

COMMENTS ON SIX SPECIES OF MARINE ANTARCTIC LITTORINACEA (MOLLUSCA, GASTROPODA)

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Summary — In contrast to temperate and tropical littorinid species, the Antarctic ones are living only in tide pools or below the intertidal zone. Is this a secondary adaptation to escape low air temperature prevailing in these southern regions, or have they never been living exposed in the intertidal zone?

A study of their phylogenetic relations on the basis of their radular morphology shows a mixing of littorinid and lacunid peculiarities, including transitional forms between the two families. So the present habit of the Antarctic Littorinidae to live below sea surface may be considered as the ancestral way or life in the whole family.

The embryonic shell, examined in three species, indicates the young animals hatching out as miniature adults, a feature already known in the arctic Littorinidae. Finally, it is shown that the shell structure is typically that of the lower Mesogastropoda.

Résumé — Contrairement aux Littorinidae tempérés et tropicaux, les Littorinidae antarctiques ne vivent que dans les flaques ou sous la zone intertidale. Est-ce une adaptation secondaire visant à échapper aux basses températures de l'air des régions antarctiques, ou ces espèces n'ont-elles jamais vécu exposées dans la zone intertidale?

Une étude de leurs relations phylogénétiques, sur la base de la morphologie radulaire, montre un mélange de caractères de Littorinidae et de Lacunidae. Aussi peut-on considérer leur mode de vie actuel, sous la surface de la mer, comme le mode de vie ancestral de l'ensemble de la famille.

La coquille embryonnaire, examinée chez trois espèces, souligne que l'éclosion se fait sous forme d'adultes en miniature, particularité déjà connue chez les Littorinidae arctiques. Enfin, il est montré que la structure de la coquille est typiquement celle des Mésogastropodes inférieurs.

The Antarctic marine Littorinacea are of special interest since they live mainly below water level, either below the intertidal zones or in tidal pools within the intertidal area. This is quite in contrast to the living mode of representatives of the Littorinidae of the tropical and northern zones. In those regions, only mem-

bers of the Lacunidae prefer to live below water level all the time, while the species of the Littorinidae settle within the intertidal zone or above it within the spray zone or outside of it near the edge of the sea (mangrove species). Therefore the question has to be answered whether the Antarctic marine Littorinacea have secondarily adapted in their mode of life to the low air temperatures of their living environment and have migrated out of the intertidal area, or whether they are representatives of an ancestral stock not specialized to live in the intertidal area, or a mixture of both.

RESULTS

LAEVILITORINA ANTARCTICA (Smith, 1902)

Synonymy : cf. Arnaud 1972a : 117, fig. 7 (radula).

Maximum size : 3,75 mm (Smith 1902).

Distribution and bathymetric range : cf. Arnaud 1972a.

Ecology : this is the characteristic and the most common species of Littorinidae of the coasts of East Antarctica. It is not found in supralittoral and mediolittoral zones, a fact obviously being related to low air temperature and icing during about ten months of the year (ice foot) on the intertidal substrates. In Adelie Land, upper specimens are observed mostly on upper plants of the brown algae *Desmarestia menziesii* just below low water level, the lowest specimens are found among the rhizoids of the large kelp *Phyllogigas grandifolius*. Here, they can find a shelter against a heavy predation (Arnaud & Hureau 1966) by the fish *Notothenia coriiceps neglecta*.

They feed on epiphytic diatoms and filamentous algae which are common on the kelps.

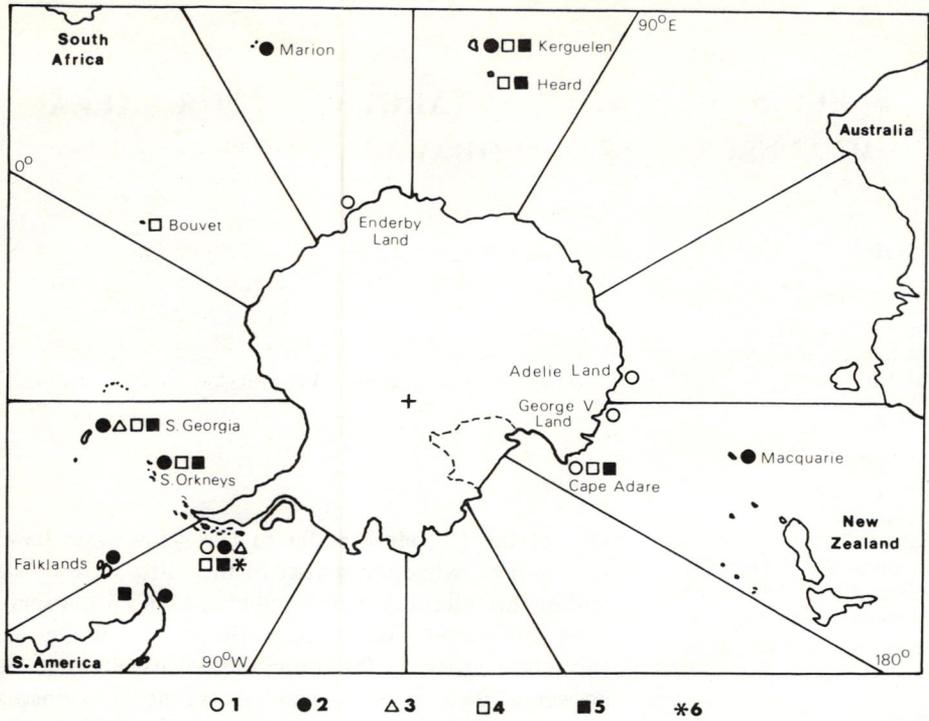
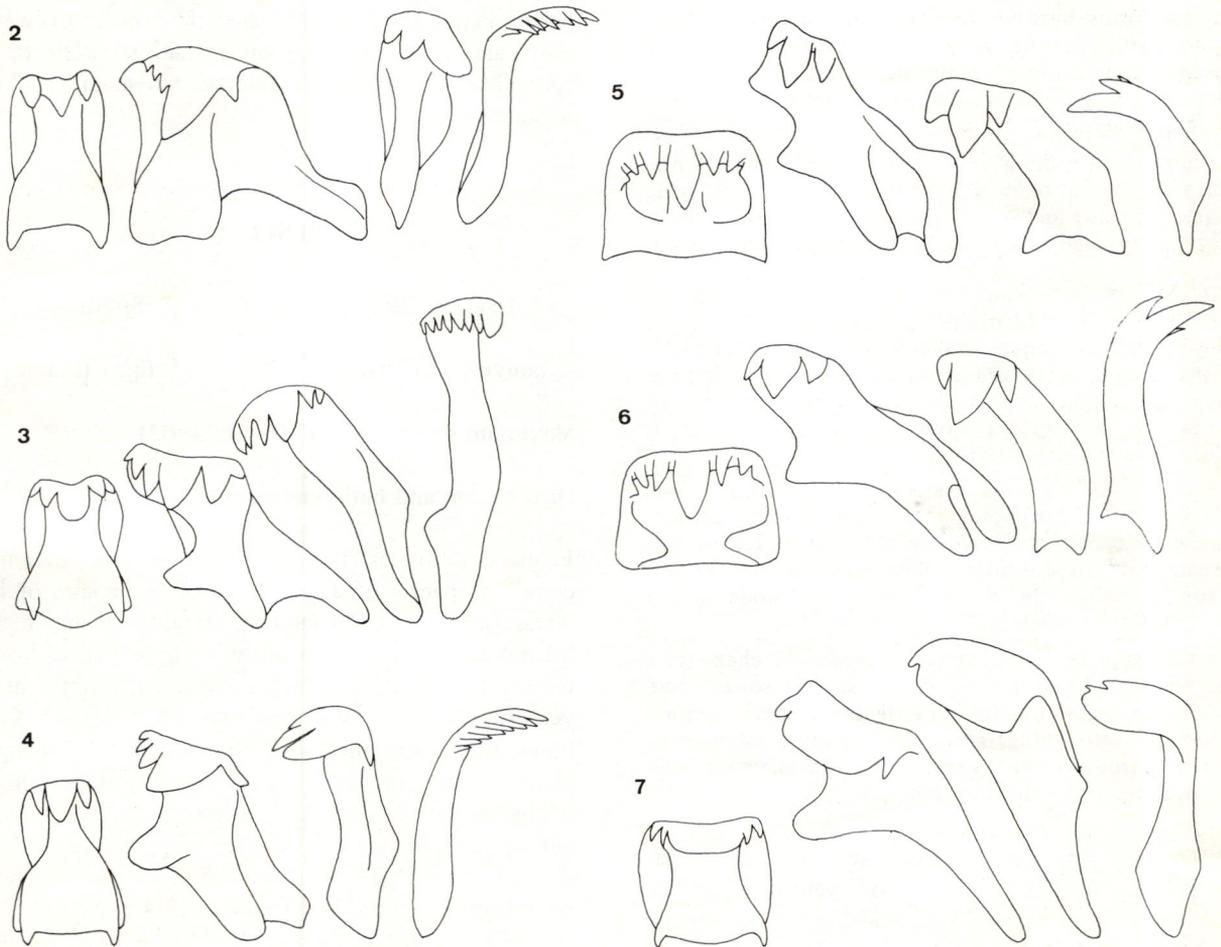


Figure 1 - Map demonstrating the occurrence of the 6 Antarctic Littorinacea studied in this work : 1. *Laevitorina antarctica*, 2. *L. caliginosa*, 3. *L. cf. umbilicata*, 4. *Pellitorina setosa*, 5. *P. pellita*, 6. *Laevilacunaria bransfieldensis*.



Figures 2-7 : Half rows of radula of *Laevitorina antarctica* (2), *L. caliginosa* (3), *L. cf. umbilicata* (4), *Pellitorina setosa* (5), *P. pellita* (6) and *Laevilacunaria bransfieldensis* (7).

Material used : Pointe Geologie archipelago, Adelie land, P.M. Arnaud coll., 1962.

Radula (Fig. 2 ; pl. 1, figs. 1-3 & 7) : the central tooth is of rectangular outline, about twice as long as wide. Its cutting edge is situated at the anterior front and forms an angle of 90 degrees with the basal platform. It shows 3-5 cusps, the central of which is pointed and the largest. The first flanking pair of cusps is also pointed and of about one half of the size of the central susp. The outer pair may be present as low rounded cusps (pl. 1, fig. 1), or both or one may be absent in other central teeth of the same radula (pl. 1, fig. 2). A central broad swelling of the anterior basal platform connects the cutting edge with the marginal swellings of the posterior portion of the basal platform, which extends into pointed posterior projections. The basal platform therefore in its anterior portion is convex, and is concave in its posterior portion. The anterior margins begin at the anterior corners of the end of the cutting edge and extend towards the central portion of the margins with even convex curve forming solid wing-like marginal lamellae.

They terminate where the posterior ridges of the basal platform reach the margins. The posterior edge is straight to concave in its course between the pointed projecting posterior corners (pl. 1, fig. 2).

The lateral tooth is the largest in the radula (pl. 1, fig. 1). It is as wide as high and of broadly triangular shape. A wide central swelling extends from a thickened posterior lobe to the cutting edge across the shovel-like, concave basal platform (pl. 1, figs. 1, 2). The latter is dominated by one solid main cusp accompanied by one small outer cusp and three continuously smaller inner cusps. The inner margin is straight, ending in a rounded posterior inner corner. The outer margin is convex from the anterior corner onward, then changes into concave in its course to a handle-shaped outer-posterior corner. The inner portion posterior edge shows a low lobe-like end of the central swelling. It forms a concavity extending into the outer posterior corner (pl. 1, figs. 1, 7).

The inner margin of the lateral tooth can be fitted into the central restriction seen on the central tooth (pl. 1, fig. 7). The outer posterior corner extends far outward. Therefore, the inner marginal tooth can rest on the outer concave portion of the basal platform of the lateral tooth. The outer marginal tooth is rooted right next to the end of the outer posterior corner of the lateral tooth (pl. 1, figs. 1, 7).

The inner marginal tooth is more closely related to the lateral tooth in shape than to the outer marginal tooth (pl. 1, fig. 3). It is twice as long as wide and of almost rectangular outline. Its cutting edge is dominated by a large central cusp accompanied by 1 outer and 2 inner smaller cusps. A swelling originates at the

base of the upward-turned cutting edge and extends across the basal platform into a knob-like central lobe of the posterior edge which is situated close to the inner posterior corner. The outer posterior corner is rounded and forms with the convex outer margin a wing like lamella flanking the central swelling on the outer side (pl. 1, fig. 3).

The outer marginal tooth is formed like a fork with slender handle and wide upturned prongs (pl. 1, figs. 3, 7). It is 3.5 times longer than the width. The straight cutting edge shows 7-8 slender and pointed cusps, the innermost being the smallest and narrowest. The basal platform is flattened and the narrow straight posterior edge forms the attachment to the radular membrane.

Embryonic shell (pl. 3, figs. 5-6 ; pl. 4, fig. 1) : the whole embryonic shell consists of about 1.7 whorl and is 0.5 mm (pl. 3, fig. 6). The well-rounded protoconch (initial cap-like portion of the shell) is evenly concave in shape and measures about 0.14 mm in width (pl. 4, fig. 1). The onset of the first strong growth lines (pl. 3, fig. 6) indicates the time of hatching. The young hatched as miniature adult like crawling individuals. The embryonic shell is sculptured by a fine striation of spiral ridges (0.3 μ m wide) which are spaced 5 μ m apart from each other on the first whorl (pl. 3, fig. 5). This sculpture is restricted to the embryonic shell and not formed after hatching (pl. 3, fig. 6 ; pl. 4, fig. 1).

LAEVILITORINA CALIGINOSA (Gould, 1849)

Synonymy : cf. Arnaud 1972b : 431 and add the following :

L. caliginosa : Kenny & Haysom 1962 : 250, 252.

? *L. cf. caliginosa* : Dell 1971 : 204.

L. caliginosa aestualis Strebel 1908 : 51 ; Powell 1951 : 107.

Maximum size : 8 mm (in South Georgia : David, 1934).

Distribution and bathymetric range : cf. Arnaud 1972b : 431. The type locality is not Royal Sound, Kerguelen, as mentioned for example by Powell (1951) but Tierra del Fuego (Gould, 1849). Mostly a very shallow water species, but sometimes caught down to 20 or even 30 m.

Ecology : this is the most common littorinid of the Antarctic Peninsula and vicinity (West Antarctica), of the subantarctic islands, and of the Magellanic regions.

It is a typical member of the "biocénose de la roche littorale" (Arnaud 1974) in these areas and lives mostly under boulders encrusted by calcareous algae, lying in tide pools or in crevices. Associated species are principally *Lasaea consanguinea* on subantarctic and

magellanic coasts (replaced by *Kidderia subquadratum* on the coasts of the Antarctic Peninsula and vicinity), large Turbellarians (*Procerodes*), chitons, and phylobryid pelecypods.

This species is almost never exposed at low tide, a probable protection against freezing temperatures (in West Antarctica) or desiccating effects of strong winds (in subpolar areas).

In fact, *L. caliginosa* is always living in sublittoral conditions (always submerged) even when it is living in the intertidal zone (under boulders lying in pools). This littorinid is also observed on hold-fasts of *Durvillea antarctica* (at Macquarie Island: Kenny & Haysom 1962) and on sublittoral seaweeds and kelps *Macrocystis* (in South Georgia: Strebel 1907 & 1908: David 1934) at the depth of about 30 m.

Simpson (1976) has published the results of an ecological and biological study of the species at Macquarie Island, which are briefly summarized here. *L. caliginosa* is very euryhaline (salinity from 18 to 35 ‰) tolerant to low temperature (as is shown by its occurrence in West Antarctica) but not to desiccation, even if it is observed only in the intertidal zone (but generally in pools). Here, it grazes the green algal film and diatoms. In an aquarium, it accepts to eat *Durvillea*, *Rhodomenia* and coralline algae but not *Macrocystis* and other algae. The reproduction is achieved by a direct, non-pelagic development within the egg cases. Its only observed predator at Macquarie Island is the Asterid *Anasterias directa*.

Material used: Kerguelen Is., from near Port-aux-Français, underface of boulders at low tide, P.M. Arnaud coll., 7 March 1970, 7 specimens.

Radula (Fig. 3; pl. 1, fig. 8; pl. 2, figs. 1-3): the radula is quite similar to that of *L. antarctica* in general outline (Martens & Pfeffer 1886, pl. 3, figs. 10-11; Powell 1951, fig. I.16) but shows many differences in detail. The central tooth is shorter and only a bit longer than the width (5:4) (pl. 2, fig. 2). The cutting edge shows 5-7 cusps with broad, rounded, central, main cusp, accompanied by 2 pairs of flanking cusps, the outer of which is the smallest. There may or not be an outermost pair of denticles present on the outer-

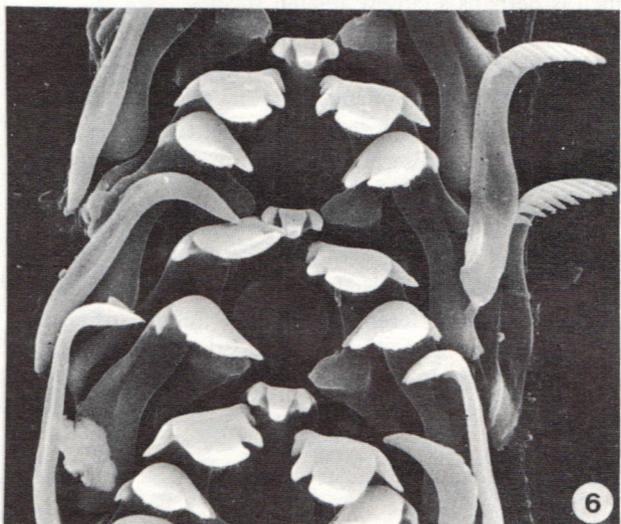
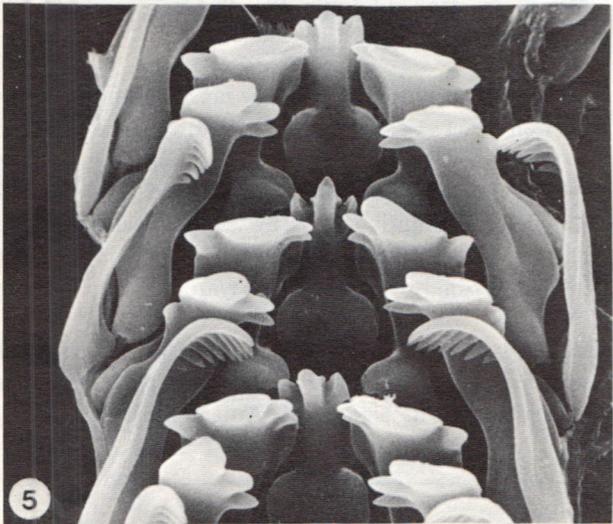
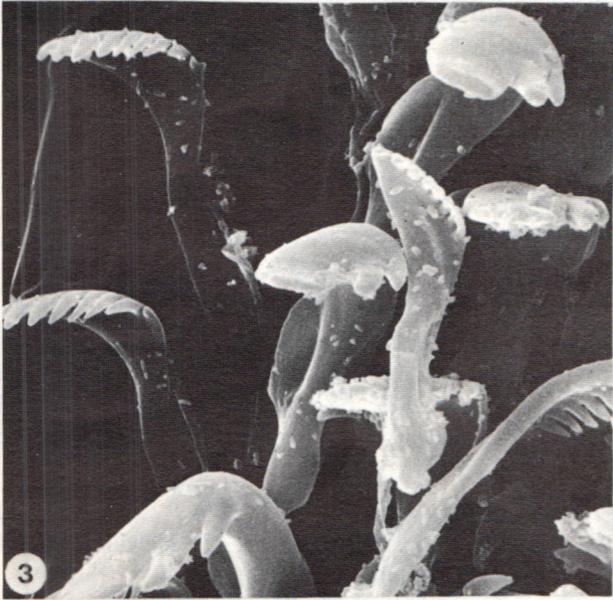
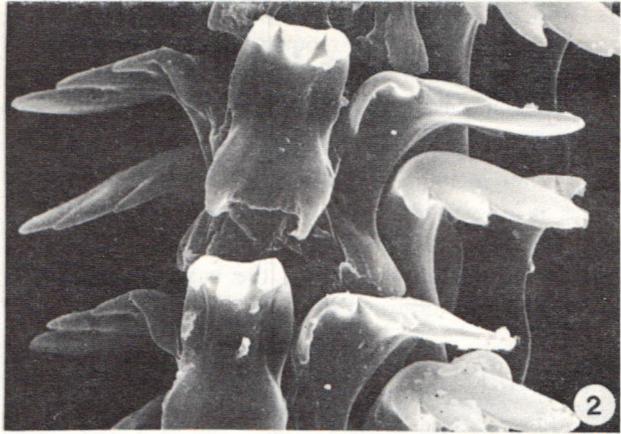
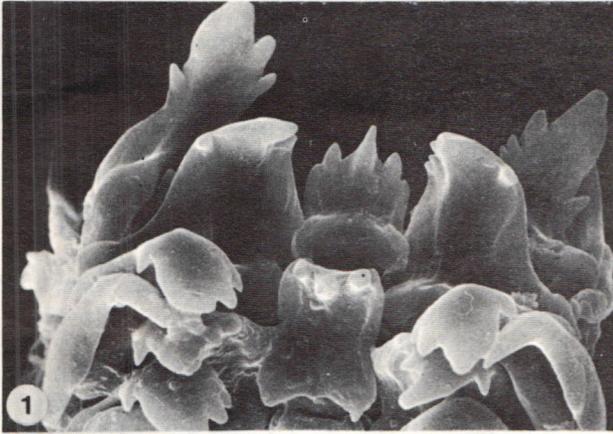
most corners of the cutting edge. A broad central swelling extends from the central portion of the cutting edge downwards, widens in its posterior course on the basal platform and extends into solid denticles extending over the posterior edge (pl. 1, fig. 8; pl. 2, fig. 1). These ridges of the posterior basal platform do not quite follow the margins but are situated a little inward, so the rounded posterior corners lie on a lower plane. The central swelling shows deeply concaved margins. A deep concavity is formed by the low lateral lamellae and the margins of the central swelling. Into this groove the rounded anterior inner corner of the lateral tooth may be fitted (pl. 2, fig. 2).

The lateral tooth is again characterized by its extended outer posterior corner, which embraces the inner marginal tooth. Therefore the latter may rest on the concave outer portion of the basal platform of the lateral tooth (pl. 2, figs. 1, 3). The outer marginal tooth is rooted right at this extension of the lateral tooth. In difference to *L. antarctica*, the central swelling of the lateral tooth extending from the base of the upturned cutting edge to the posterior edge, is split into two ridges near its base. One extends to the center of the posterior edge forming a low projecting lobe, the other is bent inward to form a thumb-like projection turned upward and not attached to the radula membrane (pl. 2, figs. 1-2). This projection helps to hold the inner marginal tooth in its resting place on the concave outer portion of the basal platform of the central tooth (pl. 2, fig. 3). The inner margin of the lateral tooth is bent upward following the rounded inner anterior corner and forms a deep indentation following the bulging base of the central tooth in its course. The base of the central tooth can be fitted into this indentation of the lateral tooth. Therefore both teeth are almost hinged to each other (pl. 2, figs. 2-3). The lateral tooth is almost as wide as high showing a rounded main cusp accompanied by 2 outer and 3-4 continuously smaller inner cusps. The outer margin is straight to weakly concave and turned upward to form the rim of the concavity of the basal platform here. The long posterior edge is attached to the radula membrane from below the inner thumb-like projection to the extended outer posterior corner.

The inner marginal tooth is similar in shape to that of *L. antarctica* about 3 times as long as wide (pl. 2,

PLATE 1

- Figure 1 - Radula of *Laevitorina antarctica* showing teeth in different degrees of spreading (x 515).
 Figure 2 - Central and lateral teeth of *L. antarctica* (x 1030).
 Figure 3 - Outer marginal, inner marginal and lateral teeth of *L. antarctica* (x 1030).
 Figure 4 - Half row of the radula of *L. cf. umbilicata* (x 1600).
 Figure 5 - Radula of *L. cf. umbilicata* (x 820).
 Figure 6 - Radula of *L. cf. umbilicata* (x 790).
 Figure 7 - Radula of *L. antarctica* (x 590).
 Figure 8 - Radula of *L. caliginosa* (x 400).



figs. 1, 3). It shows an outer wing-like extension of the outer margin, a bit less pronounced than in *L. antarctica*. The up-turned cutting edge demonstrates a rounded main cusp accompanied by 2 outer and 3 inner cusps.

The outer marginal tooth is again fork-like in shape, 3 times as long as wide and shows 8-9 cusps, the innermost of which are the smallest (pl. 1, fig. 8, pl. 2, figs. 1,3). The inner margin of the basal platform is extended into an upturned rim.

LAEVILITORINA cf. *UMBILICATA*
Pfeffer, 1886

L. umbilicata Pfeffer in Martens & Pfeffer 1886 : 88, pl. 1, fig. 12 ; Tryon 1887 : 254, pl. 46, fig. 33 ; Carcelles 1953 : 170 (under *Laevilittorina*, sic) ; Castellanos & Luna Perez 1963 : tabl. 10. *Non* Lamy 1905 : 478 *Nec* 1906a : 5 = *L. antarctica* (Sm., 1902) *fide* Lamy 1910 & 1911.

Maximum size : 3 mm (Pfeffer 1886).

Distribution and bathymetric range : South Georgia (type locality : Pfeffer, 1886), Danco coast (Castellanos & Luna Perez 1963), and Arthur Harbor (present material). Very shallow species.

Ecology : on superficial algae, according to Castellanos & Luna Perez (1963). Our material is from a stomach of *Notothenia coriiceps neglecta* and this littorinid probably is able to live on *Desmarestia* like *L. antarctica*, which is perhaps a closely related species.

Material used : Arthur Harbor, Anvers I., Palmer Archipelago, cove SE of Bonaparte Point, stomach content of *Notothenia coriiceps neglecta* caught by fish trap, 2-11 m, "Hero" cruise, J.H. Dearborn, P.M. Arnaud *et al.* coll., 16 march 1972, 2 specimens.

Radula (fig. 4 ; pl. 1, figs. 4-6) : the radula of *L. caliginosa* is very similar in shape and arrangement of teeth. The main difference lies in the number of cusps of the different teeth, but otherwise the description of the radula of *L. caliginosa* is similar to that of *L. umbilicata*.

The central tooth is longer than the width (4 : 3) and shows 3 cusps on its cutting edge. The central of these solid triangular cusps is the largest (pl. 1, figs. 4-5).

The lateral tooth is slightly wider than the length, and owns 5 cusps, one large, rounded and bilaterally flattened main cusp accompanied by 1 outer and 3 inner cusps (pl. 1, fig. 6).

The inner marginal tooth is twice as long as the width, shows a large rounded, bilaterally flattened main cusp, one rudimentary or small outer cusp and 2 continuously smaller inner cusps (pl. 1, fig. 5).

The outer marginal tooth is fork-like in shape, almost 4 times as long as the width and shows 9-10 long pointed cusps (pl. 1, fig. 5-6).

PELLILITORINA SETOSA (Smith, 1875)

Littorina setosa Smith 1875 : 69 ; 1877 : 172, pl. 9, fig. 6 ; Martens 1885 : 92 (under *Littorina*, sic) ; Watson 1886 : 575 (under *Littorina* sic) ; Tryon 1887 : 255, pl. 46, fig. 37-38.

Pellilitorina setosa : Martens & Pfeffer 1886 : 77, pl. 1, fig. 7a-b ; Strebel 1908 : 50 (under *Pellitorina*, sic) ; Thiele 1912 : 235 ; David 1934 : 127 ; Powell 1951 : 107, 109, fig. I.32 (radula) ; Carcelles 1953 : 174 ; Gaillard 1954 : 521 ; Dell 1964 : 285 ; Arnaud 1974 : 553, 556.

L. (P.) setosa : Smith 1902 : 204 ; ? Thiele 1904 : 165, pl. 7, fig. 34 ; pl. 8, fig. 47 ; Melvill & Standen 1907 : 131 (and 1909 : 101).

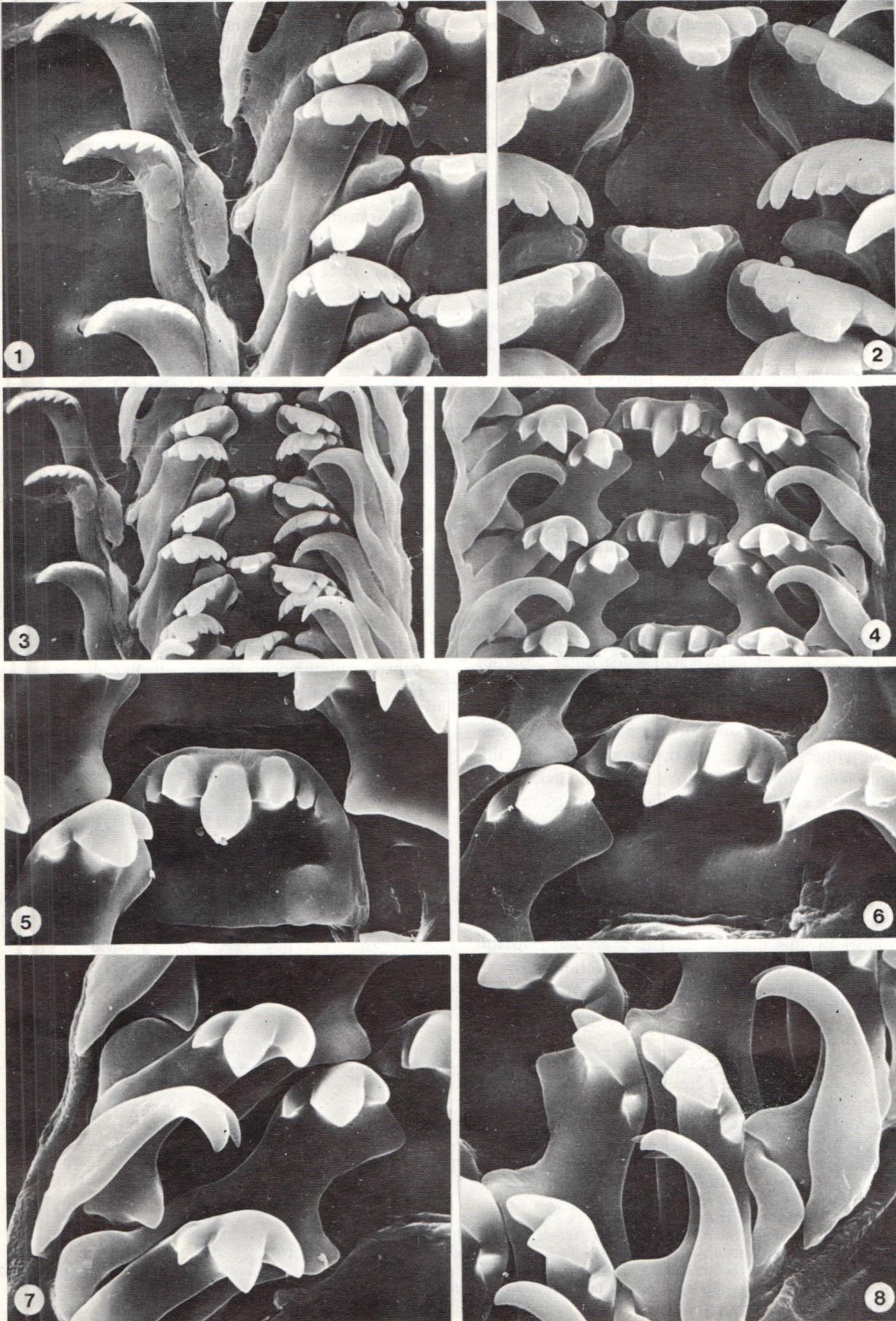
Maximum size : 14,1 mm (South Georgia : Martens & Pfeffer 1886).

Distribution and bathymetric range : South Georgia (Powell 1951, Carcelles 1953), South Orkneys (Melvill & Standen 1907, Carcelles 1953) Cap Adare (Smith 1902), Bouvet I. (Powell 1951) ; Heard I. (Dell 1964), Kerguelen I. (Smith 1875, 1877, type locality : Swain's bay ; ? Martens 1904 ; Thiele 1912, Dell 1964). From intertidal zone to may be 60 m (*fide* Powell 1951).

Ecology : species living in tide pools as well as among seaweeds or on the kelp *Macrocystis pyrifera* (among rhizoids or on its blades : cf. Arnaud 1974).

PLATE 2

- Figure 1 – Outer marginal, inner marginal and lateral teeth of *Laevilitorina caliginosa* (x 790).
Figure 2 – Central teeth of *Laevilitorina caliginosa* (x 1300).
Figure 3 – Radula of *L. caliginosa* (x 425).
Figure 4 – Radula of *Pellilitorina setosa* (x 1100).
Figure 5 – Central tooth of *P. pellita* (x 635).
Figure 6 – Central tooth of *P. setosa* (x 1100).
Figure 7 – Outer marginal, inner marginal and lateral teeth of *P. setosa* (x 1100).
Figure 8 – Outer marginal, inner marginal, and lateral teeth of *P. setosa* (x 1100).



Material used: Kerguelen I., Port Jeanne d'Arc, dredging along a *Macrocystis pyrifera* bed, 14-17 m, P.M. Arnaud coll., 12 Feb. 1970, 3 specimens.

Radula (Fig. 5; pl. 2, figs. 4 & 6-8): the radula is very similar to that of *P. pellita*. The central tooth is wider than the length (4:3), showing rounded anterior corners and angular posterior corners (pl. 2, fig. 6). The cusps of the cutting edge are rooted in vertical position right on the anterior portion of the basal platform. The central largest cusp leaves a frontal rim at its base, while the next pair of cusps extends without rim on the anterior front. There are two more pairs of much smaller cusps present on the outer sides of the cutting edge. The margins are convex and raised into a low rim. The posterior edge is straight. Two deep pits connected with each other by a less deep central region are found in the anterior central portion of the basal platform (pl. 2, fig. 6). Into these pits the extended anterior inner corner of the lateral tooth may rest in the folded radula (pl. 2, fig. 4).

The lateral tooth is wider than the length (5:4) and shows only a short cutting edge with 3 solid cusps rooted vertically on the inner anterior portion of the basal platform (pl. 2, fig. 7). The central cusp is the largest. The inner anterior edge is extended into a projection. From there onward the inner margin forms a deep concavity ending in a thumb-like projection extending from the posterior inner corner. The posterior edge is straight until reaching the outer posterior corner. The outer margin forms at first a weakly concave extension of the cutting edge. It becomes straight in a parallel course to the posterior edge. Near the outermost portion of the basal platform, this margin bulges upward and thus forms an indentation between this swelling and the posterior outer corner. A gutter-like broad extension of the outer posterior corner is therefore formed, into which the whole shaft of the inner marginal tooth can be fitted (pl. 2, figs. 7-8). The swelling at the outermost portion of the outer margin of the lateral tooth extends upward further as the inner of this margin, forming a groove. Into this groove the projection of the inner posterior corner of the following inner marginal tooth is fitted (pl. 2,

fig. 8). Therefore, the handle-like gutter shaped outer extension of the lateral tooth is hinged with its 2 neighbouring inner marginal teeth.

The inner marginal tooth is 3 times as long as wide. It shows smooth margins, the inner one concave, the outer convex, and a three-cuspid cutting edge with central cusp strongest. The inner posterior corner is extended like a thumb and project upwards (pl. 2, fig. 7-8). It forms a raised border of the flattened basal platform onto which may be rested the flat surface of the stalk of the outer marginal tooth.

The outer marginal tooth is about 4 times as long as wide, bilaterally flattened and shows an upturned cutting edge with 3 cusps (pl. 2, fig. 8).

Embryonic shell (pl. 3, fig. 7; pl. 4, fig. 3): the whole embryonic shell consists of about 1.7 whorl (pl. 4, fig. 3). The well rounded, evenly concaved protoconch measures about 0.2 mm in width. The onset of first strong growth lines indicates that the young hatched from the egg mass at this stage of shell growth with about 0.83 mm high. The embryonic shell is sculptured by spiral ridges and rows of pits between them (pl. 4, fig. 3). These pits are about 15 μ m wide and of oval outline. About 20 spiral ridges and pit rows may be counted on the first whorl. This sculpture is restricted to the embryonic shell and not continued after hatching. Following the embryonic shell the periostracum is sculptured by short bristle-like thorns arranged in rows following the course of the growth lines (pl. 3, figs. 7, 8).

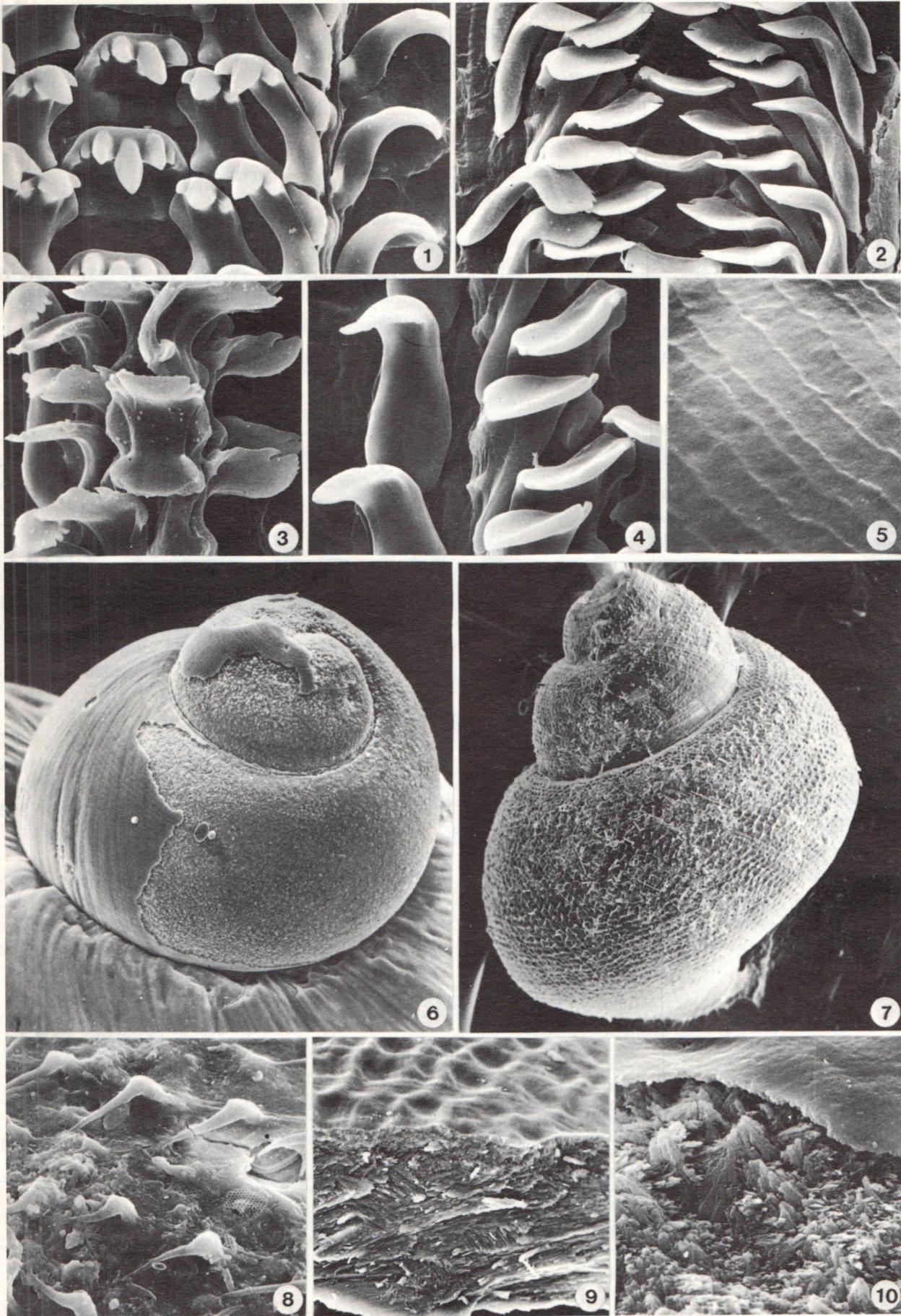
PELLILITORINA PELLITA (Martens, 1885)

Littorina pellita Martens 1885: 92; Tryon 1887: 255, pl. 46, fig. 33-41.

Pellilitorina pellita: Martens & Pfeffer 1886: 79, pl. 1, fig. 6a-c; Lamy 1905: 478, 1906a: 5, 1906b: 122, 1915: 72 (under *Pellilittorina* sic); Strebel 1908: 50 (under *Pellilittorina*); David 1934: 127; Carcelles 1953: 173; Powell 1951: 109, fig. 133 (radula); Gaillard 1954: 552; Dell 1964: 286.

PLATE 3

- Figure 1 - Half row of the radula of *Pellilittorina pellita* ($\times 390$).
 Figure 2 - Radula of *Laevilacunaria bransfieldensis* ($\times 290$).
 Figure 3 - Central tooth of *L. bransfieldensis* ($\times 380$).
 Figure 4 - Marginal and lateral teeth of *L. bransfieldensis* ($\times 530$).
 Figure 5 - Sculpture of the embryonic shell of *Laevilittorina antarctica* ($\times 1400$).
 Figure 6 - Embryonic shell of *L. antarctica* ($\times 140$).
 Figure 7 - Juvenile shell of *Pellilittorina setosa* ($\times 25$).
 Figure 8 - Sculpture of the juvenile shell of *P. setosa* ($\times 475$).
 Figure 9 - Fracture through the embryonic shell of *P. setosa* parallel to growth lines ($\times 163$).
 Figure 10 - Surface of the embryonic shell of *P. setosa* corroded away to show below the outermost shell cover the complex prismatic structure as transition into the crossed lamellar structure below ($\times 942$).



L. (P.) pellita : Smith 1902 : 204 ; Melvill & Standen 1907 : 131 (& 1909 : 101) ; 1912a : 348 (& 1912b : 122).

Maximum size : 18,2 mm (in South Georgia : Martens & Pfeffer 1886).

Distribution and bathymetric range : Burdwood Bank (Melvill & Standen 1912), South Georgia (Martens & Pfeffer 1886, Powell 1951), South Orkney Islands (Lamy 1906b, Melvill & Standen 1907, Powell 1951), South Shetland Islands (recorded here), Melchior Island (Carcelles 1953), Wandel Island (Lamy 1905, 1906a), Cape Adare (Smith 1902), Heard I. (Gaillard 1954), Kerguelen I. (Lamy 1915, Gaillard 1954). From intertidal zone to 30 m (*vide* Lamy 1905).

Ecology : this species is generally found among sublittoral seaweeds and more rarely kelps or in tide pools ; it is apparently never exposed at low tide.

Material used : King George I., South Shetland Is., Fildes Bay, stomach content of *Notothenia coriiceps neglecta*, C. A. Moreno coll., Jan. 1971, 1 dried specimen.

Radula : (Fig. 6 ; pl. 2, fig. 5 ; pl. 3, fig. 1) : the radula is very similar to that of *L. setosa*. The teeth are hinged to each other in the same way only with less pronounced projections and groove or pits as present in *L. setosa* (pl. 3, fig. 1). The central tooth is wider than the length (5 : 3). The arrangement of the 7 cusps is like that in *L. setosa* but a frontal rim is always present (pl. 2, fig. 5). The depression in the basal platform is less concave and shows no separation into two pits.

The lateral tooth is almost as wide as long, and quite like that of *L. setosa*. The inner marginal tooth is 3 times as long as the width. The only difference to that of *L. setosa* is based on the structure of the inner posterior corner, where the projection is smaller (pl. 3, fig. 1).

The outer marginal tooth is 3 times as long as the width and in contrast to *L. setosa* demonstrates a knob-like bulging inner posterior corner (pl. 3, fig. 1).

LAEVILACUNARIA BRANSFIELDENSIS
(Preston, 1916)

Pellilitorina bransfieldensis Preston 1916 : 271, pl. 13, fig. 5;

Laevilacunaria bransfieldensis : Powell 1951 : 106, 108, fig. I.29 (radula) ; Castellanos & Luna Perez 1963 : tabl. 10.

Maximum size : 5 mm (Preston 1916).

Distribution and bathymetric range : South Shetland Islands (Powell 1951), Bransfield strait (type locality), Danco coast (Powell 1951) and Arthur Harbor, Anvers Island (present material). This means a very limited distribution ! Shore species, not observed at more than a few meters deep.

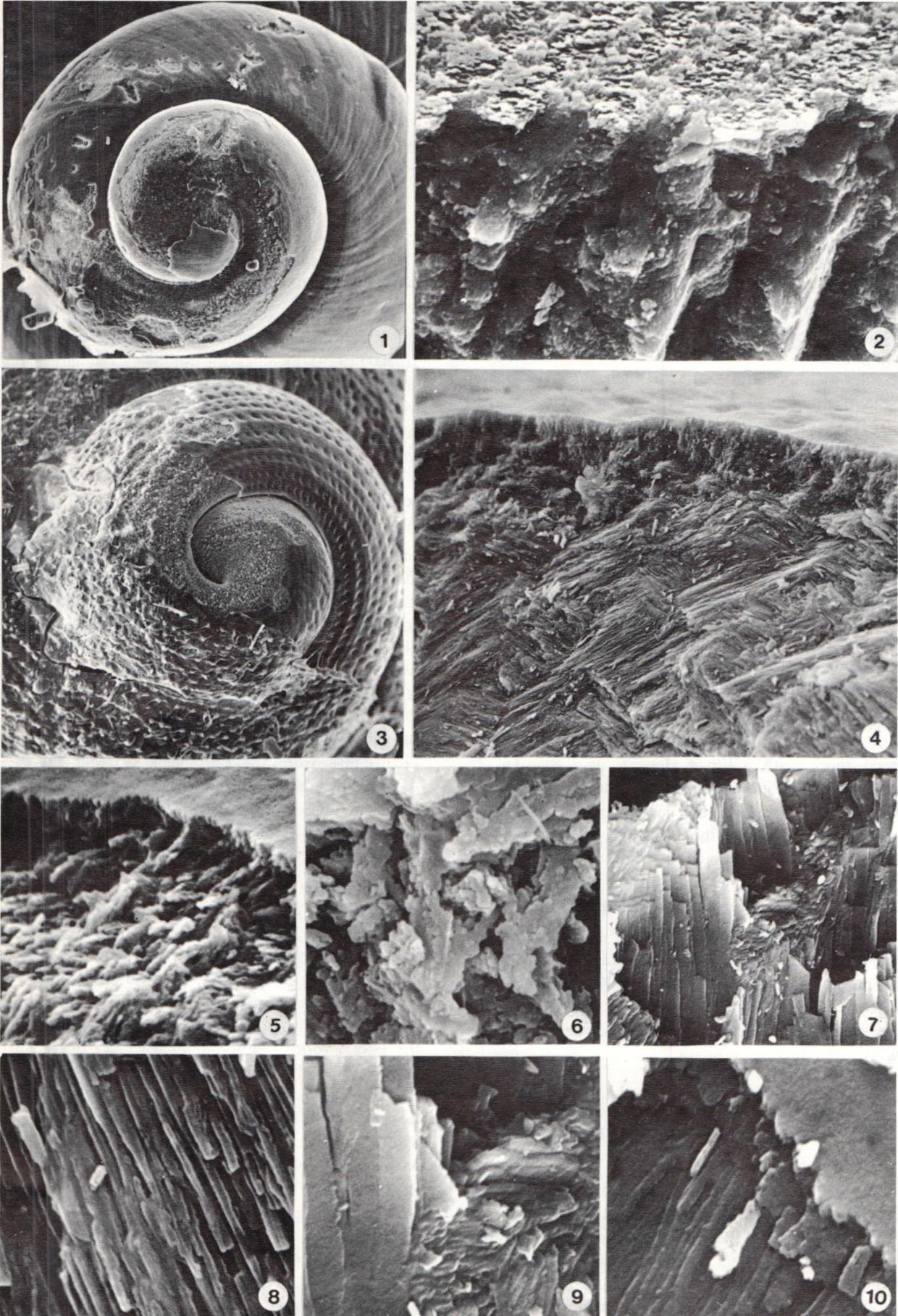
Ecology : living on superficial seaweeds of coasts relatively sheltered (tide pools, coves, etc.) as first mentioned by Castellanos & Luna Perez (1963). Most probably never exposed, and heavily preyed by nototheniid fish (as evidence by the source of Preston's and our material).

Material used : Arthur Harbor, Anvers I., Palmer Archipelago, cove SE of Bonaparte Point, stomach content of *Notothenia coriiceps neglecta* caught by fish trap, 2-11 m, "Hero" cruise, J.H. Dearborn, P.M. Arnaud *et al.* coll., 16 march 1972, 4 specimens.

Radula (Fig. 7 ; pl. 3, figs. 2-4) : the radula demonstrates scale-like appearance of all its teeth (pl. 3, figs. 2). The teeth are like a broad shovel in shape and show bilaterally flattened, straight and turned-up cutting edges.

PLATE 4

- Figure 1 - Embryonic shell of *Laevilitorina antarctica* (x 128).
 Figure 2 - Fractured shell of *L. antarctica*, vertical to growth lines, demonstrating the crossed lamellar structure (x 1400).
 Figure 3 - Embryonic shell of *Pellilitorina setosa* (x 97).
 Figure 4 - Shell of *P. setosa* fractured parallel to growth lines demonstrating the crossed lamellar structure split open parallel to the planes of the lamellae of the first order (x 400).
 Figure 5 - Corroded embryonic shell of *Laevilitorina antarctica* demonstrating outermost prismatic layer, followed by complex prismatic structure leading into the crossed lamellar structure below (x 2800).
 Figure 6 - Dendritic structure of embryonic shell of *Pellilitorina setosa* intermediate between granular outermost layer and complex prismatic structure below (x 4750).
 Figure 7 - Innermost portion of the adult shell of *P. setosa* showing transition from the crossed lamellar structure into the lamellar needle structure (x 1600).
 Figure 8 - Needle elements (lamellae of third order) in the crossed lamellar layer of the shell of *P. setosa* (x 4150).
 Figure 9 - Detail of figure 7 (x 3950).
 Figure 10 - Border of lamellar needle structure against the inner surface of the shell of adult *P. setosa* (x 4000).



The central tooth is as wide as the height and of angular outline (pl. 3, fig. 3). Its cutting edge forms an angle of about 90° with the basal platform. The broad, angular central portion of the cutting edge is straight. It is accompanied by two continuously lower and pointed cusps on each side. The outermost cusps are the endpoints of a central swelling which extends with decreasing width toward posterior direction for two thirds of the tooth-length. From there on the ridge extends outwards branching into two swellings which are shouldered by two ridge-like basal denticles. The margins of the central tooth are formed by wide lamellae, extending from the base of the cutting edge to the posterior corners in an evenly convex course. The posterior edge is evenly convex between the projecting posterior corners. Into the concave hollows of the sides of the central tooth the inner anterior corners of the neighbouring lateral teeth may be fitted.

The central portion of the cutting of the lateral tooth is broad and straight (pl. 3, fig. 2, 4). It is flanked by 1-2 pointed cusps on each side. The cutting edge stands vertically on the basal platform. The lateral tooth is higher than the width (4 : 3) and of an angular outline. Its inner margin is concave ending in a dull thumb-like projection of the inner posterior corner (pl. 3, fig. 4). On this broad projection a denticle is set. The outer margin is straight, ending in a rounded outer posterior corner. The corner is attached to the radula membrane somewhat inwards of the attachment of the inner marginal tooth and therefore hidden by it.

The inner marginal tooth is longer than the width (4 : 3) and shows a cutting edge similar to that of the lateral tooth with a broad straight main cusp (pl. 3, figs. 2, 4). Only one inner additional cusp is present. A swelling extending from the cutting edge to the inner posterior corner flanks the inner margin and extends far into posterior direction. The posterior edge between this projection of the inner corner and the rounded outer posterior corner is straight.

The outer marginal tooth is of a spoon-like shape, with broad, flattened handle and evenly upturned head and more than twice as long as the width. The broad straight outer cusp is flanked by 3 pointed smaller inner cusps. The posterior corners are rounded (pl. 3, fig. 4).

DISCUSSION OF RADULA

Troschel (1856-1863) had first grouped the families Lacunidae and Littorinidae of Thiele's classification (1929) under the heading Littorinae. Troschel had noted a constant characteristic for this group consisting of a short and wide lateral tooth which is extended into an outer posterior projection forming a rounded

indentation at its outermost end. This extension of the outer posterior corner is present in all species studied here. Based on this characteristic these species were proved to be members of the group Littorinae of Troschel's classification. The shape of the central teeth within this group is quite variable, and was considered by Troschel to reflect generic differences. Besides the closely related families Lacunidae and Littorinidae, Thiele (1929) has erected the superfamily Littorinacea and included two families of terrestrial gastropods which show quite different radular characteristics. They are most probably not very closely related to the two marine families of the Littorinacea.

The diagnosis of the genus *Laeviltorina* Pfeffer 1886 (erroneously written with 2 t) according to Thiele (1929) includes the following radular characteristics: central tooth considerably longer than the width, broadest posteriorly, with 3-5 cusps; lateral and inner marginal teeth usually with 5-6, sometimes only with 3 cusps, the main cusp considerably larger than the flanking ones; outer marginal tooth with about 10 pointed cusps.

Ponder (1976) has rearranged the diagnosis of *Laeviltorina* Pfeffer 1886 in regard to the radula as follows: "Radula with narrow central tooth, central and lateral teeth with several prominent, narrowly pointed cusps, marginals fan-shaped and multidenticulate". The general characteristics of the *Laeviltorina* radula are therefore to be considered the same as those of most representatives of the general *Littorina* and *Tectarius* (see Bandel 1974, figs. 23-59). Bandel (1974) noted in the case of 18 species of Littorinidae from the Caribbean Sea and the North Atlantic that characteristic differences could be found in the number of cusps present on the single teeth of each radula row, and all 18 studied species could be differentiated on this radula feature alone.

Laeviltorina antarctica shows 3-5 cusps on the central tooth; *L. caliginosa* owns 5-7; *L. cf. umbilicata* 3. Ponder (1976) described 3 cusps in *L. burni* Ponder, but his photograph of the fig. 1 indicates 5-7. The lateral tooth in *L. antarctica* shows 5 cusps, the central largest one accompanied by 3 inner and 1 outer smaller cusp. In *L. caliginosa* 6-7 cusps are present on the lateral tooth, with 3-4 inner and 2 outer smaller cusps besides the main cusp. *L. cf. umbilicata* owns 5 cusps on the lateral tooth in the same arrangement as seen in *L. antarctica*. *L. burni* demonstrates 5 cusps, with 2 smaller ones accompanying the main cusp on both sides (Ponder, 1976). In respect to the inner marginal tooth, *L. antarctica* and *L. burni* show the same number of cusps (4), while *L. caliginosa* shows 6 and *L. cf. umbilicata* 3-4 cusps. The number of cusps on the outer marginal tooth increases from *L. antarctica* (7-8) to *L. caliginosa* (8-9), *L. cf. umbilicata* (9-10) to *L. burni* (10).

The number of cusps that may be counted from the drawing of the radula of *L. caliginosa* presented by Powell (1951, fig. I, 26) coincides quite well with that counted in our study, with exception of the outer marginal tooth where Powell drew 16 cusps instead of 8-9. The radulae of *Laevilitorina heardensis* Dell (1964) and *L. coriacea* Melvill and Standen (Powell, 1951) also show general similarities to the other members of the genus. The base of the lateral tooth of *L. heardensis* is drawn without the typical indentations (Dell, 1964, fig. 27) and may therefore be similar to that of *L. antarctica*. Following Dell's description there are 3-5 cusps on the central tooth, 5 cusps on the lateral tooth and 6-7 cusps on the marginal teeth in this species.

Powell (1951) noted that the radulae of *Laevilitorina* and *Pellilitorina* show very distinct differences. In the definition of the genus *Pellilitorina* Pfeffer 1886, Powell noted: "Radula with a broad shallow-based central tooth, bearing five cusps, the middle one strongest, laterals with three strong cusps, marginals foliated and with several denticles". This definition is different from that offered by Thiele (1929) only in one respect. Thiele wrote that the outer marginal tooth in members of this genus shows 3 cusps, a circumstance that we can confirm. The central tooth of *Pellilitorina* is wider than the length, as Thiele noted, and shows raised convex margins. The cusps of the central tooth are rooted on the anterior platform. The marginal teeth are slender and bilaterally compressed. Powell (1951) figured the radula of both, *Pellilitorina setosa* and *P. pellita*. From his figures (I, 32, 33) the radulae of both species can not be kept apart but the figures are right in general.

The greatest difference of the *Pellilitorina* radula from the radula of other Littorinidae may be seen in the shape of the central tooth. It is quite different from the other known Littorinidae and lacks the characteristic lateral wings. The study of the radulae of the southern *Laevilitorinids* indicates a greater complexity than is suggested by their respective shells, as Powell (1951) has stated. A close systematic relation between *Laevilitorina* and *Pellilitorina* may therefore be ruled out.

The radula of *Laevilacunaria bransfieldensis* was figured by Powell (1951, fig. I, 29) and shows in general the same features as represented here. Only the strong flanking basal denticles of the central tooth and the thumb-like inner posterior projection of the lateral tooth were not drawn and noted by this author. Even with the scale-like appearance, that is due to the bilaterally flattened straight cutting edges present on all teeth in each row, the single teeth of this radula resemble those generally found within the Littorinidae. The central tooth of *Laevilacunaria*, with its wide lateral wings, is similar to the central tooth of *Laevilitorina*, and different from the bow shaped central tooth

of *Pellilitorina* having raised margins and lacking lateral wings. The radula of *Laevilacunaria bennetti* (Preston) as figured by Powell (1951, fig. I, 30) demonstrates, in general, an outline similar to that seen in *L. bransfieldensis*, but the cutting edge is resolved in denticles in contrast to the latter. Transitional radula morphology between *Laevilitorina* and *Laevilacunaria* can be noted in the genera *Rufolacunaria* and *Macquariella* as described and figured by Ponder (1976, figs. 2-4). Here we can notice the formation of long straight cutting edges on lateral and marginal teeth dented with many cusps. Ponder (1976) expressed the opinion that the *Laevilitorina* group, encompassing the Antarctic Littorinidae, is to be considered as primitive and to contain species of unspecialized Littorinidae that are in many features closer to *Lacunaria* than to *Littorina*. The radulae of *Lacunaria carinifera* A. Adams (Thiele 1929, fig. 96), *L. vineta* Forbes and Hanley (Troschel 1856-1863, pl. 10, fig. 13), *L. pallidula* (Da Costa) Meyer and Möbius, 1872, fig. 13), and *L. divaricata* Fabricius (Meyer and Möbius 1872, fig. 7) resemble those of *Laevilacunaria*. Basal denticles on the central tooth were noted only in *Laevilacunaria* but not on *Lacunaria*. These features are quite prominent in *Laevilacunaria* but very rarely seen among other members of the marine Littorinacea and up to now only known from *Littorina neritoides* Linné (Bandel, 1974, fig. 58-59).

Troschel's (1856-1863) statement that the group Littorinidae, encompassing Littorinidae and Lacunidae of Thiele's classification, contains closely related species which can best be differentiated and characterized by their radula-morphology can be confirmed in our study. Ponder's conviction that the *Laevilitorina* group, or better the group of Antarctic Littorinidae, are to be considered as transitional between the Lacunidae and Littorinidae is agreed to, but only with restriction to the genera *Laevilitorina* and *Laevilacunaria*. These genera are connected to each other by transitional forms. *Pellilitorina*, in contrast, shows so widely different central teeth that they can, on behalf of this feature, neither be considered as representatives of the Lacunidae nor the Littorinidae. Only three cusps on the outer marginal teeth are seen quite rarely among littorinid radulae (for example *Tectarius muricatus* Linné: cf. Bandel 1974, figs. 24-25) and the broad central tooth has no counterpart among known marine littorinaceans. On the other hand, both the radulae of Antarctic representatives of *Laevilitorina* and *Laevilacunaria* show the characteristics in their morphology and structure of most Lacunidae and Littorinidae from other regions of the world. To our knowledge transition between both, as noted in detail in Ponder's (1976) recent study, occur only in Antarctic regions.

If we search for radular similar to those of the marine Littorinacea outside of this superfamily, we can note similarities with some members of the superfamily

Rissoacea, and especially the families Eatoniellidae and Cingulopsidae (Ponder 1965, a,b) (both included within the family Rissoidae in Thiele's classification). Ponder has described and figured radulae of New Zealand members of these families. Members of the genus *Eatoniella* for example show central teeth transitional in shape between that of *Pellilitorina* and *Laevilitorina*. The lateral teeth also demonstrate the indentation of the outer posterior extension considered as characteristic for marine Littorinacea by Troschel. This relationship cannot be regarded as proof for a close systematic relation between the superfamily Littorinacea on one side and the superfamily Rissoacea on the other, for both superfamilies, as understood by Thiele (1929), contain families with no apparent relation aside from small size and general shell morphology. But it does demonstrate relations between Littorinidae and Lacunidae on one side, and Eatoniellidae and Cingulopsidae on the other.

DISCUSSION OF EMBRYONIC SHELL

Simpson (1976) observed a non-pelagic development of the young of *Laevilitorina caliginosa*. Miniature adults will leave the egg cases after completion of metamorphosis. Bandel (1975 a,b) described the embryonic shells of a number of Littorinidae and discussed in detail the older literature on this subject. From this study it is apparent that those species which possess a free-swimming, larval veliger stage show well-differentiated embryonic and larval shells. The embryonic shell will show another sculpture than the one formed on the larval shell (see also Richter and Thorson, 1975). This is different in such species of Littorinidae where the development within the egg mass continues until after the metamorphosis. Here only an embryonic shell is differentiated. Species with free-swimming, planktonic larvae show embryonic shells protoconchs 0.04 to 0.09 mm wide. Species of Littorinidae with complete larval development within the egg, in contrast, show wider (0.1 to 0.09 mm) protoconchs. Into the latter group *Laevilitorina antarctica* and *Pellilitorina setosa* (with 0.14 and 0.2 mm wide protoconchs) must be classified. The size of the embryonic shell also clearly delimits Littorinidae with free larval life from those which develop within the egg case. Bandel (1975a, Schemas 1 and 2; 1975b, pp. 12-14) demonstrated that the shells of hatching veligers measure between 0.1 and 0.15 mm in width, while those hatching as miniature adults measure more than 0.4 mm in width. Into the latter group *Laevilitorina antarctica* and *Pellilitorina setosa* may be included, as their shells are 0.5 and 0.8 mm high.

While *Littorina obtusata* (Linné) and *Littorina saxatilis rudis* (Maton) from the North Atlantic, which

also hatch as miniature adults (Bandel, 1975b), only show growth on their embryonic shells, the two Antarctic representatives of the Littorinidae own quite definite sculpture. It consists of spiral ridges in the case of *L. antarctica* and spiral ridges and pit rows in the case of *P. setosa*. The sculpture found on the embryonic shell of the species hatching as veliger larvae often reflects the systematic position of its carrier. This is not, or to a much lesser extent, the case in the species in which the development proceeds beyond metamorphosis within the egg mass. Here we can find similar sculptures and shell dimensions in completely unrelated members of the gastropod system. Therefore, we can gather little phylogenetic information from the sculpture of the embryonic shell of southern Littorinidae.

Southern Littorinidae hatch after completion of their metamorphosis within the egg capsule, and their representatives live below low water or always covered by water in tide pools. Therefore they confirm Mileikovsky's (1975) results that place of living and type of embryonic development are not correlated in such a way in the Littorinidae that species living below the tidal zone have free swimming larvae and those living within or above that zone have crawling young hatching. But since we have seen that Lacunidae and Littorinidae are not to be separated in the antarctic regions, this Woodward's (1909) scheme would not work any longer anyhow, because we would have to include *Lacuna*.

Thorson (1940, 1946) has found that the number of species with a free larval stage increases with the increase in water temperature; he noted no pelagic larvae in East Greenland waters. It seems that Thorson's scheme works also in antarctic waters where larval stages are held within the egg capsule.

SHELL STRUCTURE

The shell structure of *Laevilitorina antarctica*, *L. caliginosa* and *Pellilitorina setosa* was analysed. The shell of all three species is fully aragonitic and composed mainly of needle-like biocrystals arranged in the crossed lamellae structure (pl. 4, figs. 2,4). The crossed lamellar structure consists of plates inclined to each other in two directions (pl. 4, fig. 2). These plates are composed of needles (biocrystals) which are oriented parallel to the plane of each plate and are of equal orientation within each plate (pl. 4, figs. 4, 8). The plates, in literature, are usually called lamellae of the first order. The needles composing the plates or lamellae of the first order may fuse to form lamellae of the second order (pl. 4, fig. 2) measuring up to a few microns in breadth and about 0.2 μm in thickness. The lamellae of the third order composing both

lamellae of the second and the first order actually are like needles measuring $0.2 \mu\text{m}$ in diameter (pl. 4, fig. 8).

In *Laevitorina* and *Pellitorina* the lamellae of the first order only measure up to about $5 \mu\text{m}$ in width (pl. 4, fig. 2), are quite long, usually continuous throughout the breadth of the layer, and arranged regularly forming thin, discontinuous ribbons if seen from the surface of growth. Lamellae of the second order are distinct and well developed forming narrow rod-like structures. The lamellae of the third order are composed of basal elements that show angulate to polygonal or round shape and measure fractions of one micron, usually around $0.2 \mu\text{m}$.

The crossed lamellar layer forms the bulk of the shell and only one single layer is present. Transitional structures from simpler crystal arrangement into the crossed lamellar layer were observed on the embryonic shell of *Pellitorina setosa* (pl. 3, figs. 9-10; pl. 4, fig. 6) and *Laevitorina antarctica* (pl. 4, fig. 5). Here the outermost portion of the embryonic shell shows a composition of organic material intergrown with mineral particles of the size of basal elements (about $0.2 \mu\text{m}$ width) which may or may not group themselves into columnar units with the width of one basal element (pl. 3, fig. 10; pl. 4, fig. 5). This layer only measures about $1 \mu\text{m}$ in breadth.

Below this outermost portion of the shell the distinctly needle-like aggregations or rows of basal elements arrange themselves into irregular columnar units. Within each of these units the needles are arranged almost parallel to each other, but the units themselves show no preferred orientation (pl. 3, fig. 10; pl. 4, fig. 6). This layer may be called complex prismatic. In the embryonic shell the complex prismatic layer grades rapidly into the crossed lamellar layer. The transition into the complex prismatic structure is through the dentritic structure (Bandel 1977) (pl. 4, fig. 6).

In outer portions of the shell formed by the adult animal the outermost prismatic or irregular layer may first arrange itself into a sperulitic prismatic zone before changing into the complex prismatic layer.

The composition of the mineral structures of the shell of the Antarctic Littorinidae shows a construction by basal elements from the start of mineralization onward. This demonstrates that the mineral components were constructed in an immediate contact with the epithelium and can be considered as true biocrystals (Bandel and Hemleben, 1975; Bandel, 1975c).

The crossed lamellae layer of the shell may be underlaid by an inner, additional layer that is derived from the crossed lamellae layer without interruption (pl. 4, figs. 7, 9-10). Here one of the plate-directions of the crossed lamellar layer has disappeared and only the lamellae of the second and third order remain. This

layer is built in the lamellar needle structure and is made of lamellae that are composed of intergrown needles and are as one-needle thick ($0.2 \mu\text{m}$) (pl. 4, figs. 9-10).

The structure of the shell of Antarctic Littorinidae is quite like that found among many gastropods which have no nacre. One layer of crossed lamellar structure only is not so commonly found; more usual are two layers one on top of the other and arranged in such a way that plane of the lamellae of the first order of the outer layers forms a right angle to the plane of the lamellae of the first order of the inner layer. Only one layer is commonly found among archaeogastropods, marine littorinaceans and rissoaceans while other prosobranchs, pulmonates and shell-bearing opisthobranchs usually show at least 2 layers. The sequence of irregular or prismatic outermost layer, dentritic layer, gradational complex prismatic layer, crossed lamellar layer, and innermost lamellar needle layer is normally found among molluscs that show crossed lamellar structure in the composition of their aragonitic shell.

CONCLUSIONS

1) The 6 species of Antarctic Littorinacea discussed here represent 3 different types of radula morphologies, and all three fit well the definition given for the marine representatives of this superfamily by Troschel (1856-1863).

2) The study of the radulae of the Antarctic Littorinidae with the help of the scanning electron microscope, as carried out in our study and that by Ponder (1976), confirms the results presented by Bandel (1975a) that within the marine representatives of this superfamily the morphology of the radula is to be considered of great taxonomic importance. The radula morphology may both be used to separate species and genera and to trace phylogenetic lines of development.

3) Within the southern Littorinacea no clear dividing line may be drawn between the family Littorinidae on one side and the family Lacunidae on the other. *Laevitorina* can be considered as typical representative of the genus *Littorina* in the broad sense in respect to its radula morphology. *Laevilacunaria* shows much in common with *Lacuna* in respect to the radula. Both types of radulae are interconnected by intermediate forms as shown by Ponder (1976). No such interconnection was seen in respect of the *Pellitorina* radula which stands separated and shows intermediate characters of both Lacunidae and Littorinidae, and some similarity to rissoaceans.

4) Outside of the Antarctic region Littorinidae are restricted to the intertidal and supratidal zones. *Laevili-*

torina as Antarctic representative of this group lives continuously below water. Since there is a transition from the *Laevilitorina* radula morphology to radulae typical for the genus *Lacuna* of the northern hemisphere represented by *Laevilacunaria* from the southern region, this mode of life is not to be considered as secondary adaptation to the harsh environment, but reflects the mode of life of the ancestors of the intertidal littorinids.

5) The embryonic shell of the southern littorinids reflects the mode of development in its morphology, size and sculpture and is of no systematic value aside from providing additional species characteristics. The embryonic shell owns a different sculpture than the adult shell. *Laevilitorina antarctica* and *Pellilitorina setosa* hatch as fully metamorphosed miniature adults just like *Laevilitorina caliginosa* (according to Simpson, 1976) and like northern littorinids from cold water (Bandel, 1975b).

6) The shell structure of the Antarctic Littorinidae does not differ from that of many representatives of lower Mesogastropoda with an aragonitic shell. The shell consists mainly of one layer of the crossed lamellar structure with precursor structures consisting of spherulitic prismatic dendritic and complex prismatic structures and with successor structures consisting of the lamellar needle structure.

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