

Western Atlantic Species of *Nodilittorina*

22560

(Gastropoda : Prosobranchia):

Comparative Morphology and its Functional, Ecological,
Phylogenetic and Taxonomic Implications

BY

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(8 Plates; 11 Text figures)

INTRODUCTION

THE PRESENT STUDY started with the taxonomic review of some of the species dealt with herein. Soon it became apparent that not only a full-scale taxonomic revision of all the species would be the only satisfactory answer to several taxonomic and nomenclatorial problems, but that the taxonomic significance of the organs commonly utilised for classification, *i.e.*, shell, operculum, penis, radula and spawn, had to be re-assessed. This goal prompted a review of the functional morphology and the adaptational value to the animal of a given feature. Though much is left to do to answer such questions satisfactorily, there are indications that similar ecological pressures are prone to generate homoeomorphic properties in closely related species (*i.e.*, related on the genus and family level), and to recognise this, taxonomy must take account of as many organs and their properties as possible.

It may be worthwhile to recall the historical development of the taxonomic classification of our species. In the earlier part of the 19th century, all species were placed in the genus *Littorina*. Already in these early days, all nodulose shells were grouped together, although this was not always expressed in the generic classification (*e.g.*, PHILIPPI, 1846-48; REEVE, 1857-58). Later the genus *Littorina s. lat* was split in various ways; without enumerating these taxonomic arguments, it may be said that the classification pattern common to all of them was to put the spirally sculptured

species in *Littorina*, and all nodulose-species in *Tectarius*, except *Echininus cumingi* because of its multispiral operculum (*e.g.*, TROSCHER, 1856-63; TRYON, 1887; THIFLE, 1929; WENZ, 1939; CLENCH & ABBOTT, 1942). Only ABBOTT (1954a) recognised the close relationships between nodulose *Nodilittorina* and some of the spirally sculptured "*Littorina*" species and he separated *Tectarius* and *Nodilittorina*. But up to now all generic and subgeneric definitions of littorinid genera and subgenera coincide with the occurrence, resp. absence of nodulose or granulose sculpture (ABBOTT, 1954, 1974; ROSEWATER, 1970-73, 1981), in spite of the fact that the anatomical data described by these authors suggest many close relationships across the limits based upon shell sculpture.

The species concepts of West Atlantic *Nodilittorinae* reflect the development from a shell classification to a biologically oriented species classification and may be illustrated by the spirally sculptured *Nodilittorina* species. In the 19th century, all new species were proposed upon shell (and operculum) characters alone. As the differences were relatively slight and variability inevitably perceptible, BEQUAERT (1943) united all nominal species in "*Littorina ziczac*," explaining some of the shell variations by sexual dimorphism of a single species; this interpretation proved to be entirely speculative. It was not until 1969 when BORKOWSKI & BORKOWSKI (1969) split "*Littorina ziczac*" into three species, utilising radula and spawn characters for the first time in this group. By the same criteria,

BANDEL (1974) recognized a fourth species, then cautiously named "*Littorina* sp.". In this paper, BEQUAERT's "*Littorina ziczac*" is shown to be composed of seven species, three of which can be distinguished only by radula characters, while the remaining four are also recognized by their shells, and in some instances also by spawn and operculum characteristics. Also, it proved that nearly all species were inadequately named, which was due to unresolved taxonomic problems as well as to misidentifications of type material and to nomenclatorial complications.

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ABBREVIATIONS

B/K	Collections of the authors (now largely in USNM, except few retained specimens of each sample.)
BMNH	British Museum (Natural History), London, England
IRSNB	Institut royal des Sciences Naturelles de Belgique, Bruxelles
MCZ	Museum of Comparative Zoology, Harvard College, Cambridge, Massachusetts
MHNG	Muséum d'Histoire Naturelle de Genève, Switzerland
RMNHL	Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands
SMF	Forschungsinstitut Senckenberg, Frankfurt a. M., Germany
USNM	United States National Museum of Natural History, Washington, USA.
ZMK	Universitetets Zoologiske Museum, København, Denmark

Explanations: An asterisk in synonymy lists denotes the introduction of a new name of the species group applicable to the species dealt with. Localities in the "Material examined" paragraphs are proven by radula examination unless otherwise stated.

In the plate explanations, "FN" denotes the photograph number of a SEM photograph taken and filed in the Institute for Paleontology of the University of Bonn.

Comparative Morphology and its Functional Interpretation

Anatomy of Soft Parts

General Remarks: The anatomy of *Littorina littorea* was described in great detail by FRETTER & GRAHAM (1962). These authors based their description on the accounts published by LINKE (1933) and JOHANSSON (1939) on the anatomy of *Littorina littorea*, *L. obtusata* and *L. saxatilis*. MARCUS & MARCUS (1963) dissected "*Littorina ziczac*" (= *Nodilittorina lineolata*) from Brazil and compared their anatomical data with those of Johansson, Fretter and Graham, and other authors. With exception of the morphology of the penis, MARCUS & MARCUS have noted no fundamental differences in the anatomy of *Littorina littorea* and *Nodilittorina lineolata*.

Penis: The species of the genus *Nodilittorina* described in this paper possess, where known, a slender verge with an open, but deeply folded spermiduct and with one large gland at its outer side. A basal enlargement is always present.

The penis gland was described in detail by MARCUS & MARCUS (1963, fig. 16). They found that it contained glandular cells lining a central cavity with a distal opening. The gland is similar in morphology to the numerous glands described in the genera *Littorina* s. str., *Tectarius* and *Echininus*. The genera *Littoraria*, *Cenchritis*, *Fossarilittorina* and *Melarhaphé* do not have this organ.

The penis morphology of West Atlantic species is not sufficiently known to allow subgeneric groupings in the genus *Nodilittorina*. Available data are depicted in Figures 1A-1D. Information published so far on Atlantic and Indo-Pacific species suggests a six-fold subdivision of the genus *Nodilittorina*. No consistent correlation between penis morphology and other properties of the species emerges from this, but very close relationships between nodulose and non-nodulose species can be assumed:

Group 1 (Figures 1A-1C): Penis with basal enlargement, adhesive flagellum ("Haftlappen" MARCUS & MARCUS (1963)) and one gland (rarely none or two) standing upright on

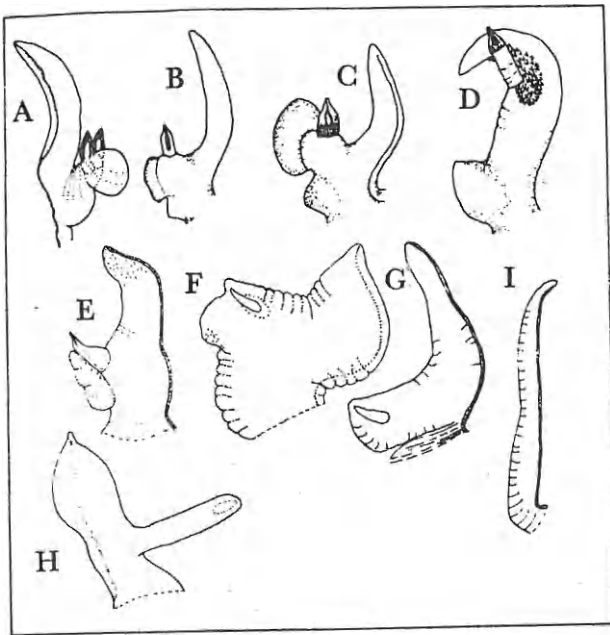


Figure 1

Penis Morphology

- A) *Nodilittorina (Nodilittorina) lineolata* (Orbigny) after MARCUS & MARCUS, 1963 ("*Littorina ziczac*," São Paulo)
- B) *Nodilittorina (Nodilittorina)* sp. after ABBOTT, 1954a ("*Littorina ziczac*" from the Bahamas; may be *N. ziczac* (Gmelin) s. str., *N. angustior* (Mörch) or *N. mordax* spec. nov.)
- C) *Nodilittorina (Nodilittorina) tuberculata* (Menke) after ABBOTT, 1954a
- D) *Nodilittorina (Tectininus) antoni* (Philipp) after ABBOTT, 1954a ("*Echininus nodulosus*")
- E) *Nodilittorina (Nodilittorina) pyramidalis* (Quoy & Gaimard) after ROSEWATER, 1970
- F) *Nodilittorina (Nodilittorina) praetermissa* (May) after PONDER & ROSEWATER, 1979 (penis probably strongly contracted)
- G) *Nodilittorina (Nodilittorina) sundaica* (Regieren-Altena) after PONDER & ROSEWATER, 1979
- H) *Nodilittorina (Nodilittorina) acutispira* (E. A. Smith) after PONDER & ROSEWATER, 1979
- I) *Nodilittorina (Liralittorina) striata* (King & Broderip) after ROSEWATER, 1981

the distal end of the basal enlargement. Caribbean species only: *Nodilittorina tuberculata*, *N. lineolata* and *N. spec. dub.* ("*Littorina ziczac*" of ABBOTT, 1954a).

Group 2 (Figure 1E): Penis with basal enlargement, and one gland recumbent on it; an adhesive flagellum is not always described: Indo-Pacific and Eastern Atlantic nodulose species placed by ROSEWATER (1970, 1981) in the

subgenera *N. (Nodilittorina)* and *N. (Granulilittorina)*: *N. pyramidalis*, *N. millegrana*, *N. granosa*, *N. helenae*.

Group 3 (Figures 1F-1G): Penis with basal enlargement and one gland incorporated in its distal part. Apparently no adhesive flagellum: Indo-Pacific and Eastern Atlantic non-nodulose species placed by ROSEWATER (1970, 1981) and PONDER & ROSEWATER (1979) in *Littorina (Austrolittorina)*: *N. sundaica*, *N. unifasciata*, *N. knysnaensis*, *N. praetermissa*, *N. cincta*, *N. punctata*, *N. africana*.

Group 4 (Figure 1H): Penial gland on a long, upright projection inserting near outer, proximal end of penis, i.e., at the same place as the basal enlargement of groups 1, 2, 3, 5; apparently no adhesive flagellum: the Australian *N. acutispira* only (PONDER & ROSEWATER (1979)).

Group 5 (Figure 1D): Penis with basal enlargement; single gland remote from it on the distal part of the verge, surrounded by "numerous, small, fleshy, opaque-white papillae" (ABBOTT, 1954a: *N. (Tectininus) antoni*, then named *Echininus nodulosus*).

Group 6 (Figure 1I): Penis slender, without any appendages: the West African *N. (Liralittorina) striata* only (ROSEWATER, 1981).

The first three groups are most closely related to each other. If the differences of the Caribbean species (group 1) prove to be significant and consistent throughout the species not yet investigated, they would be related more closely to each other than to Indo-Pacific species (groups 2, 3, 4), regardless of the presence or absence of nodulose sculpture, differences in operculum morphology and the considerable modifications of the radula in *Nodilittorina tuberculata* and *N. mordax*. In the Indo-Pacific, however, shell sculpture seems to be correlated with a penis feature, but even so the Indo-Pacific species of groups 2 and 3 would have more penis characters in common than they have with the Caribbean forms. The subgeneric name *Echinolittorina* Habe, 1956 is available for the latter, and should further anatomical evidence prove that such species as *N. tuberculata*, *N. lineolata* etc. are more closely related to each other than to their apparent Pacific analogues, e.g., *N. pyramidalis*, resp. *N. paytensis*, they would have to be classified accordingly.

The fourth group is probably related to the third; the peculiarities can be seen as modifications of the characters of the third group.

The fifth, monospecific group is sufficiently different from the rest to warrant the retention of a particular subgenus, *Nodilittorina (Tectininus)* CLENCH & ABBOTT, 1942.

The sixth group, also monospecific, has been raised to subgeneric rank recently (ROSEWATER, 1981). The penis characters fully justify this, while radula and shell properties are well within the range observed in groups 1-4.

The differences between the four first-mentioned groups appear to be minor, and in view of the number of species

not yet investigated, and the impossibility in the Caribbean species of correlating these penis properties consistently with other morphological features, these groups are united in the subgenus *Nodilittorina* (*Nodilittorina*) Martens, 1897. Synonyms of this are *Echinolittorina* Habe, 1956a, *Granulilittorina* Habe & Kosuge, 1966 and *Austrolittorina* Rosewater, 1970.

Little is known about the functional morphology of the penis appendages. It has been suggested that the gland and the flagellum secure the adhesion of the distal part of the penis in the mantle cavity of the female during copulation (LINKE 1933, 1934: "Klebdrüsen" = "sticking glands" in *Littorina littorea*; MARCUS & MARCUS 1963: "Haftlappen" = "adhesive velum" in *Nodilittorina lineolata*).

Radula: TROSCHEL (1856-63: 129) noted as a constant character of representatives of the Littorinae (in Troschel's terminology uniting the families Lacunidae and Littorinidae of THIELE'S (1929-35) terminology) a low and wide lateral tooth with a characteristically extended gutter-like, outer posterior corner connected to an embayment of the outer posterior edge. Troschel expressed the opinion that generic differences in the Littorinae of his terminology showed up in the shape of the central tooth. So, for example, the members of the genus *Lacuna* are characterized as typical representatives of the Littorinae by the morphology of their lateral teeth, and as belonging in the genus *Lacuna* by the hexagonal outline of the central teeth.

Within the genus *Littorina* Troschel differentiated 3 subgenera: *Littorina*, "*Tectus*" (= *Tectarius*) and "*Nina*" (= *Echininus*). In order to do so he used as characters the morphology (number of whorls) of the operculum and the length-width relationship of the central tooth of the radula. In his scheme Troschel came to the assumption that *Nodilittorina pyramidalis* belonged to the subgenus *Tectus* of the genus *Littorina* along with others, as for example, *Cenchritis muricatus*.

THIELE (1929: 124-127) includes *Nodilittorina* as subgenus in the genus *Tectarius* (subgenus *Tectus* of Troschel). *Tectarius* is characterised by Thiele in regard to its radula morphology in such general terms that it cannot be differentiated with these features from members of the genus *Littorina* (subgenus *Littorina* of Troschel) in contrast to Troschel's earlier proposal. Thiele held the members of both genera *Tectarius* and *Littorina* apart only by differences in the number of whorls present on the operculum and by presence or absence of nodular sculpture of the shell.

PONDER (1976) and ARNAUD & BANDEL (1978) have found in their studies of radulae of Antarctic Littorinidae that there are many features to be found transitional between Lacunidae and Littorinidae. TROSCHEL'S (1856-63) assumption that the group Littorinae, encompassing both Lacuni-

dae and Littorinidae of Thiele's classification, holds closely related species which can best be differentiated and classified by their radula morphology, was confirmed by their studies. Thus, no clear dividing line may be drawn between Thiele's families Littorinidae on one side and Lacunidae on the other side. ARNAUD & BANDEL (1978) noted a transition from the radula morphology of members of the genus *Laevilittorina* to that typical for the genus *Lacuna*. The members of the species of *Laevilittorina* studied show a radula morphology similar to typical representatives of the genus *Littorina* in the broad sense, including such shapes as are present in the radula of *Nodilittorina pyramidalis*.

Outside of the Antarctic region, as, for example, in the Caribbean area, Littorinidae are restricted to the intertidal and supratidal zones. In contrast to this circumstance in the Antarctic region, *Laevilittorina* lives continuously below water. There is a transition of morphological features from the radula present in *Laevilittorina* to radulae typical for representatives of the genus *Lacuna* of the northern hemisphere to be found in the southern region. ARNAUD & BANDEL (1978) suggested that this mode of life is, therefore, not to be considered as secondary adaptation but reflects the mode of life of the ancestors of the intertidal littorinids. However, as the taxonomic and phylogenetic relationships of the numerous taxa of the New Zealand and Antarctic region are not sufficiently known, and as the presence of *Littoraria*-like species as early as the Cenomanian points to an early adaptation to the intertidal habitat, it is not shown which taxa exhibit more primitive properties. It is even conceivable that in Antarctic waters species adapted secondarily to subtidal habitats, forced by the formation of inland and pack ice.

The radulae of 18 species of Littorinidae from the Atlantic, the Caribbean Sea and the Mediterranean Sea were described by BANDEL (1974). He differentiated, by the radula function and the radula morphology derived from that function, two different groups of littorinid species. The first of these groups was exemplified by the radula of *Littorina littorea* (Figure 2B), the function of which has been described and analysed in detail by ANKEL (1936, 1937). Reviews of these studies along with new observations were presented by FRETTER & GRAHAM (1962), RICHTER (1962) and ROSEWATER (1980), who divided this group in four, using details of radula morphology: "rhomboidal, hooded, moderate and pick." Into the first group of Bandel, a number of members of the genus *Nodilittorina* can be included, as for example the type species of the genus *Nodilittorina*, *N. pyramidalis* and also *N. ziczac*, *N. lineolata*, *N. interrupta*, *N. dilatata*, *N. vermeiji*, *N. glaucocincta*, *N. angustior* and *N. rusei*. This radula can be considered to be closely linked in its general morphology to the assumed original littorinid radula still found in some Antarctic representa-

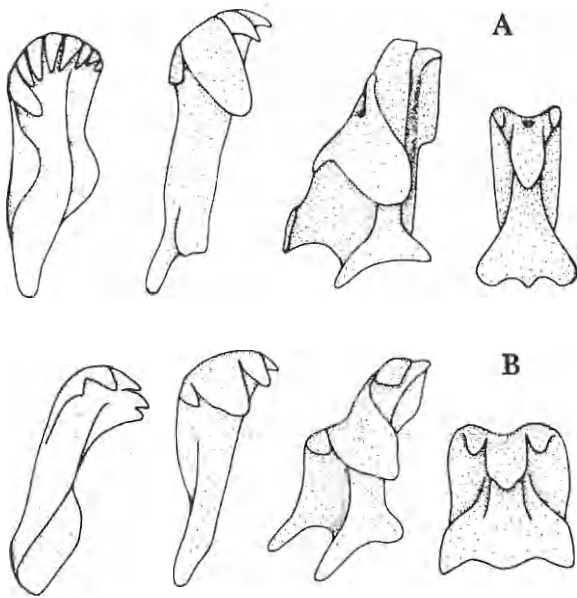


Figure 2

Radulae

- A) *Nodilittorina (N.) pyramidalis* (Quoy & Gaimard), Indo-Pacific;
 B) *Littorina (L.) littorea* (Linnaeus), European Atlantic coast

tives of this family that live below the intertidal zone. It is found among most littorinids modified only in small, but characteristic details. This type of dentition is used to rake in detritus, bite off plant material, to scrape algal crusts and shovel loose material into the mouth. It can be considered as an all-purpose instrument.

The second group of radulae described by BANDEL (1974) includes only a few species of the genus *Nodilittorina*, as for example *Nodilittorina tuberculata*, *N. mordax* and *N. antoni*. Here the lateral teeth have lost their shovel-like, concave shape and have become solid, massive cusps, larger and longer than all other teeth in each transverse row of the radula ribbon. The central tooth is reduced in size to such a degree that it has lost its function. This radula is used mainly for scraping and scratching over rock surfaces. Food material will be scratched from surfaces mainly with the lateral teeth and only the transport of loosened food material to the radula-midline is aided by the shorter marginal teeth.

Both groups of radulae found within the genus *Nodilittorina* are connected to each other by intermediate forms most probably not forming one line of descent but, at least, two (Figure 5).

The type species of the genus *Nodilittorina*, *N. pyramidalis* (Figure 2A) has a radula that in all essential features is like that of *N. ziczac*. The central tooth is about 2 times higher than wide. Its anterior front is evenly concave and the anterior corners are rounded forming the base of the 2 flanking cusps that accompany the solid, much larger, central, main cusp. A broad central swelling of the basal platform of the central tooth is continuous into the main cusp. The anterior corners of the central tooth are extended into narrow, wing-like structures that form the anterior portion of the straight margins of the tooth. In the posterior half of the basal platform the central swelling widens to form the rounded posterior corners. The lateral wings are in contact with this swelling in the posterior third of the margins. The posterior edge of the central tooth is formed by the rounded corners and, between them, an evenly concave embayment with a rounded or pointed central tongue projecting from it.

The central tooth and the lateral teeth of each row are hinged to each other in such a way that the inner raised margins of the lateral teeth rest in the concavities formed by the marginal wings and the central swelling of the central tooth. On the other hand the solid, rounded posterior corners of the central tooth project over and rest on the lower, wing-like inner margin of the lateral teeth. When the teeth are erected at the moment the radula ribbon is drawn over the front of the odontophore, the movement of the central and the lateral teeth, because of their being hinged with each other, occurs in phase with each other.

The lateral teeth also make up the largest teeth in each transverse row of teeth in the radula. It shows a wide cutting edge on its anterior front, dominated by two solid, central cusps. The inner of these cusps forms an angle larger than 90° with the basal platform of the tooth, while the outer cusp forms an angle of about 90° with it and in the folded radula stands up vertically. Both central cusps continue with their bases into a solid central swelling of the basal platform that becomes narrowest in the posterior center of the basal platform. The swelling widens again at its approach to the posterior edge. Here it forms a solid, short, thumb-like projection or denticle on the inner side that also forms the inner posterior corner. On the other side the posterior end of the central swelling ends without projection before the onset of a deep indentation of the posterior edge. This indentation forms the outer portion of the posterior edge between the central swelling and the projecting outer corner. The latter is the end of the outer margin that continues into the cutting edge. Near its outer, posterior end this margin is folded up, and, therefore, the basal platform between central swelling and outer margin is of gutter-like shape and deeply concave.

The two main cusps of the cutting edge of the lateral tooth are accompanied on both sides by one smaller denticle. The inner of these denticles is continuous into a shouldered wing with a raised inner rim. It is this wing that rests on the wing-like margin of the central tooth. The shoulder is found only in the anterior portion of the inner margin. Its raised rim ends at about half of the length of the margin, and a low, wing-like structure is present from rim end to the thumb-like, inner, posterior corner. Onto this posterior portion of the inner wing of the lateral tooth the solid, swollen bases of the central tooth are resting in the relaxed radula.

The outer raised margin of the lateral tooth will project over the outer margin of the inner marginal tooth in the relaxed radula. The inner marginal tooth rests within the gutter-like, outer, concave portion of the lateral tooth. It is attached to the radula ribbon in such a way that its cutting edge with its four cusps can be rested on the lateral tooth against the slope formed by its two outer cusps and their continuation into the central swelling. The inner marginal tooth shows a cutting edge with pointed, up-turned cusps, the second outer of which is the largest. The cutting edge and the upper portion of the basal platform form a spoon-like concavity. The posterior portion of the platform is shaped like the solid, bilaterally flattened shaft of this spoon. The inner and the outer margins are straight and there may be a basal knob present at the pointed posterior edge.

The outer marginal tooth, in the relaxed radula, rests upon the upper, flat side of the inner marginal tooth. Its up-turned cutting edge then is fitted into the spoon-like cavity of the inner marginal tooth. The outer marginal tooth is claw-like in shape and may be quite variable between species with otherwise very similar teeth. The number of cusps on the cutting edge is characteristic for species, and in this group around the type species of the genus *Nodilittorina* it counts between 6 and 9. The innermost of the cusps is the largest and commonly of triangular

outline. The others are pointed and narrow. The central shaft is solid, straight and thickened by a ridge. There are wing-like lamellae present both on the inner and on the outer margin. The lamellae are not continuous into the claw-like apical region of the tooth, but end in indentations before reaching it. The inner lamella is narrow and little prominent, while the outer forms a wide, projecting wing on the lower half of the shaft. The posterior corner is pointed. With the inner marginal lamella the base of the outer marginal tooth is hinged to the inner marginal tooth. This lamella fits into the depression present on the base of the inner marginal tooth. The marginal teeth are not only erected, but also spread sideways when the radula ribbon is pulled over the edge of the odontophore.

The radula typical of *Nodilittorina*, as described above, shows many similarities to the typical radula of *Littorina* as present in *L. littorea* (Figure 2). But there are also sufficient differences in morphology as well as in other organs to be seen to separate both genera. The central tooth of *L. littorea* is hinged with the lateral tooth just as described above for *Nodilittorina*. But in contrast to the latter the central tooth of *L. littorea* is much wider and of more rectangular shape. The lateral tooth is very similar to that of *N. pyramidalis* with only the exception that the margin of the inner wing shows less up-turned anterior shoulders. The inner marginal tooth also is very similar in *L. littorea* and the discussed group of *Nodilittorina*. It also rests in the gutter-like groove present on the outer platform of the lateral tooth. The outer marginal tooth of *L. littorea*, in contrast, is quite different from that of *Nodilittorina*. In *L. littorea* the base of the outer marginal tooth is twisted off from the main shaft and forms a separate wide base for attachment on the membrane. Aside from this base forming an angle with the shaft the latter is rounded and shows no marginal lamellae. Its claw-like apex only has five cusps.

So major differences between *Nodilittorina pyramidalis*, *N. ziczac*, *N. lineolata* and *N. interrupta* on the one hand and *Littorina littorea* on the other may be found in the shape of

Explanation of Figures 12 to 17

The early ontogenetic shell

Figure 12: *Nodilittorina (N.) millegrana* (Philippi, 1848) Port Sudan, Red Sea.

(a) Overview; × 100 FN 1714/22

(b) Overview; × 170 FN 1714/17

(c) Sculpture of larval shell; × 500 FN 1714/23

Figure 13: *Nodilittorina (N.) tuberculata* (Menke, 1828) FN 1165/6A

Nodilittorina (N.) ziczac (Gmelin, 1791)

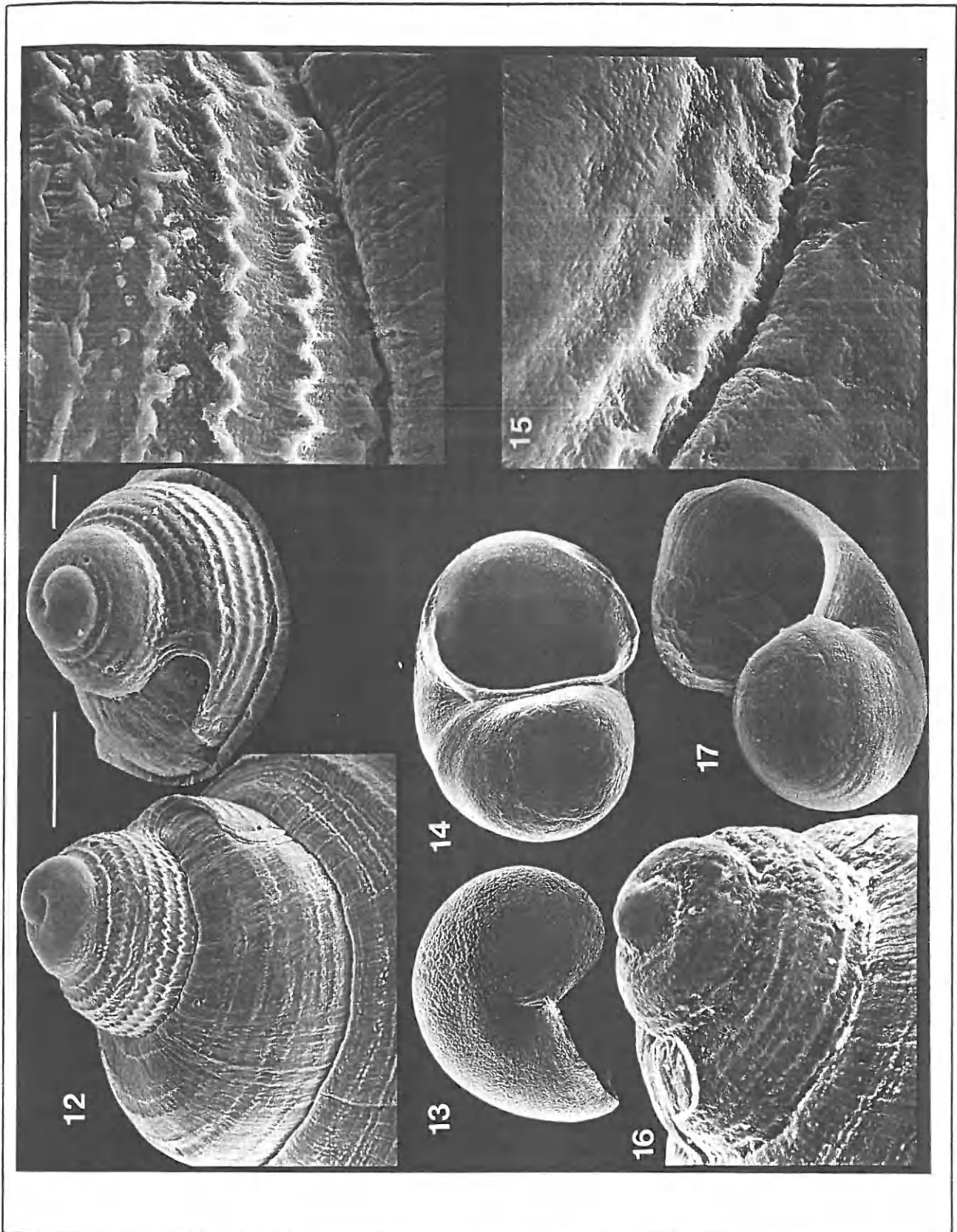
Figure 14: Embryonic shell; × 290 FN 1168/93A

Figure 15: Sculpture of larval shell; Colombia, Santa Marta; × 650 FN 2150/13

Nodilittorina (N.) interrupta (C. B. Adams in Philippi, 1847)

Figure 16: Overview. Colombia, Santa Marta. × 175 FN 2180/2

Figure 17: Embryonic shell. × 450 FN 903/29



the central tooth which is wider and more solid in *L. littorea*, and in the shape of the outer marginal tooth. The latter shows a twisted off, wide, flattened base, a rounded main shaft without marginal lamellae and fewer cusps present on the cutting edge. Such characteristics as present in *L. littorea* can also be noted, for example, in *L. saxatilis*, *L. obtusata*, *Littoraria angulifera*, *Fossarilittorina meleagris* and also in *Cenchritis muricatus* (see BANDEL, 1974).

Within members of the genus *Nodilittorina* the radula morphology as present in *N. pyramidalis*, *N. ziczac*, *N. lineolata* and *N. interrupta* is very close to that commonly present within the Littorinidae in general. But in other members of the genus *Nodilittorina* the teeth of the radula become continuously more modified until a radula morphology is reached that resembles that of *Nodilittorina antoni*.

In *Nodilittorina antoni* the central tooth has developed into a rudimentary, very narrow rod that is not solid enough to serve a function in the use of the radula. It lies almost completely hidden between the two lateral teeth. Here, on the inner margin of the solid, hammer-shaped lateral teeth a groove is present into which the narrow, flexible, central tooth can be fitted with its posterior two thirds. Therefore, only the uppermost portion of the central tooth is visible with its small, rudimentary, main cusp. Members of this species from San Salvador and Haiti, usually, show a better developed central tooth than members of this species from the Bahama Islands, where central teeth, in general, are more rudimentary.

The lateral teeth have become the dominating features in the radula of *Nodilittorina antoni*. They are large and solid and with the width of their anterior portions they also represent the width of the whole radula ribbon. The central tooth is, as we have seen above, held in a groove on their inner margins. The inner and outer marginal teeth, in the relaxed radula, are rested in the pockets formed by the lower, posterior portion of the outer margin. The inner marginal rim is present only as a narrow rudimentary projection on the inner side of the main cusp. The outer posterior corner, in its typical littorinid morphology, has disappeared and there is only a narrow lower terrace that follows the outer margin. On this terrace the marginal teeth may be rested. The cutting edge is formed mainly by a very solid, main cusp that stands vertically on the anterior portion of the tooth. There is an additional smaller outer cusp that projects sideways and forms the point of the greatest width of the radula in each transverse row of teeth. The posterior edge of the lateral tooth is rounded and formed by the end of the solid, swollen basal platform. There is no trace of a basal denticle. Aside from the longitudinal groove a crescentic depression is present on the flat, vertical inner margin

of the tooth. This groove serves no apparent function. The posterior end of each lateral tooth fits into a groove present below the cutting edge of the posteriorly following row of teeth.

The marginal teeth are very slender with straight shaft and vertically upturned cusps. The inner marginal tooth is more solid than the outer marginal tooth and shows only one solid cusp. The posterior end is pointed and flattened. The outer marginal tooth shows 2-3 cusps and a slender, rounded shaft. Individuals from San Salvador and Haiti, here again, show less reduction and, usually, 3 cusps on the outer marginal tooth. Those representatives of this species collected at Nassau show 2 to 3 cusps.

In action the teeth of the *Nodilittorina antoni* radula will spread only very little and the scraping action is carried out by the dominating lateral teeth, while the central tooth is without function and the marginal teeth can only aid in catching material scraped off by the action of the laterals. Strong wear of the main cusps of the lateral teeth is the result of this activity, while the inner marginals show less wear and the outer marginal teeth no wear.

The development of the morphology of teeth as present in *Nodilittorina antoni* can be traced step by step in intermediate species starting with the type of radula present in *N. pyramidalis*. But the radula teeth morphology of different species does not show one direct trend to develop this modified radula type. In different species, different teeth acquire new features while others may show conservative trends.

In the differentiation and reduction of the central tooth we can trace a line, as follows. The already (in comparison with most other littorinids) slender teeth of *Nodilittorina pyramidalis*, *N. ziczac*, *N. lineolata* and *N. interrupta* show all typical features, as, for example, solid main cusp of the cutting edge accompanied on its sides by smaller cusp, wing-like upper margins, and a swelling extended into the posterior basal platform. In *N. vermeiji* the general shape of the central tooth has remained like that of the former species but the marginal wings have become narrower. In the case of *N. dilatata* and *N. angustior*, in addition, the tooth becomes more elongated and is now higher than twice its width. In *N. risei* the marginal cusps of the cutting edge have migrated partially to the front of the central cusp and have split into smaller cusps. The lateral wings are extremely narrow here and the basal edge between posterior curves and central tongue is no longer concave. In *N. glaucocincta* a frontal rim has developed which carries the marginal cusps in such a way that they form a raised rim. The lateral wings are lost and the central tooth has become about 3 times higher than wide. In addition, there is no more hinging between central and lateral teeth of

each row. In *N. mordax* these tendencies have increased. A pointed long rim with raised margins forms the anterior front. In contrast to *N. tuberculata*, *N. mordax* still shows rounded basal corners, while in *N. tuberculata* these corners are angular. In *N. mordax* and *N. tuberculata* the lower margins of the central tooth can be fitted into furrows present on the inner marginal flanks of the lateral teeth. In *N. antoni*, finally, the central tooth is almost hidden in these furrows of the neighbouring lateral teeth.

We can also trace the development of the chisel-like laterals, as present in *N. antoni*, step by step. The lateral teeth of *N. ziczac*, *N. lineolata*, *N. interrupta* and *N. pyramidalis* reflect the shape which is generally found among littorinids. Typical features are seen in the wide inner rim and the marginal lamella, the central swelling which continues into the main cusps of the cutting edge, and the basal thickening of the inner posterior edge forming the thumb-like inner corner. Typical is also the extended outer corner with upturned outer margin and deep indentation between this corner and the end of the central swelling.

In *Nodilittorina dilatata*, *N. vermeiji*, *N. angustior* and *N. riisei* the two main cusps of the lateral tooth become strengthened and more prominent. The length-width relationship changes in favour of the length of the tooth. The thumb-like projection of the inner posterior corner is less pronounced than in the former group of species. In *N. glaucocincta* the lateral tooth has acquired a greater length than width and the central cusps have increased in strength even more. The major difference from the group with *N. dilatata* lies in *N. glaucocincta* in the formation of the inner flank of the tooth. Here, the marginal rim and wing is present only in the anterior portion of the inner margin. The posterior portion of this marginal flank shows a deep furrow without lamella. A thumb-like, inner base of the central swelling is present no longer.

In *Nodilittorina mordax* marginal cusps have disappeared on the cutting edge of the lateral tooth. *Nodilittorina tuberculata* no longer shows a raised rim of the outer margin, which could hold the inner marginal tooth at its place of rest, as is present in all other species mentioned before. It is only a short step away from this still wide lamella of the outer margin of *N. tuberculata* to the narrow, terrace-like outer margin of *N. antoni*. In the latter, the cutting edge of the lateral tooth has become more hammer-like in shape.

In regard to the inner marginal tooth very little difference can be seen in most of the *Nodilittorina* species discussed here. A reduction of the number of cusps is noted from the usual four to three in *N. glaucocincta*, two to three in *N. mordax* and 1 cusp only in *N. antoni*.

The outer marginal tooth again shows a different line of morphological development. The largest number of cusps is observed in *Nodilittorina ziczac* (8-9) and *N. vermeiji* (9). The former species has wide marginal lamellae while in *N. vermeiji* these lamellae are narrow. *Nodilittorina interrupta* and *N. dilatata* show 7-8 cusps; *N. lineolata*, *N. angustior* and *N. riisei* have 6-7 cusps. Here, *N. lineolata* and *N. angustior* show wide marginal lamellae while *N. riisei* has narrow lamellae. *Nodilittorina glaucocincta* and *N. mordax* have 5-6 cusps, *N. tuberculata* and *N. antoni* 2-3 cusps. All these species show no marginal lamellae.

The difference of development of these teeth demonstrates that the discussed species are not related to each other in a straight line of descent. The representatives of the genus *Nodilittorina* from the Caribbean Sea can be considered as branches of one phylogenetic line with the tendency to develop a radula with a scraping function rather than a raking and biting function as is present in littorinids in general. This circumstance enables us to differentiate, by radula features, species which otherwise show very little differences. Since we can still trace the different steps of the development towards the radula of *N. antoni* in our living fauna within the general area of the Caribbean Sea, it is quite probable that this development reflects a rather new phylogenetic achievement, restricted to the Caribbean area. This would explain the absence of similar radula features in the Indo-Pacific area. The radula type present in *Nodilittorina pyramidalis* and the group around *N. ziczac*, which must be considered as the pool from which our species development of the scraping radula has arisen, is commonly found among tropical and subtropical littorinid species from the Atlantic (see BANDEL, 1974) and the Indo-Pacific (see ROSEWATER, 1970).

This closely linking chain of development of the morphology of radula teeth demonstrates the close relation between the Caribbean species of the genus *Nodilittorina*, even though the extremes, seen isolated, seem to be quite apart. It is, therefore, considered to be of no value to construct a subgeneric differentiation of these species on radula characters alone, even though it would be a simple task to do so with the help of the radula characters demonstrated above. Radula characters have developed in different lines to similar shapes; lines that are differentiated from each other by shell characters and morphology of the egg capsules (Figure 5).

Spawn (Figure 5): Within the family Littorinidae there exists quite some diversity of the morphology and consistency of the egg masses. There are species with gelatinous egg masses, with young hatching as miniature adults from

a brood pouch, with young hatching as veliger larvae from a brood pouch and with concrete, unattached, floating egg capsules released into the water of the sea. MILEIKOVSKY (1975) has reviewed data on 39 species of littorinids from various regions of the world regarding the types of larval development. All members of the genus *Nodilittorina* listed by this author show a completely pelagic development of their larvae.

Egg capsules of members of the genus *Nodilittorina* were described by LEBOUR (1945), TOKIOKA & HABE (1953), HABE (1956b), KOJIMA (1957), WHIPPLE (1965), STRUHSAKER (1966), BORKOWSKI & BORKOWSKI (1969), ROSEWATER (1970), BORKOWSKI (1971), BANDEL (1974), ROBERTSON (1974). BANDEL (1974) has also presented a generalised scheme to show littorinid spawn as known from the literature. Here it becomes evident, that spawn is to be considered as of restricted taxonomic value within the littorinids in general. The closely related species *Littorina littorea*, *L. obtusata* and *L. saxatilis*, for example, hatch from very different egg masses. In *L. littorea* free floating egg capsules are produced from which veligers will hatch with a long free larval life. In *L. obtusata* gelatinous egg masses are glued to algal substrates. From these crawling young will hatch after a completed metamorphosis within the egg masses. In *L. saxatilis* (s.l.) crawling young will hatch after completed metamorphosis within the brood pouch of the female.

Members of the genus *Nodilittorina*, as far as is known at present, only produce spawn consisting of free floating egg capsules holding usually one egg only. Differences can be observed again within the floating egg capsules produced by many littorinids. These may be grouped in two ways, the first of which is by content: Many or few eggs per capsule, as, for example, in *Littorina littorea*, and 1 egg per capsule, as, for example, in the known representatives of *Nodilittorina*. Within such species having one egg capsule only, the shape of the capsules differentiates several groups (see BANDEL, 1974). The egg capsules of species of the genus *Nodilittorina* are characterized by a basal, watch-glass-shaped or flat wall and an upper cupola projecting over the base with a more or less wide rim. The cupola is sculptured by ridges and may show quite different ornamentation and shape, which could prove to be of taxonomic value within the genus *Nodilittorina*.

Nodilittorina interrupta, *N. lineolata*, *N. ziczac* and *N. dilatata* capsules show a broad, vertical, unsculptured, basal portion in their upper cupola and a species-specific number of ridges on the top of the cupola. In *N. tuberculata* and *N. angustior* the cupola extends into the basal rim, and a large number of step-like ridges is present. In *N. riisei* and *N. antoni* the vertical basal portion of the cupola shows additional, inclined, transversal stripes.

Egg capsules from Pacific representatives of the genus *Nodilittorina* resemble those from the Caribbean Sea. The capsules of *N. picta* (WHIPPLE, 1965, STRUHSAKER & COSTLOW, 1969) from Hawaii (= *N. hawaiiensis* ROSEWATER & KADOLSKY) are similar to those found in *N. ziczac*. *Nodilittorina millegrana* (HABE, 1956 (as *picta*); TOKIOKA & HABE, 1953; ROBERTSON, 1974) shows a striated basal portion and, therefore, resembles the egg capsules of *N. antoni*; *N. pyramidalis* egg capsules (TOKIOKA, 1950; ROBERTSON, 1974) resemble again those of *N. ziczac*.

Each spawn of *Nodilittorina* consists of a large number of egg capsules. STRUHSAKER & COSTLOW (1969) have counted between 10 and 1000 eggs per spawn on *N. picta* (= *N. hawaiiensis*). The egg masses may show some minor variation in the ornamentation of individual capsules which is not so large as to dominate their species characteristics. Spawn of *N. ziczac* from Florida (BORKOWSKI & BORKOWSKI, 1969) is quite like that of members of this species from Colombia (BANDEL, 1974).

SHELL

General Remarks: The *Nodilittorina* species dealt with here can (all but three) be distinguished by their shell characters. The differences are sometimes subtle, but are always corroborated by more obvious differences of other organs. Only *Nodilittorina riisei*, *N. glaucocincta* and *N. mordax* have virtually identical shells, but very distinct radulae. As in this case the shell was phylogenetically more conservative than the radula, it seems that shell characters are not always that variable and hence of minor taxonomic significance as is sometimes expressed in literature. Obviously, lumping of seven non-nodulose species and two nodulose species into one each, as for example, BEQUAERT (1943) and CLENCH & ABBOTT (1942) did, respectively, gave the illusion of highly variable shell characters of these assumed "species." Certainly, as all species established in the 19th century were defined by shell characters alone, it was science at its best to question the importance placed on shell characters, unless anatomical data confirmed the "conchological" concept. The data now available show that many of the ancient species have been correctly proposed. It is noteworthy that a similar process of recognition occurred in European littorinids, when HELLER (1975a) realised that at least four species had been lumped under the name of *Littorina saxatilis* (Olivi), again resulting in the deceptive picture of a "species" with extreme shell variability.

Shell Sculpture: Individual species may frequently be distinguished by their sculpture. The number of primary,

secondary and tertiary spirals, the profile of spiral ridges and furrows, the occurrence, shape and strength of nodulose beads and the way they merge or stay apart or divide themselves are useful criteria. In the genus *Nodilittorina*, however, the existence of nodulose sculpture cannot be consistently linked to other properties of the species, e.g., radula, penis, operculum or spawn characters. In fact, all anatomical and even conchological characters apart from the sculpture, the nodulose species prove to be very closely related to the non-nodulose species classified by ROSEWATER, 1970 as *Littorina* (*Austrolittorina*), while no particular relationships to other Littorinid genera with nodulose sculpture can be recognized. Furthermore, in some species (*Nodilittorina australis* (Gray), *N. millegrana* (Philippi), *N. hawaiiensis* Rosewater & Kadolsky, *N. cinerea* (Pease), *N. quadricincta* (Mühlfeld), *N. striata* (King & Broderip)) the infraspecific variability of sculpture ranges from spirally striated to granose or nodulose. A review of the entire family Littorinidae shows that nodulose sculpture has originated several times independently, as taxa showing this property have either close relationships to non-nodulose species or no particular relationships at all, not even to other nodulose taxa. These groups of nodulose species are (for genus definitions, see Table 1):

1. *Tectarius*: an Indo-Pacific group without close allies (ROSEWATER, 1972-73, as *Tectarius* (*Tectarius*)).

2. *Echininus*: another Indo-Pacific group without close allies (ROSEWATER, 1972, as *Echininus* (*Echininus*)).

3. *Cenchritis*: comprises one Caribbean species only; possibly related to *Littoraria* (ABBOTT, 1954, as *Tectarius* (*Cenchritis*); P. H. FISCHER, 1971).

4. *Nodilittorina*: worldwide, tropical and subtropical; close anatomical relations to non-nodulose species do not justify a subgeneric separation of nodulose species; even the nodulose species in this genus may be of polyphyletic origin, as they form five groups which did not necessarily originate from a common nodulose ancestor: (a) *N. pyramidalis-miliaris* (-*dilatata*?) group, (b) *N. tuberculata*, (c) *N. millegrana* group, (d) *N. (Tectininus) antoni*, (e) *N. (Liralittorina) striata*.

5. *Littorina aleutica* Dall, 1872: A nodulose species probably related to *Littorina stichana* (Philippi), *L. atkana* Dall and *L. obtusata* (Linnaeus) (see P. H. FISCHER, 1967a).

6. *Littorina brevicula* (Philippi, 1844): A species with spiral ornamentation sometimes growing rugose or nodulose; not closely related to *L. aleutica*, although to be placed in the same genus.

7. *Melarhappe nodulifera* (Kadolsky, 1973): a European Oligocene form originated from the sympatric *M. obtusangula* (Sandberger, 1859) which is entirely smooth, as are all other species of *Melarhappe*.

These examples demonstrate the impossibility of utilising the nodulose sculpture by itself in littorinid taxonomy; however, combined with other shell and anatomical features it may be helpful to recognise related groups of species, hence genera and subgenera (compare Table 1).

Colour Pattern: Highly variable colour patterns in some Gastropods (e.g., the land snail *Cepaea*) led to the conclusion that colour patterns can be assigned no or little taxonomic value. Also, this study has been conducted disregarding colour patterns of *Nodilittorina*. However, once the species were defined utilising other shell characters as well as operculum, radula and spawn characters, they turned out to have also fairly characteristic colour patterns. There is considerable variation; in our group, the most variable features are the inconstancy of ziczac lines which easily turn into straight or only slightly bent lines, and the extent of the dark brown pigmented zone in the middle of the whorls: sometimes being only a darker shade, sometimes seen in full intensity on the outer surface, it may also vary considerably in width.

Interestingly, only spirally sculptured and weakly granulose species of *Nodilittorina* seem to develop colour markings, as strong nodules certainly will obscure any markings. This, and the fact that the range of colour patterns in each species is relatively small, suggest that each particular colour pattern, or more generally speaking, the appearance of the shell surface (thus including obvious sculptures) is biologically meaningful in a given habitat. Its value in

Explanation of Figures 18 to 22

Nodilittorina (N.) ziczac (Gmelin, 1791)

Figure 18: Martinique. BMNH 1854.10.4.13.; lectotype of *Littorina d'Orbignyana* Philippi, 1847; probably original of ORBIGNY, 1842 (plt. 15, figs. 5, 8). Shell: 24.2×14.0mm. Radula:

× 280 FN 1465/11

Figure 19: Locality unknown. BMNH 1968.222. Lectotype of *Littorina debilis* Philippi, 1846. Shell: 9.2×6.4mm. Radula:

a) × 280 FN 1600/30

b) × 280 FN 1600/28

Nodilittorina (N.) lineolata (Orbigny, 1840)

Figure 20: Rio de Janeiro, part. BMNH 1854.12.4.363. Lectotype. Shell: 8.2×5.1mm, Radula:

× 480 FN 1465/63

Figure 21: Rio de Janeiro, Hapuca in Niteroi. SMF 110777. Shell: 9.6×6.7mm, Radula:

× 370 FN 1600/1A

Figure 22: São Vicente near Santos. Marcus & Marcus leg. USNM 749802. Shell: 7.9×4.1mm

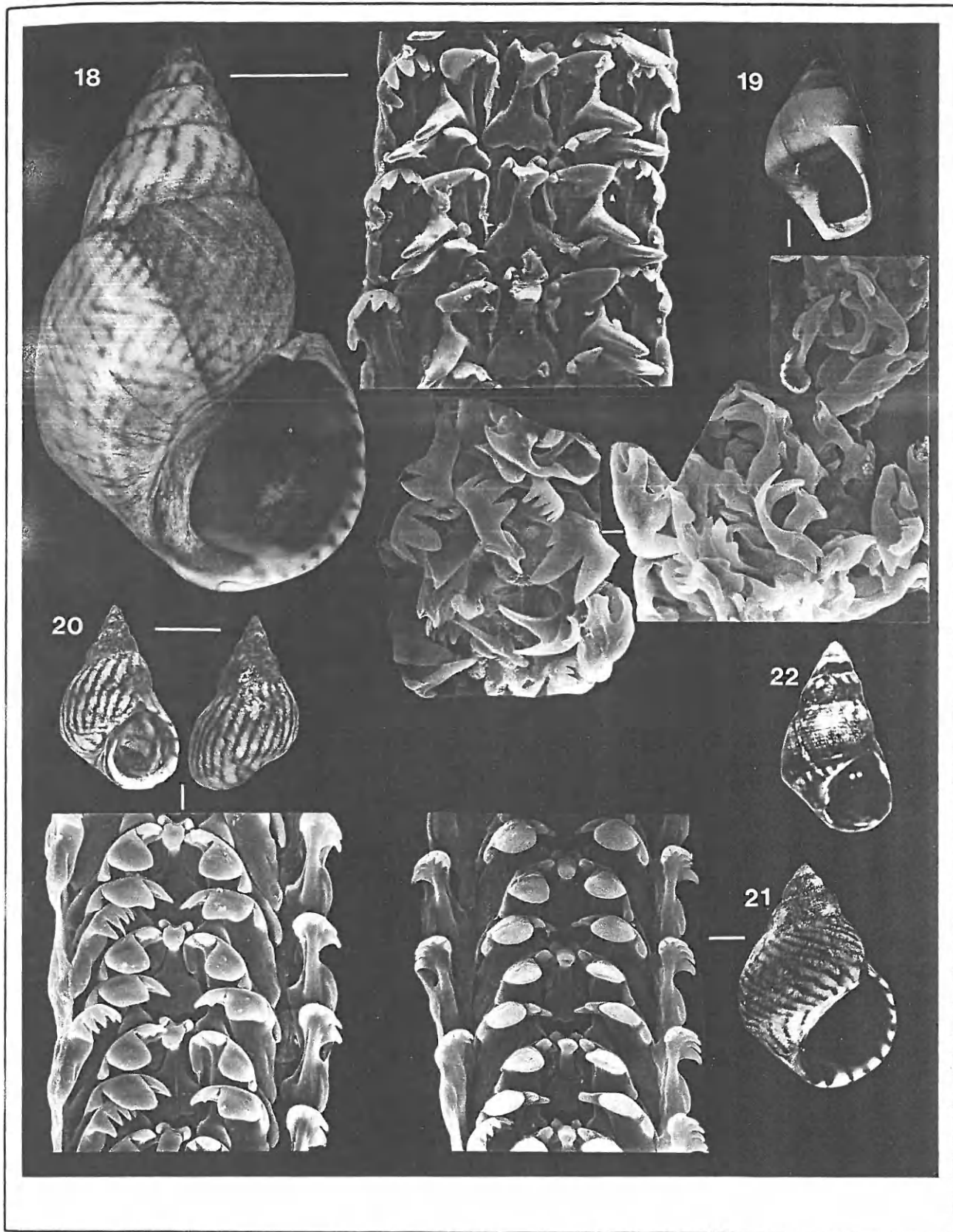


Table 1
Synopsis of the characters of the genera

Genus (with type species)	Shell				
	Size, Shape	Colour Pattern	Sculpture	Penis	Operc
<i>Littorina</i> Ferussac, 1822 (<i>Turbo littoreus</i> Linnaeus, 1758)	Large to medium; ovate to conical	Uniform or broad spiral bands, or chessboard pattern; interior brown, no white zones; columella white	Elevated spiral striae, may become very faint or nodulose	Open spermoduct; numerous glands	Horny, paucisp types A B
<i>Littoraria</i> Gray in Griffith & Pidgeon, 1834 (<i>Littorina pulchra</i> Sowerby, 1832)	Large, rarely medium or small; ovate-conical, periphery often angulate	Brown dots and oblique axial or zigzag bands, often on yellow background; interior and columella only slightly pigmented	Elevated or flattened spiral striae	Spermoduct mostly open, rarely closed; no glands, often an accessory flagellum	Horny, paucisp type A
<i>Cenchritis</i> Martens, 1900 (<i>Turbo muricatus</i> Linnaeus, 1758)	Large; ovately top- shaped; pseudumbilicate.	Surface white with rudi- mentary brown dots; interior dark brown; columella white	Rows of rounded nodules; 3 primary, equal rows	Spermoduct open; no glands nor appendages	Horny, paucisp type B
<i>Tectarius</i> Valenciennes 1832 (<i>Tectarius coronatus</i> Valenciennes, 1832)	Large, conically top-shaped; thickening at columella, interior with raised spiral ridges	Sparse brown dots or bands; columella and interior light-coloured	Rows of spiny to rounded tuber- cles; 1 primary row	Spermoduct open; numerous glands on lateral edge; papillose surface on opposite edge	Horny, mesosp
<i>Echininus</i> Clench & Abbott, 1942 (<i>Trochus cumingi</i> Philippi, 1844)	Large, top-shaped, umbilicated; interior with raised spiral ridges	As in <i>Tectarius</i>	As in <i>Tectarius</i>	Spermoduct open, with internal fold; numer- ous glands near base; swelling at base	Calcare
<i>Nodilittorina</i> Martens, 1897 (<i>Littorina pyra- midalis</i> Quoy & Gaimard, 1833)	Medium sized, ovate-conical, periphery often angulate	Uniform, or chessboard pattern, or axial zigzag lines; often dark median zone on whorls; columella and interior dark brown, one light band on umbilical side, occ. several more	Incised spiral lines or rows of granules or nodules; primary rows unequal	Spermoduct open; usually with basal enlargement and one penial gland, occ. a flagellum, rarely no appendages	Horny, paucisp types A B, or mesosp;
<i>Rissolittorina</i> Ponder, 1966 (<i>Zelaxites alta</i> Powell, 1940)	Very small, obtusely conical	Uniform brown, white band on umbilical side	Smooth	Spermoduct unknown; 1 long and slender 'filament'	Horny, paucisp type A
<i>Melarhappe</i> Mühlfeld in Menke, 1828 (<i>Turbo neritoides</i> Linnaeus, 1758)	Small, ovate-conical, periphery angulate; columella and parietal margins continuous	Uniform brown, white band on umbilical side	Smooth, rarely rounded nodules	Spermoduct partly closed; no appendages	Horny, paucisp type A
<i>Fossarilittorina</i> Rosewater, 1981 (<i>Phasianella meleagris</i> Potiez & Michaud, 1838)	Small, ovate- conical, periphery angulate; pseudumbilicus	White dots, flammules and stripes on dark brown back- ground; interior dark brown, white band on umbilical side	Spiral sculpture	Spermoduct closed; no appendages	Horny, paucisp type A

Table 1

Synopsis of the characters of the genera of the family Littorini

Genus (type species)	Shell			Penis	Operculum	Spawn, Onto
	Size, Shape	Colour Pattern	Sculpture			
<i>Littorina</i> (1822 <i>littorea</i> Linnaeus, 1758)	Large to medium; ovate to conical	Uniform or broad spiral bands, or chessboard pattern; interior brown, no white zones; columella white	Elevated spiral striae, may become very faint or nodulose	Open spermoduct; numerous glands	Horny, paucispiral types A and B	Pelagic egg cap with numerous veliger hatchin egg masses or c viparous witho veliger stage
<i>Littorina</i> (Griffith Leon, 1834 <i>pulchra</i> Gmelin, 1832)	Large, rarely medium or small; ovate-conical, periphery often angulate	Brown dots and oblique axial or zigzag bands, often on yellow background; interior and columella only slightly pigmented	Elevated or flattened spiral striae	Spermoduct mostly open, rarely closed; no glands, often an accessory flagellum	Horny, paucispiral type A	Pelagic egg cap with one egg, f shape, veliger l ing or ovovivi
<i>Littorina</i> (1900 <i>uricatus</i> Linnaeus, 1758)	Large; ovately top- shaped; pseudumbilicate.	Surface white with rudi- mentary brown dots; interior dark brown; columella white	Rows of rounded nodules; 3 primary, equal rows	Spermoduct open; no glands nor appendages	Horny, paucispiral type B	As in <i>Littoraria</i>
<i>Littorina</i> (1822 <i>coronatus</i> Linnaeus, 1758)	Large, conically top-shaped; thickening at columella, interior with raised spiral ridges	Sparse brown dots or bands; columella and interior light-coloured	Rows of spiny to rounded tuber- cles; 1 primary row	Spermoduct open; numerous glands on lateral edge; papillose surface on opposite edge	Horny, mesospiral	Unknown
<i>Littorina</i> (Clench Scott, 1942 <i>cumingi</i> Cuming, 1844)	Large, top-shaped, umbilicated; interior with raised spiral ridges	As in <i>Tectarius</i>	As in <i>Tectarius</i>	Spermoduct open, with internal fold; numer- ous glands near base; swelling at base	Calcareous;	Unknown
<i>Littorina</i> (1822 <i>pyra-</i> Quoy & Gardner, 1833)	Medium sized, ovate-conical, periphery often angulate	Uniform, or chessboard pattern, or axial zigzag lines; often dark median zone on whorls; columella and interior dark brown, one light band on umbilical side, occ. several more	Incised spiral lines or rows of granules or nodules; primary rows unequal	Spermoduct open; usually with basal enlargement and one penial gland, occ. a flagellum, rarely no appendages	Horny, paucispiral types A and B, or mesospiral	Pelagic egg cap with one egg, o flat, the other c with spiral ridg veliger hatchin
<i>Littorina</i> (1966 <i>alta</i> Carter, 1940)	Very small, obtusely conical	Uniform brown, white band on umbilical side	Smooth	Spermoduct unknown; 1 long and slender 'filament'	Horny, paucispiral type A	Unknown
<i>Littorina</i> (1822 <i>nitoides</i> Linnaeus, 1758)	Small, ovate-conical, periphery angulate; columella and parietal margins continuous	Uniform brown, white band on umbilical side	Smooth, rarely rounded nodules	Spermoduct partly closed; no appendages	Horny, paucispiral type A	Pelagic egg cap flat, with one e veliger hatchin
<i>Littorina</i> (1981 <i>illa</i> Pottiez Laud, 1940)	Small, ovate- conical, periphery angulate; pseudumbilicus	White dots, flammules and stripes on dark brown back- ground; interior dark brown, white band on umbilical side	Spiral sculpture	Spermoduct closed; no appendages	Horny, paucispiral type A	Pelagic egg cap with one egg, o flat, the other c with spiral ridg veliger hatchin

Table 1

Characters of the genera of the family Littorinidae s. str.

Axis	Operculum	Spawn, Ontogeny	Radula	Shell structure and mineralogy	Distribution, Remarks
duct; glands	Horny, paucispiral types A and B	Pelagic egg capsule with numerous eggs, veliger hatching; or egg masses or ovoviparous without veliger stage	Central tooth broad, with 3 cusps in one level; cusps of lateral and marginal teeth show minor size differentiation	Main layer calcitic; irregular prism sectors with variable orientation of prisms; inner layer of aragonitic cross lamellae may be present	Northern Hemisphere, moderate and cold zones. Subgeneric division possible
mostly glands, sessory	Horny, paucispiral type A	Pelagic egg capsule with one egg, flat shape, veliger hatching or ovoviviparous	Broad central tooth with 3-5 cusps and usually a "cockscorn" at its distal end ("hooded" type of Rosewater, 1981); very little size differentiation in cusps of lateral and marginal teeth	Crosslamellae; aragonite	Worldwide, tropic and subtropic seas. Subgeneric division including <i>Littorinopsis</i> Mörch necessary, pending anatomical data on the type species, <i>pulchra</i> Sowerby (= <i>zebra</i> Donovan, 1825)
open; or	Horny, paucispiral type B	As in <i>Littoraria</i>	Similar to <i>Littorina</i>	Crosslamellae; aragonite	Caribbean. Probably related to <i>Littoraria</i>
open; glands ridge; surface edge	Horny, mesospiral	Unknown	Narrow central tooth; lateral and marginal with low number of cusps	Crosslamellae; aragonite	Indopacific, tropical seas
open, with d; numer- near base; base	Calcareous;	Unknown	As in <i>Tectarius</i>	Crosslamellae; aragonite	Indopacific, tropical seas
open; basal and one d, occ. rarely ges	Horny, paucispiral types A and B, or mesospiral	Pelagic egg capsule with one egg, one side flat, the other convex with spiral ridges; veliger hatching	Central tooth narrow, occ. reduced, its 2 lateral cusps overtop the central cusps; cusps of lateral and inner marginal teeth of markedly different size	Crosslamellae; aragonite	Circumtropical; subtropical and tropical seas. Three subgenera: <i>Nodilittorina</i> s. str., <i>Tectininus</i> and <i>Liralittorina</i>
long	Horny, paucispiral type A	Unknown	Central tooth broad, 5 cusps; cusps of all teeth show very little size differentiation	Unknown	New Zealand, moderate zone
partly	Horny, paucispiral type A	Pelagic egg capsule flat, with one egg, veliger hatching	Central tooth broad, with basal denticles	Crosslamellae; aragonite	Europe, subtropical to moderate seas
closed; ges	Horny, paucispiral type A	Pelagic egg capsule with one egg, one side flat, the other convex with spiral ridges; veliger hatching	Central tooth moderately broad, with 3 cusps, the lateral ones not overtopping the central cusps; cusps of lateral and marginal teeth similar to primitive <i>Nodilittorina</i> teeth	Crosslamellae; aragonite	Atlantic; prob. American Pacific coast and Galapagos; tropical

natural selection, however, is at present not fully understood. HELLER (1975b) demonstrated that red shells of *Littorina nigrolineata* Gray and *L. rudis* (Maton) are significantly more frequent on red-brown cliff rocks than on others, thus acting as camouflage against visual selection by predators. Also in the West Atlantic species, protection against visual selection predators could be more important than protection against desiccation by enhanced shell reflectivity, as there seems to be no correlation between light-coloured shells and their supratidal habitat.

Even on the genus level, some elements of the colour pattern are constant in *Nodilittorina*: The major portion of the shell's interior is pigmented dark brown except a narrow band on the umbilical side. In the family Littorinidae, the genera *Melarhappe* and *Fossarlittorina* have this same colour pattern, but *Melarhappe* is very different in every other respect, while *Fossarlittorina* appears to be more closely related to *Nodilittorina* in relation to its spawn and, to some degree, its radula characters. Yet there is no support in the fossil record to confirm the hypothesis that *Melarhappe*, *Fossarlittorina* and *Nodilittorina* share a common ancestor with the same colour pattern, although this cannot be excluded with certainty.

Another colour character indicating relationships of *Nodilittorina* species is probably the fact that external colour markings in spirally sculptured species are present only in species living on American and African coasts; they are missing in the Australian and Pacific species, except in *N. acutispira* (E. A. Smith), which differs in penis characters from the other Pacific and Australian species.

In summary, if the range of colour patterns is considered, they may be of diagnostic value for both species and supra-specific groups, but they cannot be utilised isolated from other characters.

Embryonic and Larval Shells (Figures 12-17): The embryonic shell of the Caribbean representatives of *Nodilittorina* does not differ in general from such embryonic shells found among other littorinids with young hatching as veliger larvae (BANDEL, 1975a,b; RICHTER & THORSON, 1975). All embryonic shells studied up to now show weakly tuberculated to more coarsely tuberculated shells, which may or may not show growth lines. The embryonic shell of the Hawaiian *N. picta* (= *hawaiiensis*) is no exception (STRUHSAKER, 1968) and also demonstrates a finely granular sculpture.

The larval shell, secreted by the free swimming pelagic larva during its life as a member of the plankton, in contrast to the embryonic shell, shows more characteristics in its sculpture that may prove to be of high taxonomic value, if more species are studied. Up to now only the larval shell of *Nodilittorina hawaiiensis* (by STRUHSAKER, 1968, as

picta), *N. striata* and *N. miliaris* (by ROSEWATER, 1981: pl. 6, figs. E, F), *N. millegrana*, *N. striata*, *N. ziczac* and *N. interrupta* (own studies) are known from members of *Nodilittorina*. The larval shell of *Littorina littorea* was recently studied by BANDEL (1975b) and that of "*Littorina*" *neritoides* (= *Melarhappe neritoides*) by RICHTER & THORSON (1975). The larval shell of *Littoraria angulifera* was also studied by us to serve for comparison with *Nodilittorina*.

Common to all Littorinidae species mentioned with a free living veliger phase is the change in the course of growth lines after hatching. While in the embryonic shell the apertural lips were straight and show no undulations, the larval shell develops, right from first shell secretion onwards, a hooked outer lip of the aperture. Growth lines now are situated following the outline of the aperture with a strong saddle between a shallow umbilical lobe and deep apical lobe at the apertural lip. While the embryonic whorl of the shell is planispirally arranged, the 1 or 1.5 larval whorls now show a clear conspiral coiling.

Growth lines in the embryonic shell usually are weak and difficult to trace. With the onset of the growth of the larval shell growth lines become more prominent. The larval shell shows a deep and wide umbilicus. Aside from the more pronounced growth lines and their sinuous course also a more characteristic sculpture is to be seen on the larval shell in comparison to the embryonic shell. This sculpture, in the case of *Littorina littorea*, consists of tubercles of about 1 μ m width that arrange themselves into 7-8 spiral rows (BANDEL, 1975b). In *Melarhappe neritoides* tubercles at first form rows, later fuse partly to form 1-2 μ m wide discontinuous spiral ridges on a smooth surface (RICHTER & THORSON, 1975, and own observations). The larval shell here shows tubercles on the apical portion of each whorl and discontinuous ridges on the umbilical side of the larval whorl.

The larval shell of *Littoraria angulifera* encompasses 3.6 whorls and is strongly sculptured by 6-7 spiral ridges separated from each other by even, rounded grooves between them. The spiral ridges themselves are undulating in their course or straight.

The larval shell among the studied members of the genus *Nodilittorina* could be found best preserved in the species *N. millegrana* from the Red Sea (Figure 12). It consists of 3 whorls with a strong apical sinus in the outer lip. Growth lines, therefore, show a deep apical lobe and a wide, high saddle umbilically. Following the embryonic shell, that is sculptured like those of the Caribbean representatives of the genus (BANDEL, 1975a), along with the abrupt change in the course of the growth lines from straight to lobed, a rapid change in sculpture is observed. On the first half whorl produced by the free swimming larva 8-9 spiral rows consisting of strong tubercles are present. In the following

larval shell the tubercles are fused to form zic-zac shaped ridges, 7-10 on each whorl. There are quite strong individual differences to be noted in the number and the shape of these ridges. They may have a regular zic-zac course, or they may break up into rows of tubercles with short inclined ridges included, also giving a zic-zac appearance in the whole spirally arranged ornamental structure.

Nodilittorina ziczac and *N. interrupta* from Santa Marta (Figures 14-17) show a larval ornamentation very much like that seen in *N. millegrana*. But the preservation of the studied material from the Caribbean Sea was not as good as that from the Red Sea. The number of the whorls of the larval shell of individuals ready to metamorphose is 2.5-3 in the case of *N. ziczac*. The ornamentation consists of ziczac ridges as in the case of *N. millegrana*, and also 7-10 such spiral ridges are present on each whorl. In the larval shell of *N. interrupta* the zic-zac pattern is not as strongly developed as in *N. ziczac*, but still well traceable.

The larval shell of *N. striata* from Gran Canaria (Canary Islands) also shows a sculpture very much like that of the three other representatives of the genus *Nodilittorina*, thus demonstrating its close affinities to this group.

STRUHSAKER (1968, fig. 8) described and presented a drawing of the larval shell of *Nodilittorina picta* (= *hawaiiensis* Rosewater & Kadolsky) from Hawaii. The author had found that the larval life lasts 3-4 weeks from spawning to settling; 3.5 whorls are present before the larvae settle and before the animal finishes its metamorphosis from veliger to the crawling young. The larval shell of *N. picta*, according to Struhsaker, shows a more or less coarse spirally arranged zic-zac ribbing, similar to that of the members of the genus *Nodilittorina* described above.

Shell Structure: The shell structure of all members of the genus *Nodilittorina* here studied is aragonitic in composition. The needle-like biocrystals are arranged in the crossed lamella structure as is described in detail by BANDEL (1979). It is also like that of Antarctic littorinids as described by ARNAUD & BANDEL (1978).

The structure of the shell of Caribbean littorinids is like that of most marine mesogastropods. Usually two layers of the crossed lamellae structure are arranged in such a way that the plane of the lamellae of the first order of the outer layer forms almost a right angle with the plane of the lamellae of the first order of the inner layer. No differences in shell structure enabling the differentiation of species were found in the genus *Nodilittorina*.

Operculum

Characters: The common characters of all *Nodilittorina* opercula are: Operculum spirally coiled, composed of brown organic matter, edges thin and flexible, growth edge position opposite the parietal wall, spiral part opposite the columellar margin.

According to the type of coiling, three opercula types are recognised amongst West Atlantic species (Figure 3):

Type A: Operculum paucispiral, elongate, last whorl very large, its width is more than half of the operculum length; *Nodilittorina ziczac*, *N. interrupta*, *N. lineolata*, *N. rüsei*, *N. mordax*; operculum not seen: *N. glaucocincta*.

Type B: Operculum paucispiral, more circular, width of last whorl equal or less than half of operculum length: *Nodilittorina angustior*, *N. dilatata*, *N. tuberculata*, *N. vermeiji*.

Type C: Operculum mesospiral, nearly circular, width of last whorl about one fifth of operculum length: *Nodilittorina (Tectininus) antoni*

Functional Morphology: It has been suggested (STANLEY, 1979) that in Gastropod phylogeny the acquisition of the operculum afforded an improved protection against predators. In the intertidal and supratidal habitats, however, the protection against desiccation may become a more important task for the operculum (VERMEIJ, 1973). One important measure to accomplish this is the acquisition of the thin and flexible edge of the operculum: when the operculum is strongly withdrawn into the shell interior, this edge bends outwards and provides an improved closure. The flexible portion is largest at the adapical side of the operculum and least at the abapical side, so the operculum can be withdrawn further on its adapical side.

Muscle impressions on the interior side of the operculum suggest that about half of its surface is only loosely attached to the flesh and that the retractor muscle inserts on the side adjacent to the columella and the parietal wall. The insertion area is oval with a central constriction, whose tip points to the nucleus of the operculum (Figure 3B). During growth, this impression migrates in a rotating sense, marking its previous positions by internal growth lines, which are perpendicular to the external growth lines. Apparently additional operculum material is accreted on the edge of the retractor muscle scar adjacent to the palatal wall of the shell. Thickening of the operculum can be achieved best if the rotation of the muscle scar and the subsequent material accretion occur as often as possible. With the

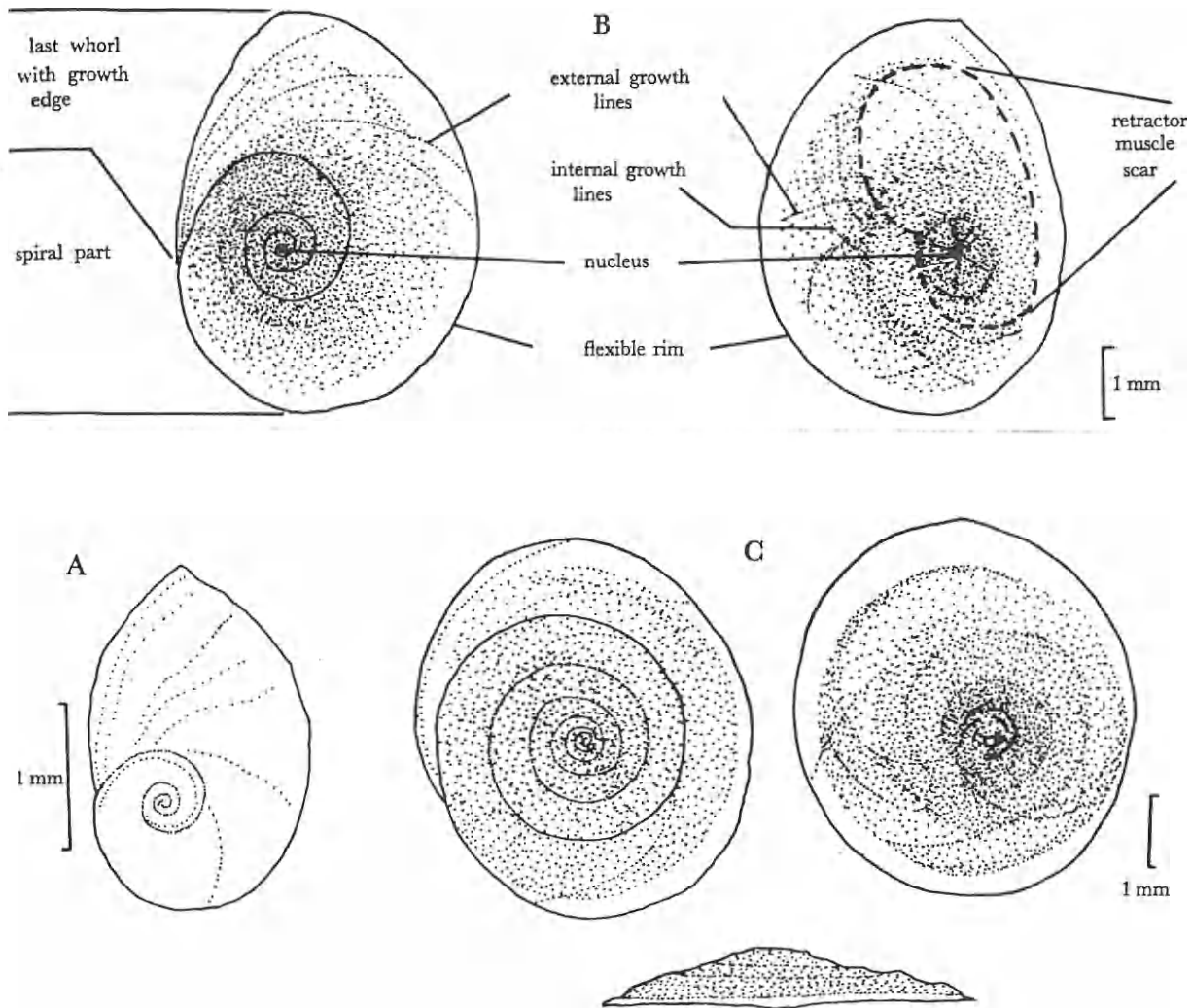


Figure 3

Opercula of *Nodilittorina* species

A) *N. lineolata* (Orbigny): paucispiral, widely coiled (type A). Per-nambuco (BMNH)

B) *N. tuberculata* (Menke): paucispiral, narrowly coiled (type B). Santa Marta, Colombia (B/K)

C) *N. (Tectininus) antoni* (Philippi): mesospiral (type C). Nassau, Bahamas (B/K); left: outer surface; right: inner surface; below: side view with inner side pointing upwards

aperture size tending to become smaller in high supratidal species as compared to low supratidal ones, this can only be accomplished by narrowing the operculum whorls to leave space for more gyrations. In fact, the most densely coiled *Nodilittorina* species, *N. antoni*, has the thickest operculum. Its flexible edge has become very narrow, but as

it is markedly concave on the exterior and convex on the interior surface, it will still provide a good closure.

The tendency of high supratidal species to build a smaller and more circular aperture coincides with the increase of the number of operculum whorls, which cause the operculum to acquire a more circular shape. So in the family Littorinidae the dense operculum coiling is a double purpose adaptation: to fit into a circular aperture and to enable the animal to thicken the operculum. In other Gastropod taxa living submerged, e.g., many Trochacea (marine) and Valvatacea (freshwater), the multi-spiral operculum appears to be just an adaptation to fit into a circular aperture.

As a third measure to prevent desiccation, the operculum may become calcified, as it is in the Indo-Pacific genus *Echininus*.

Taxonomic significance: Amongst marine Littorinidae *s. lat.*, apart from the above-mentioned West Atlantic species, the paucispiral type A was found in: *Littoraria angulifera* (Lamarck), *L. flava* (King & Broderip), *L. pintado* (Wood), *L. glabrata* (Philippi), *L. nebulosa* (Lamarck), *L. undulata* (Gray), *L. tessellata* (Philippi), *L. scabra* (Linnaeus), *L. cingulifera* (Dunker); *Fossarlittorina meleagris* (Potiez & Michaud); *Nodilittorina miliaris* (Quoy & Gaimard), *N. millegrana* (Philippi), *N. peruviana* (Lamarck), *N. punctata* (Gmelin), *N. striata* (King & Broderip); *Littorina littorea* (Linnaeus), *L. obtusata* (Linnaeus); *Melarhappe neritoides* (Linnaeus); *Laevilittorina johnstoni* (Cotton); *Macquariella kingensis* (May); *Rissolittorina alta* (Powell); *Laevilacunaria bennetti* (Preston).

The paucispiral operculum type B was observed in *Nodilittorina granosa* (Dunker), *N. pyramidalis* (Quoy & Gaimard), *N. subnodosa* (Philippi); *Littorina saxatilis* (Olivieri) group; *Risellopsis varia* (Hutton); *Cenchritis muricatus* (Linnaeus) (transitional to mesospiral); *Algamorda newcombiana* (Hemphill); *Rufolacunaria brunensis* (Beddome); *Macquariella hamiltoni* (E. A. Smith).

The mesospiral operculum (type C) is known from the genus *Tectarius* and the multispiral operculum from the genera *Echininus* and *Peasiella*.

In some instances, species with different opercula have been placed in the same genus (see *Nodilittorina*, *Littorina* and *Macquariella*), due to a combined evaluation of shell, radula, penis, spawn and operculum characters. From the considerations on the functional morphology and ecological adaptations of the operculum it is conceivable that from a stock of originally type A operculated littorinids the types B, C and the multispiral operculum evolved repeatedly, according to the pressure the supratidal environment exerted. So again, in taxonomy the operculum characters may be very misleading when considered isolated from other properties of the species, but in combination with as many other features as possible they will prove useful in recognising species groups and hence, subgenera and genera.

The subfamilies Echininae Rosewater, 1972 and Tectariinae Rosewater, 1972, founded solely on operculum characters, are thus considered unnecessary: As opercula cannot have more weight in taxonomy than any other organs, these subfamilies either have to be withdrawn or, for the sake of a consistent classification, numerous subfamilies, each comprising only one or a very few genera, would have to be created (probably one subfamily for each genus as defined in Table 1). So it is preferred to postpone a subfamilial division of the family Littorinidae until further anatomical data are known. The Risellidae and Lacunidae and the numerous taxa restricted to the South-

ern Pacific area (not mentioned in Table 1) would have to be considered in such a reclassification.

In the genus *Nodilittorina*, the mesospiral *N. antoni* constitutes the sufficiently well defined subgenus *Tectininus*. The paucispiral operculum type A occurs in most spirally striated and in the granulose species, for which the subgenera *Austrolittorina* Rosewater, 1970 and *Granulilittorina* Habe & Kosuge, 1966 have been proposed. However the penis of the spirally striated ones seems to differ between Indo-Pacific plus African species on the one hand and Western Atlantic species on the other; and there is the spirally sculptured *N. angustior* with operculum type B. These facts suggest that a subgenus *Austrolittorina* including all spirally striated Nodilittorinae would not represent natural groupings. The paucispiral operculum type B is found in *N. angustior* and in all more strongly nodulose species (*Nodilittorina s. str.*). It seems to be premature to attempt further subgeneric subdivisions based on shell and operculum characters before more anatomical data on *Nodilittorina* species are available.

Ecology and Morphological Adaptation

(Figure 4)

All species treated here live on the shoreline above medium high water level on hard substrata, mainly rocks. They remain quiescent during dry periods and become active when wetted with seawater spray by wave action. Then they feed upon films and crusts of algae, lichens, and probably also fungi and microscopic animals. All species produce pelagic egg capsules; thus, even those living most distant from the water level have to descend for spawning; correspondingly, the juveniles originating from the planktonic veliger larva have to crawl upwards from the sea level to the usual living area of the animal.

Figure 4 depicts the relative levels of habitat. No absolute heights can be given as these vary according to the coast topography and the hydrographic conditions; *e.g.*, tide and wave action. Also this zonation will be found valid only on sea cliffs with a certain amount of slope, as on flat rock benches both high and low supratidal species may live together (BANDEL, 1974a: Curaçao). For reference purposes, *Cenchritis muricatus* (Linnaeus) is also shown in Figure 4 as this is the littorinid species living most remote from the sea level.

Several papers deal with the morphological adaptations of littorinids to suit the supratidal habitat. VERMEIJ (1973) described from several localities all over the world gradients of littorinid shell morphology related to the distance of the living areas from the sea level; *i.e.*, related to the degree of desiccation and heat resistance of the animals. As a general trend, he recognised the increase of shell ornamentation and shell size and the decrease of the rela-

	<i>Cenchritis muricatus</i>	<i>Nodilittorina antoni</i>	<i>Nodilittorina angustior</i>	<i>Nodilittorina interrupta</i>	<i>Nodilittorina tuberculata</i>	<i>Nodilittorina dilatata</i>	<i>Nodilittorina riisei</i>	<i>Nodilittorina ziczac</i>	<i>Nodilittorina vermeiji</i>	<i>Nodilittorina mordax</i>
nodose sculpture	++	++	-	-	++	++	-	-	+	-
operculum type	B	C	B	A	B	B	A	A	?	A
aperture size index	155	137	172	217	171	213	216	194	174	239
▼ high water level ▼										
Ref.	BANDEL, 1974 BORKOWSKI, 1969 VERMEIJ, 1973	<i>nodulosa</i> <i>nodulosa</i>	<i>jamaicensis</i> <i>lineata</i> <i>lineata</i>	sp.	<i>tuberc.</i>	<i>dilatata</i> <i>tuberc.</i>	<i>lineolata</i>	<i>ziczac</i> " "	? <i>helenae</i>	<i>lineolata</i>

Figure 4

Supratidal zonation of West Atlantic species of *Nodilittorina* and their morphological adaptations to drought and heat

it cannot be compared accurately to habitats of the other species. Operculum type: A) paucispiral, last whorl wider than spiral part; B) paucispiral, last whorl narrower than spiral part; C) mesospiral. The aperture size index is the Ratio aperture surface : shell surface. Shell surface approximated as cone surface with base diameter = shell width, cone height = shell height; aperture surface approximated as ellipsis with long axis = mouth height, short axis = mouth width

The relative heights of the species habitats are indicated by reference to the mean high water level and to the zones of *N. ziczac*, *N. angustior* and *Cenchritis muricatus* (Linnaeus). The latter species is unrelated to *Nodilittorina* and included only for reference, as it is the littorinid living highest above sea level. Not shown are: *N. glaucocincta* (may live in the same zone as *N. ziczac*, if "*Littorina lineolata*" of Vermeij, 1973 from Jamaica is this species), and *N. lineolata*. Note that *N. vermeiji* is the sole species in its habitat, thus

(achieved by size increase) will minimise desiccation, and temperature intake will be minimised by avoiding the contact of the foot sole with the substratum, by avoiding creation of metabolic heat during dry periods and by mini-

tive mouth height with increasing distance of the habitat from the sea level. He interpreted this as an adaptation to desiccation and overheating, as a small aperture capable of being closed by an operculum and a low specific surface

missing the shell surface exposed to radiation; cooling of the animal body is maximised by a strong sculpture which increases the surface exposed to wind convection without increasing the surface liable to evaporation and to reception of radiation.

Similarly, STRUHSAKER (1968) showed that the nodulose morph of *Nodilittorina hawaiiensis* Rosewater & Kadolsky (= *Littorina picta* Philippi, 1846, non *Littorina obtusata picta* Menke, 1845) living on steep cliff slopes is larger than the smoother morph and is better adapted to dryness, high temperatures and hypersalinity, while the smooth morph living on shallow benches is much more capable of withstanding strong surges and submersion. In this species wave action is obviously another relevant selective factor not dealt with by Vermeij.

In the Red Sea, one of the authors (K.B.) observed the habitats of the nodulose, top-shaped *Nodilittorina subnodosa* (Philippi) with operculum type B and of *N. millegrana* (Philippi), which has a relatively larger aperture, an operculum type A and only beads of faint nodules (rather: granules). Confirming the trends observed by Vermeij and Struhsaker, *N. subnodosa* lives in the supratidal zone above the usual splash zone and is therefore rarely active; *N. millegrana*, however, lives in the lower part of the supratidal zone, which is frequently wetted by wave splash, down to the upper part of the permanently wet zone, enabling the animals to be more frequently active.

HELLER (1975b) indicated the importance of the camouflage effect of the shell colour in *Littorina nigrolineata* Gray and *L. rudis* (Maton), suggesting that protection against visual selection by predators is another essential selection mechanism.

Certainly there are many selection mechanisms; the littorinids have to cope, for example, with desiccation, high and low temperatures, hypersalinity and fresh water, wave action, gain of food, finding of sexual partners, maintenance of a sufficient fertility rate, protection against predators, resistance against parasites and epidemics. Also, each selection factor possibly can be tackled in several

ways. As a result, the morphological features of a species are bound to reflect a complex pattern of adaptation. It will take years of research to elucidate some of these adaptations, as Struhsaker's studies on *Nodilittorina hawaiiensis* have shown. Every simplistic approach to explain morphological features by adaptation to a certain factor of the environment may be valid within narrow ranges, but cannot be generalised, as the following exceptions to Vermeij's and Struhsaker's findings demonstrate:

- In Europe, the littorinid species living highest above sea level, *Melarhaphe neriooides* (Linnaeus), is nearly the smallest European species, certainly the least sculptured one and has still an unusually large aperture.
- In the Indo-Pacific, nodilittorines are described as living intertidally and supratidally (ROSEWATER, 1970). Amongst the intertidal species, there are several nodulose and granulose ones (*Nodilittorina quadricincta quadricincta* (Mühlfeld, 1824) (syn. *N. leucosticta* (Philippi, 1847)), *N. quadricincta biangulata* (Martens), *N. nodosa* (Gray), *N. australis* (Gray), while non-nodulose species frequently live supratidally (*N. unifasciata* (Gray), *N. punctata* (Gmelin), *N. praetermissa* (May), *N. africana* (Philippi)).

- The colour pattern of West Atlantic nodilittorines appears not to be optimal for temperature insolation, as it is mostly fairly dark. However, the intertidal Australian *N. australis* and the not particularly high living Caribbean *N. ziczac* have very light-coloured shells. The unexpectedly low variability of colour patterns suggests that they are preferentially selected, only leaving a limited variety of them to survive. Probably the protection against predators is an environmental factor exerting stronger selective pressure than the reflectivity of the shell.

Figure 4 shows also some of the properties probably related to desiccation resistance. The trends noted by VERMEIJ (1973) are clearly visible: The aperture becomes relatively smaller, and nodulose sculpture is more frequently found in species living high above water level. Also, the operculum tends to become more narrowly coiled. However, the many exceptions from this trend can be seen

Explanation of Figures 23 to 29

Nodilittorina (N.) interrupta (C. B. Adams in Philippi, 1847)
Figure 23: "Antilles." MHNG 1096/87/2. Paratype of *Phasianella lineata* Lamarck, 1822. Shell: 14.3×8.4mm, Radula:
× 360 FN 1599/14

Figure 24: Jamaica, MCZ 186123. Topotype of *Littorina ziczac interrupta* C. B. Adams in Philippi, 1847 (figured by CLENCH & TURNER, pl. 38, fig. 18). Shell: 7.8×6.0mm, Radula: × 400 FN 1599/18

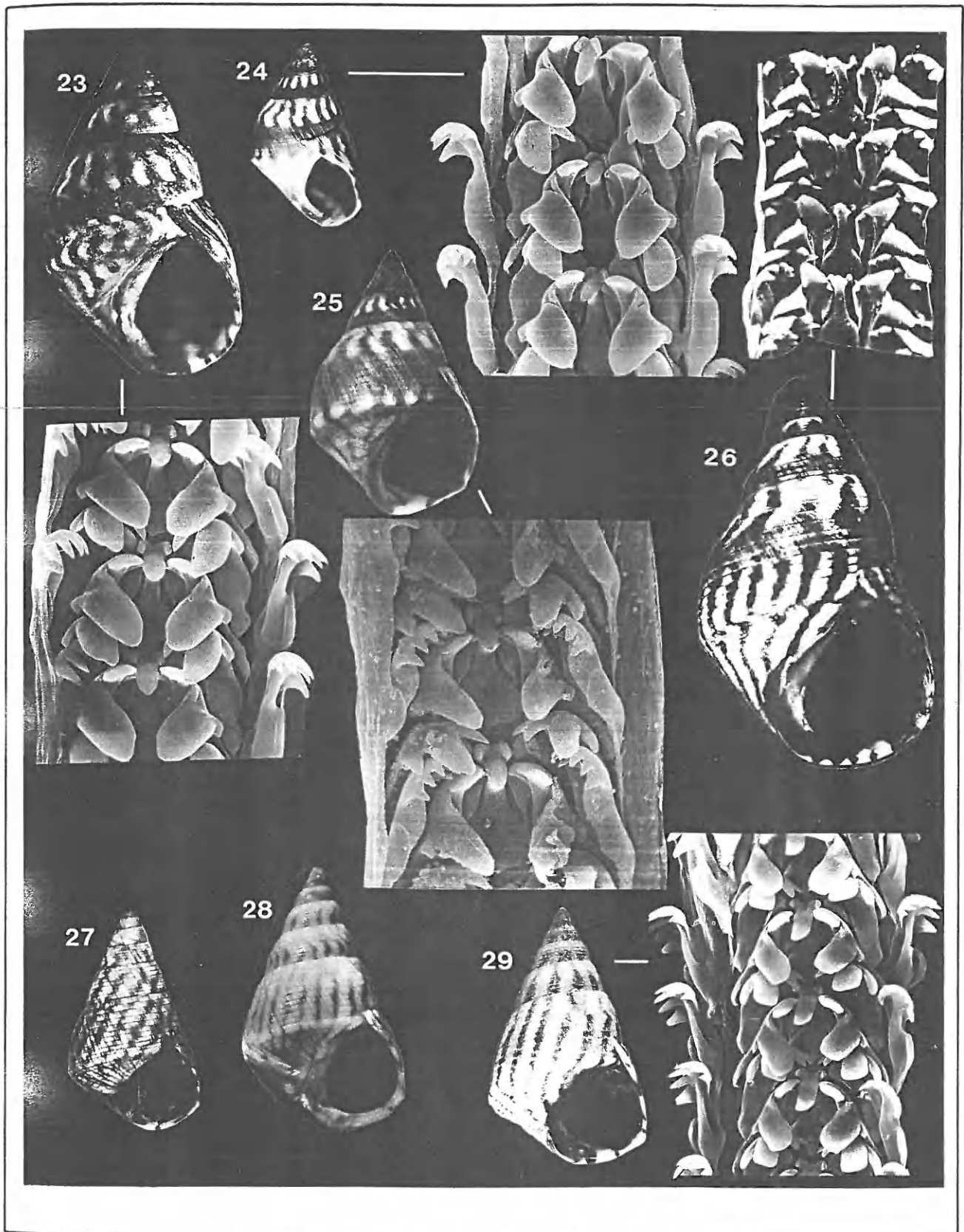
Figure 25: Lesser Antilles, St. Thomas, ZMK: Lectotype of *Littorina (Melaraphe) floccosa* Mörch, 1876. Shell: 11.7×7.5mm, Radula:
× 420 FN 1394/2

Figure 26: Lesser Antilles, St. Vincent. BMNH. Height, 16.0mm. Radula: × 330 University Erlangen-Nürnberg FN 1491
Nodilittorina (N.) angustior (Mörch, 1876)

Figure 27: Cuba, Havana. ZMK. Lectotype of *Littorina (Melaraphe) angustior* Mörch, 1876. Shell: 10.4×5.2mm

Figure 28: Cuba. BMNH 1854.10.4.128. Lectotype of *Littorina carinata* Orbigny, 1842. 11.6×7.0mm

Figure 29: Curaçao, Cornelisbaai. USNM 749809. Shell: 11.6×6.8mm, Radula: × 280 FN 1903/26



as well: *Nodilittorina interrupta* seems to have no adaptation at all to its elevated habitat, and *N. dilatata* seems to live too close to the water level, according to the criteria outlined above.

TAXONOMY

The Genus *Nodilittorina* Martens, 1897 in the Western Atlantic

Diagnosis.

Shell ovate to conical, solid; larval shell 2.5 to 3 obtusely conical whorls with spiral ziczac lines; postlarval shell sculptured with spirals or spirally arranged rows of nodules, tubercles or granules; whorls more or less angulate at periphery (may be superseded by nodules); interior of shell pigmented brown with a colourless or yellow band on the umbilical side, more unpigmented bands may be present; outer surface unicoloured, or with a broad dark median zone or axial brown stripes or both; no umbilicus; a crescent-shaped area of the outer shell surface adjacent to the columella margin may be redissolved. Operculum paucispiral to mesospiral, horny, brown. Radula with narrow central tooth, whose marginal cusps rise above the central one. Pelagic egg capsule is a circular disc, one side flat, the other one convex with spiral ridges, each capsule containing one egg. Penis with open spermiduct; presence and configuration of accessory organs are utilised and described in the subgenus diagnoses.

As discussed above, at present it is not justified to separate on a subgenus level spirally striated species from those with a granose or nodulose sculpture. The relationships between *Nodilittorina* as defined herein, and other nodulose taxa as well as the genus *Littorina* are shown in Table 1. The non-nodulose species of *Nodilittorina* used to be classified in *Littorina*; however, the low degree of relationship can easily be seen. In Table 1, the opportunity is seized to propose a new definition of the genus *Littorina* in its accustomed sense, splitting the genus as understood in current literature into the four genera *Littorina s.str.*, *Littoraria*, *Fossarlittorina*, and *Melarthaphe*, the rationale of which is considered to be obvious.

Three subgenera of *Nodilittorina* are recognised:

Nodilittorina (Nodilittorina): Penis with one (rarely none or 2) penial glands, at a variable degree in contact with the basal enlargement; this subgenus comprises the bulk of the species, i.e., with nodulose, granose and spiral sculpture; opercula type A and B; radula types "moderate," "pick" and "vestigial" of ROSEWATER, 1980.

Nodilittorina (Tectininus) Clench & Abbott, 1942: One penial gland widely apart from basal enlargement and surrounded by papillae; operculum mesospiral (type C); radula extremely vestigial. Only one species: *N. (T.) antoni* (Philippi) (= *Echminus nodulosus* Auct.)

Nodilittorina (Liralittorina) Rosewater, 1981: Penis without appendages; shell, radula and operculum characters within range of *N. (Nodilittorina)*. Only one species: *N. (L.) striata* (King & Broderip).

Key to Shell Identification (Figure 5)

(including *Nodilittorina helenae*)

1. Shell with nodulose sculpture 2
Shell spirally sculptured only; 6-8 primary spirals on visible part of whorls 6
2. Operculum mesospiral, 5-6 volutions; shell top-shaped, not conical due to convex and nodose whorls; aperture relatively small; nodes strongly developed, 2nd and 3rd row (counted from adapical row) distant from each other
N. antoni, p. 34
Operculum with maximal 4.5 volutions, paucispiral; shell shape more regularly conical 3
3. The two primary rows of nodules distant from each other, strongly unequal 4
The two primary rows of nodules closer together, subequal 5
4. Apical angle about 45°; light bands at the suture, the periphery and the umbilical side seen externally *N. helenae*, p. 37
Apical angle 50-60°; no white external bands except on the umbilical side, but nodules white *N. vermeiji*, p. 31
5. Columella abapically often dilated, sometimes a pseudoumbilicus; nodules rounded to spinose *N. dilatata*, p. 29
Columella not dilated; nodules rounded
N. tuberculata, p. 33
6. Primary spirals distinctly incised; no or sporadic intercalations of secondary spirals 7
Primary spirals more or less regularly doubling, primary and secondary spirals becoming equal, on last whorl often disappearing; interior with 2nd light band near the suture 8
7. Shell shape strictly conical; whorls gradually increasing, contours straight; height of aperture less than half of shell height; occasionally 2nd light interior band; operculum type B
N. angustior, p. 25
Shell shape ovate-conical; whorls more rapidly increasing, slightly convex; height of aperture more than half of shell height; operculum type A *N. rüsei*, p. 26;
N. glaucocincta, p. 27; and *N. mordax*, p. 28
To be distinguished by radula characters only
8. Last whorls with 15-20 very fine spirals above the suture, often extinguishing; keel reduced; narrow ziczac lines, not confluent *N. ziczac*, p. 19
Last whorls with 7-17 spirals above the suture, more incised than at ziczac; keel somewhat more pronounced; colouration more extensive 9
9. Shell up to 10mm long, slender, conical; dark brown median zone on whorls variable, absent to conspicuous; 2nd interior light-coloured band absent to present *N. lineolata*, p. 21

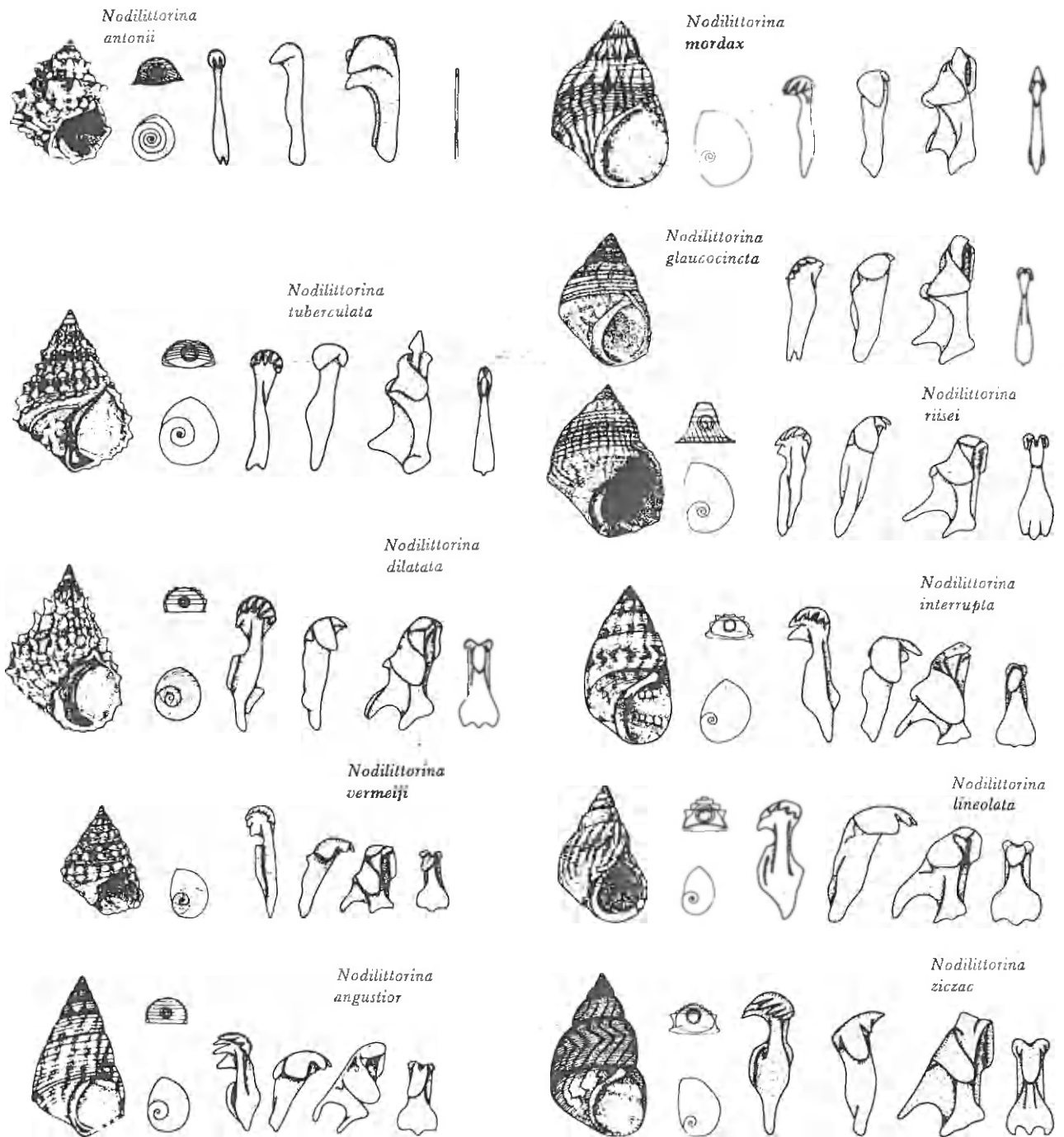


Figure 5

The West Atlantic species of *Nodilittorina*

Compilation of shell, radula, egg capsule and operculum morphological features. Arrangement of species according to similarity of characters does not necessarily imply phylogenetic relationships. In the vertical direction, the array follows the radula characters:

at the bottom species with a primitive *Nodilittorina*-type radula (e.g., *N. ziczac*) are to be found, while towards the top radula characters approach those of *Nodilittorina (Tectininus) antonii*; (after ABBOTT, 1954a; BANDEL, 1974; BORKOWSKI, 1971; BORKOWSKI & BORKOWSKI, 1969; MARCUS & MARCUS, 1963; and new)

Shell about 15 mm long (average), broader conical; dark brown median zone on whorls always broad and strongly developed; interior always with two light bands *N. interrupta*, p. 23

Key to Radula Identification (Figure 5)

(including *Nodilittorina helena*)

1. Teeth of moderate ("normal") size, inner marginal with 4 cusps, outer marginal with 7-9 cusps 2
Central tooth more or less reduced; cusp number of remaining teeth reduced, *i.e.*, inner marginal with 1-3 cusps, outer marginal with 3-6 cusps; one cusp of both lateral and inner marginal tooth greatly enlarged 9
2. Basal platform of central tooth wide 3
Basal platform of central tooth narrow 6
3. Margins of basal platform convex, thus largest width of basal platform remote from its posterior end *N. ziczac*, p. 19
and *N. helena*, p. 37
Margins of basal platform straight 5
5. Transition from the posterior portion of the basal platform to its anterior portion in the central tooth rounded
N. angustior, p. 25
Transition angulate *N. lineolata*, p. 21
6. Largest width of the central tooth near the posterior edge of the basal platform; length/width ratio of central tooth 1.7-2.2
N. interrupta, p. 23
Largest width of central tooth remote from the posterior edge of the basal platform; or basal platform rectangular 7
7. Outer marginal tooth with 8 cusps; length/width ratio of central tooth not exceeding 2.5 8
Outer marginal tooth with 7 cusps; length/width ratio of central tooth 2.5-2.8 *N. riisei*, p. 26
8. Length/width ratio of central tooth 2.1-2.3
N. dilatata, p. 29
Length/width ratio of central tooth 2.3-2.5
N. vermeiji, p. 31
9. Lateral tooth with 4 cusps 10
Lateral tooth with 1-3 cusps 11
10. Outer marginal tooth with 6 cusps; length/width ratio of central tooth 5-6 *N. glaucocincta*, p. 27
Outer marginal tooth with 7 cusps; length/width ratio of central tooth 5.6-6.5; third cusp of lateral tooth very large
N. tuberculata, p. 33
11. Lateral and inner marginal teeth with 3 cusps each, outer marginal tooth with 5-6 cusps; central tooth 6-12 times longer than wide *N. mordax*, p. 28
Lateral and inner marginal teeth with one very large, massive cusp each, outer marginal tooth with 3 cusps; central tooth tiny, with one cusp *N. antoni*, p. 34

Subgenus *Nodilittorina* (*Nodilittorina*) Martens, 1897

- * *Nodilittorina* Martens, 1897: 204. Type species: *Littorina pyramidalis* Quoy & Gaimard, 1833 (SD/ABBOTT, 1954a: 451).
- * *Echinolittorina* Habe, 1956a: 96, 98-. Type species by M: *Littorina tuberculata* Menke, 1828.

- * *Granulilittorina* Habe & Kosuge, 1966: 313, 328. Type species by M: *Granulilittorina philippiana* Habe & Kosuge, 1966 (= *Littorina millegrana* Philippi, 1848).
- * *Austrolittorina* Rosewater, 1970: 467. Type species by OD: *Littorina unifasciata* Gray, 1827.

Nodilittorina (*Nodilittorina*) *ziczac* (Gmelin, 1791)

(Figures 5, 6, 14, 15, 18, 19, 45)

- *Trochus ziczac* Chemnitz, 1781: plt. 166, figs. 1599a-b (here reproduced Figure 45) ("Sugar Islands" in the West Indies; rejected work, not binomial).
- * *Trochus ziczac* Gmelin, 1791: 3587, no. 122 (Type locality des. BEQUAERT, 1943): Barbados. Types probably lost; lectotype (herein): original of Chemnitz, 1781, plt. 166, fig. 1599b).
- * *Littorina zigzag* "Chemnitz" Orbigny in RAMON DE LA SAGRA, 1842: 210-, plt. 15, figs. 5, 8 (emendation of *ziczac* Gmelin, 1791) (here Figure 18).
- * *Littorina debilis* Philippi, 1846: 140 (no locality given; lectotype herein: BMNH 1968.222, here Figure 19). PHILIPPI, 1847: 47, plt. *Littorina* 6, fig. 7. REEVE, 1857: no. 70, plt. 14, fig. 70. KÜSTER, 1856: 22-, plt. 3, figs. 9-11.
- * *Littorina d'Orbignyana* Philippi, 1847: 162, plt. *Littorina* 3, fig. 12 (includes *zigzag* Orbigny, 1842; therefore Orbigny's original, BMNH 1854.10.4.130, is hereby designated lectotype, Figure 18 herein; type locality: Martinique).
- *Littorina ziczac*, PHILIPPI, 1847: 162-, plt. *Littorina* 3, figs. 13-14. KÜSTER, 1856: 22-, plt. 3, figs. 6-8. WEINKAUFF, 1882: 32 (part).
- *Littorina ziczac*, REEVE, 1857: no. 57, plt. 11, fig. 57. ABBOTT 1954b: 132, plt. 19, fig. E. ?LEWIS, 1960: 415- (part), figs. 11G, H (spawn). ABBOTT, 1968: 82, ?fig. 81 (penis, spawn), fig. 83.3 (shell). KAUFMANN & GÖTTING, 1970: 348-; fig. 34. BORKOWSKI & BORKOWSKI, 1969: 408-413; fig. 4c (spawn), plt. 66, figs. 5-6 (shell). BORKOWSKI 1971: 827-836, fig. 2 (spawn). BANDEL, 1974: 93-113, figs. 8 (shell); 15A-B, 17 (spawn), 18-21, 45-46 (radula). FLORES, 1973a: 13-, plt. 2, figs. 1-5. BORKOWSKI, 1975: 369-376; fig. 1C (radula). BANDEL, 1975: 15; plt. 1, figs. 1-3 (embryonic shell).
- * *Littorina* (*Melaraphe*) *zic-zac* "Chemnitz" Mörch, 1876: 137-, no. 321 (emendation of *ziczac* Gmelin, 1791).
- *Littorina* (*Melaraphe*) *ziczac*, TRYON, 1887: 251 (part), plt. 45, fig. 5 (copy REEVE, 1857).
- *Littorina* (*Melaraphe*) *ziczac*, MARTENS, 1900: 577, 583 (part). BEQUAERT, 1943: 14-18; plt. 5, figs. 1-4 (part, most synonyms and remaining figures to be excluded). ABBOTT, 1954a: 450: ?fig. 55j (penis), fig. 55k (spawn) (part: all spirally sculptured Caribbean species included here). ABBOTT, 1964: 65 (part).
- * *Littorina zigzac*, LEBOUR, 1945: 465; figs. 5a-d (spawn, veliger) (emendation of *ziczac* Gmelin, 1791).
- *Littorina* (*Littorina*) *ziczac*, ROSEWATER, 1970: 423. ABBOTT, 1974: 68; fig. 556.

Description: Shell ovate-conical, 15-20 mm long, with slightly convex, regularly increasing whorls, the last bluntly angular at the periphery; no umbilicus. Embryonic shell: one planispiral whorl, with finely granulose sculpture and growth lines; diameter 0.15 mm; aperture slightly

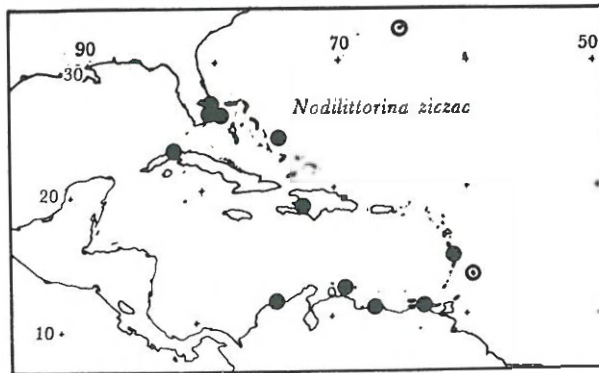


Figure 6

Distribution of *Nodilittorina (N.) ziczac* (Gmelin, 1791)

higher than wide. Larval shell not observed. **Teleoconch:** sculpture commences with 5-6 visible, incised spiral lines separated by flattened ridges; after approximately 2 whorls the number doubles; later more spirals may intercalate, bringing the number of spirals above the suture up to 15-20. Umbilical side with similar, but more closely spaced spirals. Blunt angle at the periphery made up by thickening of the shell wall. **Colour** at first brown, then gradually becoming whitish with thin axial and ziczac markings always at angles to the growth lines; interior of shell brown except a light band around the umbilicus and another, less sharply defined one near the suture; exterior pigmentation may be largely reduced, producing a nearly white shell. **Aperture** ovate, angulate adapically; columellar edge moderately broad, slightly concave, more or less brown, adapically thickening, smoothing the transition to the parietal wall by a callus with a straight interior edge. Parietal wall with thin brown shell layer. Outer lip simple. External shell surface adjacent to columella not redis-

solved. Operculum horny, brown, paucispiral, last whorl broader than half of operculum length.

Radula: basic *Nodilittorina* type (Figure 18, also BANDEL, 1974).

Spawn: LEBOUR, 1945; ?LEWIS, 1960 (figs. 11G-H only, however slightly different from the figures of other authors); BORKOWSKI & BORKOWSKI, 1969; BORKOWSKI, 1971; BANDEL, 1974; see Figure 5.

Penis: ABBOTT (1954a) figured a penis of "*Littorina ziczac*" from the Bahamas. As at that time all spirally sculptured *Nodilittorina* species were united under the name of *ziczac*, this might be a penis of *N. angustior* or *N. mordax* as well.

Types: Gmelin's *Trochus ziczac* was founded on figures and description of Chemnitz only. Dr. Knudsen (København) kindly informed us that Chemnitz had three collections at his disposal: his own, Spengler's and that of Count Moltke. The two last-named are in the Universitets Zoologiske Museum of København, but the location of his own is not known. Chemnitz stated his specimens to be present in his collection, a fact being consistent with Dr. Knudsen's statement that there is no material in København. As the species is easily recognizable in Chemnitz' figures (here refigured), the designation of fig. 1599b (Figure 45) to represent the lectotype is considered to be sufficient to stabilise nomenclature.

Philippi's *Littorina debilis* proved to be a half-grown specimen of *Nodilittorina ziczac* with a reduced colour pattern. The hereby designated lectotype had parts of the radula preserved.

In 1847 Philippi distinguished a more distinctly sculptured *Littorina d'Orbignyana* and a "true" *L. ziczac* with reduced sculpture and more pronounced axial colour lines. Such differences are often encountered in populations and are of intraspecific rank; the radula exhibits no differences. Philippi's types may be in Berlin (East), but as he included

Explanation of Figures 30 to 36

Nodilittorina (N.) riisei (Mörch, 1876)

Figure 30: Cuba. ZMK. Lectotype. Shell: 9.6×7.0 mm. Radula: × 680 FN 1394/43

Figure 31: Cuba. SME. Shell: 7.5×5.6 mm, Radula: × 370 FN 1615/1

Nodilittorina (N.) glaucocincta (Mörch, 1876)

Figure 32: Lesser Antilles, St. Jean. ZMK. Holotype of *Littorina (Melaraphe) floccosa* var. *glaucocincta* Mörch, 1876. Shell: 13.1×8.4 mm, Radula: a) × 350 FN 1382/19

b) (inner and outer marginal teeth) × 570 FN 1382/20

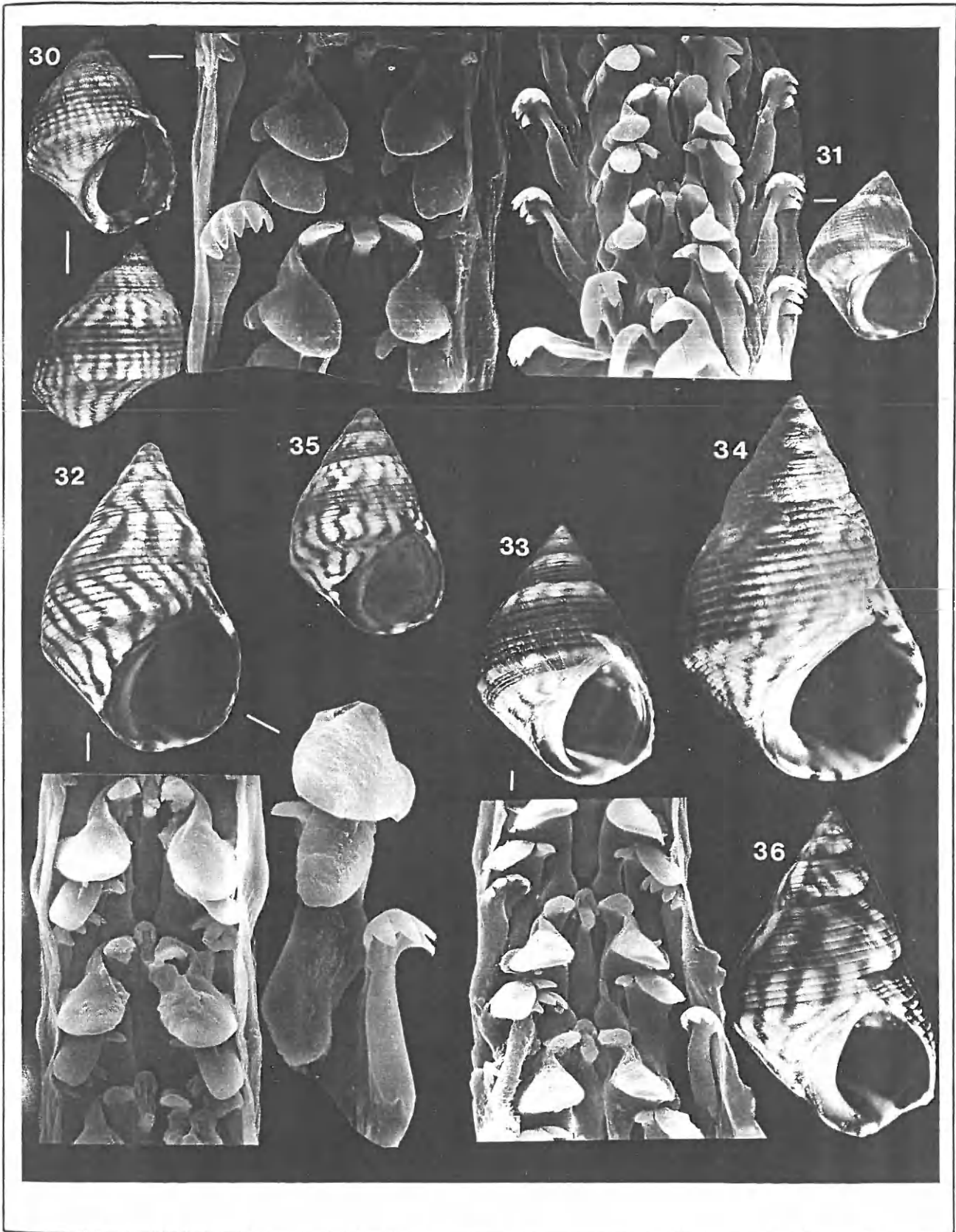
Figure 33: Jamaica. MCZ 156162. Paratype of *Littorina jamaicensis* C. B. Adams, 1850. Shell: 11.5×7.4 mm, Radula: × 370 FN 1599/4

Doubtful species, possibly *Nodilittorina glaucocincta* (Mörch, 1876)

Figure 34: Jamaica. MCZ 186133. Lectotype of *Littorina jamaicensis* C. B. Adams, 1850. 16.9×10.6 mm

Figure 35: Antilles. ZMK, labelled "*Littorina glaucocincta* Beck." 10.1×6.8 mm (compare Figure 32)

Figure 36: Martinique. BMNH 1854.10.4.139. Lectotype of *Littorina (Melaraphe) angustior* var. *fasciata* Mörch, 1876; original of ORBIGNY, 1842, pl. 14, fig. 25. Shell: 14.3×8.7 mm



the "zigzag" of Orbigny, 1842, in his *L. d'Orbignyana*, this original specimen was the only available one and is designated to be the lectotype of *L. orbignyana* Philippi, 1847.

Relationships. *Nodilittorina lineolata* and *N. interrupta* are closely allied, but differ in the slightly lower number of more pronounced spirals, a more pronounced angulation at the periphery; the egg capsule of both *N. interrupta* and *N. lineolata* has four spiral ridges instead of 5. *Nodilittorina lineolata* also is smaller, more slender; both species have more intensive colour markings and the tendency towards a dark brown median zone on the whorls. *Nodilittorina ziczac* and *N. interrupta* are sympatric in the Southern Caribbean, where *N. interrupta* inhabits a higher supratidal zone than *N. ziczac*; *N. lineolata* is geographically separated from both *N. ziczac* and *N. interrupta* and could be regarded as a geographical race of, preferably, *N. interrupta*.

Range. Bermuda, Florida, all Caribbean islands, Colombia, Venezuela; occurrence on the coast of Middle America mainland probable, but no material available.

Material examined. Bermuda (Lebour, 1945, (spawn); BMNH (shells)). Florida: Miami; Boca Raton; Key Biscayne (no radula). Bahamas: S. Bimini; San Salvador (USNM 749794 through 749797). Cuba (SMF). Hispaniola: Port-au-Prince, Cacique Island (USNM 749798). Antilles: Martinique (lectotype of *L. d'orbignyana* Philippi, 1847, BMNH 1854.10.4.130); Barbados (type locality, no material seen) untypical spawn figures by Lewis, 1960, fig. 11G-H; Curaçao, Cornelisbaai (USNM 749799). Colombia: Santa Marta (USNM 749800, 749801). Venezuela: La Guaira (RMNHL); Carupano (SMF 209798). No locality: SMF 196010 (coll. Helm, 1817, with preserved radula); lectotype *L. debilis* (BMNH 1968.222).

Nodilittorina (Nodilittorina) lineolata (Orbigny, 1840)

(Figures 1A, 3A, 5, 7, 20-22)

- * *Littorina lineolata* Orbigny, 1840: 392. (Port of Rio de Janeiro; lectotype BMNH 1854.12.4.363, Figure 20 herein) (part, synonyms excluded).
- * *Littorina lineata* ORBIGNY, 1842: 208; no. 120 (part, excl. figs. and synonyms). BORKOWSKI, 1975: 369, 371 (part, only synonym "brazilensis" = misspelling for *brasilensis* Vermeij & Porter, 1971) (not *Phasianella lineata* Lamarck, 1822).
- * *Littorina pusilla* Philippi, 1847: 164; plt. *Littorina* 3, fig. 23 ("Brasilia or Sandwich Islands" type locality restricted to Brasilia herein; types not available, might be in Berlin (East)) (not *Littorina pusilla* M'Coy, 1844: 32, pl. 5 fig. 26). KÜSTER, 1856: 11; plt. I, figs. 20-22.
- * *Littorina (Melaraphe) lineolata*, MÖRCH, 1876: 138, no. 323.
- * *Littorina (Melaraphe) pusilla*, MÖRCH, 1876: 140, no. 328. TRYON, 1887: 251; plt. 45, fig. 8 (copy KÜSTER, 1856).
- * *Littorina (Melaraphe) sp.n (or pusilla var.?)*, MÖRCH, 1876: 140, no. 329.
- * *Littorina (Melaraphe) ziczac*, BFQUAERT, 1943: 15, 17 (part, figs. excl.). MATTHEWS, 1968: 184, fig. 1. RIOS, 1970: 33 (not *Trochus ziczac* Gmelin, 1791).

- *Littorina ziczac*, MARCUS & MARCUS, 1963: 7-33, figs. 1 (shell), 3 (radula), 9 (osphradium), 15-16 (penis), 24-25 (female genitalia), 28-29 (spawn), 30 (young shell).
- * *Littorina ziczac brasiliensis* Vermeij & Porter, 1971: 448 (new name for *Littorina pusilla* Philippi, 1847, not M'Coy, 1844). Vermeij, 1973: 324.

Description: Shell ovate conical, about 10mm long, with slightly convex, regularly increasing whorls, the last angular at the periphery; no umbilicus. Apex very often heavily corroded by algae.

Teleoconch: Sculpture commences with 7 visible incised spiral lines separated by flattened ridges; this number may double later. Umbilical side with similar, but more closely spaced spirals. Angle at the periphery of variable strength, made up by thickening of the shell. Colour at apex brown, then gradually becoming whitish with axial and, in large specimens, ziczac markings always at angles to the growth lines; a conspicuous dark brown median band is rarely seen on the whorls; shell interior dark brown with a light band on the umbilical side and occasionally (in about half of specimens) a second, less distinct light band near the suture. Aperture ovate, angled adapically; columellar margin broad, very slightly concave, dark brown, adapically thickening, smoothing the transition to the parietal wall by a callus with straight interior edge. Parietal wall with brown shell layer. Outer lip simple. External shell surface adjacent to columella sometimes slightly redissolved.

Operculum: horny, paucispiral, width of its last whorl more than half of the remainder of the operculum.

Radula: is of the basic *Nodilittorina* type, with the transition from the posterior portion of the basal platform of the central tooth to its anterior portion angulate.

Spawn: (MARCUS & MARCUS, 1963) a cupola-shaped capsule with one egg, one side flat, opposite side convex with 4 spiral ridges, separated from flat side by a steep-sloped smooth zone.

Relationships: *Nodilittorina ziczac* is larger than *N. lineolata*, its spiral sculpture is weaker and commences with 5-6 spirals which may double twice; always two light bands in the interior; egg capsule with 5 ridges. *N. interrupta* is also larger, but always has a conspicuous dark brown median zone on whorls and two light interior bands, and shells of equal size are generally broader in *N. interrupta*. *N. interrupta* and *N. lineolata* are probably most closely related, but they are geographically widely separated. The shell of *N. angustior* may be very similar to *N. lineolata*, but this is regarded as homoeomorphous as both species are sufficiently distinguished by their spawn and operculum characteristics to be regarded as not closely related.

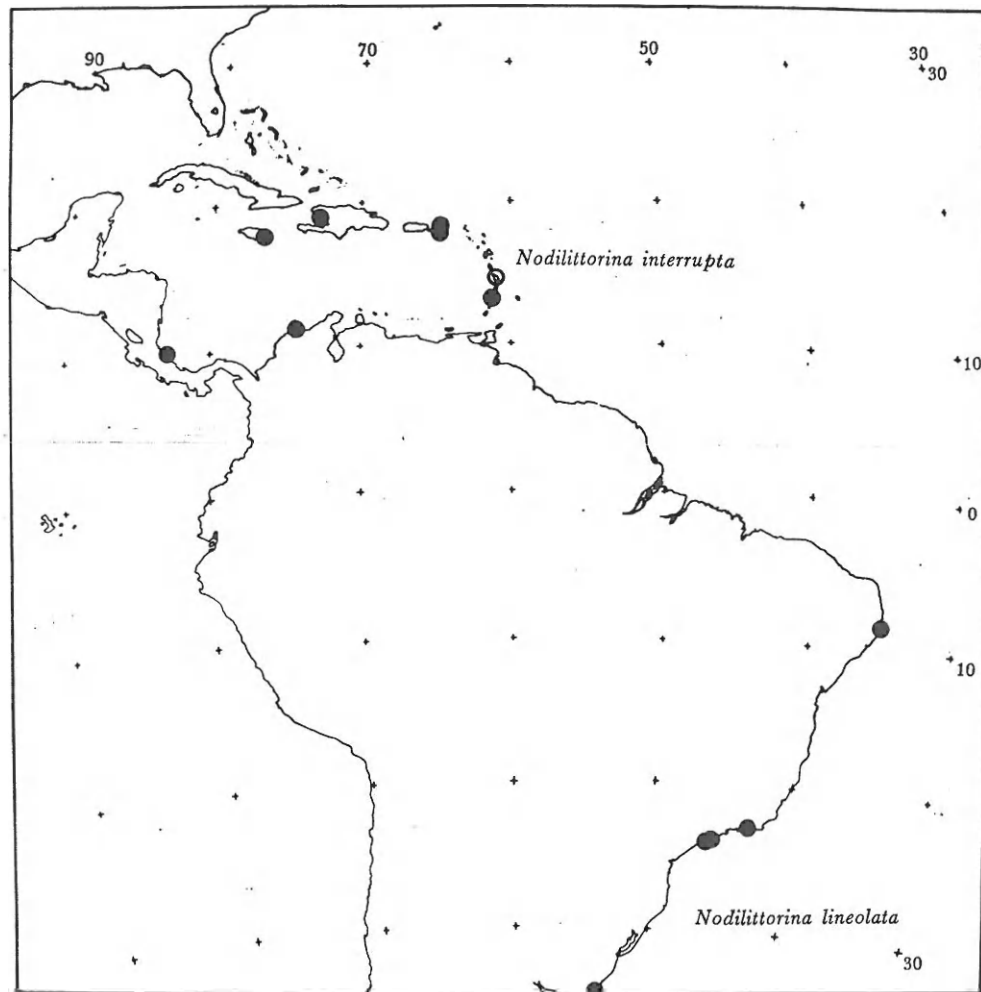


Figure 7

Distribution of *Nodilittorina (N.) lineolata* (Orbigny, 1840) and *N. (N.) interrupta* (C. B. Adams in Philippi, 1947)

Nomenclature. In recent years, the name *lineolata* Orbigny has been applied to a mixture of species encompassing *Nodilittorina interrupta*, *N. glaucocincta*, *N. riisei* and *N. mordax*. However, from Orbigny's original diagnosis it is obvious that he considered *lineolata* to be a mere variety of "*Littorina lineata* Lamarck" (= *N. angustior* according to his 1842 figures, but probably *N. interrupta* of his intention), demonstrating that he did not confuse the names *lineata* and *lineolata*:

"Cette espèce, que nous considérons comme une variété de la *Littorina lineata* des Antilles, est beaucoup plus petite. Avec les mêmes couleurs, elle est quelquefois moins anguleuse, mais ne nous paraît pas en différer spécifiquement."

The 1840 publication of Orbigny is considered to be the original publication of the name *Littorina lineolata*, although the author cited another publication of the name *lineolata*

in a paper entitled "Mollusques des Antilles." No work with such a title has been published; and as the numbers allocated to *Littorina lineolata* and to *L. columellaris* in the synonymy citations of 1840 are the same as published for *L. lineata* and *L. columellaris* in 1842, it is assumed that "Mollusques des Antilles" is a manuscript title subsequently dropped when the actual manuscript was published in Ramon de la Sagra's account of the Isle of Cuba (ORBIGNY, 1842).

By its type locality and by its preserved type specimens the identification of this species is beyond doubt. Orbigny himself, in a later study (1842) contributed further to the confusion about *Nodilittorina lineolata*, in that he included his *lineolata* in "*Littorina lineata*," even citing it as "*lineata*." Since 1847, the name *pustilla* Philippi, 1847 came into more frequent use; it was proposed for individuals with a heavily corroded spire. Although it is preoccupied, the substitution name *brasiliensis* Vermeij & Porter, 1971 is unnecessary as the name *lineolata* is without doubt available for the Brazilian species. BEQUAERT (1943: 17) selected "Barbados," one of the two so-called "Sugar Islands" cited in Chemnitz' references as type locality for both *N. ziczac* and *N. lineolata*; this selection is rejected for *N. lineolata* because it is based on Orbigny's reference to CHEMNITZ (1781: pl. 166, figs. 1600a-b (refigured Figure 45 herein)) only, which is not conspecific with the material Orbigny actually described; the selection of a lectotype (herein) supersedes this and any possible other restriction of the use of the name *lineolata* (Art. 74 a(ii) IRZN).

Distribution. South America: Brazil and Uruguay.

Material studies. Brazil: Desterro (SMF, no radula), Pernambuco (BMNH), São Vicente near Santos (USNM 749802); Prov. Rio de Janeiro, Prainha (IRSNB); Rio de Janeiro (Lectotype, BMNH 1854.12.4.363; SMF), Sao Paulo (SMF, no radula). Uruguay: Cabo Polonio, Rocha (SMF).

Nodilittorina (Nodilittorina) interrupta

(C. B. Adams in Philippi, 1847)

(Figures 5, 7, 16, 17, 23-26)

- *Phasianella lineata* Lamarck, 1822: 54 (Antilles; part, not the lectotype which is *Littoraria tessellata* (Philippi, 1847); 3 paratypes in MHNG 1096/87/2-4, Figure 23 herein) (not *Buccinum lineatum* Gmelin, 1791, which is *Littoraria (Littorinopsis) scabra* (Linnaeus, 1758)).
- *Littorina marnat* Potiez & Michaud, 1838: 279 (part); pl. 28, figs. 9-10 (St. Thomas; synonymy excluded is *N. punctata* (Gmelin, 1791): lectotype hereby designated: original of *Trochus marnat* Adanson, 1757 (pl. 12, fig. 1) = holotype of *Trochus punctatus* Gmelin, 1791, refigured by FISCHER-PIETTE, 1942: pl. 10, figs. 2a-b, from Senegal).

- *Littorina lineata*, ORBIGNY, 1842: 208 (part, excl. figs.)
- *Littorina lineata*, PHILIPPI, 1847: 163-; pl. *Littorina* 3, fig. 18. KÜSTER, 1856: 23-; pl. 3, figs. 12-13.
- * *Littorina ziczac* var. *interrupta* C. B. Adams in PHILIPPI, 1847: 164 (sub *Littorina lineata*) (no locality given; material in the C. B. Adams collection from Jamaica, MCZ 186124, here Figure 24).
- * *Littorina jamaicensis* C. B. Adams, 1850: 71 (lectotype design. by CLENCH & TURNER, 1950: 296-, 380; pl. 38, fig. 19, herein refigured Figure 34; *nomen dubium* due to lack of radula; paratypes are *N. interrupta* (Figure 24) and *N. glaucocincta* (Figure 33)).
- *Littorina lineata* var. *interrupta*, KÜSTER, 1856: 24; pl. 3, figs. 14-15.
- * *Littorina (Melaraphe) floccosa* MÖRCH, 1876: 138, no. 322 (Lesser Antilles, St. Thomas; lectotype ZMK, Figure 25 herein).
- * *Littorina (Melaraphe) angustior* var. *fasciata* MÖRCH, 1876: 139, no. 324a (refers to *Littorina lineata* Orbigny, 1842: pl. 14, fig. 25; Martinique; holotype, BMNH 1854.10.4.139, herein Figure 36. Species identification doubtful due to lack of radula, thus *nomen dubium*; not *Littorina fasciata* Gray, 1839).
- *Littorina lineata* var. *interrupta*, CLENCH & TURNER, 1950: 294, 380; pl. 38, fig. 18 (invalid paratype designation, fig. 18, MCZ 186 123; invalid lectotype designation, p. 294).
- *Littorina lineolata*, KAUFMANN & GÖTTING, 1970: 349; fig. 35 (not of Orbigny, 1840).
- *Littorina* sp. BANDEL, 1974: 93-113; figs. 9 (shell), 16A, 17 (spawn), 18-21, 46-47 (radula). BANDEL, 1975: 14-, pl. 1, figs. 4-6 (embryonic shell).

Description. Shell elongate ovate-conical, about 15mm long; whorls slightly convex, slowly and regularly increasing, the last bluntly angular at the periphery; no umbilicus. Embryonic shell: one whorl, planispiral, finely granulated, with growth lines; shell diameter 0.13mm; aperture slightly higher than wide, its margin with shallow sinuses at their sides. Larval shell 2.5 whorls sculptured with approx. 7 spirally arranged rows of granules mostly fusing to ziczac ridges; growth lines present and a terminal varix with a deep adapical sinus (Figures 16, 17).

Teleoconch: Earliest sculpture not preserved; on later whorls sculpture consists of 10 incised spiral lines above the suture, separated by flattened ridges; three more spirals below suture; only on last whorl spirals may double and simultaneously become obsolete; umbilical side with similar, but more closely spaced spirals. Blunt angle at the periphery made up by thickening of the shell. Colour of apex brown; a broad brown median zone on the visible parts of the whorls and another narrow brown zone abapical to the peripheral angle persist throughout growth; width and intensity of these zones vary, they may be less intense than axial and ziczac markings being at angle with the growth lines. Interior brown but for narrow light bands near the suture, on the umbilical side and at the peripheral angle, the latter being the least distinct and most narrow

one. Aperture ovate, angled adapically; columellar edge broad, very slightly concave, more or less brown, adapically thickening, smoothing the transition to the parietal wall by a callus with straight interior edge. Parietal wall with light brownish shell layer. Outer lip simple. External shell surface adjacent to columella sometimes very slightly redissolved. Operculum horny, paucispiral, last whorl broader than half of operculum length.

Radula: Basic *Nodilittorina* type; central tooth slightly narrowed, the sides of the basal platform are rounded.

Spawn (BANDEL, 1974): Cupola-shaped egg capsule with four ridges on top of the convex side and smooth, slightly concave steep-sloped flank.

Relationships: *Nodilittorina ziczac* differs in size, sculpture, and colour pattern, and the central tooth of the radula has a broader basal platform with strongly convex lateral edges. *N. lineolata* has sometimes a similar colour pattern, but is also different in size, sculpture, details of the central tooth and also in the operculum. *Nodilittorina glaucocincta*, also living in Jamaica, and its allies *N. riisei* and *N. mordax* usually have broader shells with a larger aperture, stronger spiral sculpture and without the adapical light-coloured interior band. However there may be shell varieties which are more slender, less intensely sculptured and showing a weak adapical interior band; these shells cannot be distinguished from some individuals of *N. interrupta* with an equally strongly sculptured shell (e.g., Figure 26) without studying the radula and the spawn. The radula of *N. interrupta* is similar only to the one of *N. riisei*, but the egg capsules are very different.

Nomenclature: *Phasianella lineata* Lamarck: The type sample is composed of this species and *Littoraria tessellata* (Philippi, 1847); BEQUAERT (1943: 13) selected the only

individual belonging to the latter species to be the lectotype. For fuller discussion see appendix.

Littorina marnat Potiez & Michaud: The figured specimen, said to be from St. Thomas, can be determined as *N. interrupta* because additional material from this locality, constituting the lectotype and paratypes of *floccosa* Mörch, 1876, proved the specific identity with *N. interrupta*. The species name of Potiez & Michaud, being that of Adanson, 1757, for the West African form known as *N. punctata* (Gmelin, 1791), is taken as an indication of the authors' intent as to which populations they considered to be typical of their nominal species, and the lectotype is designated accordingly.

Littorina interrupta: PHILIPPI (1847) mentioned and defined the specific name "*interrupta* C. B. Adams" the first time; however, he considered this a colour variety of his "*Littorina lineata*" not worthy of a name even on the variety level; i.e., the name *interrupta* is published as a synonym here. Subsequently the name has been accepted for a taxon only once (KÜSTER, 1856), but this should satisfy the requirements of availability of names published primarily in synonymy (Art. 11 (d), IRZN). In case this interpretation should be rejected, the species dealt with here would retain the specific name "*interrupta*," but the authorship had to be credited to KÜSTER, 1856. As Philippi himself did not intend to publish this name validly, he should not be cited as the author, but C. B. Adams instead.

The type of the nominal species "*interrupta*" has to be selected from the published specimens; i.e., from those Philippi had at hand; thus the selection of paratypes from the C. B. Adams collection (Museum of Comparative Zoology, Cambridge, Mass.) and of the figs. 14-15 of pl. 3 of KÜSTER (1856) as lectotype is invalid. Also the citation of the name as of "Philippi, 1856" is incorrect. Nevertheless, the specimens of the C. B. Adams collection, exhibit-

Explanation of Figures 37 to 41

Nodilittorina (N.) mordax Bandel & Kadolsky, spec. nov.

Figure 37: Bahamas, Nassau, Paradise Island, Holotype. USNM 749813. Shell: 11.8×8.9mm, Radula: × 410 FN 931/1

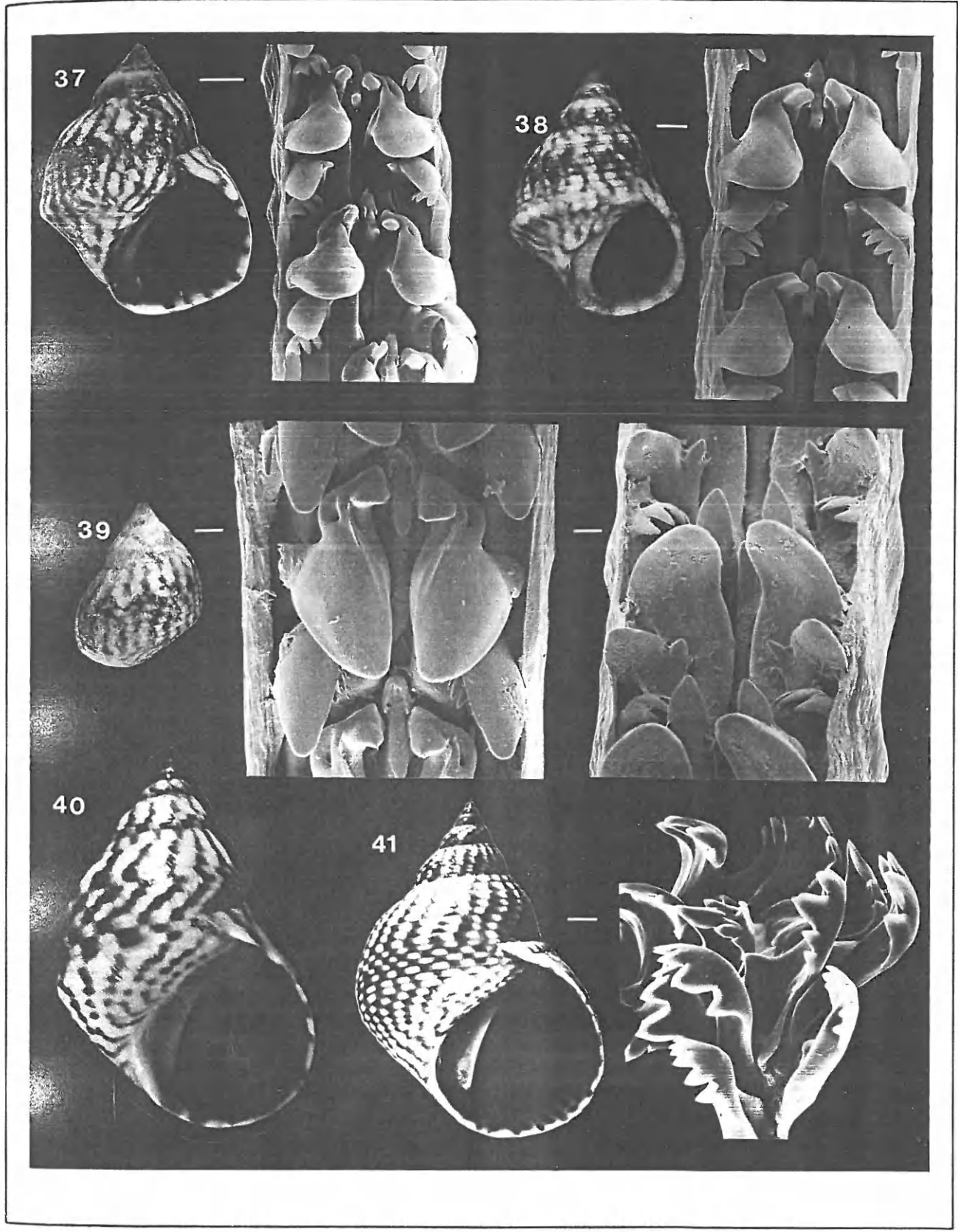
Figure 38: Curaçao, Cornelisbaai. Paratype. USNM 749816. Shell: 10.9×7.6mm, Radula (figured by Bandel, 1974 (figs. 50-51, as *jamaicensis*)) × 290 FN 1903/19

Figure 39: S. Bimini, Sunshine Inn. Paratype. USNM 749815. Shell: 7.6×5.6mm, Radula: a) × 710 FN 1427/13
b) × 710 FN 1427/15

Littoraria tessellata (Philippi, 1847)

Figure 40: Antilles. MHNG 1096/87/1. Lectotype of *Phasianella lineata* Lamarck, 1822. and of *Littoraria tessellata* Philippi, 1847. Shell: 16.6×11.0mm. Paratype figure see Figure 23

Figure 41: Haiti, Port-au-Prince, Cacique Isl., Ibo Beach. USNM 749825. Shell: 14.9×10.5mm, Radula: × 440



ing the colour variety described by PHILIPPI (1847) (see Figure 24), were very useful to identify the name "*interrupta*."

Littorina jamaicensis C. B. Adams, 1850, has to be considered as a doubtful name, as the lectotype, designated by CLENCH & TURNER, 1950, no longer contained the radula. Paratypes proved to be *N. interrupta* and *N. glaucocincta*, which can securely only be separated by their radula (and probably spawn) properties. The lectotype is a slender shell with a small aperture and strong spiral sculpture; the two first-named characters are more typical for *N. interrupta*, while the latter occurs more frequently in *N. glaucocincta*.

Distribution: Southern Caribbean Sea, from Jamaica and Hispaniola to Columbia.

Material examined. Jamaica (paratypes of *L. jamaicensis* C. B. Adams, 1850, MCZ 186123, 186124; other material, SMF); Hispaniola, Haiti, St. Marc (SMF). Lesser Antilles: St. Thomas (lectotype and 50 paratypes of *L. floccosa* MÖRCH, 1876, ZMK); St. Vincent (BMNH); St. Croix (1 paratype of *floccosa*, ZMK). Costa Rica: Limón (SMF). Columbia: Santa Marta (USNM 749803). Locality unknown: 3 paratypes of *Phasianella lineata* Lamarck, 1822, MHNG 1096/87/2-4. **Doubtful material** (no radula): Martinique (lectotype of *Littorina angustior fuscata* Mörch, 1876, (BMNH 1854.10.4.139).

Nodilittorina (Nodilittorina) angustior

(Mörch, 1876)

(Figures 5, 8, 27-29)

- *Littorina lineata*, ORBIGNY, 1842: 208; pl. 14, figs. 24, 26, 27 (not fig. 25, not *Phasianella lineata* Lamarck, 1822). BORKOWSKI & BORKOWSKI, 1969: 409-414; fig. 4B (spawn), pl. 66, figs. 1-2 (shell). BORKOWSKI, 1971: 827-836; fig. 2 (spawn). FLORES, 1973: 14-; pl. 2, figs. 6-10. BORKOWSKI, 1975: 369-376; fig. 1A (radula).
- * *Littorina carinata* Orbigny, 1842: 209; pl. 15, figs. 1-4 (Cuba; lectotype (BMNH 1854.10.4.128, here Figure 28) (not *Delphinula carinata* Woodward, 1833 nor *Turbo carinatus* Woodward, 1833, which are both forms of *Littorina litorea* (Linnaeus, 1758)). REEVE, 1857: no. 50, pl. 8, fig. 50.
- *Littorina carinata*, PHILIPPI, 1847: 163; pl. *Littorina* 3, fig. 19. KÜSTER, 1856: 19; pl. 2, figs. 28-29.
- * *Littorina (Melaraphe) angustior* MÖRCH, 1876: 139, no. 32 (type locality (hereby designated): Havana, Cuba; lectotype (hereby designated): MÖRCH collection, ZMK, here in Figure 27).
- *Littorina (Melaraphe) carinata*, MÖRCH, 1876: 139, no. 325.
- *Littorina ziczac*, WEINKAUFF, 1882: 32 (part, not figs.; not of Gmelin, 1791).
- *Littorina angustior*, WEINKAUFF, 1882: 67-, pl. 8, fig. 15 (paratype).
- *Littorina (Melaraphe) lineata*, MARTENS, 1900: 577, 583 (not of Lamarck, 1822).
- *Littorina (Melaraphe) ziczac*, BEQUAERT, 1943: 15; pl. 5, fig. 5 (part, not of Gmelin, 1791). WARMKE & ABBOTT, 1962: 52- (part), pl. 9, fig. 1.
- *Littorina lineolata*, ABBOTT, 1964: 65 (part, not of Orbigny, 1840). ABBOTT, 1968: 82; fig. 83.1. FLORES, 1973: 15-, pl. 2, figs. 11-15.

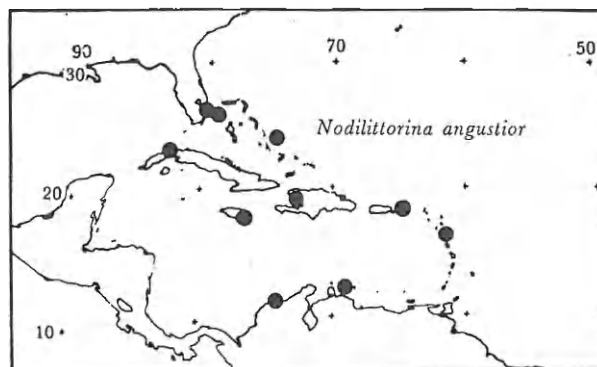


Figure 8

Distribution of *Nodilittorina (N.) angustior* (Mörch, 1876)

- *Littorina (Austrolittorina) lineata*, ROSEWATER, 1970: 423.
- *Littorina jamaicensis*, BANDEL, 1974: 95, 99, 103; figs. 10 (shell), 17 (spawn) (not the radula which is from *Nodilittorina mordax spec. nov.*; not *jamaicensis* C. B. ADAMS, 1850).
- *Littorina (Austrolittorina) angustior*, ABBOTT, 1974: 68-; fig. 560.

Description: Shell conical, about 10-15 mm long, with nearly straight but stepped contours of the whorls, the last angular to bluntly keeled at the periphery; no umbilicus.

Protoconch: About 3 whorls, brown, worn.

Teleconch: Sculpture consists of 6-7 incised spiral lines separated by flattened ridges; no or only sporadic intercalations of secondary spirals. Umbilical side with similar but weaker spirals. Angle or keel at periphery made up by shell material.

Colour: On early whorls a light zone at the adapical suture and a brown zone abapically of it; this brown zone mostly disappears during growth but may sometimes persist; oblique, closely spaced brown axial markings cover all whorls. Interior brown except two narrow bands near the suture and on the umbilical side; a third band at the peripheral angle is blurred, narrower and often obsolete.

Aperture: Small, ovate, angled adapically. Columellar edge broad, slightly concave, brown, passing without an angle to the parietal wall which is covered by a brown shell layer. Outer lip simple. Sometimes faint indications of redissolving of the external shell surface adjacent to the columellar margin.

Operculum: Horny, paucispiral, its last whorl narrower than its spiral part.

Radula: Of basic *Nodilittorina* type; in the central tooth the lateral edges are rounded at the transition from the posterior to the anterior portion of the basal platform.

Spawn (BORKOWSKI & BORKOWSKI, 1969; BORKOWSKI, 1971): Capsule cupola-shaped, with spiral ridges over the whole convex side down to the edge of the flat side.

Relationships: By its slender conical form, the relatively small aperture, the shape of the egg capsule and the narrowly coiled operculum, this species appears to be isolated amongst the Western Atlantic spirally sculptured species of *Nodilittorina*.

Nomenclature: Many authors credited the specific name "*lineata*" to Orbigny, 1842. However, Orbigny referred to *Phasianella lineata* Lamarck, 1822 which is not conspecific: the lectotype is *Littoraria tessellata* (Philippi, 1847) while the three paratypes belong to *Nodilittorina interrupta* (C. B. Adams in PHILIPPI, 1847). Possibly ORBIGNY (1842) considered his *Littorina lineata* to be *N. interrupta* but his figures show *N. angustior* and *N. cf. interrupta*, and his reference to Rio de Janeiro specimens includes *N. lineolata*.

The name "*carinata* Orbigny, 1842" was rejected by BEQUAERT (1943), BORKOWSKI & BORKOWSKI (1969) and others as a presumed homonym of *Turbo carinatus* J. Sowerby, 1819. As this species does not belong to the Littorinidae, it is neither a primary nor a secondary homonym of *Littorina carinata* Orbigny. However, two aberrant fossil varieties of *Littorina littorea* (Linnaeus), described by WOODWARD (1833) as *Delphinula carinata* and *Turbo carinatus*, make *L. carinata*, Orbigny, 1842 really after all a secondary junior homonym.

The distinction of "*lineata* Orb." (= *angustior* Mörch s. str.) and *carinata* Orb. is based on the existence of an angulate or keeled periphery, respectively. This character, however, is variable within the species. "*L. lineata*" was sometimes identified with *N. interrupta*, e.g., by PHILIPPI, 1847 and KÜSTER, 1856.

Range: The whole Caribbean Sea, as far south as Venezuela, as far north as Florida.

Material examined: Florida: Key Biscayne (no radula); Miami (USNM 749804); Boca Raton (749805); Bahamas: S. Bimini (749806); San Salvador (749807). Cuba: Lectotype and paratypes of *Littorina carinata* Orbigny, 1842, (BMNH 1854.10.4.128); Havana (lectotype and 1 paratype of *L. angustior* Mörch, 1876. ZMK); dto. (SMF). Jamaica (SMF). Hispaniola Haiti, St. Marc (SMF). Antilles: St. Thomas (ZMK: 6 paratypes of *L. angustior* Mörch, no radula); St. Thomas, near Buck Island (ZMK: 6 paratypes of *L. angustior* Mörch); St. Martin (ZMK: 5 paratypes of *L. angustior* Mörch, no radula); Guadeloupe, E. tip of Grande Terre, Pointe des Châteaux (749808); Curaçao, Cornelisbaai (749809). Colombia: Santa Marta ((749810).

Nodilittorina (Nodilittorina) riisei

(Mörch, 1876)

(Figures 5, 9, 30, 31)

- * *Littorina (Melaraphe) Riisei* Mörch, 1876: 140, no. 327 (Cuba; lectotype (hereby): ZMK, Fig. 30 herein).
- *Littorina lineolata*, BORKOWSKI & BORKOWSKI, 1969: 408-414; fig. 4A (spawn), pl. 66, figs. 3-4 (shell). BORKOWSKI, 1971: 826-840; figs. 1A, B (nurse cells), 2 (spawn). BANDEL, 1974: fig. 17 (spawn) (part). BORKOWSKI, 1975: 369-376; fig. 1B (radula). (Not *lineolata* Orbigny, 1840).

Description: Shell ovate-conical to conical-ovate, up to 17mm long, with slightly convex, regularly increasing whorls, the last bluntly keeled at the periphery.

Protoconch: Probably paucispiral, brown (only worn parts preserved).

Teleconch: Sculpture consists of 6 narrow spiral furrows separated by flattened elevated ridges; in large specimens this number may rise to 9 by intercalation of a few more furrows of equal size; further, small spiral ridges of second rank may show up in these furrows. Peripheral keel made up by thickening of the shell; umbilical side with numerous closely spaced incised spiral lines.

Colour: At first brown, then development of a light zone at the adapical suture; brown middle zone persists on all whorls in variable width and intensity; another narrow brown zone abapically of the peripheral keel. Interior dark brown except a narrow band on the umbilical side; near the suture a less intensely pigmented zone.

Aperture: Ovate, angled adapically; columellar margin broad, slightly concave, brown, passing without forming an angle into the parietal margin by a callus with straight interior margin; parietal wall with thin brown shell layer; outer lip simple. A small part of the external shell surface adjacent to the columellar margin is regularly redissolved.

Operculum: Horny, brown, paucispiral, width of last whorl larger than width of the spiral part.

Radula: Close to the basic *Nodilittorina* type, but central tooth fairly narrow, and outer marginal with 7 cusps only (instead of 8 as in many species).

Spawn: (BORKOWSKI & BORKOWSKI, 1969; BORKOWSKI, 1971): a high cupola-shaped capsule with spiral ridges on the convex side, and oblique striae on the steep and slightly concave sides.

Relationships: *Nodilittorina glaucocincta* and *N. mordax* have virtually identical shells and are only to be distinguished by their radula characters: in *N. mordax* the central tooth is much narrower than in *N. glaucocincta*, and the other teeth reduce their cusp numbers, while one cusp in the lateral and in the inner marginal tooth increases in size. *Nodilittorina interrupta*, *N. angustior* and *N. lineolata* may have similar colour patterns, but differ in other shell characters, including the presence of a second light-coloured band in the interior, as well as by their primitive radula and different egg capsules.

Range: Florida and Cuba.

Material examined: Florida: Miami (USNM 749811); Boca Raton (USNM 749812); Key Biscayne (B/K). Cuba (lectotype and 1 paratype, ZMK; other material, SMF).



Figure 9

Distribution of *Nodilittorina (N.) riisei* (Mörch, 1876), *glaucocincta* (Mörch, 1876) and *mordax* spec. nov. From Barbados (locality marked (1)) spawn similar to that of *N. riisei* was described (Lewis, 1960)

Nodilittorina (Nodilittorina) glaucocincta

(Mörch, 1876)

(Figures 5, 9, 32, 33)

- * *Littorina jamaicensis* C. B. Adams, 1850: 71 (Jamaica; lectotype S.D., by CIENCH & TURNER, 1950; 296-, 380; pl. 38, fig. 19; MCZ 186 133; of doubtful species identity due to lack of radula, refigured herein Figure 34; paratypes with radula partly conspecific with *L. glaucocincta* (Figure 33), and partly with *L. interrupta* (Figure 24). *Nomen dubium*).
- * *Littorina (Melaraphe) floccosa* var. a (*Littorina glaucocincta* Beck), MÖRCH, 1876; 138, no. 322a (St. Jean; holotype ZMK, Figure 32 herein).

Description: The shell is essentially the same as that described for *Nodilittorina riisei* and that of *N. mordax*. The radula is characterised by a very narrow central tooth, a lateral tooth with the second cusp (counted from the centre of the radula) enlarged, the inner marginal tooth with three cusps the central of which is enlarged, and the outer marginal with 6 cusps only.

Relationships: *Nodilittorina glaucocincta* can be distinguished from *N. riisei* and *N. mordax* by its radula characters only. A full discussion is given under *N. mordax*. The shell of *N. interrupta* usually is more slender, the spiral sculpture weaker and the apical light-coloured zone in the aperture is more pronounced, but some individuals may be indistinguishable by shell characters alone.

Remarks: Many literature references cannot be allocated with certainty to the synonymy lists of either *Nodilittorina riisei*, *N. glaucocincta*, *N. mordax* or *N. interrupta*, due to lack of data on the radula and spawn characters. Amongst them is the lectotype of *Littorina jamaicensis* C. B. Adams, 1850, while paratypes proved to belong to *N. interrupta* and to *N. glaucocincta*. Another one is the nominal taxon "*Littorina angustior fasciata* Mörch, 1876," which is tentatively included in *N. interrupta*, as the shell resembles this species slightly more than *N. glaucocincta*. LEWIS depicts an egg capsule from Barbados (1960: figs. 11E-E, as "*Littorina ziczac*") very similar to those of *N. riisei*. If the assumed close relationship between *N. riisei*, *N. glaucocincta* and *N. mordax* is correctly assumed, it might be the egg capsule of either *N. glaucocincta* or *N. mordax* whose proven distribution is closer to Barbados than that of *N. riisei*.

Types: The lectotype and paratypes of *Littorina jamaicensis* C. B. Adams are preserved in the C. B. Adams collection in the MCZ. The radula of a paratype could be examined.

The holotype of *Littorina floccosa glaucocincta* Mörch is kept in the Mörch collection in the ZMK; it still contained the radula. The type designation was somewhat difficult, as in the original publication Mörch named only one locality, St. Jean. In the collection, however, the only sample from St. Jean was labelled "*Littorina*..." while another sample without a proper locality ("*inter testas minutas ex Ins. Antill.*") was determined as "*Littorina glaucocincta* Beck."

The two samples contained rather similar shells (Figures 32 and 35). Probably the specimens without exact locality were the original "*Littorina glaucocincta*" of Beck, a manuscript name before Mörch, 1876, who identified with this the St. Jean specimen he had received from Unger. He probably failed to note this determination on the label, and he did not mention the Beck specimens because of their vague locality. As only the St. Jean specimen was

included in the original description, it becomes automatically the holotype.

Range: Jamaica; Virgin Islands.

Material examined: Jamaica (paratypes of *L. jamaicensis*, MCZ 186133). Virgin Islands. St. Jean (holotype of *glaucoincta*, ZMK). Doubtful material (no radula): "Antilles" (ZMK, labelled *Littorina glaucoincta* Beck). Jamaica (lectotype *L. jamaicensis*, MCZ 186133).

Nodilittorina (Nodilittorina) mordax

Bandel & Kadolsky, spec. nov.

(Figures 5, 9, 37-39)

- *Littorina jamaicensis*, BANDEL, 1974a: 95-108 (part); figs. 18-21, 50-51 (radula) (not the shell description and figure which is *N. angustior*; not *jamaicensis* C. B. Adams, 1850).
- *Littorina lineolata*, BANDEL, 1974a: 95-108; figs. 11 (shell), 36-38 (radula) (part, not *lineolata* Orbigny, 1840). BANDEL, 1974b: 13; fig. 6D (faeces).

Holotype: B/K (USNM 749813), Fig. 37 (shell, radula).

Paratypes: B/K (USNM 749814 through 749816).

Type locality: Bahamas, Nassau, Paradise Island; Bandel collected 1970.

Etymology: *mordax* (Lat.): biting, because of the large lateral teeth.

Diagnosis: A species of *Nodilittorina* with a spirally sculptured shell identical with those of *N. riisei* (Mörch, 1876) and *N. glaucoincta* (Mörch, 1876), but characterized by radula properties: The central tooth is so much reduced that it has lost its function; the third cusp of both the lateral and, to a lesser extent, the inner marginal tooth (counted from the centre of the radula) are extremely large, while the remaining cusps are very small, the marginal ones being obsolete or nearly so. This radula is very

similar to the one of *Nodilittorina tuberculata* (Menke, 1828), in which however, the outer marginal tooth has 7 cusps instead of 5-6 in *N. mordax*.

Description of the shell: Compare *Nodilittorina riisei* (Mörch, 1876); see also BANDEL, 1974, p. 99f, as "*Littorina lineolata*"; for the description of the radula see BANDEL, 1974 p. 108 (as "*L. jamaicensis*" from Curaçao and "*L. lineolata*" from Paradise Island, Bahamas). Operculum paucispiral, width of its last whorl larger than that of the spiral part.

Relationships: The indistinguishable shells found in *Nodilittorina riisei*, *N. glaucoincta* and *N. mordax* suggest very close relationships; i.e., evolution from a common ancestor probably by geographical separation, as these species are now allopatric. *N. interrupta* has very similar shell characters, but mostly a weaker sculpture and a second light-coloured band in the interior; the shape of the egg capsule and the radula demonstrate that this species is not particularly closely related to any species of the *N. glaucoincta* group. *N. tuberculata* has a radula very similar to that of *N. mordax*, but differs in every other character. Some radula properties of the species mentioned above may be compiled in Table 2:

Table 2

Radula characters of some *Nodilittorina* species.

	Length/width ratio	Cusp number of			
		Central tooth	Lateral tooth	Inner marginal	Outer marginal
<i>N. interrupta</i>	1.7 - 2.2		4	4	7 - 8
<i>N. riisei</i>	2.5 - 2.8		4 (5)	4	7
<i>N. glaucoincta</i>	3.7 - 5		4	4	6
<i>N. mordax</i>	7 - 8		3 - 4	2 - 3	5 - 6
<i>N. tuberculata</i>	6.9 - 7.5		3	3	7
<i>N. antoni</i>	(reduced)		1	1	3

Explanation of Figures 42 to 45

Nodilittorina (N.) dilatata (Orbigny, 1842)

Figure 42: Cuba, Havana. BMNH 1845.10.4.126. Lectotype. 13.9 × 10.7 mm

Figure 43: Bahamas, Nassau, Paradise Island. USNM. Radula figured by BANDEL, 1974 (figs. 48, 49)

Figure 44: Miami. USNM 749817. Shell: 13.1 × 9.4 mm, Radula: × 290 FN 1406/4

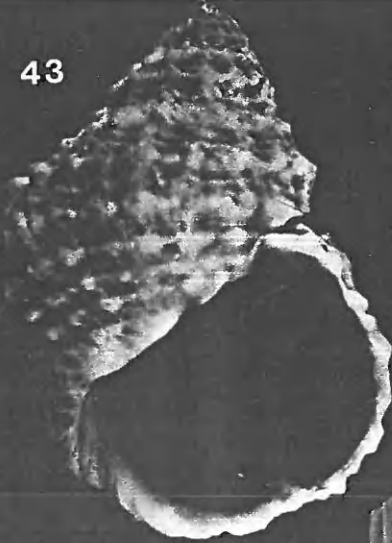
Figure 45: *Nodilittorina* species figured by CHEMNITZ, 1781. Plt. 166, figs. 1599 a, b: Lectotype figure of *Trochus ziczac* Gmelin, 1791 (= *Nodilittorina ziczac* (Gmelin, 1791)). Presumably from Barbados (BEQUAERT, 1943). Height of original figures: a) 16 mm, b) 15 mm. Plt. 166, figs. 1600 a, b: Individual cited in the original publication

of *Trochus ziczac* Gmelin, 1791 (var. β), *Phasianella lineata* Lamarck, 1822, and *Littorina lineolata* Orbigny, 1840. Presumably from Barbados (BEQUAERT, 1943); does not constitute a type figure; doubtful species identity, might be either *Nodilittorina interrupta* (C. B. Adams in Philippi, 1847), *N. jamaicensis* (C. B. Adams, 1850), *N. glaucoincta* (Mörch, 1876), *N. riisei* (Mörch, 1876) or *N. mordax* spec. nov. Height of original figures: a) 12 mm, b) 13 mm
Plt. 169, figs. 1545-1546: Lectotype figure of *Trochus nodulosus* Gmelin, 1791 (designated by CLENCH & ABBOTT, 1942: 3) from the Pacific. Height of original figure: 18 mm. The Caribbean "*Littorina*" *tuberculata* Menke, 1828, was established by comparison to this figure and accompanying description, being differentiated by its smaller size only

42



43



44



45



PI. 166 F. 1599



PI. 166 F. 1600



PI. 163 F. 1545 - 1546



Obviously, the radulae of *Nodilittorina riisei*, *N. glaucocincta* and *N. mordax* represent three stages of increasing modification of the basic *Nodilittorina*-type radula as exemplified by *N. interrupta*. The radula of *N. tuberculata* is indeed very similar to that of *N. mordax*, but a close relationship is highly improbable: it would imply that during the whole process of radula differentiation in the *N. glaucocincta* group the shell and operculum characters had remained constant, until the properties of *N. mordax* had developed, and then all of a sudden the shell and operculum characters turned into those of *N. tuberculata*. The egg capsule of *N. tuberculata* is also very different from that of *N. riisei*, while the egg capsules of *N. glaucocincta* and *N. mordax* are not yet known. Interestingly, the egg capsule of *N. antoni*, where the process of radula modification is most advanced, shows some resemblance to the one of *N. riisei*, particularly the oblique striations on the deep flank of the cupola. Shell and operculum of *N. antoni*, however, are extremely different from *N. riisei* or *N. mordax*. More anatomical data are required to trace possible relationships in more detail; it emerges already now that several properties, in particular the radular modifications towards a reduced central tooth and the remaining teeth having one very large cusp, have developed repeatedly in the West Atlantic. The subgenus *Echinolittorina* Habe, 1956, based only on the radula characters of *N. tuberculata*, is of no use in classification, as it would have to include *N. mordax*, a species certainly not closely related to *N. tuberculata*, but to *N. glaucocincta* and *N. riisei*. A subgenus *Echinolittorina* thus would have to comprise the two last-mentioned species, plus *N. mordax* and *N. tuberculata*; but no reasonable definition of a group so composed could be made.

Range: Bahamas and Curaçao.

Material examined: Bahamas: S. Bimini, Sunshine Inn (C. Edwards leg., USNM 749815) (3 paratypes); Nassau, Paradise Island (K. Bandel leg. 1970; USNM 749813-749814; holotype and 30 paratypes. Curaçao, Cornelisbaai (K. Bandel leg. 1971; USNM 749816; 22 paratypes).

Nodilittorina (Nodilittorina) dilatata

(Orbigny, 1842)

(Figures 5, 10, 42-44)

- * *Littorina dilatata* (ORBIGNY, 1842: 207; pl. 14, figs. 20-23 (type locality: Cuba, Havana; lectotype: BMNH 1854.10.4.126, fig. 42 herein). REEVE, 1857: no. 9, pl. 2, fig. 9.
- *Littorina dilatata*, PHILIPPI, 1846: 145; pl. *Littorina* 2, fig. 13.
- *Littorina (Tectarius) dilatata*, MÖRCH, 1876: 193, no. 312.
- *Littorina (Tectarius) dilatata*, WFINKAUFF, 1882: 47; pl. 5, figs. 17-19; pl. 12, figs. 1, 4.

- *Tectarius nodulosus*, TRYON, 1887: 258 (part); pl. 47, fig. 60 (copy REEVE, 1857), pl. 48, fig. 74 (copy ORBIGNY, 1842: fig. 21) (not of GMELIN, 1791).
- * *Echinella nodulosa* var. *matanzensis* RICHARDS, 1935: 257; pl. 25, figs. 26, 30, 31 (type locality: Cuba, Matanzas Province, 6.5 km NE Sabanilla in Matanzas Bay; stratum typicum: lowest marine terrace of Matanzas Bay, up to 7.6 m elevation, Quaternary; holotype: original of Richards' fig. 30, 13:11 mm, Carnegie Museum, Pittsburgh, Pennsylvania).
- *Tectarius (Nodilittorina) tuberculata* "Wood," CLENCH & ABBOTT, 1942: 2- (part), pl. 2, figs. 1-2 (not of Wood, 1828 nor of Menke, 1828).
- *Echinella trochiformis*, LÉBOUR, 1945: 466; fig. 7 (spawn, veliger) (not of Dillwyn, 1817).
- *Nodilittorina tuberculata*, ABBOTT, 1954a: 451- (part); figs. 551 (spawn, after LÉBOUR, 1945), 56a (distribution, partly). ABBOTT, 1954b: 194; pl. 19, fig. J. BORKOWSKI, 1971: 827-836; fig. 2 (spawn). BORKOWSKI, 1975: 369-376; fig. 2B (radula) (not *Littorina tuberculata* Menke, 1828).
- *Nodilittorina (Echinolittorina) tuberculata*, ABBOTT, 1974: 70 (part), fig. 570 (shell, operculum) (not of Menke, 1828).
- *Nodilittorina dilatata*, BANDEL, 1974: 95-113; figs. 12 (shell), 17 (spawn), 18-21, 48-49 (radula).
- *Nodilittorina (Granulilittorina) dilatata*, ROSEWATER, 1981: 33.

Description: Shell broadly conical, up to 18 mm long, with slightly convex, regularly increasing whorls; outline of shell controlled by nodose sculpture; sometimes a pseudumbilicus.

Protoconch: Probably paucispiral, light brown (worn parts only preserved). Diameter of embryonic shell 0.10-0.13 mm (LÉBOUR, 1945).

Teleoconch: Sculpture commences with three spiral rows of nodes; the adapical one is the smallest, the two other ones are of about equal strength, with a small part of the abapical one covered by the succeeding whorl. The entire surface is from an early stage on covered with subequal spiral threads (spiral elements of 2nd order); delicate spirals of 3rd order are preserved only on later whorls, where the spirals of 2nd order becomes nodulose; umbilical side with 2-3 smaller node rows, and spirals of 2nd and 3rd order as on the apical side; growth lines reduced in number and strength, the stronger ones squamose, but never prevailing over 3rd order spirals. Main nodes with more or less rhombic base, acute, often tending to channelled spines when their aperture-wards flank is not completely filled with shell material.

Colour: Brown pigment distributed throughout shell, lacking in nodes, 2nd order spirals and in the narrow band in the umbilical side; exterior appears bluish grey with white sculpture, interior brown.

Aperture: Roundish, angled adapically; columella margin very broad, brown, but in the abapical tip plane;

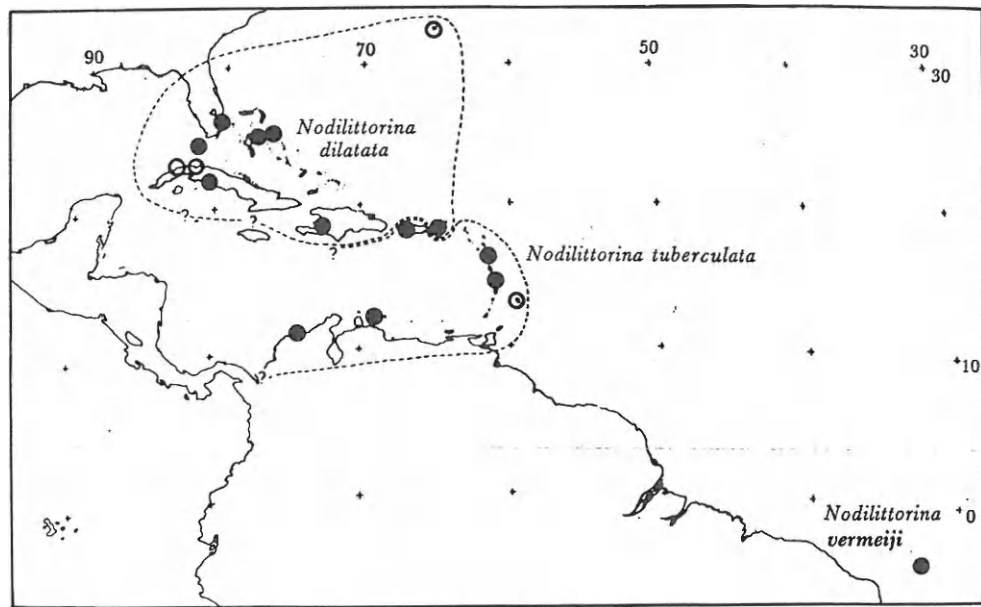


Figure 10

Distribution of *Nodilittorina* (*N.*) *dilatata* (Orbigny, 1842), *vermeiji* spec. nov., and *tuberculata* (Menke, 1828)

abapically concave, expanded, slightly recessed and protruded abapical-wards (this character intensifies with age); plane of columella margin receded against external shell surface, forming in adults a pseudumbilicus of variable size, sometimes very large and deep; columella margin passes into a thick brown parietal callus, both forming a single, gently curved arc. Outer lip simple, with channelled tips where nodes are accreted, as the accretion proceeds from the exterior to the interior. Shell surface adjacent to the pseudumbilicus sporadically redissolved, nodes of umbilical side adjacent to parietal wall regularly redissolved.

Operculum: Horny, paucispiral, width of last whorl less than half of operculum length.

Radula: Basic *Nodilittorina* type; central tooth narrow (see key p. 19).

The pelagic egg capsule is cupola-shaped, it bears five spiral ridges on its convex side and has a smooth zone adjacent to its flat side.

Synonymy: The form described by Orbigny is quite easily identified by its pseudumbilicus and its locality, which is remote from the area of the similar *Nodilittorina tuberculata*. Therefore, no uncertainty arises because of the lack of the radula of the lectotype.

The form named by RICHARDS (1935) is certainly conspecific as judged from the figures and the locality which is inside the established distribution area of *N. dilatata* and far away from that of other species; e.g., *N. tuberculata*. Richard's diagnosis, however, contradicts his figures; besides, it is not clear what he understood to be "*Echinella nodulosa*" (cited without author); 4 species can be hidden under this name:

- (1) *Nodilittorina* (*Nodilittorina*) *pyramidalis* (Quoy & Gaimard, 1833), synonymous with *Trochus nodulosus* Gmelin, 1791 (preoccupied by SOLANDER, 1766).
- (2) *Nodilittorina* (*Tectininus*) *antoni* (Philippi, 1846), misidentified by PFEIFFER (1839) as "*Littorina nodulosa*" of Gmelin, this misinterpreted subsequently to constitute the introduction of a new species "*Littorina nodulosa* L. Pfeiffer, 1839." For a detailed explanation of synonymy and nomenclature see below.
- (3) *Nodilittorina* (*Nodilittorina*) *tuberculata* (Menke, 1828), which was included in or confused with *N. nodulosa* (Gmelin) (= *N. pyramidalis*) by some authors (see synonymy below).
- (4) *Nodilittorina* (*Nodilittorina*) *dilatata* (Orbigny, 1842), as included in *N. tuberculata* and with this species in *N. pyramidalis*.

In each case, the "carinae" are not more pronounced, the remaining carinae not reduced, the lip is not "smaller" than that of any one of the 4 species, judging from Richard's figures.

Relationships: The shell is quite similar to that of *Nodilittorina tuberculata*; however, in *N. dilatata* the tubercles are often more acute, the shape is slightly broader, the last whorl larger, and the columella abapically more strongly dilated in adult specimens; in addition a pseudumbilicus encircled by a ledge may appear; the most important difference is found in the radula, while minor differences occur in spawn morphology, too. For discussion of other species see under *N. tuberculata*.

Range: From Bermuda and Florida in the North to the northern Lesser Antilles (St. Thomas) in the South.

Material examined: Bermuda (BMNH; spawn figured by LEBOUR, 1945). Florida: Miami (USNM 749817); Long Key, Key West (SMF 189493); Cuba: Havana (lectotype, BMNH 1854.10.4.126, shell only); Matanzas Bay, Quaternary (*Echinella nodulosa matanzensis* of RICHARDS, 1935); Cienfuegos (SMF 167803). Bahamas: Nassau, Paradise Islands (USNM 749818); Cat Isl., Arthur's Town (RMNHL). Hispaniola: Haiti (SMF). Jamaica (SMF). Lesser Antilles: St. Thomas (SMF 209754).

Nodilittorina (Nodilittorina) vermeiji

Bandel & Kadolsky, spec. nov.

(Figures 5, 10, 46-48)

- *Nodilittorina (Echinolittorina) tuberculata helenae*, MATTHEWS, 1968: 185; fig. 4 (not *tuberculata* Menke, 1828, nor *helenae* E. A. Smith, 1890). RIOS, 1970: 33; pl. 6.
- *Nodilittorina helenae* ssp., VERMEIJ, 1973: 325 (not *helenae* E. A. Smith, 1890).
- *Nodilittorina (Granulilittorina) miliaris*, ROSEWATER, 1975: 10. ROSEWATER, 1981: 34-35 (part, locality Fernando de Noronha only; not *miliaris* Quoy & Gaimard, 1833).

Holotype: B/K (USNM 749819) Figure 46; length 9.7 mm, width 7.5 mm.

Type locality: Isla Fernando de Noronha, Baía de Sueste (540 km NE Recife, NE. Brazil).

Etymology: G. J. Vermeij provided us with 27 specimens.

Diagnosis: A new species of *Nodilittorina* s.str. with a shell of more or less broadly conical shape, intensively brown pigmented with white, large, rounded nodules and a spiral angle of about 50-60°; the two main rows of nodules become distant and unequal during ontogenesis, the abapical row being stronger and sometimes bipartite; radula similar to that of *N. dilatata* (Orbigny, 1842); a difference from *N. helenae* and *N. miliaris* is found in the central tooth, where the transition between basal platform and the "neck" supporting the central cusp is angular in *N. vermeiji*, and rounded in *N. miliaris* and *helenae*. Operculum coiled narrowly paucispiral.

Description: Shell more or less broadly conical, solid, 14.3 mm high at maximum; whorls slightly convex, aperture less than half of shell height. Colour intensive brown exteriorly and interiorly except for a yellow band on the umbilical side and the white nodules.

Sculpture: Apex ca. 2.5 brown whorls; then 3 primary spirals originate, the strongest situated in the middle of the not overlapped part of the whorls, the abapical one is half overlapped by the succeeding whorl. These spirals are at first uniformly brown; nodules develop first on the middle row and only later on the other spirals; they are opaque-white. Probably simultaneously with the primary spirals secondary spirals develop, but they could not be observed before the third whorl due to corrosion. The first and second primary row (counted from the apex) remain closely together and may attain equal strength on the last whorl; the third primary row, which is ½ to ¾ overlapped by spiral whorls, remains free only in the last whorl where it is situated at the periphery, its nodules being now larger than those of the abapical rows; sometimes this peripheral row may split in two rows of nodules, which can be seen only on the last whorl. On the umbilical side, three irregular rows of weaker nodules, separated by a broader interval without nodules or granules from the main row of nodules, are developed. If the spiral main rows are classified as spirals of first order, spirals of second and third order are present, too: the spirals of second order cover tubercles and interstices, without forming nodules, and are themselves covered by spirals of third order; the latter are only visible at at least 20 × magnification; they are undulate and form a fine shagreen with the growth lines which are of the same width. The aperture is roundish with four blunt angles at (1) the junction outer lip / parietal wall, (2) at the junction parietal wall / columella margin, (3) at the transition columella / outer lip, (4) at the outer lip, where the abapical primary row of nodules meets it. The outer lip is simple and sharp, with faint tips where nodules are accreted, the columella is broad and somewhat deepened, concave, and slightly inclined inward, and at the base slightly pronounced abapicalwards, concave and receded.

Radula: A "normal" *Nodilittorina* radula: the central tooth is narrow but not reduced and its lateral cusps overtop the central cusp; the lateral and inner marginal teeth have four cusps each, the third (counted from the centre) being the largest; the outer marginal has eight cusps.

Operculum: Horny, brown, narrowly coiled, paucispiral, width of last whorl equals that of the spiral part; entire margin thin and flexible.

Spawn: Not known.

Relationships: *Nodilittorina vermeiji* belongs possibly to the Southern Atlantic *Nodilittorina miliaris* group, which is characterised by its sculpture: the second and third primary row of nodules are markedly distant and in most cases unequal (unlike *N. dilatata*, *N. tuberculata*, *N. pyramidalis* etc.), the abapical one being strongest and frequently bipartite; there is also a tendency to develop additional beads. The radula is the "normal" *Nodilittorina radula*. Within this group, *N. helenae* (E. A. Smith, 1890) is more slender (apical angle about 45°), the nodules are coloured with brown and the adapical ones are much smaller. *Nodilittorina miliaris* (Quoy & Gaimard, 1833) from Ascension Island has smaller, more numerous and more elevated nodules; the abapical primary row is regularly bipartite, and secondary rows of nodules are common. *Nodilittorina vermeiji*, however, differs from both *N. miliaris* and *N. helenae* apart from sculpture and shape also by the operculum, whose last whorl is more narrowly coiled (cf. Figure 5; for *N. miliaris* and *N. helenae* see ROSEWATER, 1981: pl. 3, figs. E, I) and by details of the central tooth of the radula: the transition from the basal platform to the "neck" supporting the central cusp is angular in *N. vermeiji* (Figure 47), while it is rounded in *N. miliaris* (Fig. 49) and in *N. helenae* (Rosewater, 1981: pl. 4, fig. E).

Range: Restricted to Fernando de Noronha, off the coast of Brazil.

Material examined: Fernando de Noronha (BMNH: 11 paratypes, nos. 1889.2.21.63-6, 88.6.27.52-5, 87.2.9.1831-3); ditto, Baía de Sueste (Vermeij leg. 27.6.1969 at high watermark; holotype and 6 paratypes, (USNM 749819-749820); ditto, Praia da Atalaia (Vermeij leg. 28.6.1969, 20 paratypes; USNM 749821).

Nodilittorina (Nodilittorina) tuberculata (Menke, 1828)

Figures 1C, 3B, 5, 10, 13, 52-55

- Der kleinknotige Krausel CHEMNITZ, 1781: 42 (part, only the smaller "species").

- *Trochus nodulosus* [var.] Gmelin, 1791: 3582, no. 98 ("... mari Americam meridionalem alluente"; based on CHEMNITZ, 1781).
- * *Littorina tuberculata* Menke, 1828: 25 (based on Gmelin, 1791 only; types of Chemnitz probably lost. Neotype hereby designated: Fig. 52, from Guadeloupe, deposited in USNM 749822). Menke, 1830: 44 (not Menke, 1829: 10, which is based on *Trochus nodulosus* Gmelin, 1791 (= *Nodilittorina pyramidalis* (Quoy & Gaimard, 1833))).
- * *Littorina thiarella* Anton, [1838]: 53, no. 1922 (no locality given, types probably lost).
- *Littorina nodulosa*, ORBIGNY, 1842: 205; pl. 14, figs. 11-14 (BMNH 1854.10.4.124, here Figure 53) (not of Gmelin, 1791).
- *Littorina trochiformis*, PHILIPPI, 1846b: 143; pl. *Littorina* 2, figs. 12, 14 (part, not fig. 15; not *Turbo trochiformis* Dillwyn, 1817).
- * *Littorina trochiformis* var. *minor* PHILIPPI, 1846b: 143 (based on reference to *Littorina thiarella* Anton, [1838] only).
- ?*Littorina trochoides*, PHILIPPI, 1847: 159; pl. *Littorina* 3, fig. 3 (not *Littorina trochoides* Gray, 1839).
- *Littorina (Tectus) tuberculata*, MÖRCH, 1876: 133.
- *Littorina (Tectus) tuberculata*, var. *minor*, MÖRCH, 1876: 133 (reference to *Littorina thiarella* Anton, [1838]).
- *Littorina (Tectarius) thiarella*, WEINKAUFF, 1882: 45-; pl. 5, figs. 9-11 (Guadeloupe).
- *Tectarius (Nodilittorina) tuberculatus* "Wood," CLENCH & ABBOTT, 1942: 2-; ? pl. 2, figs. 3-5 (part, *Nodilittorina dilatata* (Orbigny, 1842) included in this species; not *Turbo tuberculatus* Wood, 1828).
- *Nodilittorina tuberculata*, ABBOTT, 1954a: 451-; figs. ?55b (shell), 55d (foot), 55f (operculum), 55h (faeces), 55n (penis), 56a (distribution in part), 57b (radula). ABBOTT, 1954b: 134 (part, not fig.). ABBOTT, 1968: 82; figs. 81 (penis), ?83.10 (shell). KAUFMANN & GÖTTING, 1970: 350; fig. 38. FLORES, 1973a: 10-; pl. 1, figs. 1-4. BANDEL, 1974a: 93-113; figs. 13 (shell), 16B, 17 (spawn), 18-21, 39-41 (radula). BANDEL, 1974b: 13; fig. 6E (faeces). BANDEL, 1975: 17-; pl. 2, figs. 3, 5 (embryonic shell).
- *Nodilittorina (Echinolittorina) tuberculata*, HABE, 1956a: 98-; WARMKE & ABBOTT, 1962: 54; fig. 12a (operculum), pl. 9, fig. R (shell). ? ROSEWATER, 1970: 424; pl. 326, figs. 10, 12. ABBOTT, 1974: 70 (part; figs. and syn. *dilatata* = *Nodilittorina dilatata* (Orbigny, 1842); syn. *trochiformis* Dillwyn = *N. pyramidalis* (Quoy & Gaimard, 1833)).
- *Tectarius tuberculatus* "Wood," LEWIS, 1960: 414-; figs. 10A, B (spawn), 10D (veliger) (not *Turbo tuberculatus* Wood, 1828, not fig. 10C).

Explanation of Figures 46 to 51

Nodilittorina (N.) vermeiji Bandel & Kadolsky, spec. nov.

Figure 46: Isla Fernando de Noronha, Baía de Sueste, 540 km N.E. Recife, N.E. Brazil. Holotype 9.7 × 7.5 mm. USNM 749820

Figure 47: dito. Paratype. USNM. Shell: 7.0 × 5.3 mm, Radula: × 370 FN 1901/7

Figure 48: dito. Paratype. BMNH 1889.2.21.63. H. 8.9 mm

Nodilittorina (N.) miliaris (Quoy & Gaimard, 1833)

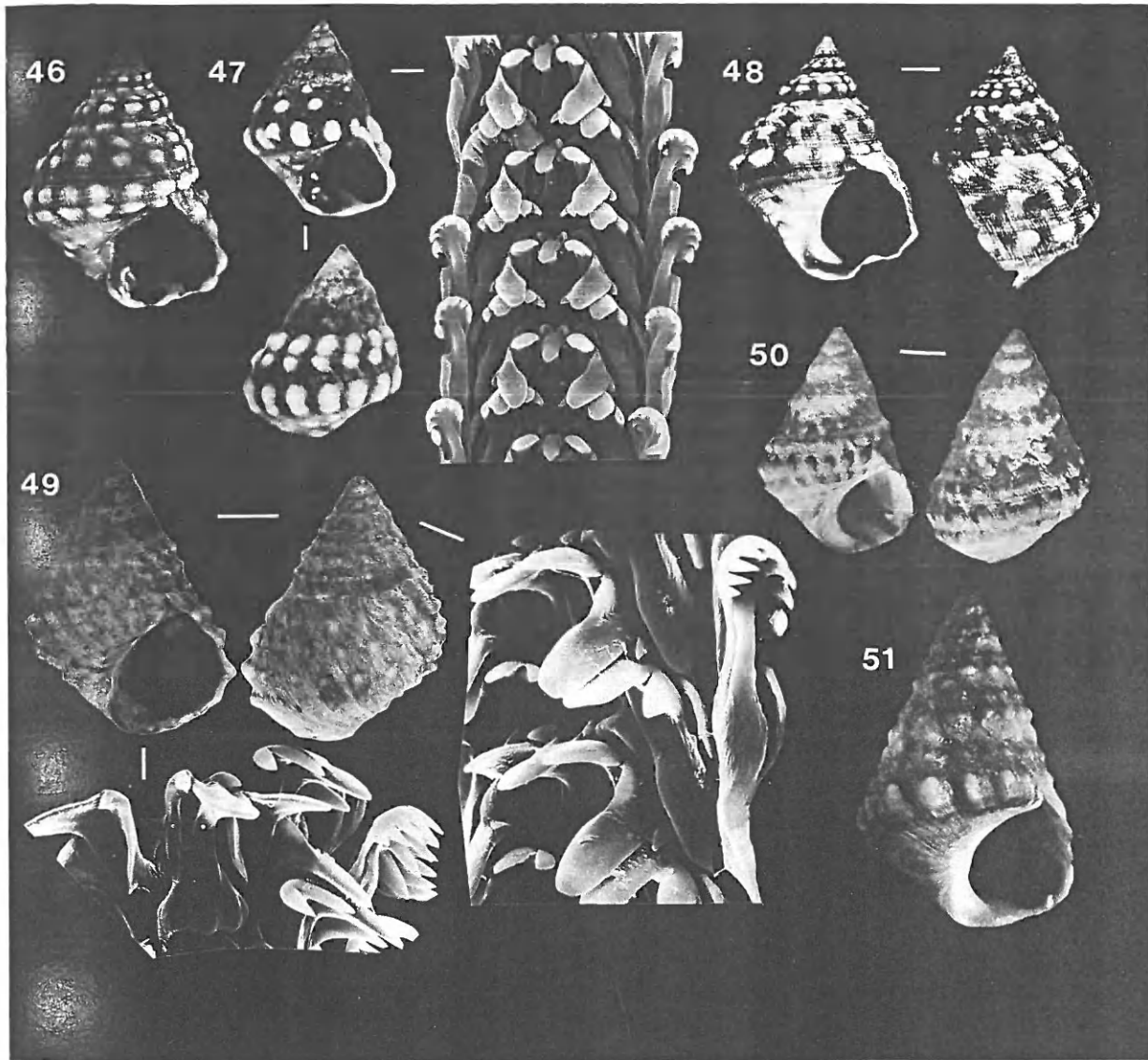
Figure 49: Ascension Island, Mac-Arthur Point. J. ROSEWATER leg. 10.7.1976 USNM 749825. Shell: 9.5 × 6.9 mm. Radula: a) × 800
b) × 930

FN University Erlangen-Nürnberg 4926, 4918

Figure 50: Lectotype of *Littorina lemniscata* Philippi, 1846. BMNH 1968.216. Shell: 8.4 × 5.7 mm. Erroneously reported from Cuba

Nodilittorina (N.) helenae (E. A. Smith, 1890)

Figure 51: St. Helena. BMNH 1889.10.1.2546. Paratype 11.6 × 7.0 mm



Description: Shell conical, 13-18mm long, with slightly convex, regularly increasing whorls; outline of shell dominated by nodose sculpture; no umbilicus. **Embryonic shell:** one slightly conispiral whorl, colourless except the red umbilicus, coarsely granulated; growth lines in its distal part; diameter 0.11mm. **Larval shell:** about 2.5 conispiral whorls sculptured with approx. 7 spirally arranged rows of granules, often fusing to ziczac lines (Figure 13).

Teleoconch: Sculpture of earliest whorls not preserved; earliest preserved sculpture consists of three spirally arranged rows of prominent nodes of which the adapical one is smaller than and more distant from the two middle rows of nodes. Nodes and interstices are covered by subequal spiral threads; in late whorls one thread in each interstice between the three rows of nodes becomes stronger, indistinctly nodulose and rarely grows into nodes of equal strength as the main nodes. The nodes are elevated but more or less rounded and circular to elongated in the spiral direction. Where only faint growth lines and no attack of cyanophyceans occur, a third order sculpture of delicate spiral threads is seen, covering the main nodes and spirals of 2nd order. The umbilical side is covered by three rows of smaller nodes, and spiral threads of 2nd and 3rd order as in the remainder of the shell.

Colour: A brown pigment is present throughout the shell but in the most elevated elements of the sculpture, *i.e.*, the nodes and in later whorls in the second order spirals; interior uniformly brown but for a light band in the umbilical side.

Aperture: Roundish, angled adapically; columella margin broad, brown, straight, abapically strongly expanded, concave (this obsolete in juveniles), recessing; adapically passing without angle into the parietal margin; parietal and protruding abapical wall with brown shell layer; outer lip simple, but in juveniles with channeled tips where the nodes are accreted (the external part of a node before the inner part being secreted). External shell surface adjacent to the columella regularly redissolved.

Operculum: Horny, paucispiral, width of last whorl about $\frac{1}{3}$ of length of operculum.

Nomenclature and types: The name *tuberculata* Menke, 1828, which has been in general use only since 1954 (ABBOTT) for the species here dealt with, and for *Nodilittorina dilatata* (Orbigny), which was re-recognized as a distinct species only in 1974 (BANDEL), is based on a rather dubious literature reference: MENKE (1828) referred to *Trochus nodulosus*, var. "minor" of Gmelin, 1791, which is entirely based on CHEMNITZ', 1781 unfigured variety of his pl. 163, figs. 1545-1546, here refigured Figure 43. These are the lectotype figures of *Trochus nodulosus* Gmelin, 1791 (non SOLANDER, 1766) (designated by CLENCH & ABBOTT, 1942: 3; invalid)

type locality: Cuba, Havana; Chemnitz: "k6mmt durch die Cookische Seereisen aus den S6dlandern" (comes by Cook's expeditions from the southern countries, [*i.e.*, the Pacific]), which can easily be identified with *Nodilittorina pyramidalis* (Quoy & Gaimard, 1833) (P. H. FISCHER, 1967b; ROSEWATER, 1970). The expression used by Gmelin, "*Trochus nodulosus* ... Habitat in oceano australo, et (minor) mari Americam meridionalem alluente ...," is interpreted not as the introduction of a variety named "minor" but as a descriptive term without nomenclatorial status. Chemnitz differentiated his "kleinere Art... aus Westindien" (smaller "species" from the West Indies) only by its smaller size. This "diagnosis" contains not the least factual substance to recognise any particular *Nodilittorina* species: Chemnitz' figure is 18mm high, but *Nodilittorina pyramidalis* varies between 5 and 24mm shell height (ROSEWATER, 1970), while *N. tuberculata* in its accustomed sense is usually between 11 and 16mm high. Further, *N. tuberculata* has a well developed row of nodules adjacent to the suture which is—as Chemnitz' figures clearly show—absent or very weak in *N. pyramidalis*. If considered a *nomen nudum*, *N. tuberculata* would gain nomenclatorial status not before M6RCH, 1876; the name would then be unavailable because of subjective homonymy with *Turbo tuberculatus* Wood, 1828 (= *Nodilittorina (Tectininus) antoni* (Philippi)) and the species dealt with here would have to be named *N. thiarella* (Anton, [1838]). Although in the original diagnosis of "*Littorina*" *thiarella* no locality is given and the types are lost, the description is sufficient to recognize *N. tuberculata* (diagnosis translated from the German):

"Ovate-conical, spire acute, five whorls with strongly stepped contours, each with a double row of closely spaced nodes separated by a shallow furrow, base finely granulated; bluish grey, nodes white; non-umbilicate; columella fairly narrow, overtopping the base and dilated; aperture roundish. Width 2.5''' , height 3'''."

As the name *thiarella*, however, has not been used in the more recent literature, as opposed to *tuberculata*, it is proposed to maintain the name *tuberculata* Menke, 1828, in its accustomed sense and as described here. The original publication is construed as follows: the reference to Chemnitz' publication is regarded as a reference to a formal diagnosis, indicating that the West Indian species is smaller than the lectotype figure of *nodulosus*; *i.e.*, smaller than 18mm. The provenance allows a choice between *Nodilittorina dilatata* and *N. tuberculata* auct. Individuals similar to Chemnitz' figures of *nodulosus* are found only amongst *N. tuberculata* auct., although the subsutural row of nodules is still more prominent than in *N. pyramidalis*. Such an individual from Guadeloupe (Figure 52) is proposed to be the **neotype** of "*Littorina*" *tuberculata* Menke, 1828.

Relationships: Radula and spawn characteristics allow a convincing distinction between *Nodilittorina dilatata* and *N. tuberculata*; shell properties are less useful, although

N. dilatata proved often to develop a spiny sculpture and a relatively broad shell, and the abapical row of nodules is more frequently covered by the succeeding whorl; also, in *N. dilatata* the columella often is more dilated, developing a groove in the umbilical region (pseudumbilicus). It is remarkable that the radula is extremely different from the one of *N. dilatata*, and almost identical with the one of *N. mordax*; it is outlined under this species, that the radula features in common are most likely homoeomorphs. Consequently, the subgenus *Echinolittorina* Habe, 1956, based solely on these radula characters, in *N. tuberculata*, is rejected. The true relationships of *N. tuberculata* are difficult to assess; the Galapagian *N. galapagensis* (Stearns, 1893) is similar in shell properties, but radula and spawn are not known. The Indo-Pacific *N. pyramidalis* (Quoy & Gaimard) has a radula more similar to the one of *N. dilatata*, while the shell differs from both *N. dilatata* and *N. tuberculata* in that the beads of nodules are largely reduced except the two main peripheral ones; and the egg capsule is insufficiently described (HABE, 1956b). In the Southern Atlantic, several closely related species, collectively named the *Nodilittorina miliaris* group, show no particular relationship to *N. tuberculata* or *N. dilatata*.

Range: Caribbean Sea, from Puerto Rico to Colombia and Venezuela.

Material examined: Puerto Rico: Rincon Lighthouse (ABBOTT, 1954a, radula fig'd). Antilles: Martinique, Sta. Lucia (BMNH 1854.10.4.124, original of ORBIGNY, 1842); Barbados (LEWIS, 1960, spawn fig'd); Guadeloupe, E. tip of Grande Terre, Pointe des Châteaux (USNM 749822, Vermeij leg.; neotype); Curaçao, Cornelisbaai (USNM 749823). Colombia: Sta. Marta (USNM 749824).

Subgenus *Nodilittorina* (*Tectininus*) Clench & Abbott, 1942

- *Tectininus* Clench & Abbott, 1942: 4. Type species by monotypy: *Echininus* (*Tectininus*) *nodulosus* "Pfeiffer" Clench & Abbott, 1942 (= *Littorina antoni* Philippi, 1846; non *Trochus nodulosus* Gmelin, 1791 which is *N. (N.) pyramidalis*).

Nodilittorina (*Tectininus*) *antoni* (Philippi, 1846)

(Figures 1D, 3C, 5, 11, 56-59)

- * *Turbo tuberculatus* Wood, 1828: 57; pl. 6, fig. 30 (no locality given; lectotype BMNH 1887.4.26.13, Figure 56 herein) (not *Turbo tuberculatus* Pennant, 1777, nor *Littorina tuberculata* Menke, 1828).
- * *Littorina scabra* Anton, [1838]: 53, no. 1920 (no locality given; types unknown) (not *Helix scabra* Linnaeus, 1758).
- *Littorina nodulosa*, L. PFEIFFER, 1839: 537- (not of Gmelin, 1791; not intended as the introduction of a new species, but of a new combination ex *Trochus nodulosus* Gmelin). PHILIPPI, 1846: 144; pl. *Littorina* 2, fig. 11 (cites Pfeiffer as author of the species name; not of Gmelin, 1791). PHILIPPI, 1847: 159; pl. *Littorina* 3, fig. 2 (copy Orbigny, 1842).

- *Littorina tuberculata*, ORBIGNY, 1842: 206; pl. 14, figs. 15-19 (Cuba, Havana; BMNH 1854.10.4.125, Figure 57 herein. Lectotype (hereby) of *Littorina Pfeifferiana* Weinkauff, 1882 and holotype of *Echininus* (*Tectininus*) *nodulosus* Clench & Abbott, 1942). PHILIPPI, 1847: 159; pl. *Littorina* 3, fig. 1 (copy Wood, 1828).
- * *Littorina Antonii* PHILIPPI, 1846: 145; pl. *Littorina* 2, fig. 18 (*Littorina scabra* Anton, [1838] included in synonymy, but not expressly proposed as a substitution name. Locality: Antilles; types unknown.).
- *Nina tuberculata*, MÖRCH, 1876: 132-, no. 310 (not Menke, 1828).
- * *Littorina* (*Tectarius*) *Pfeifferiana* WEINKAUFF, 1882: 46; pl. 5, figs. 15-16 (based on reference to L. PFEIFFER (1839), PHILIPPI (1846: *Littorina nodulosa*) and ORBIGNY (1842) only; lectotype hereby: original of ORBIGNY, 1842, figs. 16-17, BMNH 1854.10.4.125, Figure 57 herein. Type locality: Cuba, Havana).
- *Littorina* (*Nina*) *Antoni*, WEINKAUFF, 1882: 89-; pl. 5, figs. 13-14. WEINKAUFF, 1883: 227 (in syn.: *pfeifferiana* Weinkauff, 1882).
- *Echinella nodulosa*, DALL, 1889: 146-147 (not GMELIN, 1791).
- * *Echininus* (*Tectininus*) *nodulosus* "L. Pfeiffer," CLENCH & ABBOTT, 1942: 4; pl. 3, figs. 1-5 (holotype: original of ORBIGNY, 1842, pl. 14, fig. 17, BMNH 1854.10.4.125, here Figure 57; type locality: Cuba, Havana) (not *Trochus nodulosus* Gmelin, 1791, which is *Nodilittorina* (*N.*) *pyramidalis* (Quoy & Gaimard, 1833)). ABBOTT, 1954a: 458-; figs. 55a (shell), 55c (foot), 55e (operculum), 55g (faeces), 55p-q (penis), 56b (distribution), 57a (radula). ABBOTT, 1954b: 135; pl. 19, fig. H. WARMKE & ABBOTT, 1962: 54; fig. 12B (operculum), pl. 9, fig. O (shell). ROSEWATER, 1972: 510; pl. 388, figs. 18-20, pl. 390, figs. 13-15. ABBOTT, 1974: 70; fig. 572.
- *Echininus nodulosus*, ABBOTT, 1968: 82; fig. 83.9 BORKOWSKI, 1971: 827-836; fig. 2 (spawn). VERMEIJ, 1973: 321. BANDEL, 1974a: 95-113; figs. 17 (spawn), 18-21, 42-44 (radula). BORKOWSKI, 1975: 371-; fig. 2D (radula).
- *Echininus* (*Tectininus*) *antoni*, KADOLSKY, 1971: 192.

Description: Shell broadly conical, up to 20mm long with slightly convex, regularly increasing whorls; outline controlled by nodose sculpture; no umbilicus.

Protoconch: Probably paucispiral, brown (only worn parts preserved).

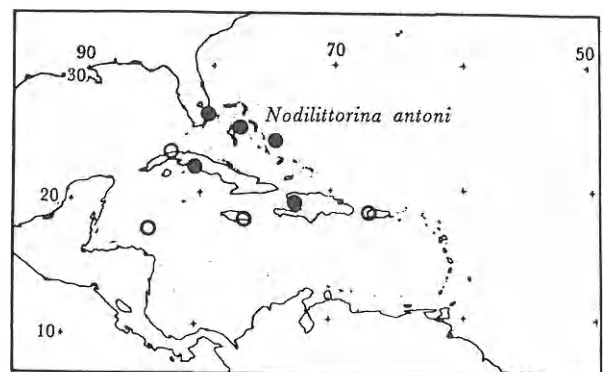


Figure 11

Distribution of *Nodilittorina* (*Tectininus*) *antoni* (Philippi, 1846)

Teleoconch: Sculpture commences with three rows of nodes, of which the adapical one is small, the middle one is large and spiny, and the abapical one is largely covered by the succeeding whorl. Spiral elements of 2nd order only preserved on later whorls: numerous subequal spiral ridges covering nodes and interstices, becoming themselves nodulose on the latest whorls. A cover of delicate spiral threads of third order is developed where growth lines are faint; otherwise the surface is densely covered by thread-shaped to squamose growth lines. The sequence of increasing width of sculpture elements is: spirals of 3rd order - growth lines - spirals of 2nd order - node rows. Umbilical side with 2-3 smaller node rows, spirals of 2nd order and growth lines as on the apical side of the shell; spirals of 3rd order only near the periphery.

Colour: Brown shell pigment uniformly distributed, lacking only in the nodes, nodules and in a band on the umbilical side; exterior surface appears in greenish grey to bluish grey.

Aperture: Subcircular, angled adapically. Columella margin moderately broad, expanded abapically, concave, recessing and slightly protruded abapically; outer edge of columella passes with an angle, inner edge with a wide arc into the parietal margin. Parietal wall with thin brown shell layer. A crescent-shaped portion of the external shell surface centred at the junction of the columellar and parietal edge is redissolved. Outer lip simple but for channelled tips where nodes are accreted as the nodes are accreted from the exterior to the interior.

Operculum: Subcircular, horny, brown, mesospiral; thicker than in other *Nodilittorina* species; external side concave, internal side convex.

The **radula** has 7 teeth in a transverse row, which are extremely modified: the central tooth is a very narrow rudiment without any function; the lateral tooth is very large, bearing one large and massive cusp and a smaller one on its exterior side; the inner marginal is small and narrow, bearing only one relatively large and massive cusp; the outer marginal is small, narrow and has three small cusps.

The pelagic **egg capsule** is cupola-shaped and bears wavy spiral ridges on the convex top and wavy oblique lines on the steep sides. (BORKOWSKI, 1971).

The **penis** is large and shows a basal enlargement and on its distal part a penis gland surrounded by small papillae (ABBOTT, 1954a).

Relationships: The penis gland being very distant from the basal enlargement, the presence of papillae on the penis and the mesospiral operculum demonstrate this

species to be unrelated to other *Nodilittorina* species. The retention of the subgenus *Tectininus* CLENCH & ABBOTT, 1942, defined by these characters, is certainly justified. The sculpture pattern, the abapical columella expansion and the pigmentation pattern are identical to that of other nodose *Nodilittorina* species; the egg capsule contains morphological elements observed in *N. riisei*. *Tectininus* has been attributed subgenerically to the Indo-Pacific *Echininus* only by its operculum characters. However, *Echininus* opercula are calcified and more narrowly coiled (true multispiral type); The width of the last whorl is 10% of the operculum length, while in *N. antoni* it is 20%. This compares better with the operculum of *Tectarius*, where the figure is 18-27%. Such opercula are named mesospiral by ROSEWATER (1972). There are sufficient differences between *Echininus*, *Tectarius* and *Tectininus* in a shell, penis and radula characters to exclude close relationships.

Nomenclature and types: KADOLSKY (1971) pointed out that L. PFEIFFER (1839) (cited as author of "*Echininus nodulosus*" as constantly as erroneously), who misidentified specimens of the species dealt with here with the Pacific *Trochus nodulosus* Gmelin, 1791 (now *Nodilittorina pyramidalis* (Quoy & Gaimard, 1833)), considered himself as author only of the combination "*Littorina nodulosa*." As a new species name, the name "*nodulosa*" has not been validly established until 1942, when CLENCH & ABBOTT named "*Littorina nodulosa* L. Pfeiffer" as the type species of their newly proposed subgenus *Echininus* (*Tectininus*). These authors expressly excluded from their synonymy list the synonyms associated by L. Pfeiffer with his "*Littorina nodulosa*." Thus, they have intentionally used L. Pfeiffer's misidentification as a name for a type species of a new subgenus. According to article 70(b) of the IRZN this constitutes the introduction of a new nominal species, *Echininus* (*Tectininus*) *nodulosus* Clench & Abbott, 1942. Their designation of a lectotype for "*Littorina nodulosa* L. Pfeiffer" has to be interpreted as a holotype designation for *Echininus* (*Tectininus*) *nodulosus* Clench & Abbott, 1942. The holotype is figured by ORBIGNY, 1842 on pl. 14, figs. 16 and 17, but not 19 which shows the operculum.

Although widely used, the name *nodulosa* Clench & Abbott cannot be maintained for this species, because of two available senior synonyms: *antoni* Philippi, 1846 and *pfeifferiana* Weinkauff, 1882. In addition, *Nodilittorina* (*Tectininus*) *nodulosus* (Clench & Abbott, 1942) would be a junior secondary homonym of *Trochus nodulosus* Gmelin, 1791, which is now classified as *Nodilittorina* (*Nodilittorina*) *pyramidalis* (Quoy & Gaimard, 1833).

An older name proposed for this species, *scabra* Anton [1838] is not available because of secondary homonymy with *Helix scabra* Linnaeus, 1758. PHILIPPI (1846) seemingly

introduced *Littorina Antonii* as a replacement name for *scabra* Anton, as he included both *scabra* Linnaeus and *scabra* Anton in the genus "*Littorina*." Although a homonymy no longer exists, since *scabra* Anton is attributed to *Nodilittorina* (*Tectininus*), while *scabra* Linnaeus is a *Littoraria* (*Littorinopsis*), names rejected as secondary homonyms prior to 1961 cannot be reinstated. Types of *scabra* Anton and *antoni* Philippi are not known, but the diagnoses and Philippi's figure agree well with this species. The type of *pfeifferiana* Weinkauff was selected from the original material of Orbigny as Weinkauff referred to literature only; thus *pfeifferiana* Weinkauff and *nodulosa* Clench & Abbott are absolute synonyms as based on the same type specimen.

Range: Between Florida in the North and Hispaniola and Jamaica in the South.

Material examined: Florida: Miami (USNM 749826). Bahamas: San Salvador (USNM 749827); Nassau, Paradise Island (USNM 749828). Cuba: Havana (Orbigny, 1842, lectotype of *pfeifferiana* Weinkauff, 1882 and holotype of *nodulosa* Clench & Abbott, 1942; BMNH 1854.10.4.125); Cienfuegos (SMF 167803). Hispaniola: Haiti, St. Marc (SMF). Jamaica (CLENCH & ABBOTT, 1942). Puerto Rico: Rincon Lighthouse (ABBOTT, 1954a; penis and radula fig'd). Bay of Honduras: Swan Island (CLENCH & ABBOTT, 1942). No locality: lectotype of *Turbo tuberculatus* Wood, 1828 (BMNH 1887.4.26.13 (no radula)).

APPENDIX

Species incorrectly associated
with Western Atlantic *Nodilittorina* species
Nodilittorina species erroneously recorded
from the Western Atlantic

Nodilittorina (*Nodilittorina*) *miliaris* (Quoy & Gaimard, 1833)
(Figures 49, 50)

- * *Littorina miliaris* QUOY & GAIMARD, 1833: 484; pl. 33, figs. 16-19 (Ascension Island; holotype MHNP, figured by ROSEWATER, 1970: 494; pl. 381, figs. 1-2; and ROSEWATER, 1981: pl. 2, fig. J).

- * *Littorina echinata* ANTON, [1838]: 53 (no locality given; types unknown; placed in synonymy of *Nodilittorina miliaris* by PHILIPPI, 1847: 160; pl. *Littorina* 3, fig. 5).
- * *Littorina granularis* GRAY, 1839: 140 (no locality given; holotype BMNH 87.4.26.9, refigured by ROSEWATER, 1970: 494; pl. 381; figs. 3-4, "eastern Atlantic").
- * *Littorina lemniscata* PHILIPPI, 1846a: 139 ("Cuba," erroneous locality; lectotype BMNH 1968.216, Figure 50 herein). REEVE, 1857: no. 6, pl. 2, fig. 6. WEINKAUFF, 1882: 91; pl. 13, figs. 5, 8.

Remarks: Present knowledge of this species suggests its restriction to Ascension Island in the South Atlantic. The form living on the coasts of Fernando de Noronha, 300 km off the Brazilian coast and 2000 km W of Ascension, has been identified with *Nodilittorina miliaris* by ROSEWATER, 1975 and 1981 and with the *N. helenae* by MATTHEWS, 1968 and VERMEIJ, 1973. The differences are outlined under *N. vermeiji*, spec. nov.

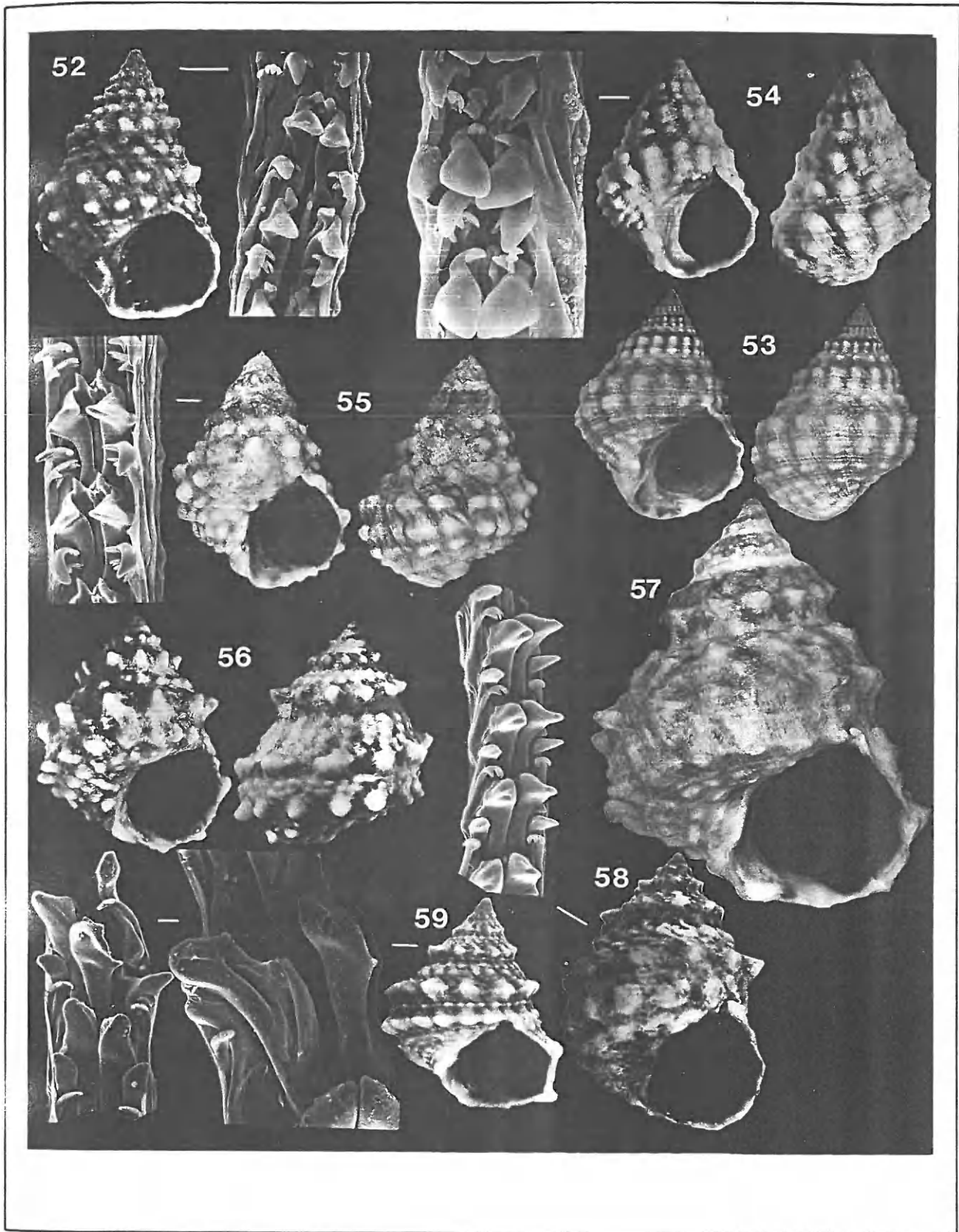
Littorina lemniscata Philippi, 1846, was originally recorded from Cuba, but has not been rediscovered there or anywhere else in the world. Examination of the lectotype, preserved without the radula, led to the conclusion to place this form into the synonymy of *Nodilittorina miliaris*. Available data on the form of Ascension Island (ROSEWATER, 1970, 1975 and 1981, and specimens received by courtesy of J. Rosewater) indicate that *N. lemniscata* is somewhat more slender and lacks secondary rows of nodules; but these differences are slight, and even if one objects to regarding them as being conspecific, *N. miliaris* would be the most closely related species to *N. lemniscata*, so far known. Particularly the numerous, small but prominent, rounded nodules seen in *N. lemniscata* distinguish also *N. miliaris* from related species, such as *N. vermeiji* spec. nov., *N. helenae* (E. A. Smith, 1890) and *N. natalensis* (Philippi, 1847).

The opportunity is seized to propose also the synonymy of *Littorina echinata* Anton, [1838] and *Littorina miliaris* Quoy & Gaimard, 1833, although the first-named had never been considered as a West Atlantic species. PHILIPPI (1847) already identified it with *Nodilittorina miliaris*, but later

Explanation of Figures 52 to 59

Nodilittorina (*N.*) *tuberculata* (Menke, 1828)
Figure 52: Guadeloupe, E. tip of Grand Terre, Pointe des Châteaux. Neotype. USNM 749822. Shell: 13.0 × 9.5 mm, Radula: × 210 FN 1641/7A
Figure 53: Martinique. BMNH. 1854.10.4.124. Original of ORBIGNY, 1842 (pl. 14, figs. 11-13). Shell: 14.1 × 11.2 mm
Figure 54: Martinique. BMNH 1854.10.4.124. Orbigny collection. Shell: 13.6 × 9.3 mm, Radula: × 265 FN 1599/23
Figure 55: Colombia, Santa Marta. USNM 749824. Shell: 13.0 × 9.5 mm, Radula: × 205 FN 956/14

Nodilittorina (*Tectininus*) *antoni* (Philippi, 1846)
Figure 56: Locality unknown. BMNH 1887.4.26.13. Lectotype of *Turbo tuberculatus* W. Wood, 1828. 13.0 × 10.8 mm
Figure 57: Cuba, Havana. BMNH 1854.10.4.125. Probably original of ORBIGNY, 1842 (pl. 14, figs. 16-17, as *tuberculata*); lectotype of *Littorina Pfeifferiana* Weinkauff, 1882; holotype of *Echininus* (*Tectininus*) *nodulosus* "Pfeiffer" Clench & Abbott, 1942. 23.1 × 14.4 mm
Figure 58: Bahamas, San Salvador. USNM 749827. Shell: 15.7 × 11.1 mm, Radula: × 130 FN 1920/6
Figure 59: Same as Figure 58: USNM 749827. Shell: 11.9 × 10.1 mm, Radula: × 212 FN 1465/7



Litorina echinata Anton was forgotten. The original diagnosis may be cited in translation from the German original:

"Obliquely conical-pyramidal, five whorls, the last fairly bulgy, $\frac{3}{5}$ of the whole, with nine rows of fairly distantly placed spines (Stacheln); in the middle of the whorl with a thread-shaped brown cirlet, greyish white, spines white, the ones of the base brown; columella broad, curved; non-umbilicate; aperture long-oval, brown, with two white stripes. One [specimen].

Variety: much narrower, last whorl half the size of the whole, less bulgy. Unicolored red-brown, with a yellow stripe. Width 4.5'''', height 7''''. One [specimen].'' [9.8 : 15.3mm].

Analysis of the diagnosis shows that in fact it corresponds best with *Nodilittorina miliaris*: Nine rows of "spines" on the last whorl indicate that beads of 2nd order are present, and that the nodules cannot be as large as, say, in *N. dilatata*; the expression used, "Stacheln," indicates that they must be elongated and pointed; the colour pattern is peculiar, but externally visible light-coloured zones are seen in the lectotype of *Littorina lemniscata* and in the closely related *N. helenae*, thus it is conceivable that in an extreme colour variation only a narrow dark cirlet is left in the middle of the whorls.

Nodilittorina (Nodilittorina) helenae (E. A. Smith, 1890)

(Figure 51)

- * *Littorina helenae* E. A. SMITH, 1890: 283; pl. 21, fig. 19 (St. Helena: lectotype BMNH 1889.10.1.2546-54, refigured by ROSEWATER, 1981: pl. 2, fig. 1; paratype Figure 51 herein).

VERMEIJ (1973) identified the *Nodilittorina* population of Fernando de Noronha with this endemic form of St. Helena. The differences are outlined under *N. vermeiji* spec. nov. *Nodilittorina helenae*, *N. vermeiji* and *N. miliaris* are certainly closely allied but distinct enough to distinguish them as separate species. The distinguishing characters of *Nodilittorina helenae* are the slender conical shell, the lack of convexity of the whorls, the weak, nodulose sculpture, the presence of two externally visible yellowish bands, one at the periphery, the other on the umbilical side, this one forming the internal light band known in all *Nodilittorina* species; nodules pigmented yellowish, not white, the two adapical primary rows very weak, the abapical one strong and bipartite, thus the 2nd and 3rd row being extremely unequal. Radula, penis and operculum were described and figured by ROSEWATER, 1981.

Nodilittorina (Nodilittorina) unifasciata unifasciata

(Gray, 1827)

- * *Littorina mauritiana* var. *crassior* PHILIPPI, 1847, Abb. Besch. Conchyl. 2: 165; pl. *Littorina* 3, figs. 15, 17a (type locality: "Cuba" (fig. 15 only) is erroneous, corrected by ROSEWATER (1970) to Australia).
- * *Littorina cubana* WEINKAUFF, 1882, Syst. Conch.-Cab. 2 (140): 68; pl. 9, figs. 2-3 (type locality: "Cuba" is erroneous, corrected hereby to Australia; types not known).
- * *Littorina (Melarhapha) ziczac*, BEQUAERT, 1943, Johnsonia 1 (7): 15 (part, only the synonyms *crassior* Philippi and *cubana* Weinkauff).
- * *Littorina (Austrolittorina) unifasciata unifasciata*, ROSEWATER 1970, Indo-Pacific Moll. 2 (11): 467-480; pl. 325, fig. 17-18; pl. 326, fig. 5; pl. 259, figs. 1-5; pl. 360, figs. 1-4; pl. 361, figs. 1A (radula), 1C (penis).

Remarks: The names *crassior* Philippi and *cubana* Weinkauff refer to shells of *Nodilittorina* with spiral sculpture and without colour markings except of a broad and blurred, slightly darker zone adapically of the periphery. No western Atlantic form has this colour pattern; they are typical, however, of the Australian *N. unifasciata unifasciata*.

Nodilittorina (Nodilittorina) knysnaensis (Philippi, 1847)

- * ?*Turbo dispar* MONTAGU, 1815, Trans. Linnæan Soc. London 11(2): 195; pl. 13, fig. 4 (type locality Poole, England, is erroneous; types not found in the Exeter Museum nor in the British Museum (Natural History); *nomen dubium et oblitum*, included in synonymy of "*Littorina ziczac* (Gmelin)" by BEQUAERT, 1943 (Johnsonia 1(7): 15) and ABBOTT, 1964 (Nautilus N.S. 78:65)). BROWN 1844, Illustr. recent conchol. Great Britain and Ireland... (2nd edition): 16; pl. 10, fig. 22.
- * ?*Littorina dispar*, BROWN, 1844, Illustrations of the Recent Conchology of Great Britain and Ireland... (2nd edit.): 128. JEFFREYS 1865, British Conchology... 3:376.
- * *Littorina knysnaensis* PHILIPPI, 1847, Abb. Besch. Conchyl. 2: 196; pl. *Littorina* 4, fig. 4 (South Africa: Caput Bonae Spei ad regionem fluminis Knysna). KRAUSS 1848, Die südafrik. Mollusken: 102.
- * *Littorina picea* REEVE, 1857, Conch. icon. 10: no. 83, pl. 15, fig. 83 (no locality given; lectotype: ROSEWATER 1970, pl. 364, figs. 19-20, BMNH 1968.320).
- * *Littorina (Austrolittorina) knysnaensis*, ROSEWATER, 1970, Indo-Pacific Moll. 2(11): 478-; pl. 364, figs. 17-23 (shell), pl. 365, fig. D (penis), pl. 369 (distribution).

BEQUAERT (1943) and ABBOTT (1964) included *Turbo dispar* Montagu, 1815, in *Nodilittorina ziczac (sensu lato)*. The original

description and figure, however, show a shell broader than *N. ziczac*, intensively dark pigmented, with a white band near the columella, and spiral furrows. This proves the species belongs to *Nodilittorina*, but the dark colour pattern without perceptible markings is quite anomalous for a Western Atlantic species. *Turbo dispar* is more likely synonymous with *Littorina knysnaensis* Philippi, 1847, as there is a particular similarity to the specimen which constitutes the lectotype of *L. picea* Reeve, 1857; the numerous small light-coloured dots reported for *N. knysnaensis* might have been obsolete or overlooked in *Turbo dispar*. As types are not preserved, the identity of *Turbo dispar* Montagu, 1815 cannot be established with certainty; thus it is preferred to consider it a doubtful and forgotten name.

West Atlantic species
erroneously attributed to *Nodilittorina*

Littoraria tessellata (Philippi, 1847)

(Figures 40-41)

- * *Phasianella lineata* LAMARCK, 1822: 54, no. 6 (Antilles; lectotype SD BEQUAERT, 1943: 13; original of DELESSERT, 1841: pl. 37, figs. 11a-b; MHNG 1096/87/1, here Figure 40) (not *Buccinum lineatum* Gmelin, 1791, which is *Littoraria scabra* (Linnaeus, 1758)).
- * *Littorina undulata* ORBIGNY, 1842: 212; pl. 15, figs. 12-14 (Martinique) (not *Littorina undulata* Gray, 1839).
 - *Littorina lineata*, DESHAYES in LAMARCK, 1843: 243.
- * *Littorina* [*ziczac* var.] *undulata* "Menke" PHILIPPI, 1847: 163 (no locality given; not of Gray, 1839).
- * *Littorina tessellata* PHILIPPI, 1847: 226; pl. *Littorina* 5, fig. 26 (Martinique; new name for *Littorina undulata* Orbigny, 1842).
 - *Littorina* (*Melarthaphe*) *nebulosa tessellata*, BEQUAERT, 1943: 13; pl. 4, figs. 8-10.
 - *Littorina* (*Austrolittorina*) *tessellata*, ROSEWATER, 1970: 423.
 - *Littorina* (*Littoraria*) *tessellata*, ROSEWATER, 1981: 26.

LAMARCK (1822) possibly intended to describe *Nodilittorina interrupta* (C. B. Adams in PHILIPPI, 1847) under the name of *Phasianella lineata*, as the three paratypes belong to that species (see Figure 23). However the only specimen of *Littoraria tessellata* in the type lot has been figured by DELESSERT (1841); DESHAYES (1843) restricted Lamarck's species to that figured by Delessert; and eventually, BEQUAERT (1943) designated this figure as lectotype. The original is refigured (Figure 40) herein and clearly shows its identity with *L. tessellata* Philippi. Other authors confused Lamarck's *lineata* with *N. interrupta*, *N. angustior* and *N. glaucocincta* group (see the synonymy lists of these species).

The attribution of *Littoraria tessellata* to *Austrolittorina* by ROSEWATER (1970) is certainly incorrect, as *L. tessellata* shows

no interior of the shell pigmented with brown, no light-coloured basal band, and the central tooth of the radula is not narrowed, its lateral cusps are on the same level with the central cusp (Figure 41). Further the penis has a basal "flap" without glands (ROSEWATER, 1981). Judging from shell and radula characters alone, *L. tessellata* appears to be most closely related to *L. undulata* (Gray, 1839) from the Pacific. The identity of the specific names *undulata* of Gray (1839), Orbigny (1842) and Philippi (1847) is by coincidence.

CONCLUSION

Evolution of the genus *Nodilittorina*
in the Western Atlantic

FOSSIL RECORD:

No suitable evidence to shed light on the evolutionary history of the genus *Nodilittorina* in the West Atlantic has emerged so far. RICHARDS (1935) reports *N. ziczac* (or perhaps any other "smooth" species) and *N. dilatata* (under the name of *Echinella nodulosa matanzensis* n. var.) from a Pleistocene raised beach (25') of Matanzas Bay, Cuba. From the Paraná Formation of Argentina, BORCHERT (1901) describes "*Littorina*" *paranensis* and "*Littorina*" *unicostalis*. The first-named he compares with *Nodilittorina angustior* (MÖRCH) and *Nodilittorina ariesensis* (Fontannes, 1879/82), the latter with "*Littorina*" *paranensis* only. Although probably belonging to *Nodilittorina*, the descriptions and figures are not detailed enough to ascertain the relationships of these species.

RECENT EVIDENCE:

The properties of the living Western Atlantic species of the genus *Nodilittorina* are visualised in Figure 5. Analysis of the properties so far known has revealed that two major features in the evolution of the *Nodilittorina* species can be recognized: speciation by geographical separation and homoeomorphology.

The speciation by (or during?) geographical isolation is shown in three species groups:

- 1) *Nodilittorina interrupta* (S. Caribbean) and *N. lineolata* (Brazil);
- 2) *Nodilittorina rüsei* (Florida, Cuba), *N. glaucocincta* (Jamaica, Lesser Antilles), and *N. mordax* (Bahamas, Curaçao);
- 3) *Nodilittorina vermeiji* (Fernando de Noronha), *N. militaris* (Ascension), *N. helenae* (St. Helena), *N. natalensis* (S.

and E. Africa) (the three last-named are not included in Figure 5 as being not Western Atlantic).

As negative evidence of the above, less closely related species overlap more or less in their geographical distribution: *Nodilittorina ziczac* and *N. interrupta* in the Southern Caribbean; *N. angustior* and *N. ziczac* in the entire Caribbean Sea; possibly *N. tuberculata* and *N. dilatata* at their northern, respectively, southern areal boundaries in the area of Puerto Rico/St. Thomas.

Homoeomorphologies occur worldwide in the family Littorinidae and are dealt with in the chapters on the taxonomic importance of the different organs. Homoeomorphologies in Western Atlantic species may be compiled here:

1) operculum type B (paucispiral, narrowly coiled) in (a) *Nodilittorina angustior*, (b) the conical, strongly nodulose *Nodilittorina* species like *N. tuberculata*, *N. dilatata* etc.

2) (possible homoeomorphs:) strongly nodulose species widely differing in anatomy: (a) *Nodilittorina dilatata*, *N. pyramidalis*, *N. miharis* group etc., (b) *N. tuberculata*, (c) *N. antoni* (a common origin of all these species is still possible, but not well conceivable with the evidence at hand).

3) egg capsule: cupola-shaped, entire convex side covered by spiral ridges: (a) *Nodilittorina angustior*, (b) *N. tuberculata*.

4) egg capsule: only top portion of the convex side covered by spiral ridges, and steep flanks with oblique striae: (a) *Nodilittorina risei* (and probably also the closely related *N. glaucocincta* and *N. mordax*), (b) *N. antoni*.

5) Radula with reduced central tooth, other teeth with reduced number of cusps, one cusp in both the lateral and the inner marginal teeth very large: (a) *Nodilittorina glaucocincta* and *N. mordax*, (b) *N. tuberculata*, (c) *N. antoni*.

Strangely enough, double homoeomorphologies occur repeatedly in the West Atlantic nodilittorines: *Nodilittorina angustior* and *N. tuberculata* (items 1 and 3), *N. tuberculata* and *N. antoni* (2 and 5), *N. mordax* and *N. antoni* (4 and 5). This circumstance would cast doubt as to whether the pertinent properties are really homoeomorphologies instead of homologies, if not the sum of all their characters would dismiss any close relationship. Apparently, when interpreting the relationship and evolution of this group of animals, one is faced with the problem of recognising numerous and repeated homoeomorphologies evolving from a repertoire of characters limited enough to not allow a further separation of the pertinent species into several genera. The problem is at present intensified by the limited knowledge of anatomical data.

For example, the available data on the penis morphology suggest that *Nodilittorina tuberculata*, *N. lineolata* and *N. ziczac* auct. (i. e., either *N. ziczac* s. str., *N. angustior* or *N. mordax*) have characters in common which distinguish them from both spirally sculptured and nodulose species of the Indo-Pacific area. If these differences prove to be consistent in the species not yet investigated, the conclusion would be possible that all Caribbean Nodilittorinae had evolved from a common source different from the ancestors of the Indo-Pacific species, thus demonstrating any characters they may share with the Indo-Pacific species to be homoeomorphologies. On the other hand, there must be close affinities between Atlantic and Pacific Middle American species, as the Atlantic and Pacific Ocean were disconnected in this area only in geologically fairly recent time.

In summary, the genus *Nodilittorina* seems to have undergone a rapid evolution in recent times (approximately since the beginning of the Miocene). One driving mechanism of this evolution is obviously geographic isolation; another one may be ecological separation as shown in the two morphs of *N. hawaiiensis* Rosewater & Kadolsky. In the species dealt with here, the first-named mechanism can be demonstrated in several species groups. The origin of these species groups, their historical development and possible migration paths, however, cannot yet be traced due to the limited amount of anatomical data of the living species and the extremely poor fossil record.

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