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Finer sculptures in euthecosomatous shells, and their value for taxonomy (Mollusca, Pteropoda).

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ABSTRACT

The protoconch in *Limacina helicoides*, *Peraclis moluccensis*, *Styliola subula*, *Cavolinia globulosa*, *C. gibbosa*, *C. inflexa* and *C. longirostris* are described; finer structures of the shell in these species and *Hyalocylis striata*, *Diacra quadridentata* and *Cavolinia tridentata* are described. The occurrence of a distinct protoconch-I and -II in Cavoliniidae is discussed as well as the taxonomic value of the structure of the ventral ribs in the Cavoliniidae mentioned.

INTRODUCTION

Recent pteropod studies (Be et al., 1972; Rampal, 1972; Boltovskoy, 1974) showed scanning electron microscope (SEM) research to contribute to the knowledge of finer structures, especially of the embryonic shells in Limacinidae and Peraclididae. Sculptures of embryonic parts proved to be specific in some cases and there are indications that taxonomic relations are reflected by finer sculptures in different species.

A critical approach of SEM research is highly necessary, however as the SEM gives no information on structural phenomena of intact objects, as the time-consuming and expensive SEM application usually prevents one from studying variations on a large piece of material. The present study also shows a lack of structural descriptions and surveys variations insufficiently. *Cavolinia globulosa* (Gray, 1850) is studied, mainly with regard to the shedding of the protoconch, to demonstrate its relation to the other Cavoliniidae. The position of the Cavoliniidae among the Thecosomata is discussed because their protoconch proves to be of a typically aberrant type. *Cavolinia longirostris* (De Blainville, 1821) is chosen to demonstrate differences between infraspecific taxa. The possibility to study *Limacina helicoides* (Jeffreys, 1877) is used to describe the embryonic shell. The origin of the material and techniques used are given with the specimens described.

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[105]

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TERMINOLOGY

When describing minor sculptures and structures in Thecosomata, it proved to be necessary to give definitions of terms especially for those phenomena which are not found in other molluscs.

A survey of terms is given below in alphabetical sequence. Terms printed in italics are correct in the author's opinion. Concepts not printed in italics should be omitted as a consequence.

Aberrant stage (c.f. Van der Spoel, 1973) — period in life cycle, after strobilation in which the animal is still in an interstitial stage.

Additional ribs — ribs formed by calcareous concretion in loose contact with the normal shell; they may be added to smooth or sculptured surfaces.

Adult — period of life in which growth stops or diminishes, and in which reproduction and a normal ratio of body and shell (c.f. minute stage) is found.

Anterior — in Thecosomata identical to oral; should be used instead of cranial. The anterior side is the side where the wings are attached or, as for the shell, the side at which the aperture is found.

Aperture — opening of shell through which soft parts protrude anteriorly.

Aperture prismatic layer (c.f. Be et al., 1972) — the prismatic layer along the aperture rim, added after the shell has grown to its final size.

Aperture spine — protrusion of aperture border (found in Limacinidae and Peraclididae).

Aperture teeth — confusing term to be replaced by aperture spine.

Caudal — confusing term to be replaced by posterior.

Caudal spine — confusing term to be replaced by protoconch.

Closing mechanism — two articulations in the aperture connecting dorsal and ventral shell halves (found in Cavoliniinae).

Closing membrane — total of calcareous layers closing the teloconch posteriorly when the protoconch has been shed.

- Columellar membrane* — calcareous membrane along the columella, elongated posterior to the aperture.
- Columellar myostracum* — (c.f. Be et al., 1972) — prismatic layer at the place of secondary attachment of the columellar muscle formed inside the helical layer before formation of a closing membrane.
- Cranial* — confusing term to be replaced by anterior.
- Dorsal* — side in Limacinidae where the mantle gland is found, in Cavoliniidae side opposite to the mantle gland.
- Dorsal lip* — shell part protruding dorsally over aperture.
- Dorsal ribs* — all sculpture lines over the dorsal side of the shell.
- Dorsal spine* — prolongation of dorsal shell side anterior to aperture in Cavoliniidae.
- Double ribs* — sculptured ribs showing two tops in cross section.
- Embryonic* — phenomena related to the period in the life cycle spent in the egg capsule.
- Embryonic ring* — transversal irregularity or ring structure between protoconch-I and -II or between protoconch-II and teloconch.
- Embryonic shell* — confusing term to be replaced by protoconch-I in most cases.
- Free hanging septa* — confusing term for the initials of the closing membrane.
- Growth rings* — irregularities in shell structure and sculpture due to fluctuations in growth speed or type of growth.
- Growth striae* — confusing term for growth rings.
- Imbricate* — the phenomenon of ribs showing a more or less hollow anterior side.
- Inner callus* — all calcareous material formed inside the inner helical layer other than aperture layer, columellar myostracum and closing membrane.
- Inner helical layer* (Be et al., 1972) — thick inner layer composed of aragonite rods arranged in helical structure, found in Cavoliniidae.
- Inner laminar layer* — (Be et al., 1972) — the same as the preceding layer, but composed of a crossed laminar aragonite structure found in Limacinidae.
- Larval shell* — confusing term to be replaced by protoconch-II.
- Lateral aperture prolongations* (= lateral aperture slits) — the part of the aperture posterior to the closing mechanisms.
- Lateral ribs* — (thickened) shell parts between posterior corners of aperture and lateral corners of protoconch mark or protoconch-I.
- Lateral spines* — lateral prolongations of the shell at the level of the posterior aperture corners.
- Lips* — confusing term for shell parts; to be used only for the oral lips of the soft parts; dorsal lips and ventral lips should be used only in that combination for shell parts.
- Longitudinal* — running in the direction of growth.
- Minute stage* — (c.f. Van der Spoel, 1967) — stage of the lifecycle in which soft parts are extremely small in relation to the shell and in which the spec-

imen is immature, while the columellar muscle is attached to its definite place.

Organic matrix — thin organic layer formed before calcification of shell.

Outer callus — all calcareous structures formed additional to shell outside outer prismatic layer.

Outer prismatic layer — (Be et al., 1972) — thin prismatic aragonite layer of shell (in Cavoliniidae).

Periostracum — (Be et al., 1972) — organic film covering outer shell surface.

Permanent shell — confusing term to be replaced by teloconch.

Posterior — hind side, where protoconch and insertion of columellar muscle in Cavoliniidae is found.

Posterior spine — confusing term to be replaced by protoconch.

Primary ribs — ribs dominating shell surfaces being higher than the secondary ribs.

Protoconch-I — shell part formed during the embryonic stage in the egg capsule.

Protoconch-II — shell part formed during larval stage before metamorphosis, in Cavoliniidae before the occurrence of minute or skinny stages.

Rostrum — (in Peraclididae) — elongation of the aperture by prolongation of the columella.

Reticulate — pattern of crossing ribs.

Secondary ribs — ribs minor to primary ribs formed in between the latter.

Septal insertion prismatic layer (Be et al., 1972) — the same structure as columellar myostracum layer.

Septal membrane (Be et al., 1972) — thin membrane on which closing membrane is formed, its presence is hypothetical and as discussed below not likely to exist.

Skinny stage — (Van der Spoel, 1967) — immature stage in life cycle in which the soft parts are small and skinny as they are torn out by the rapidly growing shell.

Spine cracks — cracks along lateral sides of protoconch-II and teloconch in Cavoliniidae.

Suture — place where two whorls in coiled shells touch each other.

Suture crests — sculptures radiating from a whorl, over the suture, to the next whorl.

Teloconch — adult shell, all parts formed after completion of protoconch-II.

Transversal — perpendicular to direction of growth.

Veliger stage — stage of life cycle between embryonic and adult stage, during which protoconch-II is formed.

Ventral — in Cavoliniidae the side in contact with the mantle gland and in Lamacinidae the opposite side.

Ventral lip — shell part bordering the ventral margin of shell aperture.

Waved ribs — sculptural ribs which, at one side, show a type of horns or points in wavy arrangement.

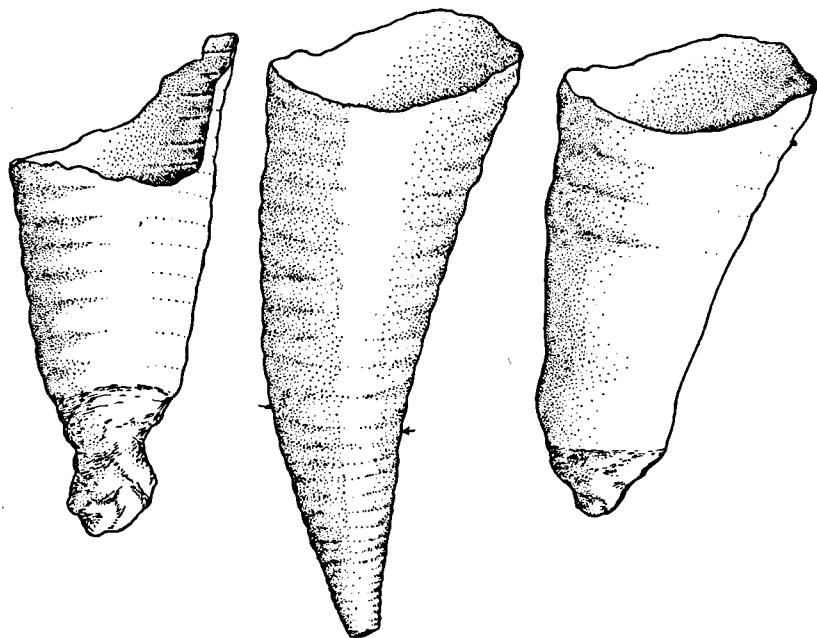


Fig. 1. *Hyalocylis striata*, three adult specimens, left and right one after damage during life, central one undamaged (5.6 mm in length), all specimens given with the same enlargement.

RESULTS

Limacina Gray, 1847 (see Rampal, 1972 and Boltovskoy, 1974)

Limacina helicoides Jeffreys, 1877; collected at 33°N 64°06'W, 27-8-1971; Ocean Acre Program, cruise 12 Stat. 5B, preserved in alcohol 70%, gold coating $\pm 190 \text{ \AA}$, subadult specimen, ZMA reg. no. 3133. (Pl. I figs. 1—5).

This is the only deepwater species in the family and the only one showing ovoviviparity. The protoconch-I, the protoconch-II, and the teloconch show different structures (Pl. I fig. 1). In other Limacinae a distinct protoconch-II is not found. It seems correct to assume that the protoconch-II is formed during the larval period spent in the female animal when the youngsters are kept in the accessory sexual gland. The protoconch-I is covered with rather coarse, more or less pyramidal, tops which are smaller when nearer to the protoconch-II (Pl. I figs. 3—4). The protoconch-II consists of $\frac{3}{4}$ whorl and shows no sculptures. Its surface is, however, not entirely smooth but dentated. An embryonic ring is clearly seen between protoconch-II and teloconch. The first whorl of the teloconch is covered with spiral lines of small grains composed by outer callus (Pl. I fig. 2). The other parts of the teloconch whorls are smooth. The suture, especially around the protoconch,

is provided with numerous small and irregular suture crests (Pl. I fig. 5). These crests are probably comparable to those formed in *Peraclis*.

Peraclididae Tesch, 1913 (see Boltovskoy, 1974)

Peraclis moluccensis Tesch, 1903 (see Boltovskoy, 1974); collected at 59°N 19°W, 19-6-1964; Cirrus Expedition, Stat. 9F, preserved in alcohol 70%, gold coating $\pm 160 \text{ \AA}$, adult specimen, ZMA reg. no. 289 (Pl. I figs. 6—8).

To show the suture crests in *Peraclididae* a photograph (Pl. I fig. 6) is added of these crests in *P. moluccensis*. The crest can be followed much longer over the whorl than in *L. helicoides* and there are clearer knobs at their beginning in the former species. Seemingly related to the suture crests are the transversal ribs near the rim of the aperture spine. In my opinion these sustaining ribs are, however, of another origin than the crests, as the structure of the shell surface between the ribs differs from the suture structure. The protoconch-I is given (Pl. I fig. 8) to show the difference with *L. helicoides*. Both species do not differ principally in these structures. When the reticulate-like sculpture of *P. moluccensis* becomes more coarse, so that the bases of the elevations touch each other, a sculpture as found in *L. helicoides* is formed.

Cavoliniidae Fischer, 1883

Creseis Rang, 1828. In all species of this genus the protoconch and teloconch are both smooth.

Styliola subula (Quoy & Gaimard, 1827); collected at 19°35'N 73°27'W; Dana Expedition, Stat. 1245V, preserved in alcohol 70%, gold coating $\pm 160 \text{ \AA}$, adult specimen (Pl. II figs. 4—5, 8).

The teloconch and protoconch are in this species smooth like in the genus *Creseis*. The protoconch-I (Pl. II fig. 8) of the present specimen shows a corroded surface, from the posteriormost top even a layer is absent. This corrosion is not caused by preservation as the remainder of the shell shows a perfectly smooth surface (upper right and lower left corner in Pl. II fig. 4). The asymmetrical, longitudinal rib in this species shows a remarkable structure at the inside (Pl. II figs. 4—5), due to mountainlike warts on the rib surface.

Hyalocyclus striata (Rang, 1828); collected at 2°57'S 99°36'E, 19-10-1929; Dana Expedition, Stat. 3860XI + XV, preserved in alcohol 70%, after formalin preservation, adult specimens (text-fig. 7).

From this species no material was available which could be used for SEM studies as the preservatives were inadequate, mostly formalin 4%. To show aberrant posterior closing membranes figure 1 is given. The central specimen is a normal shell with at its top the small, slightly convex closing membrane. The arrows alongside this specimen show the places where the shells at the left and the right are broken respectively before a new membrane has been formed. The shell length of the right and left specimen is comparable to that of juveniles. The posterior top of the left specimen resembles a protoconch

and so does, to a lesser degree, the top of the right specimen. The aperture width is, however, that of full grown shells. The present posterior structures are closing membranes and have nothing to do with the protoconch. The protruding shape of the membrane is due to secretion around the soft parts which have projected posteriorly from the broken shell. Up till now I failed to discover a specimen with a real protoconch. "*Creseis chierchiae*" of Boas (1886) is in my opinion representing the juvenile of this species.

Clio Linnaeus, 1767. The protoconchs studied in *C. pyramidata* Linnaeus, 1767, *C. cuspidata* (Bosc, 1802), *C. polita* (Pelseneer, 1888) and *C. recurva* (Childern, 1823) are of the smooth type.

Cuvierina Boas, 1886. This genus shows a smooth protoconch. The transitional and longitudinal striae on the teloconch are not studied.

Diacria Gray, 1847. This genus shows a protoconch of the smooth type.

Diacria quadridentata quadridentata (De Blainville, 1821) forma *danae* Van der Spoel, 1968; collected at 15°17'N 61°29'W, 1-4-1922; Dana Expedition, Stat. 1286V, preserved in alcohol 70%, gold coating $\pm 160 \text{ \AA}$, adult specimen, ZMA reg. no. 3144. (Pl. II figs. 1—3; Pl. X figs. 3, 11).

In this species the protoconch is shed after the larval stage when the minute stage is reached. For *Cavolinia globulosa* and *C. unicata* is demonstrated that the caudal spine in Cavoliniidae is in general identical to the protoconch. At the place where the protoconch breaks a closing membrane is formed. The membrane is secreted in the original shell before shedding takes place, in such a way that after the rupture part of the original shell forms a wall posteriorly around the closing membrane (Pl. II fig. 2). The surface of the closing membrane shows an irregular structure.

The borders of the shell aperture are formed by the aperture myostracum layer. In *D. quadridentata* and *D. trispinosa* this layer is curled outwards so that the irregular rims of the separate myostracum layers point posteriorly (Pl. II fig. 1).

The surface of the shell below the aperture rim is smooth except for the normally described sculptures and granules spread over the surfaces between the ribs. These granules are found over the entire shell also on the ventral side (Pl. X fig. 3). From this figure it is clear that the ventral side is provided with primary and secondary sculpture ribs of which there are about 18 between two primary ones. These secondary ribs are figured more enlarged in Pl. X fig. 11; the granules are shown as irregular white dots.

Cavolinia gibbosa (D'Orbigny, 1836); collected at 24°36'5N 17°27'W, 18-3-1930; Dana Expedition, Stat. 4009III, preserved in alcohol 70%, gold coating $\pm 160 \text{ \AA}$, adult specimen, ZMA reg. no. 3129. (Pl. III figs. 1—4; Pl. IV figs. 3—4; Pl. VI figs. 5—6; Pl. X fig. 12)

The ribs on the ventral side of this species show some typical characters found in most Cavoliniidae. Pl. III fig. 1 pictures the ventral ribs of which the

fourth from the top shows a double rim (Pl. III fig. 2) and the fifth from the top shows parts of an additional rib (discussed more fully under *C. globulosa*). Between the primary ribs some 12 secondary ribs are found like in *D. quadridentata*. The grains as found on the surface in *D. quadridentata* are more irregular here (Pl. III figs. 3—4).

The protoconch-I is usually broken, but in a few specimens it is still present (Pl. IV fig. 4). Protoconch-I shows a fine transversal striation (Pl. IV fig. 3), the protoconch-II shows a transversal striation as fine as that in the younger part, but with ring intervals about twice as wide. The embryonic ring between protoconch-I and -II forms a clear incision. All rings run parallel in the protoconch of this species. Under high magnification secondary rings are visible on the two protoconchs between the primary ones (Pl. IV fig. 3). Near the anterior top of protoconch-II the shell shows spine cracks (Pl. VI fig. 5), which are dichotomously branched cracks in the shell concentrated along its lateral sides. The transversal ribs, typical for protoconch-II, are disappearing here. They are replaced by a faint type of the ventral sculpture, crossed by longitudinal ribs (Pl. VI fig. 6), which remain distinctly anterior in *C. uncinata*, but which disappear rapidly in this species.

Cavolinia globulosa (Gray, 1850); collected at 3°40'5N 137°33'E, 12-7-1929; Dana Expedition, Stat. 3751IV, preserved in alcohol 70%, gold coating \pm 160 A, adult specimen, ZMA reg. no. 3126, minute specimen, ZMA reg. no. 3127 (Pl. IV figs. 1—2; Pl. VIII figs. 1—2; Pl. IX figs. 1—9; Pl. X figs. 1—2, 4—5, 7, 9).

This is the only species showing external callus in the posterior shell part forming the protoconch-II (Pl. IV fig. 1; Pl. IX fig. 4). This callus is composed of two latero-dorsal and two latero-ventral ribs beginning near the protoconch mark. This callus is present in adults and in specimens in minute stage. It was described in literature (c.f. Van der Spoel, 1967) as forming four crests over the posterior shell point. From the photographs (Pl. IX figs. 8, 6) it is clear the callus is formed in addition to the original shell. This species shows, like the preceding one, cracks along the lateral side. These protoconch cracks occurred after the formation of the striae of the protoconch-II, but they occurred in all probability simultaneously with the outer callus crests, as the crests are sometimes covered by the callus and sometimes cross the callus (Pl. IX figs. 3, 6). The cracks are usually directed transversally and rarely longitudinally.

The closing membrane — not described for this species before — is formed after shedding the protoconch but not necessarily during the minute stage. The membrane is formed during the minute or the adult stage. The closing membrane is an irregularly formed calcareous layer (Pl. IX figs. 1, 2), which is in the present specimen separated by a crack from the original shell (Pl. IX fig. 7). By its wavy and granulated character it is shown that the membrane is deposited quickly and without a fixed scheme of cristallisation. When the membrane has not yet been formed (Pl. IV fig. 1) the protoconch

cracks are still absent and the outer callus is not yet completely present. The closing membrane being formed on a previously secreted septal membrane (Be et al., 1972) is contradictory to the structure of the membrane itself. A regular calcification is to be expected on a septal membrane and not the irregular structures as usually found.

The situation on the protoconch-II (Pl. IV fig. 2) is of the normal type. The ribs on dorsal (Pl. VIII fig. 1) and ventral (Pl. VIII fig. 2) sides are composed of primary ribs and secondary ribs. Between two primary ventral ribs about 12 secondary ribs are found while between the primary dorsal ribs about 14 secondary ones are found. On the top of the primary ventral ribs additional ribs are present (Pl. IX figs. 8—9). The fact that these ribs are added to the original shell without having grown together with the shell is demonstrated in the figures 8 and 9, where in figure 8 part of the additional rib is absent. Under the additional rib the shell surface continues without interruption, and it is only somewhat more punctated under the additional rib. The posterior shell points were broken off in all investigated specimens, so that only the structure of protoconch-II could be studied.

Cavolinia uncinata uncinata (Rang, 1829) forma *roperi* Van der Spoel, 1969; collected from sediment near Frederikstadt, St. Croix (17°N 65°W, depth 500 fathoms); preserved dry, gold coating $\pm 160 \text{ \AA}$, adult specimen. (Pl. IV figs. 5—8; Pl. VIII fig. 11)

This shell from the sediment was chosen to show that the finer structures are preserved also in dead shells from the sediment. The protoconch in this species is usually present throughout life, except for the tip of protoconch-I which is frequently broken. The sculpture of the protoconch is nearly identical to that in *Cavolinia inflexa*. The protoconch-I shows closely set transversal ribs (Pl. IV fig. 6) and the protoconch-II shows the same type of ribs with mutual distances twice as wide as on the protoconch-I. An embryonic ring is absent. The last rings on the protoconch-I are interrupted by material of protoconch-II. This results in a non-parallel orientation of the striae in protoconch-I and protoconch-II (Pl. IV fig. 5). The anterior rim of protoconch-II is hard to trace as in most species. Its structure comes gradually to an end where the abrupt widening of the shell begins.

The ribs on the ventral shell side (Pl. IV figs. 7—8) are typically different from those in the other species by the reticulate pattern and the additional ribs dominating the shell.

The transversal additional ribs are formed on top of small normal ribs so that the complex of both causes an imbricate structure.

The additional ribs are so strongly developed in this species that they can be seen without magnification as white rims on the ventral surface. Between the transversal additional ribs, secondary ribs are found, but they are of variable strength and sometimes they disappear completely. The reticulate pattern of longitudinal and transversal ribs (Pl. IV fig. 8) gives rise to a hammered appearance of the shell. This hammered appearance is also found

in the posterior half of the ventral side in *Cavolinia tridentata*, *C. globulosa*, *C. gibbosa* (Pl. VI fig. 6) where it is caused by the same, though less pronounced, sculptures.

Studies with light microscope showed that this description is representative for all the infraspecific taxa of *C. uncinata*. Only minor differences can be found in the development of the rib sculpture.

Cavolinia inflexa (Lesueur, 1813); collected at 15°17'N 61°24'W, 7-4-1922; Dana Expedition, Stat. 1286V, preserved in alcohol 70%, gold coating ± 160 Å, juvenile specimen, ZMA reg.no. 3142, adult specimen ZMA reg.no. 3143. (Pl. V figs. 1—2; Pl. X figs. 8, 10).

The juvenile specimen was identified according to the criteria given by Troost & Van der Spoel (1972). The protoconch of the juvenile and the adult specimen proved to have an identical structure and both differed distinctly from juveniles of *Cavolinia longirostris*. The protoconch in the present species (Pl. V figs. 1—2) resembles that of *Cavolinia uncinata* most (Pl. IV fig. 5). The protoconch-I shows imbricate transversal ribs. A real embryonic ring is absent.

The transition between protoconch-I and protoconch-II consists of an abrupt change in rib figuration. The imbricate transversal ribs of the protoconch-II show mutual distances twice as wide as in the protoconch-I; and the perfect circular shape of the ribs is lost at the lateral side by a small undulation posteriorly. Between the protoconch ribs no secondary ribs were found. In the area of the embryonic ring the first ribs of the protoconch-II are complete, while the last rings of the protoconch-I are interrupted by material of protoconch-II.

Cavolinia longirostris (De Blainville, 1821). In this species six formae are distinguished, five of which could be studied; material of the forma *strangulata* (Deshayes, 1821) was not available. The forma *angulosa* (Gray, 1850) was used to compare the structure of the protoconch in this and the preceding species. The study of the other formae deals only with the teloconch.

Cavolinia longirostris (De Blainville, 1821) forma *longirostris* (De Blainville, 1821); collected at 19°35'N 73°27'W; Dana Expedition, Stat. 1245V, preserved in alcohol 70%, gold coating ± 160 Å, adult specimen. (Pl. II figs. 6—7; Pl. III fig. 5; Pl. V fig. 5; Pl. VI figs. 3—4; Pl. VIII figs. 3—5, 7—8).

Closure of the permanent shell after shedding of the protoconch, in this species, is a process different from that in the other species (c.f. Troost & Van der Spoel, 1972). It is a primitive filling of the opening by a folded callus (Pl. V fig. 5; Pl. VI figs. 3—4). The transformations along the lateral ribs show that the teloconch changed in shape posteriorly, so that the opening is closed by a mere narrowing. (Pl. VI fig. 1). The place where the posterior part is broken off at the level of the protoconch-II is shown by the striae of the protoconch-II on the permanent shell. (Pl. V fig. 5).

It was in this forma that the presence of a periostracum could be demonstrated. On the dorsal lip (Pl. II fig. 6) the folded remnants of this layer (Pl. II fig. 7) were easy to distinguish.

The ribs on the ventral side are of taxonomic value. The transversal ribs are to be considered as additional ribs (Pl. III fig. 5). These ribs are of a wavy regular structure, regular undulations border the anterior side of the ribs, the posterior side is nearly straight. All the waves are of the same size and the ribs have only one top. The wavy character is clear in the anterior ribs (Pl. VIII figs. 4—5), less clear in the centre of the ventral side (Pl. VIII fig. 8); the ribs at the posterior end of the ventral side are nearly straight (Pl. VIII figs. 3—7).

Cavolinia longirostris (De Blainville, 1821) forma *limbata* (D'Orbigny, 1836); collected at 15°31'N 18°05'W, 13-3-1930; Dana Expedition, Stat. 4006V, preserved in alcohol 70%, gold coating ± 160 Å, adult specimen, ZMA reg.no. 3130. (Pl. III figs. 7—8; Pl. VI fig. 2; Pl. VIII figs. 6, 9—10).

The ventral ribs in this species are stronger developed than in the other formae of this species. The additional ribs consist of a broad base with straight posterior margin and finger-like horns, projecting in groups, forming a wave-like structure anteriorly (Pl. III figs. 7—8). The ribs become smaller posteriorly (Pl. VIII fig. 10) and show only small waves at the posterior half of the ventral side (Pl. VIII figs. 9, 6). Closure of the shell posteriorly is of the same type as in the other formae (Pl. VI fig. 2).

Cavolinia longirostris (De Blainville, 1821) forma *angulosa* (Gray, 1850); collected at 15°17'N 61°29'W, 7-4-1922; Dana Expedition, Stat. 1286V, preserved in alcohol 70%, gold coating ± 190 Å, juvenile specimen, ZMA reg.no. 3139, adult specimen, ZMA reg.no. 3141. (Pl. III fig. 6; Pl. V figs. 3—4; 6—7; Pl. VI fig. 1; Pl. VII figs. 1—2, 6).

The striae on protoconch-I and protoconch-II are imbricate like in all other species, but a clear embryonic ring is present between protoconch-I and protoconch-II, while the rings in protoconch-I and -II run parallel (Pl. V figs. 3—4). This suggests a growth interruption between protoconch-I and -II, which is absent in *C. inflexa* where the embryonic ring is absent. On the other hand there is no difference in growth direction between the two parts of the protoconch in *C. longirostris*, which, however, in *C. inflexa* causes the non-parallel position of the ribs of protoconch-I and protoconch-II. The mutual distance between the rings in the protoconch-II is twice as large as in the protoconch-I (Pl. V figs. 6—7) of *C. inflexa*.

The ribs in this forma are narrower but higher than in the previous forma (Pl. III fig. 6), so that they are of a more clear-cut shape. The wavy character is lost as the anterior projections of the ribs are sharply pointed (Pl. VIII figs. 1—2). These projections are never composed of more than one horn like they are in the forma *limbata*.

Cavolinia longirostris (De Blainville, 1821) forma *flexipes* Van der Spoel, 1971; collected in the Red Sea, 6-10-1969, Stat. 4, Gulf of Aqaba off Merrat, by

Ch. Lewinsohn; preserved in alcohol 70%, gold coating $\pm 190 \text{ \AA}$, adult specimen, ZMA reg. no. 3146 (Pl. VII fig. 5).

The ribs in this forma are straight, only a flattened side (Pl. VII fig. 5; rib at the bottom) can be considered a remainder of the wavy structure found in other formae.

Cavolinia longirostris (De Blainville, 1821) forma *mcgowani* Van der Spoel, 1973; collected near Philippine Islands, 18-9-1909, Albatross Expeditions, preserved dry, gold coating $\pm 190 \text{ \AA}$, adult specimen, ZMA reg.no. 3145 (Pl. VIII fig. 3).

This forma also shows ventral ribs of the straight type without undulations. Comparing the formae *angulosa* (Pl. VIII fig. 1) and *mcgowani* (Pl. VII fig. 3), it is evident that the ribs are in principle of the same structure: rather high and clear-cut.

Cavolinia tridentata (Niebuhr, 1775) forma *bermudensis* Van der Spoel, 1974, collected at $24^{\circ}36'N$ $17^{\circ}27'W$, 18-3-1930; Dana Expedition, Stat. 4009III, preserved in alcohol 70%, gold coating $\pm 190 \text{ \AA}$, adult specimen ZMA reg. no. 3125 (Pl. VII fig. 4; Pl. X fig. 6).

In this species only the present forma could be studied, but light microscope studies with the other formae proved that great differences with these do not exist. The ventral ribs are simple, not wavy (Pl. VIII fig. 4); they are formed, like in most Cavoliniidae, by additional callus (Pl. X fig. 6).

DISCUSSION

The descriptions show that SEM studies may form an adequate method to identify even small fragments from sediment. Closely related taxa are still so different in their minor details that a carefully compiled atlas of SEM photographs may be of value for paleontologists.

The most important finding was the typical nature of the protoconch in Cavoliniidae. It was already shown (Be et al., 1972; Rampal, 1972) that the structure of the teloconch in Cavoliniidae differs considerably from that in Limacinidae. The sculpture of the protoconch-I and the protoconch-II only affirms the difference between the "theca" of Cavoliniidae and that of Limacinidae. The transversal sculpture rings on the protoconch-I are different from all structures found in coiled pteropods and they were only described for the protoconch in larvae of the gymnosomatous *Clione limacina* (Phipps, 1774) by Lebour (1931), which cannot, however, indicate any relation between Cavoliniidae and Gymnosomata.

That the rings are only sculpture rings is hard to believe because of their imbricate character, which gives the impression that the rings have a structural origin. In all species studied there was a mark between protoconch-I and protoconch-II. In some species the protoconch-II is only recognizable by its structure which differs from that in protoconch-I. In these species growth seems to proceed regularly through the embryonic and

larval stage. In other species a ring caused by an irregularity in growth separates the protoconch-I and protoconch-II, so that growth in these species is of another type.

The striation of protoconch-II usually disappears gradually anteriorly and the border between protoconch-II and teloconch is never sharply marked. This can be explained by the rapid growth during the minute stages after the larval stage, in which the entire teloconch is completed (Van der Spoel, 1967). The presence of a clearly recognizable protoconch-I and -II was not found in Peraclididae and Limacinidae (except for *L. helicoides*). The presence of protoconch-II in Cavoliniidae must have a special reason. It has been argued that pelagic molluscs in the adult stage have a way of life not different from that in the larval stage, so that the shell formation in these two stages is also identical. The theory is supported by the exceptional case of *L. helicoides*, in which the larval stage, characterized by a distinct protoconch-II is spent inside the female specimen. In Cavoliniidae a distinct protoconch-II is found which merges gradually into the teloconch. Logically one would assume that the larval stage in Cavoliniidae is more different from the adult stage than it is in Limacinidae. The occurrence of minute stages in Cavoliniidae may cause the fact that only in this family the protoconch-II is well characterized as it causes a well defined larval period before the minute stage.

The fact that the protoconch-I shows transversal rings instead of punctation or reticulation as in Limacinidae and Peraclididae shows that the Cavoliniidae are clearly separated from the other families.

Other taxonomic implications are found in the study of finer structures in the infraspecific taxa of *Cavolinia longirostris*. Waved ribs on the ventral side are found in *Cavolinia longirostris* formae *longirostris*, *limbata* and *angulosa*, while more straight ribs are found in the formae *mcgowani* and *flexipes*, which makes two groups of formae in this species. The Red Sea (*flexipes*) — Pacific (*mcgowani*) distribution is also found in other plankton species (Van der Spoel, 1971). The strong development of the lateral spines in both *mcgowani* and *flexipes*, as well as their zoogeography seem to demonstrate that *mcgowani* and *flexipes* are more related one to another than the other formae.

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TEXT TO THE PLATES

Plate I

Figs. 1—5. *Limacina helicoides*, subadult: (1) first whorl from apical — 100 x, (2) punctation on first whorl of teloconch — 500 x, (3) protoconch-I and -II with part of teloconch — 200 x, (4) protoconch-I — 1000 x, (5) suture between teloconch and protoconch — 500 x.

Figs. 6—8. *Peraclis moluccensis*, adult: (6) suture along body whorl — 500 x, (7) aperture spine — 100 x, (8) protoconch-I — 2000 x.

Plate II

Figs. 1—3. *Diacria quadridentata quadridentata*, forma *danae*, adult: (1) dorsal lip — 500 x, (2) left corner of closing membrane — 2000 x, (3) dorsal lip — 500 x.

Figs. 4—5, 8. *Styliola subula*, adult: (4) inner side of asymmetric shell rib — 500 x, (5) the same — 2000 x, (8) protoconch-I — 500 x.

Figs. 6—7. *Cavolinia longirostris* forma *longirostris*, adult: (6) dorsal lip — 500 x, (7) smooth periostracum on elongated dorsal lip — 2000 x.

Plate III

Figs. 1—4. *Cavolinia gibbosa*, adult: (1) ribs on the ventral side — 50 x, (2) two of the most pronounced ribs from previous fig. 1 — 200 x, (3) anterior top of double rib — 2000 x, (4) posterior top of the same double rib — 2000 x.

Fig. 5. *Cavolinia longirostris* forma *longirostris*, adult: base of ventral sculpture rib of Pl. VIII fig. 4 — 5000 x.

Fig. 6. *Cavolinia longirostris* forma *angulosa*, adult: base of ventral sculpture rib of Pl. VII fig. 2 — 2000 x.

Figs. 7—8. *Cavolinia longirostris* forma *limbata*, adult: (7) top of ventral sculpture rib — 2000 x, (8) base of same ventral sculpture rib — 2000 x.

Plate IV

Figs. 1—2. *Cavolinia globulosa*, adult: (1) broken protoconch showing protoconch striation, outer callus and fragments of the soft parts in the opening — 200 x, (2) striation of protoconch-II — 5000 x.

Figs. 3—4. *Cavolinia gibbosa*, adult: (3) striation of protoconch-I — 5000 x (4) protoconch-I and -II — 200 x.

Figs. 5—8. *Cavolinia uncinata* forma *roperi*, adult: (5) protoconch-I and -II — 200 x, (6) striation of protoconch-I — 1000 x, (7) ventral crossing ribs — 500 x, (8) ventral crossing ribs — 200 x.

Plate V

Figs. 1—2. *Cavolinia inflexa* forma *inflexa*, adult: (1) protoconch-I — 500 x, (2) striation between protoconch-I and -II — 1000 x.

Figs. 3—4, 6—7. *Cavolinia longirostris* forma c.f. *angulosa*, juvenile: (3) protoconch-I — 500 x, (4) transition between protoconch-I and -II — 500 x, (6) striation of protoconch-I — 5000 x, (7) striation of protoconch-II — 5000 x.

Fig. 5. *Cavolinia longirostris* forma *longirostris*, adult: striation of protoconch-II at both sides of the folds of the closing membrane — 5000 x.

Plate VI

Fig. 1. *Cavolinia longirostris* forma *angulosa*, adult: lateral rib between lateral spine and protoconch — 500 x.

Fig. 2. *Cavolinia longirostris* forma *limbata*, adult: protoconch after shedding of posterior part — 200 x.

Figs. 3—4. *Cavolinia longirostris* forma *longirostris*, adult: two sections of the closing membrane both — 5000 x.

Figs. 5—6. *Cavolinia gibbosa*, adult: (5) lateral side of protoconch — 200 x, (6) crossing ribs at posterior part of ventral side — 200 x.

Plate VII

Figs. 1—2, 6. *Cavolinia longirostris* forma *angulosa*, adult: (1) ventral ribs — 200 x, (2) two ventral ribs from a more posterior position — 500 x, (6) ventral rib — 2000 x.

Fig. 3. *Cavolinia longirostris* forma *mcgowani*, adult: ventral ribs — 100 x.

Fig. 4. *Cavolinia tridentata* forma *bermudensis*, adult: ventral ribs — 500 x.

Fig. 5. *Cavolinia longirostris* forma *flexipes*, adult: ventral ribs — 200 x.

Plate VIII

Figs. 1—2. *Cavolinia globulosa*, adult: (1) dorsal ribs — 200 x, (2) ventral ribs — 200 x.

Figs. 3—5, 7—8. *Cavolinia longirostris* forma *longirostris*, adult: (3) one of the more posterior ventral ribs — 2000 x, (4) one of the anterior posterior ribs — 1000 x, (5) ventral ribs — 200 x, (7) most posterior ventral ribs — 200 x, (8) median ventral ribs — 200 x.

Figs. 6, 9—10. *Cavolinia longirostris* forma *limbata*, adult: (6) one of the posterior most ventral ribs — 500 x, (9) median ventral rib — 500 x, (10) anterior ventral rib — 500 x.

Fig. 11. *Cavolinia uncinata* forma *roperi*, adult: crossing of ventral ribs — 1000 x.

Plate IX

- Figs. 1—9. *Cavolinia globulosa*, minute stage: (1) protoconch mark with closing membrane — 500 ×, (2) closing membrane — 1000 ×, (3) outer callus — 500 ×, (4) posterior shell part after shedding of most of the protoconch — 50 ×, (5) ventral lip — 500 ×, (6) outer callus 200 ×, (7) closing membrane — 1000 ×, (8) additional rib of which part is absent — 5000 ×, (9) intact additional rib — 5000 ×.

Plate X

- Figs. 1—2. *Cavolinia globulosa*, minute stage: (1) primary and secondary ventral ribs — 1000 ×, (2) three primary ventral ribs — 50 ×.
- Figs. 3, 11. *Diacria quadridentata* forma *danae*, adult: (3) ventral ribs — 500 ×, (11) dorsal lip — 2000 ×.
- Figs. 4—5, 7, 9. *Cavolinia globulosa*, adult: (4) ventral ribs — 100 ×, (5) one primary ventral rib — 2000 ×, (7) top of a primary rib — 10.000 ×, (9) striation of protoconch-II — 1000 ×.
- Fig. 6. *Cavolinia tridentata* forma *bermudensis*, adult: top of a ventral rib — 500 ×.
- Figs. 8, 10. *Cavolinia inflexa* forma *inflexa*, adult: (8) transition between protoconch-I and -II — 1000 ×, (10) striation of protoconch — 2000 ×.
- Fig. 12. *Cavolinia gibbosa*, adult: two ventral ribs — 200 ×.

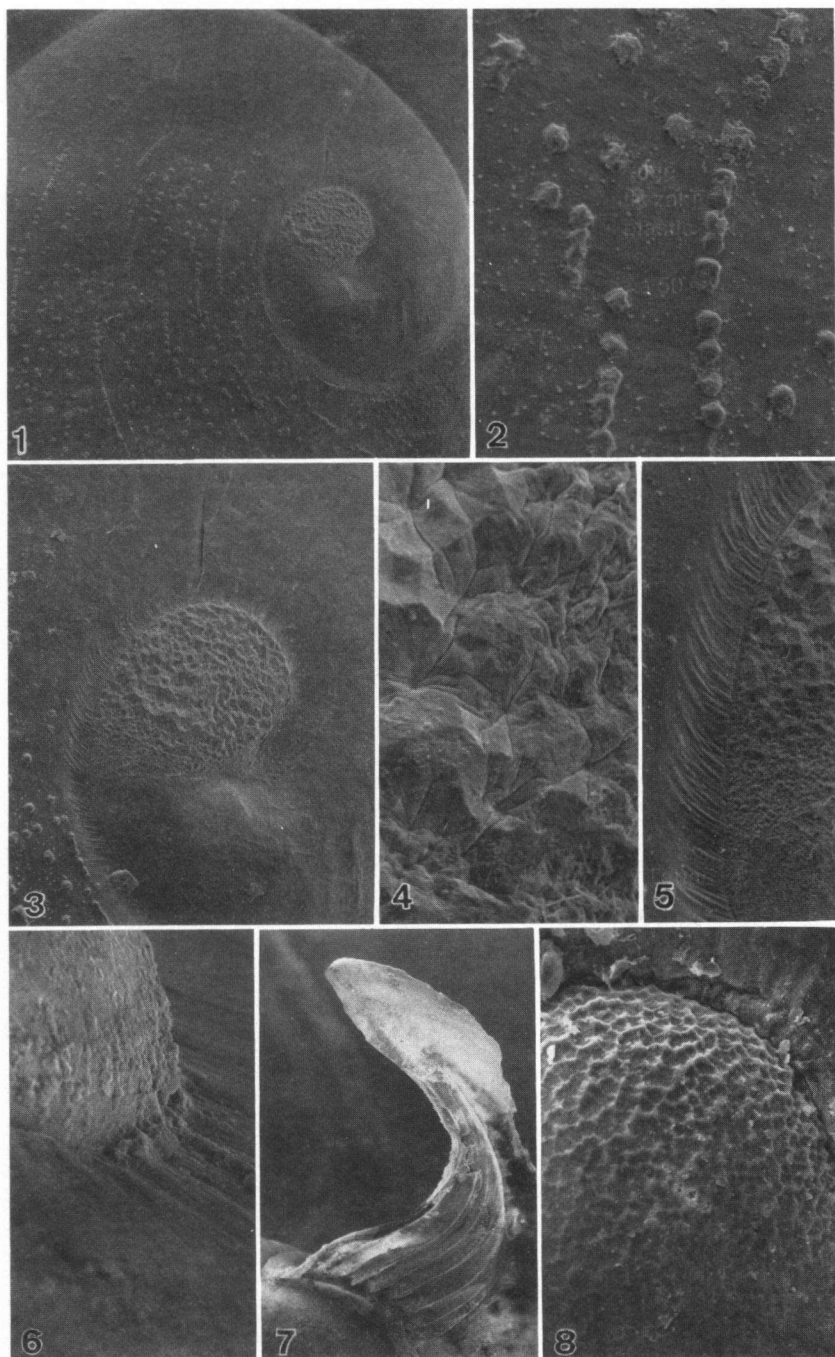


Plate I

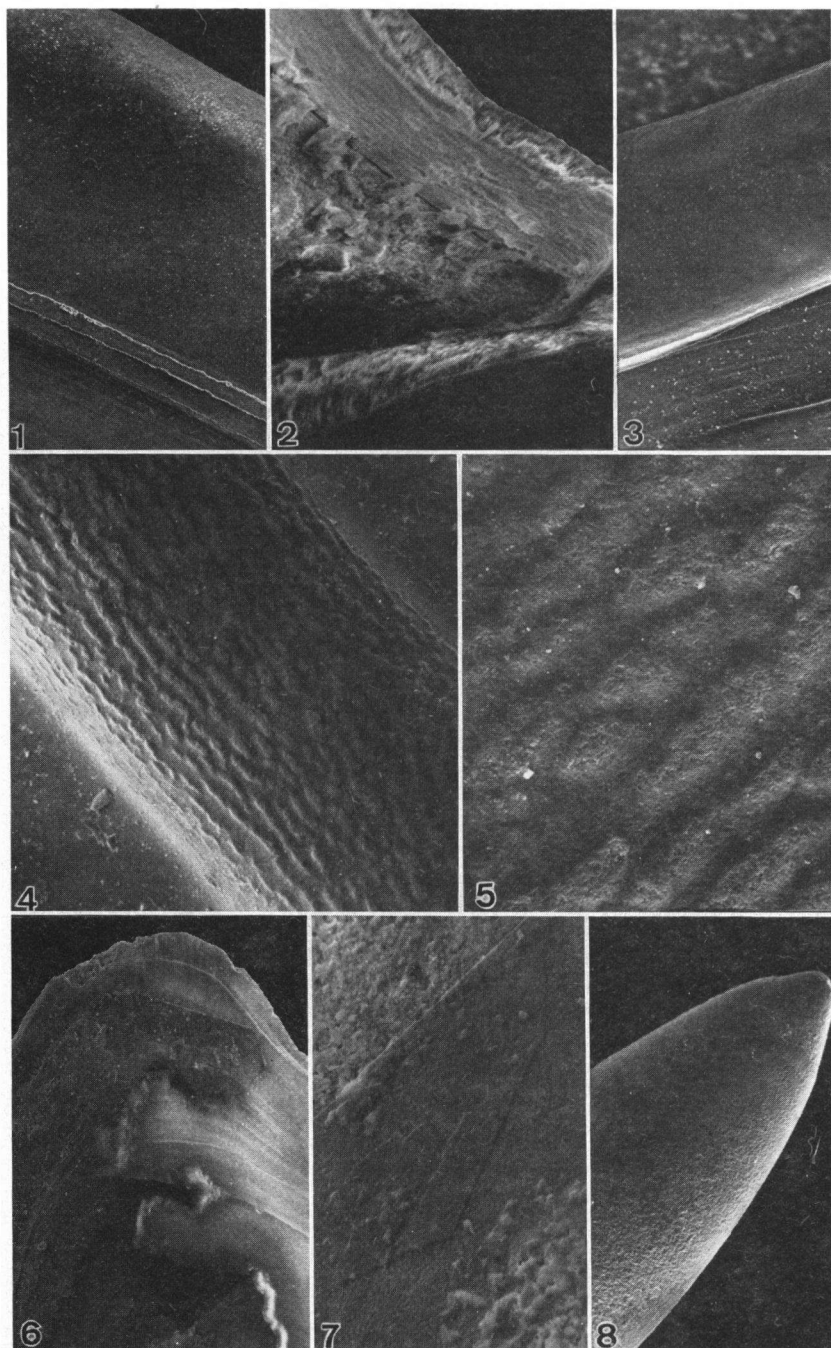


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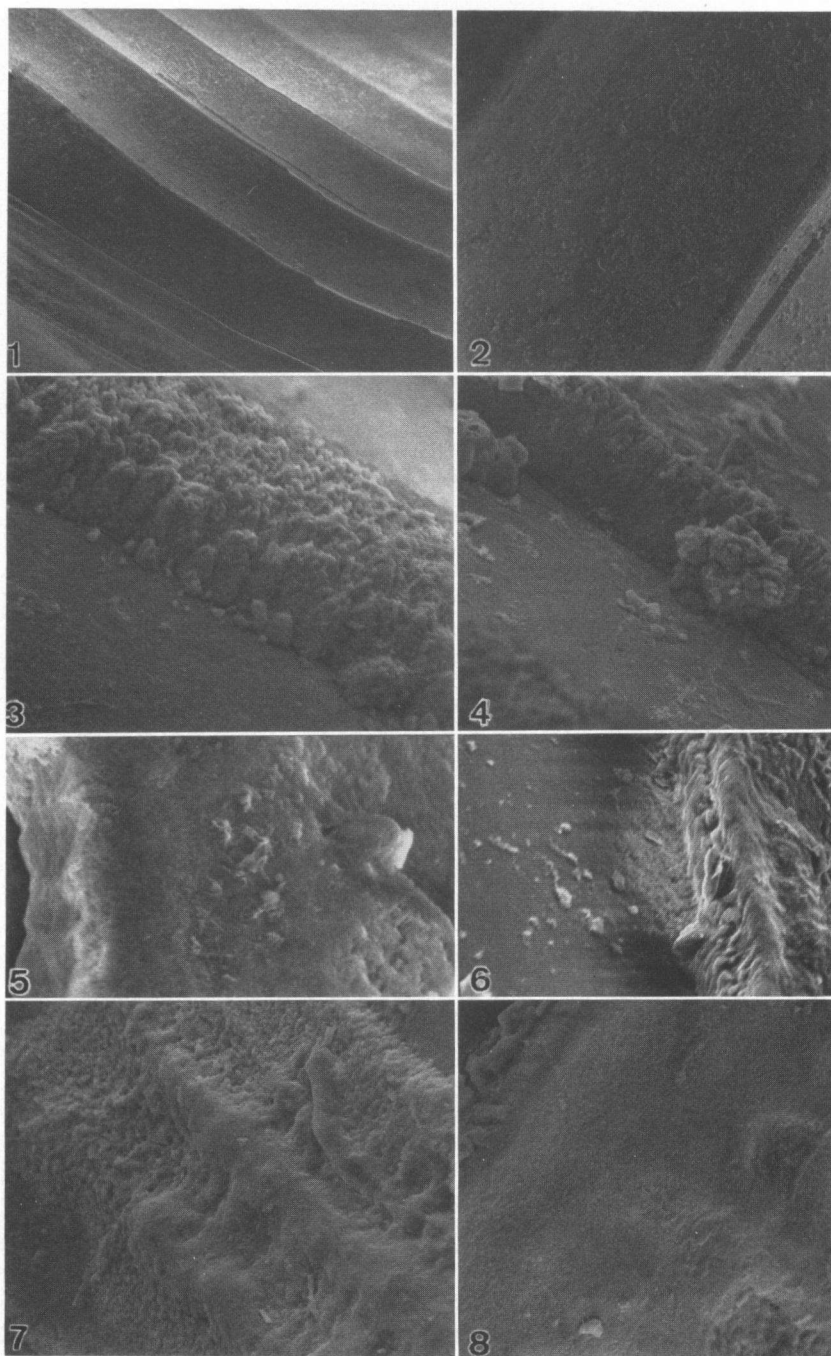


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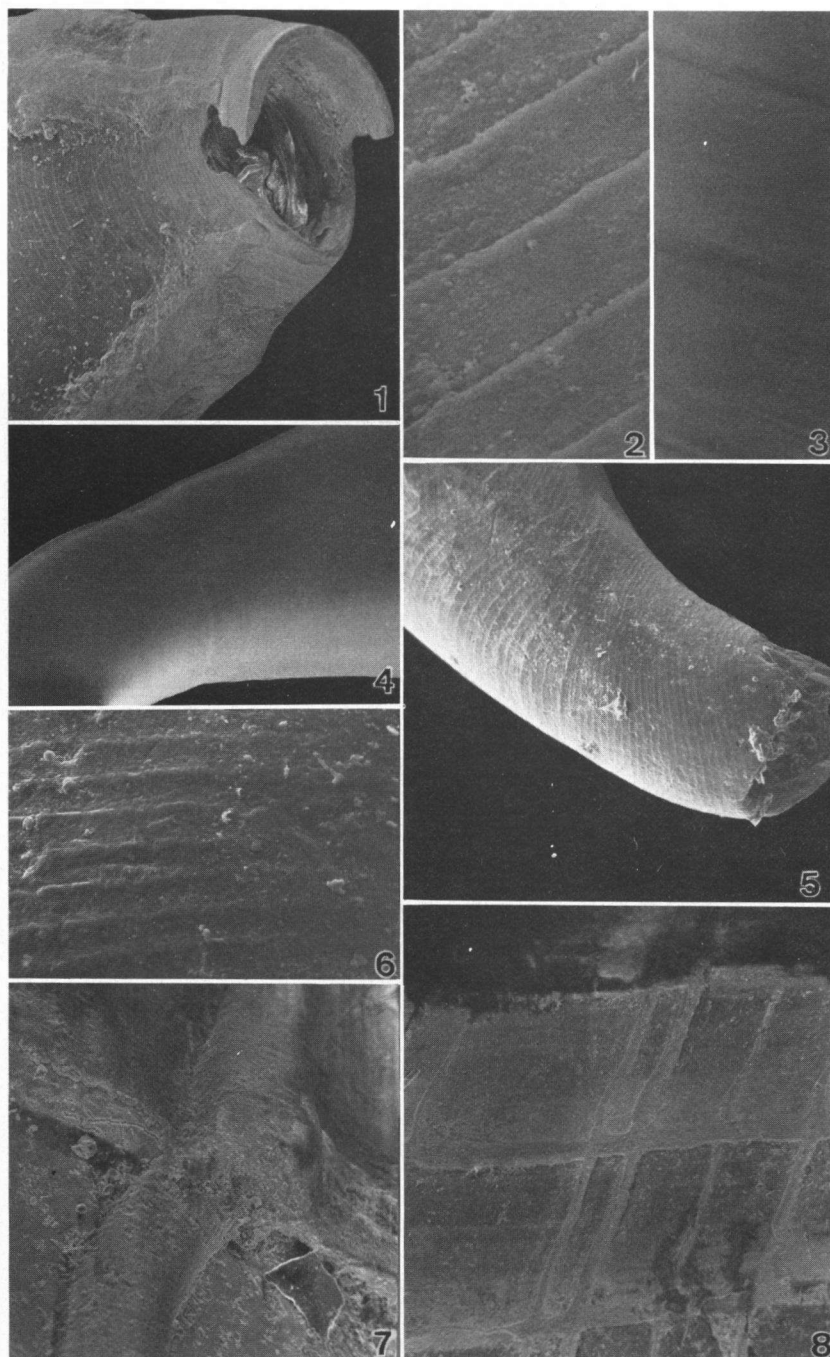


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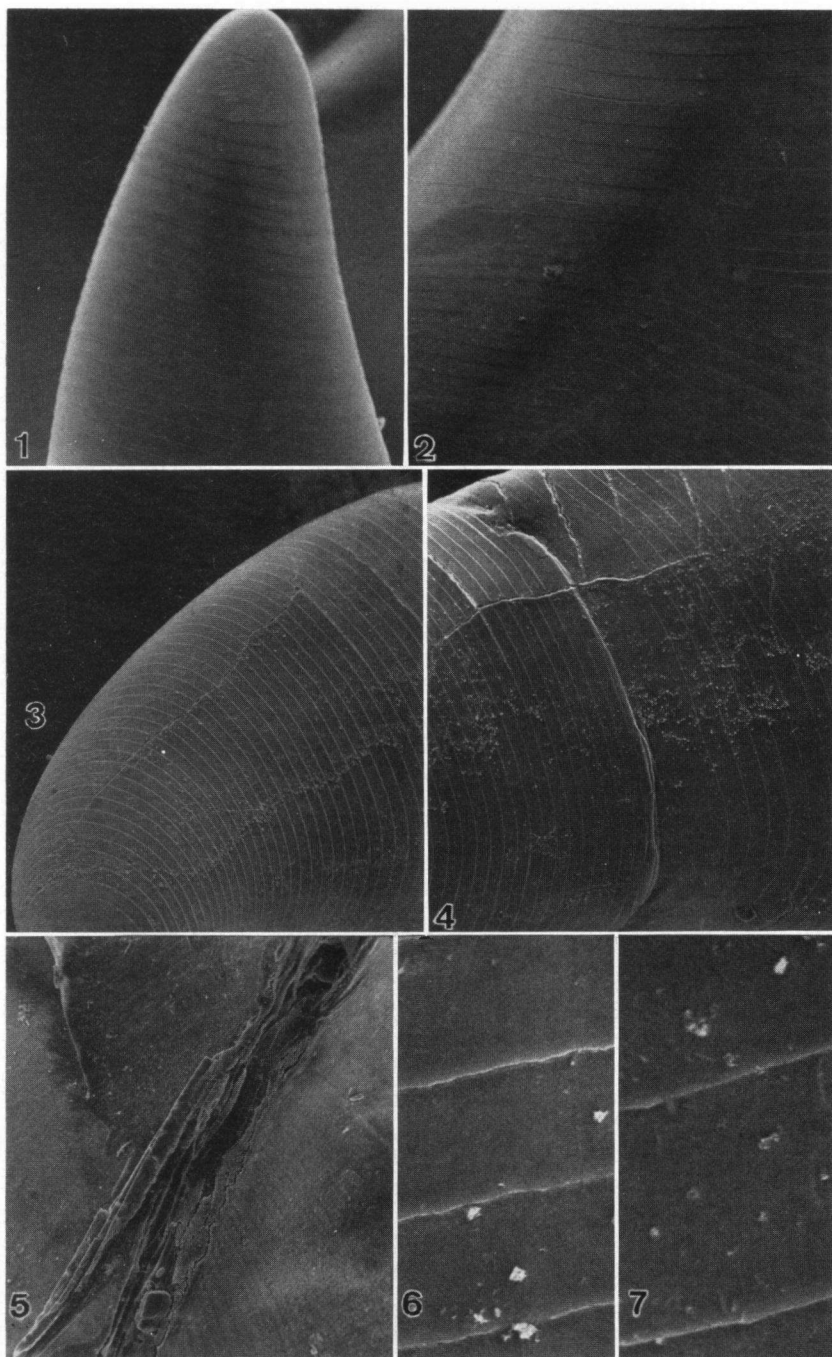


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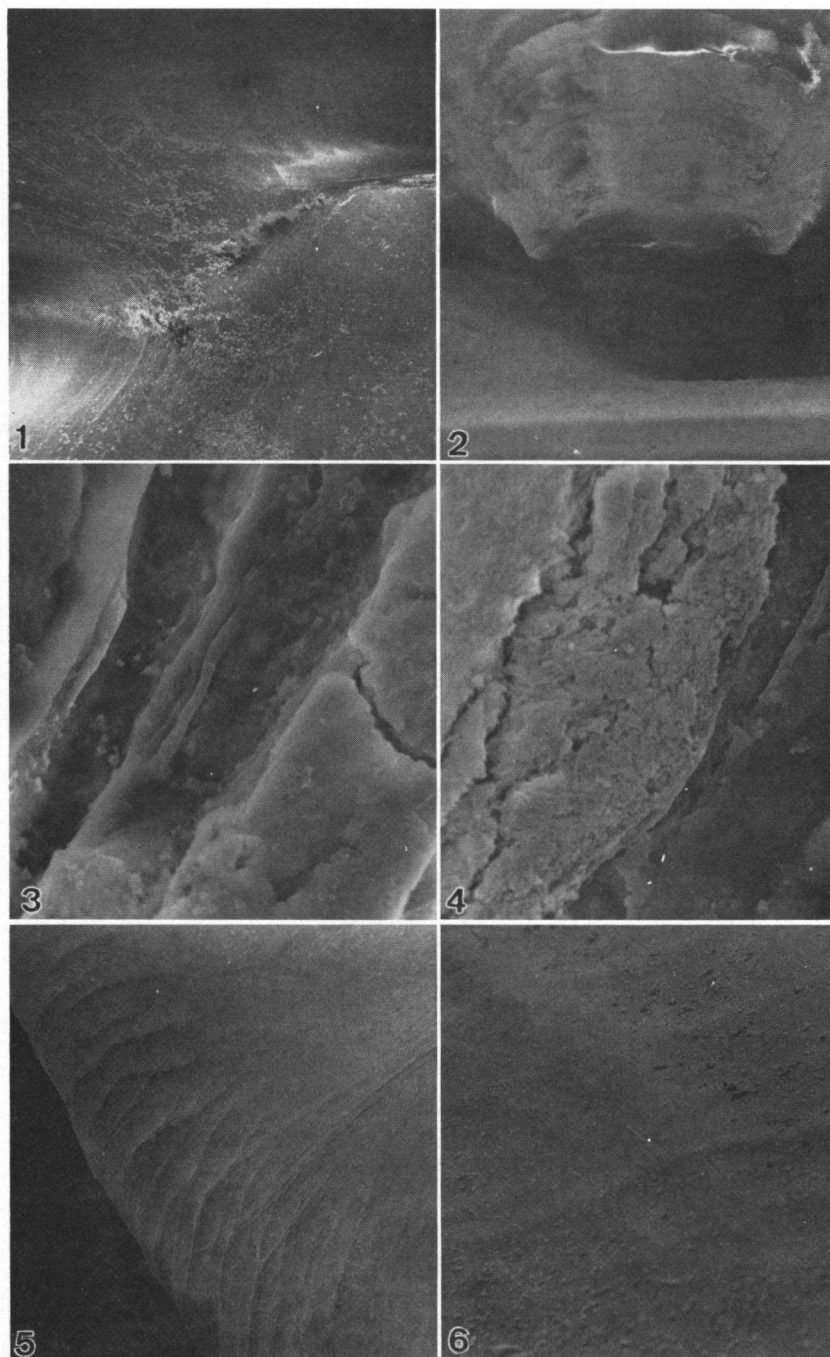


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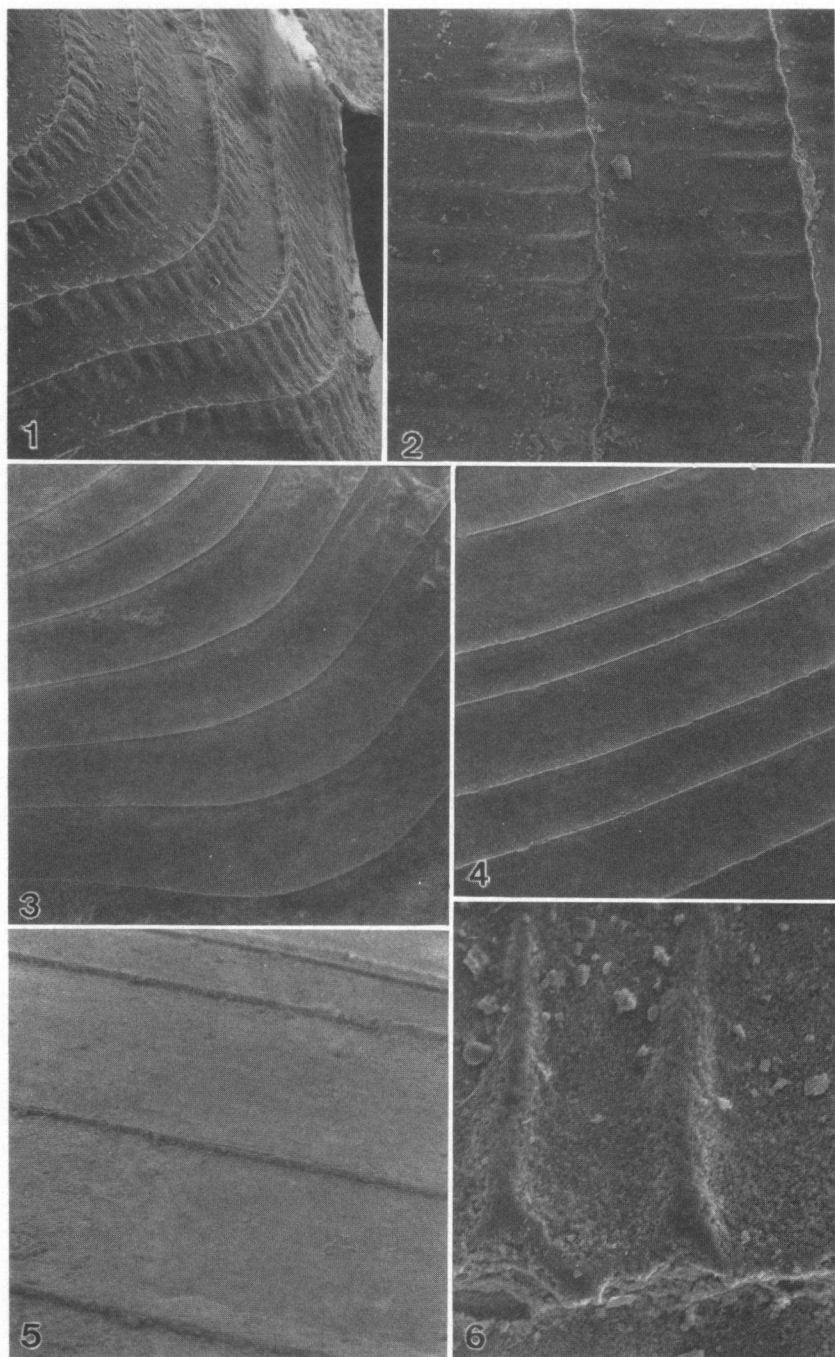


Plate VII

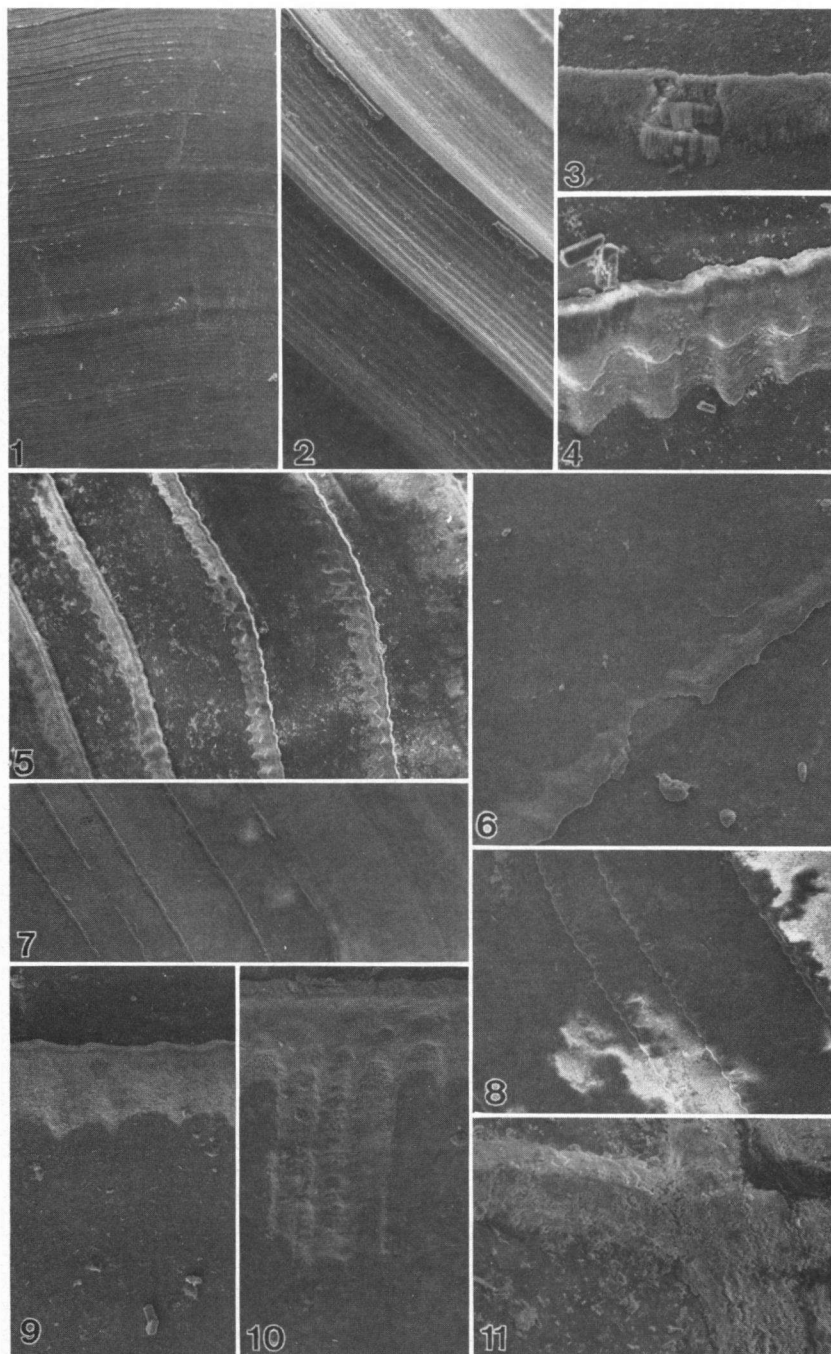


Plate VIII

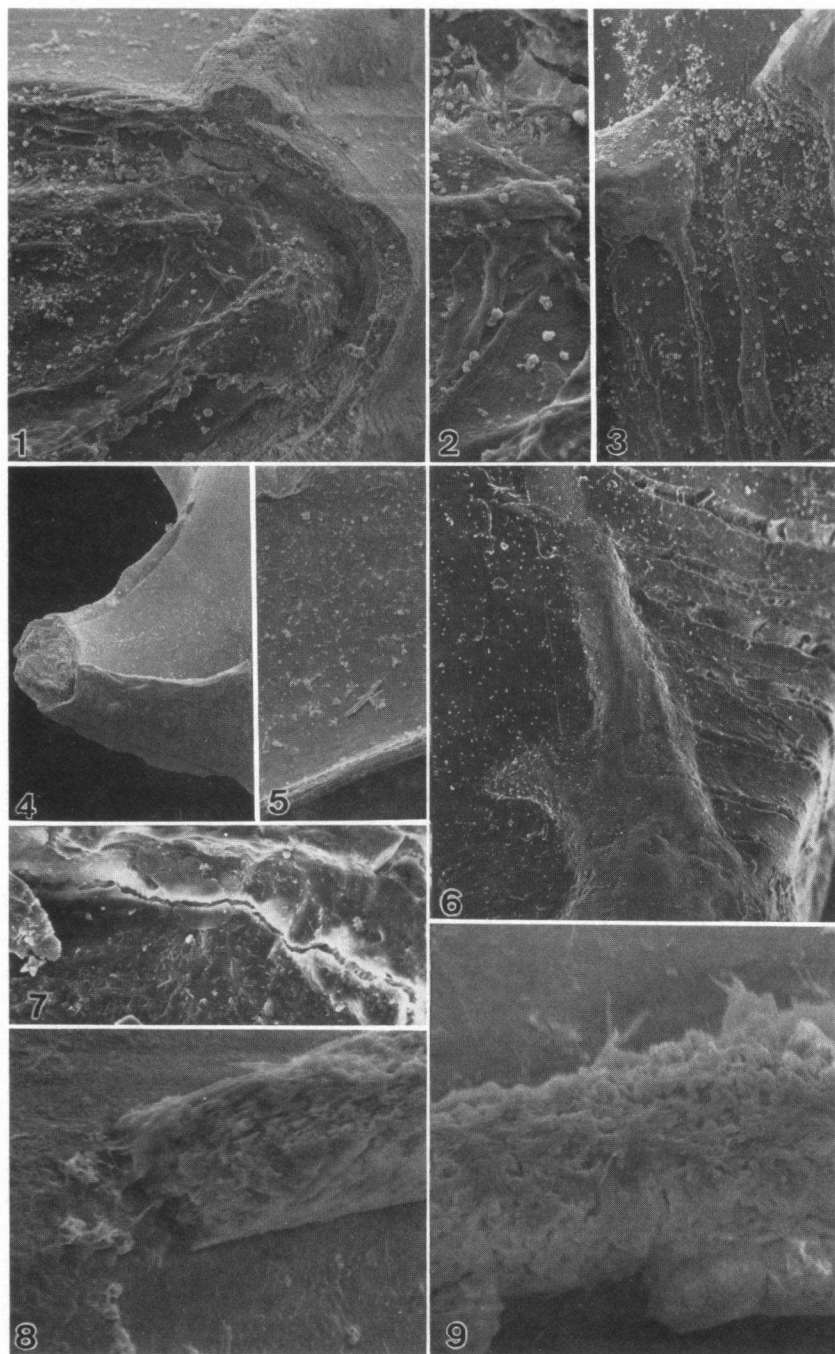


Plate IX

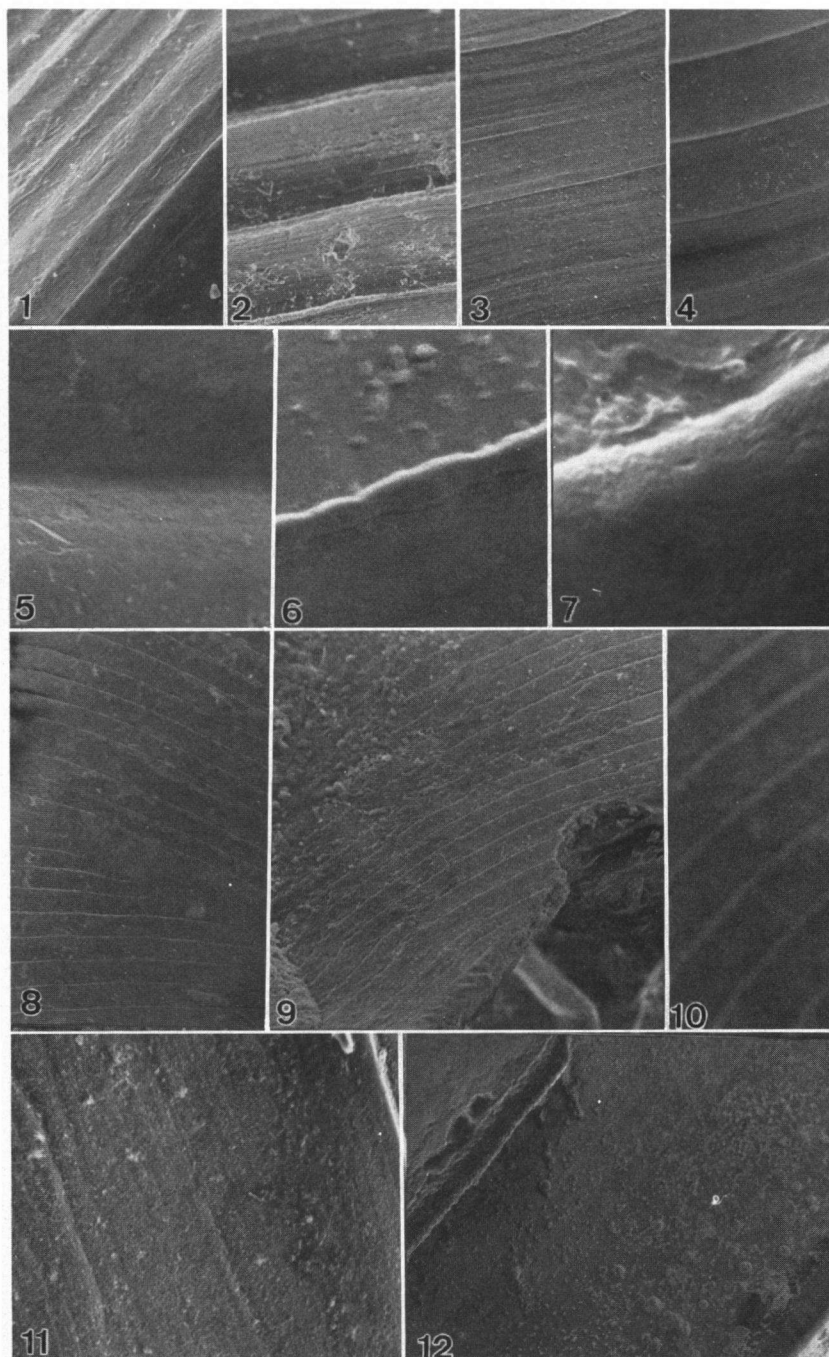


Plate X