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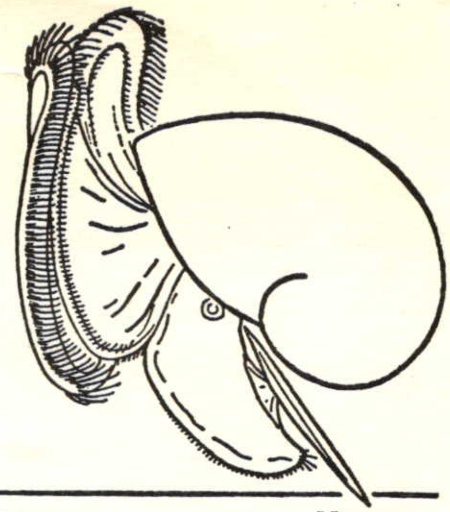

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Note: The various taxa above species are indicated by the use of different type styles as shown by the following examples, and by increasing indentation.

ORDER, Suborder, **DIVISION**, **Subdivision**, SECTION,
SUPERFAMILY, FAMILY, Subfamily, *Genus, (Subgenus)*
New Taxa

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Studies on Littorinidae from the Atlantic

BY

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(5 Plates; 22 Text figures)

INTRODUCTION

MEMBERS OF THE FAMILY Littorinidae occur as large populations on many shores ranging from the southern Caribbean Sea to the North Atlantic Ocean. Most littorinid species are restricted to hard rock substrates within or above the normal intertidal zone. Few, like *Littorina angulifera* Lamarck, 1822 and *L. nebulosa* (Lamarck, 1822), prefer wood substrates, and only *L. littorea* Linnaeus, 1758 can be found on all substrates, even on muddy bottoms. All 18 species described herein live primarily on plant material which is scraped and bitten from the substrate by the radula. ROSEWATER (1970) in light-microscope studies of many radulae indicated that the more generalized taenioglossate radula of this family offers little promise for systematic diagnosis below the generic level. Here it is demonstrated that with the scanning electron microscope clear differences in the radular morphology of 18 species of Littorinidae can be shown and used to distinguish between species. Furthermore, possible taxonomic relations can be shown more clearly and problems concerning species differentiation in the *L. ziczac* (Gmelin, 1791) and *Nodilittorina tuberculata* (Menke, 1828) groups can be solved.

In defining subgenera in the family Littorinidae the shape of egg capsules should also be considered as a valuable aid, as shown here and as previously suggested by BORKOWSKY & BORKOWSKY (1969), MARCUS & MARCUS (1963), and ROSEWATER (1970).

All individuals used in this study were collected by myself to avoid confusion about the ecological data. Material was collected from Cape Cod (Massachusetts, U. S. A.), 1965; Nassau in the Bahama Islands, 1970; Santa Marta, Colombia from 1970 to 1972; Curaçao (Netherlands Antilles) in 1971; Fuerteventura on the Canary Islands in 1972, Banyuls sur Mer (southern France), 1973; and the Wadden-Sea of the Oosterschelde in the Netherlands.

More detailed taxonomic studies especially connected with the Caribbean species are omitted in this work and will be reported separately (BANDEL & KADOLSKY, in preparation).

DESCRIPTION OF THE ENVIRONMENT

I. Santa Marta (Figures 1 and 2)

Detailed collection and observation over a period of 18 months was carried out between the fall of 1970 and the spring of 1972 in the vicinity of Santa Marta, Colombia.

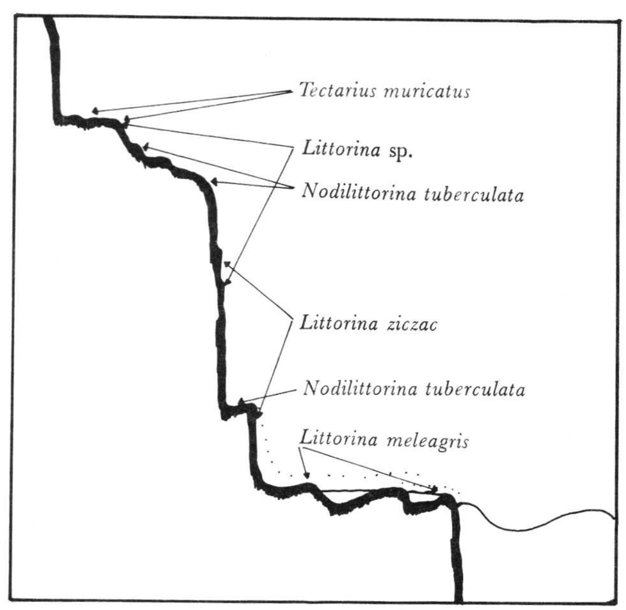


Figure 1

Transect of a cliff in the Bay of Santa Marta (Isla Morito)

The species that lives under driest conditions of all littorinids and of all marine prosobranchs in this area is *Tectarius muricatus* (Linnaeus, 1758). Individuals of this species are found in greatest abundance on flat benches of rocky shores and cliffs in areas just barely reached by spray of high seas and from strong gales. *Tectarius muricatus* has to endure long periods (months) of dryness. Members of this species can be found only rarely in the bay of Santa Marta on the islands Moro and Morito (Figure 1). Here they occupy the highest platforms carved out of the metamorphic shales by salt erosion. Only in the period between September and May, when strong winds blow almost continuously, can these animals be moistened with sea water spray and can feed on minute algae that grow on the wet rock surface. During the remainder of the year spray only rarely will reach these upper levels, and therefore all individuals remain motionless.

A thriving population of *Tectarius muricatus* is found in the Ensenada Playa Brava north of Santa Marta. Here the platform of a bench consisting of indurated calcareous dune sand receives considerable spray from comparatively heavy wave action. But here also the animals have to endure high temperatures and extreme dryness during long periods of quiet water. Some animals may even be surrounded by crusts of salt remaining from former spray water puddles, but they renew activity after being made wet by fresh sea water.

An unusual occurrence of a *Tectarius muricatus* population was observed in the mangrove belt of the southern extension of the Ensenada Chengue, north of Playa Brava. In this unusually quiet part of the bay the animals live on driftwood and dead branches piled up and anchored between the roots of living mangrove bushes and on a dry shingle beach a few tenths of a centimeter above normal water level. But here also rare high waves caused by extreme swells and unusual wind directions disturb the bay water so that waves go high enough to wet the habitat. Only then they can feed.

On rocky shores below the *Tectarius muricatus* populations *Littorina* sp. and *Nodilittorina tuberculata* populations live with a narrow to wide zone of intermixture. While *N. tuberculata* prefers flat bench surfaces with spray water basins and puddles as substrate, *Littorina* sp. is also likely to be found on vertical rock faces. The mollusks do not cling to the dry rock with their feet, but the lip of the shell is attached to it by a hard and brittle film of mucus. The strength of this film is sufficient to hold the snail to a vertical surface over long periods of time. *Nodilittorina tuberculata* will, like *T. muricatus,* survive encrustation in salt formed by the residue from evaporated spray water. Both species (*L.* sp. and *N. tuberculata*) will withstand extreme dryness and heat, for some places where they live are moistened only during certain periods of the year. The darker *Littorina* sp. avoids some of the heat of the sun by hiding in crevices and solution cavities which are especially abundant in the supratidal cliff sections. The populations of both species extend from areas of very dry conditions down into areas which are more frequently washed over by sea water. Periodically, the latter environment will not be reached by the tide and dry out. The animals are then exposed to the heat of the tropical sun. Larger pools situated in this area will periodically attain high temperatures (over 40° C) or dry out completely. Changes in the salinity of the water are large and range from saline brines (due to evaporation) to almost fresh water (due to rain). Smaller individuals of *N. tuberculata* and *Littorina* sp. prefer pools closer to the high tide line having a normal or a slightly higher salinity. When rain dilutes this pool water considerably, the juvenile animals leave it and congregate at the rim of the pool above the water surface, but they remain on a wet substrate.

Littorina ziczac (Gmelin, 1791) populations will usually be found in areas where splash and spray are common all year around and below the adult populations of *Littorina* sp. and *Nodilittorina tuberculata.* This habitat coincides with that described for this species from Margarita Island, Venezuela by RODRIGUEZ (1959). On cliffs and pebble beaches with little wave action *L. ziczac* and *L.* sp. form mixed populations, while *N. tuberculata* usually is absent. Here *L. ziczac* is also found more commonly in crevices on the shady side of larger pebbles, but *L.* sp. is common in places exposed to the sun. It can be concluded that *L. ziczac,* in general, needs more moisture even than *L.* sp. although it can endure weeks of dryness exposed to the sun. On rock cliffs more exposed to wave action where spray may moisten up to 10 m of vertical rock surface above the high tide mark, the zone of *L. ziczac* populations is distinct from that of *L.* sp. populations. Here on the island of Morito, for example (Figure 1), a 1 m to $\frac{1}{2}$ m zone of mixed populations is followed by 2 m to 3 m of pure populations above and below, respectively.

The lower range of *Littorina ziczac* populations in the whole area of Santa Marta is always distinct and coincides with the upper limit of the occurrence of *Purpura patula* (Linnaeus, 1758) in the upper splash zone. Often this muricid was seen feeding on littorinids. In places where *P. patula* populations were removed, the *L. ziczac* population expanded down to the high water line in a short time.

In rocky environments, the representative of the Littorinidae which is found in the lowest situation is the very small *Littorina meleagris* Potiez & Michaud, 1838. Individuals of this species may be found in moderately warm splash pools together with the juveniles of the 3 species *L. ziczac*, *L.* sp., and *Nodilittorina tuberculata* if water is exchanged often by splash or high waves. The animal cannot tolerate dryness. From shallow pools or depressions which are frequently renewed with sea water to a few centimeters below the water line, *L. meleagris* is very abundant, occurring in greatest numbers in the narrow normal intertidal area (only about 20cm in height in the vicinity of Santa Marta). Common predators for *L. meleagris* are represesentatives of the genera *Thais* and *Leucozonia*. Pebble beaches with little wave action are densely settled by *L. meleagris* which are on and below rocks in the intertidal area and among rocks densely covered by algal growths just below low tide mark.

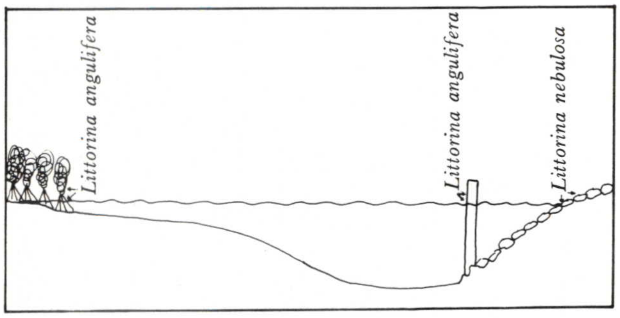


Figure 2

Transect through the estuary of the Cienaga Grande Lagoon between Santa Marta and Barranquilla (Colombia)

Littorina angulifera populations were found near *Tectarius muricatus* settlements only at the unusual locality of the Chengue mangrove belt. Here *L. angulifera* settles on living roots and branches of the mangrove bushes, while *T. muricatus* uses dead branches and washed up driftwood between bushes for attachment.

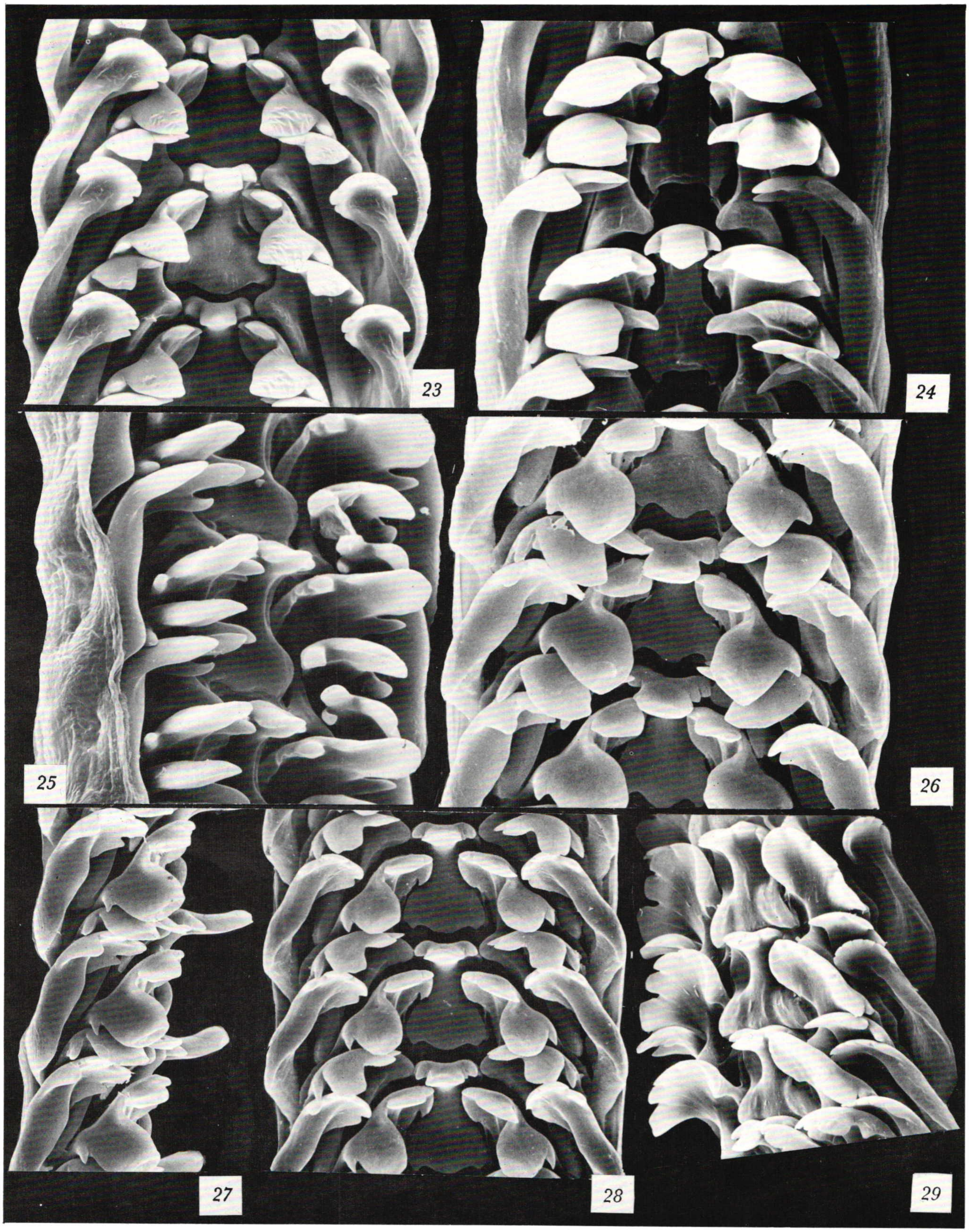
Littorina angulifera was collected on mangrove bushes growing under normal marine conditions and in brackish water lagoons. Fresh water conditions were tolerated only for short periods. This was observed in the mouth of the Cienaga Grande, a large, shallow, brackish water lagoon in the Rio Magdalena delta about 40km south of Santa Marta. Here, fresh river water from a Rio Magdalena flood had in the winter of 1970/1971 flushed out the brackish water of the lagoon. After about 2 months of fresh water flood all the rich settlements of *L. angulifera* had disappeared from the mangrove bushes of the lagoon and its estuary, even though the animals populate the bushes in heights up to 2m above the water surface (even at flood times with raised water level). Shorter periods of low salinity should be tolerated by this species. In the same Rio Magdalena flood the animals in another lagoon were exposed for at least one month to fresh water; most of these individuals survived.

The zonation of *Littorina angulifera* populations in the vicinity of Santa Marta is the same as described by Coomans (1969) for the Caribbean region in general, by Marcus & Marcus (1963) for Brasil, and by Lenderking (1954) for Florida.

At the mouth of the Cienaga Grande the environments of *Littorina angulifera* and *L. nebulosa* approach one another. *Littorina angulifera* settles on wooden pilings of an old bridge and *L. nebulosa* can be found next to it on rocks of a breakwater, covered by algae (Figure 2). This is not an unusual environment for *L. nebulosa*, but it demonstrates its tolerance to salinity changes in this estuarine milieu of the lagoon entrance. During the extended periods of freshwater outflow of the Rio Magdalena flood *L. nebulosa* populations disappeared from the estuarine area and survived only on rock piles at the seaward end of the entrance to it. The more usual habitat of *L. nebulosa* is driftwood tree trunks firmly fixed between boulders or anchored on sandy beaches within the surf zone. Strong wave action is tolerated and dense populations are usually found. All littorinids mentioned previously gather microorganisms, algae and detritus from the surface on which they live. *Littorina nebulosa* seems to be able to feed on rotting wood. Therefore, cellulose wood fibres are the principal constituent of their faeces. This is in contrast to *L. angulifera* and *Tectarius muricatus* which may also be collected from driftwood or wooden pilings, but never

Explanation of Figures *23* to *29*

Figure *23*: *Littorina littorea* from Cape Cod, Massachussetts. × 240
Figure *24*: *Tectarius muricatus* from Paradise Island, Nassau. × 480
Figure *25*: *Tectarius muricatus* from Santa Marta. × 480
Figure *26*: *Littorina saxatilis* from the Oosterschelde. × 350
Figure *27*: *Littorina saxatilis* from the Oosterschelde. × 310
Figure *28*: *Littorina obtusata* from the Oosterschelde. × 245
Figure *29*: *Littorina obtusata* from Cape Cod, Massachussetts. × 360



produce faeces consisting primarily of wood fibers (BANDEL, in press).

II. Curaçao (Figure 3)

Near the old wrak in Cornelisbaai on the leeward side of the island of Curaçao, Netherland Antilles, the beach region consists of a hard beach rock bench and limestone boulders. The seaward edge of the rock bench drops suddenly into deeper water where coral growth is evident. The transect shows pools continuously washed through by waves, without Littorinidae, followed by pools only rarely reached by a wave or only by splash, containing dense populations of *Littorina mespillum* von Mühlfeld, 1824. Members of this species are generally only found below the water line. At the water line of the more landward pools and also near pools with more saline water the 2 species *Nodilittorina tuberculata* and *L. jamaicensis* C. B. Adams, 1850, are common. The ones living at the edge or in the water of the pools usually have extensive erosions of the upper part of their spire. Others, living on rock surfaces or in more dry surroundings have well preserved shells. *Littorina ziczac* populations settle in crevices protected from the sun and the undersides of large boulders that are moistened by splash and spray.

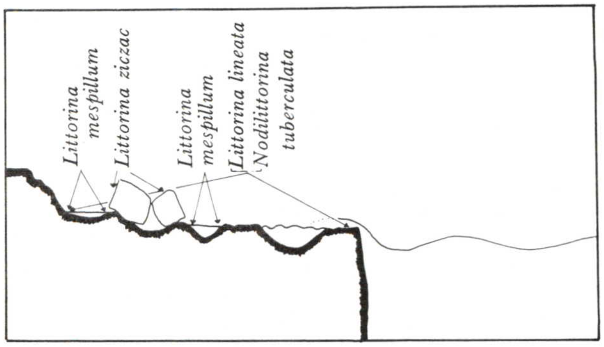


Figure 3

Beachrock-shore on the leeward side of Curaçao

III. Nassau (Figure 4)

A consolidated oolith bar at the seaward side of Paradise Island, Nassau, Bahamas, harbored a number of Littorinidae collected here in the fall of 1970. At the time of collection (1 week) the top of the bar was completely dry. The uppermost parts of the bar were settled by numerous individuals of *Tectarius muricatus* and *Echininus nodulosus* (Pfeiffer, 1832). Near the uppermost spray pools, which were in part filled with brackish water due to rain or were in part dry, *Nodilittorina dilatata* (d'Orbigny, 1841) was common. This population generally occurred in a distinctly lower zone than the former two species. Tidal pools filled with splash water refreshed by daily floods and strong waves contained numerous *L. mespillum*. Rocks from there down into the high water line were settled by *Littorina lineolata* d'Orbigny, 1840.

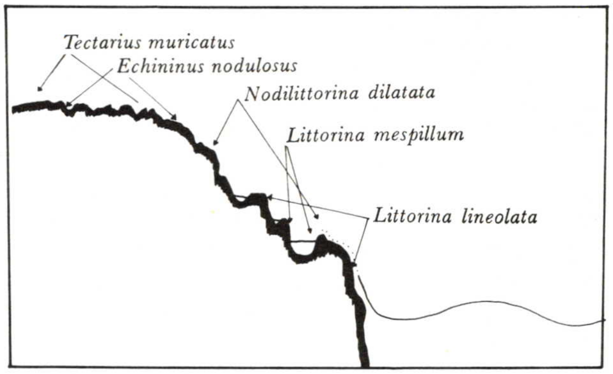


Figure 4

Transect through a limestone bar on Paradise Island, Nassau

IV. Fuerteventura (Figure 5)

The Littorinidae of the Canary Islands include 3 species: *Littorina punctata* Gmelin, 1791; *L. neritoides* Linnaeus, 1758; and *L. striata* King & Broderip, 1832. The

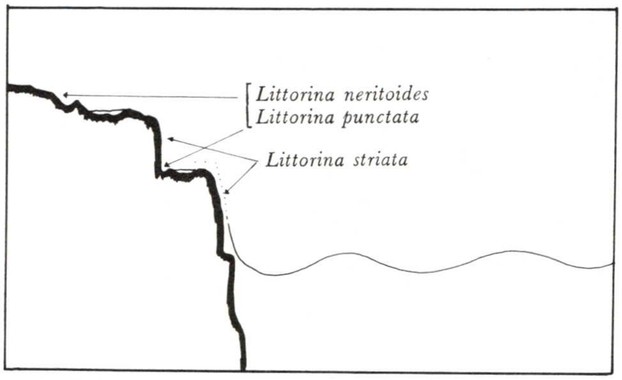


Figure 5

Transect of the Islote, a rock projection of the Island of Fuerteventura, Canary Islands transect shown here was made at the Islote, a large volcanic rock projection extending into the Atlantic Ocean at the west side of the southern part of the island Fuerteventura (Jandia) near the village of Cofete. The powerful waves cause a continuous wetting of rocks above the high tide level and at low tides during most of the year. *Littorina striata* is found from continuously wet spots up into often dry rock areas considerably above the high tide line. It may also be found in spray pools. Here it is often encountered with *L. punctata*. *Littorina neritoides* prefers areas that are high up and only moistened at high tides or if strong winds blow up splash.

On the eastern beaches of the island, more protected from wave action, tidal pools will often contain *Littorina punctata*, while *L. neritoides* prefers crevices and rock surfaces up to the high water line. This species is the marine prosobranch that ventures highest up on the beach in this area. In pebble zones it settles on larger blocks just barely reached by the sea at normal high tides.

V. Banyuls (Figure 6)

Littorina neritoides is the only representative of the Littorinidae commonly found on rock pilings, breakwaters, and cliffs everywhere in the Mediterranean Sea. It was collected from a breakwater sheltering the yacht harbor of the town of Banyuls sur Mer, a small resort town in southern France near the Spanish border. The periwinkle population is found well above the high tide mark in the spray and splash zone. The largest individuals occur furthest up and are more often seen on flat rocky surfaces, while smaller individuals prefer crevices in rocks. Very heavy seas sometimes sweep over the breakwater. Then *L. neritoides* populations may move upward. Animals trapped in small spray pools on top of the breakwater after the sea has calmed down will die if the water evaporates, leaving the snails surrounded by saline water or dry salt. The animals feed on minute algae that grow on the rocks; they move about and feed only when the surface is moist. Individuals will survive in the absence of moisture for at least 5 months (Fretter & Graham, 1962). A very detailed study on the ecology of this species was made by Lysaght (1941) on the Plymouth breakwater.

VI. Oosterschelde (Figure 7)

At the dikes and on the intertidal flats of the Oosterschelde, a fully marine embayment of the North Sea in the Rhein Delta area of the Netherlands, 3 littorinids can usually be found in great abundance. The dikes are coated with basalt columns on the seaward side up to a level well above the normal high tide line. *Littorina saxatilis* Olivi, 1792 lives just above the high water line in the zone where only splash and spray at normal high tides prevent the growth of grass. This region coincides with the line of

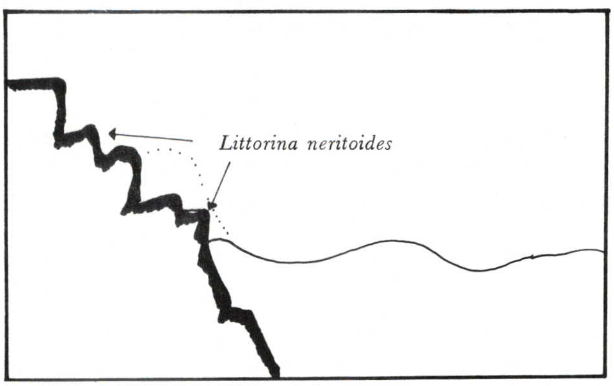


Figure 6

Transect across the breakwater of the Banyuls yacht harbor, southern France

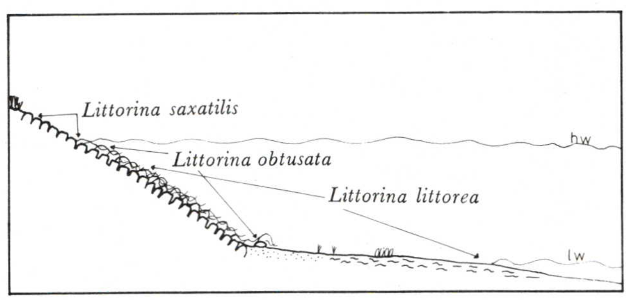
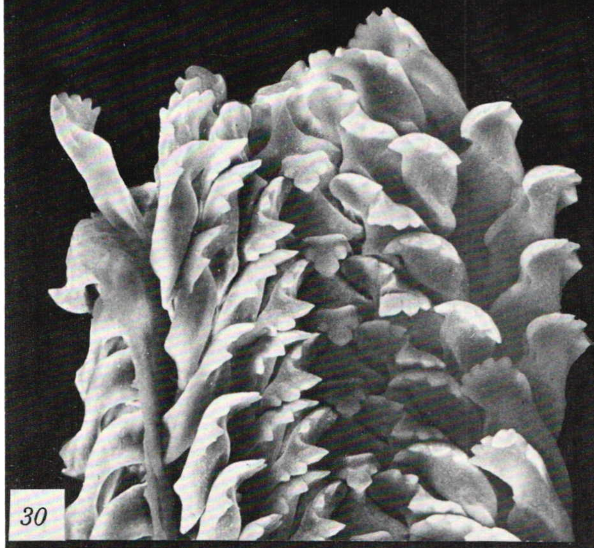


Figure 7

Transect across dike and intertidal area of the Oosterschelde, Netherlands

Explanation of Figures *30* to *35*

Figure *30*: *Littorina angulifera* from Curaçao ×170
Figure *31*: *Littorina angulifera* from Santa Marta. ×275
Figure *32*: *Littorina nebulosa* from Santa Marta. ×375
Figure *33*: *Littorina nebulosa* from Santa Marta. ×375
Figure *34*: *Littorina mespillum* from Curaçao. ×830
Figure *35*: *Littorina mespillum* from Curaçao. ×930



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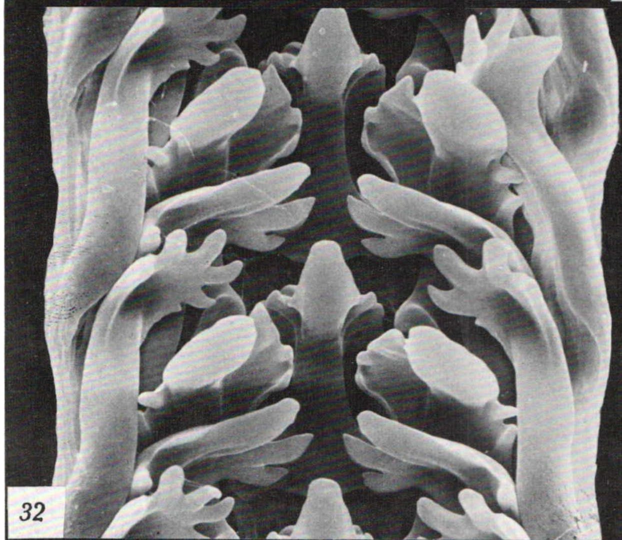

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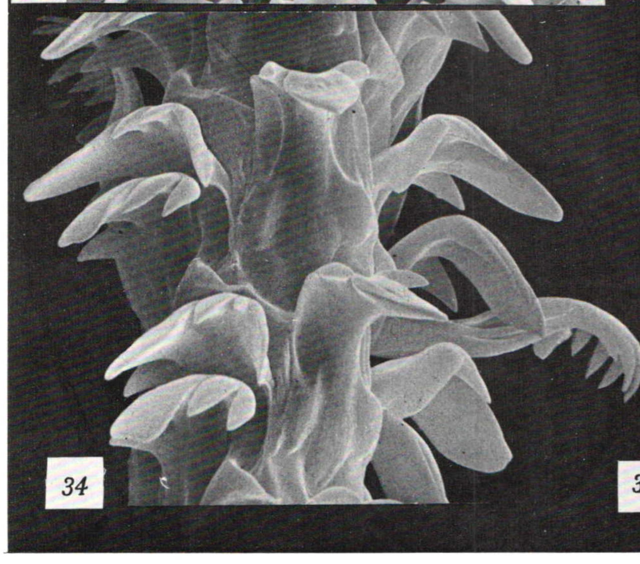

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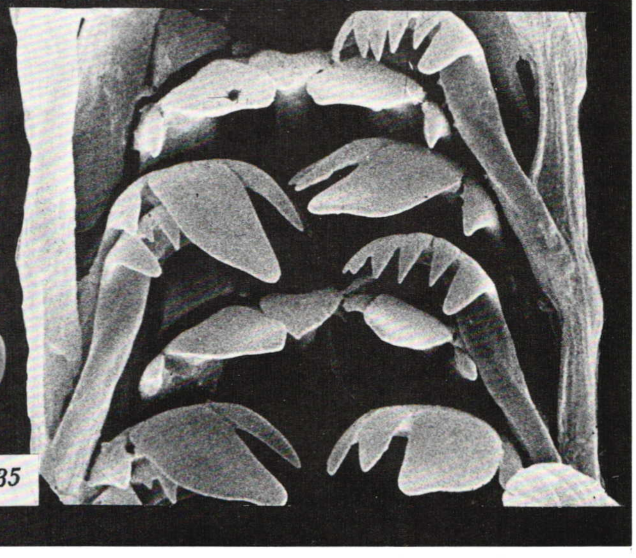

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high water spring tides (*cf.* MOORE, 1940 for British occurrence). Consequently, the rock surface is covered by fine algal growths extending down into cavities and crevices between the basalt columns. *Littorina saxatilis* usually is inactive at ebb times, but moves about and feeds when its habitat is moist. The animals are as active in slight rain as when their habitat is moistened by splash water. They feed on algal detritus and diatoms (FRETTER & GRAHAM, 1962).

Usually some individuals of this species will also enter the uppermost *Fucus*-zone, beginning just below the normal high tide line. Here the first individuals of *L. obtusata* Linnaeus, 1758 were found and also the first *L. littorea* Linnaeus, 1758. In the *Fucus* growth, which covers the whole rocky surface of the dike downward to the sand or mud bottom, *L. obtusata* is common, in lower parts with an increasing intermixture of *L. littorea*. *Littorina obtusata* feeds on the tissue of *Fucus* and anything that may have settled there (FRETTER & GRAHAM, 1962).

Littorina obtusata is restricted to rock and to algal growths on hard substrates between mid-tide and mean high water neaps (MOORE, 1940). *Littorina littorea* ranges from the high water mark down to the lowest low tide level, often a bit lower. Its upper limit of distribution can be extended by splash or by artificial sea water creeks as are commonly encountered in Yerseke at the western shore of the Oosterschelde, associated with lobster and oyster culture. *Littorina littorea* lives on rock and among small stones, on gravel or on wooden structures, even on soft sand and mud, but only if stones, boulders, tufts of weed or mussel (*Mytilus edulis* Linnaeus, 1758) clusters provide a firm base in these soft surroundings. Single old specimens may be found regularly below lowest low water, but in less dense populations than above the normal low water line. The limit of rich populations of this species can be observed in the Oosterschelde tidal flats in the presence or absence of *Ulva* growths (presence or absence of green coloration) on mussel beds and boulders. Where *L. littorea* is common, *Ulva* cannot grow, because this alga is eaten by the snails. Washed-in *Ulva* leaves attract the individuals of *L. littorea* during the first hour after the bottom has become dry again, so that up to 1000 animals may be counted in an area of 20 cm × 20 cm, all feeding on *Ulva*. Usually, all *Ulva* parts washed into the area with dense *L. littorea* populations during high tide time will be eaten completely before the arrival of the next high tide. This species also settles on rocks at the water line in brackish water like the Veerse Meer, a brackish water extension of the Oosterschelde without tidal fluctuations.

DESCRIPTION OF THE SHELL

Descriptions of *Littorina littorea, L. obtusata* and *L. saxatilis* were given by ABBOTT (1954), BEQUAERT (1943) and ZIEGELMEIER (1966). *Tectarius muricatus* was described by CLENCH & ABBOTT (1942), KAUFMANN & GÖTTING (1970) and well illustrated by ROSEWATER (1972). Descriptions and illustrations of *L. nebulosa* were published by BEQUAERT (*op. cit.*), KAUFMANN & GÖTTING (*op. cit.*), WARMKE & ABBOTT (1962), as well as descriptions of *L. meleagris*. *Littorina angulifera* was described and illustrated by BEQUAERT (*op. cit.*), MARCUS & MARCUS (1963), illustrated by ROSEWATER (*op. cit.*). *Littorina mespillum* was well documented by BEQUAERT (*op. cit.*), ABBOTT (*op. cit.*), WARMKE & ABBOTT (*op. cit.*) *Littorina punctata, L. striata,* and *L. neritoides,* with descriptions and drawings, were documented by NORDSIECK (1968). *Echininus nodulosus* was described and illustrated by CLENCH & ABBOTT (*op. cit.*) and in ROSEWATER (*op. cit.*).

The shells of individuals belonging to the *Littorina ziczac* and *Nodilittorina tuberculata* groups are described and illustrated (Figures 8 to 13) again here, to avoid confusion and to define sharply the 3 rediscovered or newly discovered species. This is necessary because they were placed by former authors studying this group into species combinations.

Littorina ziczac Gmelin, 1791 (Figure 8)

Collected along the Colombian coast from Cartagena to Guajira Peninsula and from Curaçao.

Description: Shell elongate conical, whorls 6 to 7, convex. Apex as a rule little or not eroded (submicroscopically), sutures well marked, smooth. Body whorl of adult one half of total height. Shouldered at the periphery, less distinct than in *Littorina jamaicensis, L. lineolata* and *L.* sp. First 2 to 3 whorls smooth, sculpture of remainder with very fine wavy lines, 15 to 19 on early whorls, 35 to 40 on the last whorl up to the periphery, and 25 to 35 below the periphery. The engraved spiral lines are difficult to see with the naked eye and shells seem to be glossy and smooth. Sculpture is not weaker below the periphery. Peripheral shoulder smooth and rounded, set off by a shallow rounded ridge. Aperture pear-shaped. Outer lip with a sharp edge, not thickened within, meeting the body whorl at an angle of about 45°, and channeled inside. Inner lip forming a very thin callus over the body whorl.

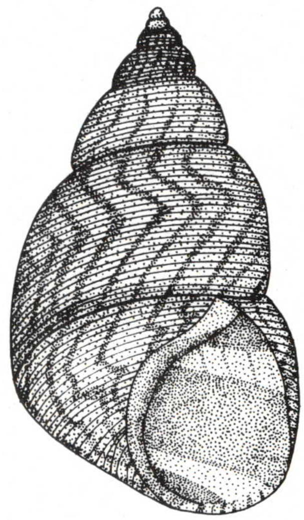

Figure 8

Shell of *Littorina ziczac*

as a rule little or not eroded (submicroscopically), microscopically always showing erosion by minute boring organisms (mostly algae). Specimens found living at the edge of tide pools sometimes decollate. Suture well marked and smooth. Body whorl of adult over one half of total height (2 : 3). In fully grown specimens the body whorl is much more convex than earlier whorls and only slightly shouldered at the periphery. Younger (also adult) specimens are more strongly shouldered.

The first 2 to 3 whorls are smooth; sculpture of remaining whorls with moderately deeply engraved spiral lines, on early whorls 12 to 17 and on the body whorl 14 to 20 up to the peripheral edge, and below the edge 10 to 14 often obsolete spiral lines. Peripheral shoulder in old whorls at the end almost smooth, on young ones forming a blunt ridge. Aperture pear-shaped, outer lip with sharp edge, not thickened within, meeting body whorl at a sharp angle forming a narrow groove. Inner lip forming a very slight callus over body whorl. Columellar area long and moderately wide, barely concave, and inclined inward. Umbilicus lacking.

Columellar area moderately large and wide, slanting inward, very weakly concave. Umbilicus lacking.

Color variable, but generally light grey, fine wavy or zigzag radial lines of light reddish-brown to dark reddish-brown on bluish or yellowish-white background. Some individuals show yellowish-white background just below the suture and bluish-white above it. Earliest whorls are dark red brown. Mouth within red brown with 2 white spiral bands, one close to the base, the other between the periphery and the suture. Outer lip white, blotched with reddish brown. Columellar area light brown.

Figured by Kaufmann & Götting (1970: fig. 34).

Littorina sp. (Figure 9)

Collected along the shores from Cartagena to the Guajira Peninsula in Colombia.

Description: Shell elongate conical, whorls generally a little less convex than in *Littorina ziczac,* 7 whorls. Apex

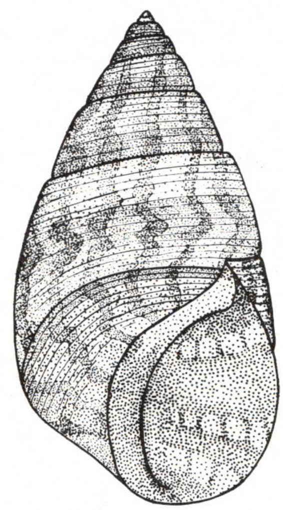

Figure 9

Shell of *Littorina* sp.

Explanation of Figures *36* to *44*

Figure *36*: *Littorina meleagris* from Santa Marta. × 790
Figure *37*: *Littorina meleagris* from Santa Marta. × 1280
Figure *38*: *Littorina striata* from Fuerteventura. × 290
Figure *39*: *Littorina striata* from Fuerteventura. × 370
Figure *40*: *Littorina punctata* from Fuerteventura. × 400
Figure *41*: *Littorina punctata* from Fuerteventura. × 400
Figure *42*: *Littorina neritoides* from Costa Brava. × 750
Figure *43*: *Littorina neritoides* from Banyuls. × 400
Figure *44*: *Littorina ziczac* from Curaçao. × 390


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Color variable, but always wavy or zigzag radial chestnut brown stripes and mostly axial lines and stripes of dark brown, grey and black on a white background. Earliest whorls dark brown. Whorl just apical to the suture white or yellowish-white in ground color, above the next suture or the peripheral edge bluish-grey to white. The axial lines may be absent or strongly developed so that the shell appears almost black. Mouth within mahogany brown with 2 white spiral bands, one close to the base, the other between the periphery and the suture. Outer lip white, blotched with reddish brown. Columellar area light brown.

Illustration by KAUFMANN & GÖTTING (1970: fig. 35) as *Littorina lineolata.* This may be *L. ziczac brasiliensis* Vermeij & Porter, 1971. Certainty cannot be evaluated from the short description, and figures were not presented. Ecological data are identical with those of *L.* sp. A *L. ziczac* described in detail by MARCUS & MARCUS (1963) probably is *L.* sp. and agrees with it in the morphology of radula and spawn.

Littorina jamaicensis C. B. Adams, 1850 (Figure 10)

Specimens collected from rocky beaches of Curaçao.

Description: Shell elongate conical with 6 to 7 flattened whorls. The apex in some individuals not eroded (submicroscopically), in others decollate (found near tide pools). Suture well marked and smooth. Body whorl of adult slightly over one half of total height (4 : 5), just as flattened as earlier whorls. Strongly shouldered at the periphery, almost at a right angle. First 2 to 3 whorls smooth, sculpture of remaining whorls with deeply engraved spiral lines, 6 to 8 on early whorls, and 9 to 11 on the last whorl up to the periphery, and 6 to 7 from the edge to the base. Sculpture in fully grown individuals sometimes weaker below the periphery and here stronger growth lines. Peripheral shoulder forming a narrow blunt ridge. Aperture pear-shaped with an edge where the peripheral shoulder ends. Outer lip with sharp edge, not thickened within, meeting body whorl at a sharp angle, and forming a narrow, slit-like channel with it. Inner lip forming a very slight callus over the body whorl. Columellar area wide, slanting inward, and smooth. Umbilicus lacking.

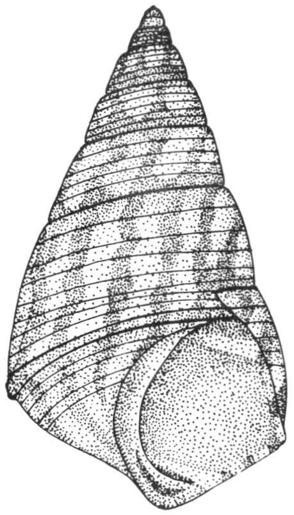


Figure 10

Shell of *Littorina jamaicensis*

Color variable, fine wavy or zigzag radial lines of dark red-brown to black, axial lines and stripes black or dark grey on a yellowish background on the apical whorl and bluish-white background on the body whorl. Earliest whorls uniformly pale reddish-brown. Mouth purplish-dark brown within, with 2 white spiral bands, a prominent one close to the base, the other, often weaker, between periphery and suture. Outer lip white, blotched with dark red-brown. Columellar area light to dark brown.

This is *Littorina lineata* of BORKOWSKI & BORKOWSKI, 1969, and probably *L. lineolata* of ABBOTT, 1964.

Littorina lineolata d'Orbigny, 1840 (Figure 11)

All shells were collected at Paradise Island, Nassau, Bahamas.

Description: Shell short-turriculate with 5 to 6 convex whorls. Apex mostly eroded. Suture well marked, smooth, Body whorl of adult over one half of total height (5 : 8), distinctly shouldered at the periphery. First 2 whorls smooth, sculpture of remaining whorls of deeply engraved spiral lines, 5 to 6 on early whorls, 8 to 9 up to the periphery on the last whorl, 6 to 8 weaker ones below the periphery. Peripheral shoulders forming a strong and broad blunt ridge.

Aperture pear-shaped, from peripheral edge to base often almost straight. Outer lip with sharp edge, not thickened within, meeting body whorl at larger angle than in *Littorina jamaicensis* and *L.* sp. (about 90°), channeled inside. Inner lip forming a strong callus over the body whorl. Columellar area moderately long and wide, inclined inward, barely concave. Umbilicus lacking.

Color not as variable as in *Littorina* sp. and *L. jamaicensis,* fine wavy or zigzag chestnut-brown radial lines crossed at the lower part of each whorl by continuous axial grey lines and lines of grey blotches. Background bluish-white. Earliest whorls uniformly pale reddish-brown. Mouth dark brown within with one white spiral band close to the base.

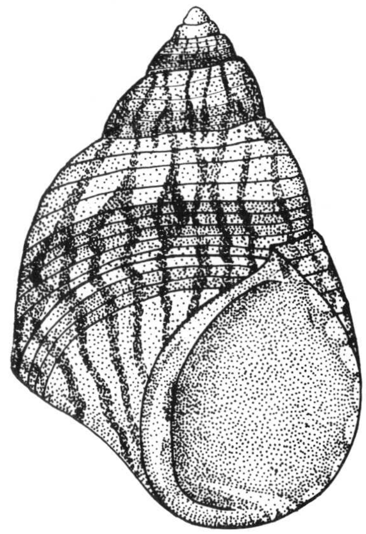


Figure 11

Shell of *Littorina lineolata*

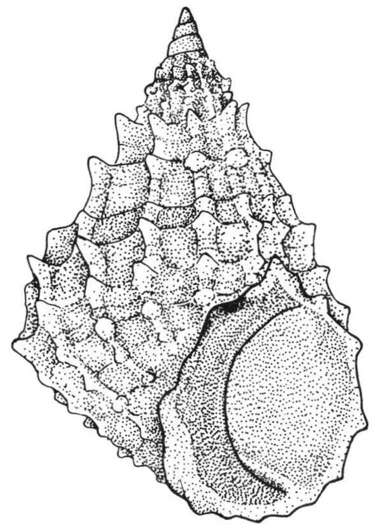


Figure 12

Shell of *Nodilittorina dilatata*

Outer lip with a very narrow white edge, blotched with reddish-brown. Columellar area red-brown.

This is *Littorina lineolata* as described by BORKOWSKI & BORKOWSKI, 1969.

Nodilittorina dilatata (d'Orbigny, 1841) (Figure 12)

Collected at Paradise Island, Nassau, Bahamas.

Description: Shell conical, broadly turriculate, whorls 7 to 8, the first flattened, later more convex. Apex, as a rule, little or not eroded (submicroscopically). Suture wavy, shallow, but distinct between more convex whorls. First 2 to 3 whorls smooth, sculpture of remaining whorls consisting of axial rows of sharp tubercules, 3 rows on early whorls, 7 to 10 beaded rows on the last whorl, between which are found 0 to 5 rough spiral threads. These threads are crossed by rather coarse growth lines. Different individuals have different beaded rows which are most prominent (2 to 4). Aperture subcircular. Outer lip with sharp edge, not thickened within, meeting body whorl at an angle of over 90°. Inner lip forming a very strong callus continuous with the wide columella and thus forming a wide shelf not inclined toward the aperture. This shelf continues to the upper corner of the aperture. Individuals with more than 6 whorls show a conical pseudo-umbilicus.

Color of the first 3 whorls pale reddish-brown, later whorls light grey to lead grey with whitish tubercles. Edge of the outer lip white with irregular light brown blotches. Columella and aperture dark brown with one clear white stripe below.

The individuals in figure 122 of CLENCH & ABBOTT (1942) closely resemble the one here described.

Nodilittorina tuberculata (Menke, 1828) (Figure 13)

Collected from Santa Marta Rodadero along the rocky shores of the Guajira Peninsula, and on Curaçao.

Description: Shell elongate conical, whorls 7 to 8, flattened. Apex in individuals may be little or not eroded (submicroscopically) or decollate (especially if collected in or near tide pools). Sutures indistinct, wavy. Body whorl of adult slightly over one half of total height (8 : 9). First 3 whorls smooth, sculpture of remaining whorls of axial bands of tubercles, 2 bands on early whorls, and 7 beaded rows on the last whorl. The 2nd and 3rd row of each whorl usually have the largest nodules. Between the beaded rows there are 1 to 4 rough spiral threads, crossed by fine regular growth lines. Aperture oval. Outer lip with sharp edge, not thickened within, meeting body whorl at an angle of about 45° and not channeled inside. Inner lip forming a moderately thick callus over the body whorl. Columella inclined inward, wide with a shallow longitudinal excavation but not forming a shelf as in *Nodilittorina dilatata*. Umbilicus lacking.

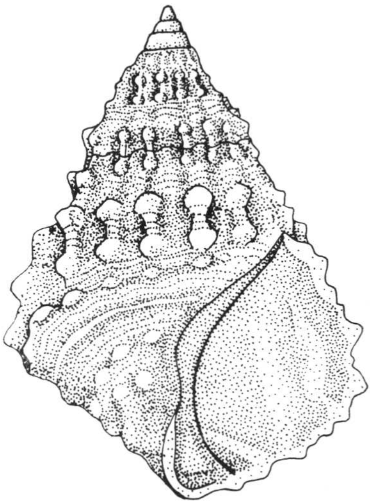


Figure 13

Shell of *Nodilittorina tuberculata*

Color brownish-grey to lead-grey with whitish to light orange tubercules. Often greenish colors due to strong algal growths on or within the outer shell surface. The first 3 whorls are light brown, edge of the outer lip white, columella and aperture dark brown with a white stripe below.

This species is illustrated by ROSEWATER (1970), illustrated and described by KAUFMANN & GÖTTING (1970).

SPAWN

Description

Littorina littorea Linnaeus, 1758

The pelagic egg capsules are disc shaped, about 1 mm in diameter, with a swelling in the center in which 1 to 5 eggs (usually 3 to 5) are accommodated. The peripheral parts of the capsule form a flat flange to the central swelling. Floating egg capsules can be found in the waters of the Oosterschelde from April until October. Eggs and veligers of this species are the most common components of the prosobranch plankton in these waters besides veligers of *Hydrobia ulvae* (Pennant). The capsules give rise to free swimming veligers on the 6^{th} day of development (*cf.* THORSON, 1946 and FRETTER & GRAHAM, 1962).

Tectarius muricatus (Linnaeus, 1758)

Individuals of this species proved to be always viviparous in the area of Santa Marta. Freshly collected females usually shed fully developed veligers if kept overnight in a jar of fresh sea water. These veligers swim actively and carry a shell with a little more than one whorl. In contrast to individuals from Santa Marta, *T. muricatus* from Bermuda (LEBOUR, 1945), from the Barbados (LEWIS, 1960), and from Florida (BORKOWSKI, 1971) produce lens-shaped pelagic capsules with a diameter of about 0.2 to 0.3 mm and with one surface more convex than the other; it is much wider than it is deep with only one egg in each capsule.

Littorina saxatilis Olivi, 1792

This viviparous periwinkle retains its eggs in the brood pouch during development. Hatched individuals crawl through the genital aperture and live in the same rock crevices as the adult animals (FRETTER & GRAHAM, 1962). The egg cocoons are almost as large as those of *Littorina obtusata* (THORSON, 1946). Of females collected at the dikes of the Oosterschelde usually a few contain young throughout the frost-free period of the year. Some groups of this species produce egg masses like those of *L. obtusata*, and fix them to hard substrates (SESHAPPA, 1947).

Littorina obtusata Linnaeus, 1758

Littorina obtusata usually deposits its gelatinous egg mass on damp, unexposed fronds of *Fucus* in the warm months of the summer in the Oosterschelde and elsewhere (FRETTER & GRAHAM, 1962; THORSON, 1946; HERTLING & ANKEL, 1927). The spawn is flat, long, oval, or kidney-shaped, with 40 to 150 $1\frac{1}{2}$ to 2 mm wide round eggs per mass. The mass is composed of 2 to 3 layers, one above the other, embedded in a resistant jelly. After 3 to 4 weeks of development inside the egg capsule, the young hatch in the crawling stage (THORSON, *op. cit.*).

Littorina angulifera Lamarck, 1822

Individuals freshly collected from normal mangrove beaches and of estuarine areas will secrete mucus containing veligers as well as eggs in all stages of development if kept overnight in a jar with fresh sea water. The eggs are all equal in shape and size (0.12 mm) as the inner egg-coverings of pelagic egg-cases in other periwinkles. The female contains eggs and larvae in its brood pouch until extreme flood tides and high waves in storms are calm. Others will move down to the water level

(Lebour, 1945; Lenderking, 1954; Marcus & Marcus, 1963) at times and release larvae. But for many individuals seen living on mangrove branches with no vertical extensions to the water surface an active movement to the water is not possible or only with considerable detours. Here, individuals contain eggs and veligers in their brood pouches and will discharge them when sea water wets them. Eggs develop within 3 days into veliger larvae with a transparent, light brown tinted shell of slightly more than one whorl

Littorina nebulosa Lamarck, 1822 (Figure 14A)

Spawn is shed in mucus strings which dissolve on contact with sea water; from it a large number of saucer-shaped capsules of about 0.4mm diameter is set free. These capsules consist of 2 unequally convex cupolas, that are fused by a ring-shaped lamella at the outer rim. The more concave side carries an additional central swelling. Each colorless, transparent pelagic capsule contains one egg surrounded by an inner transparent spherical covering. There is a gelatinous fluid between the outer capsule and the egg-covering, albumen between inner egg-covering and egg. After 4 to 5 days of development the veliger hatches, carrying a shell with little more than one whorl that has a brown nucleus and is otherwise transparent and colorless. Egg cases of *Littorina nebulosa* are very similar with those of *L. flava* King & Broderip, 1832 from Brasil, which, in contrast to *L. nebulosa,* hatch after 2 days of development (Marcus & Marcus, 1963).

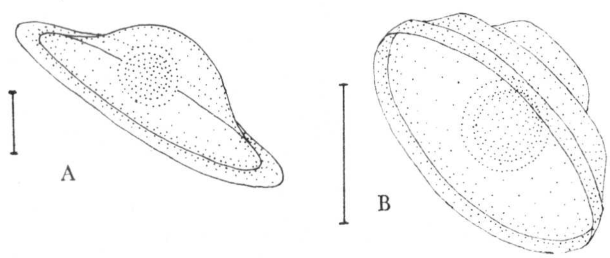


Figure 14

A: Egg capsule of *Littorina nebulosa*; B: Egg capsule of *Littorina meleagris.* Scale line 0.1mm

Littorina meleagris Potiez & Michaud, 1838 (Figure 14B)

Freshly collected individuals, if kept in a bowl of sea water overnight, produce many cupola-shaped egg capsules measuring 0.2mm in width. A cupola with 3 steps rises on a flat round basal disc. Where cupola and disc are fused, they give rise to a lamella extending outward and vertical to the plane of the basal disc. Each egg-case contains one olive-white egg with its own spherical covering. After 4 days of development a veliger hatches; its transparent shell has little more than one whorl. The egg cases produced by individuals from Florida are identical with those from Santa Marta (Borkowski, 1971).

Littorina mespillum von Mühlfeld, 1824

The spawn of this species is still unknown. Perhaps egg capsules observed by Lewis (1960) and possibly mistaken as belonging to *Puperita pupa* (Linnaeus, 1767) were produced by this species. In these capsules a rounded cupola with an intermediate ring rises on a flat basal disc. Each egg capsule contains one egg that hatches after two days.

Littorina neritoides Linnaeus, 1758

The pelagic capsule produced by *Littorina neritoides* is lens-shaped, 0.16mm wide, and contains one embryo per capsule; the egg hatches at the veliger stage (Lebour, 1935; Linke, 1935).

Littorina punctata Gmelin, 1791

Littorina striata King & Broderip, 1832

The spawn of these species is unknown.

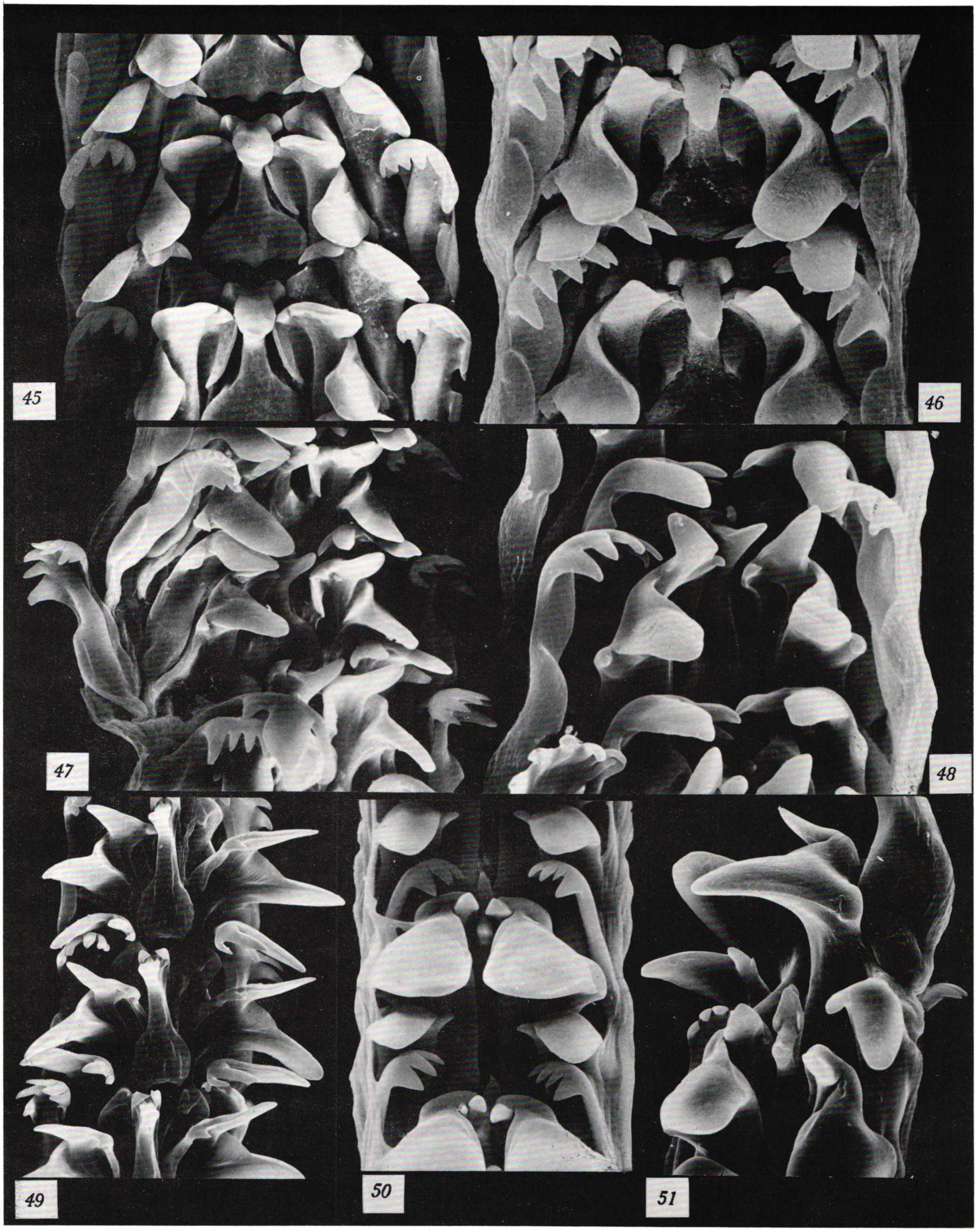
Littorina ziczac Gmelin, 1791 (Figures 15A, 15B)

Freshly collected animals, if placed overnight in a bowl of sea water, produce pelagic egg capsules throughout the year. Each capsule is about 0.2mm wide and 0.1mm high, beehive-shaped with a flat round disc at the base and a cupola above it. At the edge between both sides a lamellar collar is developed that is inclined outward. The cupola consists of a lower platform with slightly inclined sides at the base and a convex upper part sculptured with

Explanation of Figures 45 to 51

Figure *45*: *Littorina* sp. from Santa Marta. × 710
Figure *46*: *Littorina* sp. from Santa Marta. × 400
Figure *47*: *Nodilittorina dilatata* from Paradise Island, Nassau. × 600
Figure *48*: *Nodilittorina dilatata* from Paradise Island, Nassau. × 420
Figure *49*: *Littorina jamaicensis* from Curaçao. × 390
Figure *50*: *Littorina jamaicensis* from Curaçao. × 410

Figure *51*: *Littorina lineolata* from Paradise Island, Nassau. × 430



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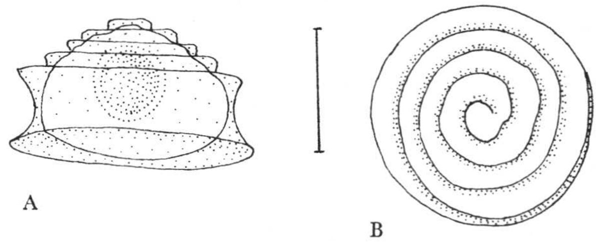


Figure 15

Egg capsule of *Littorina ziczac*: A: seen from the side; B: seen from above. Scale line 0.1 mm

a spiral consisting of a rounded ridge with 5 volutions that end bluntly at the top of the cupola. Grooves between the spiral ridges are sharp and deep. Each greenish egg of each capsule is covered by a shiny sphere suspended in the gelatinous liquid filling the outer capsule. The veliger hatches after 7 days of development; its brownish shell is transparent and has little more than one whorl. Similar capsules derived from *Littorina ziczac* from Florida and from the Bermudas were described by BORKOWSKI & BORKOWSKI (1969) and LEBOUR (1945), respectively.

Littorina sp. (Figure 16A)

Individuals of *Littorina* sp. produce, throughout the year, pelagic egg capsules of about 0.2 mm width, each of which contains one greenish egg in its spherical covering. Egg capsules have the shape of a beehive, quite similar to the shape of those of *L. ziczac*. The base is also flat and round, and the cupola consists of one larger platform at the base. But in contrast to the *L. ziczac* capsules, they usually have almost vertical sides. A lamellar collar, as the outward extension of the lower platform sides, is inclined, as the sides are. A further difference from *L. ziczac* is that the upper part of the cupola consists of 3 to 4 steps

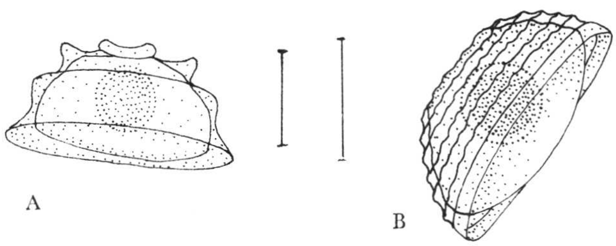


Figure 16

A: Egg capsules of *Littorina* sp.; B: Egg capsule of *Nodilittorina tuberculata*. Scale line 0.1 mm

rather than of spiral ridges. Each small platform forming a step has almost perpendicular sides, a flat roof and a sharp edge. The spawn of one female with numerous capsules usually contains also a small number of malformed capsules which may carry a smooth cupola, have an irregular or an almost spherical shape. All embryos, of irregular and regular capsules, develop in the same way if kept in a jar with fresh sea water in the laboratory. After 3 days the egg covering dissolves, liberating a transparent veliger. Its shell has more than one whorl. The veliger leaves the egg capsule at a rupture. A very similar egg capsule was described and illustrated by MARCUS & MARCUS (1963) from *L. ziczac* of Brasil.

Nodilittorina dilatata (d'Orbigny, 1841)

This species produces pelagic egg capsules of about 0.2 mm width and 0.1 mm height, and of a shape very similar to that described for *Littorina ziczac*. The only difference from it is that the cupola is sculptured with a spiral with 6 volutions rather than 5. It was described by LEBOUR under the name *Echinella trochiformis* Dillwyn from Bermuda; it was refigured by BORKOWSKI (1971) under the name *Nodilittorina tuberculata*.

Nodilittorina tuberculata (Menke, 1828) (Figure 16B)

Freshly collected animals, held overnight in a jar of fresh sea water, will produce, throughout the year, pelagic egg capsules, each holding one greenish egg in its spherical shiny covering. From a shallowly convex basal disc a cupola, sculptured with a spiral ridge of 6 to 7 volutions, rises. It differs from *Nodilittorina dilatata* by having a cupola with a rounded shape without a lower platform. At the rim between the cupola and the basal side a lamellar collar, pointing outwards, is developed. The spiral ridges form rounded steps, each separated from the next by a deep pointed furrow. The veliger, hatching after 4 days of development, carries a transparent shell with a reddish spot at the nucleus.

Littorina jamaicensis C. B. Adams, 1850

The beehive-shaped pelagic egg capsules of *Littorina jamaicensis*, measuring 0.22 mm in width, from Florida (BORKOWSKI & BORKOWSKI, 1969) are identical in shape and type of contents with capsules of *Nodilittorina tuberculata* from Santa Marta. This spawn was described under the name *L. lineata* d'Orbigny, 1841.

Littorina lineolata d'Orbigny, 1840

Pelagic egg capsules of this species were described by BORKOWSKI & BORKOWSKI (1969) from Florida. They are higher than the others (0.44 mm) and quite large with a diameter of 0.66 mm. They have a bell-shape and contain one egg each. The upper part of the cupola is sculptured by 4 steps; the base is concave and gives rise to a large outward pointing collar.

Echininus nodulosus (Pfeiffer, 1839)

Pelagic egg capsules of *Echininus nodulosus* were described briefly by BORKOWSKI (1971) without any detail. Each capsule has an 0.13 mm high cupola sculptured by wavy ridges at the top. They show close similarities to egg capsules of *Littorina lineolata,* but with a width of 0.26 mm, they are much smaller.

DISCUSSION

Two large groups of different egg masses can be distinguished in the Littorinidae. One group includes species that produce large eggs from which crawling miniature adults will hatch, as is the case in *Littorina obtusata, L. atkana* Dall, 1886 (KOJIMA, 1957), *L. sitkana* Philippi 1846 (HABE, 1958) and *L. saxatilis.* In the other, larger group the species produce eggs from which small veliger larvae with, usually, a long planktotrophic life will hatch (Figure 17).

The first group can be subdivided into 2 subgroups: one with *Littorina obtusata, L. atkana,* and *L. sitkana* which deposit gelatinous egg masses on hard substrates (rocks, plants, etc.) and the other, with *L. saxatilis,* where the eggs are retained in the brood pouch of the female until the young hatch as crawling animals. Both subgroups are closely related, since *L. saxatilis* sometimes deposits egg masses similar to those from the other subgroup (SESHAPPA, 1947).

The large group of species of the family Littorinidae producing pelagic egg capsules, may again be subdivided into 2 major subgroups: one in which each egg capsule contains but a single egg, and the other in which each capsule contains more than one egg.

The latter subgroup is formed by species with a northern range, as *Littorina littorea* from the northern Atlantic, *L. mandschurica* Schrenk (KOJIMA, 1958) and *L. squalida* Broderip & Sowerby (KOJIMA, 1957) from the northeast Pacific. The disc-shaped capsules of *L. littorea* con-

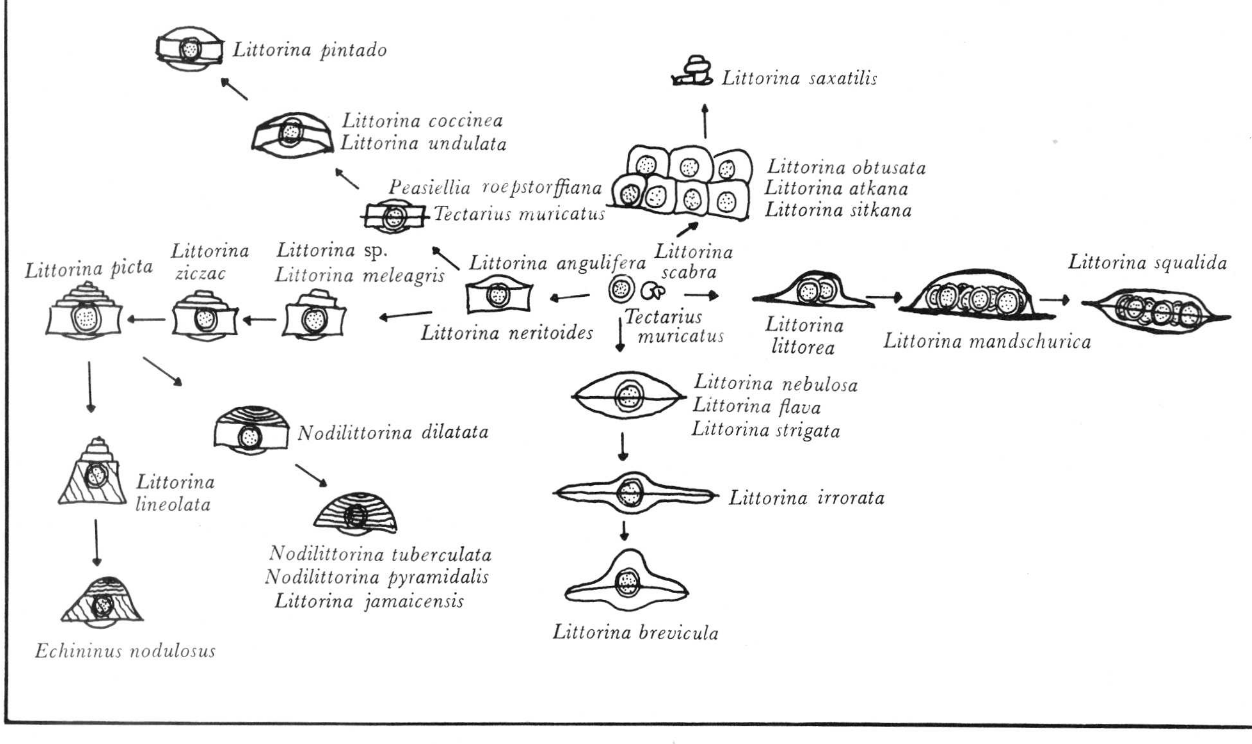


Figure 17

Generalized drawing of littorinid spawn as known from the literature tain in general 3 to 5 eggs, those of *L. mandschurica* 9 to 12 and those of *L. squalida* up to 14 or 15 eggs.

In the large subgroup of littorinids having one egg per pelagic egg capsule, 3 branches with similar egg capsule morphology can be distinguished. *Littorina angulifera, L. scabra* Linnaeus, 1758 (STRUHSAKER, 1966) and *Tectarius muricatus* produce eggs without capsule or hatch their eggs in the brood pouch of the female and release the progeny as veligers. In colder areas *T. muricatus* produces egg capsules of flat pill box shapes (LEBOUR, 1945) similar to those of *Peasiella roepstorffiana* (Nevill, 1884) (HABE, 1956), sculptured only by a median lamella. Egg capsules of even simpler shapes, without lamella, are shed by *L. neritoides*. Large inclined lateral lamellae (flotation skirts)are found on capsules of *L. undulata* Gray, 1839 and *L. coccinea* Gmelin, 1791 (ROSEWATER, 1970), and in *L. pintado* Wood, 1828. This lamella itself is sculptured with a basal groove in the last mentioned species (OSTERGAARD, 1950; STRUHSAKER, 1966; WHIPPLE, 1965).

Another branch of capsule forms contains biconvex disc-like shapes as in *Littorina nebulosa, L. flava, L. strigata* Lischke, 1871 (KOJIMA, 1958) and *L. irrorata* Say, 1822 (BORKOWSKI, 1971). Of the same general shape but with strongly unequally convex sides are the capsules of *L. brevicula* Philippi, 1844 (KOJIMA, 1957; AMIO, 1963).

The third branch is most interesting because it combines a group which also shows close relations in radula structure, but is very variable in its shell morphology. Common to all is the cupola sculptured by ridges on a flat or convex basal disc. Simple types with few steps in the cupola are seen in the egg capsules of *Littorina meleagris* and *L.* sp. Spiral ridges are found in *L. ziczac* in a wider spiral and in *Nodilittorina dilatata* and *L. picta* Philippi, 1846 (STRUHSAKER, 1966; WHIPPLE, 1965) in a tighter spiral. *Nodilittorina tuberculata, N. pyramidalis* (Quoy & Gaimard, 1833) (KOJIMA, 1957) and *L. jamaicensis* carry only a ridge-sculptured cupola on the basal disc, rounded as in *Echininus nodulosus*, but more evenly sculptured than the latter. The sculpture of *E. nodulosus* capsules resembles that of *L. lineolata* but is more rounded than the latter which is high bell-shaped.

RADULAE

Description

Littorina littorea (Figure 23)

Radulae from individuals from the Oosterschelde and from Cape Cod, Massachusetts, were studied. The radula is up to 4 cm long and 0.33 mm wide. The rachidian tooth carries 3 frontal, one large, broad median and 2 strong lateral cusps. The tooth is almost as wide as long (7 : 8) and solid. The lateral tooth is short and spade-like with 5 cusps, the inner 2 being rounded, the middle largest and the outer ones being small and pointed. The central and the 2 outer cusps form a unit, the surface of which points in a different direction than the platform formed by the inner 2 cusps. The inner marginal tooth has 4 cusps, the 2 inner ones of equal size, the third the largest and all 4 pointed. This tooth is longer than the lateral tooth but shorter than the outer marginal one, which is spoon-shaped with 5 almost equal sized denticles. The outermost cusp is triangular in outline.

The radula was illustrated in detail and its function described by ANKEL (1936, 1937). Radulae illustrated by FRETTER & GRAHAM (1962) show only 4 cusps on the lateral tooth and 5 cusps on the inner marginal, and figures in TROSCHEL (1856) show 4 cusps on the inner marginal, but only 4 cusps on the lateral tooth.

Tectarius muricatus (Figures 24 and 25)

Radulae from individuals from Paradise Island, Curaçao, and Santa Marta were studied. The radula is up to $7\frac{1}{2}$ cm long and 0.13 mm wide. The rachidian tooth carries 3 frontal cusps, the central one more prominent than the 2 lateral ones. The tooth is narrower than long (4 : 5) and is solid. The lateral tooth has 5 cusps: the inner 3 successively larger, the 4th pointed and the largest, in used parts of the radula worn to a rounded shape, and the outer small. The inner marginal tooth has 4 cusps, the 3rd is the largest. The outer marginal tooth is long and slender and carries only 3 rounded denticles.

The figure given in TROSCHEL (1856) is in general appearance correct, but in details like the number of cusps of each tooth incorrect. The central tooth of *Tectarius muricatus* illustrated by ABBOTT (1954: fig. 57) shows very little similarity to the one described here.

Littorina saxatilis (Figures 26 and 27)

Radulae from individuals from the Oosterschelde and the North Sea (Zoutelande, Netherlands) were studied. The radula is up to 3 cm long and 0.21 mm wide. The rachidian tooth carries 5 frontal cusps: the central one is much larger than the equal-sized lateral ones. The maximum width of the central tooth is less than the maximum length (3 : 2), and this tooth is solid. The lateral tooth has 5 cusps: the inner 2 small, the 3rd large and all 3 forming one plate of the tooth, while the 2 remaining ones are separated from them by a deep groove and form a platform with its axis pointing in a different direction. The 4th cusp is the largest and is rounded. The inner marginal tooth has 4 cusps of which the 3rd is the largest.The outer marginal tooth is much longer than the inner marginal one and carries 5 rounded denticles on its spoon-like concave end. The 2 inner ones are quite small.

Littorina obtusata (Figures *28* and *29*)

Radulae of individuals from the Oosterschelde and from Cape Cod (Massachusetts) were studied. The radula is up to 6cm long and 0.23mm wide. The rachidian tooth carries 5 cusps: the central is the largest and solid, the following ones successively smaller.The central tooth is very wide at its base, but still slightly longer (15 : 16). The lateral tooth is a shovel-like structure with the inner rim curved upwards. The 4 cusps of this tooth are broad and curved. Only the small outer one is pointed.The 3rd is the largest. The inner marginal tooth carries 4 cusps and is almost as long as the outer marginal tooth, which is spoon-like and carries 4 rounded denticles.

TROSCHEL's (1856) figure gives only a vague idea of the actual morphology of this radula.

Littorina angulifera (Figures *30* and *31*)

Radulae of individuals from Santa Marta and Curaçao were studied. The radula is up to $1\frac{1}{2}$cm long and 0.29mm wide. The rachidian tooth carries 5 frontal cusps consisting of a larger central one and 2 solid lateral ones, each of which has a small denticle set to the frontal side. In front of these small denticles a flat frontal plate can be seen, which continues toward the back of the tooth in a convex outline. The tooth is very wide at its base and here almost as wide as long (10 : 11), but much narrower in front. The lateral tooth is a plate-like structure made of 2 parts pointing in different directions and separated by a deep groove. The inner plate has 3 rounded flat cusps and the outer plate 4 equally indistinct cusps. The inner marginal tooth has a long shovel-like shape with 4 equally sized cusps. The outer marginal tooth is only a bit longer than the inner marginal and has 7 rounded denticles, the outermost with a triangular outline.

The lateral tooth of *Littorina angulifera* illustrated in TROSCHEL (1856) gives an incorrect picture, but the drawing published by MARCUS & MARCUS (1963) from this species differs only in showing fewer denticles on the outer marginal tooth. ROSEWATER (1970) suggested that *L. angulifera* and *L. scabra* should be considered as subspecies. The radula of *L. scabra,* as figured by Rosewater shows a number of differences in morphology when compared with *L. angulifera.* The denticles bordering the central cusps of the rachidian tooth of *L. angulifera* are absent in *L. scabra.* The frontal plate of the central tooth is straight in *L. scabra* and curved in *L. angulifera.* The lateral tooth shows more irregular sized cusps in *L. scabra.* Also the outer marginal tooth shows more irregular denticles in this species. Therefore both taxa should be considered as separate species and not as subspecies of *L. scabra.*

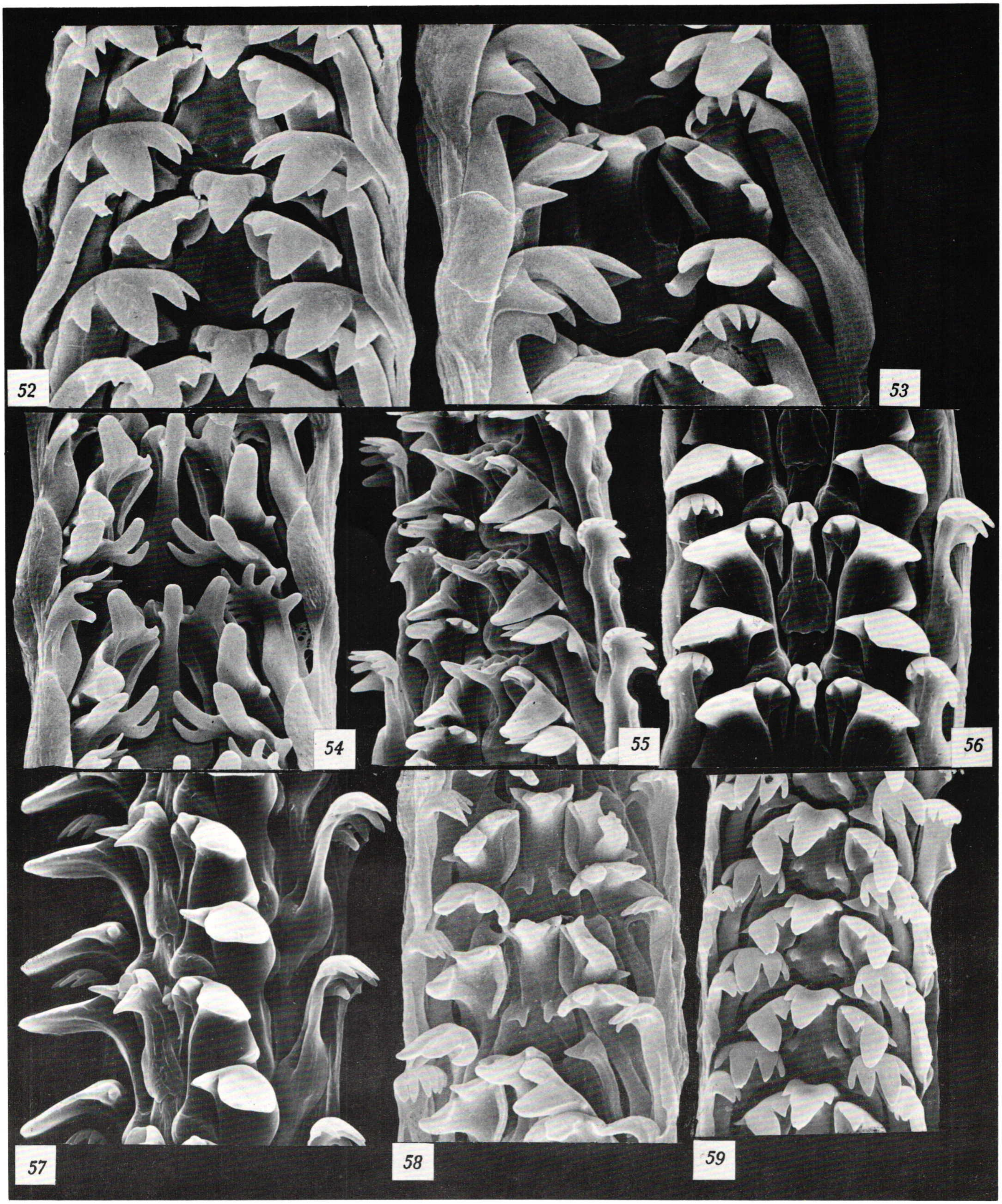
Littorina nebulosa (Figures *32* and *33*)

Radulae of individuals from Santa Marta were studied. The radula is up to 3cm long and 0.24mm wide. The rachidian tooth is similar to that of *Littorina angulifera.* It has 5 frontal cusps, a large central one and 2 nearly equal-sized smaller lateral pairs. The frontal plate is bent upward at its front edge, and this ridge is cusp-like. The frontal plate continues backwards with an approximately straight outline, ending in the basal part where this tooth is as wide as it is long. The lateral tooth has 6 cusps: the inner 3 are small and rounded, the 4th large one is rounded if seen from the front, pointed if seen from the side, and 2 outermost small pointed cusps. The inner marginal tooth carries 4 cusps and is slightly shorter than the outer marginal tooth. Both are spoon-shaped and the outer carries 6 denticles which, with the exception of the triangular outer one, are rounded.

The radula as illustrated by TROSCHEL (1856) shows none of its characteristics. The radula of *Littorina flava* was described by MARCUS & MARCUS (1963) and shows many similarities to that of *L. nebulosa.* The only difference found was the number of denticles on the outer marginal teeth and the radular width (0.35 to 0.5mm) at about the same length (3.2cm).

Explanation of Figures *52* to *59*

Figure *52*: *Littorina lineolata* from Paradise Island, Nassau. ×430
Figure *53*: *Littorina lineolata* from Paradise Island, Nassau. ×345
Figure *54*: *Nodilittorina tuberculata* from Santa Marta. ×465
Figure *55*: *Nodilittorina tuberculata* from Santa Marta. ×490
Figure *56*: *Nodilittorina tuberculata* from Santa Marta. ×360
Figure *57*: *Echininus nodulosus* from Paradise Island, Nassau. ×200
Figure *58*: *Echininus nodulosus* from Paradise Island, Nassau. ×200
Figure *59*: *Echininus nodulosus* from Paradise Island, Nassau. ×285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Littorina meleagris (Figures *36* and *37*)

Specimens were all collected in Santa Marta. The radula is up to 3mm long and 0.09mm wide. The rachidian tooth carries 3 frontal cusps, one strong median and a pair of smaller lateral ones. The tooth is more slender than that of *Littorina littorea*. The front of the central tooth is concave. It is broadest at its end and a little longer than wide (5 : 6). The lateral tooth has 5 cusps, all pointed, the 3rd being the largest. The inner marginal tooth resembles it, but has only 4 pointed cusps with the 3rd one the largest. The outer marginal tooth is much longer, slender and like an open hand with 7 finger-like pointed denticles. This is the difference from *L. mespillum* where the outer marginal tooth carries 8 denticles.

Littorina mespillum (Figures *34* and *35*)

Radulae of individuals collected at Paradise Island and Curaçao were studied. The radula is up to 1 cm long and 0.08mm wide. The rachidian tooth is quite similar to that of *Littorina meleagris* with one large central cusp, a pair of smaller laterals, and a concave end. The lateral cusps are somewhat more distant from the central cusp in *L. mespillum*. The greatest width is found at the base of the central tooth, which is longer than broad (2 : 3). The lateral tooth has only 4 cusps in contrast to *L. meleagris* which has 5. The inner marginal tooth appears quite similar to the lateral tooth, the only difference being a greater length. The longest tooth in each row is the outer marginal with the general shape of a raking hand on a long arm with 8 long, pointed denticles, the outermost of which has a triangular outline and is strongest.

Littorina neritoides (Figures *42* and *43*)

Radulae of individuals from Banyuls, Fuerteventura, Costa Brava (Spain) and Provence (France) were studied. The radula is about 1.2cm long and 0.1mm wide. The rachidian tooth differs from the central teeth of all other known littorinids in possessing 2 apical cusps on its broadened end in addition to the 3 frontal cusps. The large central frontal cusp is accompanied by 2 laterals which stand at its front forming a strongly concave frontal part. The rachidian tooth is broadest at its base and a little longer than wide (5 : 7). The lateral tooth is quadricuspate, the 3rd cusp being the largest; all cusps are pointed. The inner marginal tooth is longer than the lateral one, but of about the same width and carries 4 pointed cusps. The outer marginal tooth is narrower, but of about the same length as the inner marginal and shaped like an open hand with 7 pointed fingers.

Littorina punctata (Figures *40* and *41*)

Radulae of individuals collected at Fuerteventura and Gran Canaria were studied. The radula is up to 5cm long and 0.14mm wide. The central tooth is quite slender and almost 3 times as long as broad, measured at its end where it is broadest (2 : 5). The triangular pointed frontal central cusp is accompanied by a pair of smaller laterals standing in front of it; these are fused with their inner sides, forming a plate with a deep pit in its center, below the central cusp. The lateral and the inner marginal teeth are quite large, almost of the same length, solid, and of similar shape, with 4 cusps each, the 3rd being the largest. The outer marginal tooth is formed like a salad fork with 7 long pointed cusps and a long, slender handle.

Littorina striata (Figures *38* and *39*)

All radulae studied came from individuals collected at Fuerteventura. The radula is up to 8cm long and 0.17mm wide. The central tooth is very similar to that of *Littorina punctata*, with a strong central cusp, a pair of smaller cusps in front, and it is almost twice as long as broad, measured at its broadest place, near the base (6 : 10). Lateral and inner marginal teeth are very similar to each other and carry 4 cusps each. The outer marginal tooth has 9 long pointed cusps and is long and slender.

Littorina ziczac (Figure *44*)

Radulae of individuals coming from Santa Marta and Curaçao were studied. The radula is up to 7cm long and 0.12mm wide. The slender rachidian tooth has a large, strong central cusp which is accompanied by a pair of smaller lateral cusps at its front so that the frontal end of the tooth is quite concave. The tooth is broadest at its base and not much longer than wide (10 : 13), but of slender shape due to a decreased width in front. Lateral and inner marginal teeth are very similar to each other in shape but the latter is longer than the former. Both have 4 cusps. The slender outer marginal tooth has 7 finger-like cusps.

Littorina sp. (Figures *45* and *46*)

Radulae of individuals collected at Santa Marta were studied. The radula is up to 5cm long and 0.17mm wide. The morphology of this radula is very similar to that of *Littorina ziczac* with the only significant difference being the rachidian tooth which is more slender and twice as long as wide at the base (1 : 2). Also a strengthening and a larger size of the lateral tooth is present, but no other morphological differences from *L. ziczac* can be noted.

Littorina ziczac from Brasil, as described by Marcus & Marcus (1963), has a radula which is identical with that of *L.* sp.

Nodilittorina dilatata (Figures *47* and *48*)

Radulae studied were all derived from individuals collected at Paradise Island. The radula is up to 8 cm long and 0.17 mm wide. The tendency toward a more slender rachidian tooth is followed with the width at the end measuring only almost $\frac{1}{3}$ of the length of the tooth (2 : 5). The central frontal cusp is accompanied by a pair of slender, bent lateral cusps in front of it. The lateral tooth is shovel-like, large but thin, and carries 4 cusps, the 3[rd] being the largest. The inner marginal tooth is similar to the lateral and carries also 4 cusps. The outer marginal tooth is slender, much longer and with an end like an open hand with 7 pointed fingers.

This radula is very similar to that of *Nodilittorina pyramidalis* (Quoy & Gaimard, 1833) as described and illustrated by Rosewater (1970). The particularly blunt enlargements laterally of the outer marginal tooth mentioned by this author are also characteristic for *N. dilatata* radulae.

Nodilittorina tuberculata (Figures *54, 55,* and *56*)

Radulae of individuals collected at Curaçao and Santa Marta were studied. The radula is up to 7½ cm long and 0.12 mm wide. In this species the central tooth has become even more slender and now measures 5 times as much in length as in width (1 : 5). The central frontal cusp of the rachidian tooth is bordered by lateral cusps that are curled up and appear delicate. The lateral tooth is the most prominent in the radula. It is very solid, with a massive 3[rd] cusp and has lost the shovel-like appearance. The inner and outer marginal teeth are long and slender and spoon-shaped. The inner carries only 3 cusps, the outer 7 finger-like denticles.

The radula of *Nodilittorina tuberculata* from Puerto Rico illustrated and described by Abbott (1954) is similar to the one here described. Differences are: the lateral and inner marginal teeth carry only 2 cusps each, and the outer marginal tooth bears only 5 denticles. The inner marginal tooth in this radula is as massive as the lateral tooth, which is also in contrast to *N. tuberculata* from Santa Marta and Curaçao. Abbott mentions specimens from Habana, Cuba which have 8 denticles on the outer marginal teeth. These differences may indicate a further species differentiation in this group in the West Indies. Habe (1956) found great differences between the radulae of *N. pyramidalis* and *N. tuberculata*; this is also stated by Rosewater (1970) and confirmed in the present study.

Littorina jamaicensis (Figures *49* and *50*)

Radulae all came from individuals collected at Curaçao. The radula is up to 5 cm long and 0.17 mm wide. The central tooth is narrow and bears a large central cusp with 2 lateral cusps extending far forward, thus forming an almost pointed end of the radula. The greatest width measures only $\frac{1}{6}$ of the length of the rachidian tooth (1 : 6). Compared with the very massive lateral tooth with its big pointed 3[rd] cusp, all other teeth are small. The inner marginal tooth resembles the lateral tooth in shape, but has only 2 cusps and is smaller. The outer marginal tooth is slender but quite long with 5 finger-like denticles, one of which is very small.

Littorina lineolata (Figures *51, 52,* and *53*)

Radulae were of individuals collected at Paradise Island. The radula is up to 9 cm long and 0.11 mm wide. The central tooth is very delicate and slender and 12 times as long as wide (1 : 12). Its central cusp is small and the lateral cusps are extended into sheets forming a pointed front. The lateral tooth is large and very solid with 4 cusps, but only the 3[rd] determines the general shape of it. The inner marginal tooth is formed like a smooth concave spoon and is quite a bit longer than the outer marginal, which carries 6 denticles, the innermost of which is quite small.

Echininus nodulosus (Figures *57, 58,* and *59*)

Radulae of individuals collected at Paradise Island were studied. The radula is up to 8 cm long and 0.17 mm wide. The central tooth is only present as a rudiment and consists of a very thin rod about 20 times as long as thick (1 : 20). It is nearly hidden between the large solid high lateral teeth which are shaped like chisels. The 2 marginal teeth are smaller, the inner one with only 1 cusp and solid, the outer one with 3 cusps, the central one is minute.

Abbott (1954) illustrated and described this radula, but the very massive structure of the lateral tooth is not shown.

DISCUSSION

The radulae of all Littorinidae are constituted of identical rows of teeth, consisting of a single central or rachidian tooth flanked on each side by one lateral and two marginal teeth in each row. All the cusps of all the teeth in one radula are curved so that they point inwards. In a generalized littorinid radula the central or rachidian tooth bears one large central and one or two pairs of smaller lateral cusps. The lateral teeth are multicuspid, usually with 4 to 5 cusps and having a shovel-like, short, subangular shape. The marginal teeth are differentiated into the inner, which in most cases are similar to the lateral teeth

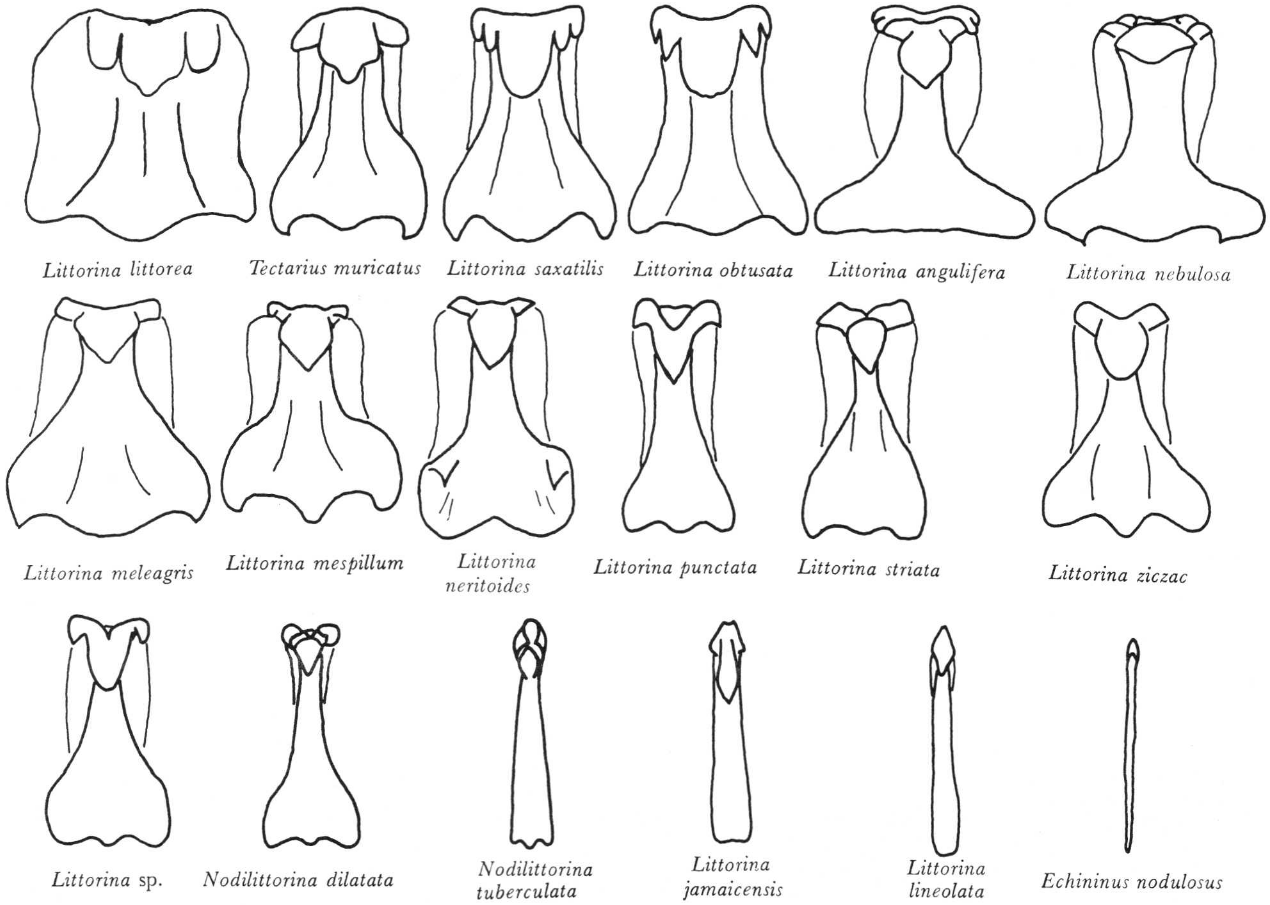

Figure 18

Generalized drawings of the rachidian teeth, frontal view

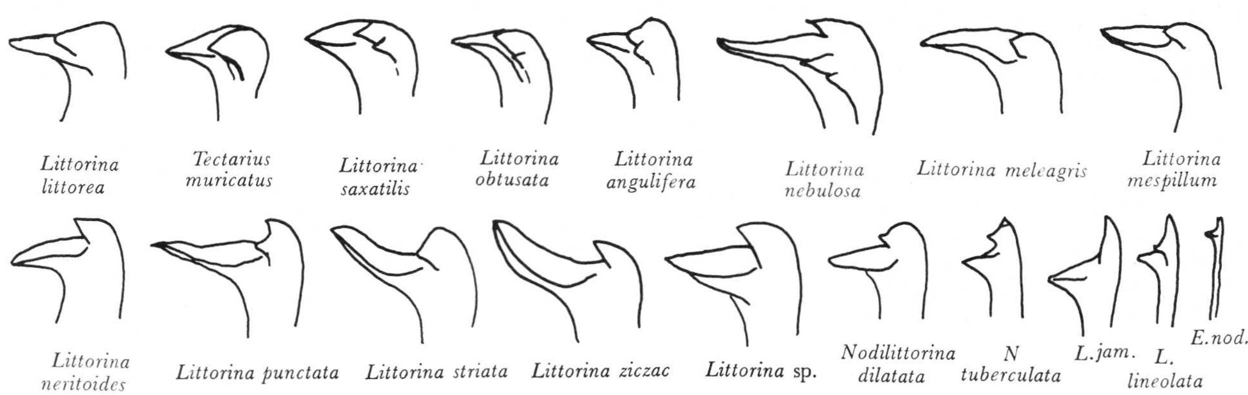

Figure 19

Drawings of the rachidian teeth, side view and usually bear 4 cusps, and the outer, which are slender and multicuspid. This radula is adapted for scraping plant growths from hard substrates, raking in detritus from hard and soft bottoms, and biting off plant material. Usually it becomes very long and the unused portions are coiled up in the radula sac.

Two different groups of littorinid species with a different radular function and resulting radular morphology can be distinguished. The first can be exemplified by the radula of *Littorina littorea,* the function of which has been studied in detail by Ankel (1936, 1937). As the odontophore (buccal mass) is moved in and out of the mouth the radula is moved backwards and forwards over the angled edge at the tip of the odontophore. Anterior to this edge the basal membrane of the radula is bent into a shallow convex shape and therefore the marginal and lateral teeth are spread sideways and the median tooth stands up. Posterior to the edge the basal membrane is bent inward into a concave shape and the teeth are folded in toward the midline. Along with this movement of the radula over the cartilage of the odontophore the mouth is moved. Therefore the recurved cusps rake detritus and algae into the midline of the interlocking cuspate teeth or bite off the plant material and transport it to the midline where everything gets caught by the cusps of the median rachidian teeth and transported into the gut. This type of feeding is found in most species mentioned here and is most common with littorinids in general (Rosewater, 1970). Differences in shape of the single teeth in most cases is therefore more an expression of phylogenetic differences and not of differences in feeding habits.

Only in one group of species – *Nodilittorina tuberculata, Littorina jamaicensis, L. lineolata,* and *Echininus nodulosus* – has the mode of feeding changed, giving rise to a radula differing in many respects from the generalized taenioglossate littorinid shape. The lateral teeth have lost their shovel-like shape and become solid, massive cusps, larger and longer than all other teeth. The median tooth is reduced in size and function is lost. If moved over the edge of the odontophore, the lateral teeth will move furthest outward, scraping with the edge over the substrate. Food material will be scratched toward the midline mainly by the lateral teeth, aided only by the shorter marginals and not by the central tooth.

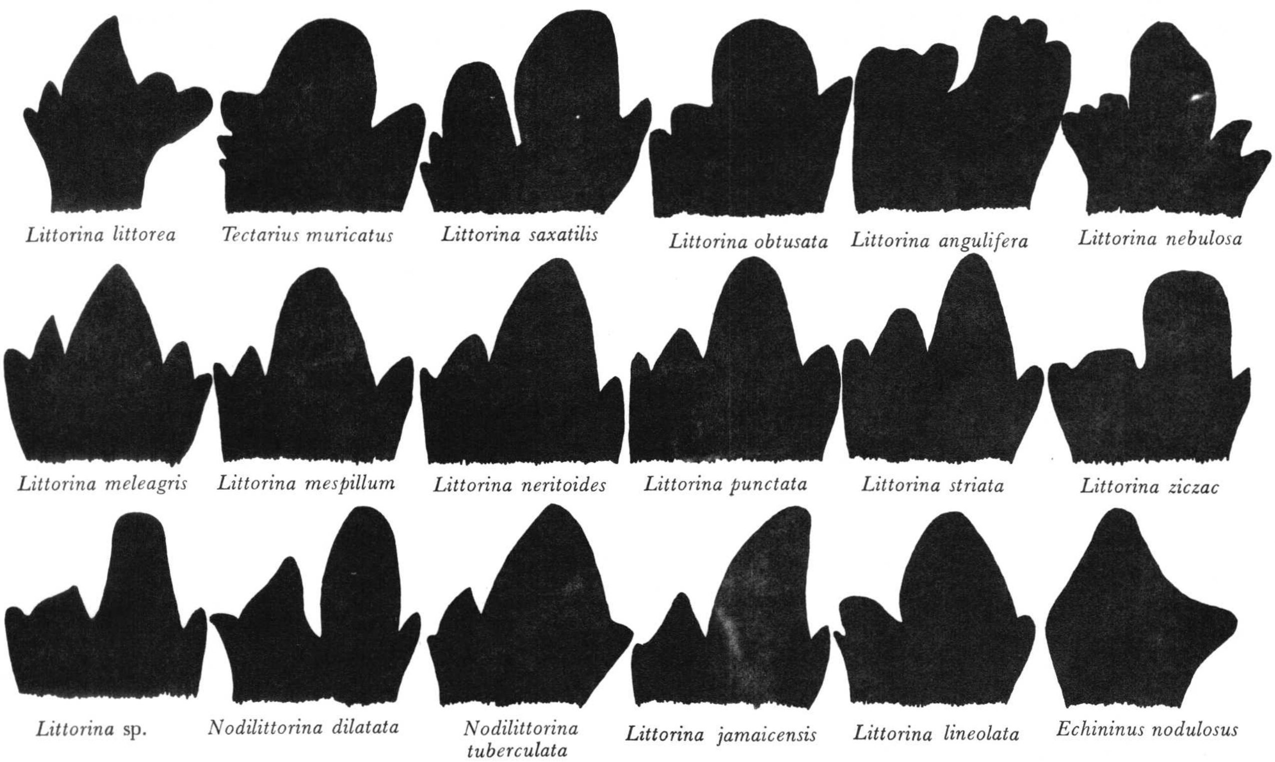

Figure 20

Lateral teeth, left side points toward the rachidian tooth

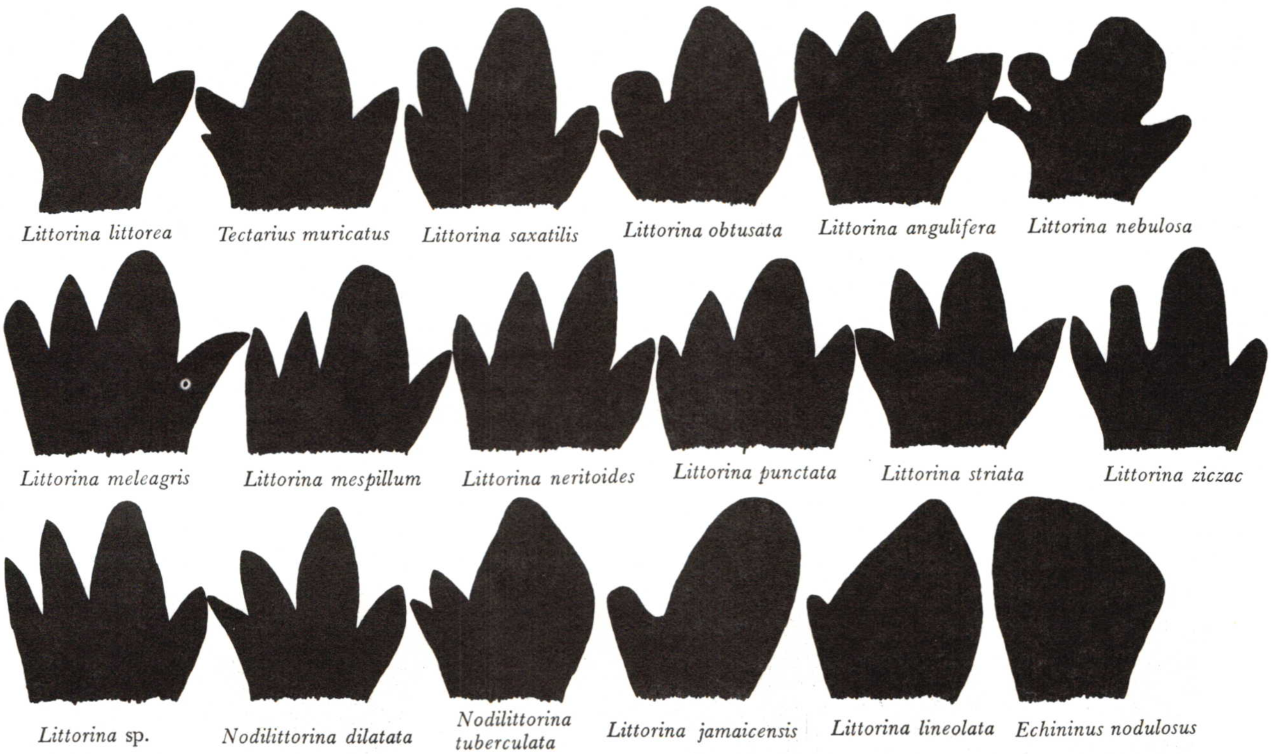

Figure 21

Inner marginal teeth, left side points toward rachidian tooth

KEY

1 Central tooth with 2 pairs of lateral cusps 3, 4
2 Central tooth with one pair of lateral cusps 9, 10
3 Length of radula less than 2 cm *Littorina angulifera*
4 Length of radula more than 2 cm 5, 6
5 Outer marginal teeth with less than 4 denticles .... *Littorina obtusata*
6 Outer marginal teeth with more than 4 denticles 7, 8
7 Central tooth with lateral cusps in front of median cusp, outer marginal tooth with 6 denticles, lateral tooth with 6 cusps .... *Littorina nebulosa*
8 Central tooth with lateral cusps at the sides of the median cusp, outer marginal tooth with 5 denticles, lateral tooth with 5 cusps .... *Littorina saxatilis*
9 Basal part of central tooth with additional pair of cusps .... *Littorina neritoides*
10 Basal part of central tooth smooth 11, 12
11 Outer marginal tooth with 3 cusps 13, 14
12 Outer marginals with more than 3 cusps 15, 16
13 Central tooth of normal shape ...... *Tectarius muricatus*
14 Central tooth rudimentary .... *Echininus nodulosus*
15 Length of radula less than 2 cm 17, 18
16 Length of radula more than 2 cm 19, 20
17 Outer marginal teeth with 8 cusps, length of radula 10 mm, ratio of width to length in central tooth 2 : 3 *Littorina mespillum*
18 Outer marginal teeth with 7 cusps, length of radula 3 mm, ratio width to length in central tooth 5 : 6 .... *Littorina meleagris*
19 Width of radula under 0.2 mm 21, 22
20 Width of radula more than 0.2 mm *Littorina littorea*
21 Central tooth width to length ratio smaller or equal 1 : 5 .... 23, 24
23 Outer marginal tooth with 7 cusps, inner marginal

tooth with 3 cusps .... *Nodilittorina tuberculata*

24 Outer marginal tooth with 5 cusps, inner marginal tooth with 2 cusps 25, 26

25 Central tooth width to length ratio 1 : 6 .... *Littorina jamaicensis*

26 Central tooth width to length ratio 1 : 12 .... *Littorina lineolata*

27 Outer marginal tooth with 7 cusps 29, 30

28 Outer marginal tooth with 9 cusps ... *Littorina striata*

29 Central tooth width to length ratio smaller than or equal to 1 : 2 .... 31, 32

30 Central tooth width to length ratio larger than 1 : 2 *Littorina ziczac*

31 Length of radula 5 cm, frontal plate of central tooth large 33, 34

32 Length of radula 8 cm, frontal plate of central tooth restricted to the area with cusps *Nodilittorina dilatata*

33 Central tooth width to length ratio 1 : 2, width of radula 0.17 mm .... *Littorina* sp.

34 Central tooth width to length ratio 2 : 5, width of radula 0.14 .... *Littorina punctata*

DISCUSSION OF PHYLOGENETIC RELATIONS

Littorina littorea is placed by Bequaert (1943) in the subgenus *Littorina* Férussac, 1822 together with *L. irrorata*. Rosewater (1970) includes *L. obtusata, L. saxatilis* and *L. ziczac* in the subgenus, using the morphology of the penis as a major taxonomic tool. From the present study it can be concluded that, with respect to the morphology of the spawn and the embryonic development, *L. littorea* has no close relationship to any of these species. With respect to the morphology of the radula, *L. irrorata, L. obtusata,* and *L. saxatilis* may be grouped together, but apart from *L. littorea. Littorina ziczac* shows affinities to other species than *L. littorea,* as discussed later.

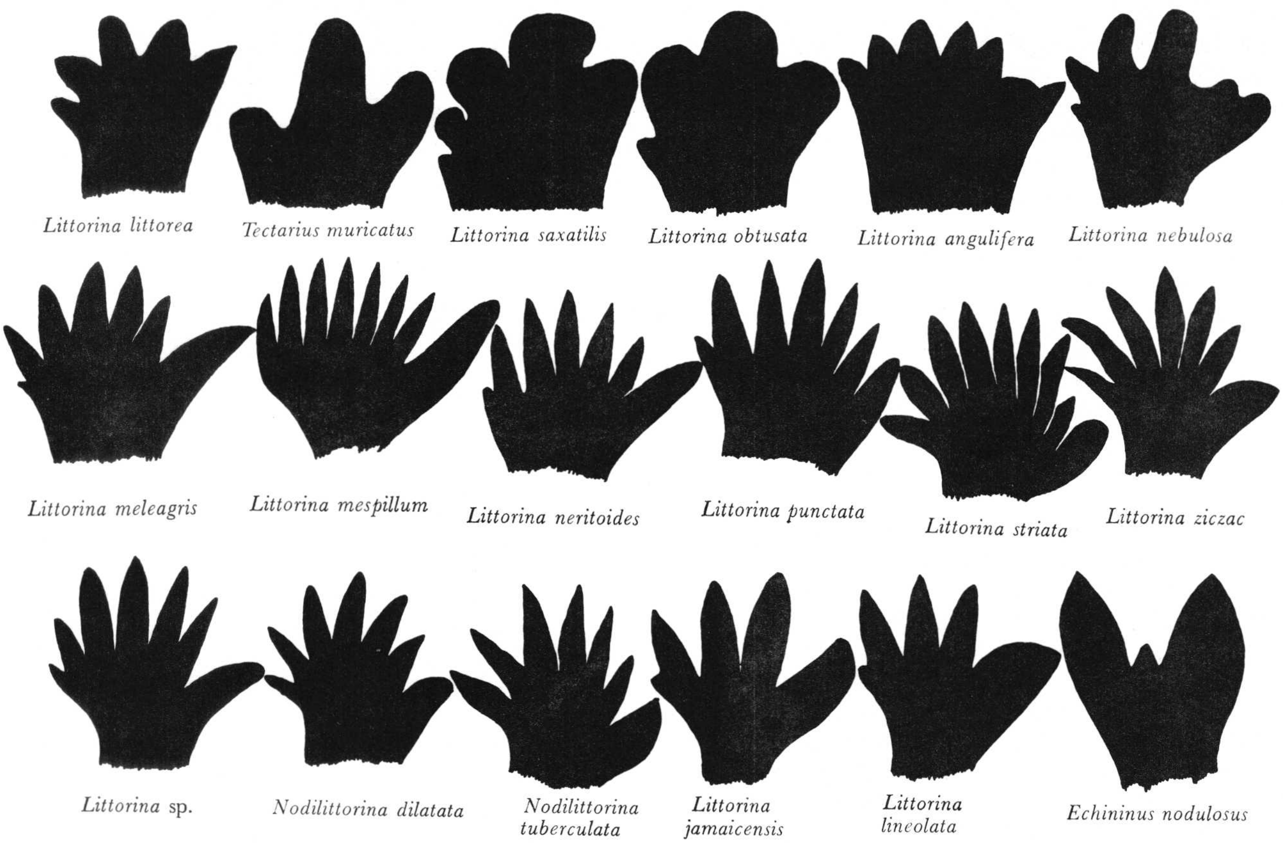

Figure 22

Outer marginal teeth, left side points toward rachidian tooth

Tectarius muricatus of the subgenus *Cenchritis* von Martens, 1900 is considered by ROSEWATER (1972) to be more closely related to *Littorina* than to *Echininus.* This can be supported and from the morphology of the radula and the type of spawn a close relationship to species such as *L. angulifera* or *L. nebulosa* could be considered, even though great differences in shell morphology cannot be overlooked.

Littorina saxatilis and *L. obtusata* are related to each other, but Bequaert considered the former to belong to the subgenus *Littorivaga* Dall, 1918 and the latter to the subgenus *Neritrema* Récluz, 1869 with *L. meleagris* and *L. mespillum.* The latter 2 species may be closely related to each other, but show differences in radula and spawn morphology and embryonic development from *L. obtusata.*

Littorina angulifera was placed by ROSEWATER (1970), together with *L. irrorata* in the subgenus *Littorinopsis* Mörch, 1876. This could be justified by similarities in radula and spawn in both species.

Littorina nebulosa is close to *L. flava* in all respects, contrary to Rosewater's suggestion who placed the former in the subgenus *Littoraria* Gray, 1834, and the latter tentatively together with *L. neritoides, L. mespillum,* and *L. meleagris* in the subgenus *Melarhaphe* von Mühlfeld in Menke, 1828. *Melarhaphe* should only contain *L. neritoides* which differs from all other littorinids by a pair of cusps on the basal part of the central tooth in the radula. Consequently also the species grouped in *Melarhaphe* by BEQUAERT (1943) should be reevaluated .

The placement of *Littorina punctata* near *L. jamaicensis* (= *lineata*) and *L. lineolata* in the subgenus *Austrolittorina* Rosewater, 1970 can only be supported if *L. ziczac* is included and close relations to *Nodilittorina dilatata* and *N. tuberculata* are accepted.

A tentative placement of *Littorina striata* into a subgenus *Granulittorina* Habe & Kosuge, 1966 (ROSEWATER, 1970) with relations to such forms as *L. punctata* and *L. ziczac* seems unjustified if the radula morphology of the three is compared.

The radula morphology of *Littorina* sp. and *L. punctata* is almost identical and close to *L. ziczac.* Therefore, 2 different subgenera, as suggested by ROSEWATER (1970) for these species are one too many.

A surprising result of this study is the close relationship of *Nodilittorina dilatata* with *Littorina ziczac, L. punctata* and *L.* sp. on one hand, and of *N. tuberculata* with *L. jamaicensis* and *L. lineolata* on the other hand. Not only radular morphology, but also radular function separate both groups from each other. However, the morphology of the egg capsules suggest a relationship between both groups.

Echininus nodulosus can be related to the last group and must not be considered as a specialized group apart from other Littorinidae.

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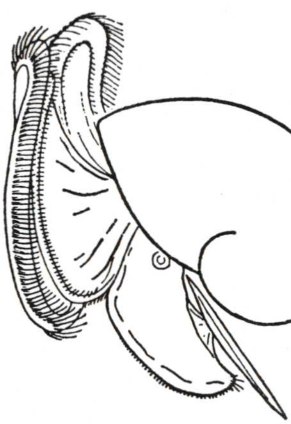

The following corrections to Figure Explanations on pages 98 through 106 and Figure referrals on pages 105 to 108 are presented with the apologies of author and editor.

The editor is particularly disturbed about this occurrence as we have been unable to find an explanation for this mixup; it is disturbing since we do not know what additional measures we must take in the future to prevent a repetition of a similar accident.

We present this page without a page number in order that it may be inserted, at the choice of the member or subscriber, where it will be of greatest assistance.

Figure *36*: *Littorina lineolata* from Paradise Island, Nassau × 430
Figure *37*: *Littorina lineolata* from Paradise Island, Nassau × 430
Figure *38*: *Littorina lineolata* from Paradise Island, Nassau × 345
Figure *39*: *Nodilittorina tuberculata* from Santa Marta × 465
Figure *40*: *Nodilittorina tuberculata* from Santa Marta × 490
Figure *41*: *Nodilittorina tuberculata* from Santa Marta × 360
Figure *42*: *Echininus nodulosus* from Paradise Island, Nassau × 200
Figure *43*: *Echininus nodulosus* from Paradise Island, Nassau × 200
Figure *44*: *Echininus nodulosus* from Paradise Island, Nassau × 285
Figure *45*: *Littorina ziczac* from Santa Marta × 440
Figure *46*: *Littorina* sp. from Santa Marta × 710
Figure *47*: *Littorina* sp. from Santa Marta × 400
Figure *48*: *Nodilittorina dilatata* from Paradise Island, Nassau × 420
Figure *49*: *Nodilittorina dilatata* from Paradise Island, Nassau × 420
Figure *50*: *Littorina jamaicensis* from Curaçao × 390
Figure *51*: *Littorina jamaicensis* from Curaçao × 410
Figure *52*: *Littorina meleagris* from Santa Marta × 790
Figure *53*: *Littorina meleagris* from Santa Marta × 1280
Figure *54*: *Littorina striata* from Fuerteventura × 290
Figure *55*: *Littorina striata* from Fuerteventura × 370
Figure *56*: *Littorina punctata* from Fuerteventura × 400
Figure *57*: *Littorina punctata* from Fuerteventura × 400
Figure *58*: *Littorina neritoides* from Costa Brava × 750
Figure *59*: *Littorina neritoides* from Banyuls × 400

The Figure numbers given with the descriptions of the radulae on pages 105 to 108 must be changed as follows:

Littorina meleagris (Figures *52* and *53*)
Littorina mespillum (Figures *34* and *35*)
Littorina neritoides (Figures *58* and *59*)
Littorina punctata (Figures *56* and *57*)
Littorina striata (Figures *54* and *55*)
Littorina ziczac (Figure *45*)
Littorina sp. (Figures *46* and *47*)
Nodilittorina dilatata (Figures *48* and *49*)
Nodilittorina tuberculata (Figures *39*, *40*, and *41*)
Littorina jamaicensis (Figures *50* and *51*)
Littorina lineolata (Figures *36*, *37*, and *38*)
Echininus nodulosus (Figures *42*, *43*, and *44*)

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