKI 1987): E - *Murstoniopsis scholtzi*, female; F - G - *Potamopyrgus jenkinsi* (F - parthenogenetic female, G - the only male found in Poland); not to scale

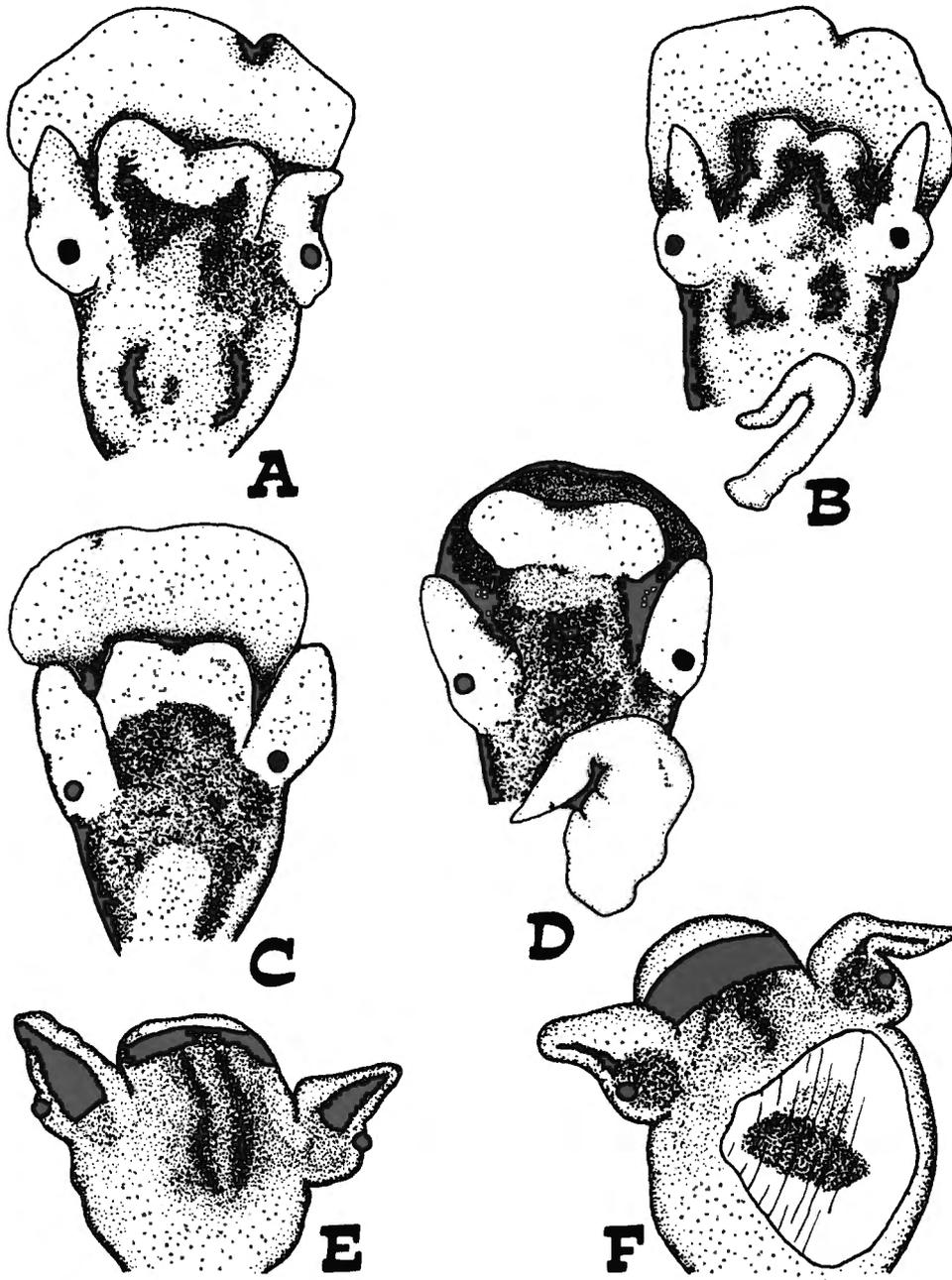
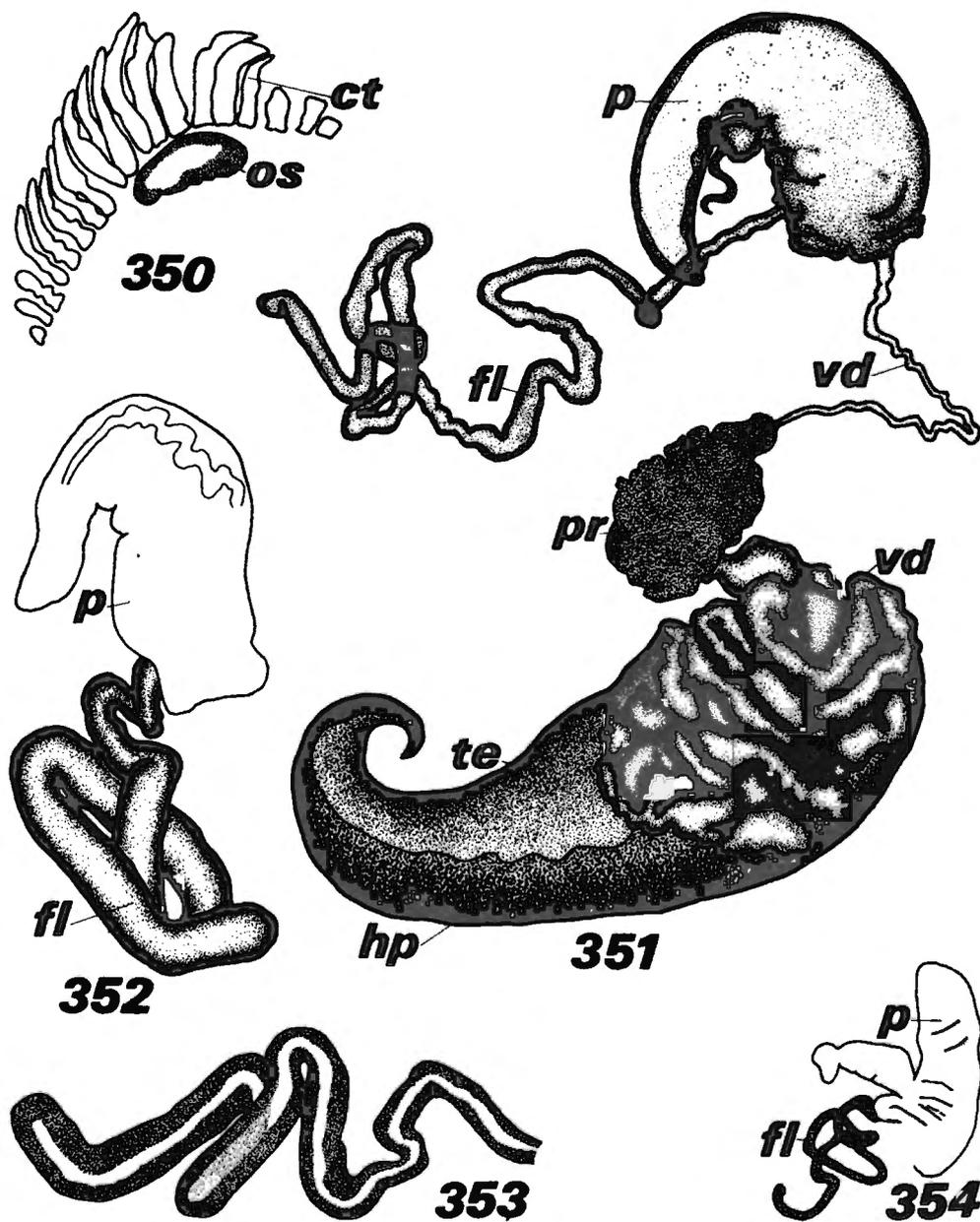
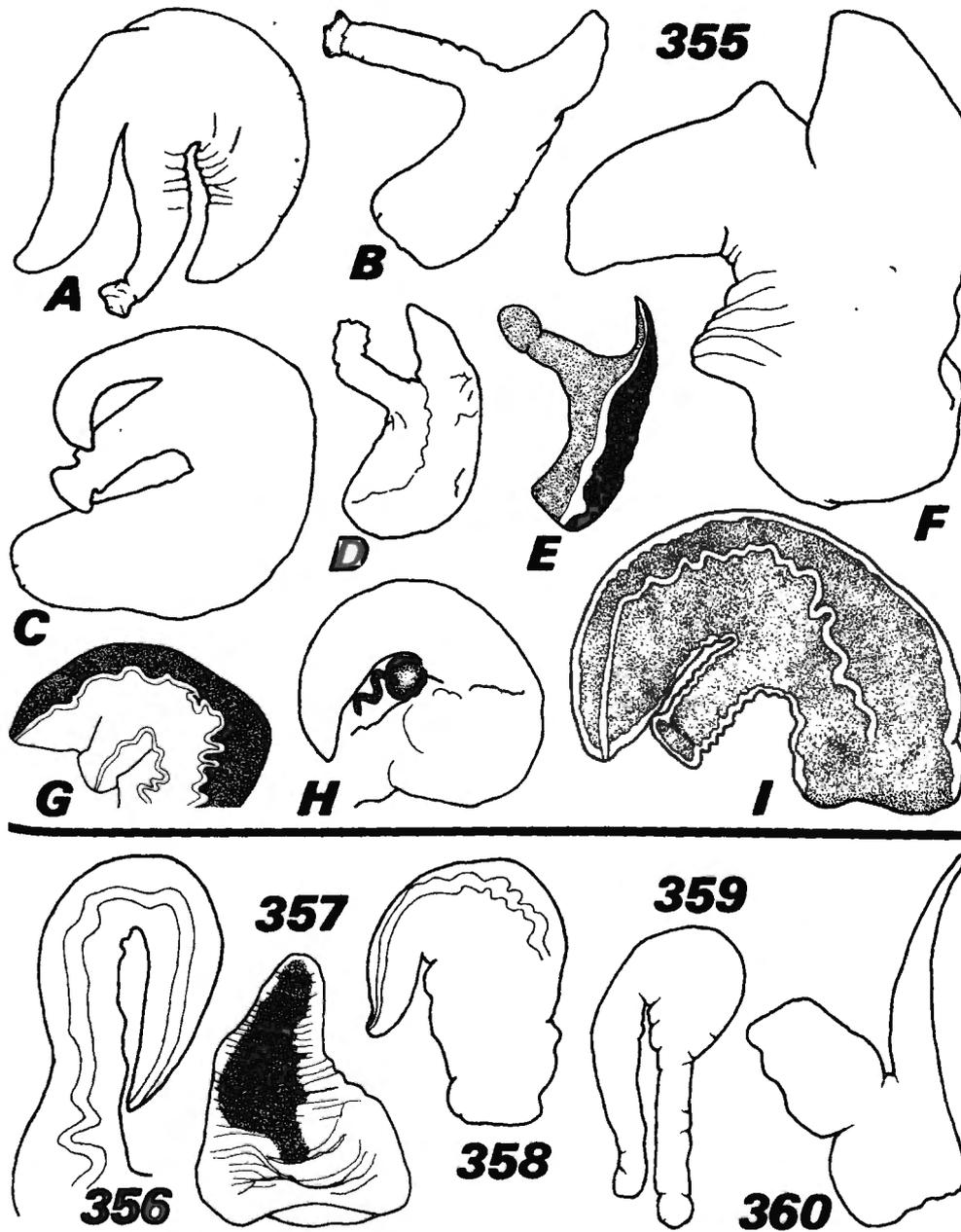


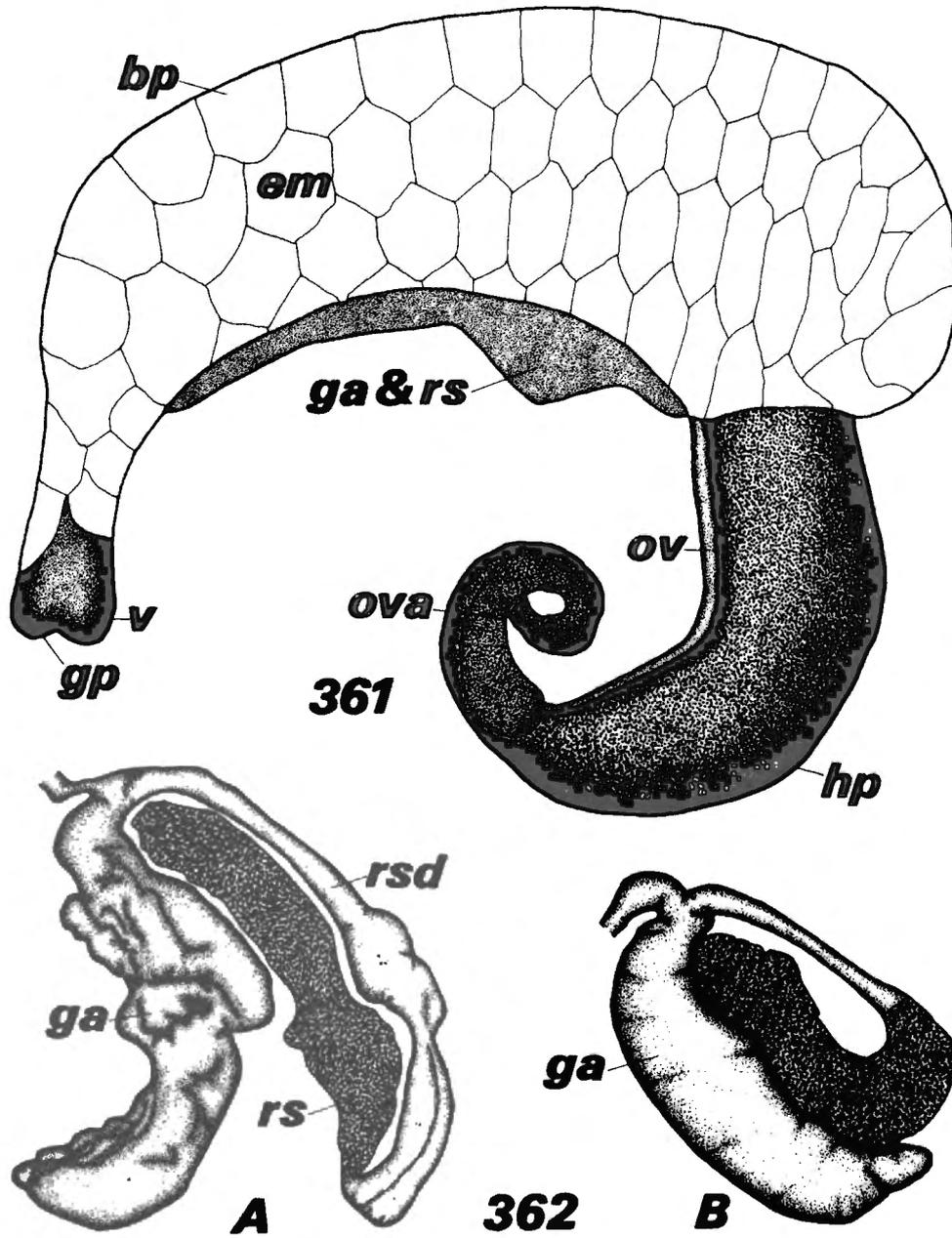
Fig. 349. Head habitus and pigmentation pattern (after FALMOWSKI 1987): A - B - *Bythinella micherdzinski* (A - female, B - male), C - D - *B. zysiontski* (C - female, D - male), E - F - *Lithoglyphus naticoides* (E - female, F - male); not to scale



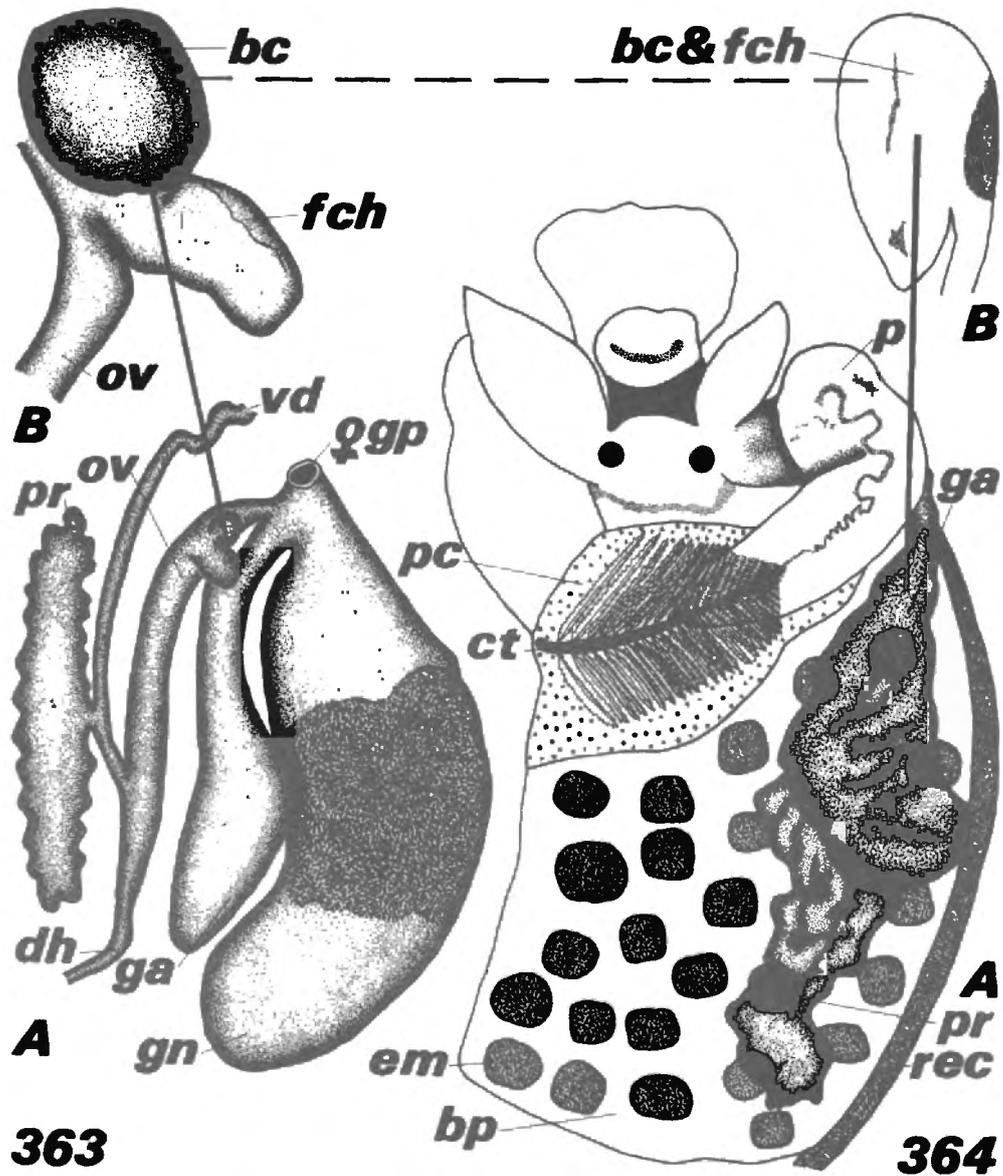
Figs. 350 - 354: Fig. 350 - ctenidium and osphradium of *Bythinella*; 351 - male reproductive organs of *Bitthymia braschei*, to show the position of the flagellum; 352 - penis with flagellum of *Bythinella zymianeki*; 353 - flagellum of *Bythinella*; 354 - penis with flagellum of *Bitthymia leachi*; 350 and 352 - 353 - after FALNIOWSKI (1987); 351 and 354 - after FALNIOWSKI (1989a).



Figs 355 - 360. Verges of some Polish prosobranch: 355 - *Dilthyria* spp., to illustrate variability range and characters (after FALNIOWSKI 1989a): A - F - *B. anteculata*, G - H - *B. leachi*, I - *B. troscheki*; 356 - *Valvata* spp.; 357 - *Lithoglyphus naticoides*; 358 - 359 - *Bythinella*: 358 - *B. zymonteki*, 359 - *B. micherdzinski*; 360 - *Marstoniopsis scholtzi*



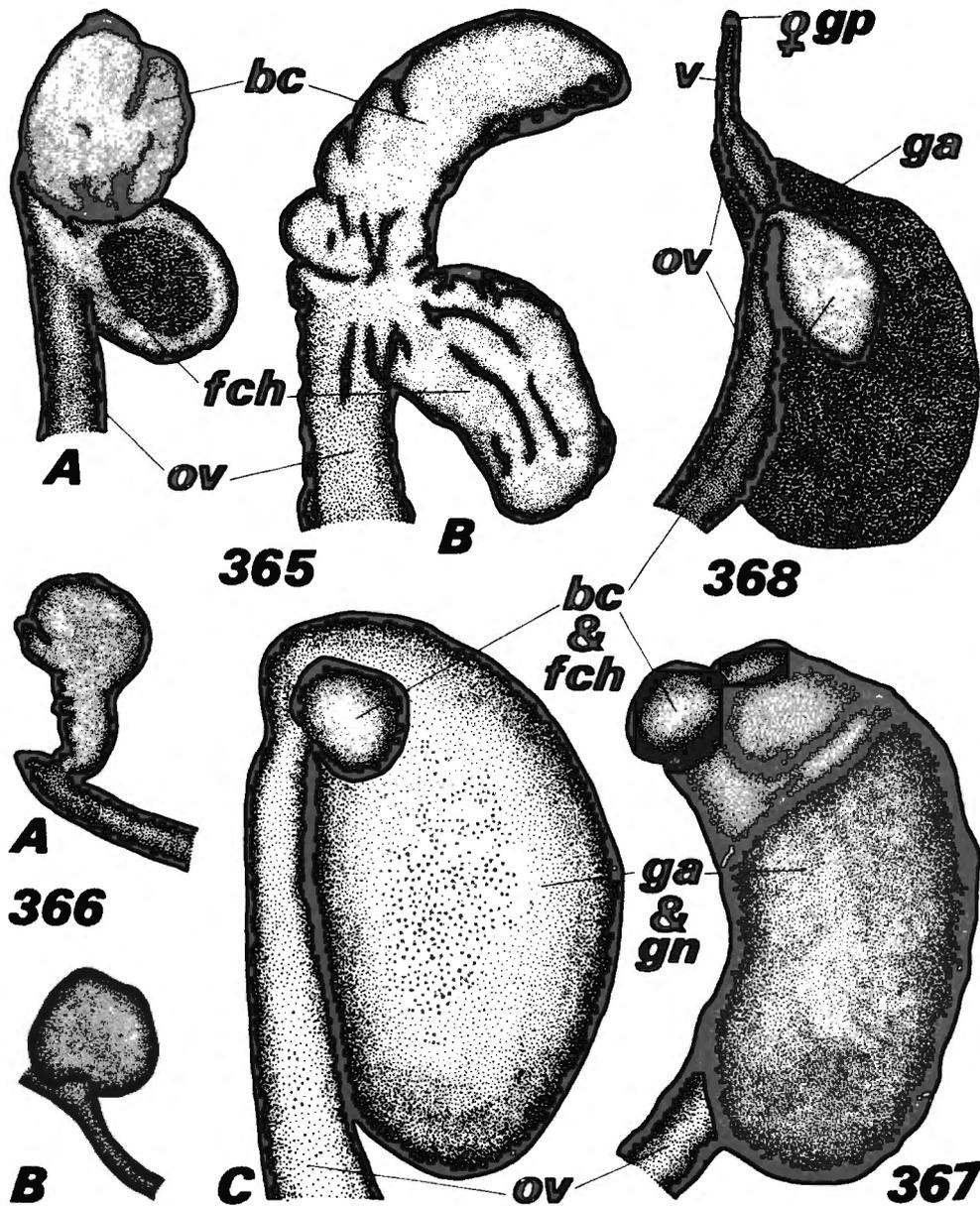
Figs. 361 - 362. Female reproductive organs of *Viparus* (after FALNOWSKI 1989a): 361 - the entire organs of *V. constrictus*; 362 - receptaculum seminis with its duct and albuminoid gland: A - *V. constrictus*; B - *V. viparus*



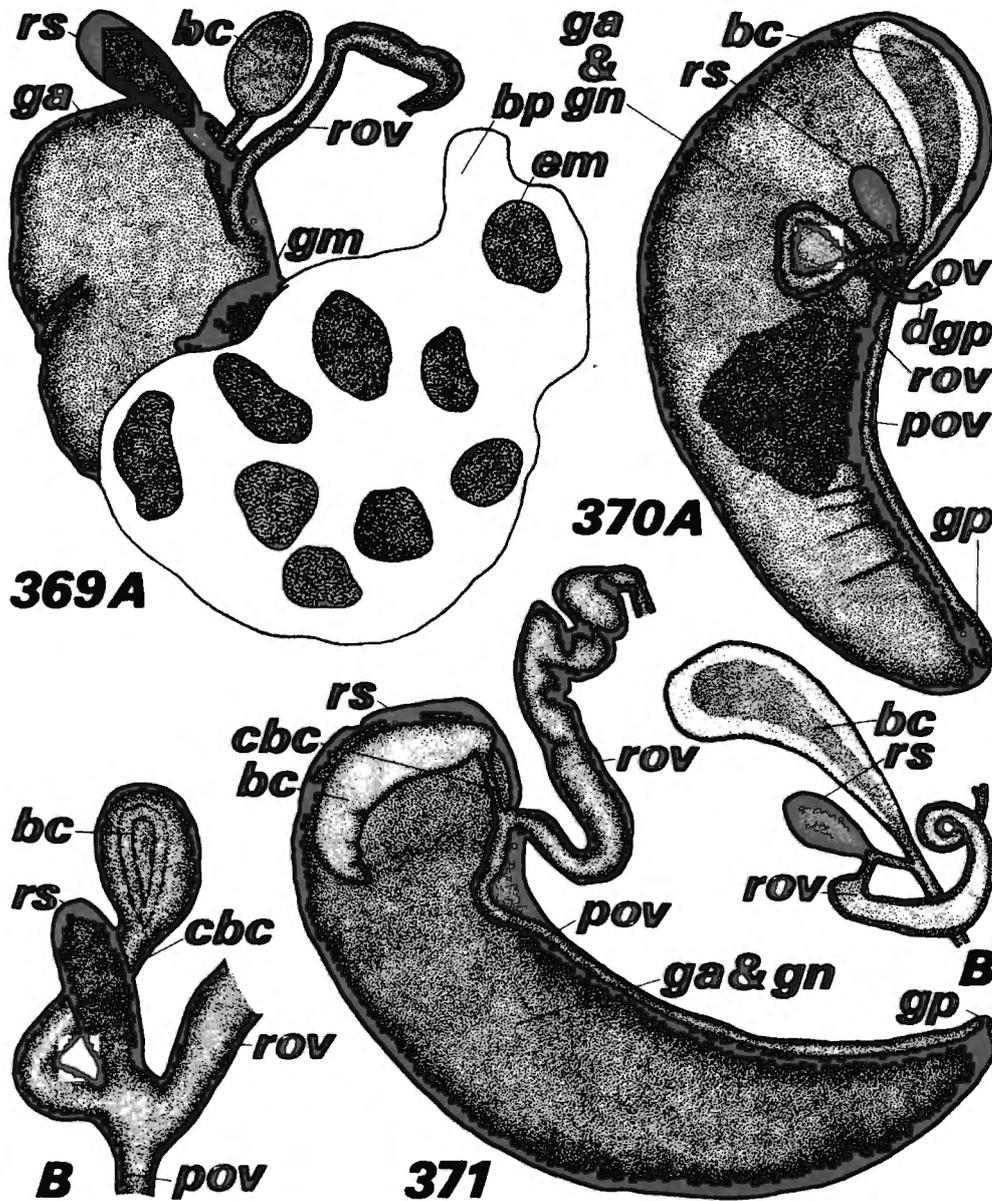
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Figs. 363 - 364. Reproductive organs of *Valvata*, gonade omitted (after FALNIOWSKI 1989a): 363 - *V. piscinalis*: A - the entire organs, B - bursa copulatrix and fertilization chamber; 364 - *V. rubicincta*: A - the organs together with the pallial cavity, head, and foot; B - bursa copulatrix and fertilization chamber



Figs. 365 - 368. Diagnostic characters in female section of valvatid reproductive organs: 365A - B - *Valvata piscinalis*, bursa copulatrix and fertilization chamber; 366 - *V. pulchella*: A - B - bursa copulatrix and fertilization chamber. C - bursa copulatrix and fertilization chamber together with glandular complex; 367 - *V. cristata*, the same as in 366C; 368 - *V. naticina*, the same as in 366C and 367; after FALNIOWSKI (1969a)



Figs. 369 - 371. Renal and pallial section of female reproductive organs of some hydrobioids: 369 - *Potamopyrgus jenkinsi*: A - whole section, B - receptaculum seminis, bursa copulatrix and oviduct; 370 - *Lithoglyphus naticoides*: A - whole section, B - receptaculum seminis, bursa copulatrix and oviduct; 371 - *Marstoniopsis scholzei*, whole section; after FALNOWSKI (1967)

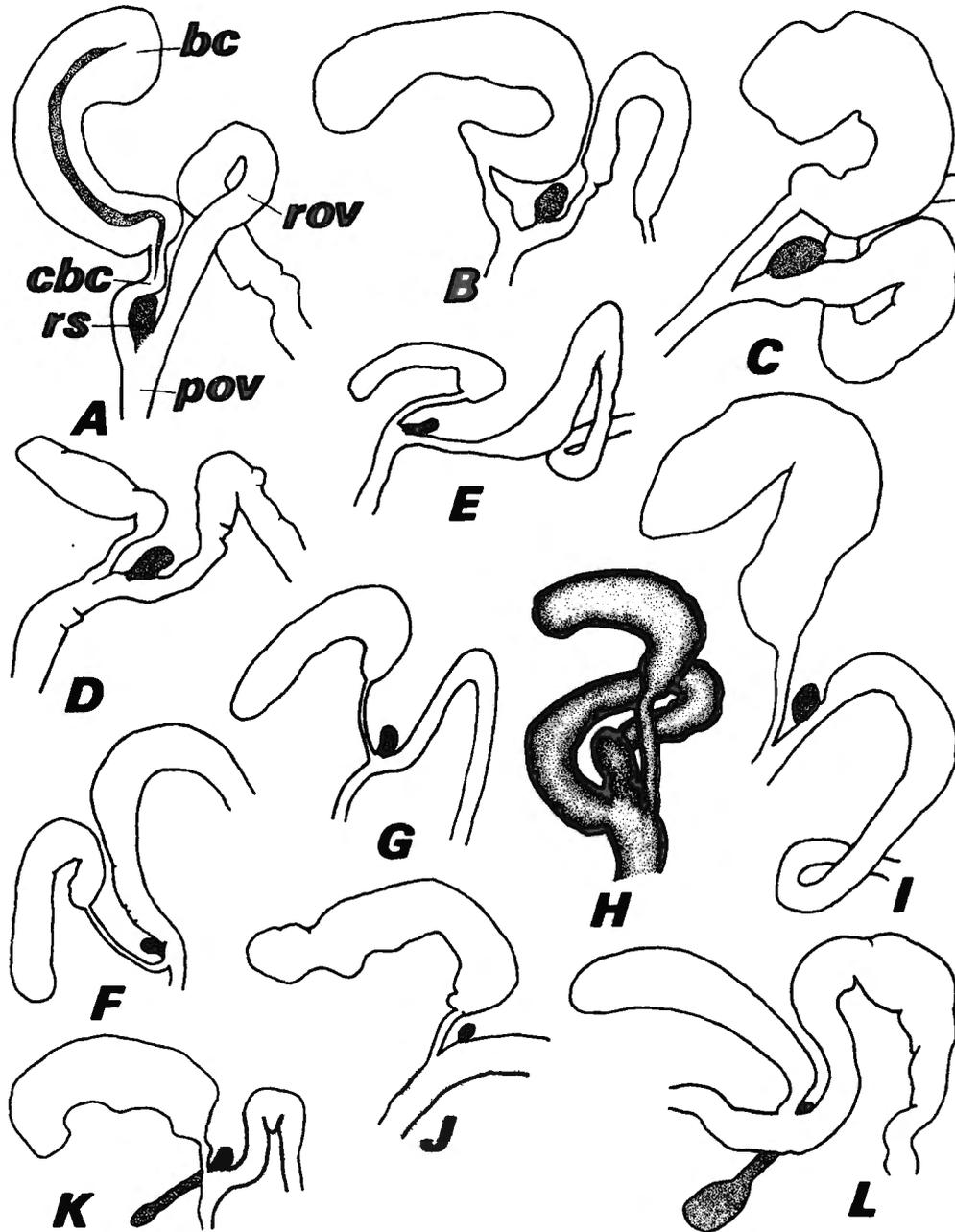


Fig. 372. Receptaculum seminis, bursa copulatrix and oviduct in the *Bythinellidae*, to show variability range and character: A - E - *Bythinella zymonteki*, F - J - *B. micherdzinski*, K - L - *Marstoniopsis scholzei*; after FALNIOWSKI (1987)

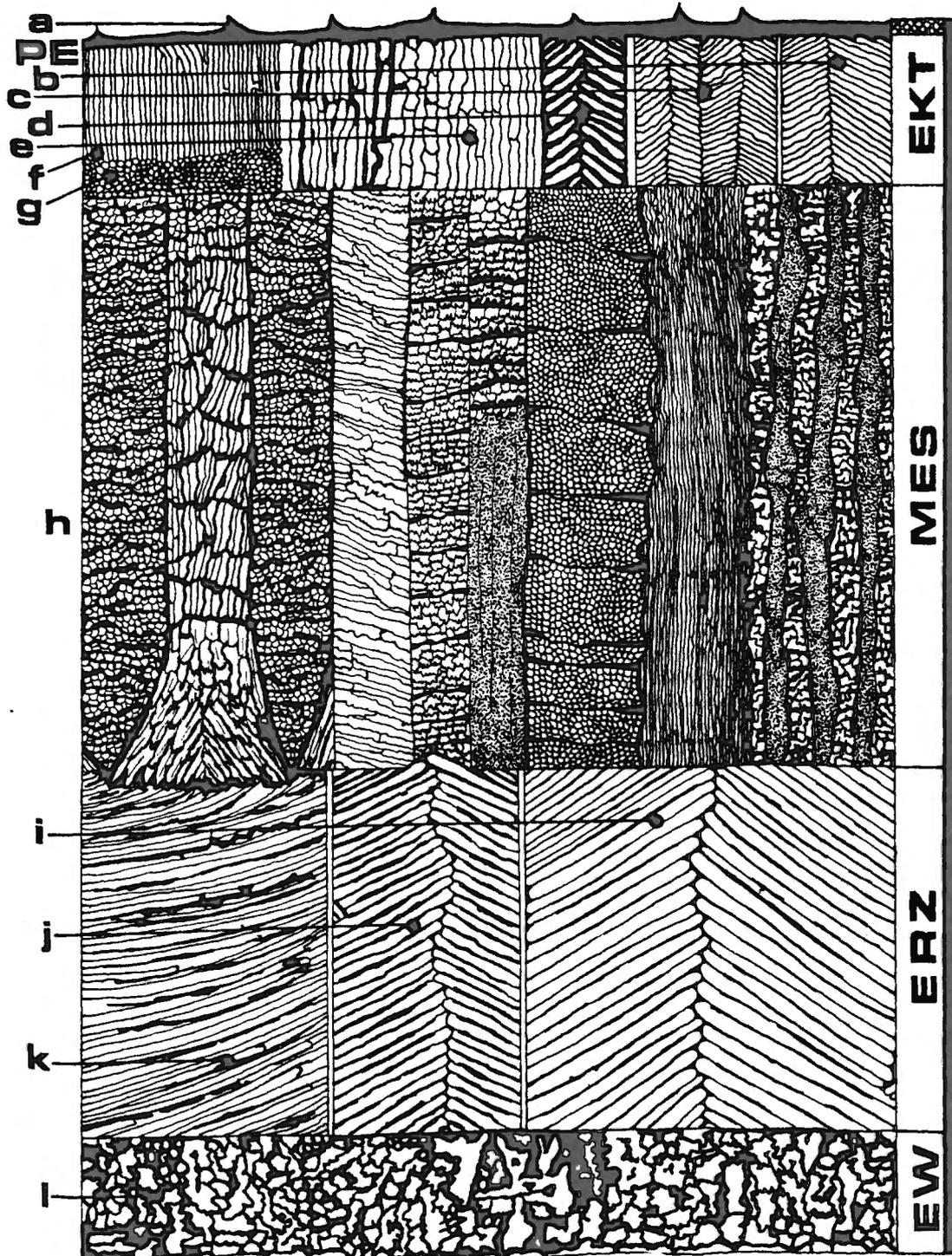
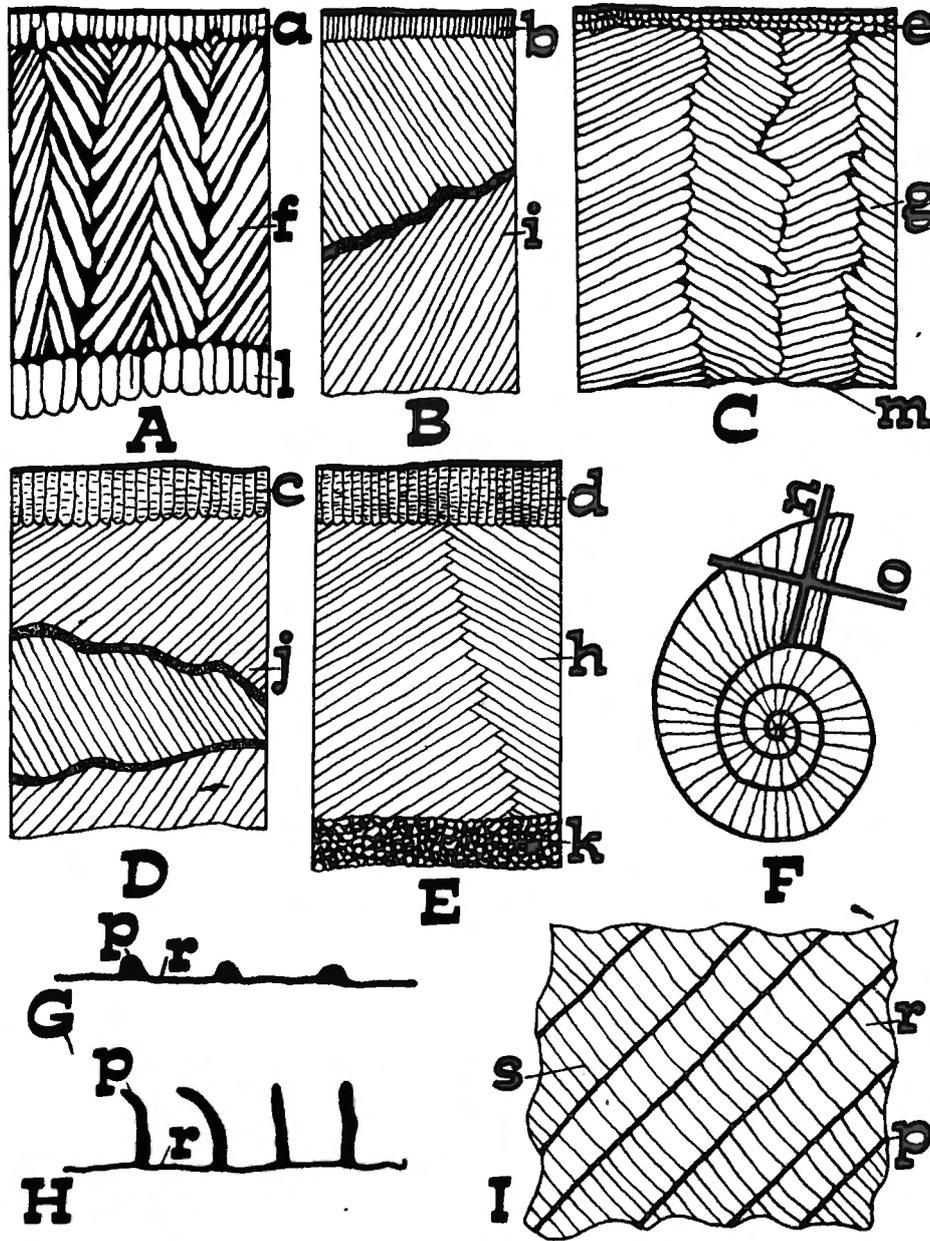


Fig. 373. General organization scheme of shell section perpendicular to growth lines (after FALNIOWSKI 1989a); for explanations to symbols, see Appendix II



Figs. 374. A - E - various modes of organization of sections parallel to growth lines, for explanations to symbols see Appendix II; F - orientation of sections: n - parallel to growth lines, o - perpendicular to growth lines; G - nonlaminar growth lines: p - growth line, r - interstice; H - laminar growth lines (abbreviations as in G); I - fragment of teleconch outer surface (abbreviations as in G, s - spiral riblet)

STRESZCZENIE

Cechy anatomiczne oraz struktury SEM tarki i muszli w systematyce szczebla gatunkowego słodkowodnych przodoskrzelnych *Mollusca: Gastropoda: Prosobranchia*: studium porównawcze ich użyteczności

Przedmiotem pracy jest porównawcza analiza użyteczności różnych cech w systematyce szczebla gatunkowego ślimaków przodoskrzelnych (*Prosobranchia*). Jej podstawą są wyniki badań autora nad 15 gatunkami ślimaków przodoskrzelnych, zamieszkujących różnego typu siedliska słodkowodne w Polsce (Appendix I zawiera ich listę, wraz z uwagami dotyczącymi ich systematyki).

Po przedstawieniu zarysu historii badań nad anatomią, tarkami, a także powierzchniami i wewnętrzną strukturą muszli, autor przedstawia stosowane przez niego metody badań powierzchni i przełomów muszli w mikroskopie skaningowym (SEM). Appendix III zawiera uwagi nad zmiennością i potencjalnymi artefaktami obserwowanymi w obrębie struktur muszli widocznych w SEM.

Następnie autor szczegółowo omawia, dla wszystkich gatunków, struktury badane w SEM – tarkę, pokrój i zewnętrzną powierzchnię protokonchy (muszli embrionalnej), zewnętrzną powierzchnię teleokonchy (makro- i mikrourzeźbienie), wewnętrzną powierzchnię teleokonchy, a na końcu – wewnętrzną strukturę teleokonchy, widzianą na przełomach prostopadłych i równoległych do linii przyrostów muszli. Opisy te są zilustrowane 336 zdjęciami SEM.

Tarki omówiono dla 13 gatunków (z uwagi na brak materiału, pominięto *Valvata cristata* i *V. naticina*), zwracając uwagę na obserwowaną dużą zmienność i słabo zaznaczające się różnice pomiędzy gatunkami (wyraźne różnice pomiędzy bliskimi sobie gatunkami stwierdzono jedynie dla *Valvata piscinalis* i *V. pulchella*). Szczegółowo opisano wszystkie rodzaje zębów i zakresy ich zmienności.

Protokonchę omówiono dla 14 gatunków (pominięto *Marstoniopsis scholtzi* z uwagi na brak dostatecznego materiału). Zauważono, że pokrój protokonchy rzadko bywa użyteczny jako cecha w systematyce na poziomie gatunku, toteż zwrócono uwagę na mikrourzeźbienie tego rejonu muszli, bardzo rzadko uwzględniane we wcześniejszej literaturze. Mikrourzeźbienie okazało się bardzo dobrą cechą wyróżniającą poszczególne gatunki w obrębie *Valvatidae*, nieco słabiej zróżnicowane międzygatunkowo wśród *Bithynidae*, a tylko niekiedy użyteczne jako cecha w obrębie *Hydrobioidea*.

Urzeźbienie zewnętrznej powierzchni teleokonchy badano głównie na ostatnim zwoju. Zarówno makro- jak i mikrourzeźbienie okazało się słabo wykształcone i nie różniące się pomiędzy gatunkami. U *Valvatidae* stwierdzono wyraźnie zaznaczające się różnice, podobnie u *Bithynidae*. W obrębie *Hydrobioidea* stwierdzono w większości gatunków obecność charakterystycznych regularnych porów leżących całkowicie w obrębie periostracum. Pory te bywają odsłonięte, przy czym proporcja powierzchni pokrytej odsłoniętymi porami do powierzchni z porami zakrytymi wykazała międzygatunkowe zróżnicowanie.

Wewnętrzne powierzchnie, badane również wyłącznie na ostatnim zwoju, omówiono jedynie dla *Valvatidae* i *Hydrobioidea* (9 gatunków). Dla wszystkich zbadanych pod tym względem gatunków okazały się one dobrymi cechami, wykazującymi międzygatunkową różnorodność przy wewnątrzgatunkowej stałości wykształcenia.

Budowę wewnętrzną teleokonchy badano także na ostatnim zwoju, oglądając w SEM jedynie przełomy dokładnie prostopadłe/równoległe do linii przyrostów muszli. Przełomy prostopadłe okazały się znacznie przydatniejsze dla celów systematyki, jako znacznie bardziej zróżnicowane i bogatsze w potencjalnie użyteczne szczegóły budowy. Odnotowano znaczną zmienność, ale też niewystępowanie jakichkolwiek dwóch gatunków o takiej samej wewnętrznej strukturze muszli.

W porównawczej analizie użyteczności poszczególnych cech, zamieszczonej dalej, omówiono najczęściej dotąd wykorzystywane cechy, jak: muszla oglądana bez użycia SEM, wieczko, zewnętrzna morfologia części miękkich, ktenidium i ostradum, męskie narządy rozrodcze, prącie, żeńskie narządy rozrodcze, a także pigmentacja części miękkich, zwłaszcza głowy. Podstawą tej części są dane zawarte we wcześniejszych pracach autora, ale najważniejsze z nich - istotne dla przeprowadzanej analizy użyteczności cech - krótko przypomniano i zilustrowano 85 rysunkami, a dla cech "makrokonchologicznych" - 62 fotografiami. Zwrócono uwagę na znaczne ograniczenia użyteczności wszystkich praktycznie cech.

W dalszej części tego rozdziału omówiono użyteczność terek, zwracając uwagę na jej znaczną ograniczoność w przypadku systematyki ślimaków przodoskrzelnych na poziomie gatunku. Zwłaszcza dotyczy to sytuacji, gdy rozpatrywany jest wyłącznie zab centralny, jak czyniło wielu badaczy. Następnie omówiono użyteczność zewnętrznej powierzchni proto- i teleokonchy. Dla tej ostatniej zwrócono uwagę na lepsze zaznaczanie się różnic międzygatunkowych w mikro- niż w makrouzależnieniu (to ostatnie tworzą linie przyrostów, spiralne żeberka, kil itp.).

Podkreślono wyraźne międzygatunkowe różnice w wykształceniu powierzchni wewnętrznej ostatniego zwoju, obserwowane dla wszystkich badanych pod tym względem gatunków. Następnie wskazano na gatunkową specyficzność wykształcenia przełomów ostatniego zwoju, zwłaszcza tych prostopadłych do linii przyrostów muszli. Obserwowana tu znaczna zmienność każe jednak analizować cały przełom, wszystkie tworzące go warstwy.

Prace uzupełnia Appendix II, przedstawiający ogólny zarys budowy muszli u omówionych tu ślimaków.