THE RADULAE OF CARIBBEAN AND OTHER MESOGASTROPODA AND NEOGASTROPODA

by

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With 346 text-figures and 22 plates

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Introduction

The classification of the recent Mollusca, especially that of the Mesogastropoda, is in such a state that it is very difficult to find one's way in the system. Specialists of certain groups of gastropods have been busy dividing the system in more and more subgroups and have created numerous new names. They have split old, well known genera into numerous new genera, often for reasons which are difficult to understand. Almost every new classification of the Mesogastropoda arranges genera, subfamilies, families and superfamilies in a different way.

Troschel (1856-1863), more than a century ago, had recognized that the radula, and not the shell of the gastropods, is the most important character that can be used to unravel the natural system of the Gastropoda. This tool can only be used on recent representatives, since fossil radulae of Gastropoda are not as yet known.

The development of the scanning electronic microscopy enables us to study the radulae with much more accuracy than is possible with light microscopy. With the radulae of a number of mesogastropods collected mainly from the Caribbean coast of Columbia and additional material for comparison from other regions, mainly the Mediterranean and the Red Sea, some branches of the natural system in this group of gastropods are traced. Many of these had already been revealed by Troschel (1856-1863) and Troschel & Thiele (1865-1893).

Material, methods, acknowledgements

Most of the radulae studied were extracted from animals that had been collected and kept under observation in an aquarium for some time. The soft tissue was destroyed in a cold KOH solution; after some days in this solution the radula could be extracted from the dissolved body tissue, usually under a microscope. The radula was rinsed in distilled water and usually cleaned ultrasonically for one to three seconds. It was then mounted, dried and coated with carbon and gold before being photographed with the scanning electronic microscope. If possible, radulae of several individuals of each species were thus prepared and mounted. Five to ten photographs were usually sufficient to describe the radula of one species and document it. The radula mounts and the shells of all Caribbean material studied have been deposited in the Rijksmuseum van Natuurlijke Historie, Leiden, the original photographs and films in the Paläontologisches Institut of the University of Bonn.

The terminology for the Mesogastropoda is elucidated with the figures 1-3. In the taenioglossate radula the central tooth (fig. 1) is accompanied by one lateral tooth (fig. 2) on each side. A pair of marginal teeth, the inner marginal tooth and the outer marginal tooth, complete each row of teeth (fig. 3). These teeth are attached to a flexible basement, the membrane of the radula. See figs. 164-167 for the terminology of the various types of radula in the Neogastropoda. The classification of Taylor & Sohl (1962) has been used to provide a framework for the various chapters.

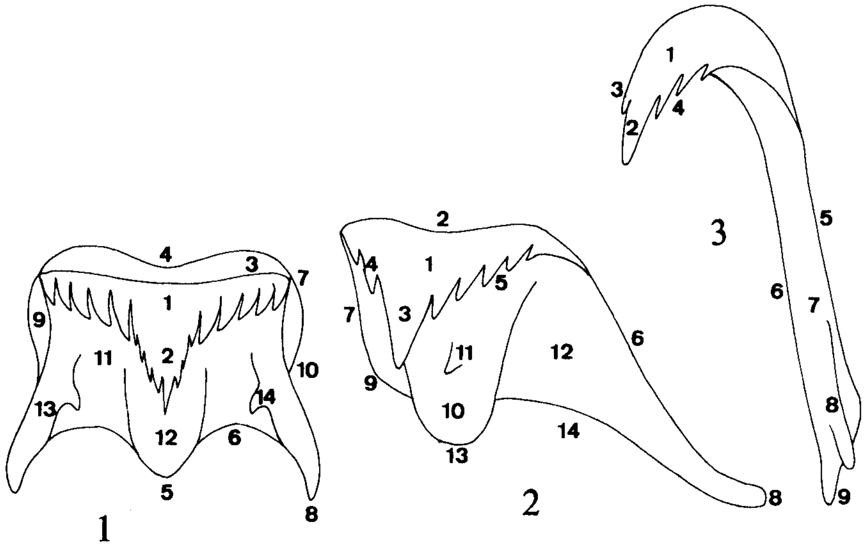

Fig. 1. Central tooth of a mesogastropod radula with the following morphological characters indicated: 1, cutting edge with main cusp and flanking cusps; 2, serrated main cusp; 3, frontal rim; 4, front or anterior front; 5, basal tongue-like projection or basal tongue; 6, base; 7, anterior corner; 8, posterior corner; 9, lateral wing; 10, margin; 11, basal platform; 12, central ridge; 13, marginal ridge; 14, basal denticle. — Fig. 2. Lateral tooth of a mesogastropod radula with morphological features indicated: 1, cutting edge; 2, front; 3, main cusp; 4, inner flanking cusp; 5, outer flanking cusp; 6, outer margin; 7, inner margin; 8, outer posterior corner; 9, inner posterior corner; 10, central swelling or central ridge; 11, basal denticle; 12, basal platform; 13, tongue-like projection of base or basal tongue; 14, base. — Fig. 3. Inner and outer marginal tooth of a mesogastropod radula with morphological features indicated: 1, apex; 2, main cusp; 3, inner flanking cusp; 4, outer flanking cusps; 5, outer margin; 6, inner margin; 7, stalk; 8, supporting ridge; 9, base.

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MESOGASTROPODA

Viviparacea

Ampullarius porphyrostomus Reeve
(pl. 1 fig. 1)

The short, sturdy radula has 28 rows of teeth. It has rectangular, central teeth that are about twice as wide as long and have a low, triangular cutting edge, situated vertically on the basal platform. The front of the central tooth is almost straight, with a shallow depression in the middle of the frontal edge. The front may have a narrow rim, forming the anterior extension of the basal platform. The cutting edge is dominated by a stout central cusp with parallel margins at its base, and has a triangular acute apex. Besides the central cusp three or four much smaller flanking cusps are present, on each side decreasing in size towards the outer edge. The corners, formed by the cutting edge and the margins, are evenly rounded. The lateral margins are straight or slightly concave, parallel to each other, and end in angular basal corners, which are also the terminal points of low ridges, extending without interruption across the basal platform to fuse with the base of the main cusp of the cutting edge. In the posterior part of the ridges, low, rounded, basal denticles are present. The base is straight or slightly concave. The basal platform is solid and is characterized by a concavity between the transversal ridges and the basal denticles, and by two additional depressions between ridges and margins.

The lateral teeth are angular, with extended outer posterior corners. The cutting edge forms an angle of about 90° with the concave basal platform and has four to five cusps. The second inner cusp is the largest and triangular in shape. From this main cusp a broad supporting ridge extends across the basal platform, ending in a central lobe on the base. Therefore, the basal edge is drawn out into a long, sturdy, raised tongue. While the inner posterior corner is rounded, the outer posterior corner is extended into a sturdy, handle-like stalk. The inner margin of the lateral tooth has a narrow, wing-like process under the innermost denticle of the cutting edge. The outer margin continues evenly curved or straight into the short extension of the outer posterior corner.

The marginal teeth are very similar to each other, both in shape and size. Their form is thorn-like and they are bilaterally compressed. The apex of a marginal tooth ends in two tips, the inner one of which is at a lower position on the cutting edge than the outer one, being also larger. While the inner marginal tooth has a broad, long stalk with a strong, median supporting ridge, the outer marginal tooth has a more slender and narrow stalk.

Ampullarius monticolus Vernhout
(pl. 1 fig. 2)

There are 33 rows of teeth in the radula.

Marisa cornuarietis (Linné)
(fig. 4; pl. 1 figs. 3, 4)

Form A (pl. 1 fig. 3), from ponds of the mouth of the Rio Magdalena. Shell with low nuclear whorls. There are 28-29 rows of teeth in the radula.

Form B (pl. 1 fig. 4), from a large lake near the road from Cartagena to Barranquilla. Shells with raised nuclear whorls. There are 28-29 rows of teeth in the radula.

DISCUSSION

The radulae of *Ampullarius porphyrostomus*, *Ampullarius monticolus*, and *Marisa cornuarietis*, collected from freshwater near and in the delta of the Rio Magdalena and from a large lake near the road from Barranquilla to Cartagena, are quite similar. Remarks on the ecology of the adult individuals and a description of the spawn and development of the young are provided by Bandel (1976a). There are no differences in the radula morphology of two populations of *Marisa cornuarietis* with somewhat differently shaped shells.

The mesogastropod superfamily Viviparacea is regarded as the most primitive of the Mesogastropoda, because of a fairly primitive nervous system (Fretter & Graham, 1962). The group is classified with the Architaenioglossa, the first superfamily (stirps) of the Mesogastropoda in Thiele's (1931) classification. With regard to their radula the snails have to be considered typical mesogastropods. Troschel (1856-1863) included his family Ampullariacea in the suborder ,,Pulmonata operculata'', where seven families belonging to the Archaeogastropoda, Mesogastropoda, and Pulmonata are united because of their ability for aerial respiration.

Taylor & Sohl (1962) have placed the families Viviparidae and Ampullariidae in the superfamily Viviparacea. The species described here belong to the family Ampullariidae of Thiele (1931), Wenz (1938), and Taylor & Sohl (1962). Thiele's definition of the radula of representatives of the Ampullariidae is as follows (translated): Radula quite short and strong; central tooth wider than long, cutting edge with triangular central cusp and two or three smaller flanking cusps on each side; lateral tooth varying in width with one or two smaller inner and two outer flanking cusps besides a large main cusp; marginal teeth solid with acute apices, almost always with one inner flanking cusp.

The species described here indicate that there may be more outer, flanking cusps on the lateral tooth than indicated in Thiele's definition. The innermost cusp of the lateral tooth is more a lamellar wing-like process of the anterior inner margin than a cusp of the cutting edge. A constant character is also provided by the ridges, and, based on these, the basal denticles on the central tooth. The ridges, but not the basal denticles, were recorded by Starmühlner (1969: fig. 169) but were not noticed by Troschel (1856-1863), Thiele (1931), or Demian (1964). Troschel (1856-1863: pl. 6 figs. 6-9) stated that there is a great similarity between the radulae of different species of the genus *Ampullarius* and also among different genera of the family Ampullariidae. Therefore, genera, subgenera, and species belonging into this family could not be kept apart by characters of the radula. Troschel's statement can be confirmed by data of Demain (1964) for the genus *Marisa*, by Starmühlner (1969) for the genus *Pila*, and by the new data concerning the genera *Ampullarius* and *Marisa*. The specimens from Columbia, in addition, show some variation in the number of cusps on the central and the lateral teeth. This makes questionable the value of minute differences stated to exist by Annandale (1921) between different members of this family.

The radula of the Viviparidae, the other family of the Viviparacea, has quite different teeth as compared to those of the Ampullariidae. The radula of *Viviparus* (fig. 5) was studied in two European species. The central tooth of *Viviparus* is less sturdy and has a concave basal platform with erect margins. The cusps of the cutting edge are weak and flexible and not solid and broad as in the Ampullariidae. No ridges and denticles are present on the basal platform.

The lateral tooth and the marginal teeth in *Viviparus* are very similar to each other. They have a bilaterally flattened, long, sheet-like stalk and a spoon- or fork-like upturned cutting edge with numerous cusps. This contrasts strongly with the Ampullariidae, where the lateral and marginal teeth differ conspicuously in their morphology (fig. 4).

Troschel (1856-1863: 87-101, pl. 7 figs. 1-6) described and figured the radulae of a number of species of Viviparidae ("Paludinae") that have the same morphology as mentioned above. Krull (1935) demonstrated the great variability of cusp-number on the cutting edge of the teeth in the radula of *Viviparus viviparus* (Linné) and noted that this number may vary within the radula of a single individual as well as the radula of different individuals. This could be confirmed here. Radulae of unhatched juveniles of *Viviparus viviparus* from the Rhine river show a variation of cusp number on individual teeth, up to two more or less cusps per cutting edge within an individual radula and between radulae of different specimens.

The radula of the Viviparidae resembles more that of the Valvatidae (superfamily Valvatacea in the classification of Taylor & Sohl, 1962) than that of the Ampullariidae. The radula of *Valvata piscinalis* Müller (fig. 6) has concave central teeth with many cusps on the cutting edge. The lateral tooth is more sturdy than

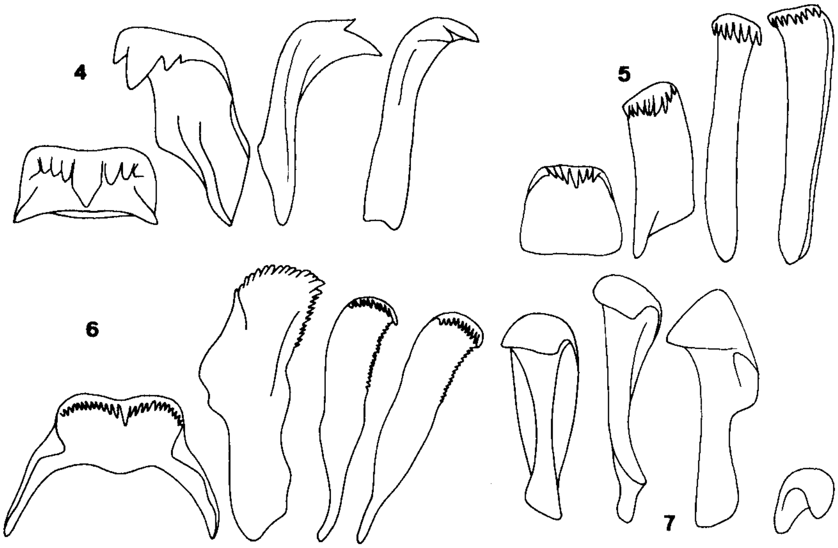


Fig. 4. *Marisa cornuarietis*, Isla de Salamanca, Columbia; × 80. — Fig. 5. *Viviparus viviparus*, the river Rhine; × 150. — Fig. 6. *Valvata piscinalis*, little lake near the mouth of the River Neretwa, Dalmatian Coast; × 400. — Fig. 7. *Cochlostoma septemspirale*, Bavaria; × 450.

in *Viviparus* and triangular in shape. The marginal teeth are slender and fork-like as in *Viviparus*. The characters used by Troschel (1856: pl. 6 figs. 13-15) and Thiele (1931: 120) with regard to the radula of the Valvatidae could also encompass the radulae found in the Viviparidae, but not those of the Ampullariidae.

Not only the shape and composition of the teeth of the Viviparidae differ from those of the Ampullariidae, but also the arrangement of teeth on the radula membrane. The teeth of *Viviparus* are attached to the membrane in such a way that there is a free space between the central tooth and the lateral teeth of each row. Lateral teeth and marginal teeth are attached in inclined rows, but also with some free space between each other. The margins of all teeth in each row do not overlap. In the folded radula the teeth are arranged in separate longitudinal rows, i.e. they are not resting on their lateral neighbours but on their anterior followers.

Marisa and *Ampullarius*, in contrast, show a much closer attachment of the teeth to each other in each transverse row of the radula. The morphology of the single teeth clearly reflects the morphology of the inner part of their lateral neighbours. The inner margin of the lateral teeth with their wing-like processes may fit in the depressions formed by the margins and the ridges present on the basal platform of the central tooth. The lateral tooth has a deep groove on the outer part of the basal platform into which the stalk of the inner marginal tooth can fit. This feature is quite like that seen in the Littorinidae. The inner marginal tooth is characterized by a strong median ridge. The outer marginal tooth can fit along almost its entire length into the groove formed by this ridge and the outer margin of the stalk. In the folded radula the outer marginal tooth fits into the concavity under the cutting edge of the inner marginal tooth.

The very different morphology and arrangement of the teeth in the radulae of Ampullariidae and Viviparidae correlates with a different mode of feeding. Members of the genera *Valvata* and *Viviparus* are microphagous feeders obtaining their food from the surface of the bottom or from the surface of aquatic plants by rasping and grasping with the radula. The food consists of small fragments of plant tissue, including algae and diatoms, as well as detritus. In addition *Viviparus* feeds with a ciliary mechanism, filtering particles from the inhalent water current and using them for food. *Ampullarius* and *Marisa*, on the other hand, cut and rasp plant material from larger sources of food. They feed on decaying as well as on fresh water plants of many kinds.

Littorinacea

Cenchritis muricatus (Linné)
(fig. 30)

The radula was figured by Bandel (1974: figs. 24, 25). It is up to 75 mm long and 0.13 mm wide and has very many rows of teeth. The central tooth is higher than wide. The basal platform is wide posteriorly and narrows anteriorly. The cutting edge has three stout cusps, the central of which is by far the largest. The tip of the central cusp is rounded and has three rounded lobes on its flanks. The lateral margins of the tooth are formed by narrow wing-like processes in the anterior part. The margins are convex. The posterior corners are extended into backward projecting points. The base is concave, with a shallow, convex tongue in its central part.

The lateral tooth is slightly higher than wide and rectangular in shape. Five cusps are present on the cutting edge, which forms a right angle with the basal platform. The fourth of these cusps is by far the largest and dominates the third cusp. The two inner cusps and the outer cusp are small. The cutting edge extends into a broad supporting ridge that continues into the inner part of the base. The inner posterior corner thus is extended into a stout thumb-like projection. Between the projection and the innermost, denticle-like cusps of the cutting edge there is a wing-like margin, which is wider anteriorly than posteriorly. Between the central supporting ridge and the extended outer posterior corner there is a wide lamellar structure, which is concave, forming a wide groove into which the stalk of the inner marginal tooth may fit. The outer posterior part of the margin is low.

The inner marginal tooth has a moderately long stalk that consists of a long thick inner part and a short flattened outer part. The tooth is more than twice as high as wide and has an upturned cutting edge with four cusps, the third of which is the largest.

The outer marginal tooth is long and slender and carries three rounded cusps on its upturned cutting edge. The stalk has a well rounded lower surface and a flattened upper surface. The base of the tooth is formed by a wide angular lamellar process, forming a right angle with the long axis of the stalk. This lamellar process has an upturned inner margin that fits into a groove between the inner and the outer posterior corners of the inner marginal tooth.

Littorina nebulosa Lamarck
(fig. 16)

The radula was figured by Bandel (1974: figs. 32, 33). It is up to 30 mm long and 0.24 mm wide and has a very large number of rows of teeth.

The central tooth is rectangular and as high as wide. The cutting edge is attached vertically to the basal platform, not quite at its anterior end. Therefore a rim, the anterior front, is present. The cutting edge is dominated by a central, sturdy cusp which is flanked by one or two much smaller cusps on each side. The basal platform has a central swelling on its anterior part, which posteriorly widens and ends in acute corners. The margins of the anterior part of the basal platform consist of wing-like processes, which extend from the rounded anterior corners to just below the centre of the margins. The base is almost straight.

The lateral tooth is angular and somewhat higher than wide. The upturned cutting edge has six cusps, the fourth of which is the largest. From the main cusp a central swelling continues across the basal platform into the thickened inner part of the base. The inner posterior corner extends into an acute, stout, thumb-like projection. The inner margin inserts anterior of this projection and continues in a concave course to meet the inner side of the innermost cusp of the cutting edge. The outer posterior corner is extended and has an upturned rim. A deep, wide groove is thus formed between central ridge and outer margin, into which groove the stalk of the inner marginal tooth fits.

The inner marginal tooth, like the lateral tooth, is spoon-like, with a concave basal platform ending anteriorly in an upturned cutting edge, which carries four cusps, the third of which is the largest. The tooth is somewhat higher than wide in front. The upper surface of the stalk is concave, the lower surface rounded, with an extended inner corner and a rounded outer corner. Between them a groove is found into which the inner margin of the outer marginal tooth fits in the folded radula.

The outer marginal tooth is about 2.5 times as high as wide and has a spoon-shaped apical part with six cusps. The stalk is sturdy, with straight margins. At the base a long rectangular lamella forms an angle of about 45° with the long axis of the stalk. The tooth is attached to the radula membrane along the inner margin of this lamella. The inner posterior corner fits into the depression found on the outer base of the inner marginal tooth.

Littorina angulifera Lamarck
(fig. 17)

The radula is up to 15 mm long and 0.20 mm wide and has a very large number of rows of teeth. It was figured by Bandel (1974: figs. 30, 31).

The central tooth is trapezoid, with a stout, thickened, triangular basal platform, wide marginal wings, and a cutting edge attached vertically not quite at the anterior end of the basal platform. Therefore, a wide frontal rim is present, often with a somewhat raised anterior edge. The angular central of the five cusps of the cutting edge is the widest. It is accompanied by a pair of increasingly smaller cusps on each side. The tooth is almost as wide as high at its posterior edge. The posterior corners are rounded; a depression in the platform is found between these corners. The base is straight. The lower frontal parts of the posterior neighbouring teeth can fit into the basal depressions. The inner lamellar process of the lateral tooth may rest in the depression formed by the central, raised supporting ridge and the marginal wings.

The lateral tooth is angular, with a wide and long outer posterior extension. The cutting edge is split up into two parts, which are separated from each other by a deep groove. The inner part of the cutting edge has three rounded, flat cusps and forms an angle of about 45° with the basal platform. The outer part of the cutting edge makes a right angle with the basal platform and has four rounded cusps. A narrow swelling on the central basal platform continues into a knob-like basal, inner corner that is arranged vertically to the basal platform. The inner margin is formed by a wide, wing-like process between cutting edge and basal projection. In the folded radula the rounded posterior corner of the central tooth fits into the depression formed by the wing-like process and the thumb-like projection. The inner marginal tooth may fit for almost its entire length into the concavity formed by the outer part of the cutting edge, the central ridge and the long extension of the outer posterior corner. The inner marginal tooth has a long, shovel-like shape with four equally sized cusps on the upturned cutting edge. It is about twice as high as wide, has a bilaterally flattened upper stalk and a strongly twisted base of the same width as the stalk. At the location of the change in direction the edge of the stalk is accentuated by a ridge ending in an outer, rounded denticle.

The spoon-like outer marginal tooth is almost three times as high as wide. It has seven rounded denticles on a weakly upturned cutting edge. The stalk is bilaterally flattened. From the stalk centre on it shows a strongly pronounced edge that continues into an acute outer corner. This edge is continuous into a wide lamellar base, that is twisted-off at almost a right angle.

All teeth in the radula are closely and hinge-like linked. The radula, therefore, is narrow when folded and wide when unfolded on the edge of the odontophore.

Littorina meleagris Potiez & Michaud
(fig. 19)

The radula was figured by Bandel (1974: figs. 52, 53). It is up to 3 mm long and 0.09 mm wide and has fewer rows of teeth than in the other Littorinidae described here.

The angular central tooth is somewhat higher than wide. The cutting edge is attached to the very front of the basal platform and has three cusps, the central of which is the strongest. From the central cusp a swelling continues across the basal platform. Just below the middle of the tooth the swelling widens to form a thickened basal part of the platform, with acute posterior corners and a low, tongue-like lobe in the centre of the base. The upper margins are formed by wide, wing-like processes. The upper part of the inner margin of the lateral teeth may fit into the depression between these processes and the central supporting ridge.

The lateral tooth is angular. Since the outer posterior corner is far extended, it is wider than high. The outer extension shows a weakly concave outer margin. A depression of the base is seen between the outer posterior corner and the swollen end of the central ridge on the base. This supporting ridge continues across the platform to the upturned cutting edge. The inner posterior corner consists of the strongly projecting, thumb-like end of the swelled base. Between this projection and an anterior, marginally upturned, lamellar process of the inner margin, a deep indentation is formed, into which fits the basal corner of the central tooth. The cutting edge has five teeth, the third of which is by far the largest.

The inner marginal tooth is fork-like, with four large cusps and a long, bilaterally flattened stalk. It is almost twice as high as wide. Its stalk may fit into the groove formed by the outer part of the lateral tooth.

The outer marginal tooth is long and slender, and its apex is formed like an open hand with seven finger-like, acute cusps. The sturdy stalk may fit into the gutter-like upper side of the inner marginal tooth. The base of this stalk has a weak twist inwards. A plate-like, narrow, lamellar process attaches the tooth to the membrane of the radula. All teeth are situated close together.

Nodilittorina ziczac (Gmelin)
(fig. 10)

The radula was figured by Bandel (1974: fig. 45). It is up to 70 mm long and 0.12 mm wide. It has a very large number of transverse rows of teeth.

The central tooth is clearly higher than wide. The cutting edge has three cusps. The marginal ones are situated somewhat more anteriorly than the acute, large, main cusp. The front is curved backward in its central part and continues in a shallow groove on the anterior face of the central cusp. The main cusp of the central tooth continues into a central swelling on the basal platform, that widens in the posterior third of the tooth to form a solid base with rounded corners.

Wing-like lamellae are present between this raised part of the basal platform and the marginal cusps of the cutting edge. The inner marginal lamella of the lateral tooth fits exactly into the depression formed by the central swelling and the lateral lamellae of the central tooth. The base has a rounded central lobe.

The lateral tooth is about as high as wide. A strong supporting ridge delimits an inner wing-like, marginal lamellar process that is broader in the anterior part of the tooth and narrower posteriorly. The wide, outer part of the basal platform is gutter-like in shape. The outer margin ends in a moderately extended, outer posterior corner, which has a raised outer margin in the folded radula, holding the outer margin of the stalk of the inner marginal tooth in position. The posterior part of the central swelling is widened and forms a rounded, thumb-like, inner posterior corner. The cutting edge has two large median cusps forming right angles with each other, and two small cusps flanking the median cusps on the outer and inner margins of the cutting edge.

The inner marginal tooth has a cutting edge with four upturned cusps. It is slender and spoon-like, with a bilaterally flattened stalk.

The claw-like outer marginal tooth has a cutting edge with seven acute cusps. The stalk is strengthened by a central supporting ridge. There are two marginal lamellae on the basal part of the stalk, one small, rounded, inner lamella, and a larger, triangular, outer lamella.

Tudora sp.
(fig. 33; pl. 1 figs. 5, 6)

The animals examined were collected from dry bushes close to the shore of the Island of Curaçao. The radula has about 190 rows of teeth.

The narrow, triangular, central tooth is longer than wide. It has a massive, concave basal platform that is curved upward vertically at its anterior end to form the cutting edge, which consists of a central cusp with sharp lateral margins only. The anterior front is evenly rounded. The lateral margins are raised and straight. The base has two marginal indentations and a wide central lobe, which is flexible and thinner than the actual basal platform and fused with the radula membrane. The shallow, concave basal platform has no basal denticles nor a central ridge, but is spoon-like and concave. The central tooth is attached to the membrane of the radula at rather a distance from the lateral teeth.

The lateral tooth is much longer than wide and of the same spoon-like appearance as the central tooth. It has a somewhat inclined, triangular outline. The inner margin is longer than the outer margin. The lateral tooth has a moderately concave basal platform with raised margins. The anterior front is regularly rounded. The straight inner margin extends into an elongated inner posterior corner; the outer posterior corner is not extended. The base is concave.

The inner marginal tooth is very slender, with a broad fork-like, concave apex on a bilaterally flattened stalk. The margins are straight and turned up, to form the concave upper surface of the stalks. The basal edge is narrow and concave. The cutting edge has five or six rounded denticles.

The outer marginal tooth is just as high as the inner marginal tooth but much wider, forming a fan-like structure. Its upper rim is turned upward to form a cutting edge, which is split along its whole course into numerous slender cusps (about 60), similar to a comb. The basal platform is smooth and somewhat concave. All teeth are independently attached to the radula membrane; they are not linked.

DISCUSSION

The superfamily Littorinacea in Taylor & Sohl's (1962) classification, following Thiele (1931), contains four recent families, viz. Lacunidae, Littorinidae, Pomatiasidae, and Chondropomidae. The radulae from the here described Caribbean species belong to the Littorinidae and Chondropomidae.

Arnaud & Bandel (1978) have shown that Troschel's (1856-1863) statement, that the group Littorininae (Littorinidae and Lacunidae of Thiele's classification) holds closely related species, which can be differentiated and characterized best by their radula morphology, may be confirmed. Ponder (1976) and Arnaud & Bandel (1978) are convinced that a group of Antarctic taxa is to be considered transitional between Lacunidae and Littorinidae. The genera *Laevilitorina* (figs. 26-28) and *Laevilacunaria* (fig. 24) are connected by such transitional forms, occurring in the Antarctic. The radulae of Lacunidae and Littorinidae thus demonstrate that these two families of the Littorinacea are closely related.

Troschel (1856-1863: pls. 4, 5) figured the radulae of several Pomatiasidae and Chondropomidae. These results have led Thiele to differentiate the subfamilies Pomatiasinae and Chondropomatinae, which were given family status in the classification of Taylor & Sohl (1962). Thiele's major arguments regarding the creation of these two (sub)families are based on differences in the dentition. While in the Pomatiasidae the cutting edge of the central tooth has a number of cusps, only one cusp is present in the Chondropomidae. The lateral tooth only has one cusp in the latter family, while in the former smaller cusps are flanking a main cusp.

Thiele's description of the radula of the Pomatiasidae mentions seven cusps for the central tooth and five for the lateral teeth. This definition has to be changed. Our own observations on *Pomatias elegans* (Müller) from Southern France resulted for the central tooth in a variation from three to five cusps, while *Pomatias laevigatum* (Webb & Berthelot) from Lanzarote (Canary Islands) has five to seven cusps (fig. 32). The number of cusps on the lateral teeth is also variable, even within the radula of a single individual. Three to six cusps were counted both in *Pomatias* from Southern France and from Lanzarote.

A further difference between the Pomatiasidae and the Chondropomidae is stated to exist in the shape and dentition of the outer marginal tooth. The Pomatiasidae are said to show a differentiation of the sheet-like tooth in an inner, fringe-like part, separated by a fissure from an outer part with mostly a smooth cutting edge (Thiele, 1931: fig. 102). Such a fissure cannot be seen in the figures given by Troschel (1856-1863: pl. 4 figs. 8-12). This fissure obviously should be regarded as an artefact that could have originated while mounting the radulae on glass slides. *Pomatias laevigatum* from Lanzarote has outer marginal teeth with strong cusps on the inner part and thin cusps on the outer part of the cutting edge (fig. 32). *P. elegans* from Southern France has comb-like cusps on the inner part and a smooth outer part of the cutting edge. *Tudora* sp. from Curaçao has comb-like cusps along the whole length of the cutting edge (fig. 33). Since a differentiation of the cusp size and shape of an inner and an outer part of the cutting edge is not consistent among the members of the Pomatiasidae, it cannot be used to differentiate between the Pomatiasidae and Chondropomidae. In the Pomatiasidae the cusp number on central and lateral teeth also shows considerable variation. It can, therefore, also not be used to distinguish members of this family from those of the Chondropomidae. The radulae of the members of both families are so similar in their general morphology, that on this character they should be synonymized.

Obviously the families of the Littorinacea can be grouped into two subgroups according to their radula structure. A close relationship between the Lacunidae & Littorinidae on one side and the Pomatiasidae & Chondropomidae on the other, cannot be defended. Thiele (1931) considered it doubtful whether to place the Pomatiasidae closer to the Littorinidae or to the Hydrobiidae. The tightly linked and very stout teeth of the Lacunidae & Littorinidae differ considerably from the spaciously arranged and unconnected teeth of the Pomatiasidae & Chondropomidae.

Searching for radulae similar to those of the group Lacunidae & Littorinidae outside the Littorinacea, one notices similarities with some members of the Rissoacea. Species of the genus *Eatoniella*, for example, have central teeth transitional in shape between those of *Pellilitorina* (fig. 20) and *Laevilitorina* (fig. 26-28). The lateral teeth also have the indentation of the outer posterior extension, considered characteristic for marine Littorinacea by Troschel (see Ponder, 1965a, b; Arnaud & Bandel, 1978).

Searching for radulae similar to those of the group Pomatiasidae & Chondropomidae, one should examine the radulae of *Valvata* (fig. 6) or *Viviparus* (fig. 5). Especially the radula of *Viviparus* compares well with that of *Pomatias*. Here the central tooth is attached to the membrane of the radula well apart from the lateral teeth. Lateral and marginal teeth are high and shovel-like in shape. The only strong difference lies in the morphology of the outer marginal tooth, which is of normal spoon-like shape in *Viviparus* and fan-like in *Tudora* and *Pomatias*. In *Valvata* the outer marginal tooth is somewhat more similar to that of *Tudora* than to that of *Pomatias*. Here the outer margin bears denticles. Such shapes could have been present in the ancestors of the Pomatiasidae & Chondropomidae. As regards the radula it would be more convincing to link the two terrestrial families of the Littorinacea more closely to members of the freshwater superfamilies Viviparacea and Valvatacea than to Lacunidae & Littorinidae.

The number of cusps found on individual teeth in the radula of *Pomatias* was found to be quite variable within individual radulae as well as between the radulae of different individuals. This contrasts with the data of Bandel (1974) on Littorinidae. Here the number of cusps on individual teeth is quite stable and can be used in the differentiation of species.

Within the Littorinidae & Lacunidae the morphology of the radula teeth provides much information that can be used to classify these families into a group of genera with the probability of a closer relationship to each other. If the radula of *Littorina littorea* (Linné) is taken as standard for comparison (fig. 8), the single teeth in each row provide important information. Unfortunately, the information gathered from the radula morphology cannot easily be fitted into the scheme of generic and subgeneric classification offered by any author in the widespread literature on this subject.

The central tooth of *Littorina littorea* is quadrangular and as wide as high (fig. 8; Bandel, 1974: fig. 23). The cutting edge is dominated by a sturdy central cusp, accompanied by one pair of lateral cusps. The main cusp is connected with a central swelling on the basal platform that splits near the posterior end to continue into the rounded posterior corners.

Troschel (1856-1863) expressed the idea that the shape of the central teeth within the Lacunidae & Littorinidae reflects generic differences. If we follow this suggestion we observe central teeth broader than in *L. littorea* in the genera *Lacuna*, *Laevilacunaria* and *Pellilitorina*. In contrast to *L. littorea*, the central teeth of *Laevilacunaria* (fig. 24; Powell, 1951: fig. I, 29; Arnaud & Bandel, 1978: fig. 7) and of *Lacuna* (Thiele, 1931: fig. 96; Troschel, 1856-1863: pl. 10 fig. 13; Meyer & Möbius, 1872: 13, fig. 7) have a bilaterally flattened, straight cutting edge and not an acute main cusp. The number of flanking cusps may vary from one to two on each side of the median cusp. The broad central teeth of *Pellilitorina* are quite different from those of all other littorinids (fig. 20) and lack the lateral wing-like processes.

Central teeth more narrow than in *L. littorea* are usually found among other Littorinidae. Fairly wide central teeth are present in *L. meleagris* (fig. 19), *L. mespillum* Von Mühlfeld (Bandel, 1974: fig. 18), *L. obtusata* (Linné) (Bandel, 1974: figs. 28, 29) and *L. saxatilis* (Olivi) (Bandel, 1974: figs. 26, 27). In these the lateral wings are wide and the cutting edge is similar to that of *L. littorea*, but in *L. obtusata* and *L. saxatilis* it has two flanking cusps on each side of the main cusp instead of one as in the other species.

A development to even more slender central teeth is seen among members of the genus *Nodilittorina* and related forms (Bandel & Kadolsky, 1982). Here a clear line of development from a typical littorinid radula to a new functional type of radula as present in *Nodilittorina antoni* (Philippi) can be discerned (Bandel, 1974). The central teeth of *Nodilittorina millegrana* (Philippi) (fig. 9), *N. pyramidalis* (Quoy & Gaimard) (fig. 11), *Littorina striata* King & Broderip (Bandel, 1974: figs. 53, 54) and *N. ziczac* (Gmelin) (fig. 10) are quite similar and have fairly wide wings and flanking cusps, mainly lateral to the central cusps and only slightly anterior of these.

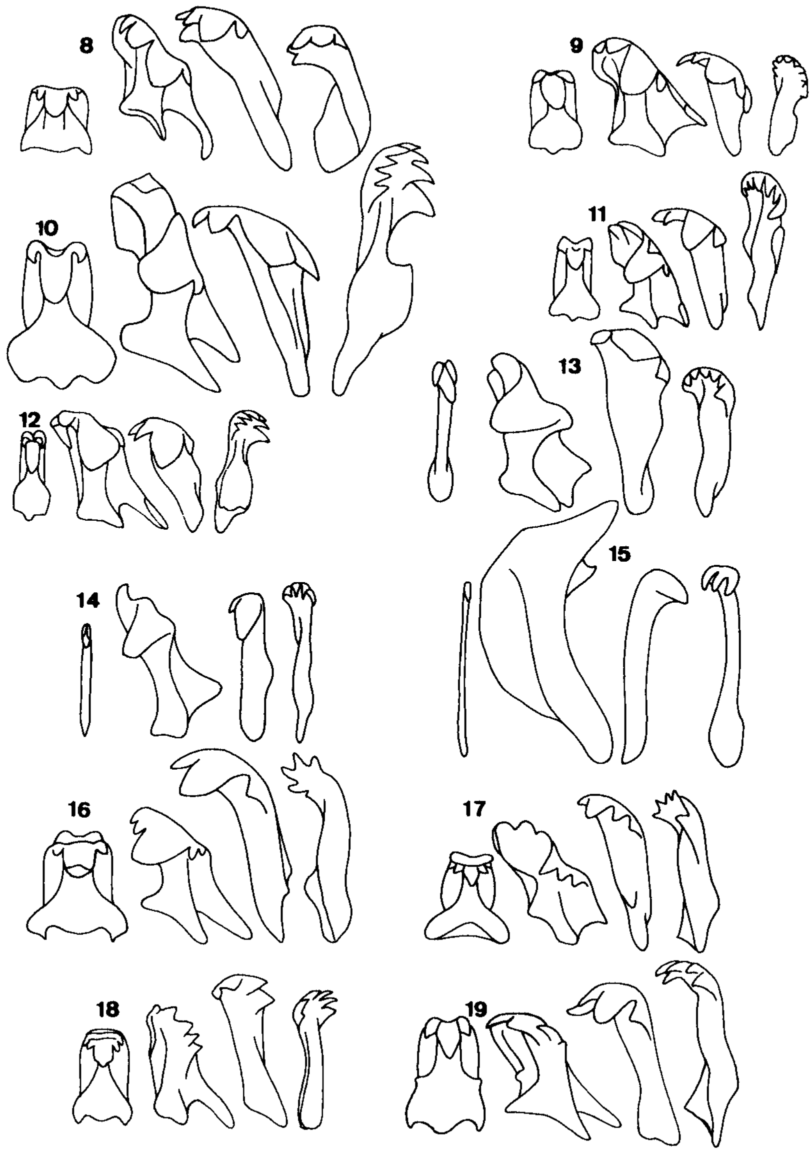


Fig. 8. *Littorina littorea*, Oosterschelde, North Sea; x 150. — Fig. 9. *Nodilittorina millegrana*, Red Sea, Port Sudan; x 250. — Fig. 10. *Nodilittorina ziczac*, Santa Marta, Caribbean; x 800. — Fig. 11. *Nodilittorina pyramidalis*, Port Sudan, Red Sea; x 250. — Fig. 12. *Nodilittorina subnodosa*, Port Sudan, Red Sea; x 220. — Fig. 13. *Nodilittorina angustior*, Curaçao, Caribbean; x 400. — Fig. 14. *Nodilittorina tuberculata*, Santa Marta, Caribbean; x 350. — Fig. 15. *Nodilittorina antoni*, Nassau, Bahama Islands; x 400. — Fig. 16. *Littorina nebulosa*, Santa Marta, Caribbean; x 160. — Fig. 17. *Littorina angulifera*, Santa Marta, Caribbean; x 160. — Fig. 18. *Littorina tessellata*, Haiti, Caribbean; x 220. — Fig. 19. *Littorina meleagris*, Santa Marta, Caribbean; x 700.

The central teeth of *Nodilittorina subnodosa* (Philippi) (fig. 12) and *N. dilatata* (d'Orbigny) (Bandel, 1974: figs. 18, 48, 49) have become narrower. The size of the lateral wings is reduced further and the flanking cusps form frontal flaps on the anterior edge. Even more slender central teeth are found in *Nodilittorina tuberculata* (Menke) (fig. 14; Bandel, 1974: figs. 18, 39, 40, 41) and some related Caribbean littorinids (fig. 13). The culmination of this development is reached in *Nodilittorina antoni* (fig. 15; Bandel, 1974: figs. 42, 43, 44.), where the central tooth is very narrow and rudimentary, and has lost its function in the radula. As Bandel (1974) has noted in this group of Caribbean species, encompassing among others *Nodilittorina tuberculata* and *N. antoni*, the morphology of the teeth has changed so much, that the function of the radula has also changed. Within this group the radula is used to scratch and scrape only and not to cut and rake.

A development from central teeth similar to those of *L. littorea* to narrower, more simple types can also be seen in another group of species. *Cenchritis muricatus* (Linné) (fig. 30) has reduced lateral wings in a central tooth that in other features is very close to that of *L. littorea. Tectarius cumingii* (Philippi) (Troschel, 1856-1863: pl. 11 fig. 7; Thiele, 1931: fig. 99; Rosewater, 1970: pl. 406A) and *T. grandinatus* (Gmelin) (fig. 31; Rosewater, 1970: pl. 394A) have central teeth which are only a little more slender than those of *C. muricatus*; these teeth of the two species are, however, completely without wings. In *Tectarius pagodus* (Linné) the cutting edge, in addition, has become simplified and has only a broad cutting blade without cusps (Rosewater, 1970: pl. 397A). In contrast to the development of the *Nodilittorina* radula, the central tooth has become simplified in its morphology in *Tectarius pagodus*, but has retained its function and size.

Another modification of the central tooth may be seen in *Littorina nebulosa* Lamarck (fig. 16; Troschel, 1856-1863: pl. 10 fig. 14), *L. angulifera* Lamarck (fig. 17; Marcus & Marcus, 1960: fig. 2) and *L. tessellata* Philippi (fig. 18). Here the cutting edge is not based right at the anterior front but somewhat behind it. Thus a more or less wide frontal plate is present. From the literature it is evident that such a feature is also found in *L. undulata* Gray (Rosewater, 1970: pl. 333A), *L. scabra* (Linné) (Troschel, 1856-1863: pl. 10 fig. 18; Barnard, 1963: fig. 37a; Rosewater, 1970: pl. 353A) and *L. irrorata* Say (Troschel, 1856-1863: pl. 10 fig. 15).

Basal denticles on the central tooth are a rare feature among Lacunidae & Littorinidae. Arnaud & Bandel (1978) noted basal denticles in *Laevilacunaria bransfieldiana* (Preston) (fig. 24) and Bandel (1974: figs. 58, 59) noted them in a more pronounced form in *Littorina neritoides* (Linné) (fig. 29). Both species, however, have little in common as regards the radulae.

Troschel (1856-1863) had recorded as a constant character of the Lacunidae & Littorinidae a short and wide lateral tooth which is extended into an outer posterior projection that forms a rounded indentation at the outermost end of the base. This feature was found in all radulae studied in this group except for species which have a radula close to that of *Nodilittorina antoni* (see Bandel, 1974).

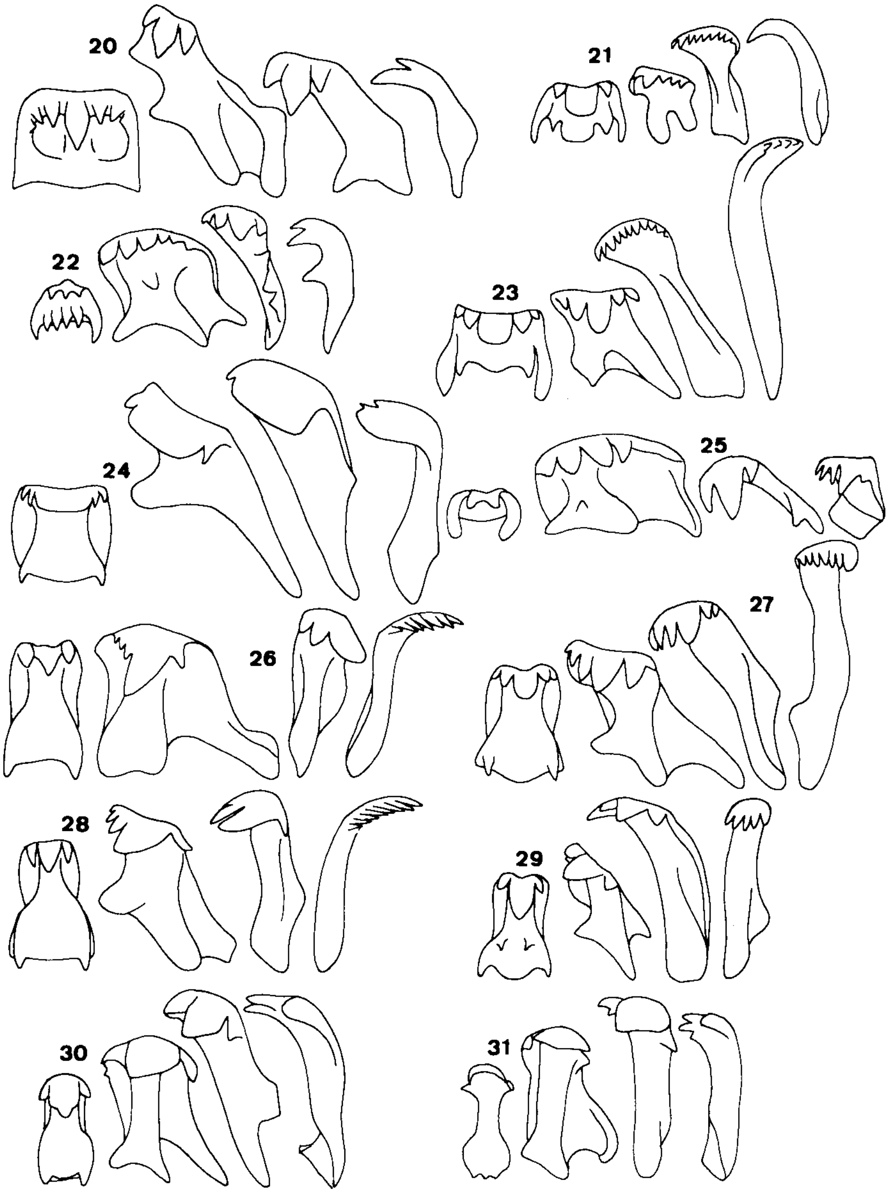


Fig. 20. *Pellilitorina setosa*, Antarctica; × 800. — Fig. 21. *Amphithalamus* sp., Santa Marta, Caribbean; × 1000. — Fig. 22. *Cingulopsis* sp., Santa Marta, Caribbean; × 650. — Fig. 23. *Pisinna punctulum*, Banyuls-sur-Mer, Mediterranean; × 1200. — Fig. 24. *Laevilacunaria bransfieldiana*, Antarctica; × 200. — Fig. 25. *Cingulopsis fulgida*, Banyuls-sur-Mer, Mediterranean; × 1000. — Fig. 26. *Laevilitorina antarctica*, Antarctica; × 600. — Fig. 27. *Laevilitorina caliginosa*, Antarctica; × 200. — Fig. 28. *Laevilitorina* cf. *umbilicata*, Antarctica; × 800. — Fig. 29. *Littorina neritoides*, Banyuls-sur-Mer, Mediterranean; × 400. — Fig. 30. *Cenchritis muricatus*, Santa Marta, Caribbean; × 230. — Fig. 31. *Tectarius grandinatus*, Phillippines, Pacific Ocean; × 60.

The lateral tooth is usually wider than high or as wide as high. In the group of Caribbean species of *Nodilittorina* the lateral tooth becomes higher, while at the same time the cusp number of its cutting edge is reduced, and the cutting edge itself becomes shortened. The central supporting ridge of the basal platform thus dominates more and more in the morphology of the tooth, until a chissel-like shape is formed. The radula thus becomes narrower until it is as wide as two lateral teeth side by side, as is the case in *Nodilittorina antoni* (Bandel, 1974: figs. 42, 43).

In the radulae of the Lacunidae & Littorinidae the inner marginal tooth fits into a gutter-like depression on the outer margin of the lateral tooth in a resting position; the inner edge of this groove is often formed by a sturdy, thumb-like projection, as in *L. littorea*. This projection prevents the stalk of the inner marginal tooth from slipping down further inward. Only in species with a strongly modified lateral tooth, e.g. *Nodilittorina tuberculata*, such a thumb is absent. Here a deep lateral groove of the lateral tooth provides a sufficient hold for the inner and outer marginal tooth. *Tectarius grandinatus* (fig. 31) also has lateral teeth which are higher than wide, without a thumb-like projection. Here the groove between the extended outer posterior corner and the stout central swelling on the outer part of the tooth is sufficiently deep to hold the slender stalk of the inner marginal tooth. As in *L. littorea*, the outer margin of the inner marginal tooth is often embraced by the raised rim of the extended outer posterior corner of the lateral tooth, but this is not a constant feature among littorinid radulae.

Usually the lateral tooth is not only linked with the inner marginal tooth but also with the central tooth. The inner anterior wing of the lateral tooth can usually fit into the depression formed by the lateral wings and the central swelling of

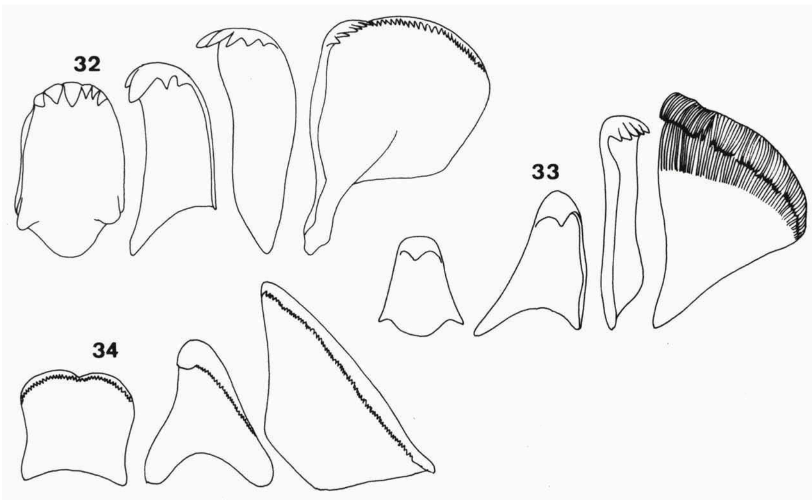


Fig. 32. *Pomatias laevigatum*, Lanzarote, Canary Islands; × 250. — Fig. 33. *Tudora* sp., Curaçao, Antillen Island; 220 × . — Fig. 34. *Rissoella caribaea*, Santa Marta, Caribbean; × 1100.

the central tooth (as in *L. littorea*). The wide base of the central tooth fits mostly into a depression between the wing-like process and the thumb-like projection of the inner margin of the lateral tooth. With the reduction of the wing size of the central tooth in the Caribbean species of *Nodilittorina* and the Indo-Pacific *Tectarius*, and, associated with it, the development of more slender shapes, the linkage between central and lateral teeth is lost.

The inner marginal tooth of *L. littorea* is very simple in shape and consists of a sturdy stalk and a spoon-like apex with four almost equal, acute cusps. Rarely, e.g. in the genus *Laevilitorina* (Arnaud & Bandel, 1978; Powell, 1951; Dell, 1964), more cusps can be counted on the cutting edge; otherwise three or four cusps are usual in the Lacunidae & Littorinidae. Less than three cusps are found only in some Caribbean species of *Nodilittorina*, leading the one-cusped inner marginal tooth of *N. antoni* (fig. 15; Bandel, 1974: fig. 21).

The outer marginal tooth, in contrast to the inner one, provides more specific information. In *Littorina littorea* the slender stalk has a claw-like upper end with five cusps and a base that is twisted inward at a right angle. The tooth is attached to the radula membrane by this lamellar base. A similar base in present in *L. angulifera* Lamarck, *L. nebulosa* (Lamarck), *L. saxatilis* Olivi, *L. obtusata* Linné and *Cenchritis muricatus* (Linné). A less twisted base is present in *L. meleagris* Potiez & Michaud, *L. tessellata* Philippi, *Tectarius cumingii* (Philippi), and *T. grandinatus*. A straight base was found in *Littorina striata* King & Broderip, *L. punctata* Gmelin, *L. natalensis* Krauss, *Nodilittorina millegrana* (Philippi), *N. pyramidalis* (Quoy & Gaimard), and *N. subnodosa*. The basal twist of the stalk of the outer marginal tooth thus differentiates three groups of littorinids. The number of cusps on the cutting edge shows very little variation and can be used for the differentiation of species (Bandel, 1974; Arnaud & Bandel, 1978).

RISSOACEA

Assiminea cf. **succinea** (Pfeiffer)
(figs. 35, 40; pl. 1 figs. 7-10)

The radula has a little more than 28 rows of teeth. The central tooth is more than two times as wide as long. It has acute posterior corners projecting sideways, straight margins, and a concave front. A wide rounded tongue-like lobe on the posterior base is accompanied on both sides by deep, rounded indentations. The cutting edge is situated on the front and follows its contour. It forms a more or less right angle with the basal platform. The acute, narrow, triangular main cusp is flanked by four or five decreasing, evenly spaced, acute cusps on each side. Three basal denticles are arranged as cusp-like projections of a ridge which extends from the middle of the basal platform in an inclined row to the basal corners. The first is the largest, the second is smaller and the third is the smallest, often developed as only a rounded, knob-like projection or even absent. The basal platform and its tongue-like projection are smooth.

The lateral tooth has a stout cutting edge, curved upward in front to form nearly a right angle with the basal platform. The strong, triangular main cusp is flanked by three or four regularly decreasing inner cusps and five or six outer cusps, decreasing in size in outward direction. The inner margin is straight, a little upturned, and ends in rounded inner corners. In the folded radula the margin can fit into the rim between the rows of denticles and the lateral margin of the central tooth. The anterior outer margin is straight; the posterior part turns outward to form the margin of a long handle-like extension of the outer basal corner. This long projection is jointed to the basal platform by a flexible connection. At its end it is twisted in anterior direction to end where the base of the inner marginal tooth is attached to the radula membrane.

The inner marginal tooth is about three times as high as wide. It has a bilaterally flattened shaft, and a bilaterally flattened apical part of spoon-like shape with erect margins, covered with about 30 slender cusps. The inner margin of the lower half of the stalk has a wide lamella, uninterrupted down to the base.

The outer marginal tooth is as long as the inner one. Its hook-like apex has about 25 thin, acute cusps distributed only on the inside of the tooth, where a broad basal lamella is attached to the lower half of the outer margin.

Zebina browniana (d'Orbigny)
(fig. 43)

The angular central tooth is about twice as wide as high. The front is deeply concave, and the cutting edge is also strongly curved. An acute main cusp is accompanied by three or four regularly decreasing flanking cusps. The margins of the tooth are convex. Anterior deep depressions are formed into which the ends of the cutting edges of the lateral teeth may fit. The outer posterior corner is cusp-like and thickened. On its upper part a low denticle may be present. The corner is separated from a large basal cusp by a deep cleft. The basal cusps are raised from the basal platform, directing backward. A somewhat angular and slightly raised, tongue-like posterior extension of the base is present between these denticles, and separated from them by a deep indentation.

The lateral tooth is 4.5 times as wide as high and has a very widely extended outer posterior corner. The upturned cutting edge has two parts. The outer part has four to six acute denticles, separate from each other. The inner part consists of the large rounded main cusp with four to six closely set, triangular, inner, flanking cusps. A low central swelling continues from the main cusp across the basal platform to the posterior base where it forms a weak lobe. A low denticle is present on the central part of this swelling. The anterior part of the inner margin forms a wing-like process that fits into the depression on the central tooth. Posteriorly the margin ends in the rounded inner posterior corner. The stalk-like, outer extension of the tooth is flat; the inner marginal tooth rests on it along its entire length. The outer posterior corner is twisted anteriorly.

The inner and the outer marginal teeth are about three times as long as wide. Their apices are turned up to form a spoon-like shape in the inner marginal tooth, being hook-like in the outer one. The inner marginal tooth has about 20 long, narrow cusps. A central ridge supports its stalk. The outer marginal tooth has about 15 low cusps on the inside of the apex, and its stalk is gutter-like in shape.

Barleeia sp.
(fig. 46)

The central tooth is rectangular and a little less than twice as wide as high. Its cutting edge has seven cusps, the central one of which is angular, forming together with the pair of cusps flanking it a right angle with the basal platform. The two outer cusps on each side of this central part of the cutting edge project forward and not upward. The front is weakly concave; the margins are straight to slightly concave, ending in acute posterior corners projecting backward. Between the cutting edge and the central part of the margin, low depressions in the basal platform are formed. The inner ends of the cutting edges of the lateral teeth may fit into these depressions. A pair of long, acute, hook-like basal cusps are attached at the posterior edge of these lateral depressions of the central tooth and project backward. The posterior part of the margin is strengthened by a ridge ending in the posterior corners. The base has low indentations between the corners and a somewhat angular, thickened, tongue-like projection.

The lateral tooth is angular and about two times as wide as high. Its upturned cutting edge has a large, angular main cusp, accompanied by four to five regularly decreasing outer cusps and two inner cusps. The anterior inner margin shows a wing-like process, under which a concavity of the margin is present. A low central swelling continues from the cutting edge to the base. A denticle is found on its lower centre. The base is straight to concave. The outer margin is straight. The outer posterior corner is extended into a long flat stalk that is twisted to the side in its outermost end. The central swelling and its denticle, the inner marginal tooth, can fit almost completely into this stalk and into the groove formed by the cutting edge.

The inner and the outer marginal teeth are of about the same length and about 3.5 times as high as wide. Their apices are hook-like, whereas their stalk is slender and straight. The inner marginal tooth has a central swelling on the stalk and eight cusps on the outer side of the acute apex. The outer marginal tooth has a gutter-like stalk and four or five cusps on the inside of the apex.

Amphithalamus sp.
(fig. 21)

The squarish central tooth is somewhat wider than high. The cutting edge has a large, square, main cusp forming ca. a right angle with the basal platform. It is accompanied by a triangular, flanking cusp on each side. Anteriorly the margins are composed of large, wing-like processes and swollen ridges forming large extended outer corners pointing backward. The anterior, inner, wing-like process of the lateral tooth fits into the depression formed by the wing-like process and the slightly raised centre of the basal platform. Two triangular, large basal denticles are slightly raised above the basal platform and project backward across the base, which has an angular, tongue-like, central projection.

The lateral tooth is as high as wide. Its cutting edge is of the same width as the tooth. It has a triangular main cusp accompanied by three outer and one inner flanking cusps. The inner margin is extended and forms a wing-like process. A deep indentation is developed below it. A central swelling continues from the main cusp of the cutting edge across the basal platform and projects in a long, tongue-like lobe backward. A deep, rounded indentation is present on the base between this lobe and the outer posterior corner. The outer margin is straight.

The inner marginal tooth is about twice as high as wide. Its apex is spoon-like with a denticulate, upturned cutting edge, which has ca. nine acute cusps. Below the concave apex the stalk is supported by a strong median ridge. The base is extended by lateral lamellae and somewhat twisted. The outer marginal tooth is as high as the inner one but hook-like in shape. A few low denticles are present on the inside of the apex whereas the outside is unarmed.

All teeth in each row of the radula fit into each other and are hinged. The upper part of the inner margin of the lateral tooth rests on the depression on the anterior margin of the central tooth. The extended posterior corners of the central tooth fit into the rounded indentation of the inner margins of the lateral teeth. The inner marginal tooth fits into the groove on the outer part of the lateral tooth. The outer marginal tooth fits with its apex into the concavity of the apex of the inner marginal tooth, whereas its stalk rests obliquely on the twisted stalk of the inner marginal tooth.

Cingulopsis sp.
(fig. 22)

The central tooth is clearly smaller than the other teeth in each row of the radula. It is triangular in general shape, with a cutting edge of only about half the width of the tooth. The tooth is somewhat wider than high, has convex margins, a convex front, and a concave base. The posterior corners are rounded and project backward. Four stout basal cusps form a transverse row and point upward with a somewhat posterior inclination. The cutting edge has three low, equally sized denticles. The lower margins of the central tooth fit into deep indentations on the lower inner margin of the lateral tooth.

The lateral tooth is irregularly oval and 1.5 times as wide as high. It is twice as high as the central tooth. The upturned cutting edge has six low, stout cusps of which the third is only slightly larger than the cusps flanking it. The upper part of the inner margin is wing-like in shape; the lower part has a deep indentation.

A sturdy central swelling continues from the cutting edge across the basal platform to the base, where it splits, forming a stout, acute, inner posterior corner and a swelling continuing on the inner base and forming more than a half of the base. A low, rounded denticle is found in the central part of the swelling on the basal platform. This denticle serves in holding the inner margin of the cutting edge of the inner marginal tooth in place when it is folded into the outer concavity of the lateral tooth. The outer margin of the lateral tooth is convex and has an upturned rim in its lower part. The outer posterior corner is acute. Between this and the basal swelling, the base forms a rounded indentation. Between the central ridge and upturned outer margin there is a deep groove, into which the inner marginal tooth may fit.

The inner marginal tooth is more than twice as long as wide. It has a straight, smooth, inner margin, an upturned cutting edge, with four cusps, and an outer margin with three cusps in its lower, central part. The lower of these three marginal cusps may disappear or only be present as a low denticle. The base of the tooth is somewhat twisted and quite broad. Into the niche formed on the outer margin between the cutting edge and the marginal cusps, the cutting edge of the outer marginal tooth may fit.

The outer marginal tooth is half as long as the inner marginal tooth. It is about twice as high as wide. The outer margin is straight in its lower part and forms a hook-like curve in its upper part. The inner margin is short and in a direct line with the cutting edge, which has three cusps. The general shape of the tooth is claw-like.

The teeth of the radula fit tightly into each other and are hinged with each other.

Rissoella caribaea Rehder
(fig. 34)

Only five teeth are found in each row of the radula. The rectangular central tooth is somewhat wider than high. The anterior corners are rounded while the posterior corners are acute. The base is concave. The low, upturned cutting edge is finely denticulate with numerous, small cusps. A furrow is present in the centre of the front. The shallow, shovel-like basal platform is smooth.

The lateral tooth is about as wide as high and about twice as high as the central tooth. It has a hook-like apex on a broad base, with sideways extended posterior corners. The attached base consists of two equally long parts that form a right angle with each other. The inner half is inclined inward, the outer half is inclined outward. The deep groove formed on the basal platform in the curve continues up to the apex of the tooth. The hook-like apex has numerous low cusps on both sides.

The marginal tooth is of a triangular, lamellar shape. It is widest at the upturned cutting edge, which has numerous, low cusps along its whole margin. The margins are straight to somewhat concave and the base of attachment is long.

In the folded radula only teeth following each other in successive rows of the radula fit into each other.

DISCUSSION

The Rissoacea are the largest superfamily of the Mesogastropoda, with more than 1300 living species (Fretter & Graham, 1962). According to Thiele (1931: 137) the superfamily Rissoacea is characterized by a radula with central teeth "often" having basal denticles. Thiele described the radula of the rissoid family Hydrobiidae as follows: The radula is short and fragile. The central tooth is widened posteriorly. It usually has one or more cusps close to the base or the lower margins. The cutting edge is mostly denticulate, rarely smooth. The lateral tooth has a more or less extended, outer basal corner. It usually has a denticulate cutting edge. The marginal teeth are long and narrow, and, as a rule, show finely or roughly denticulate cutting edges. A lamella is often developed on the outer margin of them.

The above description, after Thiele, is so general that it could encompass members of many other mesogastropod families belonging to various different superfamilies. Almost all Rissoacea next to the Hydrobiidae are covered by this definition. A few genera included in different rissoid families in fact have a radula morphology that is quite distinct from that found in the majority of the species. These genera prevent a clear superfamily or family definition as regards radula structure. This may have induced Fretter & Graham (1962) to express the opinion that the superfamily Rissoacea may be an artificial assemblage of small prosobranchs showing a general similarity of external structure.

The radulae encountered in Caribbean representatives of the Rissoacea display quite large differences, but apart from *Rissoella caribaea* they generally agree with Thiele's description of the Hydrobiidae. However, none of them is grouped with the Hydrobiidae in the literature.

The radula of *Assiminea* cf. *succinea* (Pfeiffer) from Colombia is similar to that figured and described by Marcus & Marcus (1965: figs. 35, 36) from *A. succinea vina* Marcus & Marcus and *A. succinea* from Brazil. Troschel (1856-1863: pl. 7 figs. 13, 14) described and figured the radulae of two *Assiminea* species. One of these, *A. grayana* Fleming, looks quite different from the radula of the Caribbean *A.* cf. *succinea*, whereas the other, *A. francesi* (Gray), is quite similar to it. The radula of *Assiminea grayana* was characterized again by Thiele (1931: 169, fig. 147). According to this author the Assimineidae have central teeth not wider than long, with mostly three basal denticles and lateral teeth with an intermediate extension of the inner marginal tooth. The last feature had already been noted and illustrated by Troschel, but this author had not considered the width of the central tooth and the number of basal cusps on it important characters. Comparing the radula of *Assiminea grayana* collected from the river Schelde near Antwerp (Belgium) (fig. 39) with that of *A.* cf. *succinea* from Colombia (fig. 35, 40) quite a number of differences become apparent. The central

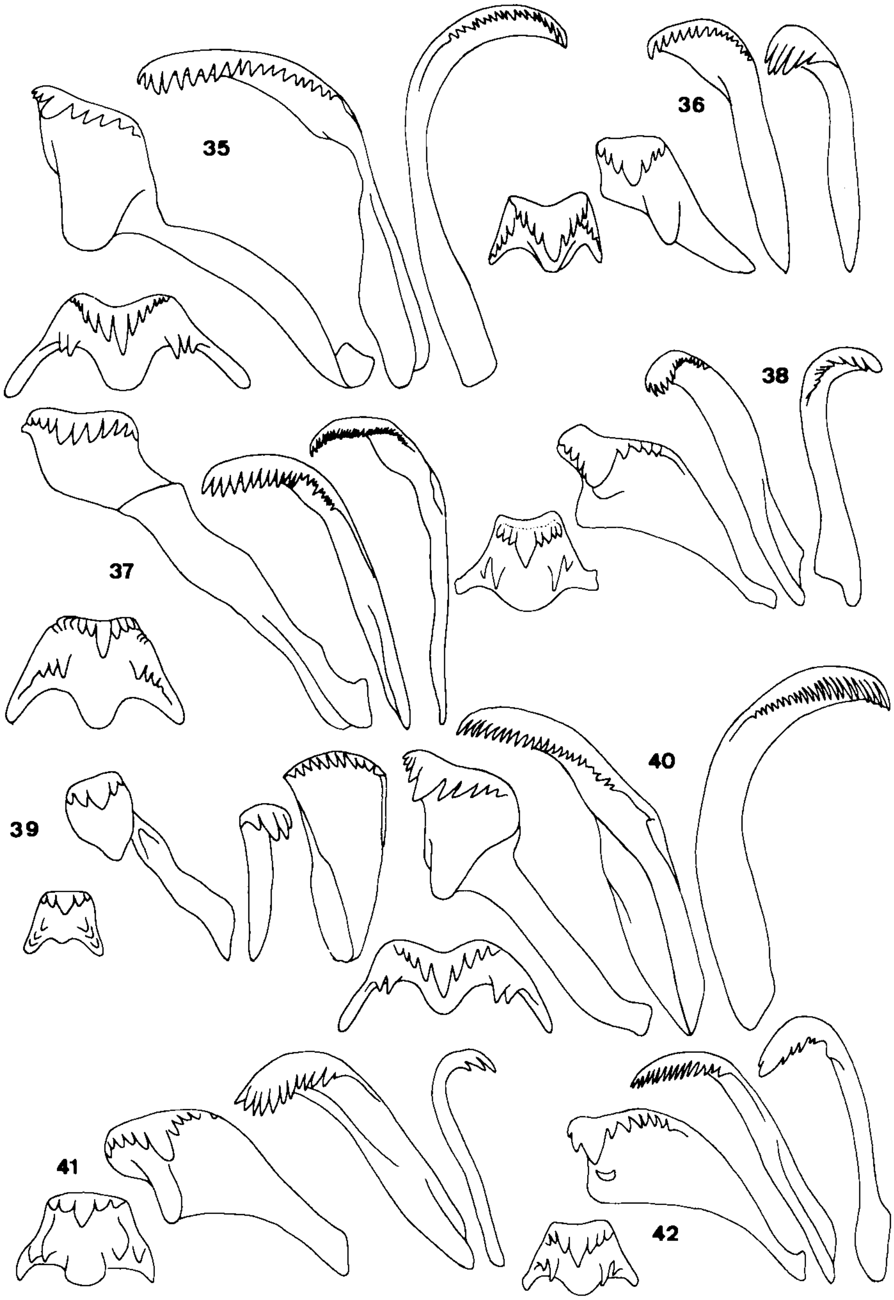


Fig. 35. *Assiminea* cf. *succinea*, a lake between Barranquilla and Cartagena, Columbia; × 800. — Fig. 36. *Bithynia tentaculata*, Laacher See, Germany; × 250. — Fig. 37. *Potamopyrgus jenkinsi*, fresh water pool near Banyuls-sur-Mer, France; × 600. — Fig. 38. *Turboella simplex*, Banyuls-sur-Mer, Mediterranean; × 500. — Fig. 39. *Assiminea grayana*, River Schelde, Belgium; × 500. — Fig. 40. *Assiminea* cf. *succinea*, Cienaga Grande lagoon, Columbia; × 800. — Fig. 41. *Setia amabilis*, Banyuls-sur-Mer, Mediterranean; × 1000. — Fig. 42. *Rissoa auriscalpium*, Banyuls-sur-Mer, Mediterranean; × 450.

tooth of *Assiminea grayana* is square and has a cutting edge almost as wide as the greatest width of the tooth. The lateral tooth has a handle-like extension of the outer posterior corner, strongly separated from the main axis of the tooth; in *A.* cf. *succinea* this extension is still in more close contact with the actual basal platform. In *A.* cf. *succinea* both marginal teeth are quite alike and have basal membranes. In *A. grayana*, however, the inner marginal tooth is slender, without lamellae, and has a cutting edge with only a few cusps, while the outer marginal tooth is greatly widened and shovel-like.

More closely related radulae to those seen in *A.* cf. *succinea* occur among members of the genus *Potamopyrgus*. The broad central tooth, as in *A.* cf. *succinea* (and *A. francesi* of Troschel), has also been noted in the genus *Potamopyrgus* by Winterbourn (1970: fig. 12a). This author discovered that within the genus *Potamopyrgus* the radulae of different species are very similar and cannot be used for taxonomic differentiation of the species. The special features of the widely extended outer posterior corner of the lateral tooth remained unnoticed. Winterbourn (1970), Seifert (1935: 238-239, fig. 2d), and Thiele (1931: 141) studied the radula of *Potamopyrgus jenkinsi* (E. A. Smith) but did not discover the flexible connection and thus the separation of the outer extension of the lateral tooth from its basal platform. The radula of *P. jenkinsi* was studied again in specimens from Southern France (fig. 37). Here the central tooth is like that of *Assiminea* cf. *succinea* in all essential details, being only slightly less wide. The lateral teeth show the same characters as noted in the Caribbean species. The outer extended posterior corner is clearly separated from the basal platform by a flexible membrane. The inner marginal teeth of *A.* cf. *succinea* and *P. jenkinsi* are similar, while the outer marginal tooth of the latter has a somewhat more spoon-shaped apex. The very close resemblance in the radulae of these Colombian and the French rissoacean species indicates that both belong to the same genus.

Krull (1935: fig. 6) showed that the central tooth of *Lithoglyphus naticoides* (Pfeiffer) (= *L. fuscus* of Troschel, 1856-1863: pl. 7 fig. 12) is very similar to that of *Potamopyrgus jenkinsi*. The radulae are similar in all essential features, only the outer posterior extension of the lateral tooth is shorter and, most probably, not separated from the basal platform. The same applies to the radula of *Bithynia tentaculata* (Linné) (fig. 36; Troschel, 1856-1863: pl. 7 fig. 8; Krull, 1935). Individuals of *B. tentaculata* from the Laacher See (Germany) were studied in detail. The central tooth of this species is less wide than that of *P. jenkinsi*, but still wider than high. In many regards it comes closer to the central tooth of *A. grayana*. Usually three or four basal denticles are present, while in *P. jenkinsi* studied three only. Krull (1935), however, showed that this feature is quite variable. Three or four basal denticles were present in Baltic representatives of *P. jenkinsi* and three to five in specimens of *B. tentaculata* from the same area. All these interconnections between the genera *Assiminea*, *Potamopyrgus* and *Bithynia*, all with usually three basal denticles on the central tooth, demonstrate the close relationships of the Assimineidae, Hydrobiidae and Bithyniidae, at least regarding the genera mentioned.

Assiminea cf. *succinea* varies between two and three in the number of basal cusps on the central tooth, with three more commonly present. Among members of the genus *Rissoa* and related genera two basal denticles are usually found. *Zebina browniana* is a Caribbean representative of this group with a rather typical radula (fig. 43). Normally the second pair of basal denticles on the central tooth is somewhat larger than in *Assiminea*. Wide central teeth, as in *Z. browniana*, have been found among Mediterranean representatives of the genera *Rissoa*, *Setia*, *Turboella*, and *Alvania* collected near Banyuls-sur-Mer in Southern France (figs. 41, 42, 44, 45). Certain small differences encountered between the species regarding the features of the central tooth are the presence or absence of a frontal rim, the size and depth of the wing-like depression on the anterior margin, the twisting and shape of the posterior corners, and the size, shape and thickness of the basal projection. The number of cusps flanking the main cusp on the cutting edge is variable, not only among different species, but also among different individuals of a single species and individual teeth within the same radula.

The lateral tooth of *Zebina browniana* is very wide due to its extremely long extension of the outer posterior corner. Usually it is not quite as wide (generally

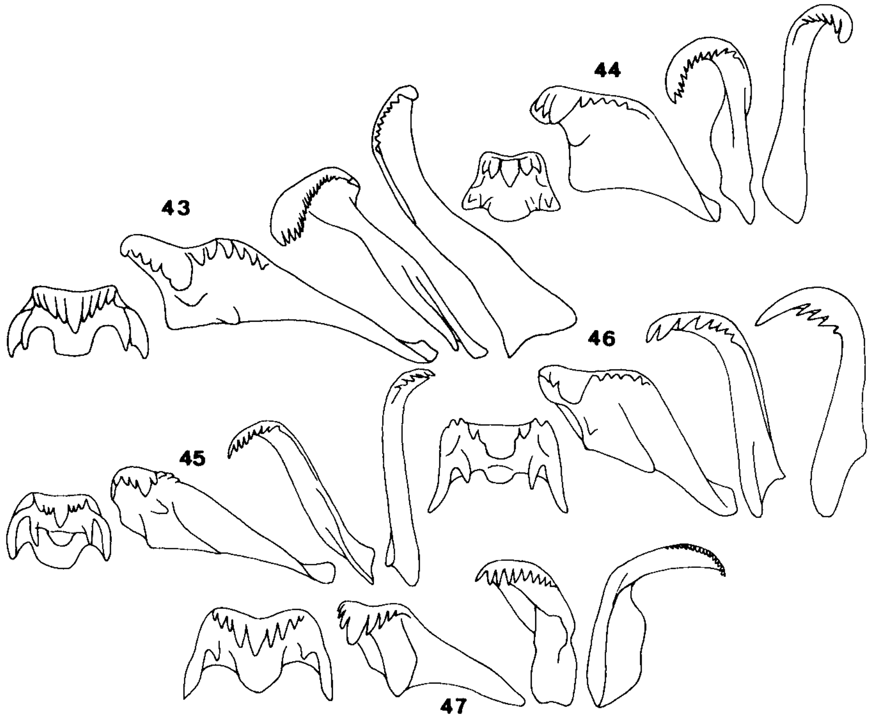


Fig. 43. *Zebina browniana*, Curaçao, Caribbean; × 200. — Fig. 44. *Rissoa violacea*, Banyuls-sur-Mer, Mediterranean; × 450. — Fig. 45. *Rissoa reticulata*, Banyuls-sur-Mer, Mediterranean; × 500. — Fig. 46. *Barleeia* sp., Santa Marta, Caribbean; × 1000. — Fig. 47. *Hydrobia cornea*, brackish water of a lagoon near Perpignan, France; × 600.

only two to three times as wide as high) among related genera. The cutting edge generally shows the arrangement of cusps as present in *Z. browniana*, with acute, loosely arranged cusps on the outside of the main cusp and closely set, triangular cusps on its side. The number of cusps is again quite variable in both individuals and among various species. The inner and the outer marginal teeth of *Z. browniana* are rather typical for the whole group, i.e. for most Rissoidea. The inner marginal tooth usually has a central supporting ridge, while the outer one has a gutter-like stalk.

The radulae of many species of the *Rissoa* group are very close to each other in their morphological features and do not support the extensive generic splitting of this group.

The outer part of basal denticles on the central tooth of *Zebina browniana* is quite small. In *Barleeia* sp. (fig. 46) these denticles are completely absent, even though the ridge from which such a denticle should project is well developed. A radula very similar to that of the Caribbean *Barleeia* is found in the Mediterranean species *Rissoa* (*Turbona*) *reticulata* (Montagu) (fig. 45). Only small differences in the shape of the cutting edge of the central tooth and the number of cusps on the other teeth are found. This might indicate a close relationship between the Mediterranean species with its strongly sculptured shell and the Caribbean species with its smooth shell.

The presence of only one basal denticle on the central tooth is also most common among radulae of different species of the genus *Hydrobia* (fig. 47). The radulae of *Barleeia* and *Zebina* from the Caribbean differ from that of *Hydrobia* in the presence of marginal lamellae on the stalk of the marginal teeth in the latter genus. These lateral lamellae on the marginal teeth of *Hydrobia* link this genus with *Potamopyrgus*, where such features are also present.

The radula of *Amphithalamus* sp. (fig. 21) differs from the rissoid radulae discussed above. This is less so with regard to the central tooth, even though it resembles that of *Laevilacunaria*, an Antarctic littorinid (fig. 24). The lateral tooth has features not seen in the Rissoidae, Hydrobiidae, Bithyniidae, or Assimineidae. A deep indentation in the outer part of the posterior base reminds the one of the littorinids, where this is a feature found among most species. The marginal teeth also differ from those of the rissoids mentioned, which have a shorter stalk. The stalk of the inner marginal tooth is twisted inward in such a way that the outer marginal tooth may fit into it. The apex of the outer marginal tooth fits into the concavity of the cutting edge and the raised central swelling of the stalk supports the outer margin of the lower stalk of the outer marginal tooth. Thus the outer marginal tooth fits very tightly into the inner marginal tooth, but in a completely different way as in *Assiminea*, *Zebina* or *Barleeia*.

A radula very similar to that of *Amphithalamus* was found in *Pisinna punctulum* (Philippi) from the Mediterranean (fig. 23). It only differs from the Caribbean species by the number of cusps on the single teeth. Radulae of similar shape have been described for members of a rissoid family not separately mentioned by Taylor & Sohl (1962), i.e. the Eatoniellidae. Ponder (1965: pl. 4 fig. 7; pl. 5 fig.

6; pl. 8 figs. 4, 14; pl. 10 fig. 5; pl. 11 fig. 11) and Barnard (1963: fig. 36) have described radulae of members of this family. While species of the genus *Eatoniella* have posterior corners similar to those of *Amphithalamus* and *Pisinna*, but no basal denticles, the *Crassitonella* species (Ponder, 1965: pl. 10 fig. 5) have six such denticles. *Amphithalamus* and *Pisinna*, therefore, have radulae with teeth intermediate between these two types of central teeth with two denticles. The essential character in *Eatoniella* is the morphology of the lateral tooth and that of the marginal teeth, which, according to Ponder's illustrations, could well be hinged and fitting into each other as in *Amphithalamus* and *Pisinna*.

Cingulopsis sp. (fig. 22) from Santa Marta has teeth which in most of their characters are quite different from those seen in the other Rissoacea, apart from the Eatoniellidae. In contrast to the Eatoniellidae, however, the central teeth are much smaller than the other teeth in a row. The dominant lateral tooth is very stout and not wide. It also has a gutter-like, outer part of the basal platform with a raised, outer margin and a deep, rounded indentation on the outer posterior base. Thus this tooth resembles that of the littorinids and the Eatoniellidae. A denticle on the central swelling resembles that seen in most rissoid radulae, but the thumb-like projection of the inner posterior corner was not observed in other rissoaceans but only in littorinids. The inner marginal tooth with its apical dentition and, in addition, a dentition of the lower outer margin, is quite a characteristic feature of *Cingulopsis*, but the way in which the inner marginal tooth is twisted and the outer marginal tooth fits into it, reminds one of the Eatoniellidae.

A radula very similar to that of the *Cingulopsis* sp. was encountered in *Cingulopsis fulgida* (Adams) from the Mediterranean (fig. 25). Here the central tooth is even more reduced in size and at the same time has lost most of the morphological features present in the Caribbean member of the genus. The lateral tooth is quite like that of the latter. The inner marginal tooth only has one cusp or denticle on the outer margin, but is quite like that of *Cingulopsis* sp. in general shape. The outer marginal tooth has the same mode of fitting into the inner marginal one and is also clearly smaller than the latter. Ponder (1965: pl. 15 fig. 12) figured the radula of *Eatonina atomaria* (Powell), which also has the characteristics of *Cingulopsis*.

Judging from the morphology of the radula there is very little evidence that *Cingulopsis*, and with it the Cingulopsidae, is related to the Rissoacea. The Rissoidae, Hydrobiidae, Bithyniidae and Assimineidae of Taylor & Sohl's (1962) classification can be considered closely related to each other from the point of view of radula morphology. In many cases it will be extremely difficult to classify a certain species in one of these families, since there is much overlap between them. The Cingulopsidae and Eatoniellidae are just as close to the Littorinidae as to the Rissoacea.

Fretter & Graham (1962) have raised the question whether some of the rissoacean families, among them the Rissoellidae should be regarded as true Rissoacea or even as Mesogastropoda at all. In the light of the data presented here this question can only be emphasized. *Rissoella caribaea* (fig. 34) has only five teeth in each row of the radula. These teeth are very different from those seen in any of the other rissoaceans studied. The shovel-like shape of the central tooth, with its strong, frontal groove and smooth basal platform, is quite unlike the stout, swollen, rissoacean tooth of the other species.

Troschel (1856-1863: pl. 10 fig. 12) figured the radula of a *Rissoella* species. Here the central tooth had split along the frontal groove and, therefore, gives the impression of a normal taenioglossate radula with a somewhat ill-defined central tooth.

The base of the central tooth in *Rissoella* is concave and there is no tongue-like projection so characteristic for rissoaceans of other families. The cutting edge consists of only the upturned basal platform and not of independent cusps attached to the basal platform. The lateral tooth, with its curved base and the hook-like cutting edge, has no counterpart among other rissoaceans. The same applies to the lamellar marginal tooth. *Rissoella glabra* (Brown) (Thiele, 1931: 178, fig. 162) and *Rissoela elongatospira* Ponder (Ponder, 1966: pl. 2 fig. 13) have teeth similar to those of *R. caribaea*. The Rissoellidae, therefore, should not be included in the Rissoacea because their radula is quite like that of the Pomatiasidae & Chondropomidae (figs. 32, 33) of the Littorinacea.

CERITHIACEA

Petalochonchus erectus (Dall)
(pl. 2 fig. 1)

The radula has 38 rows of teeth. The central tooth is angular, trapezoid, and broader at the base than it is high (ratio 7:5). The posterior corners extend into long, raised projections. They are the extensions of strong, marginal ridges that end anteriorly before reaching the triangular cutting edge, which forms an angle of about 90° with the concave basal platform. The main cusp of the cutting edge is sturdy and acute, and accompanied on each side by three to six increasingly smaller, acute denticles. The base is straight to convex. A rounded denticle is present on the inside of the anterior part of the marginal ridges. The basal platform is triangular, with its narrowest side anteriorly. Here, wing-like processes are present as the extension of the cutting edge; they merge with the middle margins. The inside of the lateral tooth fits into these anterior marginal depressions, continued as deep grooves on the lower sides of the tooth. It is thus hinged with the central tooth.

The rhombohedric lateral tooth is somewhat wider than high. Its triangular cutting edge is turned up, with acute cusps. A stout main cusp is accompanied by three to five outer and two or three inner flanking cusps. The outer margin arches and ends in a moderately drawn out, thin, outer posterior corner. From the margin on a groove extends onto the outer part of the basal platform, into which the inner posterior margin of the inner marginal tooth may fit. The base is weakly concave and ends in an inward projecting, small tip at the inner posterior corner. A central swelling connects the main cusp to the base, where it forms a raised ridge in the central part. A low denticle may be present on the middle of this shallow swelling of the concave basal platform.

The marginal teeth are of similar, hook-like shape. The long stalks have a broadened base and a central supporting ridge, ending on the inner margin at the apex of the stalk. The bilaterally flattened, acute, apical part of these marginal teeth have a dominant main cusp. The inner marginal tooth has three to five outer and two or three inner flanking cusps. The outer marginal tooth has no cusps on the outside, and two to four flanking inner cusps. All teeth are hinged and closely fit into each other.

Petaloconchus varians (d'Orbigny)
(fig. 49; pl. 2 fig. 2)

The radula has about 30 rows of teeth. All teeth are essentially like those in *P. erectus*. The wing-like processes on the anterior margin of the central tooth are even more pronounced. The grooves, depressions and ridges on the lateral tooth are also developed more clearly. The posterior part of the inner margin of the lateral tooth is wing-like and fits deeply into the lateral groove below the posterior marginal ridges of the central tooth. A deep groove runs parallel to the outer margin of the lateral tooth and ends below the cutting edge on one side, and in an indentation of the outer posterior corner on the other side. The outer marginal tooth of each row fits into a groove on the inner marginal tooth and the concavity below the cutting edge of it. The inner marginal tooth fits into the groove of the outer posterior part of the lateral tooth and the concavity below its cutting edge.

Caecum cf. **nebulosum** (Rehder)
(fig. 54)

The central tooth is somewhat wider than high, with angular posterior and rounded anterior corners. The convex cutting edge has about 11 cusps and continues from the centre of the margins along the whole front. The triangular central cusp is stout; it is accompanied by about five regularly decreasing, flanking cusps on each side. The base is straight. The basal platform shows upturned margins, is weakly concave and smooth.

The lateral tooth is about as high as wide. The cutting edge consists of about nine acute, elongated cusps. The inner margin is straight and about twice as long as the cutting edge. A low central swelling continues from the cutting edge parallel to the inner margin and forms a long lobe of the base. The outer margin is convex and inclined outward. It ends in a flexible, thin, outer posterior corner. The base consists of the wide, inner lobe and a deep indentation between it and the outer posterior corner.

The inner marginal tooth is the most prominent feature of this radula, even though it does not cover the central and lateral tooth below it, as in the two other members from this genus described. The apex, with its cutting edge on the upper and inside, is about as long as one third of the width of the tooth. It is connected to a strong outer stalk-like ridge. At the connection to this ridge the apex is bent inward and a deep groove is present here. The cutting edge ends at the groove; the cutting edge has about 15 acute cusps that are not larger than those of the lateral tooth. The apex of the inner marginal tooth has a solid, triangular platform from which the cutting edge is turned up to form a right angle. The straight inner margin continues from the outer part of this platform to the membrane of the radula. Between this and the outer margin with its stalk-like ridge a thin, lamellar basal platform is present. The tooth is fixed with its base along two thirds of its width to the membrane of the radula. The apex with its cutting edge, therefore, projects inward and fits in the space between the lateral teeth of different rows. The end of the cutting edge does not project beyond the end of the cutting edge of the lateral tooth.

The outer marginal tooth is almost as high as the inner one is wide, but consists of only a narrow stalk and a small hook-like apex with about 11 narrow, acute cusps on its inner side. The tooth is almost six times as high as wide and only attached with its narrow base. When the radula is used, the marginal teeth can be spread far out while the inner marginal tooth can only be erected. In the folded radula the gutter-like stalk of the outer marginal tooth rests on the outer ridge of the inner marginal tooth and its apex fits into the concave apex of that tooth.

Caecum antillarum (Carpenter)
(fig. 55; pl. 2 fig. 3)

The central tooth has a long-oval outline and is about twice as high as wide. The cutting edge consists of the upturned front of the basal platform and has about ten acute cusps of which the central three may be somewhat larger than the others. The base is straight and the basal platform smooth with anteriorly upturned margins.

The lateral tooth is triangular. Its cutting edge has about 11 cusps and is about as wide as the central tooth. The inner margin is straight and about twice as long as the cutting edge. A low central swelling runs from the cutting edge to a far extended basal lobe. The outer margin ends in a short, handle-like extension of the outer posterior corner. The outer part of the tooth is thin and flexible. The base has a long inner lobe followed by a deep indentation before ending in the extended outer corner.

The inner marginal tooth is of the same general shape as that described for *C.* cf. *nebulosum*. In contrast to that species it has considerably increased in size in regard to the central and lateral teeth, and these teeth are hidden below it. The eight cusps of the cutting edge are much larger than those of the central and lateral tooth. The inner ends of the apices of both inner marginal teeth in each row touch each other when erected and overlap when folded. The cutting edge of the inner marginal tooth is twice as long as that of the lateral tooth. The cutting edges of the central and lateral teeth cannot project over the rake-like cutting edge of the inner marginal tooth when the radula is in use. Therefore, they are obviously no longer functional. Only the marginal teeth are of use in the gathering of food.

The outer marginal tooth is of the same shape as in *C.* cf. *nebulosum*. It is about five times as high as wide and has about 11 cusps on its apex.

Caecum cf. **floridanum** Stimpson
(fig. 56)

The oval central tooth is as long as wide. The low cutting edge has about 20 low cusps of almost equal size and it continues around the anterior corners to end in the anterior part of the margins. In its centre the front shows a concavity. The base is concave. The basal platform is smooth and raised at the margins. The central tooth is much reduced in size as compared to the other teeth in each row.

On its inner margin the lateral tooth is three times as long as the cutting edge is wide. The cutting edge is about as wide as that of the central tooth and carries about 11 acute, slender cusps. Four to six additional cusps are present on the anterior part of the inner margin. A shallow swelling continues from the cutting edge into a far drawn out, posterior lobe on the inside of the base. This lobe is followed by a deep indentation before the base swings back into the outer posterior corner. The outer part of the lateral tooth outside of the central swelling is thin and flexible.

The inner marginal tooth is quite like that of *C. antillarum* and *C.* cf. *nebulosum* in shape. It is much larger than the central and the lateral tooth, which are almost hidden below these. When the inner marginal teeth are erected their inner ends do not quite touch as in *C. antillarum*. Their apex is much more prominent than that of the central and lateral teeth. The cutting edge is three times as wide as that of the lateral tooth. The eight or nine cusps of this cutting edge are much larger than those of the lateral tooth.

The outer marginal tooth is quite like that of *C.* cf. *nebulosum*. It has 11 cusps and is more than six times higher than wide.

Planaxis nucleus (Bruguière)
(fig. 59; pl. 2 figs. 6, 8)

The radula has about 270 rows of teeth. The central tooth is angular and about 2.5 times as wide as long. The cutting edge is bent upward to form an angle larger than 90° with the basal platform. The triangular, large median cusp is flanked by three or four increasingly smaller cusps on each side. The short margins are straight. The posterior corners are projecting far sideways and are attached to the basal platform of the tooth by a flexible part. A strong rounded denticle is attached to the outer posterior end of the margin where the lamellar posterior extensions are joined to the platform. These low, rod-like extensions are attached by their whole base to the membrane of the radula. The posterior corners end just below the inner margins of the lateral teeth. The base of the central tooth shows two lateral curves between the extended corners and a median, tongue-like process that forms the continuation of a broad supporting ridge over the base. This ridge ends in the main cusp of the cutting edge.

Apart from the extended, outer posterior corners the lateral tooth is higher than wide and has a concave basal platform and rounded, anterior corners. A central supporting ridge continues from a basal tongue across the platform to the central cusp of the cutting edge, which is turned upward, showing five to seven cusps, two or three outer ones, and three or four inner ones next to the strong main one. The margins are convex. The base is convex and has a central lobe where the central ridge ends. The inner posterior corner is rounded, while the outer posterior corner is extended into a long handle-like rod that is attached over its full length to the membrane. This rod is attached to the basal platform of the tooth by a flexible connection and ends at the insertion of the inner marginal tooth on the membrane of the radula.

The inner marginal tooth is sheet-like, about five times as long as wide, and has upturned margins. Its apex is rake-like with numerous, acute, triangular cusps. Its stalk is narrowest where it inserts onto the membrane and widest at its apex. The outer marginal tooth is just as long as the inner one and has also a sheet-like stalk. Its apex is wide and has up to 30 cusps. The cutting edge consists of the upturned anterior front of the stalk and in its centre forms an angle of more than 90°. This upper part of the stalk and the apex of the outer marginal tooth are gutter-like.

The teeth of each row dorsally fit into each other. The outer marginal tooth rests on the broad stalk of the inner marginal tooth and its apex fits just in the concavity of the apex of the latter. The stalks of both marginal teeth together may then be placed onto the long flexible extension of the lateral tooth, while their joint apices fit into the concavity of the lateral tooth.

Planaxis lineatus (Da Costa)
(fig. 57; pl. 2 figs. 5, 7)

The radula has about 100 rows of teeth. The central tooth is similar in shape to a clothes-hanger. It has far extended posterior corners and is almost four times as wide as long. Its front is curved and shows a central sinus. The cutting edge is turned upward, forming a right angle with the basal platform. It consists of one broadly triangular main cusp with two or three smaller denticles on its lateral flanks. The cutting edge extends a little into the margins, which are straight to slightly convex and continue into the extended posterior corners. The base has a strongly projecting, rounded, tongue-like, central lobe, accompanied by two rounded indentations on each side. Two pairs of basal denticles are present. The inner one consists of vertical cusps, the outer are blade-like ridges parallel to the margins. The lateral tooth may rest on the rim formed by these outer basal cusps and the outside of the inner margin.

The rhombohedric lateral tooth is almost four times as wide as high, and has a long, handle-like extension of the outer posterior corner. Its triangular main cusp is flanked by three of four inner and four outer cusps. The basal platform below the main cusp is raised to form a large, rounded denticle which causes the central portion of the basal platform to become convex. The posterior edge is attached to the membrane from the beginning of the straight inner margin to the end of the long handle-like projection forming the outer posterior corner. The outer margin is raised. Anteriorly the inner margin is raised and thickened, while posteriorly a low indentation is seen into which the extended, outer posterior corner of the central tooth fits.

The inner and outer marginal teeth form long, bilaterally flattened sheets with paw-like apices which have more than 12 narrow, acute cusps. The almost identical marginal teeth are about five times as high as wide. The teeth of each row of the radula fit into each other like in *P. nucleus*. There is considerable wear on the teeth of the used parts of the radula.

Modulus modulus (Linné)
(fig. 63; pl. 3 figs. 2, 4)

The radula has about 75 rows of teeth. The central tooth is roughly oval. In side-view there is a flat basal platform extending all the way to the front. A low, triangular crest with the cutting edge is situated on the front at a right angle with the anterior part of the basal platform. The central cusp is very strong, triangular, and acute. It is accompanied by two or three increasingly smaller, acute, triangular cusps. The cutting edge extends into a narrow rim that continues in posterior direction along the margins and slowly declines to the surface of the basal platform. The posterior corners are smoothly rounded. The posterior part of the basal platform is thinner than the anterior part and extends into a strongly convex posterior lobe on the base.

The angular lateral tooth is wider than long; it is attached to the membrane by its whole convex base. The basal platform is smooth and plane. The cutting edge is curved upward and its bilaterally flattened, rounded main cusp is accompanied by one inner and three or four outer cusps. The straight inner margin is curved upward to form a narrow rim. The outer margin is convex. The outer posterior corner of the lateral tooth is connected by a thin, flexible, folded membrane to an intermediate plate. The latter, just beyond its flexible joint with the lateral tooth, is thickened and forms a solid rod, fully attached to the membrane of the radula. The inner marginal tooth inserts on the membrane at the outer end of this intermediary rod.

Both marginal teeth are similar in shape. They are about three times as high as wide. Their shafts are gutter-like and attached to the membrane by a narrow base. The erect upper end is shovel-like bent up, with the cutting edge having four or five rounded and bilaterally flattened prongs. No wear was seen on the used parts of the radula. The central tooth is not hinged to the lateral tooth. The long stalks of the marginal teeth fit onto each other and may rest together on the intermediate plate and its continuation on the outer basal platform of the lateral tooth.

Modulus carchedonius (Lamarck)
(fig. 66; pl. 3 figs. 1, 3)

The radula has about 80 rows of teeth, which resemble those of *M. modulus*. The cutting edge of the central tooth may show two to four flanking cusps on each side of the main cusp. The basal tongue-like projection of this tooth is thickened and accompanied on both sides by depressions of the base. Such a lower part of the posterior inner margin is also present on the lateral tooth. Here a low central swelling is seen on the lower posterior platform that extends into a lobe on the inner base. The outer margin of the lateral tooth is upturned to form a flexible, folded lamella which continues into the intermediate plate, which is attached only by one narrow side. Therefore it stands up like a blade from the membrane of the radula, holding the stalks of the inner marginal tooth tightly at their resting place in the folded radula.

Cerithidea costata (Da Costa)
(fig. 65; pl. 3 fig. 6, pl. 4 fig. 6)

The radula has about 35 rows of teeth. The rounded central tooth is about as wide as high. Its frontal part has evenly rounded corners and a somewhat concave central part. The central cusp of the cutting edge is the largest and is flanked by three to five increasingly smaller cusps. The cutting edge reaches far down the margins and is attached to the very margin of the basal platform. It ends at the posterior corners from which a long, evenly rounded, tongue-like lobe takes its origin and projects backwards. The basal platform is smooth and slightly concave. Central tooth and lateral tooth are not linked but, instead, are attached well apart to the membrane of the radula.

The lateral tooth is roughly rectangular and somewhat longer than wide (if the extended handle-like projection of the outer posterior corner is disregarded). The upturned cutting edge shows a large, acute main cusp that is accompanied by two inner and three outer cusps. The margins are straight and are directed anteriorly. The inner one is raised and ends in a rounded posterior corner. The outer margin has an upturned lamellar rim that is continuous with the lamellar, flexible, rod-like extension of the outer posterior corner. This extension is as long as the lateral tooth is high and continues inclined outward up to the insertion of the inner marginal tooth on the membrane of the radula. The basal platform is smooth and somewhat concave.

The marginal teeth are very similar to each other, both in shape and size. They are about 3.5 times as high as wide, have bilaterally flattened stalks with gutter-like, upturned margins and a broadened, spoon-like apex. The cutting edge of the inner marginal tooth has five or six cusps with rounded tips. The outer marginal tooth has seven or eight narrow, sharply pointed cusps on its cutting edge. Very little wear was noted in used portions of the radula. In the folded radula the marginal teeth fit onto the posterior extension and into the concavity below the cutting edge of the lateral tooth.

Batillaria minima (Gmelin)
(fig. 60; pl. 3 fig. 5, pl. 4 fig. 5)

The radula has about 100 rows of teeth. The roughly quadrangular central tooth is slightly wider than high. Its cutting edge is dominated by the main cusp that stands erect on the frontal edge of the basal platform. The corners of the front are drawn out anteriorly to form shoulders to which the much smaller flanking cusps are attached, two at each side. The outermost of these cusps continues into a narrow ridge which runs half way down the margins. Thus, rounded grooves are formed inside the anterior margins of the tooth into which the anterior inner margins of the lateral teeth may fit in the folded radula. The straight to slightly concave margins of the central tooth end in acute posterior corners projecting outward in a curve. One pair of strong basal denticles is attached to the anterior part of a ridge that forms the edge of the anterior depressions of the basal platform and ends in the posterior corners. The base has two indentations and between it a somewhat angular or rounded, thickened, tongue-like, posterior projection.

The cutting edge of the lateral tooth is dominated by a large, triangular cusp that is flanked by two cusps on each side. The outline of the lateral tooth is rectangular, a bit longer than wide if the extended rod of the outer posterior corner is disregarded. A central swelling ends in a tongue-like process on the base. In the central part of the basal platform this swelling has a strong, rounded basal denticle. The inner margin is raised to a thickened rim. The inner posterior corner is curved and upturned so that the posterior corner of the central tooth fits below it. Between the short projection of the inner corner and the somewhat angular lobe of the central swelling the base is concave. Another concavity of the base is present outside the central lobe. A flexible rod-like extension of the outer posterior corner is the continuation of the outer margin; this extension has a raised outer margin, visible on the membrane of the radula as a low lamellar ridge. These lamellae will hold the stalks of the marginal teeth in resting position when the radula is folded. The extension is as long as the actual tooth is wide and it ends where the inner marginal tooth is attached to the membrane.

The marginal teeth are very much alike and about four times as high as wide. Both have bilaterally flattened, somewhat gutter-like stalks and upturned, claw-like cutting edges at their anterior ends. The inner marginal tooth has five and the outer marginal tooth six or seven strong and acute cusps. Only very little wear of the teeth can be observed on the used parts of the radula. All teeth fit into each other in the folded radula.

Diastoma varium (Pfeiffer)
(fig. 72; pl. 3 fig. 8, pl. 4 fig. 8)

The radula has 25-30 rows of teeth. The quadrangular central tooth is a little wider than high and has angular corners. The five to seven cusps on the cutting edge are attached directly onto the anterior part of the basal platform behind a straight frontal rim. The large central cusp is diamond-shaped and the flanking cusps decrease in size outwards. The margins are straight or slightly concave and end in somewhat elongated acute posterior corners. On the posterior basal platform ridges are present that follow the margins and end in the posterior corners. On the center of each ridge a rounded denticle is present. The base bulges slightly to form a low lobe. The basal platform is concave below the cutting edge and above the posterior ridges. The ends of the cutting edges of the lateral teeth can rest in the depressions present here; they are held in place by the basal denticle at one side and the cusps of the cutting edge at the other side.

The rectangular lateral tooth has an elongated posterior corner. The cutting edge is curved upward and has a rounded main cusp flanked by three outer and one or two inner cusps. A ridge crosses the basal platform, starting at the main cusp and ending in a lobe-like projection of the base. In its lower course this ridge is narrow and strongly raised. On its lower inside the inner margin forms a wing-like process onto which the posterior ridge of the central tooth can fit in the folded radula. The base shows a short inner and a longer outer concavity. The outer margin is raised and continuous with the acute posterior edge. Thus a wide groove is present on the outer platform of the lateral tooth, into which the stalk of the inner marginal tooth may fit.

The marginal teeth are about equal in size, slender and almost four times as high as wide. Their stalk is bilaterally flattened and their apex hook-like and acute. The inner marginal tooth has three or four inner and three or four outer cusps that flank the dominant, apical main cusp. The outer marginal tooth has a smooth outer margin and five or six cusps in the apical region of the inner margin. Only little wear could be observed in the used parts of the radula. All teeth fit well onto each other when the radula is folded.

Alaba incerta (d'Orbigny)
(fig. 71; pl. 4 figs. 1, 9)

About 35 rows of teeth are found on the radula. The rectangular central tooth is wider than long (2:3). The five teeth of the cutting edge are attached directly on the anterior part of the basal platform behind a free, straight frontal rim. The margins are concave. A strong central supporting ridge continues from the main cusp posteriorly to widen near the base, continuing with two branches into the acute posterior corners. The thus formed posterior, transversal ridge carries a pair of minute denticles. Between cutting edge, central ridge, and posterior ridge two deep depressions are formed into which the rounded anterior corners of the lateral tooth may fit exactly. The base is straight.

The lateral teeth are roughly oval in outline, with erect cutting edge and outer margin. The main cusp of the cutting edge is flanked by one or two inner and two outer cusps. In a direct line with the flattened, round main cusp a ridge-like swelling is present on the inner part of the basal platform, ending in a widely drawn out, tongue-like projection of the base. The inner margin has a deep indentation into which the posterior corner of the central tooth fits. The outer margin is extended into an upturned, large, wing-like lamella. This structure may be quite thin and often shows irregular folds in its lower part, close to the moderately extended, outer posterior corner. The base is deeply concave between lobe and outer posterior corner. A wide groove is thus formed between the central swelling and the lamellar process of the outer margin, into which the marginal teeth may fit.

The marginal teeth are about equal in size, long, and slender. The inner marginal tooth is about twice as broad as the outer one. It has a bilaterally flattened basal part of the shaft and a solid, thickened upper part of the stalk. The flattened, acute apex has a large main cusp, flanked by one outer and two inner cusps. The outer marginal tooth is widest at its base, and has an acute apex with a smooth outer margin and three or four cusps on the inner cutting edge of which the outermost is the largest. Only little wear was observed on the used portion of the radula. In the folded radula all teeth fit onto and into each other closely.

Finella dubia (d'Orbigny)
(fig. 69; pl. 3 fig. 7, pl. 4 fig. 7)

The rectangular central tooth is a little higher than wide. The five to seven teeth on the cutting edge are attached to the anterior edge of the basal platform and leave almost no frontal rim. The angle formed by the cutting edge and the basal platform is a little less than 90°. The margins are concave and end in rounded posterior corners. The base is straight. The basal platform has depressions near the central margins. The rounded ends of the cutting edges of the lateral teeth fit into these depressions. Otherwise the basal platform is smooth.

The lateral tooth is broadly ovate, with rounded corners and erect cutting edge. The strong, bilaterally flattened main cusp is flanked by one inner and four to seven outer cusps. The margins of the main cusp may be smooth or regularly serrated. A weak ridge is present on the inner part of the basal platform, ending in a moderately extended lobe of the base. The outer posterior corner is rounded and extends only very little outwards. The outer margin is smooth and may show a very narrow, flexible lamella along its whole course.

All marginal teeth are of about the same shape and length. They are slender and narrow, about three times as high as wide and have bilaterally compressed stalks, which are broadened in their lower part, having acute apices with a long main cusp on the upper part. The inner marginal tooth has three to five cusps on each side of the main cusp. The outer marginal tooth has five or six flanking cusps on the inside of the main cusp and an unarmed outer margin. No wear was observed on the teeth in the used portion of the radula. The teeth of each row may be well folded onto each other. The outer marginal tooth rests on the flat stalk of the inner one and its hook-like apex fits into the apical concavity of this tooth. Both together fold below the cutting edge of the lateral tooth, which rests with its inner margin on the central tooth.

Cerithium atratum (Born)
(fig. 76; pl. 4 figs. 4, 12)

The radula has about 50 rows of teeth. The rectangular central tooth is a little wider than long. Its cutting edge consists of five cusps which are attached directly onto the basal platform. The solid, diamond-shaped central cusp stands erect not quite at the anterior front of the platform. Thus a frontal rim is present. The flanking cusps decrease in size in outward direction and may be attached closer to the front than the main cusp. The margins are often raised anteriorly into a narrow ridge or may be on the same level as the basal platform. The posterior corners may be drawn out into points. A shallow, posterior, tongue-like projection extends from the base. Two crescentic ridges are present on the base flanking each side of the central projection. The semicircular ridges have their open sides towards the base.

The rectangular lateral tooth is about 1.5 times as wide as high and has a handle-like extension of the outer posterior corner. Its cutting edge is upturned and has a rounded or triangular main cusp with one inner and two or three outer cusps. The basal platform has a central swelling with a small, rounded denticle in the middle. This swelling extends into a strong, posterior, tongue-like projection of the base. The inner margin forms a wing-like, posterior part with a rounded, inner posterior corner. The base forms a shallow sinus between the lobe and the moderately extended, outer posterior corner. The outer margin is turned up to form a lamella.

The marginal teeth are about four times as high as wide and have a bilaterally compressed stalk. Apically they are a little wider than at their stalks. The apex has five to seven acute cusps on the cutting edge of the inner marginal tooth. The outer marginal tooth has an unarmed outer cutting edge and three to five rounded inner cusps, the outer of which is the largest. The teeth of each row can fit well onto each other when the radula is folded. The anterior shoulders of the central tooth fit on the wing-like processes of the lower inner margin of the lateral teeth.

The marginal teeth fit onto each other with their flat stalks and equally bent apices; together they fit into the groove formed by the raised outer margin and the cutting edge of the lateral tooth.

Cerithium litteratum (Born)
(fig. 81; pl. 4 figs. 3, 11)

The radula has about 50 rows of teeth, which in almost all respects are like those of *C. atratum*. Only the lateral tooth shows on its cutting edge one inner and three or four outer cusps; its outer margin is elongated to a strong, wing-like lamella.

Cerithium lutosum (Menke)
(fig. 78; pl. 4 figs. 2, 10)

About 60 rows of teeth are counted on the radula, which are quite like those of *C. atratum*, with the only difference that the outer margin of the lateral tooth is extended into a lamella as in *C. litteratum*.

Seila adamsi (H. C. Lea)
(fig. 84; pl. 5 figs. 1, 5)

The radula has about 30 rows of teeth. The central tooth is rectangular, with angular corners and straight sides. It is twice as wide as long. The cutting edge is situated right at the anterior edge of the basal platform, forming a right angle with it. It has five to seven cusps of quite unequal size. The central cusp is intermediate in size and flanked by smaller cusps on each side. The following pair of cusps is the largest on the cutting edge. A smaller pair of denticles may be present on the corners of the cutting edge. A central swelling starts in the central part of the cutting edge and continues backward across the basal platform to end in a solid, round, knob-like cusp projecting upward. Apart from this tongue-like denticle the basal platform is smooth.

The rectangular lateral tooth is wider than long (5:2). All sides are straight and all corners are angular but do not form right angles as in the central tooth. The cutting edge, with its three cusps, is attached to the inner, anterior part of the basal platform. The main, innermost cusp is solid and acute, two smaller cusps are situated on the inside. A broad swelling forms most of the outer part of the basal platform. Only a triangular, acute, outer posterior corner extends outwards from it. This broad swelling projects into a low lobe over the posterior base, which otherwise is straight.

The inner and the outer marginal teeth are quite alike in size and shape. They are about five times as long as wide, sheet-like and, with the exception of the denticulate apex, rectangular in shape. The stalk is smooth and the apex has a bunch of three to seven thin, flexible, outer, hook-like cusps, a median, hook-like cusp and a short, knob-like inner cusp. No wear was observed on the teeth of used parts of the radula. The teeth of the radula are not hinged. In the folded radula the flat marginal teeth rest on each other and all together on the flattened swelling of the outer basal platform of the lateral tooth.

Triphora nigrocincta (C. B. Adams)
(fig. 86; pl. 5 figs. 2, 3)

The rectangular central tooth is about three times as wide as long. The cutting edge consists of a row of hook-like cusps directly attached to the anterior edge of the basal platform. The centre of the cutting edge has the largest pair of cusps, which are separated from each other by a gap. Three or four more cusps are present on both sides of this pair. The outermost pair is as large as the central pair, while the intermediate cusps are somewhat smaller but equal to each other. The front is convex with a shallow lobe in the centre where the gap in the cutting edge is situated. The margins are straight, and the anterior and posterior corners have right angles. The posterior part of the otherwise smooth basal platform has a rounded, solid knob opposite the gap in the cutting edge. This short, tongue-like process projects somewhat over the straight base.

The lateral tooth is very similar to the central one, both in outline and size. It is somewhat wider than three times its own height and also shows a gap in the cutting edge. This gap, however, is not situated at the centre of the cutting edge but more outward. There are five to seven cusps on the inside of this gap, which become smaller in inward direction. Three larger cusps make up the outer part of the cutting edge. The inner margin is rounded, the outer is bulging convexly. The base is straight. A rounded basal denticle is present opposite the gap on the basal platform, which denticle projects somewhat over the base.

There are three marginal teeth which are equal in length. The inner one has a thickened, bulging, basal knob from which the thin, flexible, slender, narrow cusp arises. The intermediate marginal tooth still has a bulging base, but the actual tooth is more sickle-shaped, solid and blade-like with an acute apex. The outer marginal tooth shows only a moderate swelling of the base and is arrow- and blade-like with smooth margins. No wear was observed on teeth of the radula. The teeth are arranged side by side and not hinged. The marginal teeth cannot fit into special structures on the lateral teeth, but simply fold onto them.

Triphora turristhomae (Holden)
(fig. 95; pl. 5 figs. 4, 6)

The radula has about 200 rows of extremely small teeth. All ca. 28 teeth in a transverse row are about identical in shape and size. Usually they show three, more rarely two, hooked, solid cusps. These are attached to a short basal platform with one central basal denticle. The margins and the base are straight. No wear was noted on any tooth of the radula. The teeth are not hinged and cannot be folded onto each other.

DISCUSSION

Two conchologically very similar species of the Vermetidae, i.e. *Petaloconchus erectus* (Dall) and *P. varians* (d'Orbigny), were studied from Santa Marta specimens. Both are sessile, filter-feeding gastropods that live attached to rock and coral surfaces. *P. varians* lives in the tidal zone, mostly in the splash zone or in tidal pools. *P. erectus* lives among soft corals at a few meters of depth.

In the Vermetidae mucus threads and ribbons, produced with a gland of the foot, are often used to catch planktonic food. Boettger (1930) observed that *Vermetus gigas* Bivona caught mainly small crustaceans in this way. From time to time the mucus threads are eaten, together with the planktonic organisms stuck to them, regardless whether animal or plant. The large mucus nets which are produced at regular intervals by *Dendropoma maxima* (Sowerby), living on the crest of coral reefs in the Red Sea, are eaten by a zipper-like action of the lateral and marginal teeth, as was observed by Hughes & Lewis (1974).

The radulae of the closely related *Petaloconchus erectus* and *P. varians* are compared with those of other Vermetidae, as *Bivonia triquetra* (Bivona) (fig. 51) from the Mediterranean, *Dendropoma maxima* (fig. 50) and two unidentified Vermetidae from the Red Sea (fig. 52), which are very similar to *Petaloconchus* or *Bivonia* conchologically. The radulae of all these species proved to be very similar to those of the two Caribbean species.

The central tooth of the vermetids studied shows a trapezoidal outline, the cutting edge is wider than the anterior part of the basal platform and the sides of the cutting edge curve backward to form wing-like processes. All this was already noted by Troschel (1856-1863). The inner margin of the lateral tooth fits into the deep marginal depressions of the central tooth and into the grooves on the sides of its posterior margin. The marginal ridges of the central tooth end in long, acute, posterior corners. At the inside of these ridges one pair of rounded denticles is present. Troschel (1856-1863: pl. 13 figs. 1, 3, 4) discussed and illustrated the radulae of three species of Vermetidae and observed a pair of basal denticles in one case only, but he dit not figure this (pl. 13 fig. 4). The denticles were also overlooked by Barnard (1963: fig. 28a-d). This author described the radula of *Vermetus periscopium* Barnard and mentioned its close resemblance to that of *P. erectus*.

The lateral tooth of all species of Vermetidae studied show a triangular cutting edge and a posterior ridge that follows the inner base and carries a rounded basal denticle. A deep groove ends in the outer posterior corner or close to it on the outer part of the base. Into this groove the stalk of the inner marginal tooth may rest and held tightly in place.

The marginal teeth of the other Vermetidae studied may be even more solid than those seen in the Caribbean representatives of *Petaloconchus*, but are in

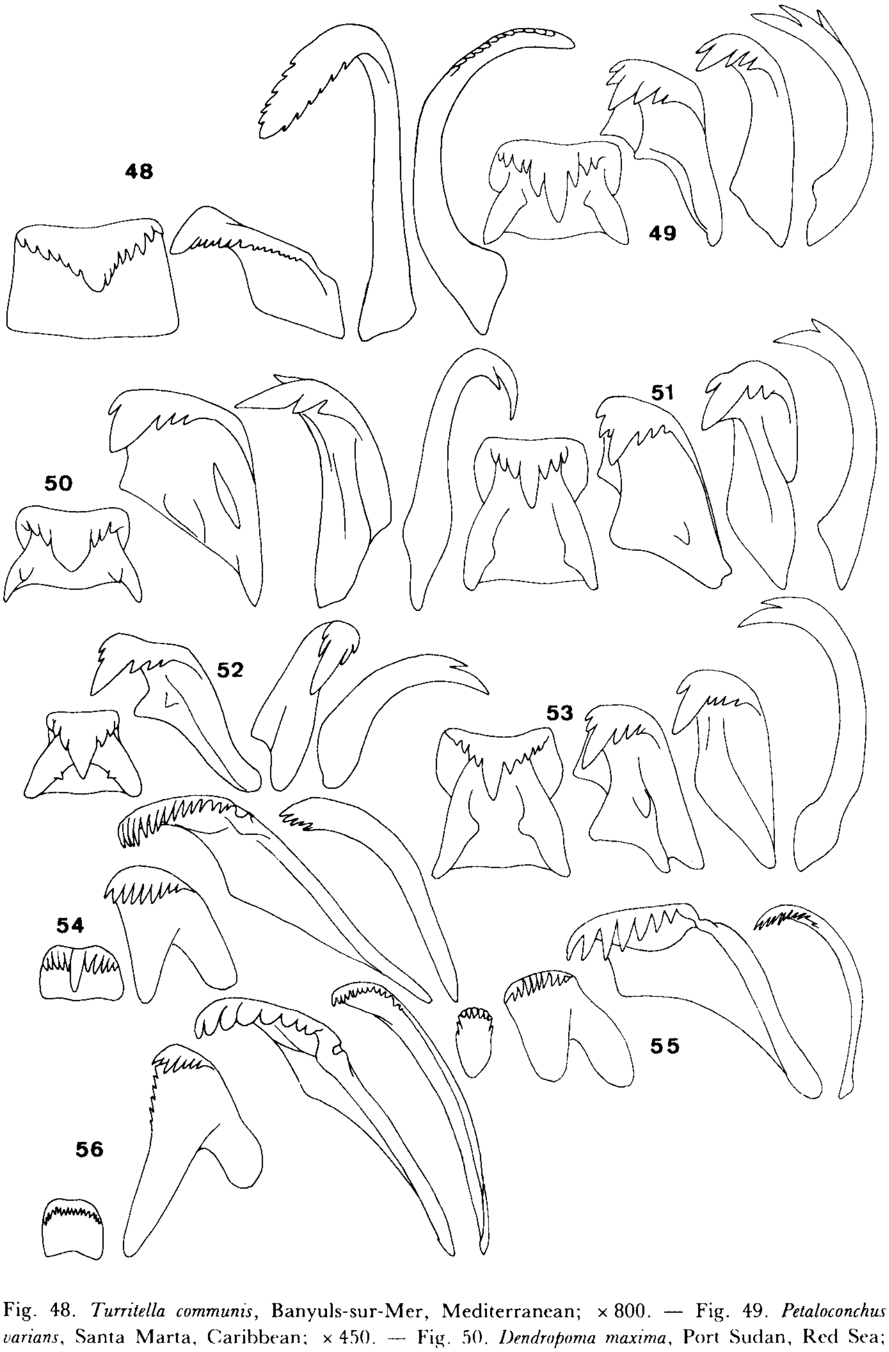


Fig. 48. *Turritella communis*, Banyuls-sur-Mer, Mediterranean; × 800. — Fig. 49. *Petaloconchus varians*, Santa Marta, Caribbean; × 450. — Fig. 50. *Dendropoma maxima*, Port Sudan, Red Sea; × 90. — Fig. 51. *Bivonia triquetra*, Banyuls-sur-Mer, Mediterranean; × 150. — Fig. 52. *Vermetus* sp., Port Sudan, Red Sea; × 100. — Fig. 53. *Vermetus* sp., Fuerteventura, Canary Islands, Atlantic Ocean; × 200. — Fig. 54. *Caecum* cf. *nebulosum*, Santa Marta, Caribbean; × 1500. — Fig. 55. *Caecum antillarum*, Santa Marta, Caribbean; × 1400. — Fig. 56. *Caecum* cf. *floridanum*, Santa Marta, Caribbean; × 2300.

general shape just like those of this genus. The outer marginal tooth never has cusps on its outer margin. Thiele's (1931: 185) description of the radula characters of the Vermetidae is quite general. Nothing is said of any of the features of the central and the lateral tooth, here considered the most characteristic of this group of gastropods. The marginal teeth of the Vermetidae in Thiele's description are characterized as quite short, while they may also be quite slender, long and thin.

Boettger (1930) thought that the radula of *Vermetus* is similar to that of *Turritella*, which is also a filter feeder. Judging from some of the data in the literature (Troschel, 1856-1863: pl. 12 figs. 11-13; Barnard, 1963: fig. 32b, c) the radulae seem to be quite close to each other. Therefore, the radula of *Turritella communis* Risso from the Mediterranean was studied (fig. 48). The extremely small radula of this species agrees quite well with data in the literature on other members of the genus *Turritella*. If compared with Vermetidae, however, none of the important features of the teeth is present. The central tooth of *T. communis* has a smooth basal platform, a concave base and neither solid, acute posterior corners nor basal denticles. This tooth is not jointed with the lateral tooth. The latter is also unmodified and smooth, showing neither a strong, basal swelling nor a deep groove on the outer basal platform. The marginal teeth of *Turritella* are hook-like as in the Vermetidae, but have a rounded apex. In contrast to *Petaloconchus* and related species the outer marginal tooth of *Turritella* is denticulate on its outer margin.

All these differences between *Turritella* on the one hand and *Petaloconchus* and *Vermetus* on the other hand show that, judging from the morphology of the radula, no close relationship between these genera, nor perhaps between the Turritellidae and the Vermetidae in general, can be assumed.

Because of the great similarity of the radulae it seems unwarranted to split the vermetids into many different genera. According to their radula morphology, *Vermetus*, *Bivonia* and *Petaloconchus* should be considered to form only one genus.

The three representatives of the Caecidae from Santa Marta collect their food with a slender proboscis. The mouth is pressed against the substrate and diatoms and other particles are collected by the action of the radula. While Morton (1975) observed that the radula of *Caecum digitulum* Hedley consists of only 13 rows of teeth, Marcus & Marcus (1963) counted 70-80 rows in *C. pulchellum* Stimpson. The latter number coincides with the species represented here.

The radulae of the two Mediterranean species *Caecum vitreum* Carpenter and *C. auriculatum* (Folin) were also studied for comparison and showed essentially the same features as those of the three Caribbean species.

The radulae of the Caecidae studied here have a small central tooth that is quite variable in the different species. In *C.* cf. *nebulosum* the semicircular central tooth is used to gather food; it has a smooth basal platform, a simple base, and a cutting edge with many cusps. The cutting edge is continuous onto the margins. The central tooth is similar in *C.* cf. *floridanum*, but here the cusps of the cutting edge have become more delicate and are reduced in size. The tooth is also provided with a less solid basal platform than that in *C.* cf. *nebulosum*. The central tooth of *C.* cf. *floridanum* is not used any more to collect food and thus has lost its function. The two Mediterranean species are somewhat intermediate in the shape of their central teeth between *C.* cf. *nebulosum* and *C.* cf. *floridanum*. The central teeth of *C. antillarum* are not functional. They are longer than wide and completely hidden below the cutting edge of the dominant inner marginal teeth.

The lateral tooth of *C. antillarum* also serves no obvious function of the radula. In shape it is like the lateral teeth in the other species studied. While this tooth, most probably, is also not functional in the radula of *C.* cf. *floridanum*, it still could serve in collecting food in the radulae of *C.* cf. *nebulosum*, *C. vitreum* and *C. auriculatum*. The lateral tooth characteristically shows a very long, low swelling that follows the inner margin into a far extended lobe of the base. The outer part of the basal platform has been reduced in thickness to such a degree that it has become flexible and largely fused with the membrane of the radula.

In *Caecum* the inner marginal tooth has become the dominant feature of the radula. It is attached along much of its width; only the apical region projects inward as far as the inner margin of the lateral tooth (in *C.* cf. *nebulosum* and the two Mediterranean caecids) or even further inward (in *C.* cf. *floridanum* and *C. antillarum*). In the last two species the strongly denticulate cutting edge of the marginal tooth, when erect, stands high above the cutting edges of the central and the lateral teeth.

Authors describing the radula of members of the genus *Caecum* have not realized that the inner marginal tooth is attached over so much of its width. Morton (1975: fig. 8b) describes the marginal tooth of *Caecum digitulum* Hedley as long and slender, with claw-like terminal cusps with minute denticles. While comparing the radula of *C. pulchellum* with that of *C. glabrum* (Montagu) Marcus & Marcus (1963) state that in both species the inner marginal tooth is the strongest and shows a scythe-like, strongly denticulate cutting edge that is somewhat separated from the straight, long shaft of this tooth. A similar picture of the inner marginal tooth was presented by Götze (1938: 77).

In contrast to the inner marginal tooth, the outer one can move freely to the outside, because it is attached to the membrane of the radula only by its narrow base, having a very slender, long stalk.

Götze (1938) expressed the opinion that the radula of the Caecidae resembles to some degree that of *Cerithium* or *Hipponix*. This idea could not be verified. Both genera have inner marginal teeth which in no way are similar to the characteristic inner marginal teeth of *Caecum* (figs. 54, 55, 56). The other teeth in the radula of *Cerithium* and *Hipponix* are also quite different from those of *Caecum* which can easily be seen by comparing the figures 73-83 and 115-117.

Marcus & Marcus (1963) suggested that Caecidae and Hydrobiidae may be related to each other. However, great differences exist between the radula of *Caecum* (figs. 54-56) and that of *Hydrobia* (fig. 47). The only factor in favour of the suggested classification by Marcus & Marcus could be found in a certain similarity of the inner marginal teeth. Those of *Hydrobia* have a lamella on the stalk and a twisted apical part not unlike that in *Caecum*. But the lamella on the base of the stalk is not attached in *Hydrobia* and the tooth serves a different function; it articulates liberally, while the inner marginal tooth of *Caecum* can only be erected.

The assignment of the Caecidae to the Cerithiacea close to the Vermetidae and the Thiaridae (Taylor & Sohl, 1962) should not be understood as indicating a close relationship between these families. The Caecidae have a radula that is essentially different from that of the Vermetidae and in most features also different from that of the Thiaridae.

The Planaxidae are represented by two Caribbean species. *Planaxis lineatus* lives just below the tidal zone, while *P. nucleus* lives within the tidal zone. Both species graze algae from the rocks. In addition the radula of *Planaxis sulcatus* (Born) from the Red Sea was studied (fig. 58); this species, just like *P. nucleus*, lives in the splash zone on more or less quiet pebble or rocky beaches.

In *P. sulcatus* the central tooth is more or less intermediate in shape to that of the two Caribbean species of the same genus. As in *P. lineatus* the extended outer and posterior corners are present as rods attached to the posterior part of the margins, but not with flexible joints as in *P. nucleus*. The basal denticles on the central tooth of *P. sulcatus* are close in shape to those of *P. nucleus*, while the triangular cutting edge of this tooth resembles more that of *P. lineatus*. The inner margin of the lateral tooth in *P. sulcatus* rests on the margins and the extensions of the central tooth in the folded radula, similar to the situation in *P. lineatus*. The handle-like, extended, outer posterior corner of the lateral tooth of *P. sulcatus* is in length and shape like that of *P. lineatus*, but articulates with the basal platform as in *P. nucleus*.

Troschel (1856-1863: 151, pl. 12 figs. 7, 8, 9) described and figured the radulae of three *Planaxis* species. He noticed the long, rod-like extensions of the central tooth and that of the lateral tooth. Troschel's drawing of the radula of *P. nucleus* (pl. 12 fig. 9) shows rather short posterior extensions of the central tooth, while the very long extension of the lateral tooth is shown correctly. Troschel, in contrast to Thiele, did not mention lamella-like extensions of the outer margin of the marginal teeth. Such lamellae are mentioned by Thiele (1931: 202-203) as characteristic for the radula of the Planaxidae. A lamella on the stalk of the outer marginal tooth was figured by Risbec (1935: figs. 14, 15) for *Planaxis sulcatus*, but this drawing does agree so poorly with the radula from *P. sulcatus* from the Red Sea, that it might represent another species.

Troschel (1856-1863: 150) described the lateral tooth of the radula of *P. sulcatus* to have a thickened area on its handle-like, posterior extension, which might easily be mistaken for a separate, little plate. In fact, Barnard (1963: fig. 32a) described and figured an accessory plate between lateral and inner marginal tooth. From the material studied here from Port Sudan it is evident that the radula of *P. sulcatus* has been characterized best by Troschel (1856-1863: pl. 12 fig. 7), it is less well figured by Thiele (1931: fig. 195a), and even worse by Barnard (1963: fig. 32a), whereas Risbec's (1935: figs. 14, 15) figures are most

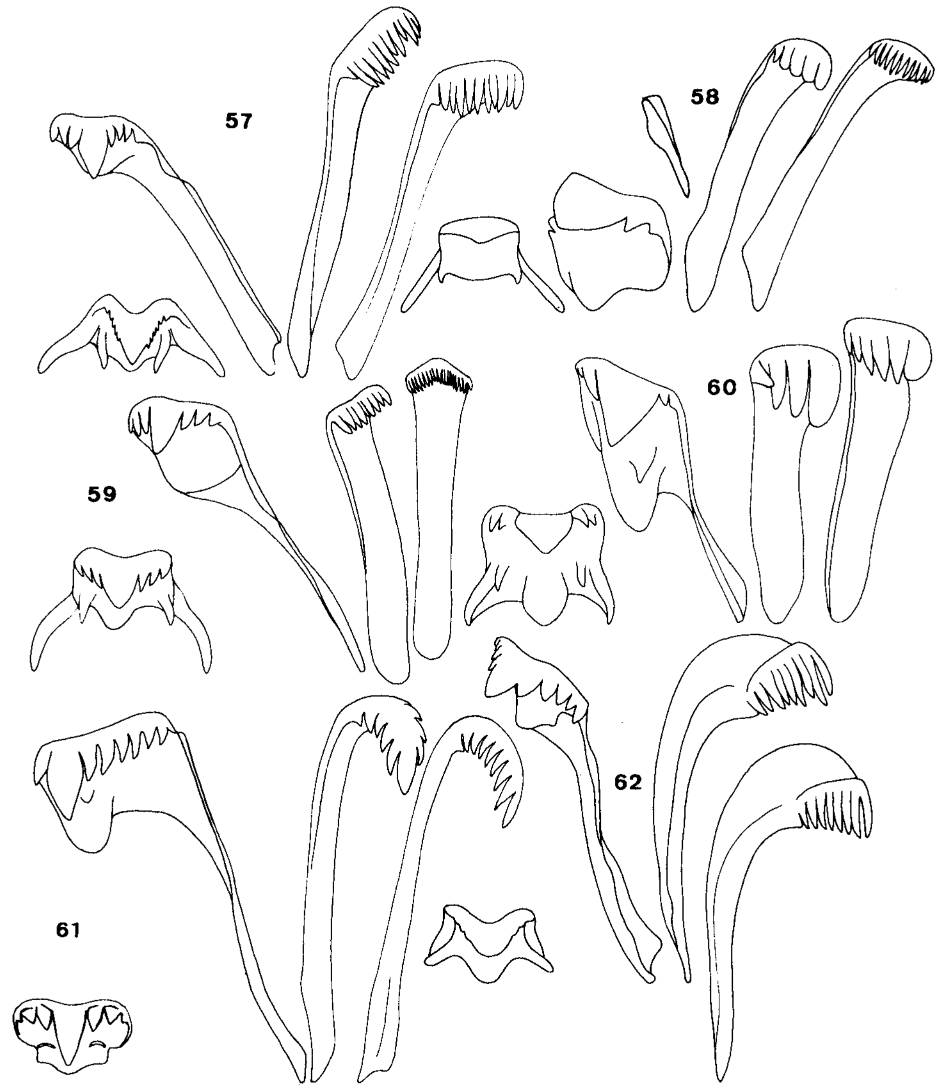


Fig. 57. *Planaxis lineatus*, Santa Marta, Caribbean; × 500. — Fig. 58. *Planaxis sulcatus*, Port Sudan, Red Sea; × 300. — Fig. 59. *Planaxis nucleus*, Santa Marta, Caribbean; × 400. — Fig. 60. *Batillaria minima*, Curaçao, Caribbean; × 400. — Fig. 61. *Rhinoclavis fasciata*, Port Sudan, Red Sea; × 250. — Fig. 62. *Amphimelania holandri*, Yugoslavia, fresh water; × 250.

aberrant. The great differences found while comparing the various descriptions and illustrations of the radula of this single species demonstrate that the literature data on radulae can only be used with certain reservations. It is also evident that Troschel's pioneer work on the radula was carried out with extreme care.

The outer posterior extension of the lateral tooth is clearly a part of this tooth but may be connected with it by a flexible part of the basal platform that could tear off during preparation of the radula for study with the light microscope. It therefore can give the impression of an independent intermediate plate between lateral and inner marginal tooth.

A radula that in most respects is very similar to that of *Planaxis* is found in *Amphimelania holandri* (Férussac) (fig. 62), a member of the Thiaridae. The central tooth of this species resembles that of *Planaxis lineatus*. The only real difference is in the absence of a pair of basal denticles in *Amphimelania*, but such denticles are known from other Thiaridae, i.e. from *Fagotia esperi* (Férussac) Thiele, 1931: 192, fig. 178).

The lateral tooth of *A. holandri* resembles that of *P. nucleus*. It also shows a flexible attachment of the long handle-like extension of the outer posterior corner. This extension is quite solid in its outer part and, therefore, was considered an intermediate rod-like tooth by Thiele (1931). The marginal teeth of *Amphimelania* are quite like those in *Planaxis*. The close morphological agreement of the radulae of the three Planaxidae and that of *Amphimelania* and other Thiaridae suggests relations between these two families.

The Modulidae are represented by *Modulus modulus* and *M. carchedonius*. Both species feed on algae which they gather from hard substrates and seagrass in shallow water below the tidal zone. An additional species from this genus, *M. tectum* (Gmelin), from the Red Sea was studied for comparison. It lives in the same type of environment as the Caribbean species of *Modulus*. The radula of *M. tectum* (fig. 64) is essentially like that of *M. modulus* and *M. carchedonius*.

Thiele (1931: 204, fig. 199) described the characters of the radula of the Modulidae as follows (translated): Radula quite short; central tooth wider than high and oval, cutting edge with five cusps; lateral tooth with moderately long cutting edge and moderately long handle-like projections of the outer posterior corner, reaching the insertion of the marginal tooth, which is long and narrow, widened at the apex, having five or six cusps. Thiele did not mention the separation between the posterior extension of the lateral tooth and its basal platform. But in his fig. 199 of *Modulus unidens* (Chemnitz) this extension is shown to be separate. Troschel (1856-1863: 144, pl. 11 fig. 15) had noted this feature and emphasized it in his description of *Modulus*. He considered the genus *Modulus* to belong to the Cerithiidae because of the similarity of the radulae of *Cerithium* and *Modulus* in spite of their conchological differences. Abbott (1974: 461, fig. 57c) figured the radula of *M. modulus*, stating that the radula of this species closely resembles that of the Rissoacea.

If the radulae of the genus *Modulus* are compared with other radulae studied here in detail, then a close similarity with the radulae of *Cerithidea* is evident (figs. 65, 68). The characteristic cutting edge of the central tooth in *Modulus*, as well as in *Cerithidea*, continues onto the margins, and the basal platform is quite smooth in the representatives of both genera. The lateral tooth is extended and this extension has developed into a quite independently thickened, rod-like structure.

Thus, according to radula morphology, a close relationship between the Modulidae and the Potamididae might be postulated.

The Caribbean members of the Potamididae studied are *Cerithidea costata* and *Batillaria minima*, which both were collected on the Netherlands Antilles. *C. costata* forms massive populations in ditches and ponds of the salinas of the island of Bonaire. Here the animals feed on the minute algae and other organisms covering the soft muddy bottom of the shallow pools. *Batillaria minima* was collected in a lagoon on the south end of the island of Curaçao. Here it forms a numerous population on seagrass and muddy bottom. Additional individuals of *B. minima* were collected in a mangrove lagoon on the island Nassau (Bahamas). Another (unidentified) *Cerithidea* species, from the Sudanese coast of the Red Sea, was studied for comparison (fig. 68). It was collected in ponds between mangroves from saline water. Here it feeds on algal and bacterial growths on the muddy bottom substratum.

All teeth in the radula of the Red Sea *Cerithidea* are essentially like those of the Caribbean *C. costata*. Only the number of cusps on the cutting edge differs and the handle-like extensions of the lateral teeth are more solid outside of their flexible connection to the actual basal platform of the teeth. The *Cerithidea* from the Red Sea has a radula that is extremely similar to that of *Modulus*.

Troschel (1856-1863: pl. 12 fig. 3) figured the radula of *Cerithidea varicosa* Sowerby, which seems to be essentially like those of the *Cerithidea* species studied here. *Cerithidea decollata* Lamarck, in contrast, seems to be quite different (Troschel, 1856-1863: pl. 12 fig. 4; Barnard, 1963: fig. 25d). Here the central tooth is higher than wide and an additional lamellar process is present on the outer marginal tooth. Such a lamellar process was also observed in *Terebralia palustris* (Bruguière) by Thiele (1931: 207, fig. 204) and figured by Barnard (1963: fig. 25c). According to Thiele, the central tooth of *T. palustris* is quite similar to that of *Cerithidea costata*. Barnard, however, figured it as being much wider than high and without the typical cutting edge that extends onto the margins.

Obviously the Caribbean and the Red Sea *Cerithidea* species belong to one genus indeed, with close relatives among the Modulidae. *Cerithidea decollata* on the other hand is sufficiently different in it its radula features to be considered a not very close relative; in view of the lamella of the outer marginal tooth it may perhaps be related to *Terebralia palustris*..

The radula of *Batillaria minima* does not look like that of *Cerithidea*. The morphology of the central tooth and the lateral tooth reminds one strongly of that of some members of the genus *Rissoa* (figs. 42, 44, 45) or *Hydrobia* (fig. 47) of the Rissoacea. Acute basal denticles and a strongly projecting, median, tongue-like process of the base are not seen in *Cerithium* and related genera, but the central teeth in *Planaxis* show similar features. The marginal teeth provide no additional information.

According to Thiele (1931: 207-208) the radulae of the Batillariinae have trapezoidal central teeth with a pair of basal denticles on their basal platform. A

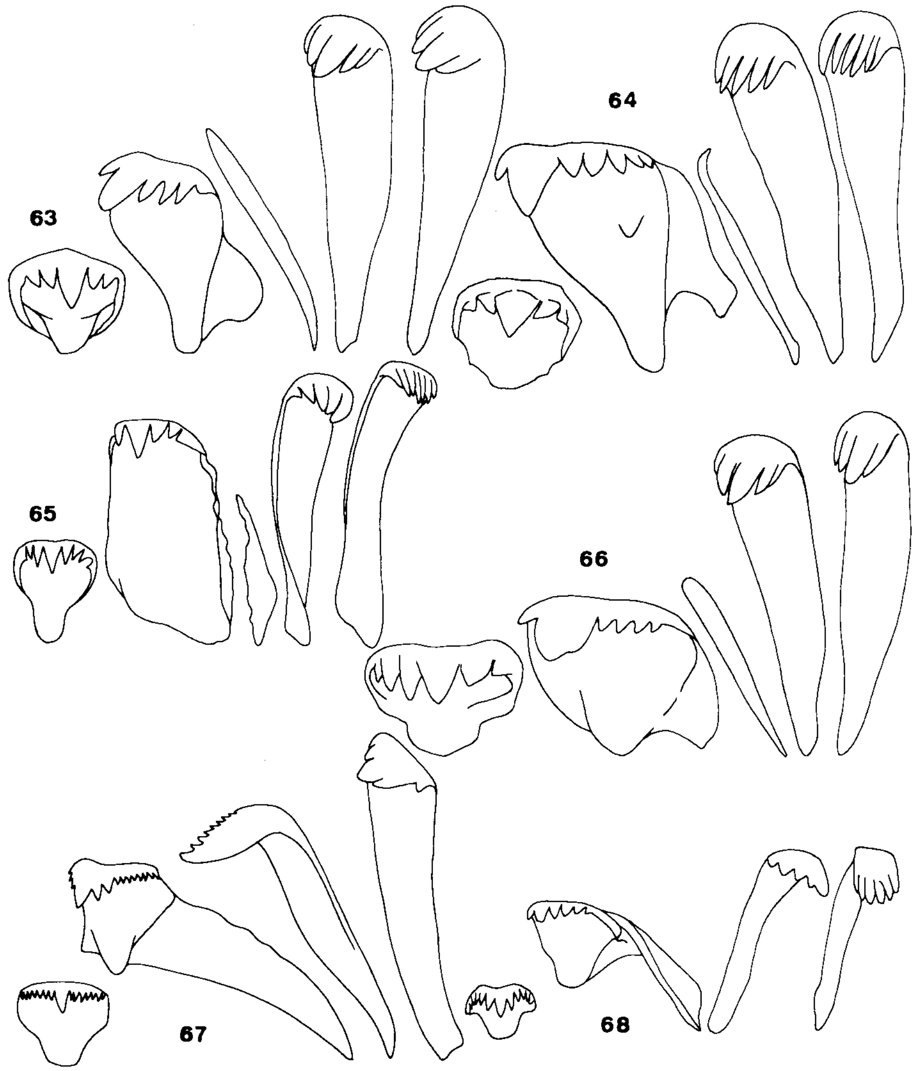


Fig. 63. *Modulus modulus*, Santa Marta, Caribbean; x 300. — Fig. 64. *Modulus tectum*, Port Sudan, Red Sea; x 200. — Fig. 65. *Cerithidea costata*, Bonaire, Caribbean; x 450. — Fig. 66. *Modulus carchedonius*, Santa Marta, Caribbean; x 320. — Fig. 67. Unidentified melaniid fresh water snail from Lake Tanganjika, Africa; x 300. — Fig. 68. *Cerithidea* sp., Port Sudan, Red Sea; x 200.

strong triangular main cusp on the cutting edge of the central tooth is flanked by one to four cusps on either side. The lateral tooth should show a moderately long, outer posterior extension, a triangular, large main cusp and few side cusps. The marginal teeth are described as long, with four to six cusps on their apex and a lamella on their margin. The radula of *Batillaria minima* does not fit well into this description. The central tooth of *B. estuarina* (Tate), figured by Thiele (1931: fig. 206a) has few of the typical characters seen in *B. minima*, apart from the general morphology of the tooth. There is no tongue-like projection of the base and the posterior corners are not acute. The description of the lateral tooth does not mention the strong rounded denticles on the main swelling of the basal platform and the composition of the outer, posterior, handle-like projection, which in *B. minima* is flexible and thin. Finally, no lamellae are found on the stalks of the marginal teeth of *B. minima*. Thus, either *B. minima* does not belong to *Batillaria*, or the definition for this subfamily has to be emended.

The great differences between *Cerithidea* and *Batillaria* indicate that both genera are not closely related.

The three small cerithiaceans *Alaba incerta*, *Diastoma varium*, and *Finella dubia* are discussed together, since there is a great confusion in the literature regarding their taxonomy. *Diastoma varium* prefers an environment of algae just below or within the tidal zone. *Finella dubia* settles in huge populations among algae developing periodically on the bottom in shallow water during the windy clear-water season, but may also be found among algae in general, especially those on seagrass in shallow lagoons. *Alaba incerta* is mainly found in *Sargassum* algae, often together with *Diastoma varium*.

Probably the food collected by these three small gastropods is similar. All are particle collectors obtaining their food from the surface of the plants on which they live. The particles are collected with the mouth and raked inside by the radula. Marcus & Marcus (1963) observed that *Diastoma varium* is also able to cut pieces from the thalli of *Ulva* and from animal carrion. *D. varium* and *Alaba incerta* also produce mucus threads with their foot while moving between the fronds of the algae. These mucus threads are sticky and trap food particles. Marcus & Marcus have observed that after a while *D. varium* ingests the mucus threads which it has produced. This type of food collecting can be regarded as primitive mucus filter feeding, similar to that seen in the sessile Vermetidae.

The radula of *Diastoma* (= *Bittium*) *varium* was described by Marcus & Marcus (1963) from Brazil. It is like that of the Caribbean representatives of this species. *Bittium reticulatum* (Da Costa) and *Bittium lacteum* (Philippi) from the Mediterranean were studied for comparison (fig. 70). The radulae of these are very similar to that of *Diastoma varium*. Abbott (1974: 106-107) classified *Bittium reticulatum* with the subfamily Bittiinae and *Diastoma varium* with the subfamily Diastominae. The great similarity of the radulae of the three species mentioned above indicates their close relationship, which should result in placing them in a single genus, certainly not in two different subfamilies.

The radula of *Diastoma varium* is also very similar to that of *Alaba incerta*, but there are sufficient differences to keep them apart from each other. *Bittium*, *Diastoma* and *Alaba* are close to each other as regards radula morphology and also close to members of the genus *Cerithium* (figs. 73-83). The radula of *Litiopa melanostoma* Rang was described and figured by Troschel (1856-1863: pl. 11 fig. 14). It seems to be essentially like that of *Diastoma*. If this proves to be correct,

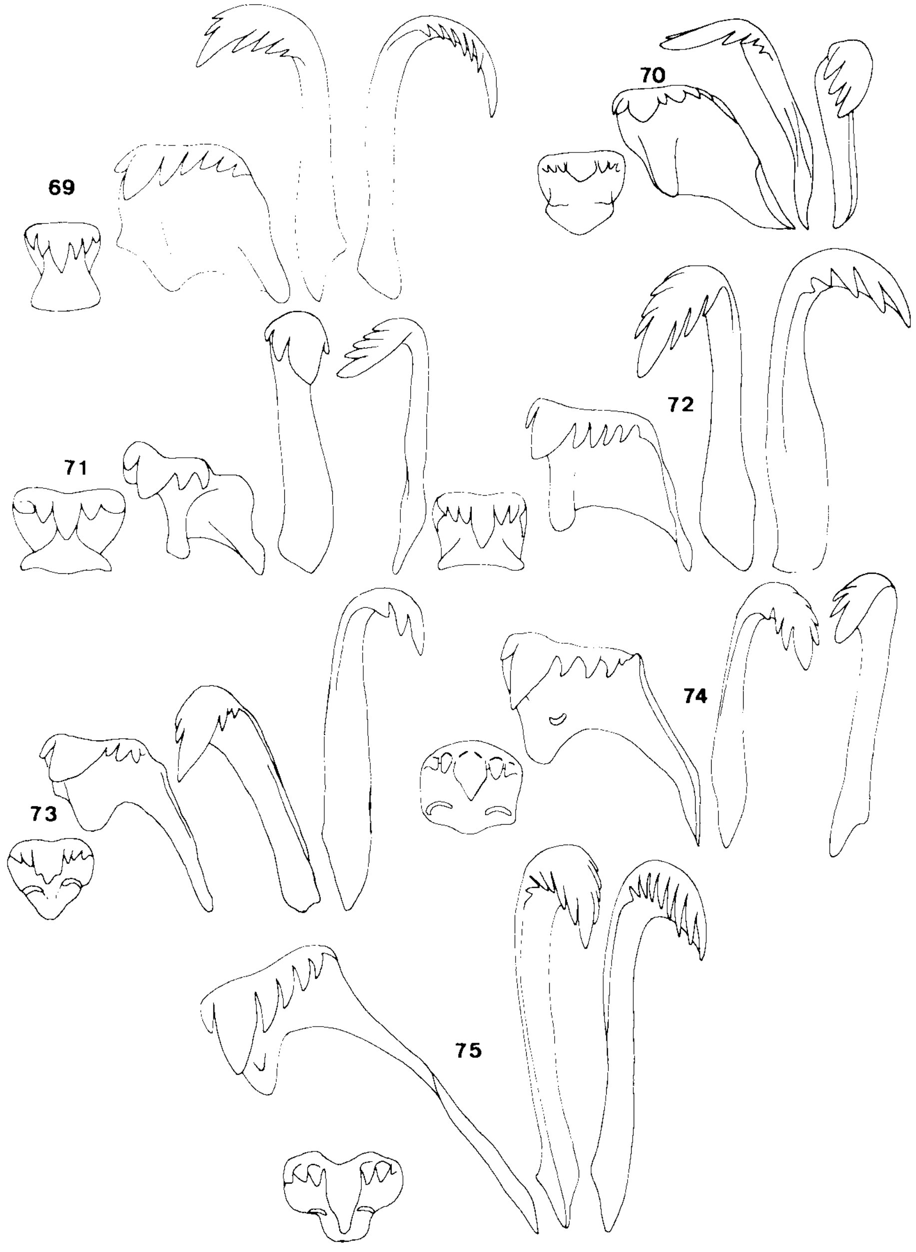


Fig. 69. *Finella dubia*, Santa Marta, Caribbean; × 850. — Fig. 70. *Bittium reticulatum*, Banyuls-sur-Mer, Mediterranean; × 350. — Fig. 71. *Alaba incerta*, Santa Marta, Caribbean; × 450. — Fig. 72. *Diastoma varium*, Santa Marta, Caribbean; × 500. — Fig. 73. *Cerithium rupestris*, Banyuls-sur-Mer, Mediterranean; × 160. — Fig. 74. *Cerithium erythraeonense*, Port Sudan, Red Sea; × 200. — Fig. 75. *Rhinoclavis aspera*, Port Sudan, Red Sea; × 300.

then the genus *Litiopa* can also be included in this group of closely related genera of small cerithiaceans.

Finella dubia, in contrast, shows quite different radula features, that set it well apart from the other species. Thiele (1931) classified *Finella* with a family of its own: Finellidae. He characterized it by a radula with central teeth higher than wide, becoming narrower in posterior direction. The lateral tooth shows a short, rounded, outer posterior corner. These characters could be confirmed by the present author. In addition *Finella dubia* has a smooth basal platform in both the central and lateral tooth, where *Bittium*, *Diastoma* and *Alaba* show denticles and ridges.

When the literature is consulted, considerable confusion regarding the placement of the species discussed here is found. Thiele (1931) grouped *Finella* in the Finellidae, *Alaba* in the Litiopinae of the Cerithiidae, and *Bittium* (including *Diastoma varium*) in the Cerithiinae of the same family, together with *Cerithium*. A complication is that Thiele (1931: 211) lists *Alabina cerithoides* Dall (= *Finella dubia* according to Abbott, 1974) among the members of the genus *Bittium*, although this species fits into his own description of the Finellidae. In Abbotts's (1974) classification *Finella dubia* is considered a member of the Diastominae, together with *Diastoma varium*; *Alaba incerta* in contrast is placed in the Cerithiopsinae; *Seila adamsi* is also listed as belonging to this subfamily, but this species is certainly not closely related to *Alaba* if the radula morphology is taken into account (figs. 71, 84). Keen (1963) grouped *Alabina* (= *Finella*), *Bittium*, *Diastoma* and *Seila* among the Cerithiidae, while *Alaba* is placed in the Litiopidae. Judging from the morphology of the radula, *Finella dubia* can easily be differentiated from *Bittium reticulatum*, *B. lacteum*, *Diastoma varium*, and *Alba incerta*. The last four species are to be considered fairly close also to members of the genus *Cerithium*.

The food of the three *Cerithium* species of which the radulae were studied, consists of algae and organic matter and is picked up from the substrate with the help of the radula. The radula can be used for collecting particles from substrates but also to cut and shred algae and other plant material as well as for sweeping and grazing. Among members of the genus *Cerithium* the collecting of food is quite similar and mostly consists of particle collecting on different substrates of the typical habitat of each species. *C. atratum* prefers sandy and muddy bottom in shallow water in the open sea. *C. litteratum* is found on rocky substrates which are covered by algae and *C. lutosum* collects food on muddy and sandy bottoms and eats decaying plants in lagoons.

Houbrick (1974) figured the radulae of all three species of *Cerithium* studied here and those of three additional Caribbean representatives of the genus. He noted that the number of cusps on individual teeth of one and the same radula is often variable and, therefore, concluded that the radulae in *Cerithium* are of no taxonomic value. As a matter of fact the three species studied here have a basically identical radula morphology. In Houbrick's figures (p. 15, 18, 29, 30, 34, 38, 44) and descriptions many features now seen on the radulae of *Cerithium* were not noted, as for example the very characteristic crescentic basal ridges of the posterior part of the basal platform of the central tooth. This feature had already been described and figured by Marcus & Marcus (1964: fig. 5) quite correctly in their study on *C. atratum*. Also not noted was the ridge crossing the basal platform of the lateral tooth and, along with it, the central denticle present here. The inner and outer marginal teeth are illustrated correctly by Marcus & Marcus. Houbrick's sketch of the outer marginal tooth shows small denticles on the outer margin of its apex, where actually no denticles are present.

The radula of *Cerithium vulgatum* Bruguière, described and figured by Troschel (1856-1863: 141, pl. 11 fig. 11), has the same morphology as those of the Caribbean species. This was verified on restudied material of this species collected in the Mediterranean. Troschel, like Houbrick, had not seen the crescentic denticles on the basal platform of the central tooth and the median ridge of the lateral tooth. But in addition Troschel had observed the absence of cusps on the outer margin of the outer marginal tooth, a feature that also was mentioned in Thiele's (1934: 210) description of the family Cerithiidae. A simplified type of drawings of radulae of some New Caledonian members of the genus *Cerithium*, which provides no essential information, was given by Risbec (1943).

For comparison the radulae of *Cerithium vulgatum* (fig. 79) and *C. rupestris* Risso (fig. 73) from the Mediterranean, *C. rueppelli* Philippi (fig. 80), *C. echinatum* Lamarck (fig. 82), *C. erythraeonense* Lamarck (fig. 74), *C. columna* Sowerby (fig. 77) and *C. nesioticum* Pilsbry & Vanatta (fig. 83) from the Red Sea were studied. The data clearly demonstrate that noticeable similarity in radula exists among species of the genus *Cerithium* from different parts of the world; all radulae studied show the characters of those of the Caribbean species. The central tooth may be more rounded, as in *C. erythraeonense* (fig. 74), or the posterior, tongue-like projection may be more or less extended over the base. The wing-like lamella of the outer extension of the lateral tooth may be larger (fig. 81) or smaller (fig. 80) and a denticle may be present on its basal platform.

A comparison of the radulae of two members of the genus *Rhinoclavis*, viz. *R. fasciata* (Bruguière) (fig. 61) and *R. aspera* (L.) (fig. 75), with the radula of *Cerithium*, demonstrates that these genera do not only differ in their mode of life. Both species, collected in the Red Sea, live in the sand and mainly move within the sand. The central tooth of *Rhinoclavis* is more oval in outline than that of *Cerithium* and has rounded corners. The cutting edge shows a tendency to be continuous with the margins. Crescentic basal denticles on the basal platform are very indistinct or absent. The lateral tooth has a longer, handle-like extension of the outer posterior corner than that in *Cerithium* and the cutting edge has more cusps. Thus the radula of *Rhinoclavis* is intermediate between that of *Cerithium* and *Cerithidea* or *Modulus*.

In his description of the radulae of members of the Cerithiidae Thiele (1931) mentions the presence of a lamella on the lower part of the inner marginal tooth. Such a lamellar process was not found in the species of *Cerithium* and *Rhinoclavis* studied now, and can, therefore, not be considered characteristic for the Cerithiidae to which, without doubt, all of them belong.

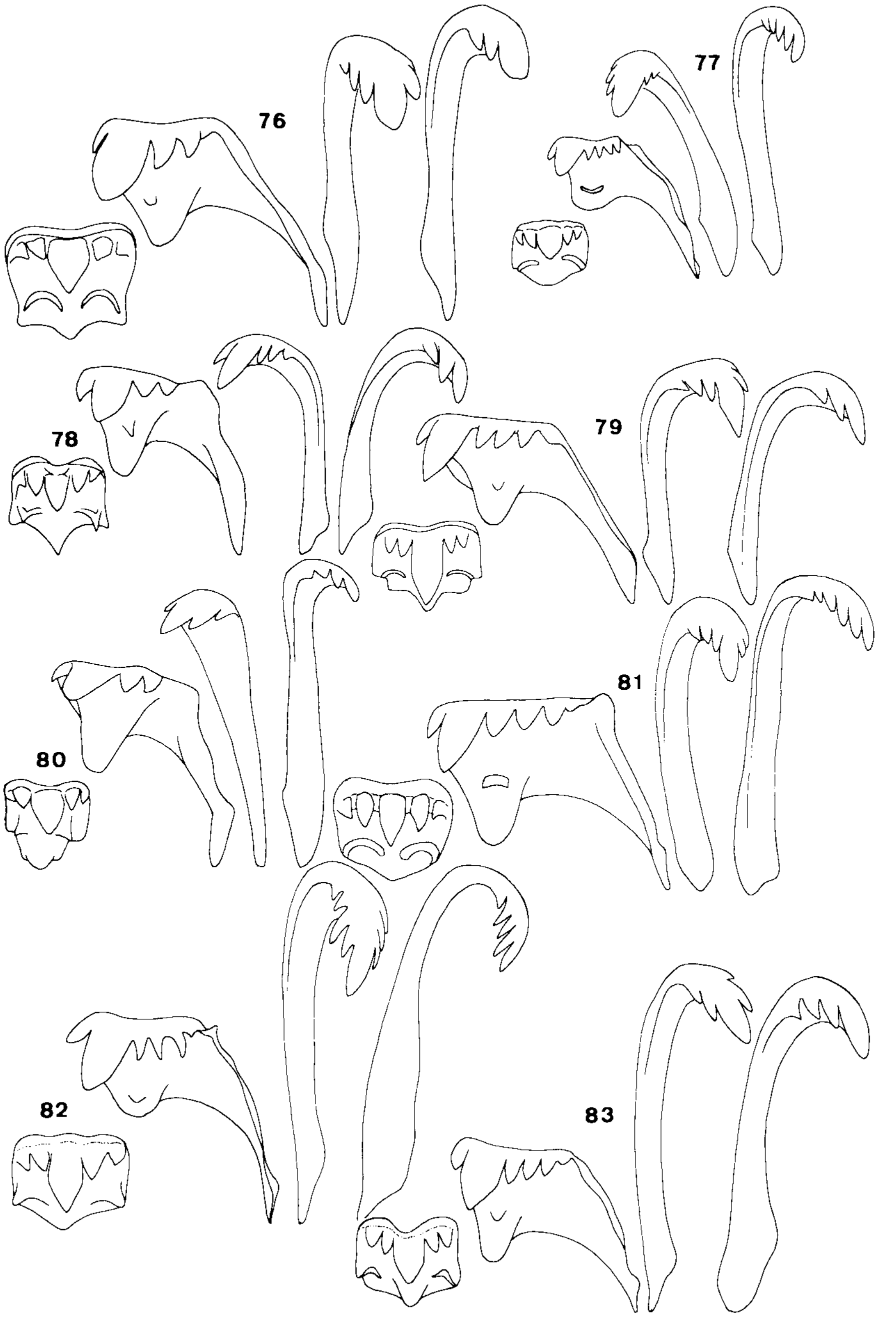


Fig. 76. *Cerithium atratum*, Santa Marta, Caribbean; × 350. — Fig. 77. *Cerithium columna*, Port Sudan, Red Sea; × 120. — Fig. 78 *Cerithium lutosum*, Santa Marta, Caribbean; × 250. — Fig. 79. *Cerithium vulgatum*, Banyuls-sur-Mer, Mediterranean; × 150. — Fig. 80 *Cerithium rueppelli*, Port Sudan, Red Sea; × 250. — Fig. 81. *Cerithium litteratum*, Santa Marta, Caribbean; × 300. — Fig. 82. *Cerithium echinatum*, Port Sudan, Red Sea; × 200. — Fig. 83. *Cerithium nesioticum*, Port Sudan, Red Sea; × 250.

The anatomy of various *Cerithium* species from the Western Atlantic was examined by Houbrick (1974: 48, 49), who found a close resemblance to *Littorina*, which had been studied in great detail by Fretter & Graham (1962). According to Houbrick, only the reproductive tract of *Cerithium* is clearly different. A similar reproductive tract is present in members of the Turritellidae, Cerithiidae, Thiaridae and Potamididae. Johansson (1947, 1953, 1956) suggested that this similarity reflects a common ancestry of the members of these families. The similarity in radula observed here among most of the Cerithiidae, Thiaridae and Potamididae studied, supports this view.

The similarity of the radula of the otherwise quite different *Cerithium* species strongly suggests a close taxonomic relationship. This contradicts the opinion of Sunderbrink (1929), who compared *Cerithium* and *Melanopsis* and concluded that the morphology of the radula is subject to frequent changes in the course of the evolution. He, therefore, regarded the radula of no great value in taxonomy. Sunderbrink referred to Ihering (1909) in order to invalidate Troschel's opinion of the taxonomic value of the radula; Ihering expressed the view that Troschel was misled by the similarity of the radula of littorinids and cerithiids by classifying *Litiopa* and *Modulus* with the Cerithiidae, instead of the Littorinidae. There is no question now who was right. Next to conchological characters, the radula structure should be studied in great detail to elucidate the natural system of the Mesogastropoda.

Whereas a certain similarity of the radulae of the cerithiacean families Thiaridae, Planaxidae, Modulidae, Potamididae, Diastomidae and Cerithiidae may be observed in many cases, such a relation to the Cerithiopsidae cannot be established. Each tooth of the radula of *Cerithiopsis* and *Seila* is sufficiently different from what is found in the above cerithiacean families to classify these genera elsewhere.

According to Fretter (1951) *Cerithiopsis tubercularis* (Montagu) feeds on the tissue of sponges. The snail ingests the tissue by sucking through a comparatively long proboscis. When the mollusc is feeding, with the proboscis thrust through an osculum to reach the soft tissue of the sponge, the jaws loosen the tissue, which is then raked into the buccal cavity by numerous fine radula teeth. A similar mode of feeding is found in *Seila adamsi*, which also feeds on incrusting sponges, but here feeding activities were not observed in detail.

According to Fretter (1951: fig. 2) the marginal teeth of the radula show finer cusps in *Cerithiopsis tubercularis* than in *Seila adamsi*. The lateral and central teeth of *Cerithiopsis* are similar to those in *Seila*, according to Fretter (1951), Troschel (1856-1863: 142) and Thiele (1931: 216). Our studies on two Mediterranean representatives of the genus *Cerithiopsis*, have revealed very different teeth (figs. 85, 92).

Thiele (1931: fig. 220) figured the radula of *Seila terebralis* (C. B. Adams) and Barnard (1963: fig. 25a) that of *S. africana* Bartsch, both of which are very similar to that of *Seila adamsi*. The radula of *Seila* shows similarities to the radulae of Triphoridae and Architectonicidae (Epitoniacea). Next to *Cerithiopsis*, *Seila* and

Eumetula (all with similar radulae) Thiele (1931) also included in his family Cerithiopsidae, *Cerithiella* and *Laiocochlis*, which, judging from his figures and descriptions (1931: 217-218, figs. 218, 221) do not have the same type of radula.

The radula of *Seila adamsi* is quite similar to that of *Triphora nigrocincta* (fig. 86), while the radula of *Triphora turristhomae*, at first sight, has nothing in common with these two species. Marcus & Marcus (1963: fig. 70) figured the radula of *Triphora* cf. *nigrocincta* from Brazil, which is quite like that of the triphorid from Santa Marta studied here. These authors found only two marginal teeth, which makes the Brazilian radula look like that of *Seila adamsi*. Fretter (1951: fig. 4) figured and described the radula of *Triphora perversa* (Linné) from Plymouth. Since the figure of this radula is quite schematic, it was studied again in animals collected in the Mediterranean (fig. 87). It is evident that this radula is extremely similar to that of *T. nigrocincta*, with the only difference that seven marginal teeth are present in *T. perversa* and not two or three. In contrast to the observations of Fretter, the marginal teeth have no cusps here, while Fretter noted that their distal end is frayed out into fine pliable processes.

Another species of *Triphora* from the Mediterranean (fig. 88) has a radula perhaps more like that of *T. perversa* from Plymouth. Here the central tooth is not as wide as the lateral tooth and shows a marginal swelling quite like that in *Seila adamsi*. The three long oval, marginal teeth have slender, flexible cusps. The Triphoridae of the Mediterranean should be revised. Special emphasis should be placed on the radula and the larval shell since there seems to be a lot of variation in the shape of the adult shell.

A radula of what was identified as *Triphora* cf. *aspera* (Jeffreys) (figs. 89, 91) from the Mediterranean was also studied. It represents a type intermediate between the *Seila* radula and that of *Triphora turristhomae*. In *T.* cf. *aspera* 17 teeth are present in each row, which are all developed as the central and lateral teeth of *T. perversa* and *T. nigrocincta*. The slender marginal teeth of these last two species have been lost, but the other two teeth are split up into three to six smaller ones each. A radula similar to that of *Triphora* cf. *aspera* may have been the original of the drawing of a "*T. perversa*" radula by Fischer (1887: fig. 445).

A fourth triphorid, from Banyuls-sur-Mer, has 23 teeth per row (fig. 90). The central and lateral teeth are almost identical in shape and have three cusps each. They are rectangular and provided with a basal, tongue-like projection. The ten (on both sides) marginal teeth also have three cusps and are tapering toward the margins of the radula. The central cusp of these marginal teeth has developed into a long flexible rod.

Thiele (1931: 219) records many rectangular to quadrate teeth with two or three points for the radula of the Triphoridae. The radula used for his description must be considered similar to that of *T. turristhomae*.

Kosuge (1966) studied 16 Triphoridae species and distinguished four groups. Only a few of the species studied here fit into one of these groups, the others are intermediate. Kosuge divides the Triphoridae into three subfamilies, mainly because of differences in the morphology of the radula. He recognized 11

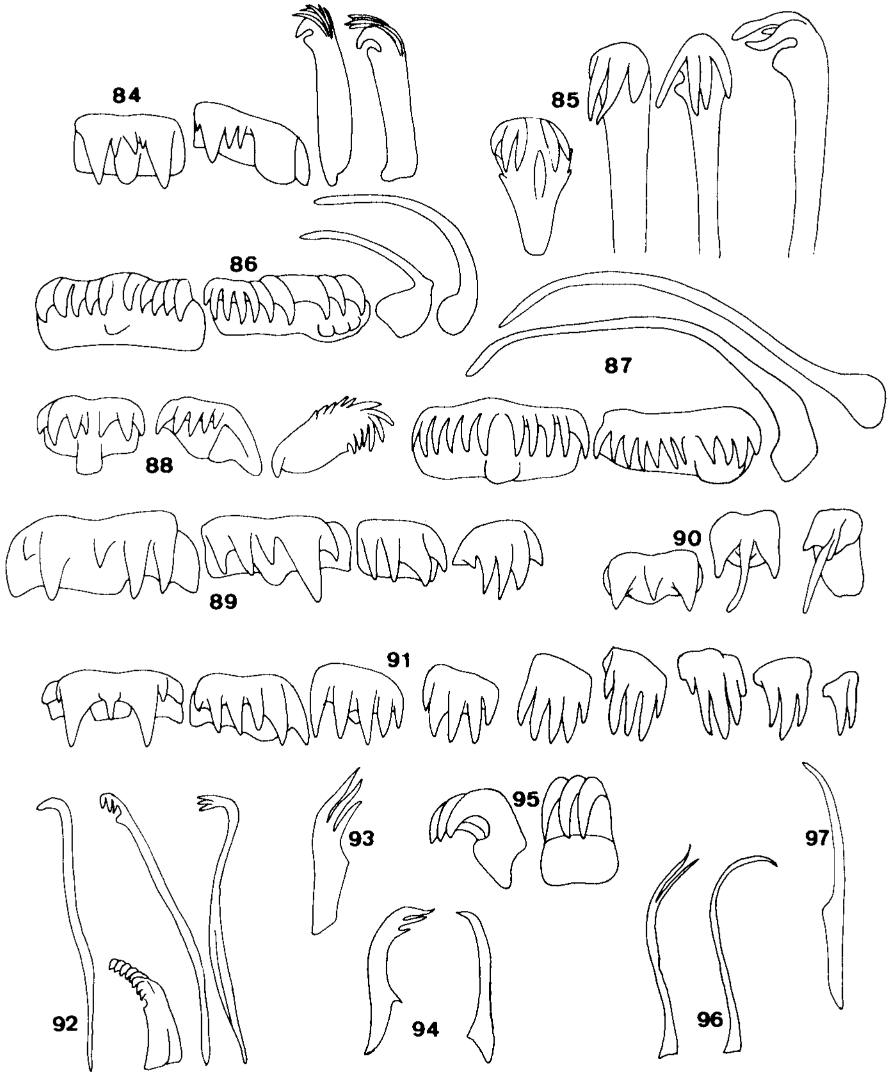


Fig. 84. *Seila adamsi*, Santa Marta, Caribbean; x 1000. — Fig. 85. *Cerithiopsis* cf. *minima*, Banyuls-sur-Mer, Mediterranean; x 3000. — Fig. 86. *Triphora nigrocincta*, Santa Marta, Caribbean, only two of the marginal teeth drawn; x 2100. — Fig. 87. *Triphora* cf. *perversa*, Banyuls-sur-Mer, Mediterranean; x 2000. — Fig. 88. *Triphora* sp. 1, Banyuls-sur-Mer, Mediterranean, there are three equal marginal teeth; x 2000. — Fig. 89. *Triphora* cf. *aspera*, Banyuls-sur-Mer, Mediterranean, variety of the type figured as complete half row in fig. 91; x 2000. — Fig. 90. *Triphora* sp. 2, Banyuls-sur-Mer, Mediterranean, the row holds three central teeth like the left and 20 lateral teeth like the right (23 teeth per row); x 2000. — Fig. 91. *Triphora* cf. *aspera*, Banyuls-sur-Mer, Mediterranean, half row of radula; x 2000. — Fig. 92. *Cerithiopsis* cf. *rugulosa*, Banyuls-sur-Mer, Mediterranean; x 900. — Fig. 93. *Epitonium lamellosum*, Santa Marta, Caribbean; single tooth; x 300. — Fig. 94. *Scala clathrus*, Banyuls-sur-Mer, Mediterranean; x 250. — Fig. 95. *Triphora turristhomae*, Santa Marta, Caribbean; two single teeth; x 4500. — Fig. 96. *Architectonica nobilis*, Santa Marta, Caribbean, marginal and central tooth; x 220. — Fig. 97. *Janthina exigua*, Santa Marta, Caribbean, single tooth; x 120.

genera, based mainly on radula features, since all these genera are conchologically very similar. Kosuge assumed that the ancestral forms of the Triphoridae had both numerous teeth and cusps; from these forms the various types are thought to have evolved by decrease of the number of teeth and differential loss of cusps. Since the radula of the Cerithiopsidae is taenioglossate, Kosuge believes that the Triphoridae are not related, this in contrast to what most authors assume because of the close conchological similarity of Triphoridae and Cerithiopsidae. Kosuge also considers the shape of the cusps in the radula of the Cerithiopsidae to be very different from that in the Triphoridae. He states that the Triphoridae are closely related to other Mesogastropoda as regards their anatomy and concludes that the Triphoridae should be grouped in a new suborder, the Heterogastropoda, with Mathildidae, Architectonicidae and Epitoniidae. This suborder should be regarded as intermediate between Mesogastropoda and Neogastropoda.

Risbec (1955) stated that the Triphoridae are different from Cerithiidae in their radula characters, which according to this author, resemble those of the Neogastropoda. This view is difficult to follow for there are no Neogastropoda known with a radula similar to that of the Triphoridae, especially not in the Columbellidae, which were considered by Risbec to be the closest relatives of the Triphoridae.

Marcus & Marcus (1963) examined the stomach content of *Triphora* cf. *nigrocincta* and found spicules of sponges. Kosuge (1966) noted that the triphorid snails he had studied were frequently found among various sponges, on which they crawl and in which they partly or completely bury themselves. Fretter (1951) has described the feeding activities of *T. perversa* in detail. The protruded proboscis is thrust through the osculum of the sponge, seeking soft tissue. When the proboscis is fully everted, a pair of jaws is brought to its tip; the teeth of the radula are situated ventrad to the jaws. The Triphoridae here studied from the Caribbean and the Mediterranean were all collected from sponges. Thus, the triphorids prefer the same type of food as the cerithiopsids, their closest relatives in respect of the radula. Since all species compared, including *Seila*, feed on the tissue of sponges, the various types of radula encountered cannot be considered a purely functional adaptation to this food. Moreover, the extremely diverse types of radula in the triphorids and cerithiopsids suggest that almost any radula can serve to feed on sponge tissue.

Contrary to Kosuge's opinion, the primitive *Triphora* radula is taenioglossate, as in *T.* cf. *nigrocinta* from Brazil (Marcus & Marcus, 1963), and close to the radula of *Seila*, a member of the Cerithiopsidae. There may be two developmental types or a mixture of these in the evolution of the triphorid radula. In the first there is a multiplication of the number of cusps on the central and lateral teeth, together with a splitting of these teeth into a few to numerous new teeth. The second type shows an increase in the number of the slender sickle- or blade-like marginal teeth. The extremes in the first type would have a radula as in *Triphora turristhomae*; those of the second type would have a radula similar to that found in

Architectonica nobilis (fig. 96) or *Epitonium lamellosum* (fig. 93). The Triphoridae exhibit an extreme variability of the radula both in shape as well as in the number of cusps. The radula in this family, therefore, should be considered a most valuable tool for systematic evaluation, as suggested already by Kosuge (1966).

ARCHITECTONICACEA AND EPITONIACEA

Architectonica nobilis (Röding)
(fig. 96; pl. 2 fig. 4)

The radula has about 60 rows of teeth. Each row consists of 12-14 equally long, hook-like acute teeth. The teeth of the central part of each row have one cusp only, while those of the marginal part have an apex that is split into two or three cusps. The base is somewhat widened and concave. The inner margin shows a groove and the outer margin a ridge. The ridge of a tooth can fit into the groove of its neighbour when the radula is folded.

Epitonium lamellosum Lamarck
(fig. 93; pl. 5 figs. 8, 10)

The radula has about 80 rows of teeth, which are all attached to the membrane in such a way that their apices point towards the middle of the radula and their axes are inclined somewhat anteriorly. Each row consists of about 160 single teeth. The middle line of the radula is a parting between teeth pointing to it from one side and those pointing to it from the other side. The teeth are all of the same general outline. They are sickle-like, bilaterally flattened and have three slender cusps on the apex. Usually the outer one of these cusps is the largest. The outer margin is straight and about five times as long as the inner margin. The latter is concave and ends in a lobe on the inner posterior corner. The base is long. When the teeth are erected, their shafts form an angle of about 45° with the membrane.

Janthina exigua Lamarck
(fig. 97; pl. 5 figs. 7, 9)

The brush-like radula has about 28 teeth in each row. The teeth are all of the same shape but differ in size. The smallest are found in the centre of the rows whereas the size increases outwards. Each tooth is slender thorn-shaped. The straight base is wide and attaches the tooth along more than one third of its length in such a way that its apex points inward and foreward. When erected, each tooth forms an angle of about 45° with the membrane of the radula. The apex is curved inward and ends in one slender cusp. The inner margin is concave and has only two thirds of the length of the convex outer margin. The inner posterior corner is angular, the outer posterior corner is acute.

DISCUSSION

In the radula of the members of the Architectonicidae, Epitoniidae and Janthinidae described a larger number of teeth is present in each transversal row than is normally found in taenioglossate mesogastropods.

Architectonica nobilis lives on sandy bottom between sea grass at a few meters depth. It was collected in the bay of Santa Marta and in other bays in the region. At daytime *A. nobilis* usually rests in the sand. In contrast to other gastropods with a similar mode of life, it is burried in the sand with the apex of the shell pointing downward and the foot closest to the surface. *A. nobilis* feeds on actinian-like coelenterates. Large polyps are attacked close to their base. Here the gastropod rasps a hole in the epidermis of the base and extends its proboscis into its prey, feeding on it until its death. Robertson, Scheltema & Adams (1970) have found that *Philippia radiata* (Röding) feeds on the polyps of hermatypic stony corals. Like *A. nobilis* it lives hidden in coarse sand near its prey and crawls out to feed at night.

Thiele (1931: fig. 169) and Robertson (1970: fig. 9) have described and figured the radula of *Philippia hybrida* (Linné). It has only five teeth per row. In general shape these teeth are very similar to those of *Architectonica*. Troschel (1861: 93-98, figs. 10-12) had noted the great similarity between the radulae of *Architectonica* and *Philippia* in the arrangement and shape of the cusps, but in contrast to Robertson's statement, he did not record the same number of teeth per row for *Philippia* and *Architectonica*. Troschel has not recorded the number of teeth in the radula of *Philippia* (Troschel & Thiele, 1866-1893: 156).

Because in the radula of *Philippia* the inner teeth have more cusps on their apices than the outer, Robertson thought that this arrangement would generally be found in radulae of the Architectonicacea. He, therefore, expressed the opinion that the observations of Troschel & Thiele (1866-1893: pl. 15 fig. 4) and Thiele (1931) were not correct, i.e. that in the radula of *Architectonica* the inner teeth do not show only one cusp, while the outer teeth may not show two or three cusps. When the radula of *Architectonica nobilis* is taken into account, however, the observations of the first authors on the radula of *Architectonica perspectiva* Lamarck can be considered correct.

Troschel & Thiele also observed a decrease in size of the teeth in each row of the radula of *A. perspectiva*. This is not seen in *A. nobilis*, where all teeth are about equal in size. According to Thiele's definition the radula of *Architectonica* (= *Solarium*) should have 28 teeth in each row. This number can no longer be regarded as correct, since only 12-14 are present in the radula of *A. nobilis*.

The food-uptake of *Epitonium* has not been observed. Robertson (1970) assumed that *Epitonium* species most likely feed on coelenterates. Ankel (1936) suggested that *Scala clathrus* (Linné) feeds upon sea anemones. Thorson (1958) observed that an American epitoniid, *Opalia crenimarginata* (Dall), was feeding on the anemone *Anthopleura* by pushing its proboscis into the tissue of the prey and sucking it for hours or even days. The radula of *Scala clathrus* from the Mediterranean was studied for comparison (fig. 94). Here each row of the radula has only about 50 teeth. In contrast to *Epitonium*, the outer teeth of each row have only one cusp and have a rounded stalk, while the inner teeth are very similar to those in *E. lamellosum*, with three to five cusps on their apices.

Troschel & Thiele (1866-1893) have studied the radulae of three species of the Epitoniidae. Thiele (1929) added data on some more species from this family. He defined the radula of the Epitoniidae as having more or less numerous, simple, hook-like teeth per row, that have acute apices with two or three cusps. The number of cusps is more variable than Thiele thought and the number of teeth in each row probably varies from species to species.

Janthina lives free floating on its own mucus raft and catches planktonic coelenterates, especially the floating *Velella* (see Wilson & Wilson, 1956). According to Fretter & Graham (1962) *Janthina* feeds on *Velella* by gradually clearing its tentacles and blastostyles from the underside of the float until only the horny skeleton remains. *Velella* is attacked and held by the hook-like teeth of the radula, that can be projected from the mouth. Radulae of various *Janthina* species were described and figured by Troschel & Thiele (1866-1893: pl. 14 figs. 1-11); all show essentially the type of teeth of *Janthina exigua*.

Troschel stated that the architectonicid radula is somewhat different from that of the Janthinidae and Epitoniidae, but differing even more from that of other prosobranch families. In the literature it has been suggested that the epitoniid radula has developed convergently with that of the architectonicid species as a consequence of identical food. While architectonicid radulae range from a modified taenioglossate radula to a ptenoglossate type, a taenioglossate type radula of the Epitoniidae and Janthinidae is so far unknown.

The difference of the radula of the Architectonicidae and Epitoniidae is mainly found in the attachment of the teeth to the membrane. In the former this attachment is narrow, while in the latter it seems to be wider. The Janthinidae would provide an intermediate width of the base. The question has to be put whether these small differences in the radulae should be used to assign these groups of gastropods to different superfamilies. The similarities of the radula are matched by similarities of the proboscis. Robertson (1970) noted that the oesophagus of *Philippia* is quite like that of *Epitonium* in its structure and function. But again, as with the radula, the convergence is interpreted as being the result of similar food requirements, i.e. the cuticularized lining of the architectonicid and that of the epitoniid oesophagus, preventing injury from the nematocysts of their prey, is interpreted to have evolved twice independently.

An ancestor of the Architectonicacea as well as of the Epitoniacea might have been similar to certain species of the Cerithiopsidae or Triphoridae, classified with the Cerithiacea by Taylor & Sohl (1962). The radula of both *Cerithiopsis* cf. *rugulosa* (Sowerby) (fig. 92) and *C.* cf. *minima* (Brusina) (fig. 85), collected in the Mediterranean, are taenioglossate, but the single teeth have become very much higher than wide. A radula like that of *Cerithiopsis* cf. *minima* would need little change to look like that in *Philippia* (see Thiele, 1931: fig. 169; Climo, 1975: fig.

4A). An elongation of the teeth together with a tendency to multiply in number, as in many Triphoridae, would result in radulae as found in *Architectonica*. A multiplication of the marginal teeth of the Cerithiopsidae or Triphoridae (figs. 84, 86, 88) with sickle-like or lamellar marginal teeth, and the reduction of the central teeth, could lead to radulae as found in the Epitoniacea.

Strombacea

Xenophora conchyliophora (Born)
(fig. 98; pl. 7 fig. 1)

The radula has about 45 rows of teeth. The central tooth is roughly heart-shaped. The rounded anterior edge is evenly excavated. A rounded, tongue-like projection dominates the base, which is fused with evenly curved, concave margins due to the absence of posterior corners. The tooth is wider than long (3:2), being widest anteriorly. The cutting edge forms an angle of about 90° with the basal platform. It consists of a large, rounded central cusp, accompanied by three or four much smaller flanking cusps on each side.

The rounded lateral tooth is shovel-like, wider than long (5:4), and has a smooth cutting edge which is upturned from the basal platform. The inner margin is convex and ends in a small denticle projecting from the inner posterior corner over the posterior edge. Apart from that the base is smooth and straight. The outer posterior corner is somewhat extended. The smooth basal platform is raised somewhat at its margins. It is connected with the membrane of the radula by a short, flexible, folded connecting process.

The marginal teeth are uniform, quite long (about seven times as high as wide), bilaterally flattened, and equally wide from the base to the apex. Their apices are hook-like curved, with smooth, margins, crenulated in the apical region. The teeth of the radula are not hinged. The marginal teeth may be folded onto the lateral and central teeth. They are too long to fit into the concavities formed by the lateral teeth.

Strombus pugilis Linné
(fig. 100; pl. 6 fig. 11)

The radula has about 40 rows of teeth. The oval central tooth has roughly angular corners. It is almost twice as wide as long, with an upturned cutting edge forming an angle of about 90° with the basal platform. The cutting edge consists of one long, acute, main cusp that is flanked on both sides by three to five smaller cusps. The cusps on the anterior corners are broader than those of the inner part of the cutting edge. The margins of the tooth are convexly rounded, somewhat raised, and end in evenly rounded to angular posterior corners. The base is straight or weakly convex. The basal platform is plain and somewhat concave.

The lateral tooth is roughly angular and almost as long as wide. The upturned cutting edge is dominated by one large cusp that is accompanied by five to nine much smaller outer cusps and one or two inner cusps. The outer margin is curved upward and extends into a thin, wrinkled lamella which continues into the outer posterior corner. Both the inner and the outer posterior corners are angular and not extended. The inner posterior corner has two angular indentations between margin and base. The basal platform shows a diagonal broad, shallow central swelling.

The inner marginal tooth is similar to the outer one in shape and length. Both are about nine times as long as wide, very slender, and evenly curved. Their stalk is broadest at its base and tapers towards the apex. In both teeth the outer margin is not denticulate, while the inner shows a cutting edge with seven triangular cusps on the inner marginal tooth and eight on the outer one. The teeth of the radula are not hinged. The marginal teeth can be folded over the lateral and the central teeth. There are no traces of wear on the used part of the radula.

Stombus gigas Linné
(fig. 102; pl. 6 fig. 12)

The radula was extracted from juvenile individuals; it has about 40 rows of teeth. The central tooth is almost twice as wide as long. At its anterior front it is almost twice as wide as at its base. The cutting edge is situated at the extreme anterior front of the basal platform and consists of one solid, large, main cusp that is accompanied by three flanking cusps on each side. The smallest, outermost cusps of the cutting edge extend as projections over the anterior corners. The main cusps are inserted somewhat posterior to the flanking cusps. The margins of the tooth are evenly curved and deeply concave. The posterior corners are angular and the base is evenly convex. The basal platform is plain.

The oval lateral tooth is somewhat wider than high (4:5). Its outer posterior corner is extended into a short projection in which the wrinkled thin lamella of the upturned outer margin ends. The inner margin is straight and ends with two angular indentations in the posterior corner. The cutting edge has triangular, bilaterally flattened cusps, varying in number and size, and decreasing in size in outward direction. Four to six cusps may be counted up to the main cusp and one or none on its inside. The cusps may split or fuse in consecutive teeth of an individual radula.

The marginal teeth are uniform, long and slender and evenly curved in their apical part. They are broadest at their base, decreasing slowly in diameter of the stalk from there on. Their outer margins are not denticulate. The inner marginal tooth has five and the outer one six acute cusps on the long cutting edge of the inner margin.

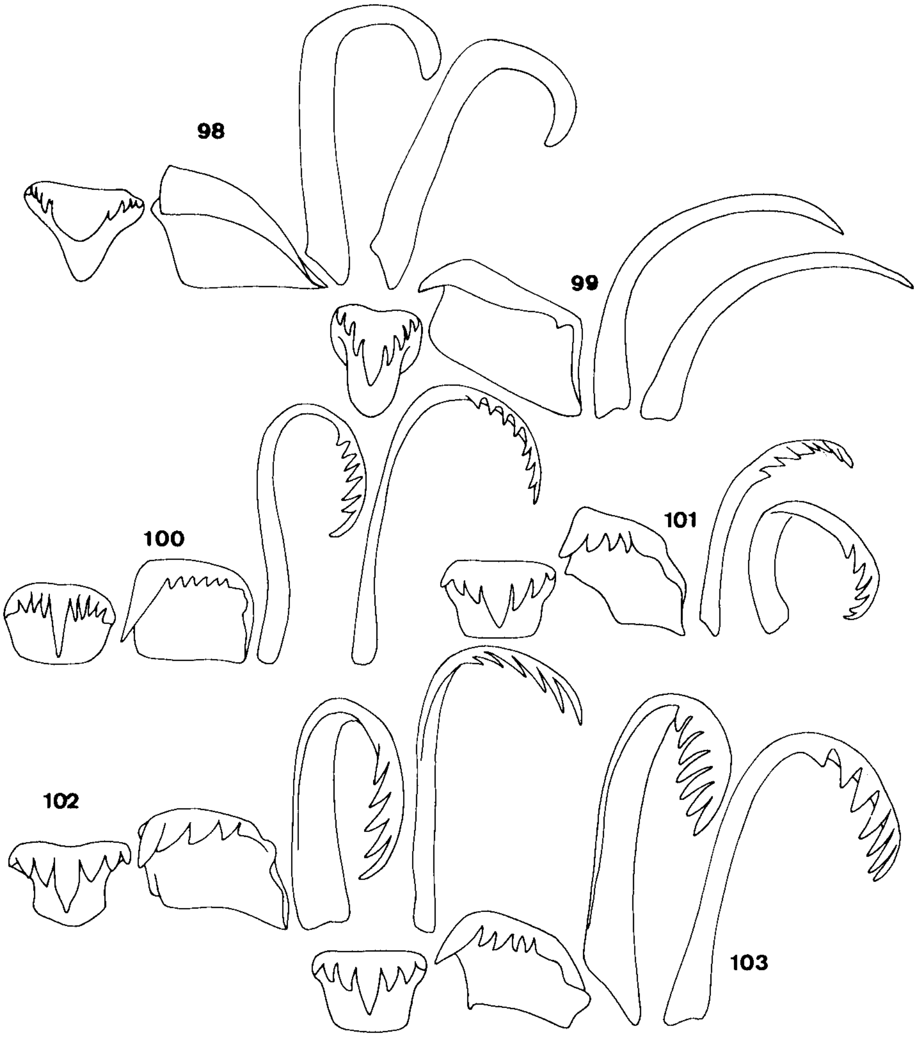


Fig. 98. *Xenophora conchyliophora*, Santa Marta, Caribbean; × 80. — Fig. 99. *Aporrhais pespelicani*, Banyuls-sur-Mer, Medditerranean; × 170. — Fig. 100. *Strombus pugilis*, Santa Marta, Caribbean; × 45. — Fig. 101. *Strombus raninus*, Santa Marta, Caribbean; × 40. — Fig. 102. *Strombus gigas*, Santa Marta, Caribbean, (juvenile); × 210. — Fig. 103. *Strombus gallus*, Curaçao, Caribbean; × 45.

Strombus raninus Gmelin
(fig. 101; pl. 6 fig. 10)

The radula has about 40 rows of teeth. The central tooth is roughly rectangular, wider anteriorly than along its base. It is wider than high (3:2). The cutting edge is curved upward and rooted on the front of the basal platform. A strong, triangular, main cusp is accompanied by three flanking cusps on each side, which are regularly decreasing in size. The outermost of these cusps may extend into a rim that is continuous around the anterior corner, ending on the anterior part of the margins; these margins are evenly curved outward anteriorly, showing a concave indentation posteriorly. The posterior corners are rounded and the base is straight. The smooth basal platform appears weakly concave.

The oval lateral tooth is wider than long (3:2). The upturned cutting edge shows bilaterally flattened, triangular cusps, which become gradually smaller in outward direction. Their number varies between five and seven since individual cusps may fuse or split. The outer margin is extended into a broad lamella that is upturned, ending in an angular outer posterior corner. The inner margin is slightly raised. The basal platform appears concave, with only a weakly raised central swelling. The base is straight between the two angular corners.

The marginal teeth are quite uniform, being about five times as high as wide. They have bilaterally flattened stalks and are almost equally wide from the base up to the apex; the stalks and the apex are evenly curved. The inner marginal tooth may have six to nine and the outer one six to seven triangular cusps, only on the inside of the teeth. The inner marginal teeth are folded between the cutting edges of the lateral and the central teeth, with their cutting edges pointing downward. There are no traces of wear on teeth of the used part of the studied radulae.

Strombus gallus Linné
(fig. 103; pl. 6 fig. 9)

The radula has about 45 rows of teeth. It is quite like that of *Strombus raninus* in all features.

DISCUSSION

Xenophora conchyliophora lives in muddy to sandy or gravel substrates at two to six metres depth in the bay of Santa Marta and similar bays along the Caribbean coast of Columbia. *Strombus pugilis* lives on sandy to muddy bottoms among seagrass, usually in open bays. *Strombus gigas* prefers deep, but protected, lagoons and bays, usually also covered by marine angiosperms. *Strombus raninus* can be found in small populations in shallow water of open bays, and, in large populations, in shallow reef lagoons with seagrass. *Strombus gallus* was collected at about four metres depth among seagrass and coral-limestone rubble off the shore of the biological station of Curaçao.

The faecal pellets of *Xenophora conchyliophora*, *Strombus raninus*, *S. gigas* and *S. pugilis* consist largely of compact sediment particles (Bandel, 1974). Faeces are produced in great quantities by the feeding animals, demonstrating that they swallow much anorganic material with their food. The Strombacea are generally accepted to be herbivorous (Jung & Abbott, 1967; Robertson, 1961). The food of

Xenophora neozelanica Suter consists of the surface layer of muddy silt together with its living and dead organic constituents (Morton, 1958). This food is scooped up by the rake-like central and lateral teeth. Morton (1958) suggested that the mode of feeding of *Xenophora* resembles that of the deposit feeder *Aporrhais*, which, according to Yonge (1937), only lives of plant material. Members of the genus *Strombus* pick up food with their long snout. The surface of the sediment, rich in diatoms filamentous algae, is brushed and the food is raked in with the help of the radula just as was observed by Morton in *Xenophora*.

Thiele (1931: 249) generally characterized the superfamily Strombacea (i.e., the Xenophoridae, Struthiolariidae, Aporrhaidae and Strombidae) by a radula that has a central tooth with a sturdy, acute, denticulate cutting edge, moderately wide lateral teeth, and long and narrow marginal teeth. In fact, the radula morphology and the leaping type of locomotion are shared between the Xenophoridae and the Strombidae. With respect to the shell shape there is no similarity between the Xenophoridae and the Strombidae, nor to the other two families of the Strombacea. Morton (1958), therefore, considered the Xenophoridae not to belong into this superfamily. He stated that Calyptraeacea and Xenophoridae have certain tendencies in common and are related to each other. Therefore, in his opinion the Xenophoridae should be removed from the Strombacea and associated with the Calyptraeacea, as was done by Taylor & Sohl (1962). Morton thinks that both Xenophoridae and Calyptraeacea are derived from the Aporrhaidae (phylogenetic diagram: see Morton, 1958: fig. 3). Morton also noted that the radula of *Aporrhais* is very similar to that of *Xenophora*.

The radula of *Aporrhais pespelicani* Linné from the Mediterranean was studied for comparison (fig. 99). Judging by its morphology, *Aporrhais* and *Xenophora* are closely related, as Morton suggested and as was implied by Troschel (1856-1863: 190), but if we compare the radula of *Xenophora* and *Aporrhais* with that of members of the genera *Crucibulum* (fig. 110), *Calyptraea* (fig. 111), *Capulus* (fig. 113), or *Crepidula* (figs. 112, 114, 118), the difference becomes quite evident. The general shape of the central tooth is different in both groups. In the Calyptraeacea the central tooth is not heart-shaped as in *Xenophora* and *Aporrhais*, but rectangular. The basal platform of the central tooth in the Calyptraeacea is not smooth, but has ridges, a feature not found in the Strombacea or in *Xenophora*. The same holds true for the lateral teeth; in the Calyptraeacea a basal ridge is present, that cannot be found in the Strombacea. Instead, a minute denticle on the inner posterior corner of the lateral tooth is found in *Xenophora* and *Aporrhais*, which denticle is similar again to that of the Strombidae, where it often is more pronounced. The marginal teeth of *Xenophora* and *Aporrhais* are very long and slender, more so than those of the Calyptraeacea studied. If these teeth are denticulate, they always have an unbroken outer margin in the Strombacea, and a denticulate anterior margin. In the Calyptraeacea, however, only the outer marginal tooth has a smooth outer margin, while the inner one is denticulate on both sides of the apex.

Troschel (1856-1863: pl. 17 fig. 7) figured the radula of *Xenophora trochiformis* Born, which is very similar to that of *X. conchyliophora* and *X. corrugata* (Reeve) (see Suter, 1908). The figure of the radula of *X. neozelanica* Suter, in Morton (1958: fig. 1c), shows smooth cutting edges with teeth otherwise like those of *X. conchyliophora*. An intermediate radula, with a denticulate central tooth but smooth lateral and marginal teeth, was described and illustrated by LeLoeuff, Intes & Marche-Marchad (1971: fig. 8) for *X. senegalensis* P. Fischer.

The Caribbean *Strombus pugilis*, *S. gigas* and *S. raninus* can be identified by using the morphology of their radulae. Obviously *S. raninus* and *S. gallus* are closely related; their radulae are practically identical in shape. Troschel (1857-1863: 193-194, pl. 16 fig. 12) described and figured the radula of *S. pugilis*. Only his description and figure of the lateral tooth do not agree with the data presented here. Troschel did notice the main cusp of the cutting edge, but not the smaller flanking cusps that are also present there. Troschel's incomplete observation was copied in Abbott's (1960) description of the radula of the subgenus *Strombus* s. str. Here the lateral tooth is supposed to be very sturdy, conical and devoid of smaller cusps, while in fact it is almost square, showing a number of flanking cusps on its cutting edge.

The radula of *Strombus gigas* was described by Troschel (1857-1863: 198). This description differs slightly from ours. Maybe Troschel studied the radula of an adult, perhaps even old, individual (central tooth 0.75 mm wide), while the radulae studied here were from juveniles.

For comparison some Strombidae from the Red Sea have been studied, viz. *Strombus (Gibberulus) gibberulus* Linné (fig. 104), *S. (Lentigo) fasciatus* Born (fig. 107), *S. (Canarium) mutabilis* Swainson (fig. 106), *S. (Canarium) erythrinus erythrinus* Dillwyn (fig. 108), *S. (Tricornis) tricornis* Humphrey (fig. 105) and *Lambis truncata sebae* (Kiener) (fig. 109). The radulae of the various Strombidae (including *Terebellum*, see Jung & Abbott, 1967: pl. 319 fig. 3), have very much in common, as shown by figs. 100-109.

In his study on the Indo-Pacific members of the Strombidae Abbott (1960) stated that the radulae in *Strombus* show little specific diversity, but considerable intraspecific variation. He, therefore, considered radula characters of secondary importance in comparison with conchological characters within this family. However, Abbott also stated that the presence of a basal denticle near the inner posterior corner of the lateral tooth is important for the classification into some of the subgenera of *Strombus*. He also found that some of the radula characters are correlated with the marine provinces in zoogeography, rather than with assumed phylogenetic relationships. Abbott unfortunately does not go into detail here and, therefore, this statement remains somewhat mysterious. It is unclear why *Strombus fasciatus* (fig. 107), with a distinct basal denticle on the lateral tooth, is grouped by Abbott among the members of the subgenus *Lentigo*, in which according to his definition (Abbott, 1960: 117) no "basal peg" is found.

The radula morphology does not reflect the subgeneric nor even the generic classification of the Strombidae adopted by Abbott. On the other hand there

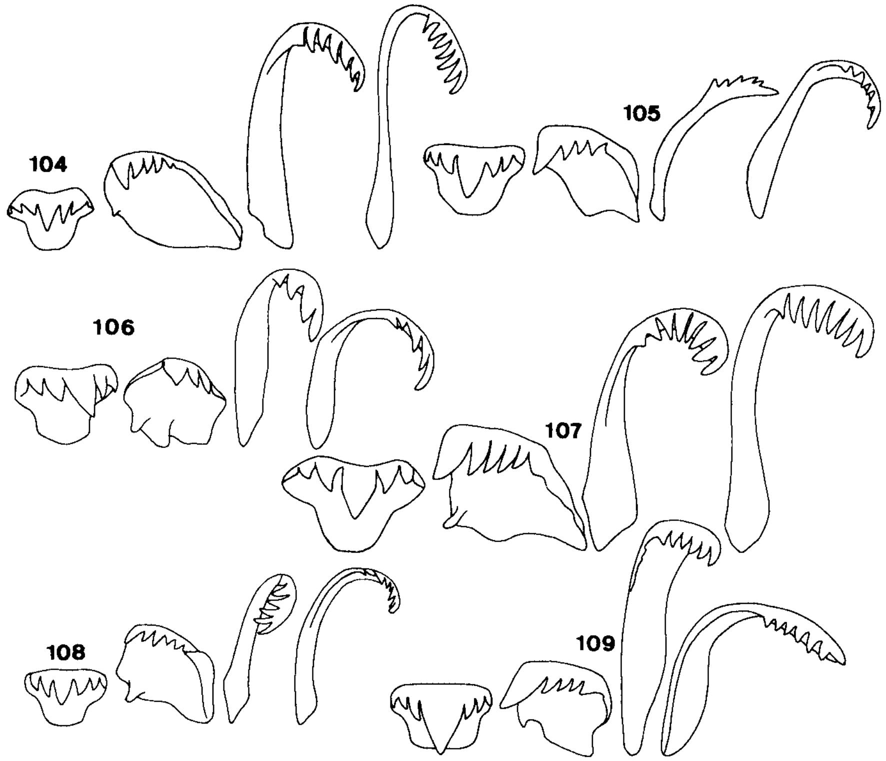


Fig. 104. *Strombus gibberulus*, Port Sudan, Red Sea; × 90. — Fig. 105. *Strombus tricornis*, Port Sudan, Red Sea; × 45. — Fig. 106. *Strombus mutabilis*, Port Sudan, Red Sea; × 90. — Fig. 107. *Strombus fasciatus*, Port Sudan, Red Sea; × 20. — Fig. 108. *Strombus erythrinus erythrinus*, Port Sudan, Red Sea; × 80. — Fig. 109. *Lambis truncata sebae*, Port Sudan, Red Sea; × 45.

seem to be sufficient differences between radulae of many species to tell them apart. The intraspecific variation mentioned by Abbott is much smaller than the differences found between most species; it only concerns the number of cusps on the cutting edges of the different teeth, where a considerable variation is encountered indeed. Judging by the radula morphology, *Lambis* (fig. 109) could well be considered only a subgenus of *Strombus*, as Thiele (1929: 255) suggested. The radula morphology makes clear that the Strombidae studied here are closely interrelated. Radula characters alone do not allow a splitting into genera and subgenera.

Radulae of the Struthiolariidae were described and figured by Powell (1951: fig. I[35-37]). The radulae of the different genera are similar to each other and seem to be somewhat intermediate between those of the Xenophoridae and the Strombidae.

Calyptraeacea and Hipponicacea

Cheilea equestris (Linné)
(fig. 117; pl. 6 figs. 2, 6)

The short radula has 35-40 rows of teeth. The central tooth is about five times wider than high and roughly triangular. Its anterior front consists of a low cutting edge with a large, central, acute, main cusp and six to eight flanking cusps on each side, which are all of about the same size. The anterior corners are also the posterior corners of the tooth since no margins are developed. The basal platform is narrow and plain. The base is attached to the radula membrane by only about one half of its length in its central part. The base shows a rounded central lobe and straight, long sides. The outer parts of the tooth overlap onto the inner platform of the lateral teeth and are thus hinged with them.

The lateral tooth is about three times wider than high. Its cutting edge is dominated by one large, triangular cusp, situated close to the inner margin. It is accompanied by four to five small inner and 9-11 outer cusps, gradually decreasing in size. The inner margin is curved outward and ends at a rounded posterior corner. It is hidden below the side of the central tooth. The outer margin is very long and straight, ending in an elongated posterior corner. This outer extension is solid and thickened, and continues into the sturdy basal platform of the tooth. The straight and smooth base between inner and outer corners is attached to the radula membrane over its whole length.

The marginal teeth are all about equally long and have slender stalks, which are oval in cross section, with hook-like apices. The apex of the inner marginal tooth is triangular and bilaterally flattened. Its main cusp is accompanied by four to five outer and five inner, much smaller, acute cusps. The apex of the outer marginal tooth is thorn-like, with a solid, acute, narrow main cusp, accompanied on the inner margin by only one or two minute denticles. In the folded radula the marginal teeth fit onto each other and together they fold into the concavity below the cutting edge of the lateral tooth, with their stalks resting in a groove on the surface of the solid outer extension of this tooth. No traces of wear were found on the used parts of the radula.

Crucibulum auricula (Gmelin)
(fig. 110; pl. 6 figs. 1, 5)

The radula consists of about 35 rows of teeth. The rectangular central tooth is somewhat wider than high, and slightly less wide at the front than at the base. The cutting edge is attached not quite on the anterior edge of the basal platform. Therefore, a flattened, convexly curved, frontal rim is formed. The cutting edge is dominated by an acute, triangular main cusp that is accompanied on each side by two or three smaller cusps. The convex margins are raised posteriorly and end in little, elongated, rounded, or acute posterior corners. The basal platform is slightly concave and, apart from a low central swelling, smooth; its base is straight.

The lateral tooth is more or less ovate, twice as wide as high, and has a straight base. The cutting edge is upturned and consists of a large, triangular main cusp that is accompanied by two smaller inner cusps and four or five smaller outer cusps, gradually decreasing in size. The outer margin is straight to convex and ends in a thin, rounded, outer posterior corner. A knob-like denticle projects from the posterior side of the central part of the basal platform and continues into a ridge that runs towards the outer posterior corner. There is a deep groove between the raised outer margin and the ridge of the basal platform; this groove ends in the outer posterior corner. The stalk of the inner marginal tooth fits into this depression.

The marginal teeth are high, all about equally long, and have hook-like apices. The inner marginal tooth is very sturdy and has a broad stalk and a triangular main cusp on a flattened apex. Inside the apex there are four cusps, gradually decreasing in size; the outside has only minute denticles. The outer marginal tooth is thin and slender and ends in an acute apex with only one thin, central cusp. In the folded radula all teeth fit closely onto each other. There are no traces of wear on the teeth of the functional part of the radula.

Crepidula convexa Say
(fig. 118; pl. 6 figs. 4, 8)

The radula consists of about 30 rows of teeth. The quadrangular central tooth has a narrow front and a wide base and is about as wide as high; it has a triangular cutting edge, which is inserted a little posterior of the anterior edge of the basal platform. Consequently, there is a narrow frontal rim that follows the convex front. The triangular main cusp dominates the cutting edge and the three to five cusps on each side of it are more a serration of its flanks than independent cusps. The margins are straight to convex and end in rounded posterior corners, together with broad, flat, inclined ridges that originate on the anterior basal platform just below the main cusp of the cutting edge. The posterior part of the basal platform consists of a broadly triangular lower part, bordered by the ridges, and the straight or concave base.

The rounded triangular lateral tooth is about twice as wide as high; it is quite similar in shape to that of *Crucibulum auricula*. Its upturned cutting edge is dominated by a triangular main cusp, flanked by three or four inner and seven to eight outer cusps. The inner margin is straight, ending in a rounded posterior corner. The straight base is accompanied by a ridge, which is almost parallel to it. This ridge originates in the lower central part of the concave basal platform; together with the raised outer margin it runs along a groove that ends in the outer posterior corner.

The marginal teeth are quite different from each other. The inner marginal tooth has a solid, bilaterally flattened, moderately long stalk (four times longer than wide) and an acute cutting edge with a hook-like main cusp. This cusp is serrated with seven or eight inner and six or seven outer denticles. The outer marginal tooth is slender, and fragile, and its stalk is round in cross section; this tooth is slightly shorter than the inner marginal tooth and much thinner (ten times longer than wide), having a narrow, hooked apex with a smooth outer side and a serration of one to four minute denticles on the inner side. All teeth of the radula fit onto each other in the folded radula. Only little wear was noted on the functional teeth.

Crepidula plana Say
(fig. 112; pl. 6 figs. 3, 7)

The radula consists of about 35 rows of teeth. The central tooth is bottle-shaped and only a little higher than wide; its anterior part is only about half as wide as its posterior part. There is a narrow rim between the vertical cutting edge and the front. The cutting edge follows the course of the convex front and is dominated by a high, diamond-shaped main cusp that is accompanied by two or three smaller flanking cusps on each side. Anteriorly the margins are curved inward, more posteriorly they turn outward, running convexly curved towards the evenly rounded posterior corners. Posteriorly the margins are raised and form narrow ridges that end in the corners. The basal platform has a broad, low, central elevation and, therefore, is convex, in spite of the raised margins. The base is straight to slightly convex.

The more or less oval lateral tooth has a straight inner margin and a long convex outer margin. The triangular cutting edge is upturned; it is dominated by a bilaterally flattened, triangular main cusp, that is accompanied by three or four inner and five to nine somewhat irregular outer cusps. The outer margin is raised, ending in a moderately extended outer posterior corner. The base is straight. There is a minute, ridge-like basal denticle on the lower central part of the basal platform. On the outer basal platform there is a broad, shallow, gutter-like groove, ending in the outer posterior corner.

Both the outer and the inner marginal tooth are similar in shape, but the inner is more sturdy. The latter has a flattened stalk, is about five times as long as wide, and has an acute, hook-like apex. The long main cusp is accompanied by a serration of the 8-16 inner and five or six outer denticles. The thin outer marginal tooth is about seven times as long as wide, having a smooth outer margin, a hook-like main cusp, and a serrated inside with five to eight denticles. In the folded radula the teeth fit onto each other. Only little wear was noted on the teeth of the functional part of the radula.

DISCUSSION

The radulae of *Cheilea equestris* (Hipponicacea) and *Crucibulum auricula*, *Crepidula convexa* and *C. plana* (all three Calyptraeacea) were studied after specimens from Santa Marta. All these species are living attached to hard substrates, either rock or shells of living and dead molluscs. The filter feeding of *Capulus ungaricus* (Linné) was described in detail by Orton (1962) and Yonge (1938). In a comprehensive study Werner (1953, 1957) analysed the feeding methods of the Calyptraeidae, based on detailed data on *Crepidula fornicata* (Linné). The Caribbean representatives of the Calyptraeidae and Hipponicidae here studied, feed like *C. fornicata*. Usually the radula is only used to pick up particles which have been caught by a mucus-ciliary filter system. The food particles are concentrated in mucus packages or rods before being swallowed. The food is only grasped and transported into the pharynx, without scraping or grazing in advance.

Cernohorsky (1968) noted considerable wear of the radula teeth of *Hipponix conicus* (Schumacher), and Richter (1961) described the same for *Crepidula fornicata*. Richter observed that the latter does not only use the radula to pick up the mucus food-rod provided by the ciliary mucus filter feeding system, but also uses its radula to clean the shell margin from growths of organisms. The radula is also used as a weapon. Richter observed that *Crepidula* bites off the intruding proboscis of carnivorous neogastropods. *Cheilea equestris* was also observed while cleaning the surface of the substrate with its radula before moving to a new holdfast. It also cleans the margins of the shell from growth. However, in all Caribbean species studied, the teeth of the part of the radula that had been used in the collection of food, showed very few signs of corrosion.

Cernohorsky (1968: fig. 1), studying *Hipponix conicus* (Schumacher), found considerable similarity between the Hipponicidae and the Capulidae when members of the genera *Cheilea* and *Capulus* are compared. He, therefore, expressed the opinion that *Hipponix conicus* would better be classified somewhere close to the Capulidae, within the Calyptraeacea, rather than with the Hipponicidae, Hipponicacea. *Cheilea equestris*, according to this author, should be classified with the Hipponicacea. In contrast to this, Abbott (1974) placed *Cheilea equestris* in the Crepidulidae (= Calyptraeidae) between *Calyptraea* and *Crucibulum* and assigned *Hipponix* and *Capulus* to the Hipponicidae.

The radula of *Capulus ungaricus* (Linné) was studied by Troschel (1856-1863: 161-162, pl. 13 fig. 14). From his illustration it seems to be more similar to the radula of *Crucibulum auricula* than to that of *Cheilea equestris*. Individuals of *Capulus ungaricus* from the Mediterranean were studied for comparison (fig. 113). The radula is quite close to that of *Crucibulum auricula* (fig. 110) in the general morphology of the teeth, but shows a different type of denticulation on the cutting edges. There are a large number of very small denticles on the central and the lateral teeth, while the marginal teeth are not denticulate. However, the radula of *Capulus intortus* Lamarck, studied by Barnard (1963: fig. 11e), seems to resemble that of *Cheilea equestris*.

Studying Thiele's characterization of the Amalteidae (= Hipponicidae), the Capulinae (= Capulidae in Taylor & Sohl, 1962) and the Calyptraeidae, we can find only very few and insignificant differences between these groups with regard

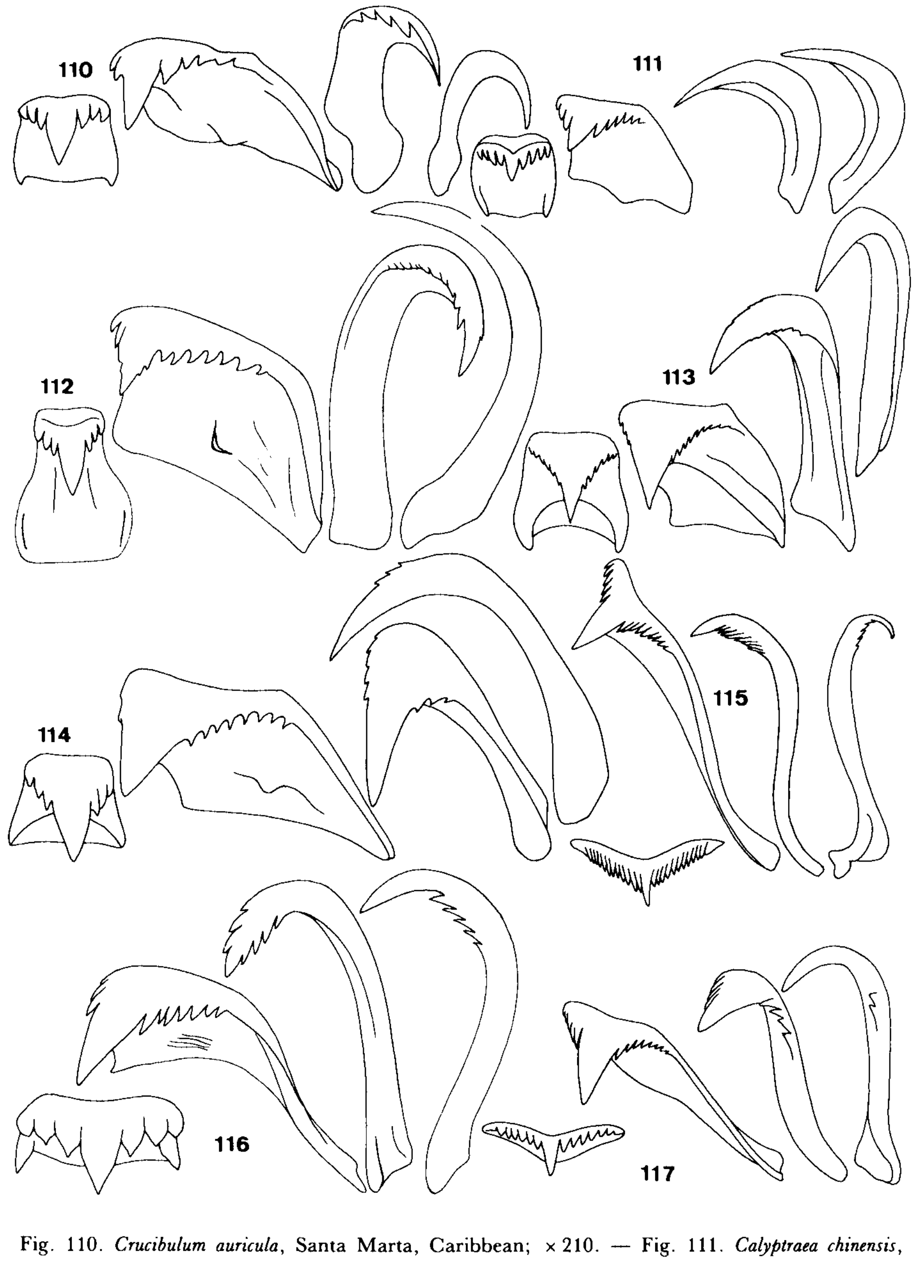


Fig. 110. *Crucibulum auricula*, Santa Marta, Caribbean; × 210. — Fig. 111. *Calyptraea chinensis*, Banyuls-sur-Mer, Mediterranean; × 200. — Fig. 112. *Crepidula plana*, Santa Marta, Caribbean; × 400. — Fig. 113. *Capulus ungaricus*, Banyuls-sur-Mer, Mediterranean; × 200. — Fig. 114. *Crepidula fornicata*, the Oosterschelde, North Sea; × 200. — Fig. 115. *Cheilea cicatricosa*; Port Sudan, Red Sea; × 130. — Fig. 116. *Hipponix conicus*, Port Sudan, Red Sea; × 250. — Fig. 117. *Cheilea equestris*, Santa Marta, Caribbean; × 300.

to the radula. According to Thiele, all radulae ar short, the triangular central teeth and the wide lateral teeth have denticulate cutting edges, whereas the marginal teeth are long and acute. The Capulinae only differ from the other groups by a less conspicuous dentition of the lateral tooth, and the shape of the marginal teeth, which are not denticulate. The central tooth of the Hipponicidae is described as very wide, in contrast to the somewhat narrower central tooth of the Calyptraeidae.

According to Troschel, and in contrast to the much later conclusions of Thiele, the Calyptraeidae and the Capulidae should not be separated. He considered the Hipponicidae quite different with respect to their radula. Troschel attached much value to the width of the central and the lateral teeth, but he did not notice the intermediate character of the radula of *Hipponix conicus* (Troschel, 1856-1863: pl. 13 fig. 15).

The morphology of the spawn and its mode of fixation enable one to differentiate three groups of genera within the discussed members of the Hipponicacea and the Calyptraeacea (Bandel, 1976). The first group contains *Hipponix* and *Cheilea*, with egg capsules attached to the parent animal, the second consists of *Capulus*, where the egg masses are kept free in the mantle cavity, and the third encompasses *Crepidula*, *Calyptraea* and *Crucibulum*, with egg capsules attached to the hard substrate below the shelter of the shell of the mother. The embryonic and the larval shells of *Cheilea equestris* are quite similar to those of *Hipponix conicus* from the Red Sea (own observation), differing considerably from those of *Crucibulum* and *Crepidula*.

If we accept Cernohorsky's opinion that a close relation exists between *Hipponix conicus* and members of the Calyptraeacea, and if we also assume a close relation between *Hipponix conicus* and *Cheilea equestris*, because of their characteristic larval and embryonic shell sculpture and the attachment of their eggs, we have to except a closer relationship between the limpet-like species now usually placed in two different superfamilies. With respect to their radula morphology, the two extremes, *Cheilea* and *Crepidula*, are connected by intermediate forms. *Cheilea cicatricosa* (Reeve) from the Red Sea (fig. 115), for example, has even wider and lower central teeth and wider lateral teeth than *C. equestris*. A variation in the dentition among members of the same species from different localities is observable in *Cheilea equestris*. While Cernohorsky (1968: fig. 3) observed many minute denticles on the outer marginal tooth in individuals from the Fiji Islands, specimens from Santa Marta have only two minute denticles at the same tooth.

Hipponix conicus collected in the Red Sea (fig. 116) and on the Seychelles have a radula identical to that of individuals of this species studied by Troschel from the Philippines and studied by Cernohorsky from the Fiji Islands. The radula of *H. conicus* is similar to that of *H. australis* Quoy & Gaimard, described and figured by Risbec (1942). This type of radula is transitional because it has wide lateral and central teeth as in *Cheilea*, but the central tooth is rectangular and its lower margins are raised, ending in projections of the posterior corners as in

Crucibulum. The radula of *Capulus ungaricus* is transitional to that of *Crepidula fornicata* Linné (fig. 114) and of *C. convexa* (fig. 118). The radula of *Crucibulum auricula* is similar to that of the two *Crepidula* species, but also to that of *Calyptraea chinensis* (Linné), which has been collected in the Mediterranean (fig. 111). The narrowest central tooth is found in the radula of *Crepidula plana*.

According to Risbec (1955) the Hipponicacea are not closely related to the Fossaridae and Vanikoridae as Thiele (1931) suggested, but may rather be considered cerithiaceans adapted to a sedentary life. Risbec found the anatomy of Hipponicidae very much like that of the Cerithiidae, and also noted that the radulae of both groups are quite similar. This does not seem to be true when the radulae of *Cerithium* (figs. 73-83) are compared to those of the Hipponicacea discussed here.

If we look for radulae similar to those of the Hipponicacea and Calyptraeacea among members of other mesogastropod families, it becomes apparent that the *Cheilea*-like radula stands quite apart. However, the more unspecialized *Crucibulum*, *Calyptraea* and *Crepidula* radulae are somewhat similar to radulae found among Vermetidae. If we compare the radula of *Petaloconchus varians* (d'Orbigny) (fig. 49) (Vermetidae) with that of *Crucibulum auricula* (fig. 110) (Calyptraeidae), the similarities and differences between the members of these two families, classified with different superfamilies, become apparent. The central teeth are of the same general outline, but while in *P. varians* strong posterior marginal ridges are present, only traces of swellings may be noted on the basal platform of the central tooth of *C. auricula*. The lateral tooth of *P. varians* is nearly completely like that of *C. auricula*, only the shape of the inner margin differs. The deep groove on the outer basal platform of the lateral tooth, that ends in the outer posterior corner, is quite characteristic. The inner and the outer marginal teeth are essentially the same in both species. The way in which the teeth are folded onto each other is very similar in both species, but the central and the lateral teeth of the vermetids are more closely hinged than those of the calyptraeids. A comparison of the conchological features of the members of the Calyptraeacea and Hipponicacea on the one hand and the Vermetidae (Cerithiacea) on the other, show great differences, but the way of life is quite similar. Both are almost sessile, and are filter feeders using mucus to catch food particles.

Since the species of Hipponicacea and Calyptraeacea are all sedentary, filter feeding animals, attached to some hard substrate, the wide variation in radula patterns is of taxonomic importance. The variation between the radulae of the various species studied here can be used to differentiate the species and genera among these conchologically so variable gastropods.

LAMELLARIACEA

Trivia pediculus (Linné)
(fig. 120; pl. 7 fig. 2)

The radula consists of about 50 rows of teeth. The squarish central tooth has concave margins and a concave front. The cutting edge is almost vertically attached to the basal platform; the central cusp is triangular and sharply pointed. One smaller denticle on each side is fused with its lower margin; there are three or four smaller, but among each other equally large, cusps on each side of the main cusp. A central supporting ridge runs across the basal platform from the main cusp to a shallow, tongue-like projection of the base. The posterior corners are elongated into points.

The angular lateral tooth is slightly higher than wide. The base has a long median "tongue" at the end of a central swelling, that extends from the very sturdy, central main cusp across the convex basal platform. The margins vary from straight to convex. The outer part of the cutting edge has six denticles, while the inner part only has one rounded denticle, right below the main cusp. The basal platform is thickened in its centre. Consequently, the rounded anterior corner of the central tooth fits into the inner depression of the lateral tooth, while the stalk of the inner marginal tooth fits into the outer depression of its basal platform.

The sturdy, sickle-shaped marginal teeth are all about equal in size. Their base is sturdy and broad, and their apices are hook-like and acute. The basal part of the stalk is oval in cross section, while its upper part is triangular. On the inner margin of the acute apex, the inner marginal tooth has one or two denticles, which may be rudimentary. The outer marginal tooth may have one small denticle on the inside of the apex, or smooth margins all over. The marginal teeth rest on each other, fitting together on the lateral tooth. No wear was observed on those teeth of the radula that had been used for gathering food.

DISCUSSION

Trivia pediculus was the only member of this superfamily from the Caribbean, which was studied. The species lives on the underside of rocks and coral blocks in water deeper than 1 m. The radula of *Trivia pediculus* had already been studied by Troschel (1856-1863: 214, pl. 18 fig. 2). The radulae of other members of the genus *Trivia* were described by Barnard (1963: fig. 6a, b), Thiele (1931: fig. 282) and Cernohorsky (1968: fig. 5). The last author noted that *Trivia oryza* (Lamarck) has a wider central tooth than found in *T. pediculus* and also quite strong basal denticles. Individuals of this species from the Red Sea were studied for the present work (fig. 121). For comparison the radula of *Trivia europaea* Montagu from the Mediterranean was also analysed (fig. 119). The central tooth of *T. oryza* proved to be clearly wider than that of *T. pediculus*, but basal denticles as illustrated by Cernohorsky were not found, only acute posterior corners. In contrast to the central tooth of *T. pediculus*, those of *T. oryza* and *T. europaea* have a smooth basal platform without marginal depressions. The sturdy lateral tooth is uniformly developed in the three species of *Trivia*, only with fewer cusps in *T. oryza* than in *T. pediculus*, and only low denticles on the cutting edge in *T. europaea*. In *T. oryza* the marginal teeth have more flanking cusps on their inner margins than in *T. pediculus*, whereas they are completely smooth in *T. europaea*.

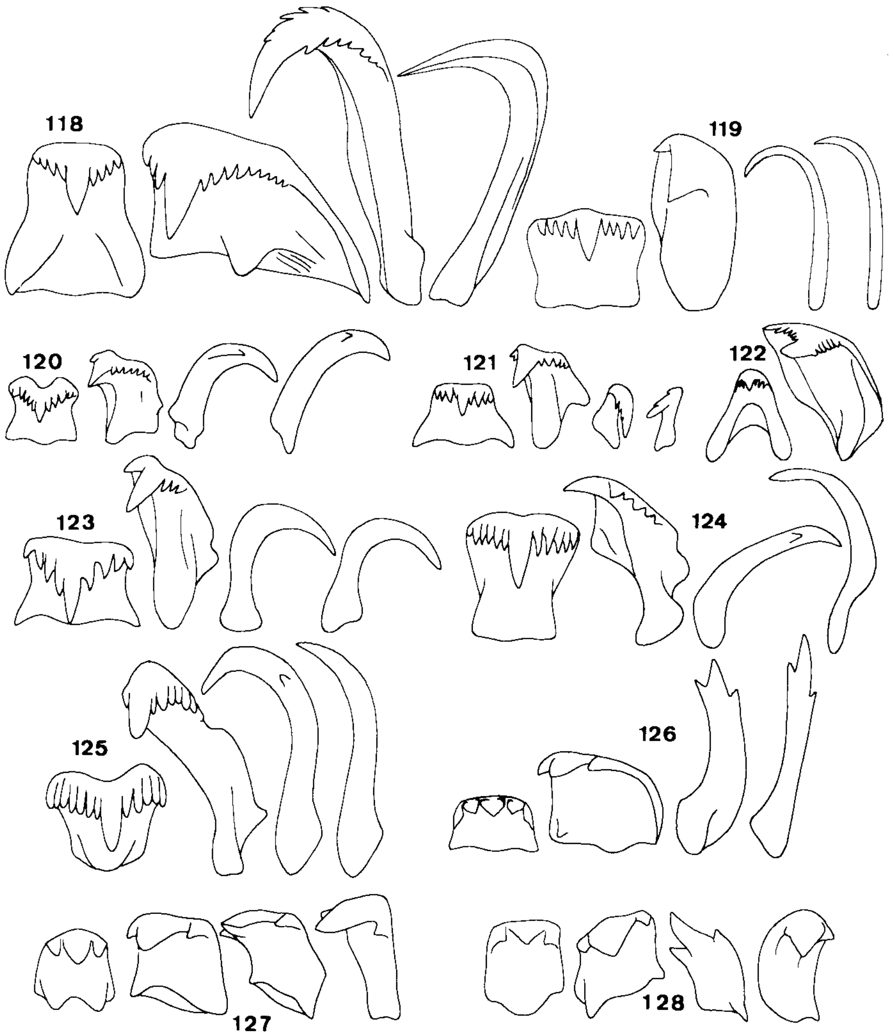


Fig. 118. *Crepidula convexa*, Santa Marta, Caribbean; x 300. — Fig. 119. *Trivia europaea*, Banyuls-sur-Mer, Mediterranean; x 250. — Fig. 120. *Trivia pediculus*, Santa Marta, Caribbean; x 100. — Fig. 121. *Trivia oryza*, Port Sudan, Red Sea; x 150. — Fig. 122. *Lamellaria latens*, Banyuls-sur-Mer, Mediterranean; x 55. — Fig. 123. *Velutina undata*, Banyuls-sur-Mer, Mediterranean; x 800. — Fig. 124. *Erato voluta donovani*, Banyuls-sur-Mer, Mediterranean; x 600. — Fig. 125. *Erato* sp., Port Sudan, Red Sea; x 1400. — Fig. 126. *Cypraea staphylea*, Port Sudan, Red Sea; x 130. — Fig. 127. *Cypraea pantherina*, Port Sudan, Red Sea; x 50. — Fig. 128. *Cypraea erosa nebrites*, Port Sudan, Red Sea; x 90.

Troschel (1856-1863: 214, 216) had noted a close similarity between the radulae of *Trivia* and *Erato*, and placed these genera together in the "Triviacea". He had them separated both from the conchologically similar Cypraeidae because of their radula morphology. *Erato voluta donovani* Schilder from the Mediterranean (fig. 124) confirms Troschel's results. The typical lateral tooth and the marginal teeth are quite similar to those of *Trivia*. The central tooth is somewhat higher than even that of *T. pediculus* and also has low marginal depressions like this species. The lateral tooth of *E. voluta donovani* has a very strong median swelling, extending into a basal process even more strongly projecting than in *Trivia*. The teeth of *Erato* are folded in the same way as those of *Trivia*. In an unidentified *Erato* species, collected from the Red Sea (fig. 125), the central swelling of the central tooth bulges posteriorly and the tooth is wider in front than at the base; the lateral tooth is clearly higher than wide and its central swelling has developed into a sturdy, median, tongue-like projection of the base.

The radula of *Velutina undata* (Brown), studied in individuals from the Mediterranean (fig. 123), is even more similar to that of *Trivia oryza* than that of *Erato*. It also agrees in a general way with the radula of *Velutina laevigata* Pennant, figured by Troschel (1856-1863: pl. 14 fig. 2). This supports the opinion of Fretter & Graham (1962: 626-629), who classify *Trivia* and *Erato* together with the Lamellariacea. According to the illustrations of Thiele (1931: fig. 279) and Marcus (1959: fig. 4), the radula of *Marseniopsis pacifica* Bergh, also a limpet-like representative of the Lamellariidae, is quite similar to that of *Erato voluta donovani*.

A typical radula of members of the genera *Trivia*, *Erato*, and *Velutina* has a rectangular central tooth with cusps of the frontal cutting edge, vertically attached to the basal platform, which is smooth or has a central swelling, whereas its posterior corners, whether rounded or acute, do not project into swellings or denticles. The very sturdy lateral tooth is higher than wide, with a sturdy central cusp from which a median swelling originates that continues into a thickened, often raised tongue of the base. This central ridge is accompanied by an inner and outer lower part of the basal platform onto which the neighbouring central and the inner marginal tooth may rest. The marginal teeth are slender, with a hook-like apex, that may have smaller flanking cusps or denticles on its inside.

Velutina, *Trivia*, and *Erato* live on tunicates, rasping them with the radula. Fretter & Graham (1962) described how these gastropods touch the tunicate individual with their long proboscis and scrape off the most nutritious parts. Our own observations indicate that *Trivia pediculus* also feeds on tunicates that usually are attached on the underside of rocks. The faecal pellets of *T. pediculus* contain the remains of the tough cellulose body walls of their food (Bandel, 1974). The feeding of *Velutina velutina* was observed by Diehl (1956). The predatory gastropod opens the tunicate by drilling a hole into the leather-like outer skin by mechanical rasping of the radula. Then the proboscis is stretched through the hole and is held quite still, the mouth is opened and closed rythmically and the radula is moved from ventral to dorsal.

The family Lamellariidae that has been selected to represent the Lamellariacea has members with a reduced radula, i.e. where the marginal teeth are lacking. The radulae of *Lamellaria perspicua* (Linné) and *L. latens* (Müller) from the Mediterranean were studied for comparison. They demonstrate the features of the radulae of *Lamellaria* species quite well (fig. 122). Taki (1972: text-figs. 11-18) reviewed and figured many *Lamellaria* radulae known from the literature. The central tooth usually has posterior bifurcate swellings and the cutting edge has a somewhat twisted main cusp, similar to that on the central tooth of *Erato*. As in *Erato* the radula is asymmetrical. The greatest similarity between the radulae of *Trivia*, *Erato*, and *Velutina* on the one hand and *Lamellaria* on the other, can be seen in the morphology of the lateral tooth. It has a strong median ridge, projecting into a posterior process of the base. At both sides of this central swelling the basal platform is low and grooved, but the grooves are no longer functional in the folded radula, since marginal teeth are absent and the central tooth is attached to the membrane of the radula at quite a distance from the lateral tooth. Not in all *Lamellaria* species the central tooth has conspicuously bifurcating marginal ridges. According to Barnard (1969: 645) the base is straight in *Lamellaria capensis* (Bergh) and no ridges are present there. The bifurcation noted by most authors is also present in *L. latens* and *L. perspicua* (see also Marcus, 1959: fig. 9). Actually it is only a bifurcation of the thickened anterior part of the basal platform of the central tooth. Between the two ridges formed in this way there is a thin, lamellar central portion of the basal platform; the weakly concave base is formed by this thin platform. Like in *Trivia*, *Erato*, and *Velutina*, *Lamellaria* uses its radula to feed on tunicates.

Judging after the radula structure it would seem quite sensible to follow Troschel's (1856-1863: 185) advice to split the Lamellariacea into two groups, i.e. (1) species with a complete taenioglossate radula, like *Trivia*, *Erato*, *Velutina* and *Marseniopsis*, and (2) species with only three teeth in each transversal row, like *Lamellaria*. This arrangement does not agree well with the conchological differentiation of this group into genera with *Cypraea*-like shells like *Trivia* and *Erato*, and those with a limpet-like shell such as *Velutina* and *Lamellaria*.

Cypraeacea

Cypraea zebra Linné
(fig. 135; pl. 7 fig. 3)

The radula consists of about 95 rows of teeth. The central tooth is roughly quadrangular and as wide as long; it has a well rounded front. The cutting edge is perpendicular to the basal platform; it has a sturdy main cusp, flanked by one smaller, rounded cusp on each side. The basal platform has two levels. A lower level is visible on the concave margins and the straight, central part of the base; the second level with straight margins and a concave base is placed on top of the other front. The base of this second level is drawn out into rounded projections at the corners, while the basal corners of the lower level of the platform are rounded. The margins of the tooth are step-like and the tooth itself is very sturdy and thickened.

The quadrangular lateral tooth is as wide as long. Its upturned cutting edge is dominated by a very sturdy, long, main cusp that is situated at the inside of the cutting edge and is flanked by one smaller cusp on each side. The margins and the posterior edge are straight. As in the central tooth there is a decrease in thickness of the basal platform near the margins forming a lower rim. This rim is quite narrow on the inner margin and somewhat wider on the outer. A large basal denticle attached to the basal platform near the inner posterior corner projects upward and backward over this corner.

The uniform marginal teeth are similar to the lateral tooth. The apex of the marginal teeth is dominated by an acute main cusp that is accompanied on the outer side only by a minute denticle. The margins are straight; the inner margin is shorter than the outer one. Therefore, the inner posterior corner is rounded, whereas the outer one is acute. The base is straight and about half as wide as the tooth is high. All teeth have a very thick basal platform; they often split in their center during the preparation of the radula. The teeth of the radula hardly fit onto each other in the folded radula.

Cypraea cinerea Gmelin
(fig. 137; pl. 7 fig. 4)

The radula consists of about 90 rows of teeth. The quadrangular central tooth has a well rounded front; it is somewhat higher than wide. The cutting edge is perpendicular to the basal platform and consists of one large sturdy cusp, from which a broad supporting ridge extends onto the concave basal platform, ending in its anterior part. The curved raised margins extend backward, ending in acute posterior corners. Near the corner there is a ridge that starts at the middle of the margin and ends in a rounded, short projection. The base between these two projections is straight or shallowly concave.

The rectangular lateral tooth is about twice as high as wide. It is about half as wide as the central tooth, but equally high. The tooth is sturdy and massive and has a cutting edge that is dominated by a stout cusp, accompanied by one much smaller cusp on each side. The base is only a little wider than the cutting edge and also convexly rounded. A sturdy acute denticle is attached to the outer part of the posterior basal platform; it projects upward, being inclined backward, without extending over the base. Otherwise the basal platform is smooth and concave since the margins are somewhat raised.

The two uniform marginal teeth are somewhat smaller but otherwise similar to the lateral tooth. The marginal teeth have a sturdy main cusp, accompanied by a smaller denticle on each side. The front and the base are rounded. A strong basal denticle projects from the outer posterior part of the basal platform over the rounded outer posterior corner. The teeth are set well apart from each other. The functional part of the radula showed some wear on all teeth of each transversal row.

Cypraea spurca acicularis Gmelin
(fig. 139; pl. 7 fig. 5)

The radula consists of about 85 rows of teeth. The rectangular central tooth is longer than wide (2:3). Its cutting edge is perpendicular to the basal platform. The stout acute main cusp is accompanied by one smaller flanking cusp on each side. Apart from a slight excavation in the centre the front is straight. The posterior corners are rounded and slightly raised, with shallow ridges that accompany the straight margins ending in them. The base extends into a smoothly curved, shallow, tongue-like process, which is the continuation of a low, rounded, central swelling of the basal platform.

The rectangular lateral tooth is larger than the central tooth and about as high as wide. Its cutting edge is curved upward, forming an angle larger than 90° with the basal platform. The sturdy main cusp is acute; it is accompanied by one inner and one outer denticle. The margins are straight and end in rounded posterior corners. A very stout, large cusp is attached to the basal platform near the inner posterior corner, projecting over it. The basal platform bulges convexly and is accompanied by a depression near both margins.

The uniform marginal teeth are dominated by long main cusps that are curved upward and inward, forming an angle of over 90° with the basal platform. This main cusp is accompanied by one small cusp on each side. The convex basal platform is quadrangular and almost twice as long as wide. In contrast to the lateral tooth, the marginal teeth have a basal denticle projecting from the outer posterior corner, while the inner posterior corner is well rounded. In the folded radula the apex of the outer marginal tooth rests on the basal platform of the inner marginal tooth. Apart from that the radula shows very little connection of the single teeth to each other. The teeth in the part of the radula that had been in use show some wear.

Cyphoma gibbosum (Linné)
(fig. 148; pl. 7 fig. 6, pl. 8 fig. 1)

The radula consists of about 150 rows of teeth. The central tooth is wider than high (8:5), with a weakly curved front and a rounded base. The margins cannot be separated from the base since they continue into each other without posterior corners. Only the lower part of the base, which is regularly curved, is attached to the membrane of the radula. The cutting edge is regularly curved upward, forming an angle of about 90° with the basal platform, which is smooth. The cutting edge has five to eight cusps, of which the central one is the largest. There is a lot of variation both in size and number of the flanking cusps. The central tooth is not linked to the lateral teeth.

The lateral tooth is much higher than the central tooth and consists of a triangular, posterior basal platform that continues into a sickle-shaped, anterior part. The outer margin is evenly convex and the inner margin is straight. The stout sickle-like, upper part of the tooth continues into a strong supporting ridge, which extends along the inner margin into the bulbous inner posterior corner. There are two or three minute, outer, flanking denticles, whereas the inside of the cutting edge is smooth. In the folded radula the lateral teeth point inward with their hook-like apices; in the unfolded radula they point outward.

The narrow, triangular, inner marginal tooth is sheet-like; it is fixed to the membrane by its acute end and its broad apex has 14-18 comb-like cusps, each with one to three points. The inner margin is straight. The outer margin is slightly concave and extends into the anterior, outer end of the cutting edge, forming a long, rod-like cusp from which six or seven cusps arise which gradually become shorter. The other cusps of the cutting edge may only branch near their apices.

The outer marginal tooth is also triangular, and ends in a comb-like cutting edge with rod-like cusps that have two or three points. The many (30-35) individual cusps are narrower and shorter than those on the cutting edge of the inner marginal tooth. The inner margin is straight and long, the outer one is extended so as to form a lobe, and short. The base is very long and constitutes almost the whole outer rim of this tooth. In some individuals the teeth of used parts of the radula are conspicuously eroded. Usually the cusps of the central tooth are completely worn away, while the marginal teeth show little wear. In this radula only the marginal teeth are hinged. The consecutive rows of the radula are very close to each other. Thus the high lateral and marginal teeth of following rows overlap strongly. The central teeth are so close together that they also overlap; therefore, they have a shallow cavity on their lower surface which fits onto the rounded basal platform of the tooth in front of it.

Simnia acicularis (Lamarck)
(fig. 144; pl. 7 fig. 7, pl. 8 fig. 2)

The radula consists of about 100 rows of teeth. The rectangular central tooth is about four times as wide as long. The cusps of the cutting edge are attached directly to the posterior part of the basal platform; there is an irregular, narrow rim between these cusps and the convex front. The triangular, acute, main cusp is the largest, having two or three secondary cusps on its flanks; it is accompanied by three to eight unequal cusps of smaller size on each side. The number, size and arrangement of these flanking cusps is very variable among individual teeth of a single radula. The short margins end in acute posterior corners. The base is convex.

Between central and lateral teeth a broad zone of the membrane is free of teeth. The triangular lateral tooth is long and slender and broadest at its base. The bilaterally flattened basal platform has a convex inner and a concave outer margin. The outer posterior corner is somewhat elongated into a short handle-like extension. The apex of the tooth is extended into an acute, long, stout main cusp, which is curved and hook-like. The inner margin of the apex has seven to ten small, acute cusps that are more a serration of the inner flank of the main cusp. The outer margin of the apex has one to three denticles.

The marginal teeth are very similar to those of *Cyphoma*. The inner marginal tooth is triangular; its comb-like apex has about 20 hooked, equally long, narrow cusps. The outer marginal tooth is broadly triangular in shape, with a comb-like cutting edge that is curved upward, with 50 cusps of the same shape and size as those on the inner marginal tooth. Near the outer margin of the cutting edge the cusps decrease in length. The radula has the same type of folding and tooth connection as in *Cyphoma*.

DISCUSSION

Three representatives of the Cypraeidae have been studied. *Cypraea zebra* is a rare species, found among reef debris at 0.5 to 10 m depth. *C. cinerea* occurs somewhat more commonly in the area of Santa Marta, also living among stones and reef debris at 0.5-4 m depth. *C. spurca acicularis* is extremely rare in the region of Santa Marta, being found under boulders at about 2 m depth. The faecal pellets of *C. cinerea* are purely organic; in *C. spurca acicularis* they consist of a mixture of organic material and sponge spicules.

The genus *Cypraea* has been subject to extreme splitting and lumping. Taxonomic criteria used for splitting have often been entirely conchological. The first author splitting *Cypraea* on the basis of both radula and shell morphology has been Troschel (1856-1863: 203-205), who considered the general outline of the central tooth in the radula most important. He differentiated between a rounded triangular and a rounded quadrangular shape and additionally used the presence or absence of denticles, raised projections or ridges near the base of the central tooth, and differences in the morphology of these basal denticles. His first genus, *Cypraea* s. str., is characterized by a central tooth that has no raised parts near its base. This genus is subdivided into four subgenera, mainly according to the outline of the central tooth. Troschel's second genus *Aricia* Gray, has raised posterior ridges on the basal platform of the central tooth; three subgenera are based again on the general outline of the central tooth. Troschel considered the two genera to constitute the family Cypraeidae. Thiele (1931) subdivided this group, which he called Cypraeinae, into six genera; in his classification one of Troschel's genera was ignored, and two of his subgenera were raised to generic rank. Schilder & Schilder (1938-1939) considered Thiele's Cypraeovulinae and his Cypraeinae together to constitute a family; these authors divided the recent Cypraeidae into 24 genera.

Kay (1960a, b), revising the generic classification of the Cypraeinae, discussed several classifications proposed in the extensive literature on this group of attractive gastropods, e.g. 52 genera for the approximately 150 species of Linné's *Cypraea*. Kay studied the soft parts of 88 *Cypraea* species and concluded that the Cypraeinae consist of only the original single genus, *Cypraea*.

Here the radulae of 17 species of *Cypraea*, including the three described from Santa Marta, are compared with each other. Thirteen species were collected near Port Sudan in the Red Sea, and one, *Cypraea tigris* L. at the Seychelles. As Troschel (1856-1863) had noted, the radula of almost every species can be differentiated from that of the other species of the genus. While comparing these radulae (figs. 126-142) it becomes evident that the four types of radulae differentiated by Kay (1960) intergrade with each other.

The central tooth is either rectangular, as in the three Caribbean species and most of the species from the Red Sea, or it is triangular as in *C. carmelopardalis* Perry (fig. 142), *C. lynx* L. (fig. 141) and *C. carneola* L. (fig. 140). The basal platform is smooth in the species just mentioned and in *C. spurca acicularis*, *C. annulus* L. (fig. 133), *C. erosa nebrites* Melvill (fig. 128) and *C. turdus* Lamarck (fig. 134). Basal denticles seem to change into projecting basal corners as in *C. annulus* and *C. isabella* L. (fig. 136). There are denticles on the basal platform of the central tooth in *C. pantherina* Solander (fig. 127), *C. arabica* L. (fig. 132), *C. erythraensis* Sowerby (fig. 131), *C. crassites notata* Gill (fig. 129), *C. caurica* L. (fig. 130), and *C. tigris* (fig. 138). Central teeth intermediate between the triangular and the rectangular type are present in the radulae of *C. isabella*, *C. tigris* and *C. staphylea* L. (fig. 126).

The lateral teeth are broad and usually tricuspid. Exceptions with two outer flanking cusps are *C. crassides notata*, *C. erythrensis*, *C. carmelopardalis*, *C. lynx*, and *C. carneola*. Usually there are one or two basal denticles; two have been observed in the radula of *C. tigris*, *C. erythrensis*, *C. arabica* L. and *C. annulus*. The basal denticle is only found on the inside of the lateral tooth in *C. spurca acicularis*, *C. zebra* and ten of the species from the Red Sea. It is situated on the outside in *C. cinerea* Gmelin and *C. isabella* only. Crovo (1971: fig. 4, 5) distinguished between the extremely similar *C. zebra* and *C. cervus* after the presence of a split lateral tooth, found in the latter species only. While studying radulae of *C. zebra*, and other *Cypraea* species such split teeth were often encountered. This feature clearly is an artifact, produced by the extraction and mounting of the teeth. The radulae of *C. zebra* and *C. cervus* L. are practically identical.

The location of the basal denticle on the inner marginal tooth is also variable, independent of the location of the basal denticle on the lateral teeth. As in *C. zebra*, *C. spurca acicularis* and a number of Red Sea species, the radulae of the species of the subgenus *Zoila*, illustrated by Wilson & McComb (1967: pl. 334) have basal denticles on the inside of the lateral tooth and on the outside of the marginal teeth.

The way in which the teeth are situated in the folded radula differs considerably among the species of *Cypraea*. All members of this genus studied show a central tooth that is not linked with the lateral teeth. Apart from this, we can distinguish the following six transitional stages:

1. *C. crassides notata*, *C. erythrensis*, *C. staphylea* and *C. caurica* with slender marginal teeth that are hinged at their base. In the folded radula the outer marginal tooth rests on the inner marginal tooth; both together fit onto the con-

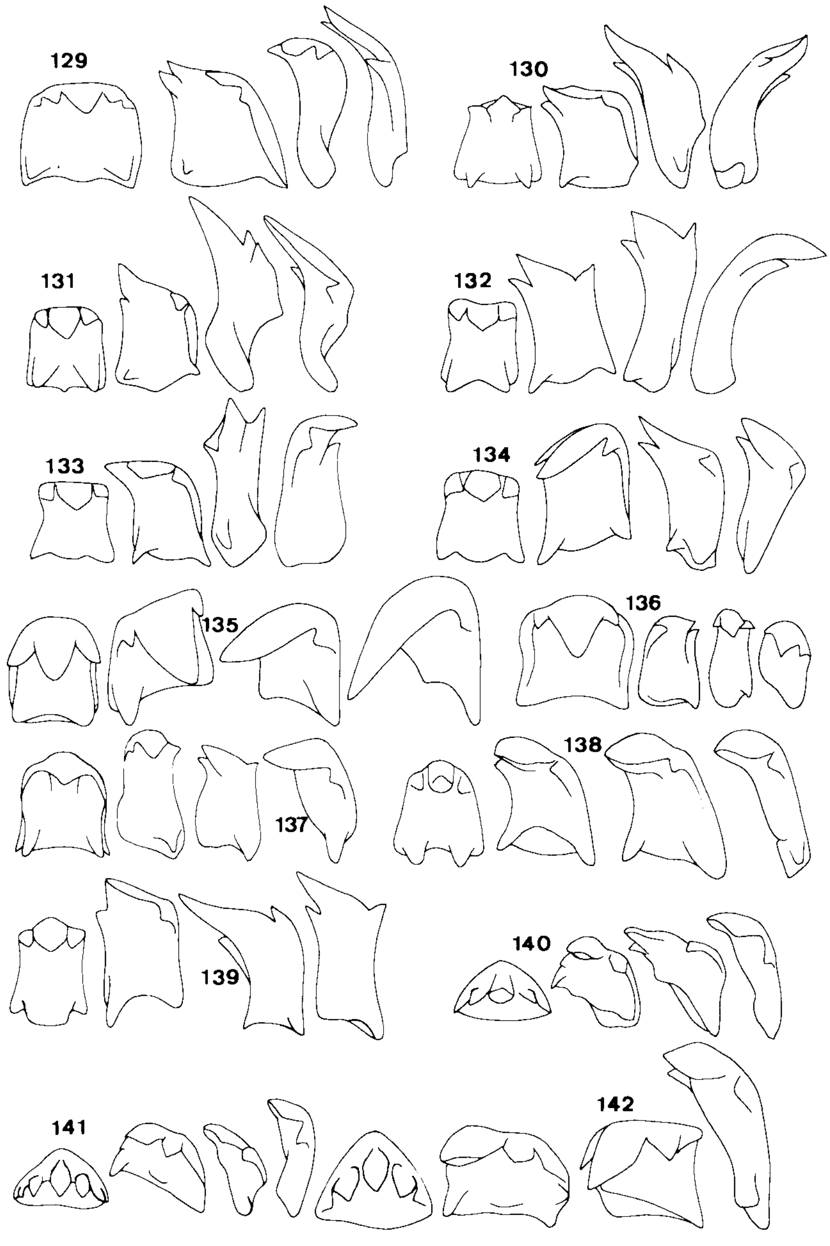


Fig. 129. *Cypraea crassites notata*, Port Sudan, Red Sea; × 80. — Fig. 130. *Cypraea caurica*, Port Sudan, Red Sea; × 70. — Fig. 131. *Cypraea erythraeensis*, Port Sudan, Red Sea; × 90. — Fig. 132. *Cypraea arabica*, Port Sudan, Red Sea; × 50. — Fig. 133. *Cypraea annulus*, Port Sudan, Red Sea; × 90. — Fig. 134. *Cypraea turdus*, Port Sudan, Red Sea; × 130. — Fig. 135. *Cypraea zebra*, Santa Marta, Caribbean; × 50. — Fig. 136. *Cypraea isabella*, Port Sudan, Red Sea; × 120. — Fig. 137. *Cypraea cinerea*, Santa Marta, Caribbean; × 120. — Fig. 138. *Cypraea tigris*, the Seychelles, Indian Ocean; × 30. — Fig. 139. *Cypraea spurca acicularis*, Santa Marta, Caribbean; × 90. — Fig. 140. *Cypraea carneola*, Port Sudan, Red Sea; × 80. — Fig. 141. *Cypraea lynx*, Port Sudan, Red Sea; × 90. — Fig. 142. *Cypraea camelopardalis*, Port Sudan, Red Sea; × 75. — Fig. 143. Not present.

cave basal platform of the lateral tooth, their apices resting below the cutting edge of the lateral tooth.

2. *C. turdus* with an arrangement of the marginal teeth similar to that of group 1, but with the teeth less closely linked at their bases.

3. *C. annulus*, *C. arabica* and *C. erosa nebrites* have marginal teeth that fit onto each other and together, with their apices, into the concavity of the lateral tooth. The marginal teeth are quite independently attached to the membrane of the radula.

4. *C. carneola*, *C. lynx* and *C. carmelopardalis* have the teeth well apart from each other. The inner marginal tooth is attached along much of its width, and only the outer marginal tooth can be moved outward. The outer marginal tooth fits onto the inner marginal tooth; it is held in place by the strong, basal swelling and the raised, outer anterior corner of the inner marginal tooth.

5. *C. zebra*, *C. spurca acicularis*, *C. pantherina* and *C. tigris* have teeth that are not linked, but the cutting edge of the inner marginal tooth projects somewhat inward. The outer marginal tooth rests with its apical part only on the outer margin of the inner marginal tooth.

6. In *C. cinerea* and *C. isabella* all teeth have a similar rounded, shovel-like shape and do not project over or fold onto each other. They are attached to the membrane well apart from each other.

The general similarity of the radulae of the various *Cypraea* species and the transition stages in radular morphology connecting the extremes, should be regarded as a strong support to Kay's (1960) views.

The two species of the Ovulidae studied from Santa Marta were observed to feed on the polyps of gorgonarian corals. *Cyphoma gibbosum*, the larger of the two, eats the flesh of these anthozoans along with much of the calcareous skeleton, leaving only the black central axes of the branches. The much smaller *Simnia acicularis* also feeds on these colonial coelenterates but does not eat much skeletal material. Specimens of both species are often seen feeding together on the same sea fan. This type of food, i.e, small polyps of large coelenterate colonies, seems to be normal for members of the Ovulidae. The radulae of three additional species of this family, viz. *Simnia carnea* (Poiret), *S. nicaensis* Risso and *Primovula coarctata* (Adams & Reeve) were studied for comparison (figs. 145-146). *S. carnea* and *S. nicaensis* were collected from gorgonarians in the Mediterranean, while *Primovula coarctata* was found on encrusting coelenterates in the Red Sea. The radulae of these three species are quite similar to that of *Simnia acicularis* from the Caribbean. The central tooth in the latter is wider than those of *Primovula coarctata* and of *Simnia carnea*. The central tooth of *Simnia nicaensis* is even less wide and almost like that of *Cyphoma gibbosum*.

Regarding the morphology and dentition of the lateral teeth, *Cyphoma gibbosum* has the largest and most sturdy type. Here the triangular basal platform is very stout and wide, and the hook-like apex has a smooth edge. The lateral tooth of *P. coarctata* also has a wide triangular basal platform, but the apex is less far extended forward and it is denticulate. In *Cyphoma gibbosum* the lateral tooth is much

Fig. 144. *Simnia acicularis*, Santa Marta, Caribbean; × 400. — fig. 145. *Simnia nicaensis*, Banyuls-sur-Mer, Mediterranean; × 210. — Fig. 146. *Primovula coarctata*, Port Sudan, Red Sea; × 300. — Fig. 147. *Simnia carnea*, Banyuls-sur-Mer, Mediterranean; × 230. — Fig. 148. *Cyphoma gibbosum*, Santa Marta, Caribbean; × 100.

higher than the central one; in *P. coarctata* both are of similar size. The lateral teeth of *Simnia acicularis*, *S. nicaensis* and *S. carnea* are similar to each other. Here the outer posterior corner is elongated to form a handle-like extension, which is not thickened. Thus the posterior basal platform is not broadly triangular as in *Cyphoma gibbosum* and *Primovula coarctata*. With regard to the marginal teeth no differences could be found between the radulae discussed here.

Troschel (1856-1863: 216) had studied the radulae of three species of Ovulidae and, for the first time, had noted the striking differences to those of the Cypraeidae. Both the illustration and description of the radula of *Cyphoma gibbosum* (op. cit.: pl. 18 fig. 7) are correct, apart from the lateral tooth, which was drawn somewhat too small and short and without the triangular basal platform. Thiele (1931: 272, fig. 290) noted the great width of the base of the lateral tooth in *Cyphoma*, but otherwise apparently described worn teeth, i.e. with strongly worn cutting edges of the central and the lateral tooth.

The radula of *Simnia uniplicata* Sowerby was figured by Troschel (1856-1863: pl. 18 fig. 8); it is very similar to that of *S. acicularis*. The lateral tooth might be too short in Troschel's illustration and an extended outer posterior corner might have gone unnoticed. The last structure most probably is present in this radula and has been observed in a number of species of the genus *Primovula* by Azuma & Cate (1971: figs. 17, 18), Cernohorsky (1968: fig. 3) and Barnard (1963: fig. 6c). Members of the genera *Kuroshiovolva* and *Phenacovolva* (Azuma & Cate, 1971: figs. 19, 21), *Calpurnus* (Cernohorsky, 1968: fig. 1), *Crenavolva* (Cate, 1975: fig. 13) and *Volva* (Barnard, 1959: fig. 6d) seem to have similar, handle-like extensions of the outer posterior corner of the lateral tooth as present in *Simnia acicularis*, *S. nicaensis* and *S. carnea*. A member of the genus *Pseudosimnia* (Azuma & Cate, 1971: fig. 24) seems to have a sturdy extension of this tooth, perhaps similar to that in *Primovula coarctata*.

Figures of the central teeth of the radula of the Ovulidae in the literature show some variation in the width of the tooth, comparable to what is observed in the here studied species. This feature seems to be only of taxonomic importance on the species level. This is different with regard to the lateral tooth. Here a development has taken place from a more normal mesogastropod type of lateral tooth, with a moderate extension of the outer posterior corner (as still well developed in *Simnia nicaensis*), to such types with a strengthened outer margin (as in *Primovula coarctata*), and, finally, to a solid triangular basal platform (as in *Cyphoma*). These features of the lateral tooth may reflect relationships on a generic level. The sheet-like marginal teeth seem to be a family character.

All studied radulae of the Ovulidae are very variable in size, number and arrangement of the cusps on the cutting edges of the teeth. The general shape of the central tooth and the morphology and size of the lateral tooth, however, are quite stable in the various species and differ considerably among the members of the Ovulidae.

Troschel (1856-1863) observed sufficient differences between the radulae of *Amphiperas ovum* L., *Cyphoma gibbosum* and *Simnia uniplicata* to justify a generic separation of these three species, but he also noted enough common features to classify them into one well defined family. Thiele (1931: 270) places the same genera in his subfamily Amphiperasinae, classified with Triviinae, Pediculariinae, Jenneriinae, Cypraeovulinae and Cypraeinae in the Cypraeidae. Keen (1963) united three of Thiele's subfamilies to a family Ovulidae, with two more families forming the Cypraeacea. Abbott (1974) and Taylor & Sohl (1962) proposed somewhat different classifications. Almost every taxonomic study published since Troschel's time has treated the Ovulidae in a different way.

The conchological differences within the Ovulidae are comparable to those of the Cypraeidae and do not justify an extensive splitting into genera. The known radulae are very similar to each other. Cate (1974) has recently split this family into no less than 41 genera for purely conchological reasons. This kind of splitting of a rather uniform group of gastropods serves no useful purpose.

The relationships of the Ovulidae with the Cyraeidae and the Eratoidae, are difficult to envisage when only the structure of the radula is taken into account. The lateral tooth of the Ovulidae is quite unlike that of the Eratoidae, the latter having a strong central supporting ridge that ends in a basal lobe. It also differs from that of the Cypraeidae, where the lateral tooth is angular or oval, with a short, rounded posterior corner. When the marginal teeth are considered, the differences are even more obvious. Sheet-like teeth with a comb-like cutting edge are seen neither in the Eratoidae nor in the Cypraeidae.

The radulae illustrated by Thiele (1931: 269-270, figs. 284-286) of members of his subfamilies Jenneriinae and Pediculariinae show marginal teeth with many cusps on the cutting edges, but with slender stalks. Also the lateral teeth differ strikingly from those of the Ovulidae and are split into two parts. Judging after the radula, the Ovulidae could be just as well classified with the Eratoidae to be included in the Lamellariacea as with the Cypraeidae in the Cypraeacea. The radula of the Ovulidae is more different from those of both these families than these families differ from each other.

NATICACEA

Natica canrena (Linné)
(fig. 149; pl. 8 fig. 3)

The radula consists of about 100 rows of teeth. The angular central tooth is about twice as wide as high. The straight front is less wide than the base. The cutting edge is attached to the anterior edge of the basal platform, forming an angle of about 90° with it. The acute, stout, main cusp is accompanied by one flanking cusp on each side. The margins are straight and inclined outward: they end in acute posterior corners that project over the base. Two stout basal denticles are attached to the posterior part of the central platform, projecting somewhat upward and backward across the straight base; these denticles rise from a plain basal platform.

The lateral tooth is like a hand with a spread thumb. Its cutting edge is evenly curved upward and the basal platform is thus concave. The cutting edge has a stout, triangular, main cusp accompanied by two inner and one outer flanking cusp. The inner margin and the raised outer margin are weakly concave. A swelling follows the base, extending into a thumb-like cusp projecting inward from the inner posterior corner. The outer posterior corner is very wide and angular. A broad gutter-like depression of the basal platform ends in this corner. The groove is bordered by the thumb-like basal cusp and its ridge-like continuation on the base at one side and by the cutting edge and its continuation, the raised outer margin, at the other side. The inner marginal tooth fits closely into this depression of the lateral tooth. The thumb-like, sturdy cusp serves two functions. It holds the marginal teeth in position and it acts as a hinge for the lateral teeth of the consecutive rows. Into the depression formed between the thumb-like projection and the inner margin of the lateral tooth the acute posterior corner of the central tooth may fit.

The inner marginal tooth is more than twice as high as wide. It has a very strong and bilaterally flattened stalk and an acute, hook-like apex with two cusps, the outer of which being the largest. This tooth fits over almost its entire length into the groove of the lateral tooth.

In the folded radula the outer marginal tooth fits into the upper side of the inner marginal tooth, which is somewhat concave. It is slightly longer than the inner marginal tooth and more slender in outline. Its stalk is rounded, ending in an acute curved apex with only one point.

Natica livida Pfeiffer
(fig. 151; pl. 7 fig. 10)

The radula consists of about 40-50 rows of teeth. It is essentially like that of *Natica canrena* as regards the outline of the teeth, the number of cusps on the cutting edges, and the structure of the teeth. The central tooth is a little less than twice as wide as high. Its base is convex and the outer posterior corners are somewhat less extended. The lateral tooth and the inner marginal tooth are quite like those of *N. canrena*. The outer marginal tooth is as wide and long as the inner marginal one.

Polinices hepaticus (Röding)
(fig. 152; pl. 7 fig. 9)

The radula consists of about 80 rows of teeth. With respect to the number of cusps on the cutting edges and the general morphology of the teeth it agrees with the radula of *Natica canrena*. The central tooth is twice as wide as high. The shape differs from that of *N. canrena* only in the form of the base, which is convex like in *N. livida*, and in the concave front. The basal denticles project more upward than backward. The marginal teeth are of equal length.

Polinices lacteus Guilding
(fig. 150; pl. 7 fig. 8)

The radula consists of about 90 rows of teeth; all are quite like those of *Polinices hepaticus*.

DISCUSSION

Natica canrena is the largest of the four Naticacea discussed and lives in sand from the tidal region to great depths; *N. livida* is the smallest species, occurring from about one meter depth onward in all soft substrates from mud to sand. *Polinices hepaticus* is common between seagrass and in other sandy and silty environments below one meter depth. *P. lacteus* prefers environments close to the shore and occurs in sand as well as gravel bottoms. All species feed on molluscs, mainly those living in or on the sandy substrate. They reach the soft parts of their prey by drilling a hole into their shell. Paine (1963) observed that *P. duplicatus* (Say) prefers thick-shelled bivalves as food (93%) but also eats polychaetes. Ziegelmeier (1954) studied the feeding activity of *Lunatia nitida* (Donovan) in detail. The radula he figured for this species (1954: fig. 106) agrees, as far as can be judged from his drawing, in all essential features with that of the four Naticacea studied here. Ziegelmeier has found that the teeth of the radula play a vital role in the excavation of the bore hole. This would explain the noticeable wear of the teeth that is usually encountered in the functional part of the radulae. This wear can hardly be considered to result from the cutting of soft tissue of the bivalves only.

Troschel (1856-1863: 169) had studied the radulae of a number of species of the Naticidae and came to the conclusion that this group of gastropods represents a natural entity, with members that are all closely related to each other. The radulae figured by Troschel (1856-1863: pl. 14 figs. 13-18, pl. 15 figs. 1-16) illustrate that the great similarities between the radulae of the four Caribbean species might indicate a general feature among Naticacea. Troschel concluded that in the Naticidae the radular morphology cannot be used to distinguish genera; this should be done by conchological characters.

For comparison the radulae of *Natica hilaris* (Sowerby) from the Red Sea (fig. 153) and *Lunatia fusca* (Blainville), *N. intricata* (Donovan) and *N. stercusmuscarum* (Gmelin) from the Mediterranean were also studied. All of them show the same general type of radula with only minute differences. The number of cusps on each tooth is very stable among members of these species and even among members of most other species of the Naticidae. Usually there are three cusps on the central tooth, four on the lateral tooth, two on the inner marginal tooth and one on the outer marginal tooth. Only rarely the central tooth only shows one cusp on its cutting edge (Troschel, 1856-1863: pl. 14 fig. 10; Powell, 1951: fig. J51; 1967: fig. 2) or five cusps on the cutting edge (Thiele, 1931: fig. 272).

The inner marginal tooth rarely has only one cusp (like the outer marginal tooth), as in the genus *Falsilunatia* (Powell, 1951: figs. J47, 48, 49; Barnard,

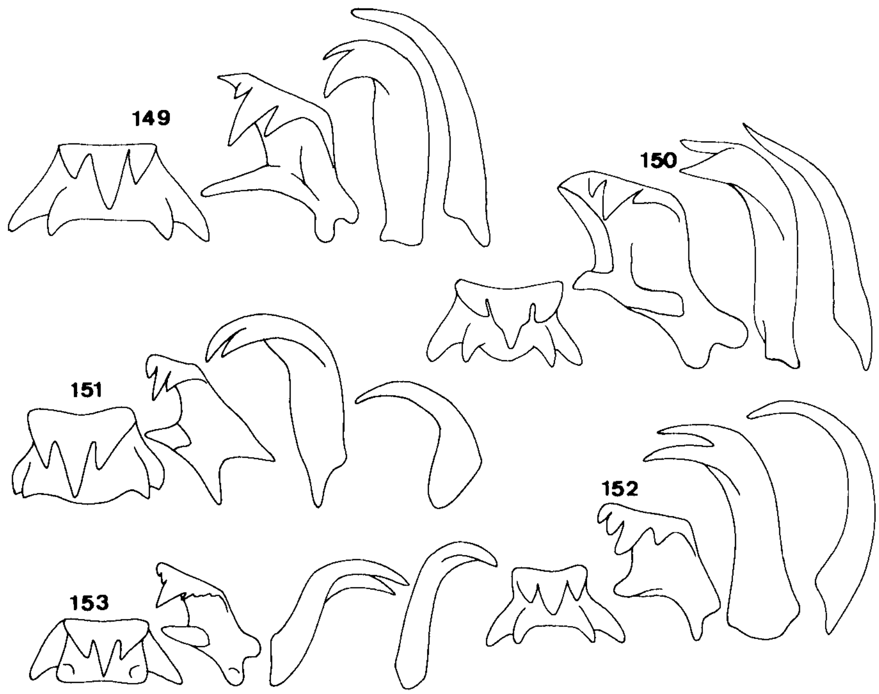


Fig. 149. *Natica canrena*, Santa Marta, Caribbean; x 300. — Fig. 150. *Polinices lacteus*, Santa Marta, Caribbean; x 200. — Fig. 151. *Natica livida*, Santa Marta, Caribbean; x 600. — Fig. 152. *Polinices hepaticus*, Santa Marta, Caribbean; x 400. — Fig. 153. *Natica hilaris*, Port Sudan, Red Sea; x 250.

1963: fig. 7e), in which also the front of the central tooth is more rounded than usual in Naticidae. Most of the many members of the Naticidae studied by Powell (1951) from the Antarctic seas and by Cernohorsky (1971) from the Fiji Islands have radulae as figured by Troschel or in the present paper.

Fretter & Graham (1962) expressed the opinion that the Naticacea are rather different from the ancestral Monotocardia, having various specialized features. In contrast to this, the radula does not seem to be that much specialized. It is quite similar to that of *Ampullarius*, regarding the central and lateral tooth, and even in more detail with regard to the marginal teeth (fig. 4). Also some Littorinidae (figs. 8, 16-20) have similar radulae, especially when the lateral teeth are compared. Similarities are also seen with members of the Calyptraeidae (figs. 110-114) and Vermetidae (figs. 49-53).

TONNACEA

Cassis madagascariensis Lamarck
(fig. 160; pl. 8 fig. 5)

The radula consists of about 80 rows of teeth. The angular central tooth is about twice as wide as long. The cutting edge is turned upward, forming about a right angle with the basal platform. The front is straight. Apart from the slightly larger central cusp and the smaller outermost cusps, the 9-13 cusps of the cutting edge are about equal in size. The margins are concave, ending in sideward extending, cusp-like posterior corners. Between these the base is evenly convex.

Between the central and the lateral tooth, a crescentic, stout, rod-like intermediate tooth is present, which is not connected to either one of these teeth. This intermediate tooth inserts on the membrane below the outer posterior corner of the central tooth, reaching the inner posterior corner of the lateral tooth.

The claw-like lateral tooth has six to eight long, acute cusps. Its basal platform is evenly curved from the short, straight base into the erect cutting edge which is about 2.5 times wider than the base. A very short, concave outer margin ends in an acute, denticle-like outer posterior corner. The inner margin is long and evenly concave, ending in a rounded inner posterior corner.

Between the lateral tooth and the inner marginal tooth a transverse, narrow, lamella-like, straight rod is attached to the membrane of the radula. This subsidiary tooth is narrower than the crescentic, inner intermediate tooth between the central and the lateral tooth. The evenly wide lamella takes its origin below the outer margin of the lateral tooth and is not attached to it. It reaches to the posterior edge of the inner marginal tooth. This intermediate tooth may have a membranous connection both with the outer posterior corner of the lateral tooth and with the inner basal corner of the inner marginal tooth.

The marginal teeth are very similar to each other in shape. They are long and slender, with their greatest width in the central part. The stalk is somewhat bilaterally flattened and about six times as high as wide, ending in an acute apex. The cutting edge is situated on the inner margin only. The inner marginal tooth has four or five acute cusps and the outer one two to four. In the folded radula the marginal teeth rest on each other and, all together, on the cutting edges of the lateral teeth in their row. The marginal teeth, folded inward from both margins of the radula, meet with their apices in the centre of the radula. Teeth which have been used in food collecting, especially the central and the lateral teeth, show considerable wear.

Cassis tuberosa (Linné)
(pl. 8 figs. 4, 7, 8)

The radula is like that of *Cassis madagascariensis*.

Charonia variegata (Lamarck)
(fig. 155; pl. 9 figs. 1, 2)

The radula consists of about 100 rows of teeth. The angular to crescentic central tooth is almost three times as wide as high. The central cusp of the cutting edge is the largest; near its base it is often fused with one or two flanking cusps. It stands erect right at the frontal edge, while the five to seven flanking cusps are attached somewhat more posteriorly. The frontal rim is curved upward to the anterior corners; just below these the margins form a deep sinus, but apart from that they continue straight into thickened, rounded, elongated posterior corners. The base may be weakly convex or straight between these corners. The basal platform is narrow, plain, and smooth.

At the posterior corner of the central tooth there is a narrow, wrinkled, short subsidiary tooth that connects this corner with the inner posterior corner of the lateral tooth.

The sturdy, thorn-shaped, lateral tooth is about twice as high as wide and has a hook-like apex. Apart from a central lobe, its base, attaching it to the radula membrane, is straight to weakly convex. The basal platform has a central swelling that extends into the large, acute main cusp. One inner cusp and three or four outer cusps flank the main cusp on the cutting edge. The inner margin is straight, the outer convex. The posterior corners are angular and not elongated.

The marginal teeth are all about equally long and slender, about six times as high as wide, with straight stalks and evenly curved acute apices. Their basal part is the thickest and here a cross section is almost round; the teeth are somewhat flattened apically. Only the inner marginal tooth has one to three denticles on the inner margin of its apex, whereas the outer marginal one is smooth. In the part of the radula that had been used for food collecting only little wear was noted. In the folded radula the lateral teeth are twisted inward until the main cusps of the laterals of one row touch each other in the centre of a radula ribbon. The marginal teeth fit onto each other, folding inward with their apices and extending over the central line of the radula ribbon.

Distorsio clathrata (Lamarck)
(fig. 163; pl. 8 fig. 6)

The radula consists of about 70 rows of teeth. The broadly triangular central tooth is almost 3.5 times as wide as high. The triangular cutting edge is much shorter than the base; it is turned upward, forming about a right angle with the basal platform. It consists of a sturdy, acute, triangular, main cusp, flanked by three or four cusps on each side, which become gradually smaller. The front is evenly curved and is continuous with the margins, which end in acute posterior corners. The base between these corners is evenly concave. The narrow basal platform is smooth.

Between the central and the lateral tooth there is an intermediate, very narrow, long, transverse, rod-like tooth, which is attached to the membrane between the central teeth. This tooth reaches to the inner posterior corner of the lateral tooth.

The lateral tooth is about 3.5 times as high as wide. It is attached to the membrane with a short base and with the outer margin. The inner margin is straight and long, bordering a narrow, inner part of the basal platform, whereas the bulk of it is thickened by a swelling that begins in the main cusp of the cutting edge and ends in the outer posterior corner. A large, sturdy denticle projects upward on the posterior center of this swelling. The cutting edge is dominated by a triangular, stout main cusp that is accompanied by one inner and eight to ten smaller outer cusps.

The uniform, sickle-shaped marginal teeth are about three times as high as wide and bilaterally flattened; they have a smooth, acute apex. In the folded radula the marginal teeth fit onto each other and, together, onto the short stalk-like outer part of the lateral tooth; their apices only reach to the outer end of the cutting edge of the lateral tooth. The lateral teeth fold down, but do not touch the central tooth.

Cymatium pileare (Linné)
(pl. 9 fig. 3)

The radula has about 65 rows of teeth. The central tooth is more or less angular, with deeply indented margins, whereas cutting edge and base are about equal in length. The tooth is about twice as wide as high. The central front part is concave; on the sides it is well rounded. The cutting edge has stout cusps, situated along a straight line almost at the anterior edge of the basal platform. The acute, diamond-shaped, central main cusp is the largest; the four or five flanking cusps become gradually smaller. The deep indentation of the margin is just wide enough for the insertion of the inner corner of the base of the lateral tooth to the membrane. The posterior corners are situated on the end of the indentations of the margins and project outward. The base is straight or slightly convex. A swelling from the main cusp continued onto the basal platform ends before reaching the centre of the latter. Otherwise the basal platform is smooth.

The triangular lateral tooth is about as wide as high. It is dominated by an acute, triangular cusp that is slightly curved upward. The basal platform is also curved. The tooth is widest at its base. The inner posterior corner projects inward and is connected with the main cusp by a concave to straight inner margin. A curved central swelling runs from the main cusp across the basal platform to the posterior outer corner, forming a very conspicuous ridge on the posterior outer part of the basal platform. The outer cutting edge has four to five increasingly smaller cusps. The outer margin forms a lamella with a wing-like upper part and a lower part which is fully attached to the membrane. The lateral tooth, therefore, is attached along its base and the posterior half of the outer margin.

The marginal teeth are sickle- to thorn-like in general shape. The inner marginal tooth has a concave basal platform and a narrow, acute apex. There may be one to three rudimentary flanking cusps, generally on the inner cutting edge, sometimes also on the outer cutting edge. The outer posterior corner extends into a projecting point. The outer posterior margin is concave and here the bulbous base of the tooth hinges with the base of the outer marginal tooth. The outer marginal tooth has a rounded stalk and a bulbous base. An inner process in this base fits into the depression of the basal part of the inner marginal tooth. The slender outer marginal tooth is evenly curved and ends with an acute apex without flanking cusps. Sometimes the functional teeth of the radula show considerable wear.

Cymatium vespaceum (Lamarck)
(pl. 9 fig. 4)

The radula has about 75 rows of teeth. The central tooth has a convex front and four or five flanking cusps besides the main cusp. The other teeth of the radula are similar to those of *Cymatium pileare.*

Cymatium krebsii Mörch
(fig. 154; pl. 9 fig. 5)

The radula has about 60 rows of teeth. The central tooth has a front that is concave in its centre. Its cutting edge has four or five flanking cusps besides the main cusp. The other teeth of the radula are similar to those of *Cymatium pileare.*

Cymatium nicobaricum (Röding)
(pl. 9 fig. 8)

The radula has about 90 rows of teeth. The central tooth has a convex front and five or six flanking cusps on the cutting edge. The other teeth of the radula are similar to those of *Cymatium pileare.*

Cymatium moritinctum caribbaeum Clench & Turner
(pl. 9 fig. 7)

The radula has about 120 rows of teeth. The central tooth has a convex front and five or six flanking cusps on each side of the main cusp of its cutting edge. The other teeth of the radula are similar to those of *Cymatium pileare.*

Cymatium muricinum (Röding)
(pl. 10 fig. 1)

The radula has about 60 rows of teeth. The central tooth has a front that is concave in its centre. Its cutting edge has five or six flanking cusps on each side of the main cusp. The other teeth of the radula are similar to those of *Cymatium pileare*.

Cymatium parthenopeum (Von Salis)
(pl. 9 fig. 6)

The radula has about 65 rows of teeth. The central tooth has a front that is concave in its centre. Its cutting edge has five or six flanking cusps on each side of the main cusp. The lateral tooth has six or seven cusps on the outer flank of the main cusp. The other teeth of the radula are similar to those of *Cymatium pilaere*.

Cymatium labiosum (Wood)
(fig. 158; pl. 10 fig. 2)

The radula has about 45 rows of teeth. The central tooth is much wider in front than at its centre; at its base it is almost as wide as in front. It has a handle-like shape and is higher than wide (4:3). The cutting edge forms about a right angle with the basal platform. It is dominated by a stout, triangular, main cusp, which is flanked by three to five increasingly lower cusps on each side. The front is strongly convex. The margin is curved inward, forming a wide sinus and ending as an outward projecting posterior corner. The base is straight. The basal platform is strongly convex, due to a central swelling that continues from the cutting edge to the base.

The lateral tooth, with its posterior corner, is attached to the membrane where the lateral sinus of the central tooth forms a gap. The tooth is triangular and about as high as wide. It is dominated by an acute, stout, main cusp, that arises on the inner corner of the cutting edge. There are three to five stout, small, outer flanking denticles. A strong swelling runs from the main cusp across the basal platform, ending in the outer posterior corner; in its posterior part a strong basal denticle is formed. The inner margin is straight and ends in an inner, rounded posterior corner. The basal platform, between the central swelling and the inner margin, is deeply concave. The inner margin, with its posterior part, is attached to the membrane. The lateral tooth is closely linked to the central tooth.

The inner marginal tooth is rather similar to the lateral tooth, being only more slender, and without a wing formed by the platform between the inner posterior corner and the central swelling. The central swelling of the inner marginal tooth originates at the cutting edge and ends in the base of the tooth in a long and strongly projecting inner posterior corner. The base is concave and the outer posterior corner is angular. Two to four flanking cusps are found on the outer margin of the acute apex. The outer marginal tooth is almost as long as the inner marginal tooth, but it is more slender and sickle-shaped. The apex is smooth.

The teeth of each row are very closely hinged and may fit onto each other in the folded radula. The central tooth, with the flanks of its cutting edge, provides the resting place for the main cusp of the cutting edge of the lateral tooth. The latter is inserted on the membrane below the marginal indentation of the central tooth. A deep, gutter-like groove on the outer part of the lateral tooth provides the place into which the inner marginal tooth can fit tightly with its stalk. Inner marginal tooth and outer marginal tooth are hinged at their bases. The latter can fit into the gutter-like depression of the inner marginal tooth.

Bursa thomae (d'Orbigny)
(fig 162; pl. 10 fig. 4)

The radula has about 70 rows of teeth. The semicircular tooth has a high, narrow, triangular cutting edge, that only has one third of the width of the tooth. The tooth is 2.5 times as wide as high. The cutting edge is dominated by a thin main cusp, flanked by two or three smaller cusps; it forms ca. a right angle with the basal platform. The straight to slightly convex margins are inclined outward. They end in rounded posterior corners. The base is straight between the far backward projecting corners. The margins are followed by strong ridges that merge with the anterior, narrow part of the tooth. The posterior part of the basal platform is thin and stretched out between the marginal ridges, thus giving the impression that the base is deeply concave. On the ridges, near the posterior corners, there is a pair of strong basal denticles. Closer to the corners a narrow ridge may project from the swelling, and here there may be another pair of smaller denticles.

There is an intermediary tooth between the central and the lateral tooth. It arises at the posterior basal corner of the central tooth, towards the inner posterior corner of the lateral tooth. It is about half as wide as the central tooth and consists of a narrow flexible rod.

The triangular lateral tooth is higher than wide (4:3); it is dominated by a long, acute main cusp on the inner part of the cutting edge. One or two stout inner and five to seven increasingly smaller outer flanking cusps accompany the main cusp. The inner margin is straight, ending in an angular, inner posterior corner. The convex outer margin continues into the cutting edge, and ends on a rounded outer posterior corner. A strong swelling continues from the cutting edge to the outer posterior corner. This ridge branches near the outer posterior corner and forms a thickened, acute projection on the inner part of the handle-like, outer end of the tooth. There is also an acute process on the outside of the outer posterior corner. Between these branches of the ridge, there is a groove into which the inner margin of the inner marginal tooth may fit.

The inner and the outer marginal tooth are about equal in length and evenly curved upward. The long-triangular inner marginal tooth has a bilaterally flattened, concave basal platform, with a straight base. The inner posterior corner is rounded, while the outer posterior corner is extended and acute. The tooth is about three times as long as wide. Its acute apex has no or up to three minute cusps, only on the inner side. The slender, sickle-like, outer marginal tooth has a narrow base and an apex with smooth margins. In the folded radula the lateral teeth rest with their inner margins on the intermediary teeth. The inner marginal tooth fits into the groove on the outer, broad, stalk-like extension of the lateral tooth. The outer marginal tooth fits onto the inner marginal tooth. The central tooth is not hinged with the other teeth of each row; all other teeth are hinged by their bases. Only very little wear could be noted on the functional teeth.

Bursa granularis cubaniana (d'Orbigny)
(pl. 10 figs. 3, 8)

The radula has about 80 rows of teeth, which are similar to those of *Bursa thomae*.

Tonna galea (Linné)
(fig. 159; pl. 10 fig. 5)

The radula has about 40 rows of teeth. The triangular central tooth has a very sturdy cutting edge, consisting of a single triangular cusp. Its flanks continue into rounded anterior corners and from here onward to the acute posterior corners. A ridge with a sharp upper part starts on the posterior corners and continues into the main cusp, ending in its apex and supporting it. On the central part of this ridge there is a stout, acute denticle. Between the outer margin and the supporting ridge, on each side of the tooth, there is a concave flank onto which the inside of the lateral tooth fits tightly in the folded radula. The base of the central tooth is straight, and the central part of the basal platform is low. Seen from aside, the whole central tooth has a hook-like appearance, since its basal platform is evenly curved into the cutting edge.

The lateral and marginal teeth are quite uniform in general shape, with stout, thorn-like structures, triangular in cross section. The inner margin of the lateral tooth is straight, up to its lower part, where a deep indentation separates it from a short, wing-like basal part. The inner posterior corner is angular. The outer margin is straight. A strong supporting ridge extends into a bulging posterior projection. On both sides of the tooth, between outer and inner margins and the median ridge, deep grooves are formed. On the basal part of the outside of the tooth this groove is deepened; the lower inside of the inner marginal tooth may fit here when the radula folds.

The inner marginal tooth lacks the wing-like structure of the inner margin that is present in the lateral tooth. The margins are straight and have an acute edge. A strong median supporting ridge is accompanied on both sides by grooves. The base of the inner marginal tooth is hinged to that of the outer marginal tooth. The outer marginal tooth is more sickle-like, with a concave, gutter-like inside and a rounded outside. All teeth fit tightly onto each other in the folded radula, thus forming a smooth, upper surface of the radula ribbon.

When unfolded, each hook-like tooth is erected and spread, and the radula has an effective holding function.

DISCUSSION

The representatives of the family Cassididae feed on sea urchins (e.g. sand dollars). They reach the soft parts of their prey by drilling one to many holes through the calcareous plates of the corona. Sea urchins of regular, rounded shape, with a large, internal lumen, can usually be emptied through one hole. The flat shells of the sand dollar have to be penetrated with several holes to reach all the soft parts dispersed between the pillars of the corona. In order to eat the food, the carnivorous gastropod creeps up to its prey, takes hold of it with its raised anterior foot, and searches with its long extensible, proboscis for a place on the corona where to penetrate it. The protective movements of the spines of the sea urchin stop when the secretion of mucus from the proboscis touches and immobilizes the epidermis around the spines.

The mode of feeding of the two *Cassis* species from the Caribbean is the same as that of *Cassidaria echinophora* (Linné) from the Mediterranean (fig. 161). The radula of the three species of Cassididae mostly show no wear of the last used teeth. The hole into the hard calcareous shell of sea urchins, therefore, cannot be drilled by mechanical means, i.e. with the help of the teeth of the radula, but must be made by dissolving with the help of acid and enzyme secretions. Abbott (1968) thought that *Cassis madagascariensis* lives mainly on *Diadema antillarum*, a sea urchin with very long and brittle spines. In contrast to this, aquarium and field observations in the region of Santa Marta have shown that *Diadema* was only attacked when the predator was starved. Otherwise other, less agile echinoids, with shorter and less brittle spines, were preferred. Work (1969) found that *C. tuberosa* ate all echinoids it encountered. Our own observations confirm this; other observations on the feeding habits of cassids are summarized by Abbott (1968).

Troschel (1856-1863) described the radulae of two *Cassis* species, among these *C. tuberosa* (pl. 18 figs. 9, 10). His drawings are comparable to those represented here, with one major difference. Troschel only noticed the ribbon-like intermediary teeth between lateral and inner marginal tooth, but not the intermediary teeth between central and lateral tooth, even though these are much more sturdy. The radula of *Cassis cornuta* (Linné) was figured by Thiele (1931: fig. 295a) after Troschel (1856-1863: pl. 18 fig. 9), quite unchanged, and therefore also without the subsidiary tooth between the central and lateral teeth. These mistakes were repeated by Abbott (1968: pl. 19), where a radula of *C. cornuta* is illustrated again, but even more simplified. The many other radulae of Cassididae, described and figured by Abbott (1968), should be restudied more thoroughly. Because essential details are not given by this author, a comparison with these radulae is impossible as yet. In Barnard's (1963: fig. 1c) description and illustration of the radula of *Phalium* no more details are found than in Abbott's drawings. Troschel (1856-1863: 223) mentioned a short intermediary tooth between the lateral and the inner marginal tooth in members of the genus *Phalium*. His figures (1856-1863: pl. 18 figs. 12, 13) show a radula that is similar in shape to that of *Cassis*. Troschel's figure and description of *Cassidaria echinophora* shows no intermediary teeth (1856-1863: 223, pl. 18 fig. 15). Individuals from this species collected in the Mediterranean were studied for comparison (fig. 161). Their radulae demonstrate the differences which can be seen within the family Cassididae with regard to this feature, even though no differences in the mode of feeding are known.

The genera *Distorsio*, *Charonia* and *Cymatium* are considered Cymatiidae. *Charonia variegata* may eat echinoids, holothurians, and asteroids. In the aquarium it may even be kept on a diet of fish, mussel, and crab meat. In the Laboratoire Arago at Banyuls-sur-Mer, France, *Charonia* was kept for years and produced fertile spawn every year. In the aquarium at Santa Marta a sea cucumber of the same length as the carnivorous snail was devoured completely in the course of one day. To cope with such a large prey, the proboscis was greatly extended and slowly pushed over the sea cucumber, which was swallowed whole. *Charonia* snails gain access to the interior of an echinoid by drilling a hole through the buccal membrane which surrounds the chewing apparatus (Aristotle's lantern), where no calcareous plates are present and only organic material has to be penetrated. Most probably the radula is not used much while drilling, which is carried out mainly chemically. The radula is used to cut and collect the interior soft parts within the echinoid corona. Only the contents of the intestines of the sea urchin are left behind when *Charonia* has finished eating. Small asteroids are swallowed whole. *Charonia* grips large asteroids with the foot and the sturdy outer lip of the shell. Usually the prey will then detach one arm. It will do so especially when it is drugged by mucus produced by the foot of the snail. While the remainder of the prey is held with shell and foot, its detached parts are swallowed whole one by one. It was never observed that *Charonia* drilled a hole through calcareous matter, as was reported by Hirsch (1915).

Clench & Turner (1957: 113) state that the radula of *Charonia* is quite distinct from that of *Cymatium*. This had already been noted by Troschel (1856-1863: 232, pl. 19 fig. 11), who considered this genus well defined by its radula morphology. The central tooth is quite different from that in the other genera of the Tonnacea. The other teeth in the *Charonia* radula resemble those of *Distorsio* in general shape, but are more slender. If the illustration of the radula of *Charonia pustulata* (Euthyme) by Barnard (1963: fig. 2e) is correct, the shape of the central tooth may be variable within this genus.

The feeding habits of *Distorsio* are not known. In the aquarium animals were fed on pieces of fish meat and lived for a long time on this diet. The radula of *Distorsio clathrata* is quite similar to that of *D. anus* (Linné), figured by Cernohorsky (1967: fig. 13), and with a little less detail by Troschel (1856-1863: pl. 20 fig. 1). Both authors did not figure nor mention the narrow, transversal tooth between the central and the lateral one. Clench & Turner (1957: pl. 132) noted and illustrated intermediary teeth of *Distorsio* radulae as very narrow but solid cross beams.

The representatives of *Cymatium* and *Bursa* are classified with two different families, Cymatiidae and Bursidae, but their food requirements are similar. They feed on molluscs, barnacles and tube dwelling worms. The here studied species of these genera were kept in an aquarium on a diet of living *Cerithium*. During feeding the prey is held by its shell with the foot of the carnivore. The aperture of the prey is kept closed and smothered with the anterior part of the foot. The long proboscis is then extended through a fold in this part of the foot into the aperture. The flesh of the prey is completely eaten, with bites of the radula and only the empty shell is discarded.

Day (1969), in a study of the feeding habits of *Argobuccinum*, mentioned that according to literature data *Cymatium australasiae* (Perry) drills holes through the shells of oysters in order to reach the soft parts. Such feeding habits, resembling those of naticid and muricid gastropods, was never noticed in any *Cymatium* and *Bursa* collected near Santa Marta, even though individuals of all species were kept in the aquarium for a long time together with different bivalves. Day observed that *Argobuccinum* feeds on sabellarid polychaetes without destroying their tubes.

The family Cymatiidae, with its four genera of Thiele's 1931 classification presents, as it seems, also four different types of radula morphology. Within the genus *Cymatium* the radula morphology usually is non-specific. Three species from the Red Sea, studied for comparison, viz. *C. pileare*, *C. trilineatum* (Reeve) and *C. hepaticum* (Röding), and *C. corrugatum* (Lamarck) from the Mediterranean, have radulae just like those of the Caribbean species. Among the radulae of studied *Cymatium* species only one exception was found, viz. *Cymatium labiosum* of the subgenus *Tritoniscus* according to Abbott's (1974) classification. Here the radula is much more similar to that of *Argobuccinum pusillum* (Broderip) from the Red Sea, which could be studied for comparison (fig. 156), than to that of the other Caribbean *Cymatium* species. The figures of the radula of *Argobuccinum (Gyrineum) gyrinum* (Linné) by Cernohorsky (1967: fig. 12) provide little information apart from the shape of the central tooth, which is not wider than long, as in *Cymatium labiosum*. The radulae of various members of the genus *Argobuccinum* as illustrated by Barnard (1963: figs. 2a, b, c) and Arnaud & Bevrois (1971: fig. 4) cannot be used for comparison here, since the figures lack the necessary detail. Judging from Troschel's figures (1856-1863: pl. 20 fig. 11) of the radula of *Argobuccinum argus* (Gmelin), this is closer to that of *Bursa*. Thiele's figure (1931: fig. 300) of the radula of *Argobuccinum murrayi* (Smith) resembles that of *Cassidaria echinophora*. There is still much confusion regarding the genus *Argobuccinum*, possibly to be cleared by closer examination of the radulae. *Cymatium labiosum* does not belong to the genus *Cymatium*, but is close to the subgenus *Gyrineum* of the genus *Argobuccinum*.

The radulae of the other members of the genus *Cymatium*, as far as known, are basically the same. The subgenera *Ranularia* (*C. moritinctum caribbaeum*),

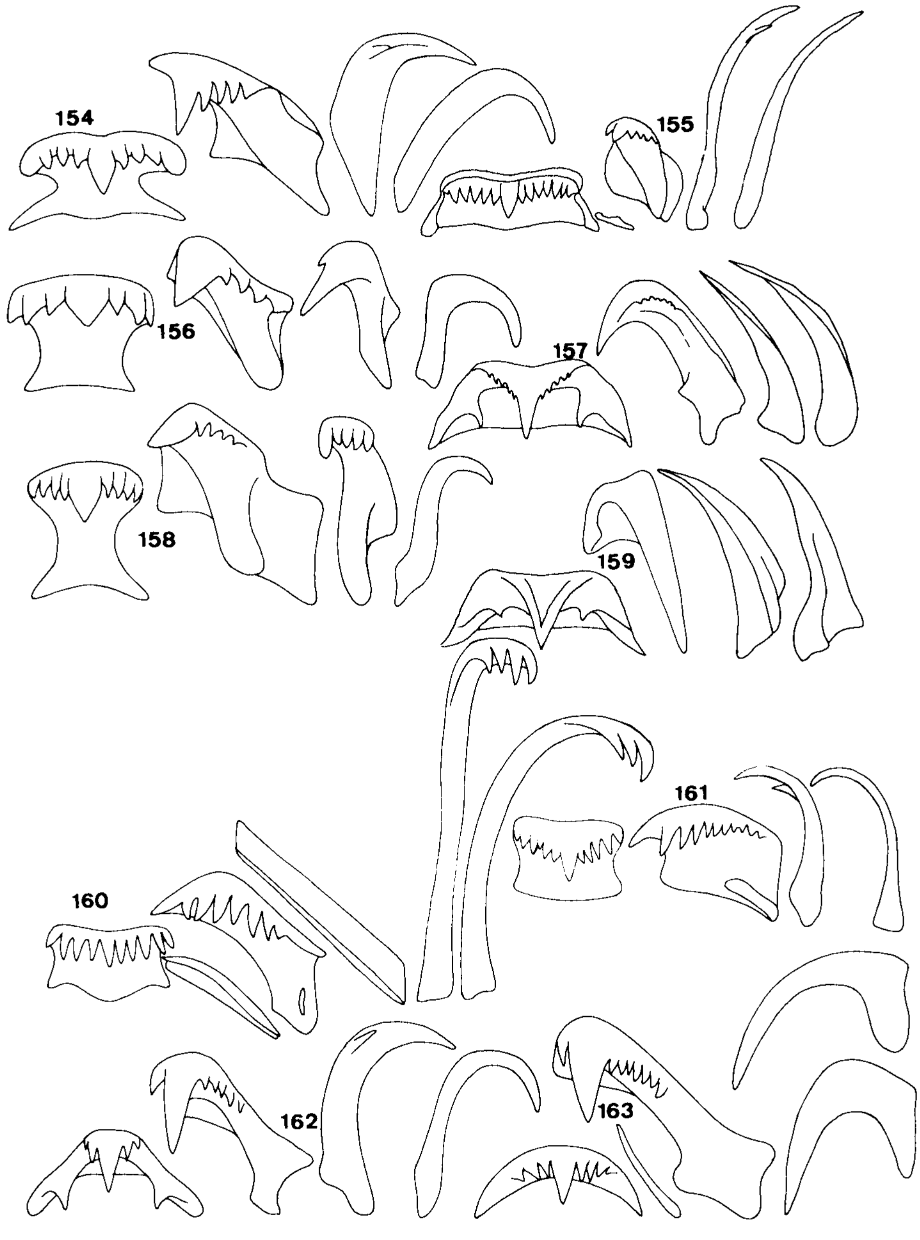


Fig. 154. *Cymatium krebsii*, Santa Marta, Caribbean; x 250. — Fig. 155. *Charonia variegata*, Santa Marta, Caribbean; x 60. — Fig. 156. *Argobuccinum pusillum*, Port Sudan, Red Sea; x 350. — Fig. 157. *Malea pomum*, Port Sudan, Red Sea; x 90. — Fig. 158. *Cymatium labiosum*, Santa Marta, Caribbean; x 300. — Fig. 159. *Tonna galea*, Santa Marta, Caribbean; x 15. — Fig. 160. *Cassis madagascariensis*, Santa Marta, Caribbean; x 90. — Fig. 161. *Cassidaria echinophora*, Banyuls-sur-Mer, Mediterranean; x 170. — Fig. 162. *Bursa thomae*, Santa Marta, Caribbean; x 220. — Fig. 163. *Distorsio clathrata*, Santa Marta, Caribbean; x 430.

Cymytriton (*C. nicobaricum*), *Septa* (*C. pileare, C. krebsii, C. vespaceum*), *Gutturium* (*C. muricinum*) and *Monoplex* (*C. parthenopeum*), cannot be distinguished by their radula morphology. Also Troschel (1856-1863: 235) was not able to distinguish the radulae of members of the subgenus *Gutturium* and *Simplum* (= *Septum*). Clench & Turner (1957) figured the radulae of most of the here described species of *Cymatium* (pl. 113 figs. 2-11) and noted the surprising uniformity. Clench & Turner expressed the opinion that regardless of what modifications have taken place in the morphology of the shell, the embryonic whorls, and the opercula, the radula has remained relatively unchanged. My own studies on the embryonic and larval shell indicate, however, that there is also very little variation in most of these characters among the *Cymatium* species. Only the morphology of the adult shell and the operculum can provide characters for the splitting of *Cymatium*.

The radula teeth of *Bursa thomae* and *B. granularis cubaniana* are very similar. These radulae are like those of *Bursa granularis* (Röding) from the Red Sea, which was studied for comparison. The radula of *Bursa granularis* is also figured by Cernohorsky (1967: fig. 3), who studied the radulae of two further species of this genus. All these radulae are quite alike. Troschel (1856-1863: pl. 19 figs. 4-10) had studied the radulae of eight different species of the genus *Bursa* and stated that it may be impossible to distinguish these species by radula characters, although the radula morphology of the genus *Bursa* clearly differs from that of all other genera. The differences in the illustrations of radulae of the Caribbean species of *Bursa* noted by Abbott (1958: text-figs. 1, 2) may well be due to individual variations in cusp numbers to a different degree of wear of the teeth. With regard to *B. thomae* and *B. granularis cubaniana*, which were also studied by the present author, the differences indicated by Abbott could not be found in the material from Santa Marta.

Tonna galea prefers rippled bottoms of coarse sand and here preferably hunts holothurians. A large individual, that had just been collected, ate three sea cucumbers in the aquarium within two days. Each of the holothurians was as long as the shell of the *Tonna* snail. The proboscis can be expanded very much and takes hold of the cucumber at one end, swallowing its prey whole. The radula here serves as a holding apparatus, which hooks into the tough skin of the holothurian. A secretion rich in sulphuric acid is produced during feeding activities; it may serve to anaesthetize the prey and stop its motion.

Tonna galea has a radula which is quite characteristic and apparently quite different from that in other genera of the Tonnacea. If we look at the radula of *Malea pomum* (L.) (fig. 157), collected in the Red Sea, we can see similarities to the radula of *Bursa thomae* (fig. 162), but also to that of *Cassidaria echinophora* (fig. 161). The most similar is the radula of *Tonna galea* (fig. 159), however. Troschel (1856-1863: 227) expressed the view that there is a close relationship between Tonnidae and Bursidae. Such a close relationship might also exist between Tonnidae and Cassididae. Troschel (1856-1863: pl. 19 fig. 3), Fischer (1887: fig. 415), Barnard (1963: fig. 1a), and Turner (1948: pl. 75 fig. 4) figured radulae of different *Tonna* species. All seem to be very similar to that of *Tonna galea*.

The radulae of the Tonnacea from the Caribbean and those of species from the Red Sea and the Mediterranean studied for comparison, indicate a wide variation of shape of the individual teeth.

A rather basic type of radula similar to that of some members of other families is found in *Cassidaria echinophora* (fig. 161). Here the central tooth is very similar to that of *Trivia oryza* (fig. 121) and *Velutina undata* (fig. 123) of the Lamellariacea, or *Crucibulum auricula* (fig. 110) and *Calyptraea chinensis* (fig. 111) of the Calyptraeacea. The lateral tooth is characterized by a broad groove on the basal platform, ending on the outer posterior corner and accompanied by a raised outer margin and a basal ridge. Such a feature is present in the above Calyptraeacea and in the Vermetidae. The marginal teeth are quite like those in most Naticidae (figs. 149-153), with two cusps on the inner marginal tooth and an acute apex on the outer one. But these teeth are also similar to those in the Lamellariacea and Calyptraeacea mentioned before. From the data provided by Barnard (1963: fig. 16) and Thiele (1931: fig. 277) it seems that the radula of members of the genus *Oocorys* is similar to that of *Cassidaria*.

The resemblance of the radula of *Cassidaria* to that of quite unrelated other groups indicates that this radula type is the least differentiated one in the Tonnacea, from which the other types may have developed. It also suggests that the Tonnacea could be distantly related to the Calyptraeacea, Lamellariacea and Naticacea.

Turner (1948) stated that members of the Tonnacea have radulae that vary just as much within each of the five families, as among the families. Turner expressed the opinion that the radulae are often so close to each other in their morphology, that with regard to this feature a relevant genus could be placed in any family of the Tonnacea. Even though this impression may be in part the result of the rather general type of description and illustration of tonnacean radulae in the literature, the assignment of *Bursa*, *Cymatium*, *Argobuccinum*, *Distorsio*, and *Charonia* to families is quite subjective. If we consider the radulae and the conchological differences of the genera *Bursa*, *Cymatium*, *Charonia* and *Distorsio*, it becomes very difficult to understand why *Bursa* should constitute a separate family (Bursidae), while the other genera should be classified together in another family. From the point of view of the radula morphology all these genera are equally different from each other.

If we consider the radula of *Cassidaria echinophora* being the closest to the ancestral radula of the Tonnacea, two directions of development from the general mesogastropod radula type become obvious. One of these lines leads to a narrower, more closely folded radula, the other leads to a wider radula, with large spaces and accessory plates between the teeth of each row.

In the development of a narrower radula with more closely hinged teeth, as seen in *Cassidaria*, two trends may be observed: (1) a development towards the *Cymatium* type radula, and from there to the *Argobuccinum pusillum* & *Cymatium labiosum* type; (2) a development to a radula as in *Malea pomum*, finally differentiating to a radula as observed in *Tonna galea*. The development of a broader radula ends with (1) the *Cassis* type, or (2) the *Charonia*-like radula. *Distorsio*, in some way, represents an intermediate type. The *Bursa* radula is about as closely spaced as the radula of *Distorsio*.

While differentiating, the single teeth have changed their morphology, their hinging, and their folding onto each other. In the development from a *Cassidaria*-like radula to the *Cymatium*-like radula, the lateral tooth is moved inward. This results in a deep notch in the margin of the central tooth, to provide the space for this change in the position of the lateral teeth on the membrane. The outline of the lateral tooth is changed and becomes higher than wide. The marginal teeth become somewhat stouter, but in general their shape remains unchanged. The *Cymatium* radula needs only little change to be transformed into the narrow *Argobuccinum pusillum* & *Cymatium labiosum* radula type. All teeth simply have lost some of their width and, therefore, have become longer and more closely spaced.

To progress from the *Cassidaria* radula to that of *Malea pomum*, the central tooth undergoes great changes. The question must be asked whether the central tooth of *Cassidaria* may not itself have become simplified. It may have lost a supporting ridge and basal denticles. We may assume that the central tooth of an even more ancestral tonnacean radula than that present in *Cassidaria*, had these features, which are so widespread among mesogastropods. Ridge and denticles became quite pronounced in *Malea pomum*. The central part of the basal platform was lowered and this part of the platform was enlarged. In this way the *Malea*, but also the *Bursa* type of central tooth may have had its origin. In the development of the hook-like lateral and marginal teeth of *Malea* and *Tonna*, the base of the lateral tooth is shortened and along with that its attachment to the membrane of the radula decreased in width. Intermediate lateral teeth are seen in the radula of *Bursa*. To progress from the radula of *Malea* to that of *Tonna*, the cutting edges were simplified and the teeth moved even closer together and became more sturdy.

During the development of the *Charonia* radula, the central teeth did become greatly widened and, at the same time, quite short. A similar development of the central tooth may be postulated for the Ficidae (Troschel, 1856-1863: pl. 20 fig. 12). In *Charonia* a short intermediary tooth bridges the gap between central and lateral tooth. Lateral and marginal teeth have not become widened, but lengthened instead. An intermediary rod bridging the distance between central and lateral tooth is also found in *Distorsio*. The intermediary teeth both of the *Charonia* as well as of the *Distorsio* radula must have been developed from the central tooth. In the case of *Charonia* the rod most probably has arisen from extended posterior corners, while in the case of *Distorsio* it is more likely that a thickening of the base has been the precursor of the intermediary rods. These thickenings remained functional when the posterior part of the basal platform of the tooth decreased in thickness until it was reduced. Thus both the arrangement of the intermediary teeth and the wide spacing of consecutive central teeth in the radula ribbon can be explained this way.

The widening of the *Cassis* radula is brought about mainly by the subsidiary teeth which both might have developed from the posterior corners of the lateral tooth. It is also possible, however, that the intermediary tooth between central and lateral tooth has developed from extensions of the posterior corners of the central tooth. The intermediary teeth have become quite independent structures of uncertain origin. The other teeth of the *Cassis* radula have not become wider in comparison to those of the *Cassidaria* radula; only the marginal teeth have lengthened considerably.

NEOGASTROPODA

Muricacea

Murex recurvirostris rubidus F. C. Baker, 1897
(fig. 171; pl. 11 figs. 1, 3)

The radula has about 150 rows of teeth. The angular central tooth is almost four times as wide as long. The anterior front is shallowly concave, the posterior edge straight to slightly convex. The convex margins, ending in rounded anterior and posterior corners, are somewhat inclined outward posteriorly. The cutting edge, with five cusps, is attached slightly anterior of the central part of the basal platform. The central main cusp and the two marginal cusps are so wide at their base that, at their insertion, they almost reach the frontal edge. These three cusps are almost equal in length and quite sturdy. While the central cusp usually is smooth, the marginal cusps may have one to three transverse wrinkles, nodules or ridges on their basal anterior part. A pair of small, acute cusps is situated between the three larger cusps. The cutting edge forms nearly a right angle with the posterior basal platform. Neighbouring central teeth are attached to the membrane of the radula so close to each other that, in the relaxed radula ribbon, the anterior corners of a tooth rest on the base of their anterior neighbour touching the posterior base of the marginal cusps. Thus the frontal rim of the basal platform covers the smooth posterior part of the basal platform of the next tooth.

The lateral tooth is sickle-shaped and unicuspid, with a sharp inner and a rounded outer margin. It is about twice as long as wide near its base. The base is straight to slightly concave and inserts distant from the central tooth, leaving a ribbon of the radular membrane between lateral and central teeth devoid of teeth.

Murex recurvirostris woodringi Clench & Farfante, 1945
(fig. 168; pl. 11 figs. 2, 4)

The radula has 220 rows of teeth. The morphology of the central and lateral tooth is quite like that of *Murex recurvirostris rubidus*, with only minor differences on the central tooth, which is somewhat narrower and almost five times as wide as long. The anterior corners are more rounded and the margins more strongly convex. The central cusp sometimes has crenulations at its base, consisting of one to three folds or ridges. The marginal cusps always have lateral ridges, on the outer flank up to six and on the inner flank up to four. Sometimes these ridges form denticles on the sides of the marginal cusps.

Murex pomum Gmelin, 1791
(fig. 172; pl. 11 figs. 5, 7)

The radula has about 140 rows of teeth. The central tooth is quite similar to that of both subspecies of *M. recurvirostris*. It is more than five times as wide as long and has an arrangement of cusps on its cutting edge like that in *M. recurvirostris*. The central cusp is wide, triangular, and more sturdy than the marginal cusps, which are just as long but more acute and narrower. The marginal cusps have a steep inside and an evenly inclined outside. There is a ridge or an additional cusp on the inside of the marginal cusps, while the central cusp is smooth. Sometimes one of the pair of small intermediate cusps splits up into smaller cusps. The outer anterior side of the marginal cusp extends in a swelling into the bulging anterior corner. Between these, the evenly, weakly concave, anterior front is accompanied by a narrow frontal rim of about half the width of the posterior part of the basal platform.

The sickle-shaped lateral teeth are about twice as long as wide at their base. Their inner margin is sharp to form a cutting edge, while the outer margin is rounded. The base is straight, the inner posterior corner is acute, whereas the outer corner is rounded.

Murex brevifrons Lamarck, 1822
(fig. 173; pl. 11 figs. 6, 8)

The radula has about 130 rows of teeth. The angular central tooth is about four times as wide as long. The margins end in angular corners and are weakly inclined outwardly in posterior direction and straight. The anterior front has a central lobe and two concavities between this and the erect anterior corners. The corners and the central lobe are the ends of swellings supporting the central and the marginal cusps of the cutting edge. The central cusp is acute and has smooth sides. The inner marginal cusps are serrated by small rounded denticles on their cutting edges and have a denticle at their anterior lower part. The cutting edge inserts on the front of the basal platform and forms an evenly curving entity with it, nearly reaching a right angle between the convex posterior edge and the tip of the central cusp. There is a pair of small, acute, intermediary cusps between the larger central and marginal cusps.

The lateral teeth are slender, sickle-shaped, and more than twice as long as wide at their base.

Morula nodulosa (C. B. Adams, 1845)
(fig. 199; pl. 11 fig. 9)

The radula has about 150 rows of teeth. The angular central tooth is about four times as wide as long. The margins are straight, whereas front and base are convex. The cutting edge is dominated by a large, hook-like, acute central cusp. It is rounded anteriorly, ending in a low lobe of the anterior front. On the posterior side it is flattened, forming a smooth, evenly bent plane with the basal platform; there is nearly a right angle between the tip of the cusp and the convex posterior edge. The cutting edge is curved, with the central cusp at the front and the lateral cusps at the posterior corners. The central cusp is accompanied by a pair of small, acute cusps. The second largest cusps, comparable to the marginal cusps in the central tooth of *Murex*, are also acute and curved hook-like, but less so than the central cusp. These cusps are accompanied by two small cusps on each side. The outermost cusps of the cutting edge are formed by the extended outer basal corners. Consequently, the cutting edge holds 11 cusps.

The sickle-shaped lateral tooth is more than twice as long as wide and has a broad basal part. The base is straight, the inner margin is sharpened into an edge, and the outer margin is rounded. The apex is curved so as to look like a hook; and in profile the outline of the inner margin is that of a semicircle.

Purpura patula (Linné, 1758)
(fig. 194; pl. 11 fig. 10, pl. 12 fig. 1)

The radula has about 130 rows of teeth. The angular central tooth is more than three times as wide as long. Its anterior front is straight, its margins are inclined in posterior direction and straight, its base is evenly convex. The cutting edge has five cusps, the strongest of which is situated at the centre, the second largest at the margins, and the small ones between these. The cusps are slightly curved backward and the cutting edge forms less than a right angle with the basal platform. There is a characteristic fissure in the lower part of the central cusp, closed below and above. The marginal cusps often show a crenulation of their outer margins.

The lateral teeth are sickle-shaped and stout. Their upper part is almost straight and they are slightly longer than wide at their base. The inner margin is sharpened into an edge and the outer margin is rounded.

Thais haemastoma Linné, 1758
(figs. 190, 191; pl. 12 figs. 2, 3-5)

The radula has about 130 rows of teeth. The angular tooth is about five times wider than long. Its basal platform is narrow and almost completely occupied by the vertical cutting edge, with the exception of a narrow frontal rim and a slightly wider posterior rim. Three main cusps are present, the central one of which is the largest. It is triangular, shark-tooth-like, and bilaterally flattened. In different ontogenetic stages the marginal cusps look different. In the large, adult, individual they are triangular, with a central swelling that ends in bulging lobes on the otherwise straight anterior front. The wing-like, bilaterally flattened inner flanks of these cusps have two to many cusps or serration denticles. The outer flanks have up to ten small cusps increasing in size in outward direction. These denticles are continuous with ridges on the anterior flank of the cutting edge. Smaller, juvenile individuals have marginal cusps with only four or a few more outer denticles and no wing-like extension of the inner flank. Here the outermost denticle of the cutting edge appears larger and there may even be an outermost pair of independent cusps, which are no longer to be regarded part of the serration of the flanks of the marginal cusps.

The sickle-shaped lateral tooth is almost twice as long as wide and has a solid base. The inner posterior corner projects as a small hooked denticle while the base is convex.

Thais rustica (Lamarck, 1822)
(fig. 192; pl. 12 figs. 6, 7)

The radula has about 170 rows of teeth. The central and lateral teeth are very similar to those of small individuals of *Thais haemastoma*. The central tooth is longer than that of *T. haemastoma*, being only three times as wide as long. Its basal platform is broader, and so are the rims in front and posterior of the insertion of the central, vertical cutting edge. The marginal cusps have one or two inner and three or four outer denticles on their flanks. The outermost cusp on the corners of the cutting edge are independent and insert right on the posterior corners.

The lateral tooth also shows a hook-like projection of the inner posterior corner.

Thais deltoidea (Lamarck, 1822)
(fig. 193; pl. 12 figs. 8, 9)

The radula has about 200 rows of teeth. The angular central tooth is about 3.5 times wider than long. The central main cusp is acute, concave at the posterior side, and supported by a central swelling on the anterior side. This swelling ends in a small lobe at the evenly concave anterior front. The central cusp is flanked by one small cusp on either side, which may split up into two unequal ones. The following, large marginal cusps have a smooth inner flank and a smooth or crenulated outer flank. On the lower part of the outer flank there are increasingly larger denticles, the outermost of which tend to become independent small cusps. The cutting edge is provided with rounded denticles, projecting from the posterior corners. The central cusp and the lower part of the cutting edge together form a shovel-like concavity with the posterior part of the basal platform; there is about a right angle between the cusp tips and the posterior edge.

The sickle-shaped lateral teeth are almost twice as long as wide at their base. The inner posterior corner is acute, but has no denticle.

Ocenebra rosea (Reeve, 1856)
(pl. 12 fig. 10, pl. 13 fig. 1)

The radula has about 500 rows of teeth. The angular central tooth is twice as wide as long. The anterior front has erect anterior corners and a stout central lobe, bulging where the central cusp is inserted on the basal platform. The anterior part of the margins is concave, in the middle these are inclined outward and posteriorly they are straight, ending in acute posterior corners. Near the corners the base is concave and forms a central, convex lobe. The cutting edge is curved; with its central cusp it is attached near the front, while the marginal cusps are attached near the posterior corners. The posterior slope of the cutting edge is deeply concave, forming a smooth, spoon-like profile with the basal platform. The main cusp is hook-like, with a rounded anterior flank. The marginal cusps consist of one inner, lower, rounded denticle and one outer, more triangular denticle. Their outer flank may be smooth or may exhibit a low, rounded dentition; it reaches the basal platform before reaching the margins. In the relaxed radula the rounded front of the central cusp fits into the spoon-like concavity of the cutting edge of the tooth in front of it.

The lateral teeth are simple and sickle-like in outline. They are almost twice as long as wide at their base.

Aspella anceps (Lamarck, 1822)
(fig. 176; pl. 13 fig. 3)

The radula has about 100 rows of teeth. The angular central tooth is more than four times as wide as long. Its anterior front is evenly concave, its posterior edge evenly convex. The margins are inclined outward in a posterior direction ending in bulging anterior and rounded posterior corners. The cutting edge is attached to the central part of the basal platform and inclined into a backward position, forming a sharp angle with the posterior part of the basal platform. There are five smooth, acute cusps; the central one is the largest, followed by the marginals.

The lateral teeth are sickle-shaped, almost twice as long as wide. They have evenly curved margins.

Aspella paupercula (C. B. Adams, 1850)
(fig. 177; pl. 13 fig. 4)

The radula has about 100 rows of teeth. It is similar to that of *Aspella anceps*; only the intermediate cusps of the cutting edge of the central tooth are more slender than those of *A. anceps*.

Favartia cellulosa (Conrad, 1846)
(fig. 175; pl. 13 figs. 2, 5)

The radula has more than 100 rows of teeth. The angular central tooth is almost three times wider than long. The front has rounded corners, followed by a straight to concave part and a stout central lobe, where the central cusp is inserted on the basal platform. The base is convex; it is accompanied by a narrow posterior part of the basal platform that forms a right angle with the cutting edge. While the central cusp is attached to the frontal part of the basal platform, the following cusps are inserted increasingly further backward, and the outermost form an extension of the posterior corners. The main cusp is flanked by one smaller intermediate cusp on each side. These are followed by the second strongest marginal cusps and finally the outermost ones, which are almost as large as their neighbours. The seven cusps of the cutting edge all have smooth flanks.

The lateral teeth are sickle-like and about twice as long as wide near their base.

Favartia alveata (Kiener, 1842)
(fig. 186; pl. 13 figs. 6, 7)

The radula has about 100 rows of teeth. The angular central tooth is less than twice as wide as long. Apart from a strongly bulging central lobe, its frontal edge is straight. The margins are weakly inclined outward in a posterior direction ending in angular, somewhat projecting posterior corners. The posterior edge bulges outward convexly. The cutting edge is strongly curved, with a central cusp attached to the frontal edge and the other cusps attached in one line near or at the posterior edge. Between the central cusp and its flanking cusps there is a deep concavity, into which a part of the anterior supporting ridge of the neighbouring posterior tooth may fit. The marginal cusps, projecting onto the posterior part of the basal platform, are flanked on their insides by one small acute cusp and on their outside by denticles which are continuous as ridges in an anterior direction. The outermost cusps of the cutting edge are situated above the posterior corners, projecting over them. Seven distinct single cusps may be counted on these teeth.

The lateral teeth are sickle-shaped and slender at their apices and more than twice as long as wide at their base.

DISCUSSION

When the above described radulae of the Muricacea are compared to each other, their great similarity becomes evident. Some groups of similar forms can be distinguished, however. The two subspecies of *Murex recurvirostris* and *Murex pomum* belong close together. Another group of species with very similar teeth is formed by *Thais haemastoma* and *T. rustica*. The radula of *Thais deltoidea* is more similar to that of *Morula nodulosa* than to that of the other members of the genus *Thais*. *Aspella anceps* and *A. paupercula* can hardly be differentiated at all with regard to the morphology of the radula, as well as that of the egg cases (see Bandel, 1976a), while adult and embryonic shell (Bandel, 1975a) are clearly different. The *Favartia alveata* radula (fig. 186) is similar to that of *Ocenebra blainvillei* (Payraudeau) (figs. 181, 183), but not to that of *Favartia cellulosa*.

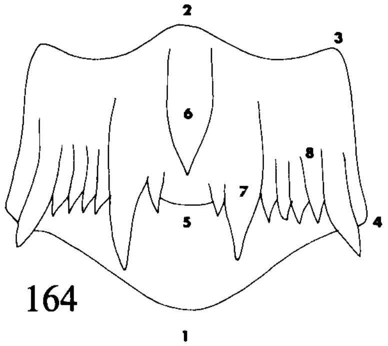
If some radulae of Muricacea from the Red Sea, the Mediterranean and the North Sea, that could also be studied, are included here, the group of *Murex recurvirostris* & *M. pomum* (figs. 168, 171, 172) can be extended by *M. trunculus* L. (fig. 170; Bandel, 1977: pl. 1 fig. 1), *M. brandaris* L. (fig. 169; Bandel, 1977: pl. 1 fig. 2) and *M. angulifera* Lamarck (fig. 174). In some radulae of *M. recurvirostris rubidus* some intermediary cusps may be lost; if so the central teeth are similar to those of *Pterynotus* sp. (fig. 187).

Radulae similar to that of *Murex brevifrons* (fig. 173), with very smooth, acute cusps and erect central and marginal parts of the front, are known from *Maculotriton serriale* (Deshayes) (fig. 178) and *Drupa cancellata* (Röding) (fig. 200). The type represented by *Morula nodulosa* (fig. 199) and *Thais deltoidea* (fig. 193) was also found in *Ocenebra edwardsi* (Payraudeau) (fig. 182; Bandel, 1977: pl. 2, fig. 2) and *Drupa rubusidaeus* Röding (fig. 196). *Thais haemastoma* and *T. rustica* radulae (figs. 190-192) are similar to that of *Drupa hadari* Emerson & Cernohorsky (fig. 198). Radulae intermediate between those of *Ocenebra blainvillei* (figs. 181, 183; Bandel, 1977: pl. 1 figs. 4, 5) and *Favartia alveata* (fig. 186), the latter with a deeply concave central part of the central tooth below the main cusp, can be noted in *Ocenebra erinacea* L. (fig. 184; Bandel, 1977: pl. 2 fig. 4) and *O. craticulata* (Brocchi) (fig. 179; Bandel, 1977: pl. 2 figs. 5, 6).

Purpura patula (fig. 194), with its central fissure of the main cusp of the central tooth, stands apart because of this feature, which may be limited to this species only.

The lateral teeth of all species mentioned and figured here are quite similar to each other, whereas great differences in the morphological details of the central teeth can be found. With the aid of these differences most species can be kept apart. Juvenile individuals may be conspicuously different in the shape of the cutting edge as compared to adult specimens of the same species. This is exemplified in the case of *Thais haemastoma*, but was also noted in *Ocenebra blainvillei*, where the typical morphology of the adult central tooth (fig. 181) is not yet developed in the juvenile; also the number of cusps differs.

The Muricacea are conchologically well differentiated and usually can easily be recognized and subdivided according to shell shape. Thiele (1929) accepted 17 genera in this family, two more than Troschel & Thiele (1865-1893) had distinguished (but not with the same names). Vokes (1964) listed 36 taxa. In only a limited number of cases the radula morphology suggests the same generic classification as the one based on shell morphology. If the numerous literature data on the radulae of this family are consulted, it also becomes evident that sometimes these data are not detailed enough (Barnard, 1959; Vokes, 1964; Radwin & Wells, 1968).



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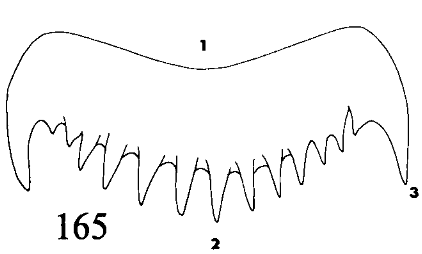

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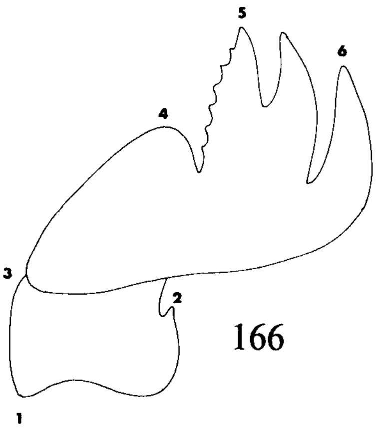

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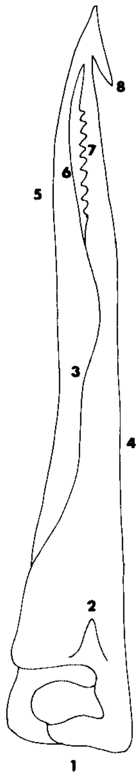

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Fig. 164. Central tooth of a neogastropod radula of the muricid type with the following characters indicated: 1, posterior base; 2, front with bulging supporting ridge of central cusps of the cutting edge; 3, anterior corner; 4, posterior corner; 5, basal platform; 6, cutting edge; 7, flanking cusps; 8, serration of denticles. — Fig. 165. Central tooth of a neogastropod radula of the vexillid type with 1, front; 2, cusp bearing the posterior base; 3, corners. Similar teeth are present in the nassariids, olivellids and marginellids. — Fig. 166. Lateral tooth of a neogastropod radula of the columbellid type with: 1, the main stalk of the tooth with a wing-like projection; 2, denticle; 3, the posterior corner; 4, basal cusps of the cutting edge; 5, central cusps, that rarely are serrated; 6, apical cusps. — Fig. 167. Lateral tooth of a neogastropod radula of the conid type, consisting of a hollow, needle-like structure with large opening at the base (1) and a slit-like opening at the apex (5). The outer margin (3) of the sheet forming the hollow tooth is seen as a suture (3) along the length of the shaft (4) of the tooth. Usually the base has a denticle (2) and the inner margin of the apical aperture is often serrated by denticles (7), while the outer margin is often undented here (6). The apex (5) has barbs (8) and is arrow-head or harpoon-like in shape.

Cooke (1919) already wrote, that the characters of the radula of the various species of *Thais* give little support to a subdivision of the genus based on the form of the shell. In this group, together with *Thais*, representatives of the genera *Nucella*, *Morula* or *Drupa* could also be placed (Troschel & Thiele, 1865-1893; Cooke, 1920; Barnard, 1959; Wu, 1965; Arakawa, 1965; Cernohorsky, 1969; Runham, 1969; Emerson & Cernohorsky, 1973).

Radulae with five almost equal cusps, as in *Aspella* as characterized by Thiele (1929: 293), also seem to occur in *Attiliosa* (Emerson, 1968), *Calotrophon* (McLean & Emerson, 1970) and *Trophon* (Barnard, 1959). Radulae with only tricuspid central teeth, as in *Jopas situla* (fig. 180) and *Pterynotus* sp. (fig. 187), are also found in *Drupa*, *Thais* (Barnard, 1959), *Homalocantha* (Cernohorsky, 1967), *Nassa* and *Rapana* (Arakawa, 1964).

Emerson & Cernohorsky (1973: 4) stated that the radula of *Morula* is muricine in appearance, while that of *Drupa* is weakly modified *Thais*-like, i.e. approaches that of *Murex* sensu strictu. However, a *Morula* radula figured by Cernohorsky (1969: fig. XX) resembles that of *Ocenebra erinacea* (fig. 184) and *Favartia alveata* (fig. 186). The latter was still called *Ocenebra alveata* by Troschel & Thiele (1865-1893: pl. 11 fig. 10), a name which seems more appropriate in view of the radula. Central teeth like those of *Favartia alveata* in general shape are illustrated by Radwin & D'Atillio (1970) for members of the genera *Muricopsis*, by Emerson & D'Attilio (1970) for the genus *Murexiella*, by Emerson & D'Attilio (1969) for *Murexsul*, and by Barnard (1959) for *Tritonalia*.

This discussion demonstrates that this classification probably does not reflect the natural system of the Muricacea. Many of the present genera combine species with strikingly different radulae. Therefore, a restriction in the number of genera, would be advisable until we have more data additional to the morphology of the adult shell.

Radwin & Wells (1968) discuss the Muricidae from both sides of Florida and the feeding habits of some of these species. These authors recognized that the radula of each of the species studied proved to have distinctive characters. *Murex recurvirostris rubidus*, *Murex pomum*, *Favartia cellulosa* and *Thais floridana* are figured. The first two are generally similar to those of the same species studied in the present paper; the third taxon is not similar at all to *F. cellulosa* from Santa Marta. The radula of *Thais floridana*, as figured by Radwin & Wells (1968: fig. 10), with strongly serrated marginal cusps, strongly resembles that of large individuals of *Thais haemastoma*. Radwin & Wells (1968) discuss the question whether *T. floridana* should be considered a subspecies of *T. haemastoma*. According to the radulae, egg capsules and embryonic shells of *T. haemastoma* from the Mediterranean (Bandel, 1977: pl. 1 fig. 6), the Canary Islands and the Caribbean, Bandel (1976a) concluded that *T. floridana* can only be regarded as an ecological form of *T. haemastoma*. In the aquarium, juvenile specimens from populations of typical *T. "floridana"* collected in the Gulf of Morrosquillo and from Santa Marta-Rodadero could be transferred into typical adult *T. haemastoma* by an abundance of food (mainly fish meat and thin shelled mytilids). Also the radulae of the *T.*

floridana stage up to the *T. haemastoma* stage were studied. The central teeth change from simple marginal cusps to dented, thickened and extended marginal cusps. There only remains the puzzling differences with Troschel & Thiele's (1865-1893: pl. 12 fig. 4) and Radwin & Wells' (1968: fig. 10) figures and descriptions.

Muricids from the Caribbean feed on other molluscs. *Murex recurvirostris rubidus* can penetrate a thick-shelled bivalve like *Anomalocardia* spec. within a day. It then thrusts its long proboscis into the clam and, with rasping and biting action of the radula, consumes all the flesh. Dead fish are also eaten and will attract *Murex pomum*. The usual food of the latter species consists of bivalves; thin-shelled species are opened by the snail by pressing its foot between the shell margins and breaking them apart. When this has resulted in a hole which is large enough for the thin and long proboscis, the gastropod starts consuming the tissue. Thick-shelled bivalves are usually bored at the shell margins and not in the more central parts of the valves as is done by *M. recurvirostris* and *M. brevifrons*. This position of the hole is of advantage because the margins of the shell are less thick than the other parts of the valves.

Murex brevifrons bores through shells of bivalves and gastropods. It will drill a hole through the shell of a large *Atrina* within 12 hours and may even get through the thick shells of full-grown *Spondylus* or *Chama* and gastropods like *Strombus*, *Thais* or *Vasum*.

Morula nodulosa, *Ocenebra blainvillei*, *Aspella anceps*, *A. paupercula*, *Favartia cellulosa*, and *F. alveata* were all observed to bore holes through the valves of pelecypods. All preferred bivalves when kept in the aquarium. *Morula nodulosa* will also detach patelloid gastropods from the substrate without boring a hole through their shell, and then consume their tissue.

Thais haemastoma is attracted by carrion, but usually feeds on barnacles and molluscs. Individuals of all sizes were kept over long periods in the aquarium and numerous field observations on the feeding snails never showed a drilling behaviour. Bivalves of the genera *Pinna*, *Atrina*, *Pteria*, and *Brachidontes* are opened by breaking the shell margins with the force of the foot, which was also observed in *Murex pomum*. Thick-shelled bivalves such as *Crassostrea*, *Chione*, and *Anomalocardia* are grabbed by the foot, which pulls on both valves. Usually within a short period the bivalves open, probably also unter the influence of a poisonous secretion produced by the gastropod.

Thais rustica prefers small herbivorous gastropods as food but may also eat bivalves, opening them as *T. haemastoma* does; no holes are drilled by this species. *Thais deltoidea* and *Purpura patula* occur on rocky shores. Both live on limpet-like gastropods and chitons. They detach their prey with their foot and the production of poisonous secretions.

With the exception of *Purpura patula* the feeding habits of the here discussed Muricidae are not reflected by the shape of the central tooth of the radula. *Purpura patula*, with its profusion of poisonous secretion in a quiet environment, i.e. without turbulent water to dilute this secretion, can use its radula on soft tissue only. Therefore, the reduction of the strength of the main cusp by the open fissure is not disadvantageous. This fissure was thought to be an internal tube of the main cusp of the central tooth opening at its apex by Troschel & Thiele (1865-1893: 126, pl. 12 fig. 1).

Usually in the Muricidae the main cusp of the central tooth is very stout and shows wear in the functional part of individual radulae, regardless whether they reach their prey by boring or not. As Runham (1969) demonstrated for *Nucella lapillus* (L.) the central teeth may be worn, while the lateral teeth in the same row are less or not worn. This also applies to the radulae here studied. The lateral teeth always show little or no wear, while the main cusp of the central tooth may be chipped or worn down to a round shape. However, most radulae studied, even of very effective borers like *Murex brevifrons*, showed very little or no wear of the central teeth at all. As Graham (1940) described for species of the genera *Nucella* and *Ocenebra*, mollusc prey is held by the foot of the snail. The anterior region of the foot forms a groove through which the proboscis is thrust and enveloped. Graham observed that the odontophore is continuously active then, being constantly pushed out to rasp the shell with the teeth. Since this author did not detect any acid production, he thought that the boring of shells by the Muricidae is purely mechanical.

Carriker (1969) has studied the boring activity of Muricidae in detail. He found that upon contact with the shell surface the anterior end of the odontophore is drawn foreward in a licking motion, scraping the cusps with their apices across the surface. In *Urosalpinx* an accessory boring organ secretes a substance, which dissolves the shell; a small part of the weakened shell is then removed by the radula and swallowed. Microhardness tests revealed, that the radula teeth range from slightly softer to slightly harder than oyster shell. Carriker observed, that because of the unfolding of the radula with over 180° at the central plane of the odontophore, only the central teeth come into contact with the shell surface. The primary function of the lateral teeth is to tear or cut off bits of flesh when feeding. The lateral tooth is curved in the form of a sickle, the inner margin is like a curved blade; the basal part, attached to the radular membrane, represents the handle. Upon erection the curved part of each tooth points upward from the membrane.

Since the radula plays no, or only a minor part in shaping the borehole, this is, as Carriker showed, primarily the product of dissolution by the secretion of the accessory boring organ. The drilling of a hole by the Muricidae, therefore, can well be compared with the way in which some members of the Tonnacea make a hole in the corona of sea-urchins.

The discussion of Radwin & Wells (1968) on the morphology of the central teeth of some Muricidae and the type of food the animals may have access to, seems quite pointless. In contrast to their opinion, *Favartia cellulosa* does not only consume thin or soft-shelled prey, but may also bore neat holes through solid bivalve shells. *Murex pomum* was observed by Radwin & Wells (1968) to bore very large holes through the shells of its prey; this was not observed in Santa Marta.

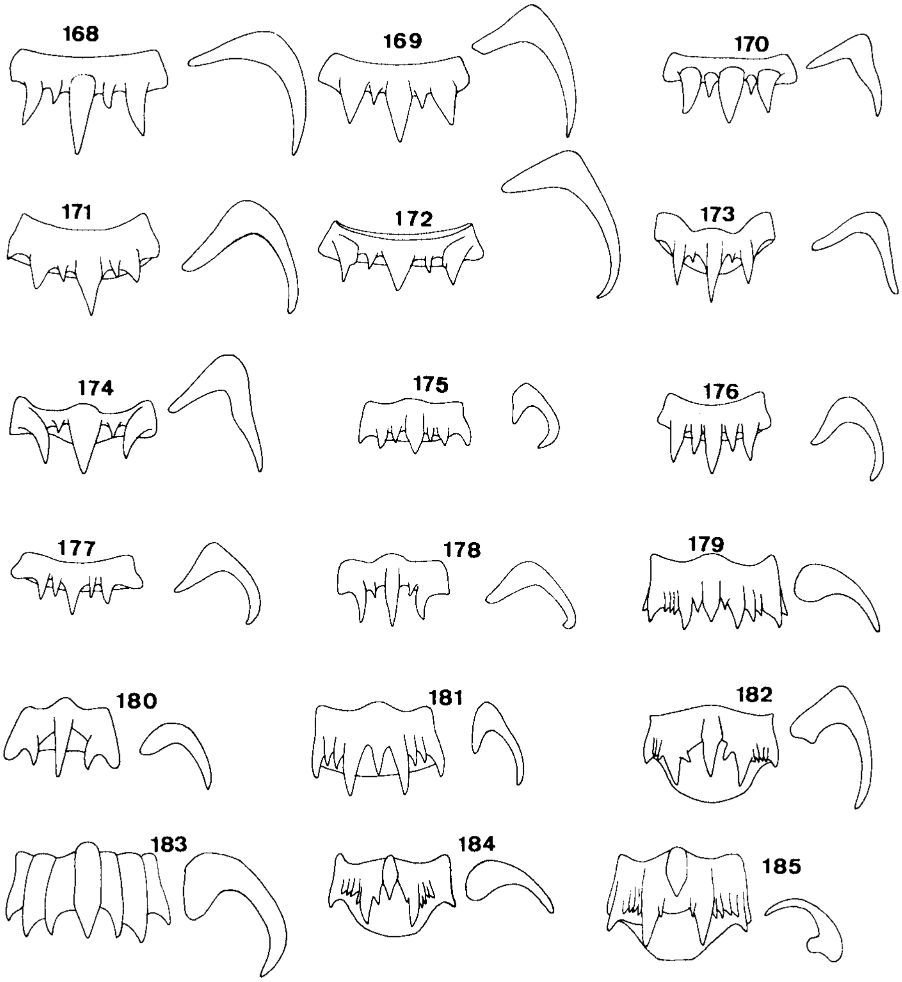

Fig. 168. *Murex recurvirostris woodringi*, Santa Marta, Caribbean; x 60. — Fig. 169. *Murex brandaris*, Banyuls-sur-Mer, Mediterranean; x 70. — Fig. 170. *Murex trunculus*, Banyuls-sur-Mer, Mediterranean; x 60. — Fig. 171. *Murex recurvirostris rubidus*; Santa Marta, Caribbean; x 10. — Fig. 172. *Murex pomum*, Santa Marta, Caribbean; x 45. — Fig. 173. *Murex brevifrons*, Santa Marta, Caribbean; x 50. — Fig. 174. *Murex angulifera*, Port Sudan, Red Sea; x 45. — Fig. 175. *Favartia cellulosa*, Santa Marta, Caribbean. x 350. — Fig. 176. *Aspella anceps*, Santa Marta, Caribbean; x 300. — Fig. 177. *Aspella paupercula*, Santa Marta, Caribbean; x 170. — Fig. 178. *Maculotriton serriale*, Port Sudan, Red Sea; x 210. — Fig. 179. *Ocenebra craticulata*, Banyuls-sur-Mer, Mediterranean; x 150. — Fig. 180. *Jopas situla*, Port Sudan, Red Sea; x 80. — Fig. 181. *Ocenebra blainvillei*, Banyuls-sur-Mer, Mediterranean; x 150. — Fig. 182. *Ocenebra edwardsi*, Banyuls-sur-Mer, Mediterranean; x 170. — Fig. 183. *Ocenebra blainvillei*, Banyuls-sur-Mer, Mediterranean; x 700. — Fig. 184. *Ocenebra erinacea*, Banyuls-sur-Mer, Mediterranean; x 150. — Fig. 185, *Ocenebra cinerea*, Cornwall, Atlantic Ocean; x 320.

Burkenroad (1931) observed *Thais haemastoma*, which drilled within 12 hours through the shell of *Crassostrea*, prefering the ventral shell-edge for the borehole. Wells (1958) observed in *Murex fulvescens* that it opened *Crassostrea* mainly by pulling its valves apart and chipping the posterior margin, while Radwin & Wells (1968) observed the species to drill holes. All this seems to indicate some variation between the feeding habits of geographically separate populations of the same species.

Wu (1965) expressed the opinion that the distinctive drupine and moruline radula patterns seen in the species he investigated, may be directly associated with feeding habits. From the study of stomach content Wu concluded that *Drupa ricina* lives on a varied diet, including carrion, sponges and holothurians, while *Morula granulata* eats dead organisms as well as molluscs, which are reached by making holes. The observation on the feeding habits of *D. ricina* is not conclusive. Both the radulae of *D. ricina* and that of *M. granulata* are morphologically similar to the here studied Caribbean species that bore the shell of their prey. Salvat (1970) came to the conclusion that *Drupa ricina* and *D. morum* are herbivorous, while Kay (1971) observed *D. morum* to eat molluscs, barnacles, worms and Sipunculida. Taylor (1968) observed that *D. morum* was feeding on barnacles, while *Morula granulata* preferred molluscs and barnacles, thus feeding on the same type of prey as the muricids from the Caribbean.

Barnacles, worms and molluscs, and carrion of vertebrates make up the food of most Muricidae (Spight, 1976; Marcus & Marcus, 1960; Clench, 1947). All members of the muricids subsisting on such food have sickle-shaped lateral teeth. Where a muricid has developed a food preference for coelenterates, as in *Morula chrysostoma* (fig. 197) and the genus *Drupella* (Cooke, 1895; Thiele, 1929; Peile, 1939; Arakawa, 1957; Barnard, 1959; Cernohorsky, 1969), the shape of the lateral teeth is changed. The lateral teeth here resemble the marginal teeth of Heteropoda (Richter, 1961, 1974) or the teeth of *Architectonica* (fig. 96) and *Janthina* (fig. 97), all of which feed on coelenterates. *Morula chrysostoma* was observed to feed on a variety of stony corals on the reefs, to a depth of 15 m and more, as well as in the lagoons, where it is over one meter deep, in the area of Port Sudan, Red Sea.

With the exception of *Drupella*, the food requirements and the mode of obtaining the food is quite similar among the different members of the muricids. Therefore, the considerable differences in the morphology of the central tooth among the various species of this neogastropod branch can be considered of great taxonomic value, a pattern not disturbed by specific adaptations to a certain type of food.

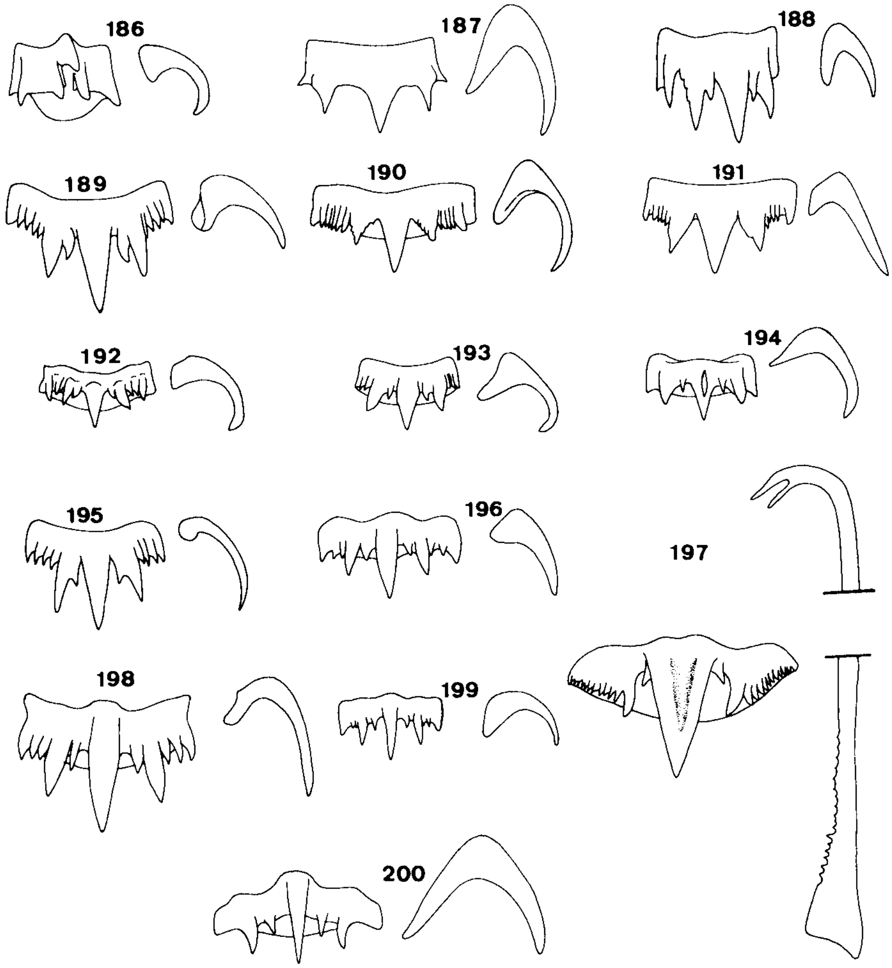

Fig. 186. *Favartia alveata*, Santa Marta, Caribbean; x 450. — Fig. 187. *Pterynotus* sp., Port Sudan, Red Sea; x 120. — Fig. 188. *Nucella lapillus*, Dutch coast, North Sea; x 200. — Fig. 189. *Drupa morum*, Port Sudan, Red Sea; x 150. — Fig. 190. *Thais haemastoma* (*haemastoma*), Santa Marta, Caribbean; x 50. — Fig. 191. *Thais haemastoma* (*floridana*), Santa Marta, Caribbean; x 100. — Fig. 192. *Thais rustica*, Santa Marta, Caribbean; x 100. — Fig. 193. *Thais deltoidea*, Santa Marta, Caribbean; x 90. — Fig. 194. *Purpura patula*, Santa Marta, Caribbean; x 70. — Fig. 195. *Drupa* sp., the Seychelles, Indian Ocean; x 150. — Fig. 196. *Drupa rubusidaeus*, Port Sudan, Red Sea; x 160. — Fig. 197. *Morula chrysostoma*, Port Sudan, Red Sea; x 220. — Fig. 198. *Drupa hadari*, Port Sudan, Red Sea; x 220. — Fig. 199. *Morula nodulosa*, Santa Marta, Caribbean Sea; x 210. — Fig. 200. *Drupa cancellata*, Port Sudan, Red Sea; x 420.

BUCCINACEA, COLUMBELLIDAE

Columbella mercatoria (Linné, 1758)
(fig. 245; pl. 13 fig. 8)

The radula has about 120 rows of teeth. Like in the radulae of all discussed columbellid species, the central tooth has no cusps nor cutting edge and is fully attached to the membrane of the radula. It is 2.5 times wider than long. Its anterior front is evenly convex, while the posterior base is curved concavely at the sides and straight in its central part. The posterior corners are acute.

In all columbellids the lateral tooth is attached to the membrane of the radula by a short posterior edge, extending into a fully attached projection of the outer posterior corner, that may be twisted out of the direction of the longitudinal axis of the lateral tooth. Here the base is extended into a wing-like posterior corner, oriented almost vertically to the basal platform. This lamella-like extension has a denticle at its outermost end. The lateral tooth is three times as long as wide. The basal cusp of the cutting edge is rounded and low, it extends into a hook-like top curved towards the longitudinal axis of the tooth. The central cusp is the largest, bilaterally flattened, and beak-like; the apical cusp is acute.

Anachis sparsa (Reeve, 1859)
(fig. 241; pl. 13 figs. 9, 10, pl. 14 fig. 1)

The radula has about 120 rows of teeth. The central tooth is wider than long (4:3) and has a weakly convex anterior front; its margins are slightly inclined outward in a posterior direction, and the posterior edge is weakly concave. The corners are rounded or angular.

The lateral tooth is almost four times as long as wide. The posterior edge has two wing-like extensions, viz. a smaller one at the inner posterior corner and a larger, angular one at the outer posterior corner, twisted away from the main axis of the tooth. These wings, together with the short base, form the attachment to the membrane. The basal cusp on the cutting edge is broad and rounded. The central cusp is hook-like, somewhat wider and shorter than the acute and long apical cusp.

Anachis brasiliana (Von Martens, 1897)
(fig. 240; pl. 14 fig. 2)

The radula has about 220 rows of teeth. The central tooth is twice as wide as long and, because of its concave posterior edge, is almost crescentic in shape. The anterior corners are rounded and the anterior front is straight. The margins are convex and end in acute posterior edges. The posterior basal platform is somewhat lower than its anterior part.

The lateral teeth are almost 2.5 times longer than wide. The base extends in a broad, long and solid extension of the outer posterior corner. The basal cusp is low, rounded and situated close to the inner posterior corner. The central cusp is smaller than the apical cusp and also acute, hook-like in shape.

Anachis pulchella (Blainville, 1829)
(fig. 243; pl. 14 fig. 3)

The radula has about 75 rows of teeth. The rectangular central tooth is almost five times wider than long. The anterior front and the posterior edge are straight or slightly concave; the margins are inclined in such a way, that the anterior corners are rounded, while the posterior corners are angular or acute.

The lateral teeth are 3.5 times longer than wide. The base is curved into a sturdy wing-like long extension. The basal cusp is drawn out into a lamella with its outer edge curved outward. This cusp extends over more than one half of the length of the tooth. The central cusp is bilaterally flattened, triangular, and beak-like in shape. The longer, but less wide, apical cusp is hooked and acute.

Anachis obesa (C. B. Adams, 1845)
(fig. 244; pl. 14 fig. 5)

The radula has about 100 rows of teeth. The rectangular central tooth has rounded corners and straight to slightly convex sides. It is almost twice as wide as long.

The lateral tooth is about three times as long as wide. Its outer base is curved into a stout wing-like extension. The basal cusp is low and rounded triangular, situated close to the inner posterior corner. The central cusp is hooked and acute, like the apical cusp, but shorter.

Anachis spec. 1
(fig. 242; pl. 14 fig. 4)

The radula has about 135 rows of teeth. The central tooth is more than twice as wide as long. The anterior front and the margins are rounded convexly. The posterior corner is angular to acute and the posterior edge concave. The posterior basal platform is somewhat lower than its broader anterior part. See also Bandel (1974: 281, 282).

The lateral teeth are three times as long as wide. The inner posterior corner is extended into a rounded lamella, the outer posterior corner is twisted and drawn out into a short wing-like extension. The basal cusp is rounded and ends at about midway of the tooth. The central and the apical cusps are similar in shape, acute and curving; the central one is the shortest of both.

Anachis spec. 2
(fig. 252; pl. 15 fig. 3)

Anachis cf. *semiplicata* Stearns, 1873

The radula has about 100 rows of teeth. The rectangular central tooth is slightly wider at the posterior edge than at the anterior front. It is almost twice as wide as long and has straight sides.

The lateral tooth is more than three times longer than wide. The base is twisted to form a stout and short extension. The basal cusp is low and rounded. The central cusp is acute, beak-like, and somewhat shorter and broader than the acute, curving, apical cusp.

Anachis lafresnayi (Fischer & Bernardi, 1856)
(pl. 15 fig. 4)

The radula has over 100 rows of teeth. The quadrangular central tooth is about twice as wide as long and has straight sides.

The lateral tooth is three times as long as wide. Its base is extended outward, twisted, ending in a stout wing-like structure. The basal cusp is low and rounded, situated near the inner posterior corner. The central and apical cusps are slender and curving, the apical one is slightly larger.

Anachis sp. 3
(fig. 253)

The radula is like that of *Anachis lafresnayi*.

Nitidella nitida (Lamarck, 1822)
(fig. 248; pl. 14 fig. 6)

The radula has about 90 rows of teeth. The central tooth is almost four times as wide as long. The margins and the anterior front form one continuous convex line. The posterior edge is straight, ending in acute corners.

The lateral tooth is three times as long as wide. Its base is twisted over its full width, forming a broad attached basement, which ends along a straight margin. The basal cusp is low and long, ending with a small hook-like apex, curved towards the longitudinal axis of the tooth. The bilaterally flattened central cusp is beak-like and somewhat shorter than the narrower, more sturdy apical cusp.

Nitidella laevigata (Linné, 1758)
(fig. 249; pl. 14 figs. 9, 10, pl. 15 fig. 1)

The radula has about 120 rows of teeth. The central tooth is low and almost seven times as wide as long. Its anterior front is somewhat concave and the posterior edge slightly convex, so that the width is the same along almost is entire course. The anterior corners are rounded, the posterior corners angular to acute.

The lateral teeth are about two times as long as wide. Their base is twisted to form a short extension, ending with a straight margin. The triangular basal cusp ends midway the tooth. The bilaterally flattened central cusp is dominant, in outline it forms almost a semicircle; it has an upper beak-like blade, separated from the lower part of the cusp by an indentation. The lower cutting edge of the cusp is serrated by six or seven denticles. The apical cusp is hook-like, acute and stout. The lateral teeth are often worn down to the central stalk in the used parts of the radula.

Mitrella ocellata (Gmelin, 1791)
(fig. 238; pl. 14 fig. 7)

The radula has about 200 rows of teeth. The central tooth is about three times as wide as long. Its anterior front is straight, the posterior edge concave. The anterior corners are rounded, the margins convex and the posterior corners angular to acute.

The lateral tooth is about three times as long as wide. The inner posterior corner is extended into rounded wing-like structures. The outer posterior corner extends into a broad, fully attached wing-like lamella, twisted away from the main stalk of the tooth. The basal cusp ends with an acute tip, curved towards the longitudinal axis of the tooth. The central and the apical cusps are acute, slender and similar in shape; the central one is slightly shorter.

Mitrella argus d'Orbigny, 1842
(fig. 239; pl. 14 fig. 8)

The radula has about 120 rows of teeth. The central tooth is only slightly wider than long (5:4), somewhat less wide at the straight anterior front than at the slightly convex posterior edge. The margins are convex.

The lateral tooth is about three times longer than wide; at its base it is evenly twisted extending into a long basal plate. The basal cusp is low, moderately long and angular at its apex. The central cusp is beak-like, bilaterally widened and shorter than the acute, curved, apical cusp.

Mitrella lunata (Say, 1826)
(fig. 237; pl. 15 fig. 2)

The radula has 100 rows of teeth. The rectangular central tooth has straight sides and is 1.5 times wider than long.

The lateral tooth is about three times longer than wide. The posterior outer corner is extended into a short acute wing. The basal cusp, situated close to the inner posterior corner is blunt. The central cusp is somewhat shorter than the apical cusp; both are similar in shape, acute and curved hook-like.

Nassarina monilifera (Sowerby, 1844)
(fig. 250; pl. 15 fig. 5)

The radula has about 150 rows of teeth. The central tooth is slightly wider than long and has a straight anterior front and posterior edge, and weakly convex margins, ending in rounded corners.

The lateral tooth is almost three times as long as wide. The basal cusp also forms the acute, inner posterior corner. The outer posterior corner is extended wing-like, without being twisted away from the tooth axis. The central cusp is bilaterally flattened, triangular to hook-like; the slightly longer apical cusp is hook-like and acute.

Aesopus stearnsii (Tryon, 1883)
(fig. 254; pl. 15 fig. 7)

The radula has about 120 rows of teeth. The central tooth is almost twice as wide as long. The anterior corners are rounded, the margins are convex. The anterior front is straight and the posterior edge concave. The posterior corners are angular.

The lateral tooth has three rounded cusps, the basal cusp near the inner posterior corner and another two situated more anteriorly. The outer posterior corner is moderately extended.

Antillophos candei (d'Orbigny, 1842)
(fig. 251; pl. 15 fig. 6)

The radula has about 120 rows of teeth. The central tooth is more than twice as wide as long. Its posterior edge is straight, ending in angular corners. The margins are convex, ending in evenly rounded anterior corners. The anterior front is convex to straight.

The lateral teeth are almost three times as long as wide. At their base they are twisted, ending in a platform with straight edges. The lower, rounded, broad, basal cusp extends from close to the inner posterior corner to about half the length of the tooth. The central and apical cusps are hooked, slender and acute; the apical one is the largest.

DISCUSSION

Marcus & Marcus (1962) had studied a number of Brazilian columbellids and found that their radulae were rather uniform. They found differences, however, in the shape and size of the individual teeth in different species, that enabled them to distinguish species by radula characters alone. Troschel & Thiele (1865-1893) distinguished only two genera in the Columbellidae, viz. *Columbella* and *Pyrene*. In their opinion these may be differentiated by the presence or absence of a denticle-like extension of the basal lamella on the lateral teeth, and the spacing of the cusps on these teeth. This feature was rediscovered by Radwin (1977), who stated that the horizontal dimensions and the degree of flexure of the lateral teeth and the sharpness of their cusps vary and are useful characters to divide the family into two subfamilies, viz. Columbellinae and Pyreninae. Thiele (1924), in a study on the radulae of most groups of Columbellidae, concluded that only the two genera suggested by Troschel can really be differentiated within this family. Thiele emphasized the importance of the extension of the basal part of the lateral tooth. If this extension is of moderate size and undivided, the columbellid in question belongs to *Pyrene*; if the extension is split up into two or three separate lamellar denticles, the species should be classified with *Columbella*. Thiele (1924, 1929) also assigned *Nitidella* to the genus *Columbella*.

In our Caribbean material the *Columbella* group is represented by *Columbella mercatoria* only. Both *Nitidella nitida* and *N. laevigata* do not have the characters to assign them to the *Columbella* group. *Columbella rustica* (L.) (fig. 247; Bandel, 1977: pl. 2 fig. 7, 8) from the Mediterranean has a radula similar to that of *C. mercatoria*. Of the eight Brazilian columbellids studied by Marcus & Marcus (1962), only *C. mercatoria* was considered to belong to the *Columbella* group.

When the 17 columbellid species from Santa Marta are compared with each other, it will be noted that even a differentiation into two groups, as mentioned before, is difficult to defend. Looking at single characters in the morphology of the teeth, the additional denticle on the basal lamella can only be found in *C. mercatoria*. Extensions of the inner posterior corner of the lateral tooth can be observed in *Anachis sparsa* (fig. 241), *Anachis* spec. 1 (fig. 242), and *Mitrella ocellata* (fig. 238). The extension of the outer posterior corner is not twisted away from the main stalk of the lateral tooth in *Anachis obesa* (fig. 244), *Nassarina monilifera* (fig. 250), and *Aesopus stearnsii* (fig. 254). An inward curving hook of the basal cusp may be seen in *Mitrella ocellata* (fig. 238), *Nitidella nitida* (fig. 248), and *Columbella mercatoria* (fig. 245). A similar variation is seen in the length and the location of the basal cusp in various species. All these characters could be considered as important as the presence or absence of a denticle on the basal, twisted lamella. Radwin's (1977: 404) optimism with regard to the taxonomical importance of the morphology of the cusps and the base of the lateral teeth is not supported by these data.

The shape of the central tooth is also not a useful generic character. Narrow teeth are found in *Columbella mercatoria* (fig. 245), *Anachis pulchella* (fig. 243) and *Nitidella laevigata* (fig. 249). Almost square teeth are seen in *Mitrella argus* (fig. 239), *M. lunata* (fig. 237), *Nassarina monilifera* (fig. 250), *Anachis sparsa* (fig. 241), *A. obesa* (fig. 244), *A. lafresnayi* and *A.* sp. 3 (fig. 253). The other species have central teeth with intermediate shapes.

Apparently the morphology of the columbellid radula cannot be used to clarify higher systematic relationships.

Marcus & Marcus (1962) suggested that the two different types of columbellid radulae may be related to feeding. They thought that herbivores have broader

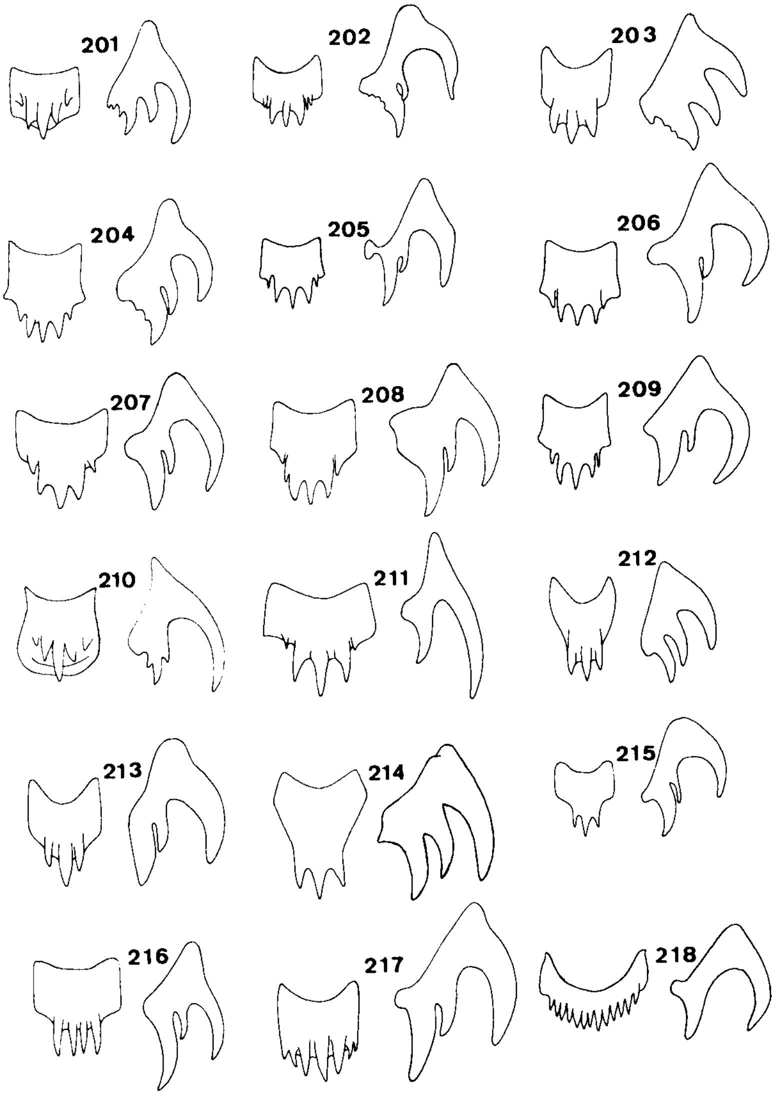

Fig. 201. *Engina turbinella*, Santa Marta, Caribbean, specimens similar to *E. corinnae* Crovo, 1971; x 700. — Fig. 202. *Cantharus undosus*, Port Sudan, Red Sea; x 120. — Fig. 203. *Cantharus* sp., Port Sudan, Red Sea; x 420. — Fig. 204. *Pisania tincta*, Santa Marta, Caribbean; x 420. — Fig. 205. *Pisania pusio*, Santa Marta, Caribbean; x 70. — Fig. 206. *Pisania auritula*, Santa Marta, Caribbean; x 80. — Fig. 207. *Pisania dorbignyi*, Banyuls-sur-Mer, Mediterranean; x 300. — Fig. 208. *Pisania auritula*, Santa Marta, Caribbean; x 100. — Fig. 209. *Pisania striata*, Banyuls-sur-Mer, Mediterranean; x 200. — Fig. 210. *Engina turbinella*, Santa Marta, Caribbean; x 500. — Fig. 211. *Engina mendicaria*, Port Sudan, Red Sea; x 420. — Fig. 212. *Engina bicolor*, Banyuls-sur-Mer, Mediterranean; x 270. — Fig. 213. *Dolicholatirus cayohuesonicus*, Santa Marta, Caribbean; x 80. — Fig. 214. *Euthria cornea*, Banyuls-sur-Mer, Mediterranean; x 200. — Fig. 215. *Colubraria swifti*, Santa Marta, Caribbean; x 320. — Fig. 216. *Busycon canaliculatum*, Woods Hole, Atlantic Ocean, unhatched juveniles; x 250. — Fig. 217. *Pusia* aff. *pulchella*, Santa Marta, Caribbean; x 150. — Fig. 218. *Nassarius* sp., Port Sudan, Red Sea; x 80.

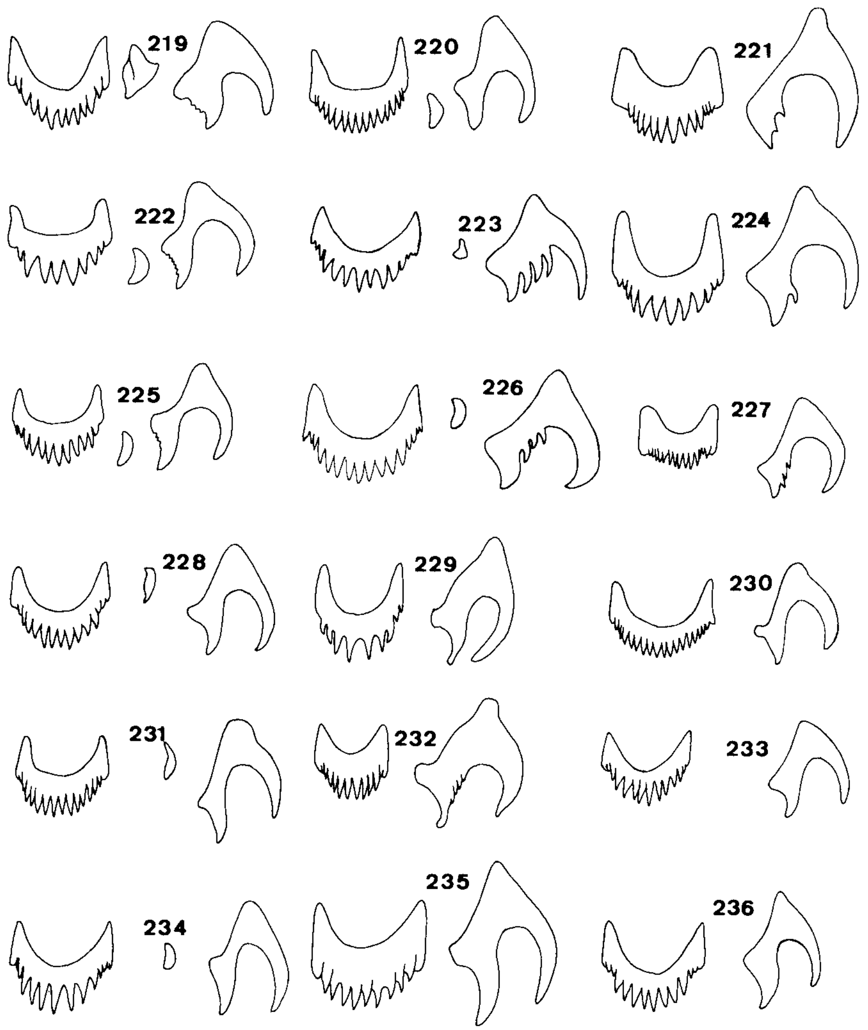

Fig. 219. *Nassarius granus*, Banyuls-sur-Mer, Mediterranean; × 120. — Fig. 220. *Nassarius* cf. *coronatus*, Port Sudan, Red Sea; × 80. — Fig. 221. *Nassarius albus* (male), Santa Marta, Caribbean; × 130. — Fig. 222. *Nassarius livescens* (female), Port Sudan, Red Sea; × 120. — Fig. 223. *Nassarius neriteus*, Banyuls-sur-Mer, Mediterranean; × 150. — Fig. 224. *Nassarius albus* (female), Santa Marta, Caribbean; × 160. — Fig. 225. *Nassarius livescens* (male), Port Sudan, Red Sea; × 120. — Fig. 226. *Nassarius corniculus*, Banyuls-sur-Mer, Mediterranean; × 80. — Fig. 227. *Nassarius vibex*, Santa Marta, Caribbean; × 100. — Fig. 228. *Nassarius trivittatus*, Cape Cod, Atlantic Ocean; × 90. — Fig. 229. *Nassarius incrassatus* (female), Banyuls-sur-Mer, Mediterranean; × 100. — Fig. 230. *Nassarius vibex*, Santa Marta, Caribbean; × 100. — Fig. 231. *Nassarius* cf. *kieneri*, Port Sudan, Red Sea; × 70. — Fig. 232. *Nassarius incrassatus* (male), Banyuls-sur-Mer, Mediterranean; × 100. — Fig. 233. *Nassarius pygmaeus*, Banyuls-sur-Mer, Mediterranean; × 180. — Fig. 234. *Nassarius reticulatus*, Banyuls-sur-Mer, Mediterranean; × 80. — Fig. 235. *Engoniophos unicinctus* (female), Santa Marta, Caribbean; × 140. — Fig. 236. *Nassarius costulatus*, Banyuls-sur-Mer, Mediterranean; × 160.

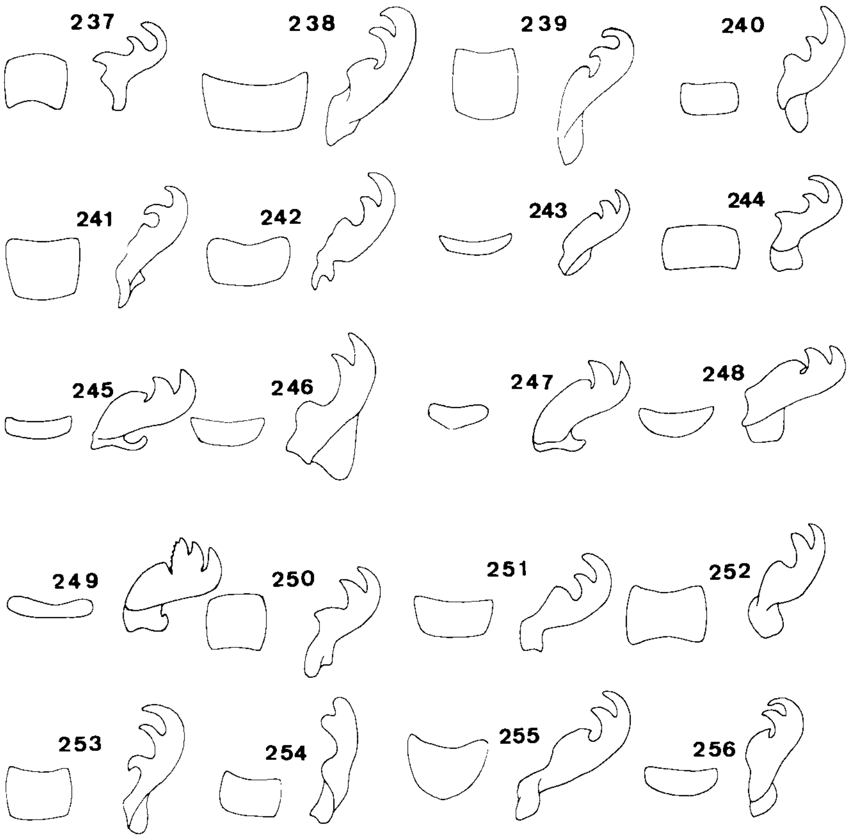

Fig. 237. *Mitrella lunata*, Santa Marta, Caribbean; × 400. — Fig. 238. *Mitrella ocellata*, Santa Marta, Caribbean; × 300. — Fig. 239. *Mitrella argus*, Santa Marta, Caribbean; × 400. — Fig. 240. *Anachis brasiliana*, Santa Marta, Caribbean; × 200. — Fig. 241. *Anachis sparsa*, Santa Marta, Caribbean; × 310. — Fig. 242. *Anachis* sp. 1, Santa Marta. Caribbean; × 330. — Fig. 243. *Anachis pulchella*, Santa Marta, Caribbean; × 100. — Fig. 244. *Anachis obesa*, Santa Marta, Caribbean; × 350. — Fig. 245. *Columbella mercatoria*, Santa Marta, Caribbean; × 60. — Fig. 246. *Columbella fulgurans*, Port Sudan, Red Sea; × 220. — Fig. 247. *Columbella rustica*, Banyuls-sur-Mer, Mediterranean; × 90. — Fig. 248. *Nitidella nitida*, Santa Marta, Caribbean; × 100. — Fig. 249. *Nitidella laevigata*, Santa Marta, Caribbean; × 90. — Fig. 250. *Nassarina monilifera*, Santa Marta, Caribbean; × 700. — Fig. 251. *Antillophos candei*, Santa Marta, Caribbean; × 250. — Fig. 252. *Anachis* cf. *semiplicata*, Santa Marta, Caribbean; × 400. — Fig. 253. *Anachis* sp. 3, Santa Marta, Caribbean; × 400. — Fig. 254. *Aesopus stearnsii*, Santa Marta, Caribbean; × 1000. — Fig. 255. *Anachis* sp., Port Sudan, Red Sea; × 210. — Fig. 256. *Pyrene* sp., Port Sudan, Red Sea; × 90.

radulae, with thicker plates, than carnivorous species. An extreme representative of the herbivores among the Columbellidae is *Nitidella laevigata* which subsists on the alga *Sargassum* (Bandel, 1974: 273). This species has thin and comparatively weak central teeth, whereas its lateral teeth have a modified cutting edge, and are not particularly strengthened if compared with other columbellid radulae.

The feeding habits of some of the species mentioned here were discussed by Bandel (1974: 271-273). In the aquarium *Columbella mercatoria* can be fed with green algae, but it also eats carrion. In its natural environment, on rocks and algal growths, within or just below the tidal area, the snails will feed on algae and everything of animal life between these, found on rocks, algal fronds or seagrass leaves. *Nitidella laevigata* consumes *Sargassum* up to the stem or the larger veins in the leaves. It will also readily accept fish in the aquarium. *Mitrella argus*, *Anachis obesa* and *Mitrella lunata* eat hydroids and other small animals. In the aquarium *Anachis sparsa*, *A. avara brasiliana*, *A. pulchella* and *Mitrella ocellata* were observed while feeding on fish.

The radulae of the studied Columbellidae, apart from that of *Nitidella nitida*, vary only in details, which may have no importance in obtaining their specific food. The radula is constructed for cutting, tearing and hooking. The movement of the lateral tooth during biting is from a position with cusps directed away from the central tooth toward the central tooth. The movements and shape of the lateral teeth should enable the radula to get a very effective hold on soft tissue or filamentous algae, which in conjunction with the retraction of the buccal mass, should result in tearing off pieces of tissue. The lower part of the inner margin of the lateral teeth is sharpened and blade-like, so tissue may be cut during the movement of these teeth against the plate-like central teeth.

In *Nitidella laevigata* cutting is aided by the saw-like border of the blade-like central cusp of the lateral tooth. The special modification of these teeth cannot be considered to reflect a primitive mode of feeding of *N. laevigata*, as in herbivorous ancestors of the Columbellidae or the Neogastropoda. It should be considered a newly evolved adaption to *Sargassum* as food, a plant which cannot be used as such by the omnivorous ancestors of *N. laevigata*, which probably had a normal columbellid radula, similar to that of *Anachis pulchella* or *Nitidella nitida*.

Abbott (1974) considered *Anachis brasiliana* (Von Martens) a subspecies of *A. avara* (Say). If we compare the egg capsules of both species (Scheltema, 1968; Bandel, 1974) we note differences, indicating that *Anachis avara* and *A. brasiliana* are separate species. The radula of *A. avara* was illustrated by Scheltema (1968: fig. a). The lateral tooth has a basal cusp provided with an acute hook, directed inward, in *A. avara*, which is not present in *A. brasiliana*. This suggests a specific status of both taxa, as could also be concluded from the study of Marcus & Marcus (1962), in which the differences between the radulae of *A. brasiliana* and that of *A. avara* are also clearly represented.

Antillophos candei, assigned to the Buccinidae by Abbott (1974), proves to be a columbellid species by its typical columbellid radula. *A. candei* is the type species of *Antillophos*. The species is quite variable in the sculpture of the adult shell, but the embryonic shells are very characteristic. The egg capsule of *A. candei* is described by Bandel (1976b: fig. 18).

Anachis pulchella from Brazil as studied by Marcus & Marcus (1964) and the species called *A. pulchella* in the present study are different in radula morphology. The central teeth are much longer in the Brazilian species and the basal cusps of the lateral teeth are more acute and narrower than in the Colombian species. This indicates that the Brazilian and the Colombian "*Anachis pulchella*" are different species. The *A. pulchella* radula figured and described by Radwin (1977: 416, fig. 15) is similar to that of Santa Marta; according to Radwin, the range of this species does not extend further south than Panama, however.

Buccinacea, Buccinidae and Melongenidae

Engina turbinella (Kiener, 1835)
(fig. 210; pl. 15 fig. 9)

The radula has about 70 rows of teeth. The central tooth is almost as long as wide. Its anterior front and the margins are straight. The posterior corners are rounded and the posterior edge curves evenly. The cusps of the cutting edge are attached right to the basal platform; three close to each other in the central part and, on each side of this group and separated form it by a cleft, there is an additional smaller one. The central cusp is the largest, the following are increasingly smaller. All cusps are acute and slender, and attached to the posterior central part of the basal platform in such a way that they form a sharp angle with the platform. The cutting edge is shallowly U-shaped, following in its course the outline of the posterior edge. The central cusp is so long that, when the tooth is observed from above, its apex extends beyond the posterior edge.

The lateral tooth is fang- to hook-like and has two or three cusps. The outer margin is rounded, evenly arched and ending in an acute outer posterior corner at one side and the tip of the main cusp at the other side. This cusp is somewhat longer than the straight to concave posterior edge. The latter ends in the angular inner posterior edge. If there are two additional cusps, these are about equal in size, only reaching one-third of the length of the main cusp. The hook-like central cusp is smooth; the inner cusp has a smooth outer flank and two to four very variable denticles on the inner flank. When there is no central cusp, there may be a denticle on the outer flank of the inner cusp. The number of cusps is variable, and the lateral teeth of one row may have two cusps at one side and three at the other.

Pisania pusio (Linné, 1758)
(fig. 205; pl. 16 fig. 1)

Pisania auritula (Link, 1807)
(figs. 206, 208; pl. 16 fig. 3)

The radula of *Pisania pusio* and that of *P. auritula* are so much alike that they are described together. *P. pusio* has about 80 rows of teeth and *P. auritula* 150 rows.

The central tooth is almost as long as wide. The cusps are situated at the posterior edge; this edge constitutes the cutting edge. The concave anterior front and the straight margins are attached to the membrane, while the posterior edge, with the five acute cusps, is free. The three central cusps are evenly spaced and of equal size. The outermost pair of cusps is separated from the central cusp by a cleft, forming a furrow on the posterior basal platform. These marginal cusps are much smaller and usually more slender in shape than the central cusps.

The lateral tooth is slightly wider than long. The outer margin continues from a rounded posterior corner to the tip of the main cusp in an even curve. The posterior edge is straight, until reaching the posterior inner corner, which is extended into a knob-like swelling. The hook-like central cusp is slender and the smallest of the three; the more straight inner cusp measures about half the length of the main cusp. There is no serration on the inner margin.

Pisania tincta (Conrad, 1846)
(fig. 204; pl. 15 fig. 10, pl. 16 fig. 2)

The radula has about 100 rows of teeth. The central tooth resembles that of the *P. pusio* & *P. auritula* radula; it is slightly longer than wide. The concave anterior front and the straight margins are attached to the membrane, while the posterior edge, which is the cutting edge with three to five cusps, remains unattached. The three central cusps are equal in size and always present, whereas both or one of the outermost cusps may be absent.

The lateral tooth resembles that of *Engina turbinella*. It has three cusps, the outer of which is the largest. The central cusp is the smallest and quite variable in length and width. The inner cusp has a smooth, strongly curving outer flank and a convex inner flank with two low denticles.

Dolicholatirus cayohuesonicus (Sowerby, 1878)
(fig. 213; pl. 16 fig. 4)

The radula has about 100 rows of teeth. The central tooth is as long as wide. It is attached to the membrane with its concave front and the straight to convex margins. The sides of the posterior edge are inclined towards the three central cusps of the cutting edge. These cusps continue in swellings onto the basal platform. The central cusp is the largest one.

The lateral teeth are similar to those of *Pisania pusio* in shape. They are somewhat longer on the outer margin than wide at their straight posterior edge. The inner posterior corner is knob-like extended. The hook-like cusps are unequal in size; the outermost is the largest, the innermost the second largest, whereas the central is the smallest.

Colubraria swifti (Tryon, 1881)
(fig. 215; pl. 16 fig. 5)

The radula has about 100 rows of teeth. It very much resembles that of *Dolicholatirus cayohuesonicus*. The central tooth is about as long as wide. The straight margins and the concave anterior front are attached to the membrane up to the basal corners. The margins are only half as long as the whole tooth. The sides of the cutting edge, or posterior edge, are inclined concavely towards the three stout cusps of which the central one is slightly larger than the other two.

The lateral tooth is about as wide as high. The three cusps are hook-like, with smooth flanks. The outermost cusp is the largest, the innermost is second in size, whereas the central one is the smallest. The posterior edge begins at a rounded outer corner, ending in a moderately widened inner posterior corner.

Melongena melongena (Linné, 1758)
(fig. 271; pl. 17 fig. 1)

The radula has about 60 rows of teeth. The central tooth is somewhat wider than long (5:4) and attached to the membrane with its concave anterior front and the straight margins. The three equally sized cusps extend from the posterior edge and are evenly spaced, each having the same length as the margins.

The lateral tooth has two cusps, of which the outer one is the largest. The tooth is twice as long as wide and has a straight posterior edge and angular posterior corners. The outer margin is evenly curved, ending in the tip of the cusp. The inner margin of the inner cusp ends before reaching the posterior corner, which bulges inward.

DISCUSSION

Troschel & Thiele (1866-1893: 69) based the "family" on the number of cusps on the lateral teeth, which should be between two and four, and the characters of the central tooth, which was said to be usually wider than long, with seven cusps at most, situated on the straight posterior edge. This definition excludes the Fasciolariidae, for these have more cusps on the lateral teeth, as well as the Nassariidae with crescentic central teeth and over seven cusps on their cutting edge. If we study the figures on plates 6-8 in Troschel & Thiele's (1865-1893) extensive study, we get an impression of the considerable amount of variation within the limits of the definition. To demonstrate some extreme forms of "Fusacea", the radulae of *Buccinum undatum* L. and *B. humphreysianum* Bennet from the North Sea and the Mediterranean respectively (figs. 269, 270), and *Volema pyrum* (Gmelin) (fig. 272) from the Red Sea are illustrated.

Thiele (1929) has split the "Fusacea" into the families Buccinidae and Galeodidae (= Melongenidae). Other classifications were offered by Taylor & Sohl (1962) and Keen (1963).

Cernohorsky (1971) in a paper on Pacific Buccinidae, noted that several genus groups proposed for the Indo-Pacific buccinid species appeared to be superfluous. Abbott (1974) considered the Caribbean species *Pisania tincta* and *P. auritula* congeneric. Consequently, the Mediterranean species usually called *Pisania striata* (Gmelin) (fig. 209; Bandel 1977: pl. 3 fig. 8, pl. 4 fig. 2) and *Cantharus dorbignyi* (Payraudeau) (fig. 207; Bandel, 1977, pl. 3 fig. 7), with radulae almost identical to those of the Caribbean species of *Pisania*, should also be assigned to a single genus, viz. *Pisania*. Cernohorsky (1971) stated that several genera have been classified with separate families, although their radulae suggest a close relationship. The same author admitted, however, that a classification of buccinid genera entirely based on radula characters would in many instances give incongruous results in case other characters of the animals are taken into account. This can be illustrated by comparing the radula of *Dolicholatirus cayohuesonicus* with that of *Pisania tincta*; both radulae are very similar, but not the shells. The same applies to the radulae and other characters of *Colubraria swifti*, *Euthria cornea* (L.) (fig. 214; Bandel, 1977: pl. 3 fig. 5) and *Engina bicolor* (Cantraine) (fig. 212; Bandel, 1977: pl. 3 fig. 6) from the Mediterranean. Cernohorsky's conclusion, that the buccinid radula is often more reliable in distinguishing between species, than in separating genera, can be accepted in the light of these data.

Well-differentiated species such as *Pisania pusio*, *P. auritula*, *P. striata* and *Cantharus dorbignyi*, have radulae which are practically identical. In addition it should be noted that the size and number of cusps on individual teeth can vary considerably within the radula of a single species.

Cantharus undosus (L.) (fig. 202) and *Cantharus* spec. (fig. 203), both from the Red Sea, have denticles on the inner margin of the lateral tooth, as in *Pisania tincta*. Cernohorsky (1971: figs. 62, 63) noted that this feature is typical for tropical members of the genus *Cantharus*. Robertson (1957: figs. 16, 17) figured similar radulae, but his figures of *Pisania tincta* show no such serrations of the lateral tooth. This author noted that the radula of *P. tincta*, *P. pusio* and *P. auritulus* have lateral teeth without specific characters. According to Robertson, only *Cantharus cancellarius* (Conrad) and *C. multangulus* (Philippi) from the Caribbean have lateral teeth with crenulated margins and central teeth like those of the *Pisania* species. Apparently, the crenulated or smooth inner margins in this species occur in different geographic populations. Therefore, this character of the radula cannot be considered important for the definition of the genera *Pisania* and *Cantharus*.

The cusp of the lateral teeth may vary in number within a species, or even in a single specimen. In a single *Pisania striata* radula from the Mediterranean, a variation between four and seven cusps was noted (Bandel, 1977: 206), which is more than Troschel & Thiele's (1865-1893) definition of their "Fusacea" allows. This radula resembles that of certain Fasciolariidae, especially the genera *Latirus* (figs. 257, 259) and *Leucozonia* (figs. 261, 263).

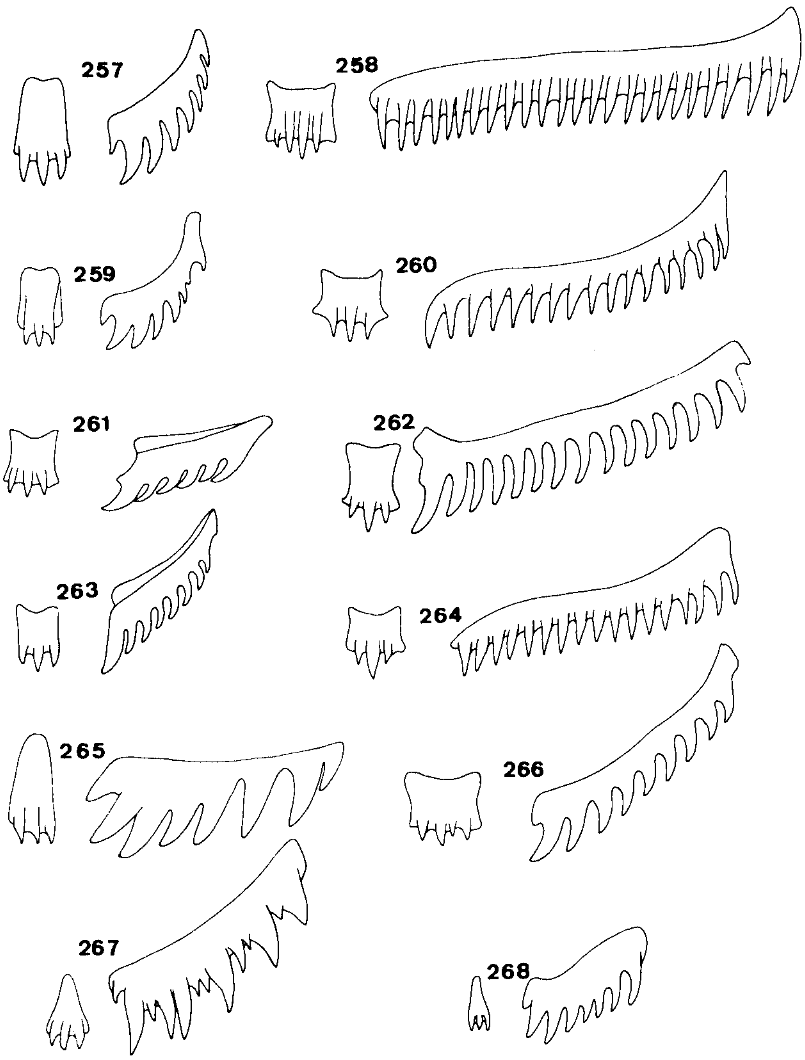

Fig. 257. *Latirus infundibulum*, Santa Marta, Caribbean; × 200. — Fig. 258. *Fasciolaria trapezium*, Port Sudan, Red Sea; × 100. — Fig. 259. *Latirus turrites*, Port Sudan, Red Sea; × 320. — Fig. 260. *Fasciolaria tulipa*, Santa Maria, Caribbean; × 90. — Fig. 261. *Leucozonia ocellata*, Santa Marta, Caribbean; × 320. — Fig. 262. *Latirus smaragdulus*, the Seychelles, Indian Ocean; × 250. — Fig. 263. *Leucozonia nassa*, Santa Marta, Caribbean; × 150. — Fig. 264. *Fasciolaria filamentosa*, Port Sudan, Red Sea; × 80. — Fig. 265. *Latirus angulatus*, Santa Marta, Caribbean; × 400. — Fig. 266. *Latirus polygonus*, Port Sudan, Red Sea; × 300. — Fig. 267. *Peristernia nassatula*, Port Sudan, Red Sea; × 600. — Fig. 268. *Fusus rostratus*, Banyuls-sur-Mer, Mediterranean; × 500.

Engina turbinella has a cutting edge of the central tooth still attached to the central part of the basal platform. Apart from that the radula is quite similar to that of *Pisania tincta*, more so than indicated by Cernohorsky (1971: fig. 64). *Engina mendicaria* (Linné) (fig. 211) from the Red Sea has central teeth with the cusps attached to the posterior edge, as in *Pisania*, and quite similar, lateral teeth, with always only two cusps, however. Here again, within the genus *Engina*, the crenulations of the inner cusp of the lateral tooth can be present or absent.

The radula of *Engina mendicaria* (fig. 211) is very similar to that of *Melongena melongena* (fig. 271), in spite of all conchological difference between these members of obviously different families, Buccinidae and Melongenidae. While very juvenile individuals of *Busycon canaliculatum* (L.) (fig. 216) from Cape Cod have a radula similar to that of *Melongena melongena* (fig. 271), the usually considered more closely related *Volema pyrum* (fig. 272) from the Red Sea has quite different central teeth, with only two horn-like cusps, attached near the posterior corners. The evolution of such forms may be traced by studying intermediate forms, as constituted by *Pugilina morio* (L.). The radulae of the other *Melongena* species from the Western Atlantic are like that of *M. melongena* (Clench & Turner, 1956: pl. 96). *Volema paradisaica* (Röding) (Barnard, 1959: fig. 306) and *Melongena nodosa* (Lamarck) (Thiele, 1929: fig. 362) also have a central tooth with three cusps, but the central cusp is reduced in size here, as in *Pugilina morio*.

Colubraria swifti (fig. 215) and *Dolicholatirus cayohuesonicus* (fig. 213) have radulae which are quite similar to each other. Abbott (1958: text-fig. 4) described and figured the radula of *D. cayohuesonicus* and suggested that this radula might represent the most highly modified of the fasciolariid radulae, resembling that of the Vasidae. Since the Vasidae (figs. 273-276) have quite different teeth, whereas the Fasciolariidae are characterized by a different number of cusps on the lateral teeth and narrower central teeth, *Dolicholatirus* should be placed among the Buccinidae. Here we find similar radulae in *Engina bicolor* (fig. 212) and *Euthria cornea* (fig. 214).

Cernohorsky (1975: 196) shows that *Colubraria swifti* is closely related to species of the genus *Caducifer*, which itself is also closely related to *Pisania*.

Kosuge (1967) assigned *Phymorhynchus tenuis* Okutani to the Buccinidae; the species was originally considered to belong to the Turridae. The radula of this species is also similar to that of *Dolicholatirus cayohuesonicus*, which, on purely conchological terms, could also be classified with the Turridae. Here the radula proves to be of great value for the classification of conchologically confusing species.

The habitats of most of the species dealt with here is described by Bandel (1976b). The *Pisania* species live among rocks. *P. pusio* and *P. auritula* accept small living gastropods and fish as food when kept in the aquarium. The gastropods prey was held by the foot during feeding, while the proboscis was thrust into the aperture and all soft tissue was removed from the shell. Fish is eaten by extending the long proboscis into it; the radula then bites off pieces. *P. pusio* and *P. auritula* occur between the tidal zone and 2 m of depth, whereas *P.*

tincta lives at over 2 m depth. These species feed on small mollusks, barnacles and worms, found on and among the rocks.

Engina turbinella has an extremely variable shell. Forms with shells very close to that figured by Abbott (1974) as *Engina corinnae* Crovo are found in deeper water, while the more common forms of *E. turbinella* are found under stones in shallow water and most commonly among coral rubble and in crevices. The radulae of these varieties are identical in shape (pl. 15 figs. 9, 10). The food of these species mainly consists of worms.

Dolicholatirus cayohuesonicus and *Colubraria swifti* are often found together in shallow water among rocks. Both snails look for prey under rocks and among the algae on the upper surface of the rocks. In the aquarium, both species were not attracted by fish. Their faeces clearly indicate their food to consist of animal tissue, probably that of worms (Bandel, 1974b: 21).

When held in the aquarium *Melongena melongena* preferably consumes bivalves of the genera *Tellina* and *Tagelus*. Populations of *M. melongena* are mainly restricted to areas settled by these thin-shelled, gaping bivalves. The carnivorous gastropod reaches the bivalves, which live at about 30 cm depth in silty bottom, by digging into the substrate until the long, extended proboscis can reach the prey. In the aquarium species of the bivalve genera *Chione*, *Anomalocardia* and *Brachidontes* were also consumed, if no other food was available. *Crassostrea* was never eaten. Fish is preferred to any of the hard-shelled clams. Young individuals of *Melongena* did also feed on barnacles.

The proboscis of *Melongena corona* (Gmelin) is also very long, as shown by Clench & Turner (1956: pl. 97). Hathaway & Woodburn (1961) observed that this species can feed on oysters. These authors suggested that *M. corona* feeds on a wide variety of living and dead material and is to be regarded a scavenger. It was also observed that *M. melongena* consumed different types of animal remains, but in its natural environment it prefers deep burrowing, thin-shelled, gaping bivalves.

BUCCINACEA, NASSARIIDAE

Nassarius vibex (Say, 1822)
(figs. 227, 230; pl. 16 figs. 9, 10)

The radula has about 70 rows of teeth. The central tooth is about three times as wide as long. The anterior front is deeply concave and the acute, anterior corners extend anteriorly. The front and the straight margins are attached to the membrane. There are 13 to 17 cusps attached to the free posterior edge; 7 to 11 central cusps are equal in size, whereas the marginal ones become increasingly smaller. All cusps are acute and narrow. The number of cusps on the evenly convex cutting edge of the central tooth is not related to sex. In rare cases the shape of the central tooth is more angular, with an even more deeply concave front and a straight posterior edge.

The lateral tooth has two cusps; the outer one is almost as long as the posterior edge, and the inner one is about half its length. The hook-like cusps may have smooth margins and the internal cutting edge is evenly curving. In many specimens the outer flank of the inner cusp is serrated by one to five acute denticles. In one radula the inner cusp was irregularly denticulate, with a high, narrow, thumb-like, innermost denticle on its apex.

Nassarius albus (Say, 1826)
(figs. 221, 224; pl. 16 figs. 7, 8)

The radula has about 60 rows of teeth. The dimensions and shape of the central tooth vary in relation to sex. The central tooth of the female is 2.5 times wider than long. It has a widely curving anterior front, ending in anteriorly elongated corners. The margins are straight and attached to the membrane, as is the front. The posterior edge is also the cutting edge; it is less strongly curved than the front and has 10-15 acute cusps, seven of which are more or less equal in size, whereas the marginal ones become increasingly smaller.

The central tooth of the male is about 1.5 times wider than long. It has a deeply concave anterior front, angular (but not acute), anterior corners and straight to convex margins. The cutting edge is strongly curved and has 13-18 cusps; the central cusp is the longest and widest one, whereas the cusps become increasingly smaller towards the margins.

The lateral teeth show no differences between male and female radulae. Each tooth has two cusps; the outer one is about twice as long as the inner one. The tooth is longer than wide (4:3) and its posterior edge is straight. The outer flank of the inner cusp may be smooth or serrated by one to four minute to large, acute denticles. Kaicher (1972: fig. 3) has described only radulae of females of this species.

Engoniophos unicinctus (Say, 1825)
(fig. 235; pl. 16 fig. 6)

The radula has about 70 rows of teeth. The central tooth is about 2.5 times wider than long. The evenly concave front and the straight margins are attached to the membrane. The anterior corners are acute. The regularly, convexly curved posterior edge has 9-12 acute cusps, of which the central eight are almost equal in size. There are no characters of the radula correlated to the sex of the animal in question.

The lateral tooth looks like that of *Nassarius albus* and *N. vibex*, it is slightly longer than wide and has one larger outer and one smaller inner, hook-like cusp. The inner cusp always has smooth flanks. The inner posterior corner is extended into a short swelling.

DISCUSSION

The shape of the radula clearly indicates that *Engoniophos unicinctus* belongs into the family Nassariidae and not to the Buccinidae, as was suggested by Abbott (1974). The habits of this species and the structure of the egg capsules also show the close relationship between *E. unicinctus* and *Nassarius vibex* (Bandel, 1976b). Animals of all three species described here, spend much time hidden in the soft bottom substrate, with only the siphon extending over the surface, testing the water currents for the flavour of potential food. A dead fish, crab or bivalve will trigger the resting snail into action. A source of food may attract snails from a few meters distance. The extensible proboscis can be stretched to nearly twice the length of the snail itself. It is inserted into the tissue and sawing movements of the radula inside the proboscis rasp and hook pieces of meat and transport it into the mouth. Gore (1969) has found that *Nassarius vibex* may attack injured animals. Most Nassariidae are omnivores and facultative scavengers. Brown (1969), in an extensive study on *Ilyanassa obsoleta* (Say), was able to show that this snail is primarily a deposit feeder, feeding activity on large algae and grazing on algal scum. *I. obsoleta* posesses a crystalline style, a structure considered to be typical for purely herbivorous molluscs. Brown noted that even though *I. obsoleta* consumes mainly plant material, it has an obvious preference for the flesh of dead animals.

The radula of *I. obsoleta* is figured and described by Troschel & Thiele (1865-1893: 97, pl. 8 fig. 22); it looks similar to that of *Nassarius vibex*. Troschel & Thiele (1865-1893: 88) noted that some *Nassarius* species display sexual dimorphism in their radula, as described before in *N. albus* (figs. 221, 224). *N. incrassatus* (Ström) from the Mediterranean (figs. 229, 232), also clearly has this kind of dimorphism (Bandel, 1977: 211, pl. 5 figs. 5, 6). Less pronounced, but still obvious, is the sexual dimorphism in the radula of *N. livescens* (Philippi) from the Red Sea (figs. 222, 225). In the radulae of this species there is a small intermediate tooth above the inside of the posterior edge of the lateral tooth. *N. corniculus* (Olivi) (fig. 226) and *N. granus* (Lamarck) (fig. 219), both from the Mediterranean, clearly also have this additional tooth (Bandel, 1977: 208, 209; pl. 4 figs. 5, 6). Many species of *Nassarius* have such an additional tooth, as may be concluded from the figures given by Troschel & Thiele (1865-1893: pl. 8 figs. 7-22) and Barnard (1959: fig. 22), as well as in the present paper (figs. 219, 220, 222, 223, 225, 226, 231, 234). It probably represents the relict of a true lateral tooth. In Neogastropoda such relict teeth are also found in *Olivella* (figs. 283-285, 287, 289), but here there is a reduced marginal tooth, functioning as an outer plate-like tooth.

The denticles between the two cusps of the lateral tooth, which may be developed in *Nassarius vibex* (fig. 227) and *N. albus* (figs. 221, 224), are a constant feature of the *N. corniculus* radula (fig. 226; Bandel, 1977: pl. 4 fig. 6); in *N. neriteus* they have developed into two or three stout central cusps between the inner and the outer cusp (fig. 223; Bandel, 1977: pl. 5 fig. 1). With respect to the morphology of the lateral teeth the Nassariidae are similar to most Buccinidae. Only the characteristic central tooth of the nassariids differentiates their radula from that of other buccinids.

BUCCINACEA, FASCIOLARIIDAE

Leucozonia nassa Gmelin, 1791
(fig. 263; pl. 17 fig. 5)

The radula has about 250 rows of teeth. The rectangular central tooth is longer than wide (4:3). The straight anterior front and margins are attached to the membrane. Three cusps, of which the central one is the largest, are attached to the convex posterior edge. The cusps continue as swellings on the posterior part of the basal platform.

The lateral teeth are almost five times wider than long. Their posterior edge is straight; the cutting edge has eight cusps, the outermost of which is the smallest, the innermost the largest. All intermediate cusps are about equal in size and are hook-like curved.

Leucozonia ocellata (Gmelin, 1791)
(fig. 261; pl. 17 fig. 6)

The radula has about 180 rows of teeth. It resembles very much that of *Leucozonia nassa*. The central cusp has the same dimensions, but the anterior front and the margins are concave, not straight. The three cusps of the cutting edge are equal in size and continuous as swellings on the posterior basal platform. They do not all point in the same direction, as in *L. nassa*; the two marginal ones are slightly inclined to the sides with their apex. The lateral teeth are almost six times wider than long and have the same arrangement of cusps as in *L. nassa*; there are six or seven hook-like cusps. In contrast to *L. nassa*, the inner margin of the lateral tooth has a long extension, which points backward and is connected with the posterior edge by a lamella. A denticle on the centre of the inner margin projects inward; in *L. nassa* this denticle is hardly noticeable.

Latirus infundibulum (Gmelin, 1791)
(fig. 257; pl. 17 fig. 7)

The radula has about 90 rows of teeth. The central tooth is twice as long as wide. Its anterior front is deeply concave in its centre and forms rounded corners with the straight margins. Margins and front are attached to the membrane of the radula. The posterior edge has three large, claw-like cusps, the central of which is slightly larger than the other two.

The lateral tooth is more than two times wider than long (9:4), it has an evenly curved, weakly concave posterior edge and seven or eight hook-like cusps. From the outer margin onward the cusp size increases, up to the sixth cusp, which is the largest. There is always a smaller inner cusp, and sometimes an even smaller cusp below it. This innermost cusp may be reduced to a denticle on the inner margin, just above the angular inner corner.

Latirus angulatus (Röding, 1798)
(fig. 265; pl. 17 fig. 8)

The radula has about 180 rows of teeth. Their shape very much resembles that of *L. infundibulum*. The central tooth is also twice as long as wide, but it is narrower at the anterior front than at the cutting edge. The narrow front is almost straight, with a small indentation at its centre. The three cusps of the cutting edge are not as claw-like as in *L. infundibulum*, but more triangular in shape.

The lateral tooth is about three times as wide as high and has the arrangement of cusps as in *L. infundibulum*, and also an evenly curved posterior edge. There are eight or nine cusps; the innermost is the smallest, sometimes being only a denticle on the inner margin.

Fasciolaria tulipa (Linné, 1758)
(fig. 260; pl. 17 figs. 9, 10)

The radula has about 90 rows of teeth. The rectangular central tooth is attached to the radula membrane by its straight to slightly concave anterior edge and the slightly concave margins. The posterior edge runs from the angular posterior corners to the margin of the outer flank of two slightly smaller marginal cusps, accompanying a symmetrical central cusp.

The lateral teeth are almost six times as wide as long and have 17-25 acute cusps. Apart from the outermost two, which are smaller, and the innermost one, which is larger, all cusps are equal in size. The inside of the posterior edge is straight to slightly concave, whereas the outside is more strongly curved. The innermost cusp ends of in angular shoulder, extending as inner margin to the angular posterior corner.

DISCUSSION

Troschel & Thiele (1865-1893: 61) characterized the radula of the Fasciolariidae. The lateral teeth are said to be very wide, with many cusps; the central teeth are quadrangular and less wide than the lateral teeth. The central teeth are called narrow, which applies to the Caribbean species here described. *Latirus polygonus* (Gmelin) (fig. 266), *Fasciolaria trapezium* (Linné) (fig. 258) and *F. filamentosa* Lamarck (fig. 264), however, have central teeth which are wider than long and, therefore, cannot be called narrow.

The lateral tooth of the Fasciolariidae is not unlike that in some Buccinidae, but wider, as can be concluded while comparing *Pisania striata* (fig. 209) and *Buccinum undatum* (fig. 270). A consistent difference, besides the number of cusps, between the lateral teeth of Caribbean Fasciolariidae and those of the Buccinidae, is the orientation of the cusps with regard to their size. While in the buccinid radulae the outermost cusp is the largest, the innermost or at least an inner cusp is the largest in the Fasciolariidae. This can also be noticed by comparing Troschel & Thiele's figures (1865-1893: pl. 5 figs. 12-19, pl. 6 figs. 1-3) and Barnard's illustrations (1959: figs. 12, 19, pl. 6 figs. 1-3). The lateral teeth of *Fusus rostratus* (Olivi) (fig. 268) from the Mediterranean have outer cusps reaching the same size as the inner cusps, resembling what is seen in the buccinid radula.

Transitional forms between the radulae of *Latirus* and *Leucozonia* species from the Caribbean and those of *Fasciolaria* species, with the many narrow cusps, can be observed in *Latirus smaragdulus* (L.) (fig. 262) from the Seychelles. The radulae mentioned so far have a quite even and regular arrangement of the cusps on the lateral teeth. *Latirus turrites* (Gmelin) (fig. 259) from the Red Sea has a modified outer part of the cutting edge. The lateral teeth of *Peristernia nassatula* (Lamarck) (fig. 267) from the Red Sea have a very variable dentition on the lateral teeth, with alternating smaller and larger cusps. This dentition is variable to such a degree, that within one radula almost no lateral tooth is exactly like the other.

Along with the variation of cusp size and cusp number in individual radulae and in radulae of different individuals of the same species, seen in various Fasciolariidae, there may also be an increase in cusp number when the snail matures. Wells (1970) noted an increase from 8 to 17 cusps of the lateral teeth in *Fasciolaria hunteria* (Perry), and from 15 to 35 cusps in *F. tulipa*, parallel to an increase in shell size. Abbott (1958: text-fig. 4) observed the same phenomenon in *Leucozonia nassa*.

Marcus & Marcus (1962) found setae and teeth of polychaetes in the intestines of *Leucozonia nassa* from Brazil. In Santa Marta *L. nassa* and *L. ocellata* were seen to feed on small molluscs and on barnacles on rocky cliffs. *Latirus infundibulum* and *L. angulatus* prey on worms and bivalves, less commonly on carrion. In the aquarium *Latirus* and *Leucozonia* were fed with fish, opened clams and barnacles. Bivalves with thin shells (*Brachidontes* spec.) can be opened by all four species studied, by chipping the margins of the valves with the snail's foot. Moderately sized, thick-shelled bivalves were opened without any visible trace of mechanical damage to the valves after they had been held by the foot of the gastropod for some time.

Fasciolaria tulipa is a voracious hunter of gastropods of all kinds, with the obvious exception of Toxoglossa. *Conus* and *Terebra* species were never attacked and did not show any escape reactions on contact with *F. tulipa* (Bandel, 1976b). The prey is held by the foot, closing the aperture of its shell. The long proboscis is then thrust into the aperture through a fold in the anterior part of the foot. All soft tissue of the prey is removed from its shell. A prey with about half the body weight of that of *F. tulipa* was totally consumed within 12 hours. *Fasciolaria trapezium* from the Red Sea was commonly found feeding on various species of Strombidae in the same way as *F. tulipa* does.

Wells (1963) observed that *Pleuroploca gigantea* (Kiener) from Florida daily consumes 3% of its own volume. Paine (1963) reported as food of *Fasciolaria tulipa* and *F. hunteria* (Perry) mainly gastropods, but also bivalves, tube dwelling worms and carrion. Wells (1958) observed *F. hunteria* scraping encrusting organisms and scales from a small area of the upper valve of an oystershell by a combined action of the radula and the outer lip of its shell. The cleaned margin is then chipped, until the proboscis can enter. This behaviour resembles that of *Thais haemastoma* or *Murex pomum* from Santa Marta.

VOLUTACEA, OLIVIDAE

Oliva reticularis Lamarck, 1810
(fig. 278; pl. 18 fig. 1)

The radula has about 100 rows of teeth. The central tooth is roughly triangular and about three times wider than long. the tricuspid cutting edge occupies about half the width of the tooth and extends to the posterior corners with sharp edges. The ridge of the cutting edge is attached to the central part of the basal platform; it is strongly inclined backward and thus extends over the base. The three cusps are acute and curved down fang-like. The outer ones are more stout than the central cusp. The anterior is concave, the margins and the posterior base are straight and hidden below the cusps in its central part.

The lateral tooth is sickle-shaped, with a flattened base and a hook-like apex. It is two times as long as wide at its base. While its upper surface is evenly rounded, the lower surface, near the base, is gutter-like and shallowly concave.

Central and lateral teeth overlap considerably in the relaxed radula. There is ample space between the attached part of the central tooth and its neighbouring lateral teeth in each row. No wear was noted.

Jaspidella jaspidea (Gmelin, 1791)
(fig. 279; pl. 18 fig. 2)

The radula is very similar to that of *Oliva reticularis*, regarding the shape of the individual teeth as well as the arrangement of the teeth. The central tooth is only about two times as wide as long and the three cusps of the cutting edge are somewhat more sturdy and oriented more upward than in *Oliva reticularis*. Thus the posterior base is better visible. The margins are inclined somewhat anteriorly and the front is less concave.

The lateral teeth have a very wide, flattened base that forms an almost lamellar extension. They are even more spatulate in their lower part than those of *Oliva reticularis*. Only very little wear could be noted on the functional parts of the radula.

Olivella adelae Olsson, 1956
(fig. 287; pl. 18 fig. 4)

The radula has about 35 rows of teeth. The central tooth is very broadly triangular to crescentic. Its cutting edge on the straight to slightly concave base, is not attached to the radula membrane, so that it can be erected when the radula is drawn over the edge of the odontophore. The tooth is almost three times wider than long and longest in its centre; the margin is formed by an extended area where front and cutting edge meet. The basal platform is smooth, near the cutting edge it becomes raised somewhat. The cusps of the cutting edge are very variable, in arrangement as well as in number. There may be two larger ones in the centre, or only one in (nearly) central position. If there are two such cusps, they may have one to four smaller intermediate cusps. On the cutting edge there may be 20 to 40 cusps, usually decreasing in size towards the margins. The arrangement and the number of cusps vary among the various rows of teeth in a single radula.

The lateral teeth are attached to the radula membrane, well apart from the central tooth, but are linked to the marginal teeth. The sickle-shaped lateral tooth is about four times longer than wide at its base. Its upper surface is rounded, its lower surface flattened to shallowly concave. The base has an indentation that fits onto the basal edge of the marginal tooth.

The marginal tooth is sturdy. It is attached to the radula membrane with its whole basal platform; there is no cutting edge, but a smooth surface only. Neighbouring marginal teeth are set very close to each other. When the chain of teeth is bent over the odontophore, the sharp edges will be pushed up and will press against the outer part of the base of the lateral teeth, erecting it.

Wear, i.e. broken-off cusps of the cutting edge, was observed on the central teeth only.

Olivella nivea (Gmelin, 1791)
(fig. 289; pl. 18 figs. 6, 7)

The radula has about 35 rows of teeth. It is like that of *Olivella adelae* in shape and arrangement of the teeth. The front of the central tooth is evenly curved and the tooth is about five times as wide as long. The cusps on the cutting edge are not quite as variable in arrangement as in *O. adelae*. A pair of main cusps is separated from each other by one or two narrow, small, intermediate cusps. On each side of the central pair there are 8 to 16 smaller cusps, generally decreasing in size towards the margins.

The lateral tooth is about three times longer than wide at its base and sickle-like in shape, with a gutter-like lower side and a rounded upper surface. The rectangular marginal tooth is solid and sturdy, and about twice as wide as long. The outer base of the lateral tooth can fit into a groove in the inner margin of the marginal tooth. Thus there is a close connection between lateral and marginal teeth.

Olivella dealbata (Reeve, 1850)
(fig. 284; pl. 18 fig. 3)

The radula has about 40 rows of teeth. In general shape and arrangement the teeth are similar to those of *Olivella adelae*. The central tooth is about three times wider than high. Its front is strongly convex and merges in its central part with the radula membrane. The cutting edge is weakly concave and the claw-like teeth are curved upward more than in the other discussed *Olivella* species. The about 13 main cusps on the cutting edge become somewhat smaller towards the margins; they are separated from each other by one to three denticles. The margins are drawn out into long tips.

The sickle-shaped lateral teeth are somewhat wider and more gutter-like than in the other *Olivella* species. They are three times longer than wide at their base. The convex base fits with its outside into a groove on the inside of the inner margin of the marginal tooth. This groove is bordered by a short marginal ridge that continues into a sharp ridge along the posterior base of the rectangular marginal teeth. These are almost as long as wide and are attached very close to each other. The movement of the fully attached marginal teeth across the edge of the odontophore should be understood in relation with the hooking of the lateral tooth while biting. The movement of the central tooth is independent of these two outer teeth.

Olivella petiolita (Duclos, 1835)
(fig. 285; pl. 18 fig. 5)

The radula has about 35 rows of teeth. It is similar to that of *Olivellae adelae*. The central tooth is somewhat more than twice as wide as long and has a straight cutting edge with two or three main cusps, separated from each other by two or three smaller, intermediate cusps. On each side of the central cusps there are about 15 increasingly smaller cusps. The basal platform is triangular, but the front is evenly convex. Thus there is a step-like edge between both, following the sides of the front.

The sickle-shaped lateral teeth are gutter-like and have a denticulate, frontal blade from base to top. The inner corner of the base is extended and thickened; each lateral tooth is in contact with two marginal teeth at its base. The marginal teeth are rectangular and slightly overlap with their respective bases and fronts.

Olivella perplexa Olsson, 1956
(fig. 283)

The radula is intermediate between that of *Olivella petiolita* and *O. adelae*.

Olivella acteocina Olsson, 1956

No radula was found.

DISCUSSION

Regarding the morphology of their radulae, it is quite evident that *Oliva* and *Jaspidella* on the one hand and *Olivella* on the other, belong to groups that cannot be considered closely related, in spite of the fact that their shells are often extremely similar. The differences in radula morphology were noted already by Troschel & Thiele (1865-1893: 107), who did not draw the necessary taxonomical conclusions, however. Troschel & Thiele (1865-1893: pl. 10 figs. 13, 14) had seen that the marginal teeth of *Olivella* are independent from the lateral teeth, and not connected to them as was assumed by Thiele (1929: fig. 391). Marcus & Marcus (1959) have shown that *Oliva* and *Olivella* not only differ regarding their radula characters, but also in the organisation of their soft parts. These authors had noted a number of muricacean features in *Oliva* and the related *Lintricula*, while *Olivella* shows more volutacean affinities. They suggested an origin of the Olividae neither directly from the Muricacea nor from the Buccinacea, but from the common root of both, followed by a development of *Oliva* and *Olivella* parallel to each other. This view is accepted here. It seems quite unlikely that *Olivella* has developed from certain small species of *Oliva* or allied forms, as suggested by Olsson (1956), because there are no transitional forms known between the radula types of: (1) *Oliva*, *Ancilla* (Troschel & Thiele, 1865-1893: pl. 10 figs. 15-17; Thiele, 1929: fig. 385), *Amalda* (Ponder, 1968: figs. 20-27), *Lintricula* & *Olivancillaria* (Marcus & Marcus, 1959: figs. 28, 29), and (2) *Olivella*.

The mode of feeding of *Olivella* differs from that of *Oliva*. *Olivella* swallows entire prey, consisting of small bivalves, foraminifera, small crustaceans and other animals living in soft sediment or between algae (Marcus & Marcus, 1959). *Oliva*, in contrast, feeds on pieces of soft tissue and does not devour its prey entirely. Its prey consists of carrion, molluscs, etc. *Oliva* takes hold of its prey with its foot and totally enwraps it. The prey is then paralysed and its tissue is dissolved by salivary secretions. Soft tissue is eaten with the help of bites by the radula, located on the tip of the proboscis. This mode of feeding was also observed in *Lintricula* by Marcus & Marcus (1959). The way of feeding is reflected in the shape of the radula. While *Oliva* uses its radula to bite off pieces of soft tissue and to transport small soft material into the mouth, quite similar to e.g. *Murex*, the radula of *Olivella* is used to get hold of a prey and to pull it into the mouth in one piece.

The different *Olivella* species have very similar radulae, as has been reported by Olsson (1956: figs. 13-19, 21-13, pl. 16 figs. 1-4). The separation of *Olivella* and *Oliva*, suggested by the present author mainly because of radula morphology, and by Marcus & Marcus (1959), mainly based on anatomical differences, has not yet been generally accepted. Abbott (1974: 233), for example, assigned *Jaspidella* with its *Oliva*-like radula to the subfamily Olivellinae, rather than to the Olivinae, as was suggested by Olsson (1956).

VOLUTACEA, MITRIDAE

Mitra nodulosa (Gmelin, 1791)
(fig. 291; pl. 19 fig. 7)

The radula has about 80 rows of teeth. The rectangular central tooth is about twice as wide as long and very sturdy. Its front is straight and slightly shorter than the weakly convex base. The margins are inclined somewhat and raised at their posterior edge into the lowermost pair of denticles. In addition there are five stout cusps, attached to the central part of the basal platform; the central one is somewhat larger than the others. The cusps are curved backward somewhat with their apices, giving a claw-like appearance to the cutting edge. The central teeth of different rows are situated close to each other but do not partially overlap.

The lateral teeth are situated well apart from the central tooth. They are almost eight times wider than long and their basal platform becomes thinner towards the sides. At its inner margin the posterior corner is formed by a stout cusp. The first cusp of the cutting edge is broadly attached to the basal platform. There are nine or ten increasingly smaller cusps on the cutting edge, which is shifted to the posterior edge; in its outermost third it is constituted by an indistinct ridge on this edge only. The sturdy teeth are shallow S-like in shape; they overlap only with the inner three larger cusps of the cutting edge. When pulled over the edge of the odontophore, the teeth point upward with their cusps, but cannot be erected, since they are attached with their whole basal platform.

Mitra cf. **nodulosa** (Gmelin, 1791) (small form)
(fig. 288; pl. 19 fig. 8)

The radula is like that of *Mitra nodulosa* s. str. Only the width-length relation and the cusp number of the teeth differ. There are five cusps on the central tooth instead of seven. The lateral tooth is only two times as wide as long; its cutting edge is denticulate up to almost the outer margin.

Vexillum puella (Reeve, 1845)
(fig. 282; pl. 19 fig. 10)

The radula has about 40 rows of teeth. The arched central tooth is narrow and about four times as wide as high. The cutting edge is situated on the posterior base. Its cusps are long and acute, with the central one slightly smaller than the adjoining cusps. Only the most marginal cusps become increasingly smaller. There are seven cusps on each side of the central cusp. The cutting edge is mainly curved convexly, only near the margins it is turned backward to form acute corners. Here also the front ends, which has a deeply concave centre.

The sickle-like lateral tooth is about three times as long as wide at its base. It is attached to the radula membrane well apart from the margins of the central tooth. Its base is wide and fully attached by a straight to convex edge. The tooth is flattened below, becoming narrower up to the hook-like cusps.

Vexillum dermestinum (Lamarck, 1811)
(fig. 281; pl. 19 fig. 9)

The radula has about 40 rows of teeth which are similar to those of *V. puella*. Only the number of cusps on the cutting edge of the central tooth differs. There are five cusps on each side of the central cusp; all cusps are about equal in size.

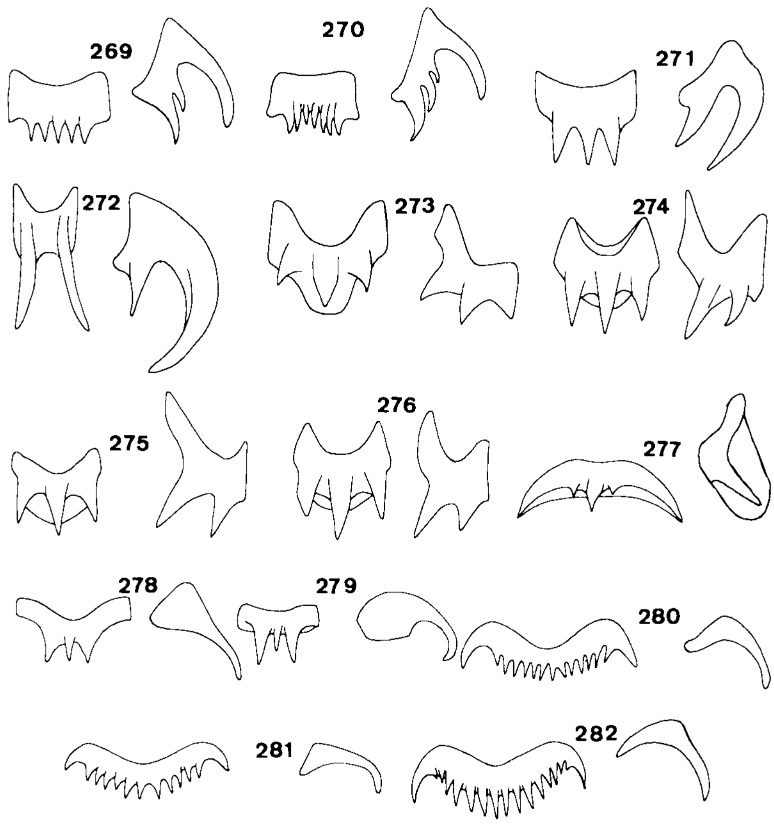

Fig. 269. *Buccinum humphreysianum*, Banyuls-sur-Mer, Mediterranean; x 50. — Fig. 270. *Buccinum undatum*, Oosterschelde, North Sea; x 40. — Fig. 271. *Melongena melongena*, Santa Marta, Caribbean; x 90. — Fig. 272. *Volema pyrum*, Port Sudan, Red Sea; x 45. — Fig. 273. *Vasum capitellum*, Curaçao, Caribbean; x 120. — Fig. 274. *Vasum turbinellum*, Port Sudan, Red Sea; x 90. — Fig. 275. *Vasum muricatum*, Santa Marta, Caribbean; x 60. — Fig. 276. *Vasum ceramicum*, Port Sudan, Red Sea; x 50. — Fig. 277. *Turbinella angulata*, Santa Marta, Caribbean; radula of just hatched individual, x 300. — Fig. 278. *Oliva reticularis*, Santa Marta, Caribbean; x 150. — Fig. 279. *Jaspidella jaspidea*, Santa Marta, Caribbean; x 180. — Fig. 280. *Vexillum hendersoni*, Santa Marta, Caribbean; x 160. - Fig. 281. *Vexillum dermestinum*, Santa Marta, Caribbean; x 210. — Fig. 282. *Vexillum puella*, Santa Marta, Caribbean; x 260.

Vexillum hendersoni (Dall, 1927)
(fig. 280; pl. 20 fig. 1)

The radula is quite similar to that of *V. puella* and *V. dermestinum*, apart from the number of cusps on the cutting edge of the central tooth. Each central cusp is accompanied by six cusps on both sides. No wear was noted on teeth of the functional part of the radula.

DISCUSSION

The Mitridae were subdivided into two subfamilies, viz. Mitrinae and Vexillinae, by Thiele (1929: 337). According to Troschel & Thiele (1865-1893: 67-68) the Mitrinae might be more closely related to the Fasciolariidae than to the Vexillinae (Strigatellacea); it was also noted, however, that there are constant differences between mitrid and fasciolariid radulae with regard to the position of the cusps on the cutting edges, and the general morphology of the central tooth. Troschel & Thiele (1865-1893: 102, pl. 9 figs. 11-16) placed *Vexillum* and *Thala* in a separate family, close to harpids, olivids, muricids and thaidids in radula structure, stating that there is a great difference between Mitridae and Vexillidae regarding both lateral and central teeth. The comb-like central tooth of the Vexillidae is narrow and arched, in contrast to the square and angular sturdy one of the Mitridae; the lateral tooth of the Vexillidae is always simple and sickle-like, while that of the Mitridae is bigger than the central tooth and usually has many cusps.

Cernohorsky (1970) has studied a large number of mitrids and found that the radula pattern of *Mitra* and *Vexillum* is so dissimilar, that both genera should be classified with different subfamilies. This author expressed the opinion that the radula of *Cancilla* is intermediate between the radulae of *Vexillum* and *Mitra*; it is supposed to have a central tooth similar to that of *Vexillum* and a lateral tooth similar to that of *Mitra*, Thus the genus *Cancilla* would fill the broad gap separating *Mitra* from *Vexillum*. The radulae of three species of *Cancilla* figured by Cernohorsky (1966: figs. 31, 32; 1971: fig. 7), however, are well within the range of variation of typical mitrid radulae. Many mitrid radulae are already known, see Barnard (1959), Cernohorsky (1965, 1966, 1970, 1971, 1972), Cate (1967) and Ponder (1968, 1971, 1972). The variation in lateral teeth is documented here by the radulae of: (1) *Mitra cornicula* (L.) from the Mediterranean (fig. 286), with the lateral teeth denticulate along their whole width, (2) *Mitra* cf. *fissurata* (Lamarck) from the Red Sea (fig. 292), with one cusp strongly enlarged and the others missing or reduced in number, (3) *Mitra* spec. from the Red Sea (fig. 290) with an extended front. The radulae figured in the literature reveal that the shape of the central tooth varies from one-cusped in *Scabricola* (Cernohorsky, 1966: fig. 33), to eleven-cusped in *Mitra* (Cernohorsky, 1966: fig. 14).

Ponder (1972) concluded that, because of their anatomy, the Vexillidae should be considered a separate family, different from the Mitridae. This view is supported by Maes & Raeihle (1975), who found that the Vexillidae, on the basis of their anatomy, reproductive biology, and radula morphology, should not be considered closely related to the Mitridae, this in contrast to Troschel & Thiele (1865-1893). Barnard (1959), Cate (1967), Cernohorsky (1966), Maes & Raeihle (1975), McLean (1967) and Thiele (1929) have illustrated radulae of numerous Vexillidae, all with the characters that have been found in the here described species. Obviously Mitridae and Vexillidae are quite unrelated families.

VOLUTACEA, TURBINELLIDAE

Turbinella angulata (Lightfoot, 1786)
(fig. 277; pl. 17 fig. 4)

Only radulae of recently hatched specimens could be studied. These have about 70 rows of teeth. The arched central tooth is almost three times as wide as long. The front is evenly convex and somewhat overlaps onto the straight or slightly concave central part of the base of the following tooth. Near its margins the base is concave; front and base meet in one rounded corner, where also a ridge arises, which follows the front. On the central part of this ridge there are three cusps of the cutting edge, occupying only the central third of the width of the tooth. The central cusp is the largest one; all three cusps are erect, with a claw-like twist backward.

The lateral tooth is attached to the radula membrane distant from the central tooth. It is of a simple shape, with a flat basal part and a hook-like, acute upper part. The tooth is broadly attached with its base and only slightly longer than wide. The inner margin is evenly convex, while the outer margin extends outward in a central shoulder. The tooth is shovel-like in shape and has a solid cusp.

Vasum muricatum (Born, 1778)
(fig. 275; pl. 17 fig. 3)

The radula has about 100 rows of teeth. The angular central tooth has a concave front, a convex base and straight margins. It is somewhat wider than long. The cutting edge is situated in the centre of the basal platform, with three hook-like, stout, erect cusps, which are slightly inclined posteriorly. The outer cusps are attached close to the margins of the basal platform. The central teeth in a row overlap somewhat and there is a small pit on the upper surface of the central cusp, where the following tooth rests with the tip of its central cusp in the folded radula.

The lateral tooth has two cusps and is about as large and sturdy as the central tooth; it is as wide as long and the two cusps are centrally attached. The front is concave and the base convex; the margins are straight with angular corners. The teeth are situated close to each other on the radula membrane.

Vasum capitellum (Linné, 1758)
(fig. 273; pl. 17 fig. 2)

The radula has about 130 rows of teeth. It is similar to that of *Vasum muricatum*. The cusps are a little stouter and the teeth slightly wider.

DISCUSSION

Both *Vasum muricatum* and *Turbinella angulata* feed on worms, hidden in the sediment or among rocks. The snails reach their prey with an extremely extensible proboscis (Bandel, 1975b, 1976b), that follows the worms into their tubes. Even though both species are quite similar to each other in their mode of feeding, they have quite different radulae. In spite of this difference and in spite of Troschel & Thiele's (1865-1893: 85) suggestion to create a separate family for *Vasum* and allied species, *Vasum* and *Turbinella* are usually placed together in the family Turbinellidae (= Vasidae, = Xancidae) (Thiele, 1929; Abbott, 1950, 1959, 1974). There is very little variation in the morphology of the teeth, both in *Vasum* and allied species (Troschel & Thiele, 1865-1893: pl. 8 fig. 6; Thiele, 1929: fig. 405; Abbott, 1959: pl. 2), and in *Turbinella* (Thiele, 1929: fig. 407; Abbott, 1950: pl. 89 figs. 2, 3). *Vasum turbinellum* (L.) and *Vasum ceramicum* (L.) (figs. 274, 276) from the Red Sea are similar to *Vasum* species from the Caribbean.

The radula of *Turbinella* (fig. 277) is very similar to that of olivids, like *Jaspidella jaspidea* (fig. 279), especially with regard to the lateral tooth with its broad flattened base. Other turbinellid genera as *Benthovoluta*, *Ptychatractus*, *Surculina* and *Metzgeria*, have radulae that are similar to that of *Turbinella* (Cernohorsky, 1973: figs. 1-6; Thiele, 1929: fig. 409). Most of these have central teeth which are less wide than in *Turbinella* and, therefore, closely approach *Oliva* and *Jaspidella*.

The radula of *Vasum* more resembles those of the Melongenidae (figs. 271, 272), generally considered a family close to the Buccinidae. Clench & Turner (1970: pl. 173 figs. 1, 2) illustrate the radula of *Odontocymbiola*, a genus of the Volutidae, which has characters of both a *Vasum* and a *Melongena* radula. Here a central tooth with three cusps, which is about as long as wide, is accompanied by lateral teeth with two cusps and broad bases. In *Odontocymbiola* the cusps are turned backward, but attached centrally; this combination of characters is transitional between what is known from *Melongena* and *Vasum*.

A close relationship of *Melongena* and *Volema* on the one hand and *Vasum* on the other, is also suggested by the mode of development of the young in the egg capsules (Bandel, 1975a) and the morphology of the egg capsules themselves, which is similar in representatives of all three genera (personel observations on *Melongena melongena* and *Vasum muricatum* from the Caribbean and *Volema pyrum* from the Red Sea). The embryonic development and the structure of the egg capsules are quite different in *Turbinella* (Bandel, 1975b).

VOLUTACEA, VOLUTIDAE AND MARGINELLIDAE

Voluta virescens Lightfoot, 1786
(fig. 299; pl. 19 fig. 1)

The radula has about 45 teeth, arranged in a narrow series of central teeth only. Each tooth is about twice as wide as long and the cutting edge is situated along the base. Each tooth is attached to the radula ribbon with only the anterior part of the basal platform, up to the slightly concave front; the denticulate base is free and can be erected when the radula is pulled over the edge of the odontophore. In the folded radula the cutting edge considerably overlaps the preceding tooth; the tips of the cusps of the cutting edge correspond with grooves on the upper surface of the tooth. The stoutest cusps are the two blunt marginal ones, which are continuous with their outside into the straight margins. Between these and the acute central cusps there are 7-12 narrow and acute cusps, very variably arranged along both sides of the cutting edge. The basal platform is strengthened by swellings on both margins.

Voluta musica Linné, 1758
(fig. 298; pl. 19 fig. 2)

The radula has about 45 rows of single teeth and is similar to that of *Voluta virescens*. The cusps on the cutting edge are arranged more regularly. There are eight or nine, acute, equally sized cusps, at about equal distances from each other between the sturdy, acute, marginal cusps. The tips of the cusps of neighbouring teeth do not correspond with pits on these teeth.

Marginella lavalleana d'Orbigny, 1842
(fig. 296; pl. 19 fig. 6)

The minute radula has a series of over 100 strongly overlapping teeth. The triangular central tooth is about as wide as long. The front is arched concavely; the cutting edge is situated at the base. The teeth are attached to the radula membrane along a narrow zone following the front; when pulled over the edge of the odontophore they are erected with vertical cutting edges. The cutting edge has one large, triangular, acute, central cusp and four slightly smaller cusps on each side, with the lowest near the posterior corner.

Persicula interruptolineata (Mühlfeld, 1816)
(fig. 295; pl. 19 fig. 4)

The minute radula has a series of about 70 central teeth, which are overlapping strongly in the folded radula. The broadly crescentic teeth are about twice as wide as long. The cusps on the cutting edge are situated at the front and the erected tooth is claw-like in shape, with a concave lower side. One or two of the central cusps are larger than the others; on each side of the cutting edge there are three to seven cusps, which are variably arranged on different teeth of the same radula. The teeth are attached to the radula membrane by a narrow zone at the frontal basal platform only; when erected they are still in touch with each other.

Persicula pulcherrima (Gaskoin, 1849)
(fig. 294; pl. 19 fig. 5)

The radula is a minute, narrow ribbon with a series of over 100 central teeth. The single teeth are similar to those of *P. interruptolineata*, but more narrowly crescentic in shape, and slightly more than half as long as wide. The teeth are attached close to each other. There is no largest central cusp; the 7-14 cusps of very uneven size are very variable, even in a single radula.

Prunum prunum (Gmelin, 1791)
(fig. 304; pl. 18 fig. 9)

The radula has only a series of 30 to 50 central teeth, which strongly overlap. Each ribbon-like tooth is ten times as wide as long and has an almost straight front and base. The cutting edge is situated at the base and consists of about 30 cusps, which are arranged in such a way that one or two smaller cusps follow after each larger one. The cusps have pits, corresponding with the tips of the cusps of the next tooth. The tooth is attached to the membrane with two-thirds of its frontal basal platform only; the posterior third is free and can be erected when the radula is pulled over the edge of the odontophore.

Prunum marginatum (Born, 1778)
(fig. 303; pl. 18 fig. 8)

The radula has a series of about 40 teeth and is very similar to that of *Prunum prunum*. The surface of the basal platform also has pits, into which the cusps of an adjoining tooth can fit. Each tooth is rectangular and about six times as wide as long. The front is straight and fully attached to the membrane, while the base is free, bearing the cutting edge with its 30 to 35 cusps. Usually there are two to seven smaller cusps between two stronger ones. No wear was noted.

Hyalina lactea (Kiener, 1841)
(fig. 301; pl. 19 fig. 3)

About 40 saw-like central teeth form the radula, in which adjoining teeth do not overlap in the folded radula. The teeth are rectangular and about four times as wide as long. The cutting edge is situated very close to the base, extending a little above it. It consists of 10-15 about equally sized, acute, erect cusps, that are curved claw-like backward. Thus they somewhat extend over the base and are arranged along the whole width of the tooth. The whole basal platform of the tooth is attached to the radula membrane.

Hyalina avena (Kiener, 1834)
(fig. 300; pl. 18 fig. 10)

The radula, with a series of 45 teeth, is very similar to that of *Hyalina lactea*. The rectangular teeth are about four times as wide as long. In contrast to the situation in *H. lactea*, they are attached to the membrane only along a narrow zone of the frontal basal platform and the cutting edge is also the base of the tooth. The teeth are flat plates, which have pits on their upper surface where the cusps of the tooth attached in front of it fit in the folded radula. In the folded radula the teeth overlap considerably; in the operational radula they are erected over almost their entire length. The cutting edge has a central, narrow, large cusp, which is accompanied on each side by 8-11 smaller cusps, separated from each other by rounded interstices. No wear was noted.

DISCUSSION

The radulae of Marginellidae and Volutidae are both characterized by the presence of only one tooth in each row. As regards the morphology, three types can be differentiated.

Rectangular teeth (the first type) are present in *Hyalina* and *Prunum* (figs. 300-304). The teeth of *Hyalina* are less wide than those of *Prunum*. The arrangement of the cusps and their number on the individual teeth, are very variable in most species. Narrow rectangular teeth of moderate width are also known from *Volvaria* (Troschel & Thiele, 1865-1893: pl. 5 fig. 8; Coan, 1965) and *Marginella* (Barnard, 1959: fig. 1c). Teeth as wide as those of *Prunum* are described for *Marginella* (Thiele, 1931: fig. 427; Barnard, 1959: fig. 1d; Coan & Roth, 1966: fig. 1). Even wider and thinner teeth, with an extremely high number of cusps on the cutting edge, are known from *Afrivoluta* (Coan, 1965: fig. 9).

The second type of teeth is crescentic in shape, as in *Persicula* and *Marginella* (figs. 293-297). Such forms have frequently been described for *Persicula*, as for example by Troschel & Thiele (1865-1893: pl. 5 fig. 11), Thiele (1931: fig. 425), Coan (1965: fig. 5), and Barnard (1969: fig. 10c).

The third type of teeth is broadly triangular, with thickened margins, as in *Voluta* (figs. 298, 299). Such margins are also known for the radula of *Lyria* (Cosel & Blöcher, 1977), which differs from that of *Voluta* in the number of cusps on the cutting edge. The central teeth of recently hatched individuals of *Voluta musica* are quite similar to those of *Persicula* (figs. 295, 297), as has been published by Clench & Turner (1970: pl. 173 fig. 3). Only during later stages, the *Voluta* tooth develops its characteristic morphology.

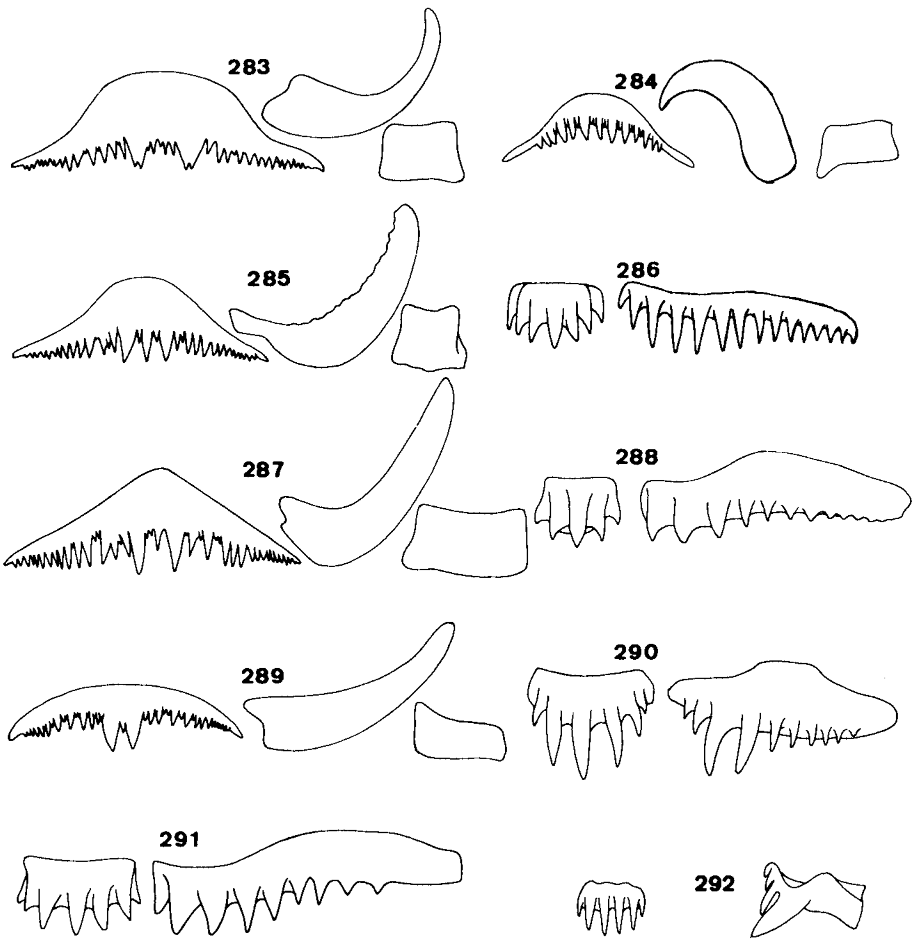

Fig. 283. *Olivella perplexa*, Santa Marta, Caribbean; x 320. — Fig. 284. *Olivella dealbata*, Curaçao, Caribbean; x 220. — Fig. 285. *Olivella petiolita*, Santa Marta, Caribbean; x 260. — Fig. 286. *Mitra cornicula*, Banyuls-sur-Mer, Mediterranean; x 230. — Fig. 287. *Olivella adelae*, Santa Marta, Caribbean; x 300. — Fig. 288. *Mitra* cf. *nodulosa*, Santa Marta, Caribbean small form; x 240. — Fig. 289. *Olivella nivea*, Santa Marta, Caribbean; x 120. — Fig. 290. *Mitra* sp., Port Sudan, Red Sea; x 250. — Fig. 291. *Mitra nodulosa*, Santa Marta, Caribbean large form; x 210. — Fig. 292. *Mitra* cf. *fissurata*, Port Sudan, Red Sea; x 80.

Barnard (1969: 615) had also observed the three types of radula in the Marginellidae. In addition he noted a fourth type, with narrow V-shaped teeth with a single cusp, similar to what is seen in *Harpa* (Troschel & Thiele, 1865-1893: pl. 10 fig. 1).

Regarding the attachment of the central tooth to the radula membrane, the species here discussed also indicate a development from a fully attached central tooth with an upright cutting edge, as in *Hyalina lactea* (pl. 19 fig. 3), to a blade-like form, attached only along a narrow zone in front, as in *Hyalina avena* (pl. 18 fig. 10). According to Troschel & Thiele (1865-1893: pl. 5 fig. 10) and Coan (1965: fig. 8), the teeth of the marginellid genus *Cystiscus* have an even more upright cutting edge, which is still situated centrally on the basal platform, and

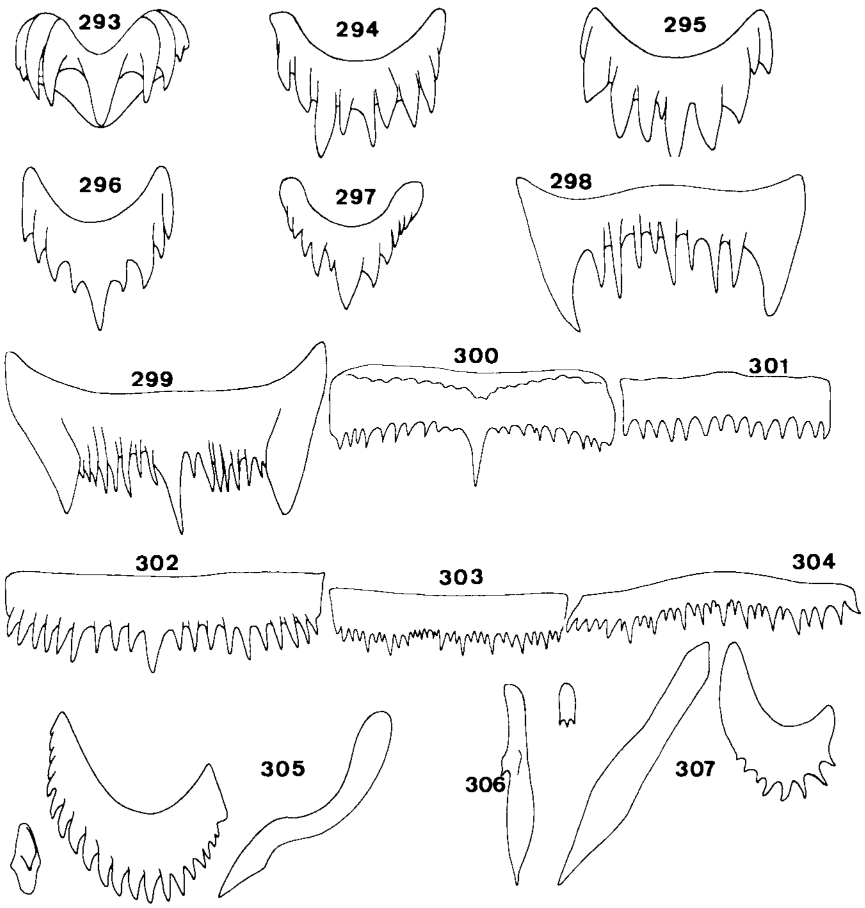

Fig. 293. *Marginella* sp., Port Sudan, Red Sea; × 2000. — Fig. 294. *Persicula pulcherrima*, Santa Marta, Caribbean; × 1500. — Fig. 295. *Persicula interruptolineata*, Santa Marta, Caribbean; × 750. — Fig. 296. *Marginella lavalleana*, Santa Marta, Caribbean; × 1500. — Fig. 297. *Persicula miliaria*, Banyuls-sur-Mer, Mediterranean; × 1000. — Fig. 298. *Voluta musica*, Curaçao, Caribbean; × 100. — Fig. 299. *Voluta virescens*, Santa Marta, Caribbean; × 200. — Fig. 300. *Hyalina avena*, Santa Marta, Caribbean; × 180. — Fig. 301. *Hyalina lactea*, Santa Marta, Caribbean; × 700. — Fig. 302. *Hyalina* sp., Port Sudan, Red Sea; × 200. — Fig. 303. *Prunum marginatum*, Santa Marta, Caribbean; × 90. — Fig. 304. *Prunum prunum*, Santa Marta, Caribbean; × 70. — Fig. 305. *Crassispira* sp., Santa Marta, Caribbean; × 240. — Fig. 306. *Drillia* sp. (1), Santa Marta, Caribbean; × 220. — Fig. 307. *Drillia* sp. (2), Santa Marta, Caribbean; × 320.

consists of three cusps mainly, similar to what is known for the central teeth of quite a number of neogastropod groups. The next step from a fully attached tooth with an erect cutting edge near the base, is a cutting edge on the base as in *Prunum*. Together with this, a differentiation either into a crescentic shape, as in *Persicula*, or into a blade-like shape, as in *Hyalina* and *Prunum*, could have taken place. Very little attachment along only the frontal part of the basal membrane, as in *Hyalina avena* or *Persicula*, finally allows the teeth to be erected even more when the radula is pulled over the edge of the odontophore. This development might have occurred independently along several lines. Ponder (1973) suggested Mitridae, Volutidae and Volutomitridae, with three teeth in each row, as different ancestors. Marcus & Marcus (1959) suggested that the Olividae may have been the ancestors of the Marginellidae and other groups with a central tooth only. *Odontocymbiola*, which, according to Clench & Turner (1970: pl. 173 fig. 1, 2) is a volutid, has a radula with a bicuspid lateral tooth with a broad base; this genus has to be considered basically buccinid, with radulae as found in *Melongena* or *Vasum*.

Radulae that consist of only a series of central teeth with cusps might have independently evolved from various neogastropod groups.

Conacea, Conidae and Terebridae

Conus mus Hwass, 1792
(fig. 324; pl. 21 figs. 1, 2; pl. 22 fig. 1)

The radula consists of a series of rows with two lateral teeth only, one being the other in reverse. The slender, hollow tooth is about seven times longer than wide at its base and consists of a sheet that is rolled up to $1^1/_4$ whorl. The suture of the sheet ends in a rounded basal knob. From there it is continuous with a wide undulation up to the central constriction of the shaft, continuing straight to the outer margin of the apical opening of the tooth, and ending in a tip with a barb. The inner margin of the apical aperture has nine or ten hook-like denticles. The aperture occupies only the upper fifth of the tooth.

Conus jaspideus pygmaeus Reeve, 1844
(fig. 318; pl. 21 figs. 3, 4; pl. 22 fig. 2)

The arrangement of the teeth is like that in *Conus mus*. The short hollow tooth is about four times longer than wide at its base and has a very broad basal part, with a large adapical opening. There is a conspicuous denticle on the upper shoulder of the base. The tube-forming sheet has $1^1/_4$ whorl; its margin is almost straight. The shaft begins with a strong constriction, delimiting it well from the basal knob. Above the middle of the shaft there is a rapid decrease in diameter. At the apex, the outer and the inner margin of the sheet turn outward. Thus a spindle-shaped, wide, apical opening without marginal serrations is formed. The acute, triangular apex is flattened, with a stout barb on the side below the opening and a small one opposite the big one, just below the apex.

Conus regius Gmelin, 1791
(fig. 345; pl. 21 figs. 5, 6; pl. 22 fig. 22)

The arrangement of the teeth is like that in *Conus mus*. The stout hollow tooth reaches its greatest width at its base; it is about seven times longer than wide. The sheet forming the tube forms a straight suture along the shaft and is rolled up into $1^1/_2$ whorls. The base, with its large, round, adapical opening, is shouldered; on this shoulders there is a low, strong basal denticle. The lower part of the shaft is columnar; its upper third, with a long, slit-like, apical opening, tapers toward the apex. The apical aperture is quite complicated in structure. The outer margin has a barb, projecting from below the aperture, and a second one, opposite to it on the apical tip. The inner margin has two bifid, acute cusps near the base of the opening. Where these cusps merge, there is a hole, through which a long acute tongue-like process points in an apical direction. This lamella is an extension of the outer part of the sheet. Above the bifid basal cusps the inner margin is denticulate, with up to nine denticles.

Conus testudinarius Hwass, 1792
(fig. 343; pl. 21 figs. 7, 8; pl. 22 fig. 3)

The radula and the individual teeth are very similar to those of *Conus regius*. There is only a somewhat larger lamellar extension penetrating through the cavity next to the bifid cusps of the inner margin of the apical aperture. This extension is clearly composed of two lamellae.

Conus spurius phlogopus Tomlin, 1937
(fig. 335; pl. 21 figs. 9, 10; pl. 22 fig. 5)

The radula is similar to that of *Conus mus*. The teeth are twelve times as long as wide at their base. There is a small basal denticle. The margin of the sheet forming the narrow tube-like tooth almost undulates along the side of the shaft, becoming the outside of the very long slit-like apical opening, that runs along the upper half of the tooth. The inner margin is thickened and serrated by three rows of denticles, the upper 19-22 of which are quite sturdy and hook-like. The tip of the tooth is flattened and triangular, with a small barb.

Terebra taurinus Lightfoot, 1786
(fig. 314; pl. 21 figs. 11, 12; pl. 22 fig. 6)

The radula has about ten rows of two teeth. Each tooth is about ten times longer than wide at its base and consists of a sheet-like basal platform that is rolled up to form a tube. The edge of the base is curved outward, forming a rim around the circular adapical opening. In its central part the outer margin of the sheet, running along the hollow shaft, which looks like an injection-needle, has two deep lobes and a rounded saddle in between. The apical opening of the shaft is slit-like and situated close to the apex. The tooth tapers regularly towards the acute apex, which has a single hook-like barb.

Terebra cinerea (Born, 1778)
(fig. 315; pl. 21 figs. 13, 14; pl. 22 fig. 7)

The arrangement of the teeth is like that of *Terebra taurinus*. The hollow tooth is about seven times longer than wide and decreases slowly in diameter from its base to the apex. The base is curved upward with its margin, forming a regular rim around the circular adapical opening. The crenellated outer margin of the sheet-like basal platform, which is rolled up, runs straight along the side of the shaft. There is a spindle-like apical opening below the acute apex, which has one tiny barb.

Terebra protexta Conrad, 1845
(fig. 313; pl. 21 fig. 15, pl. 22 fig. 9)

The radula has about eight rows with two teeth each. The hollow, slender tooth is about nine times as long as wide. The shaft has about the same diameter over most of its length. The margin of the base is curved outward, forming a somewhat irregular rim around the circular adapical opening. The sheet-like basal platform is rolled up, to form a symmetrical tube; its outer margin is straight. The apical opening is situated just below the acute apex.

Terebra spec.
(fig. 316; pl. 21 fig. 16, pl. 22 fig. 8)

The arrangement of the teeth is like that in *Terebra taurinus*. The hollow, slender tooth is about nine times as long as wide. Its base is curved to form a broad rim surrounding the circular adapical opening. From its base on the shaft first decreases in diameter, then it becomes wider again, until it has reached two-thirds of its length; in its upper third the shaft decreases rapidly in diameter, finally ending in a needle-like tip. In this narrow upper part the central tube opens with a slit-like aperture.

DISCUSSION

The structure of the teeth of Conidae and Terebridae was first described by Troschel (1848: 547), who suggested that the hollow teeth looking like the needle of a hypodermic syringe are used by the snails to convey poison into their prey. Kohn (1959) has studied the feeding of *Conus* in detail and shows that the harpoon-like teeth are really used to harpoon the prey, which is engulfed afterwards with the expanded mouth as Alpers (1931, 1932) has described.

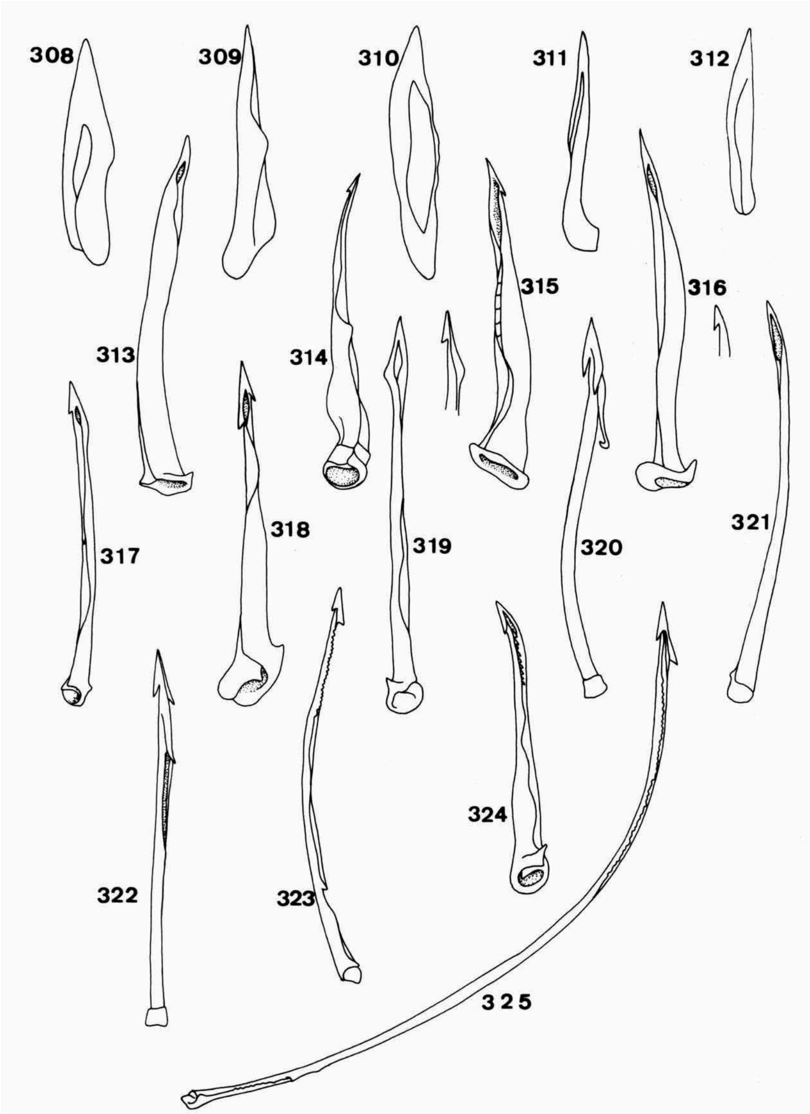

Fig. 308. *Polystira albida*, Santa Marta, Caribbean; × 410. — Fig. 309. *Drillia solida*, Santa Marta, Caribbean; × 250. — Fig. 310. Turrid spec., Port Sudan, Red Sea; × 200. — Fig. 311. *Crassispira leucocyma*, Santa Marta, Caribbean; × 160. — Fig. 312. *Crassispira albomaculata*, Santa Marta, Caribbean; × 210. — Fig. 313. *Terebra protexta*, Santa Marta, Caribbean; × 220. — Fig. 314. *Terebra taurinus*, Santa Marta, Caribbean; × 50. — Fig. 315. *Terebra cinerea*, Santa Marta, Caribbean; × 300. — Fig. 316. *Terebra* sp., Santa Marta, Caribbean; × 450. — Fig. 317. *Conus sanguinolentus*, Port Sudan, Red Sea; × 60. — Fig. 318. *Conus jaspideus pygmaeus*, Santa Marta, Caribbean; × 150. — Fig. 319. *Conus rattus*, Port Sudan, Red Sea; × 70. — Fig. 320. *Conus striatus*, Port Sudan, Red Sea, juvenile individual; × 40. — Fig. 321. *Conus lividus*, Ceylon, Indian Ocean; × 50. — Fig. 322. *Conus striatus*, Port Sudan, Red Sea, adult individual; × 22. — Fig. 323. *Conus pennaceus*, Port Sudan, Red Sea; × 17. — Fig. 324. *Conus mus*, Santa Marta, Caribbean; × 80. — Fig. 325. *Conus textile*, Port Sudan, Red Sea; × 17.

Kohn, Nybakken & Van Mol (1972) found that the various parts of a tooth, shaped as in *C. regius*, have different functions. The apex of the tooth, with its serrated cutting edge and acute triangular shape, serves to penetrate the cuticle of the prey. The barbs and the hook-like denticles fix the tooth in the body of the prey. The venom enters the prey via the hollow tube of the tooth, through the apical opening. The extended base, with its denticle, anchors the tooth to the proboscis during the process of piercing and ingestion.

Lim (1969) has tried to correlate the feeding habits of different *Conus* species with the morphology of their teeth, referring to previously published data by Endean & Rudkin (1965). In principle there are three types of prey hunted by *Conus*, viz. worms, molluscs and fish. Kohn (1959) grouped the radulae of cones feeding on different prey according to the morphology of the tooth-base and the presence or absence of a basal denticle. The radulae of the Caribbean cones described in the present paper belong to two types: *C. mus*, *C. jaspideus pygmaeus*, *C. regius* and *C. testudinarius* have the vermivorous type, while *C. spurius phlogopus* has the molluscivorous type. According to Kohn (1956) the piscivorous type of cone injects the tooth and accompanying venom into a fish; the tooth is not retained in the proboscis and, therefore, there is no basal denticle. Characteristic teeth of fish-eating cones are those of *C. geographus* L. (fig. 336) and *C. striatus* L. (figs. 322, 320), both from the Red Sea. When the tooth is discharged, the proboscis retracts, leaving the tooth in the fish. When the poison has paralysed the fish and it has become motionless, the mouth of the cone expands and the prey is engulfed (Kohn, 1956).

A typical molluscivore type of tooth is present in *C. textile* L. as figured from the Red Sea (fig. 325). Kohn (1959) found that *C. pennaceus* Born (fig. 323) also feeds on gastropods. He reported that when the prey is stung, the radula tooth is completely freed from the proboscis; up to six teeth may be injected into a single prey.

Among the worm-eating cones Kohn (1959) found differences in the shape of the teeth reflecting preferences for certain types of worms. According to Kohn, species such as *C. rattus* Hwass (fig. 319) and *C. lividus* (fig. 321) from the Red Sea keep the tooth in the proboscis while the worm is extracted from its tube after the injection of the poison. These teeth also have a basal denticle. *C. rattus* extracts polychaetes from their tubes, whereas *C. lividus* feeds on enteropneusts (Kohn, 1959).

The structure of the radula teeth was used to distinguish *C. mediterraneus* Bruguière (fig. 332) from *C. guinaicus* Hwass which can hardly be kept apart on their shell morphology (Bandel & Wills, 1977: figs. 24-29).

A fair number of mainly Red Sea *Conus* species were studied together with those from the Caribbean (figs. 317-346), which clearly proved the importance of the radula for taxonomic purposes.

Teeth of *C. jaspideus pygmaeus* (fig. 318) are similar to those of *C. taeniatus* Hwass (fig. 331); the latter, however, have five or six denticles on the inner margin of the aperture. No such denticles are present in *C. sanguinolentus* (fig. 317), which has more slender teeth than *C. jaspideus pygmaeus*.

Teeth of *C. coronatus* Gmelin (fig. 329), *C. semivelatus* Sowerby (fig. 338), *C. erythraeensis* Reeve (fig. 330), *C. fulgetrum* Sowerby (fig. 334), *C. pusillus* Lamarck (fig. 339) and *C. piperatus* Dillwyn (fig. 328) are similar to those of *C. mus* (fig. 324). Most but not all of these teeth can be well differentiated from each other by their length/width relation, size of the basal denticle, number of denticles on the inner lip of the aperture, and shape of the outer margin.

The teeth of *C. arenatus* Hwass (fig. 342) are comparatively stout and, in this respect, transitional between those of the foregoing species and *C. regius* (figs. 345, 346). Even more like *C. regius* and *C. testudinarius* (fig. 343) from the Caribbean is *C. gladiator* Broderip from the Pacific coast of Mexico (fig. 344), but this species lacks the typical additional sheet in the apical aperture of *C. regius*.

Very slender teeth, similar to those of *C. spurius phlogopus* (fig. 335), are found in *C. geographus* (fig. 336) from Port Sudan. *C. spurius* Gmelin from Florida has a radula which could not be distinguished from that of *C. spurius phlogopus* from the Colombian coast.

Species like *C. terebra thomae* Gmelin (fig. 333), *C. flavidus* Lamarck (fig. 327), *C. vexillum sumatrensis* Hwass (fig. 340) and *C. striatellus* Link (fig. 341), all from the Red Sea, have teeth similar to those of *C. virgo* L. (fig. 337), which differs, however, by a barb on the outer margin of the sheet at the central part of the shaft. Such a barb was also observed, a little lower on the shaft, on the teeth of the first two members of the next group.

Slender long teeth with conspicuous barbs on their apices occur in *C. textile* (fig. 325), *C. pennaceus* (fig. 323) and *C. striatus* (figs. 320, 322). While in *C. pennaceus* the base and the apex of the teeth are quite similar to those of *C. textile*, the latter species has much longer teeth than the former. It should be mentioned here, however, that juveniles of *C. striatus* have shorter teeth than adult specimens, indicating that length/width relations should be carefully interpreted if used for taxonomic purposes.

The radulae of three *Terebra* species from the Great Barrier Reef, described by Mills (1977), are very similar to those of the *Terebra* species from the Caribbean. All three Australian species have a concavity near the base, much like that of *T. taurinus* (fig. 314). The other three Caribbean species here described do not have such a cavity. The so-called "bridges", observed in *T. cinerea* by Marcus & Marcus (1960: 39, fig. 8) were not observed in the radulae studied by Mills (1977: 261), but they are well visible in *T. cinerea* from Santa Marta (pl. 21 fig. 13). This feature, which already had been reported by Troschel & Thiele (1865-1893: pl. 2 fig. 10) probably represents a special supporting device for the teeth, holding the sheet margins of the tooth together. The other terebrids from Santa Marta do not show this character.

Terebrid teeth are most probably used in a similar way as *Conus* species do, viz. to catch, paralyse and fix the prey, which is swallowed afterwards. In the terebrids such prey probably consists in most cases of worm-like animals (Marcus & Marcus, 1960; Miller, 1975; Mills, 1977).

CONACEA, TURRIDAE

Crassispira sp.
(fig. 305; pl. 20 fig. 2)

Each row in the radula has five teeth. The thorn-like central tooth is the smallest. It is about three times longer than wide and has a strongly arched front and base, and weakly convex to concave margins. There is a single cusp attached to the basal platform, slowly ascending into a hook-like tip; its posterior part forms a concavity with the posterior part of the otherwise flat basal platform, which is completely attached to the membrane.

The crescentic lateral tooth is about three times wider than long. Its front is concave; with its inner corner it is attached more anteriorly to the membrane than with its posterior corner. The base forms the cutting edge and ends in the corners. There are 16 to 19 acute cusps on the cutting edge, regularly arranged and decreasing in size only near the margins.

The marginal tooth is long and slender and about eight times longer than wide at its base. The stalks are evenly rounded on their upper side and gutter-like below. The base is rounded and only slightly wider than the stalk. The apex is like an arrowhead, with a sharp tip and two marginal barbs; it is bilaterally flattened. In side view the teeth are evenly curved inward, observed from above they are a shallowly S-shaped.

Drillia solida C. B. Adams, 1830
(fig. 309; pl. 20 fig. 8)

The radula has over 30 rows of teeth, with only two teeth in each row. These teeth are attached to the membrane, very close to each other, so that their rounded posterior side fits into a groove on the anterior side of the tooth of the row behind. Each thorn-like tooth is more than five times longer than wide and very sturdy. The base is rounded. The upper two thirds of the tooth are slightly twisted away from the base, so that all apices point backward. The hook-like apex is acute.

Drillia spec. 1
(fig. 306; pl. 20 fig. 4)

The radula has about 15 rows with four teeth in each row. There are no central teeth. The lateral tooth is thin and merges with its front with the membrane. It is about twice as long as wide and has a cutting edge on the base with three or four thin, acute cusps. In comparison with the stout marginal tooth, the lateral teeth are quite small and inconspicuous. The knife-shaped marginal tooth is about four times longer than wide. The base has a lamellar wing on its outside and ends with a shoulder and a denticle on the inside. The basal part of the tooth is about oval. The greatest width is reached in the upper part of the tooth. Both margins have sharp edges, while the basal platform is flattened. The apex of the blade-like upper part is acute. The marginal teeth are about three or five times longer than the lateral teeth.

Drillia spec. 2
(fig. 307; pl. 20 fig. 3)

There are about 21 rows of teeth in this radula. As in *Drillia* spec. 1 each row has four teeth only. The lateral tooth is not rudimentary here and looks like that of *Crassispira* spec. The front is evenly concave and the tooth is attached only along a narrow zone here. The cutting edge on the base has eight cusps, the inner, central ones being the largest. The teeth are about twice as wide as high.

The marginal tooth is about seven times longer than wide. It is bilaterally flattened and has a convex upper surface and a concave lower side. The basal part is narrower than the upper third, in which the tooth is widest, before it gradually decreases in width upwards to the tip. This tooth is similar to that of *Drillia* spec. 1, but it has no basal lamella nor a denticulate shoulder.

Crassispira albomaculata (d'Orbigny, 1842)
(fig. 312; pl. 20 fig. 5)

The radula has about 35 rows of teeth, each row with two symmetrical teeth only. The spindle-like tooth has an acute apex and a rounded base. It is about five times longer than wide and bilaterally flattened, with a lamella on the inner flattened side, beginning near the base and ending below the apex with a separate inner cusp.

Crassispira leucocyma Dall, 1883
(fig. 311; pl. 20 figs. 6, 9)

The radula has about 30 rows of teeth, with two teeth in each row. The tooth is a slender tube, which is about seven times longer than wide at its base; the base has a wide opening. The tube consists of a sheet-like basal platform which is rolled up; the outer margin only slightly overlaps the inner margin. The tube opens in the upper half of the tooth with a long apical slit. The apex is acute.

Polystira albida (Perry, 1811)
(fig. 308; pl. 20 fig. 7)

The radula has about 40 rows of teeth, with two teeth per row only. The teeth are acute, spindle-shaped, and consist of a deep gutter-like basal platform, with the margins touching at the base, and widely opening in the middle of the tooth. The acute, blade-like apex is bilaterally flattened.

DISCUSSION

The Turridae constitute the largest family of marine gastropods. They are represented from the intertidal zone down to the abyssal zone in all seas (Powell, 1964). Troschel & Thiele (1865-1893) have classified the Turridae, the Conidae and the Terebridae under the joint heading of Toxoglossa; the Cancellariidae were also included because of their very specialized radulae, although there were thought to be very special characters, not shared by other families, in this group. Ponder (1973) considered the Cancellariacea a separate superfamily of the Neogastropoda, independent of the other two superfamilies Muricacea and Conacea (= Turridae, Conidae & Terebridae).

Thiele (1924) assigned the Turridae to the Conidae and accepted only the Terebridae as another family within the Toxoglossa. Powell (1964) has split the Toxoglossa into five separate families. According to this author the radulae of the Turridae show several distinctive types, ranging from (1) a most primitive form with central, lateral and marginal teeth, and (2) a series of radulae characterized by the absence of lateral teeth and an enlargement of the central tooth, to (3) the toxoglossan condition, in which only the marginal teeth, one on each side, remain. The prototypic radula of Powell's classification resembles that of *Crassispira* spec. (fig. 305). Powell suggests that the reduction of the radula teeth first eliminates the lateral teeth and later on the central tooth. From the series of turrid radulae in the present paper it becomes evident that the central tooth may be lost first (*Drillia* spec. 2: fig. 307), before the lateral tooth becomes rudimentary (*Drillia* spec. 1: fig. 306) and, after that is lost altogether (*Crassispira albomaculata*: fig. 312). Powell (1964: 230) noted that the fully developed toxoglossan radula, as in *Crassispira leucocyma* (fig. 311) for example, is not correlated with obvious shell characters.

McLean (1971: 115) has stated that there are two basic radular types in the Turridae. In the first group the radular ribbon has a strong basal membrane and the marginal teeth are sturdy. In the second group there are marginal teeth only, which are hollow and truly toxoglossan; the basal membrane of the radula is vestigial. Feeding mechanisms in these two groups differ markedly. In the first group the teeth are used to rake in or bite off food; in the second teeth are used to harpoon and to inject poison into a prey, as in Conidae and Terebridae. McLean rejects Powell's view that groups with different radulae may be closely related and offers a classification based on both radula and shell characters.

According to McLean's classification *Crassispira* spec. belongs to the subfamily Clavinae, *Drillia* spec. 1 and *Drillia* spec. 2 would be close to members of the genus *Calliclava* of the Clavinae because of their reduced lateral teeth. *Polystira albida* (fig. 308) fits into the Turriculinae, with wishbone-shaped marginal teeth. *Crassispira albomaculata* (fig. 312) would fit into the Crassispirinae, with the duplex type of marginal teeth, in which a narrow, accessory limb is superimposed on the main shaft. *Drillia solida* (fig. 309) could be grouped with the Strictispirinae, with stout and massive marginal teeth, elbow-shaped and therefore

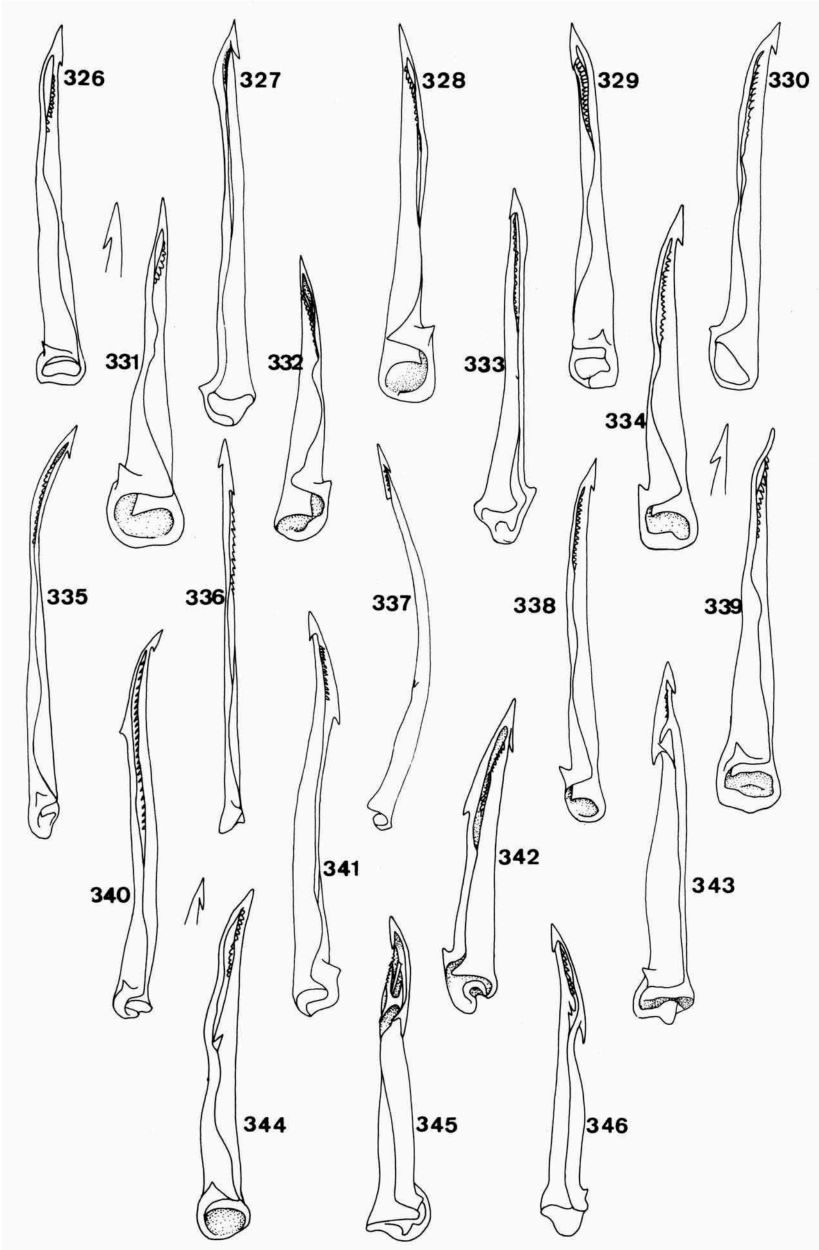

Fig. 326. *Conus arenatus*, Port Sudan, Red Sea; × 60. — Fig. 327. *Conus flavidus*, Port Sudan, Red Sea; × 80. — Fig. 328. *Conus piperatus*, Ceylon, Indian Ocean; × 140. — Fig. 329. *Conus coronatus*, Port Sudan, Red Sea; × 100. — Fig. 330. *Conus erythraeensis*, Port Sudan, Red Sea; × 90. — Fig. 331. *Conus taeniatus*, Port Sudan, Red Sea; × 210. — Fig. 332. *Conus mediterraneus*, Banyuls-sur-Mer, Mediterranean; × 100. — Fig. 333. *Conus terebra thomae*, Port Sudan, Red Sea; × 60. — Fig. 334. *Conus fulgetrum*, Port Sudan, Red Sea; × 170. — Fig. 335. *Conus spurius phlogopus*, Santa Marta, Caribbean; × 80. — Fig. 336. *Conus geographus*, Port Sudan, Red Sea; × 18. — Fig. 337. *Conus virgo*, Port Sudan, Red Sea; × 40. — Fig. 338. *Conus semivelatus*, Port Sudan, Red Sea; × 80. — Fig. 339. *Conus pusillus*, Port Sudan, Red Sea; × 120. — Fig. 340. *Conus vexillum sumatrensis*, Port Sudan, Red Sea; × 30. — Fig. 341. *Conus striatellus*, Port Sudan, Red Sea; × 30. — Fig. 342. *Conus arenatus*, the Seychelles, Indian Ocean; × 30. — Fig. 343. *Conus testudinarius*, Santa Marta, Caribbean; × 30. — Fig. 344. *Conus gladiator*, Sonora, Mexico, Pacific Ocean; × 60. — Fig. 345. *Conus regius*, Santa Marta, Caribbean; × 30. — Fig. 346. *Conus regius*, Curaçao, Caribbean; × 40.

close to the genus *Cleospira* (McLean, 1971: fig. 88). *Crassispira leucocyma*, with its hollow teeth like the needle of a hypodermic syringe, would fit into the Clathurellinae.

Ponder (1973; fig. 2, No 8) has suggested that the toxoglossan radula might have evolved from a reduced rhipidoglossate radula. He considered the radula shown by *Crassispira* spec. (fig. 305) as closest to this ancestral type.

The Turridae, Conidae and Terebridae might be considered to form a separate branch of the Neogastropoda, most probably derived from the mesogastropods and possibly independent from the other Neogastropoda.

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PLATES

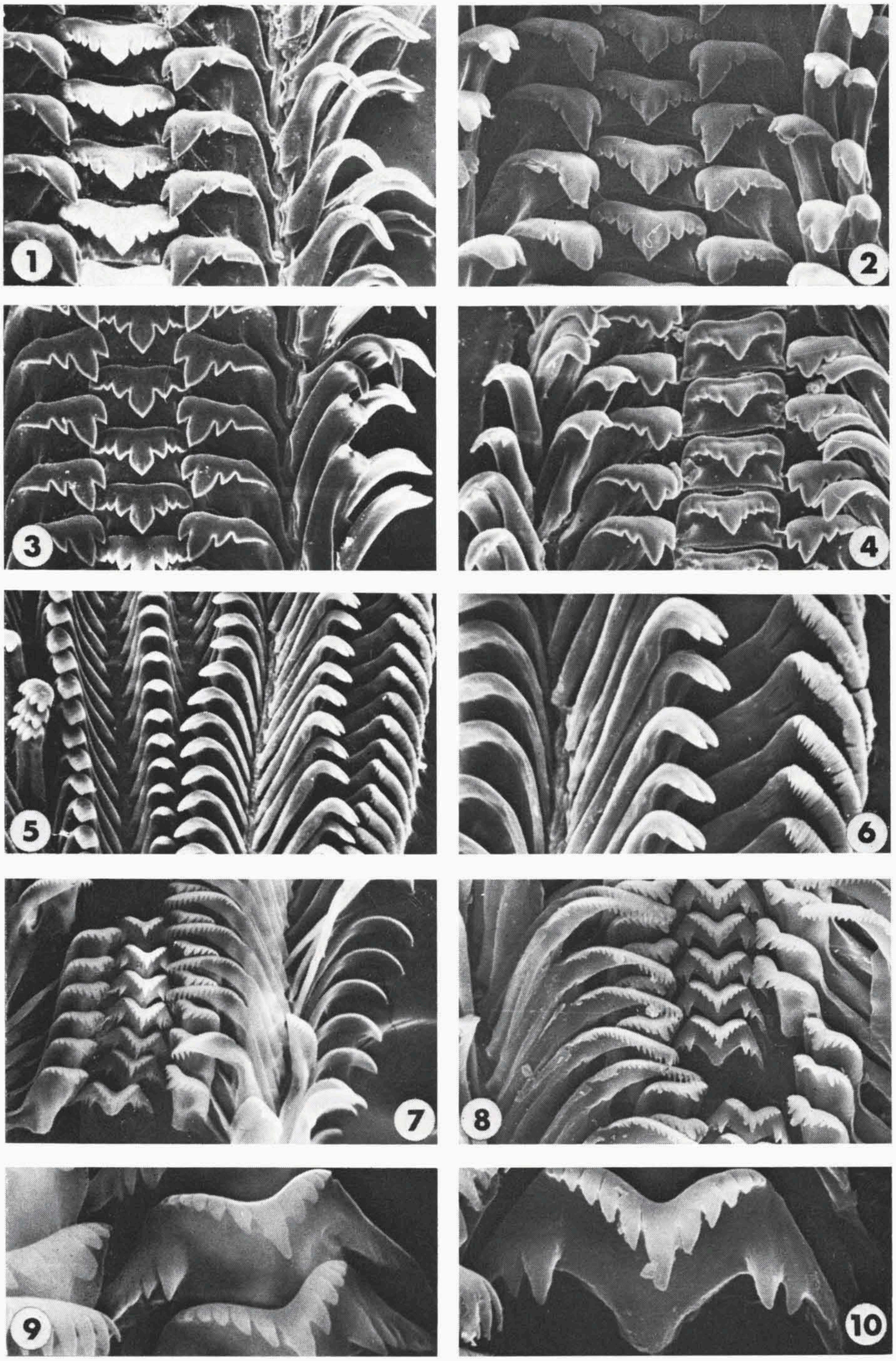


Fig. 1. *Ampullarius porphyrostomus*; × 37. — Fig. 2. *Ampullarius monticolus*; × 40. — Figs. 3-4. *Marisa cornuarietis*; 3, × 53; 4, × 53. — Figs. 5-6. *Tudora* sp.; 5, × 127; 6, marginal teeth, × 254. — Figs. 7-10. *Assiminea* cf. *succinea*; 7, × 308; 8, × 422; 9, central tooth (of fig. 7), × 1540; 10, central tooth (of fig. 8), × 2000.

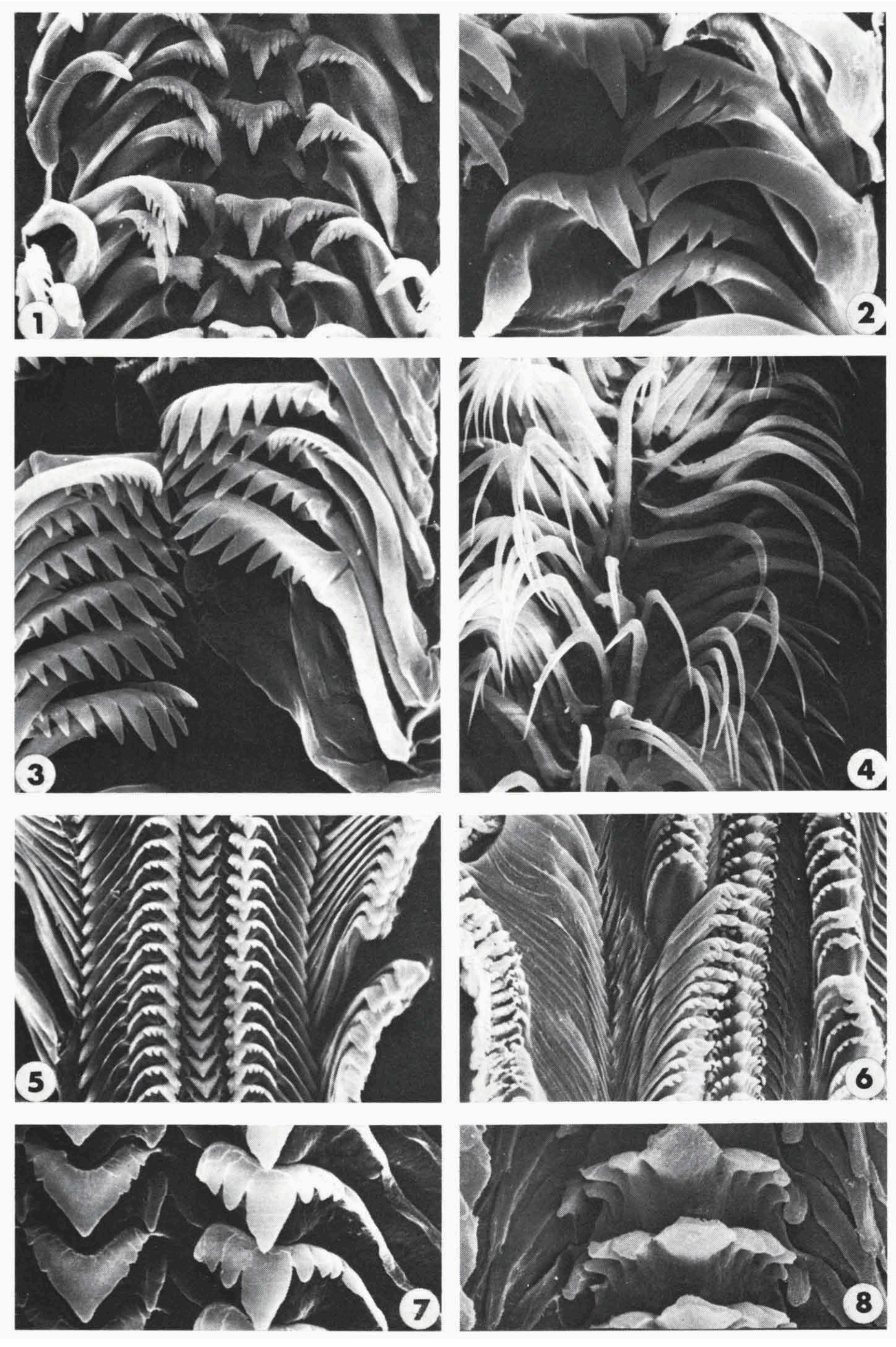


Fig. 1. *Petaloconchus erectus*; × 190. — Fig. 2. *Petaloconchus varians*; × 580. — Fig. 3. *Caecum antillarum*; × 1110. — Fig. 4. *Architectonica nobilis*; × 285. — Fig. 5. *Planaxis lineatus*; × 210. — Fig. 6. *Planaxis nucleus*; × 150. — Fig. 7. *Planaxis lineatus*, central and lateral tooth; × 833. — Fig. 8. *Planaxis nucleus*, central tooth; × 600.

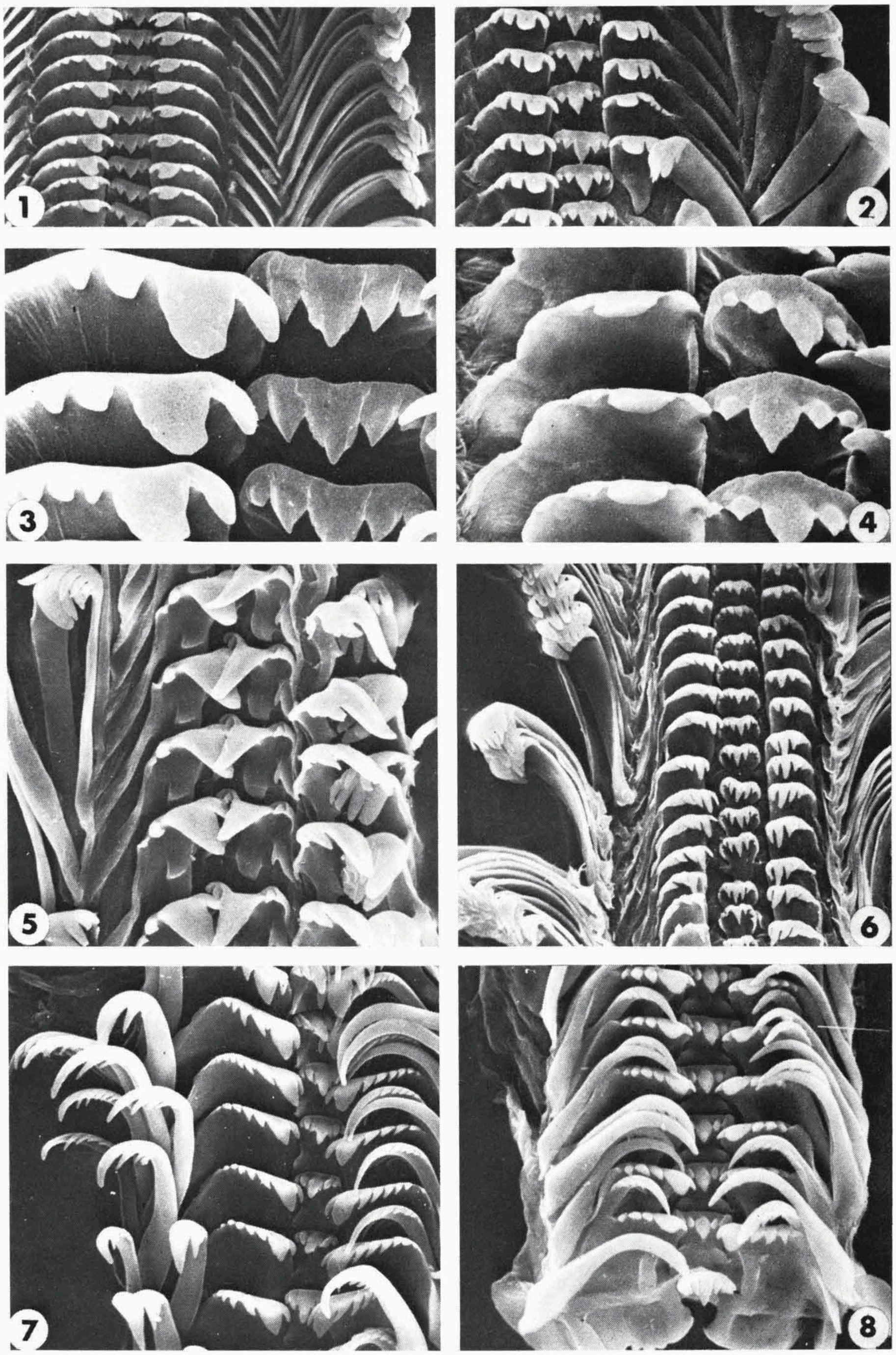


Fig. 1. *Modulus carchedonius*; × 130. — Fig. 2. *Modulus modulus*; × 150. — Fig. 3. *Modulus carchedonius*, central and left lateral tooth; × 530. — Fig. 4. *Modulus modulus*, central and lateral tooth; × 455. — Fig. 5. *Batillaria minima*; × 320. — Fig. 6. *Cerithidea costata*; × 255. — Fig. 7. *Finella dubia*; × 630. — Fig. 8. *Diastoma varium*; × 420.

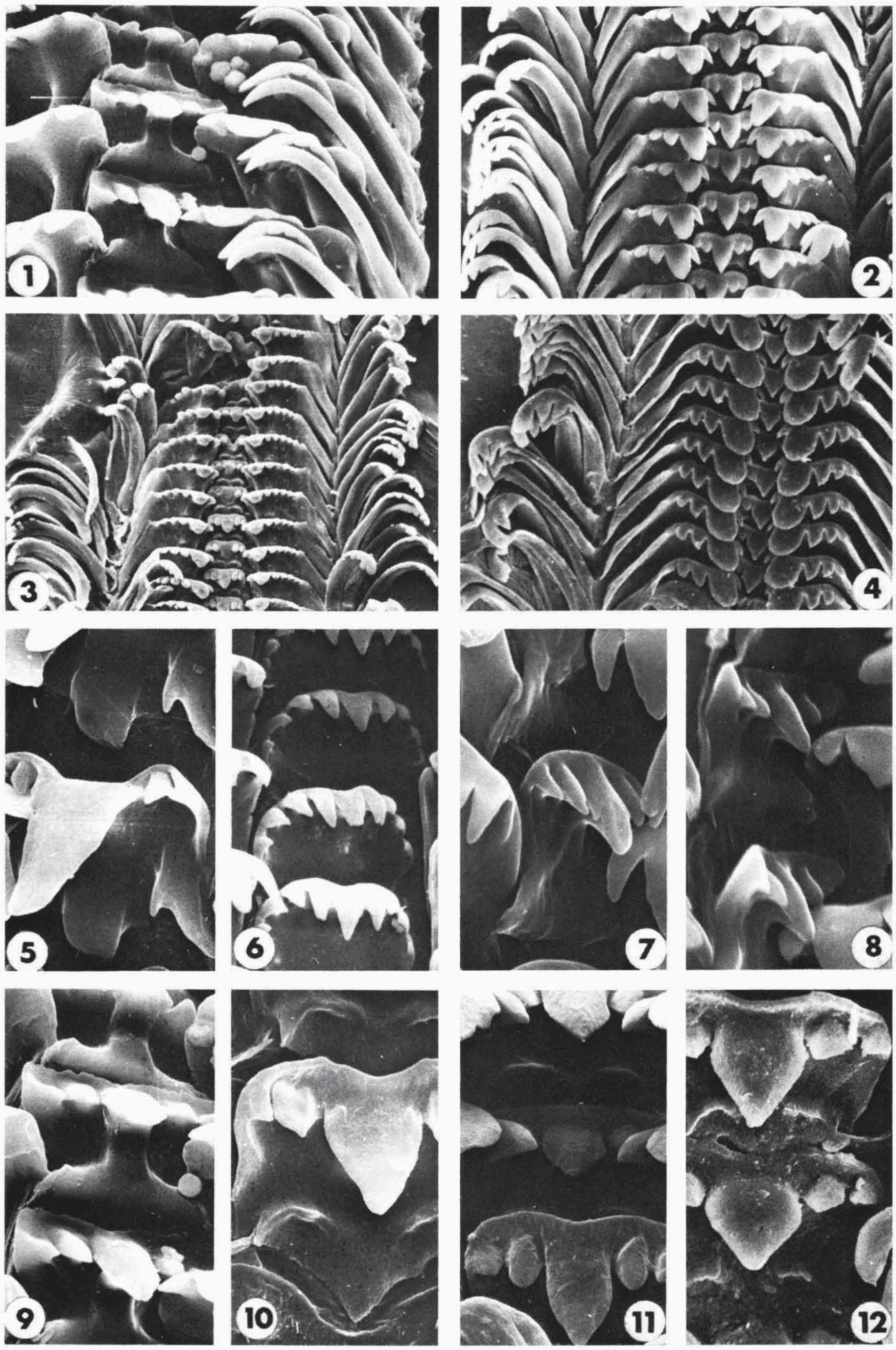


Fig. 1. *Alaba incerta*; × 420. — Fig. 2. *Cerithium lutosum*; × 150. — Fig. 3. *Cerithium litteratum*; × 95. — Fig. 4. *Cerithium atratum*; × 90. — Fig. 5. *Batillaria minima*, central tooth; × 550. Fig. 6. *Cerithidea costata*, central tooth; × 940. — Fig. 7. *Finella dubia*, central tooth; × 1940. — Fig. 8. *Diastoma varium*, central tooth; × 1060. — Fig. 9. *Alaba incerta*, central tooth; × 665. — Fig. 10. *Cerithium lutosum*, central tooth; × 850. — Fig. 11. *Cerithium litteratum*, central tooth; × 470. — Fig. 12. *Cerithium atratum*, central tooth; × 600.

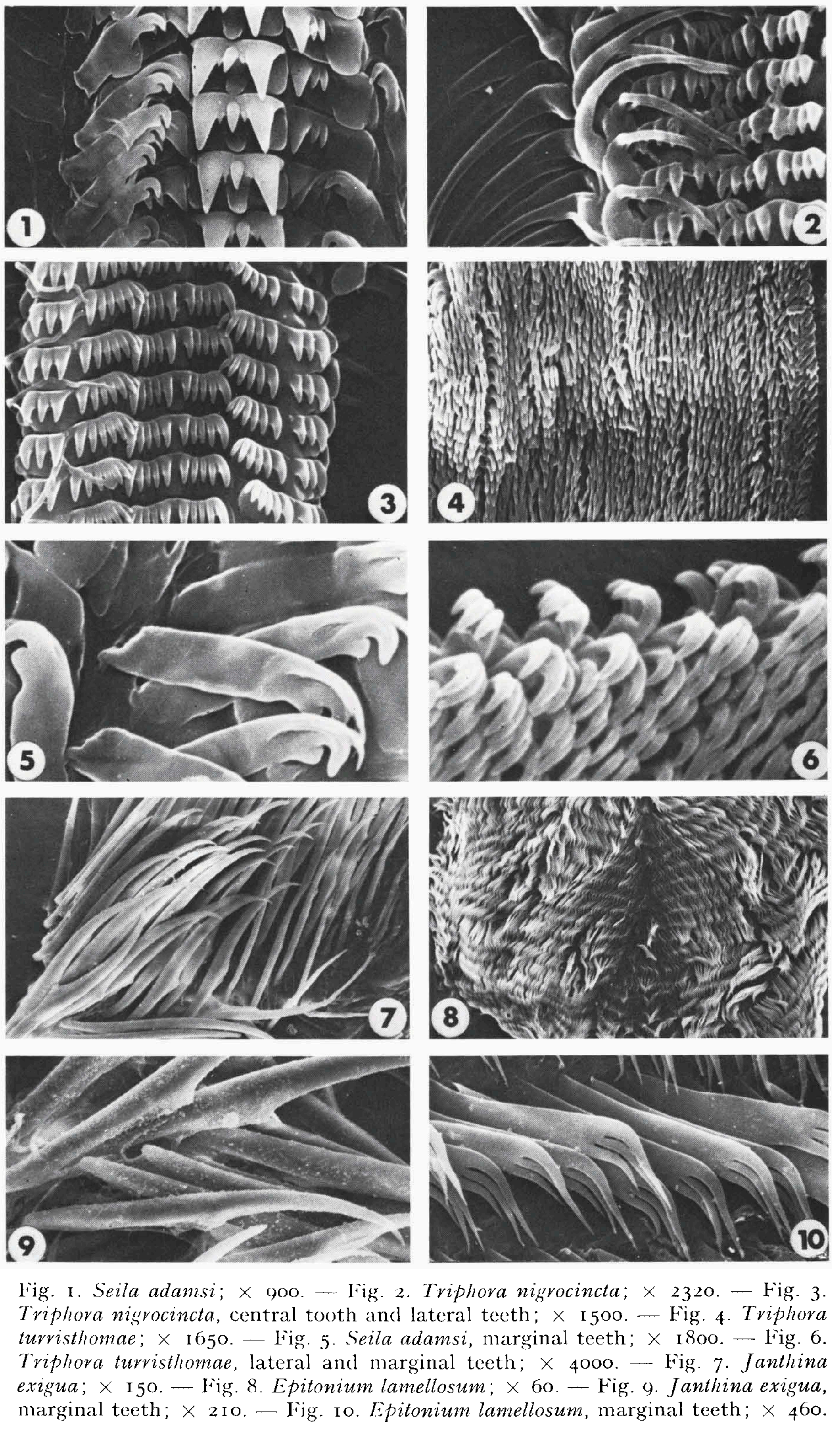


Fig. 1. *Seila adamsi*; × 900. — Fig. 2. *Triphora nigrocincta*; × 2320. — Fig. 3. *Triphora nigrocincta*, central tooth and lateral teeth; × 1500. — Fig. 4. *Triphora turristhomae*; × 1650. — Fig. 5. *Seila adamsi*, marginal teeth; × 1800. — Fig. 6. *Triphora turristhomae*, lateral and marginal teeth; × 4000. — Fig. 7. *Janthina exigua*; × 150. — Fig. 8. *Epitonium lamellosum*; × 60. — Fig. 9. *Janthina exigua*, marginal teeth; × 210. — Fig. 10. *Epitonium lamellosum*, marginal teeth; × 460.

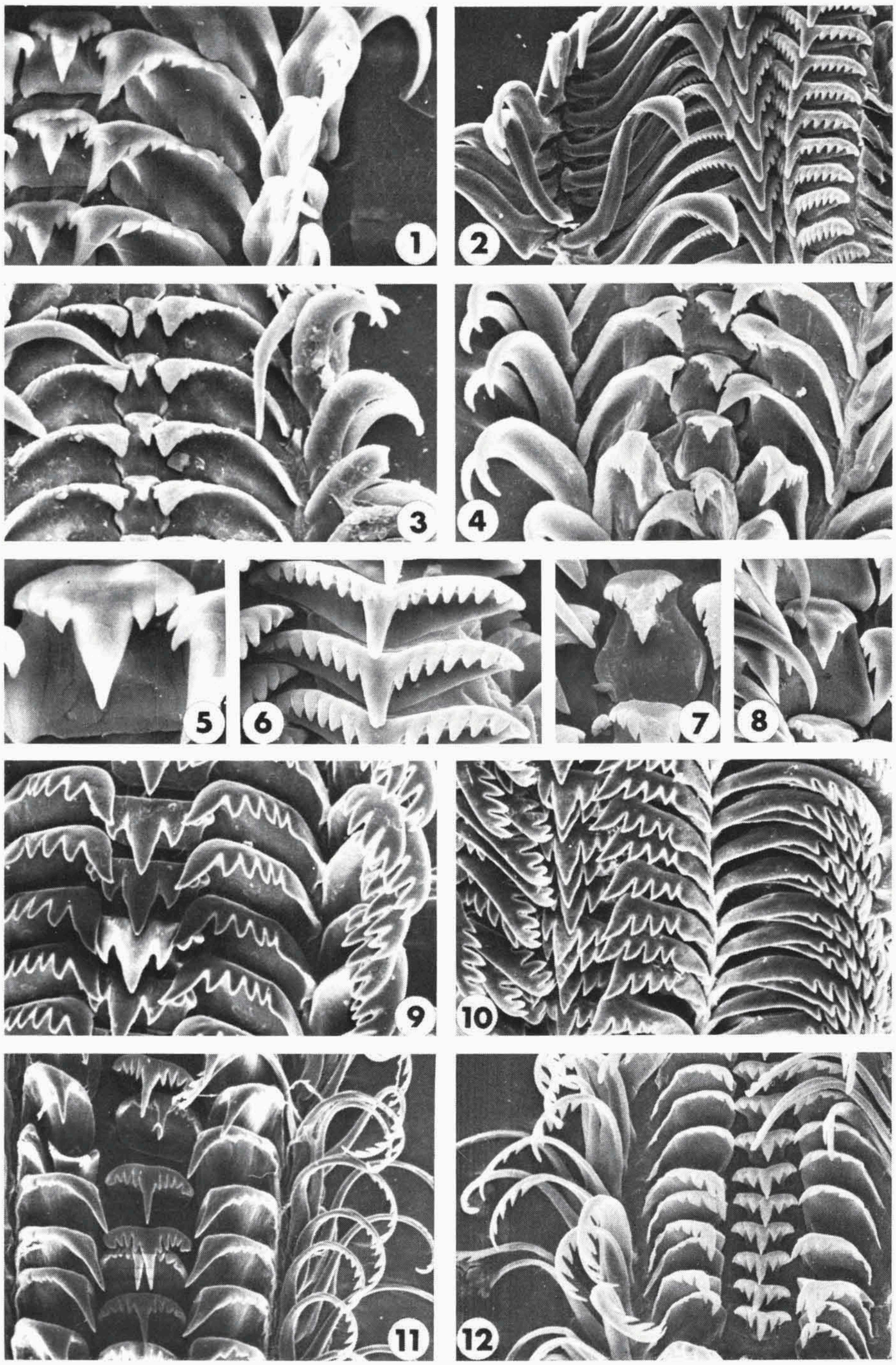


Fig. 1. *Crucibulum auricula*; × 220. — Fig. 2. *Cheilea equestris*; × 180. — Fig. 3. *Crepidula plana*; × 200. — Fig. 4. *Crepidula convexa*; × 180. — Fig. 5. *Crucibulum auricula*, central tooth; × 445. — Fig. 6. *Cheilea equestris*, central tooth; × 410. — Fig. 7. *Crepidula plana*, central tooth; × 380. — Fig. 8. *Crepidula convexa*, central tooth; × 290. — Fig. 9. *Strombus gallus*; × 43. — Fig. 10. *Strombus raninus*; × 44. — Fig. 11. *Strombus pugilis*; × 39. — Fig. 12. *Strombus gigas*; × 130.

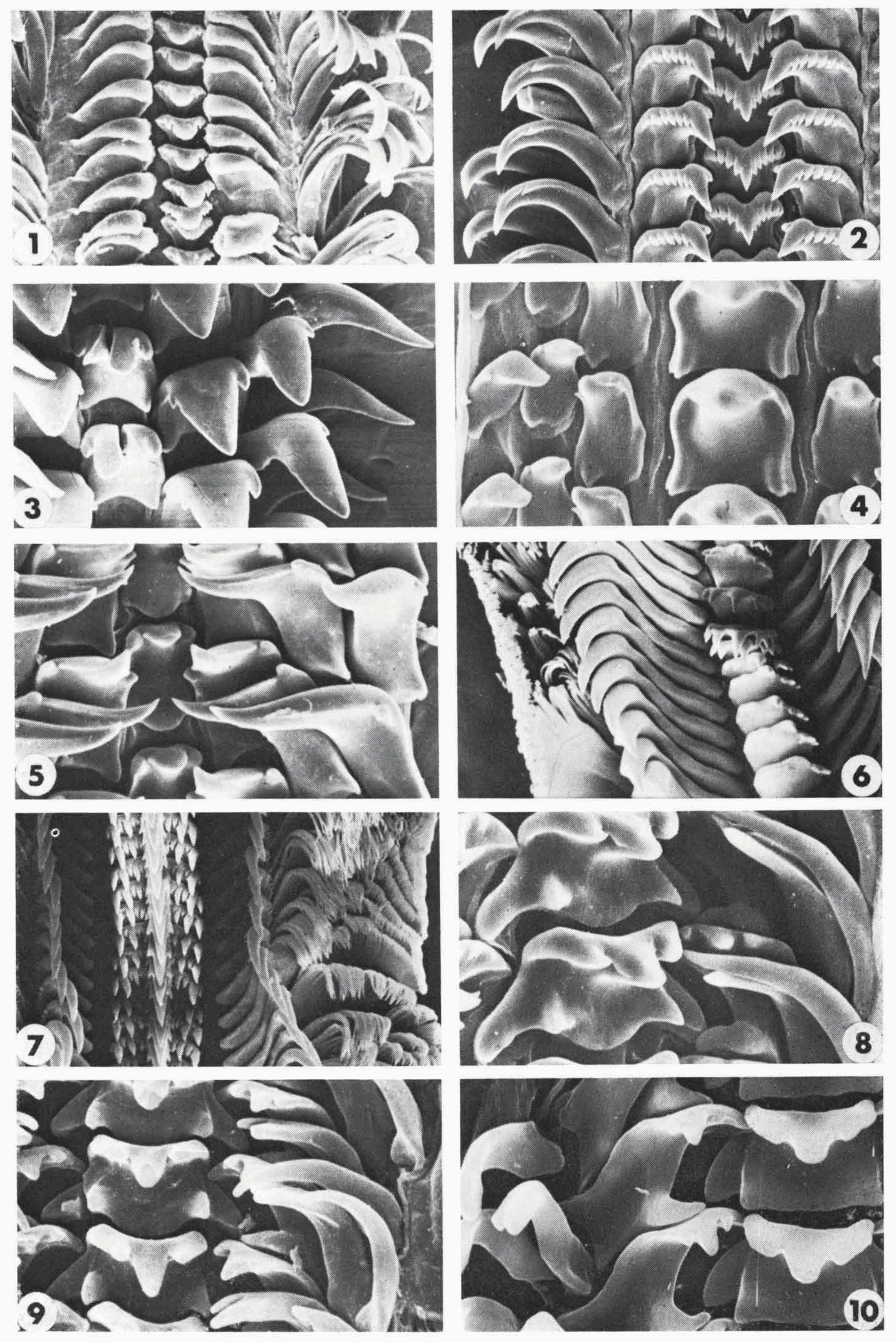


Fig. 1. *Xenophora conchyliophora*; × 42. — Fig. 2. *Trivia pediculus*; × 120. — Fig. 3. *Cypraea zebra*; × 44. — Fig. 4. *Cypraea cinerea*; × 100. — Fig. 5. *Cypraea spurca acicularis*; × 97. — Fig. 6. *Cyphoma gibbosum*; × 75. — Fig. 7. *Simnia acicularis*; × 155. — Fig. 8. *Polinices lacteus*; × 250. — Fig. 9. *Polinices hepaticus*; × 360. — Fig. 10. *Natica livida*; × 900.

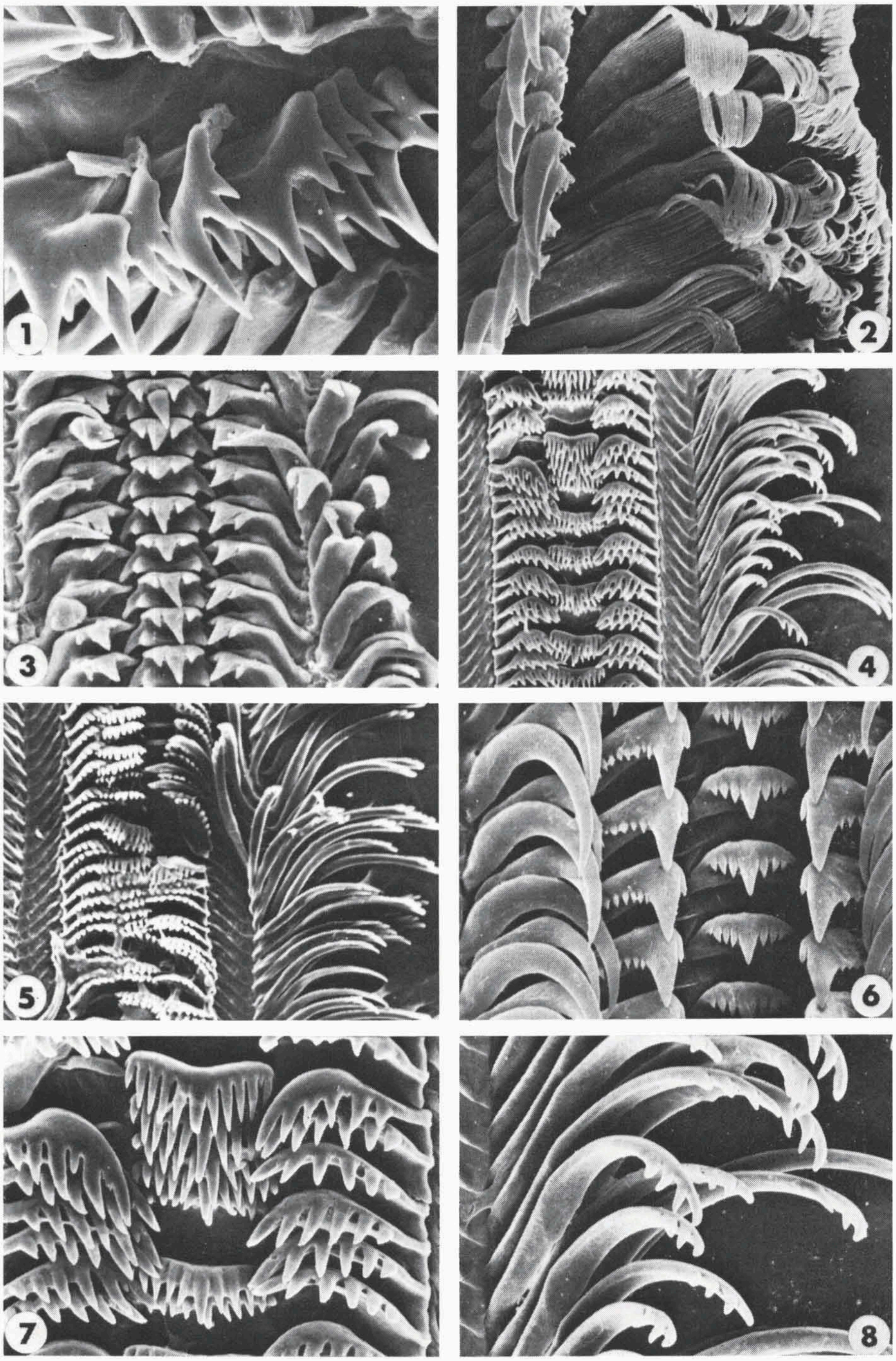


Fig. 1. *Cyphoma gibbosum*, central tooth; × 170. — Fig. 2. *Simnia acicularis*, lateral and marginal teeth; × 380. — Fig. 3. *Natica canrena*; × 115. — Fig. 4. *Cassis tuberosa*; × 45. — Fig. 5. *Cassis madagascariensis*; × 50. — Fig. 6. *Distorsio clathrata*; × 300. — Fig. 7. *Cassis tuberosa*, central and lateral teeth; × 120. — Fig. 8. *Cassis tuberosa*, marginal teeth; × 120.

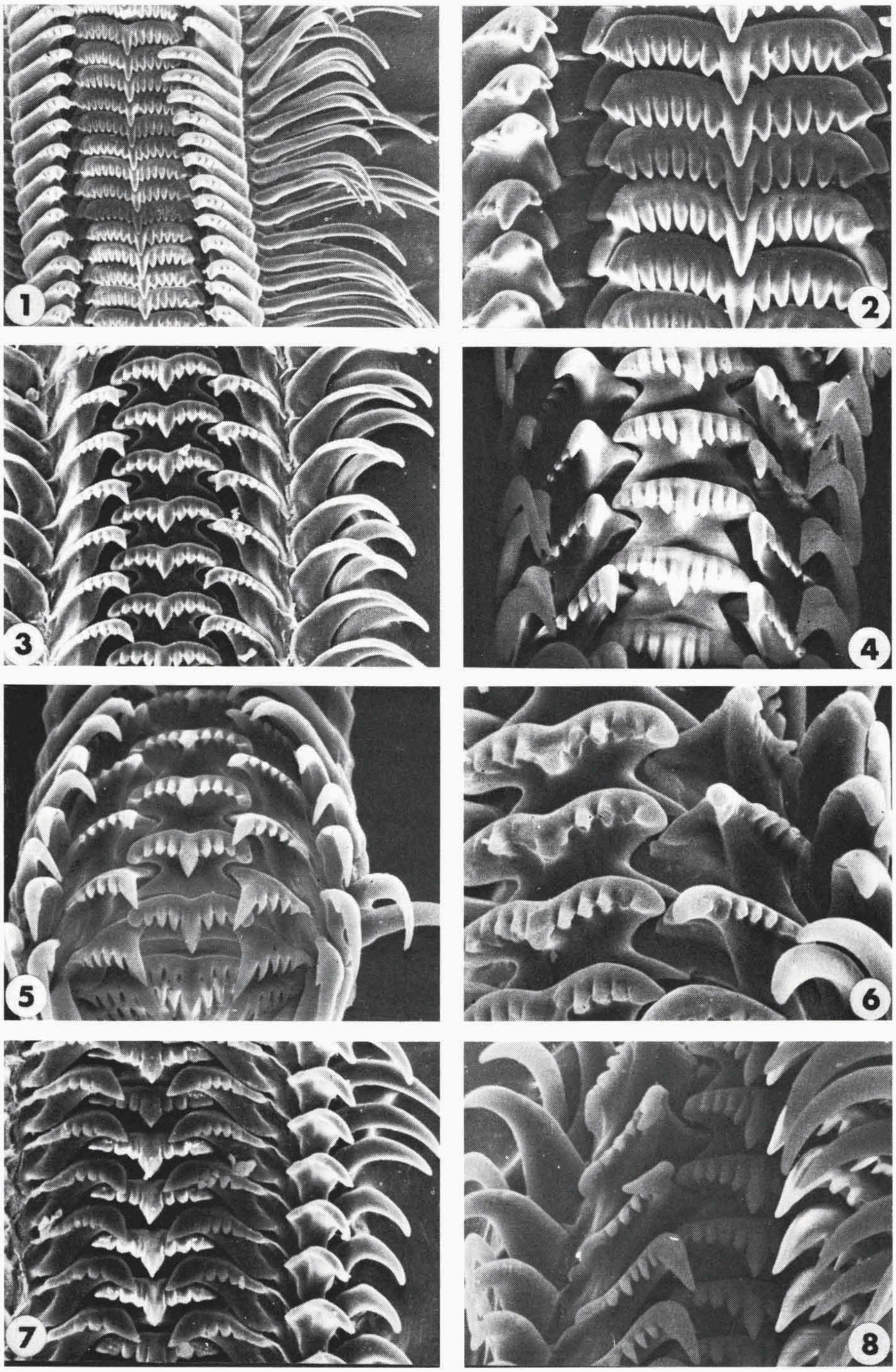


Fig. 1. *Charonia variegata*; × 35. — Fig. 2. *Charonia variegata*, central and lateral teeth; × 90. — Fig. 3. *Cymatium pileare*; × 150. — Fig. 4. *Cymatium vespaceum*; × 285. — Fig. 5. *Cymatium krebsii*; × 200. — Fig. 6. *Cymatium parthenopeum*; × 300. — Fig. 7. *Cymatium moritinctum caribbaeum*; × 100. — Fig. 8. *Cymatium nicobaricum*; × 210.

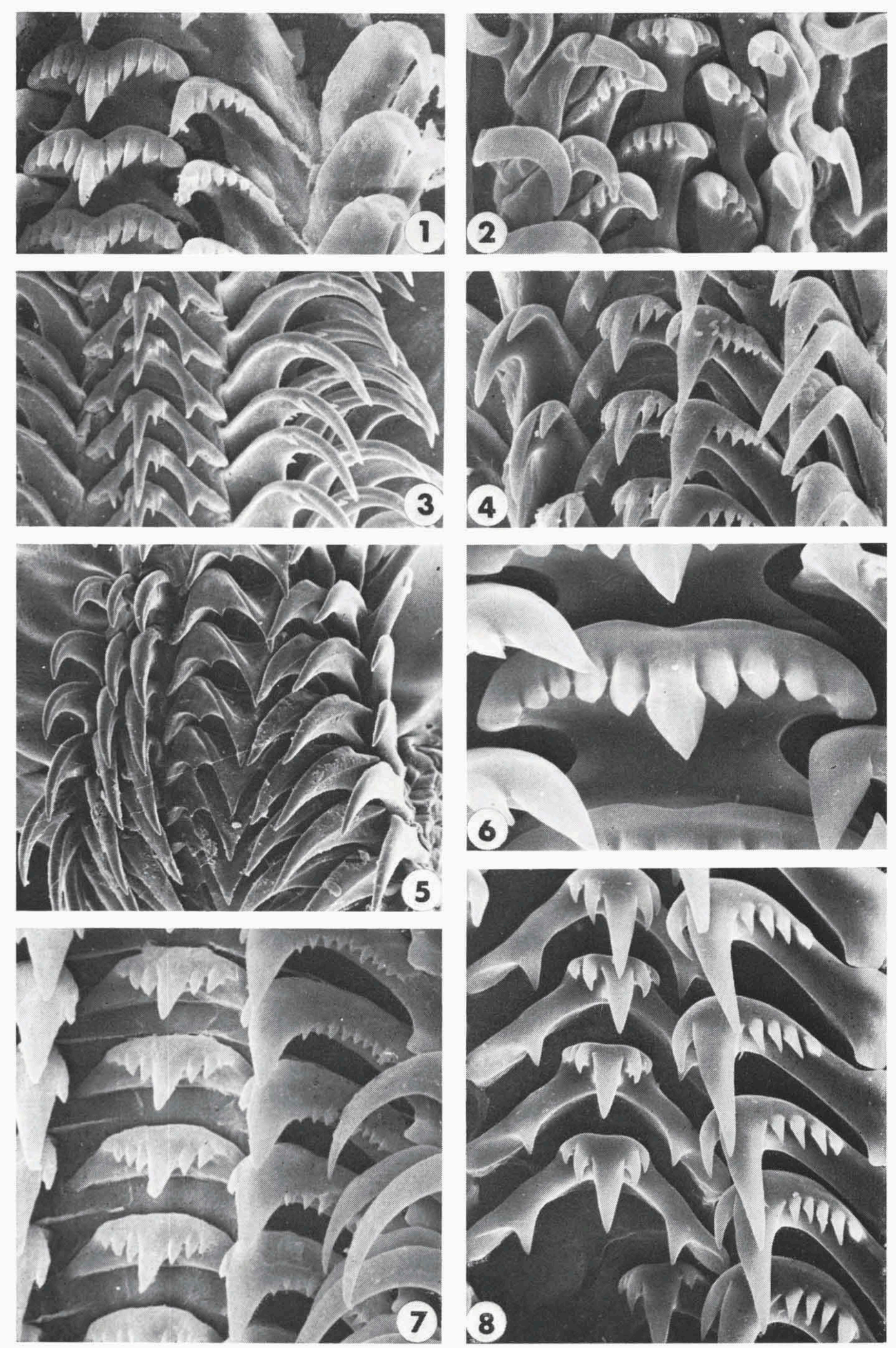


Fig. 1. *Cymatium muricinum*; × 360. — Fig. 2. *Cymatium labiosum*; × 345. — Fig. 3. *Bursa granularis cubaniana*; × 100. — Fig. 4. *Bursa thomae*; × 250. — Fig. 5. *Tonna galea*; × 15. — Fig. 6. *Cymatium pileare*, central tooth; × 500. — Fig. 7. *Distorsio clathrata*, central and lateral teeth; × 380. — Fig. 8. *Bursa granularis*, central and lateral teeth; × 350.

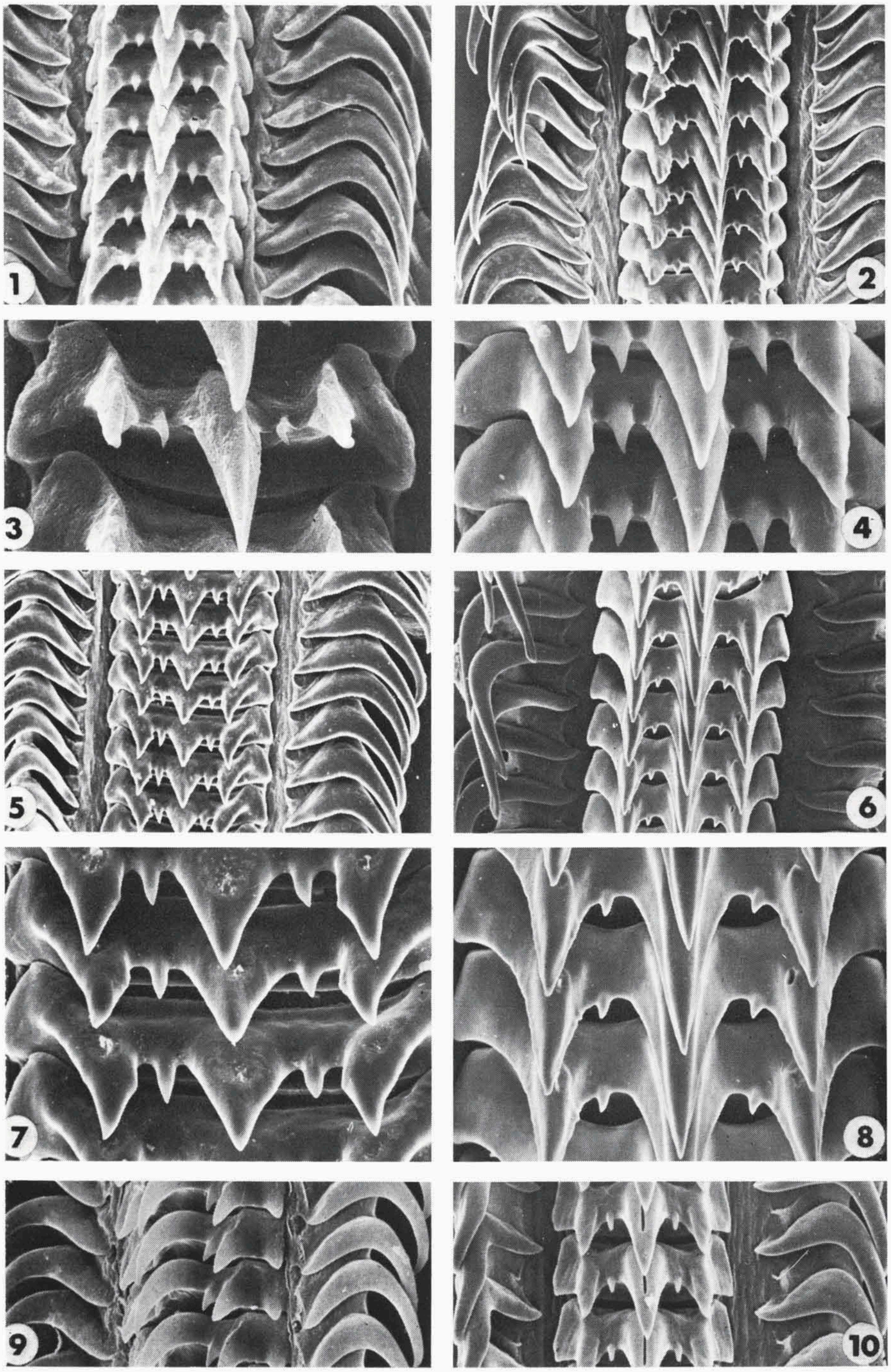


Fig. 1. *Murex recurvirostris rubidus*; × 115. — Fig. 2. *Murex recurvirostris woodringi*; × 100. — Fig. 3. *Murex recurvirostris rubidus*, central tooth; × 350. — Fig. 4. *Murex recurvirostris woodringi*, central tooth; × 195. — Fig. 5. *Murex pomum*; × 75. — Fig. 6. *Murex brevifrons*; × 100. — Fig. 7. *Murex pomum*, central tooth; × 170. — Fig. 8. *Murex brevifrons*, central tooth; × 185. — Fig. 9. *Morula nodulosa*; × 370. — Fig. 10. *Purpura patula*; × 105.

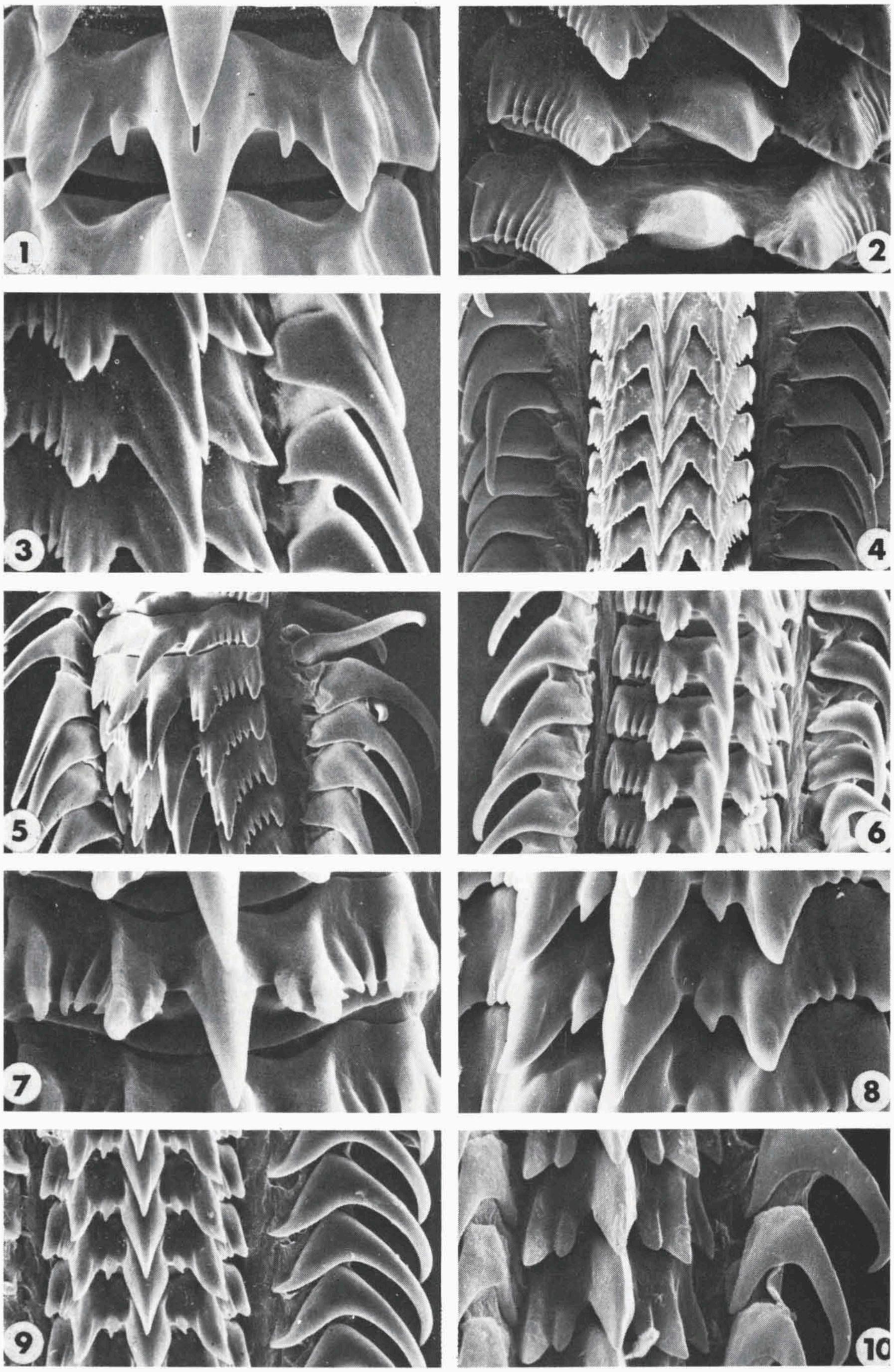


Fig. 1. *Purpura patula*, central tooth; × 250. — Fig. 2. *Thais haemastoma haemastoma*, central tooth; × 170. — Fig. 3. *Thais haemastoma floridana*; × 290. — Fig. 4. *Thais haemastoma haemastoma*; × 75. — Fig. 5. *Thais haemastoma floridana*; × 88. — Fig. 6. *Thais rustica*; × 170. — Fig. 7. *Thais rustica*, central tooth; × 340. — Fig. 8. *Thais deltoidea*, central tooth; × 440. — Fig. 9. *Thais deltoidea*; × 190. — Fig. 10. *Ocenebra rosea*; × 570.

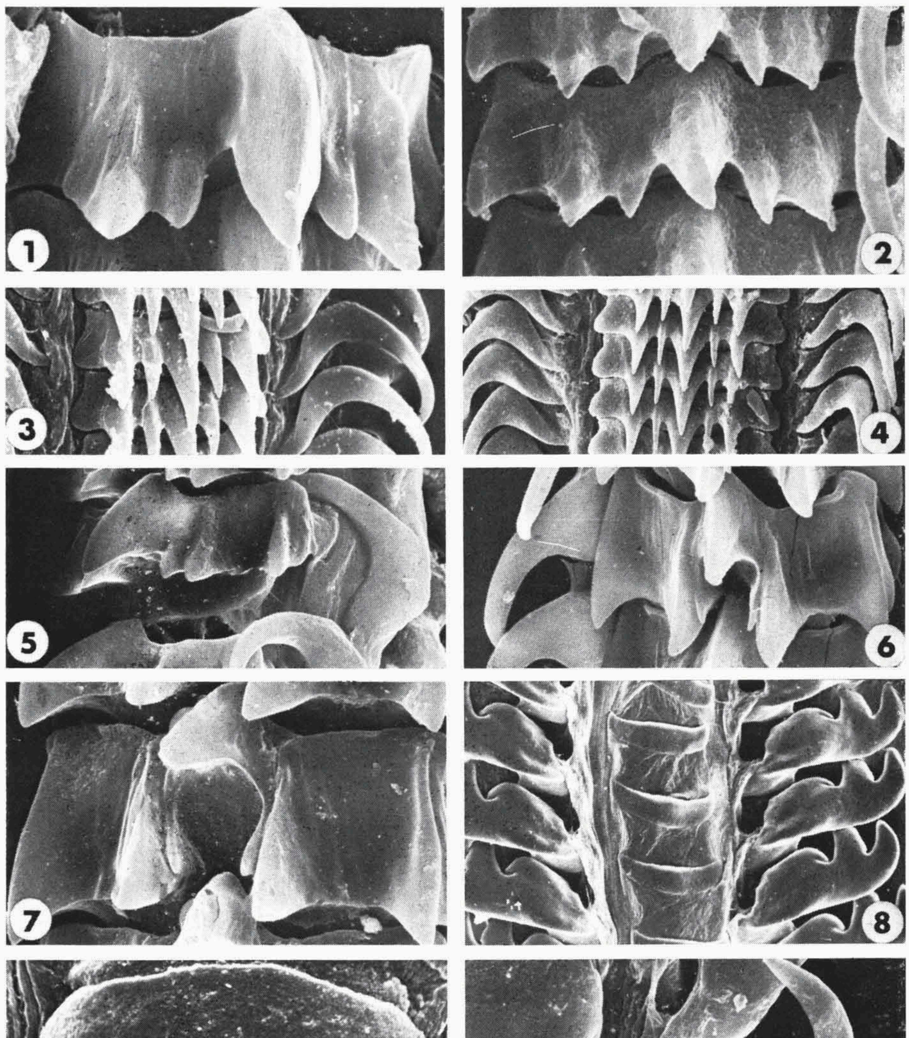


Fig. 1. *Ocenebra rosea*, central tooth; × 1150. — Fig. 2. *Favartia cellulosa*, central tooth; × 1230. — Fig. 3. *Aspella anceps*; × 580. — Fig. 4. *Aspella paupercula*; × 330. — Fig. 5. *Favartia cellulosa*; × 760. — Fig. 6. *Favartia alveata*; × 830. — Fig. 7. *Favartia alveata*, central tooth; × 1200. — Fig. 8. *Columbella mercatoria*; × 115. — Fig. 9. *Anachis sparsa*, central tooth; × 1550. — Fig. 10. *Anachis sparsa*, lateral tooth; × 820.

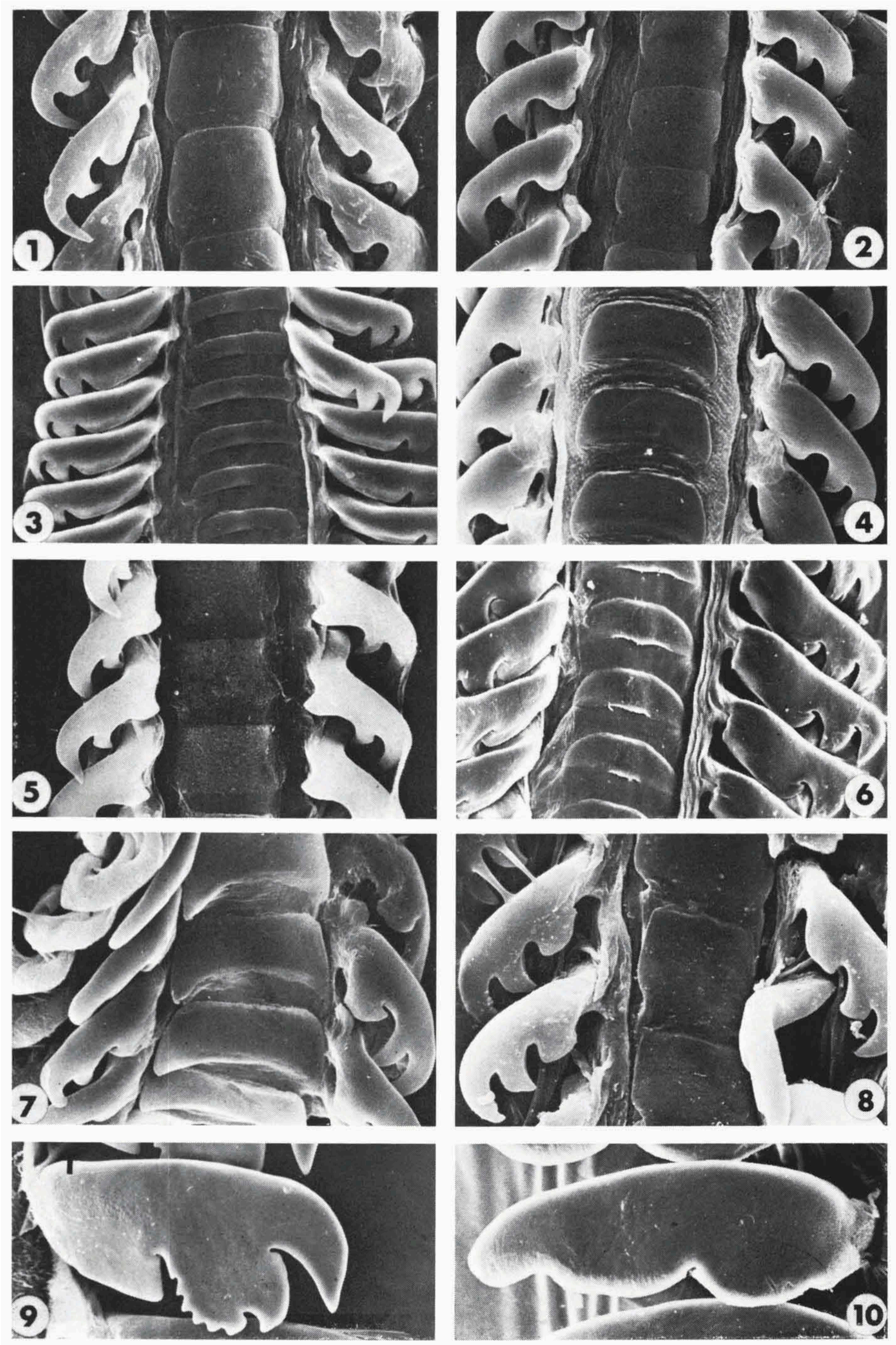


Fig. 1. *Anachis sparsa*; × 440. — Fig. 2. *Anachis brasiliana*; × 330. — Fig. 3. *Anachis pulchella*; × 150. — Fig. 4. *Anachis* sp.; × 460. — Fig. 5. *Anachis obesa*; × 515. — Fig. 6. *Nitidella nitida*; × 155. — Fig. 7. *Mitrella ocellata*; × 470. — Fig. 8. *Mitrella argus*; × 560. — Fig. 9. *Nitidella laevigata*, unused lateral tooth; × 380. — Fig. 10. *Nitidella laevigata*, used lateral tooth with worn cutting edge; × 390.

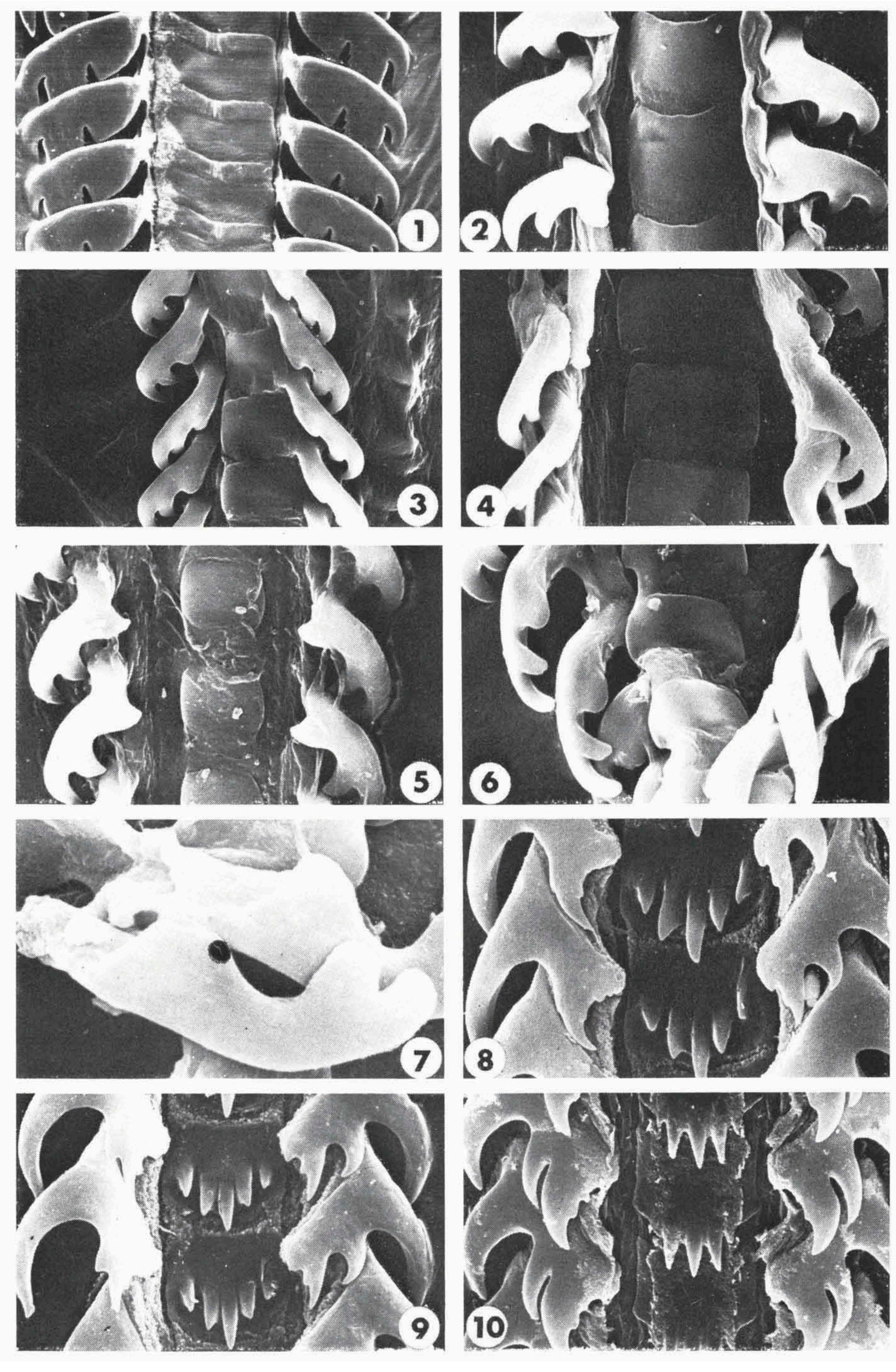


Fig. 1. *Nitidella laevigata*; × 119. — Fig. 2. *Mitrella lunata*; × 760. — Fig. 3. *Anachis* cf. *semiplicata*; × 390. — Fig. 4. *Anachis lafresnayi*; × 390. — Fig. 5. *Nassarina monilifera*; × 760. — Fig. 6. *Antillophos candei*; × 430. — Fig. 7. *Aesopus stearnsii*, lateral tooth; × 2640. — Fig. 8. *Engina* cf. *corinnae*; × 1030. Fig. 9. *Engina turbinella*; × 830. — Fig. 10. *Pisania tincta*; × 630.

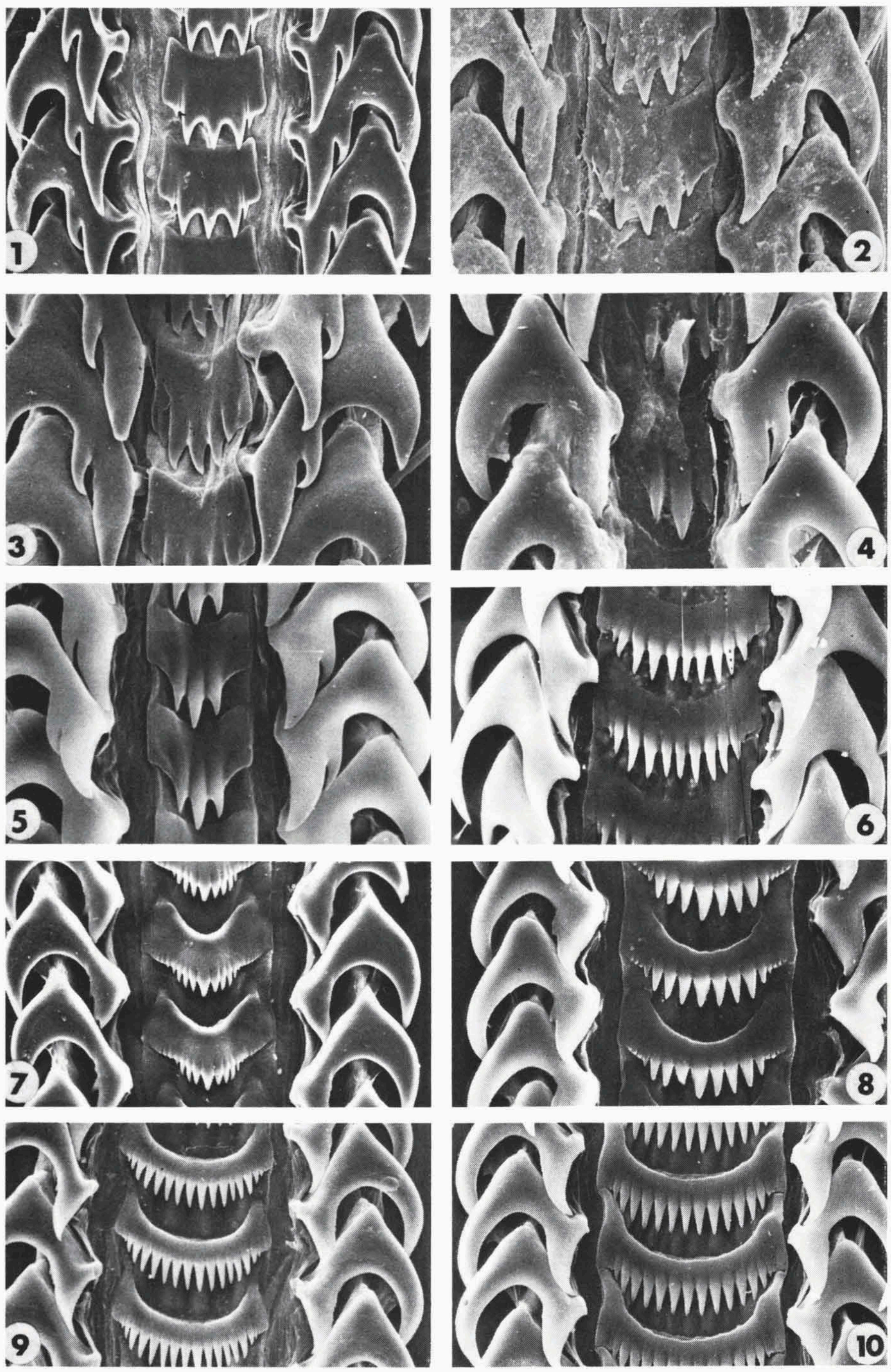


Fig. 1. *Pisania pusio*; × 102. — Fig. 2. *Pisania tincta*; × 410. — Fig. 3. *Pisania auritula*; × 120. — Fig. 4. *Dolicholatirus cayohuesonicus*; × 420. — Fig. 5. *Colubraria swifti*; × 380. - Fig. 6. *Engoniophos unicinctus*; × 245. — Fig. 7. *Nassarius albus*, male; × 136. — Fig. 8. *Nassarius albus*, female; × 245. — Fig. 9. *Nassarius vibex*, male; × 135. — Fig. 10. *Nassarius vibex*, female; × 200.

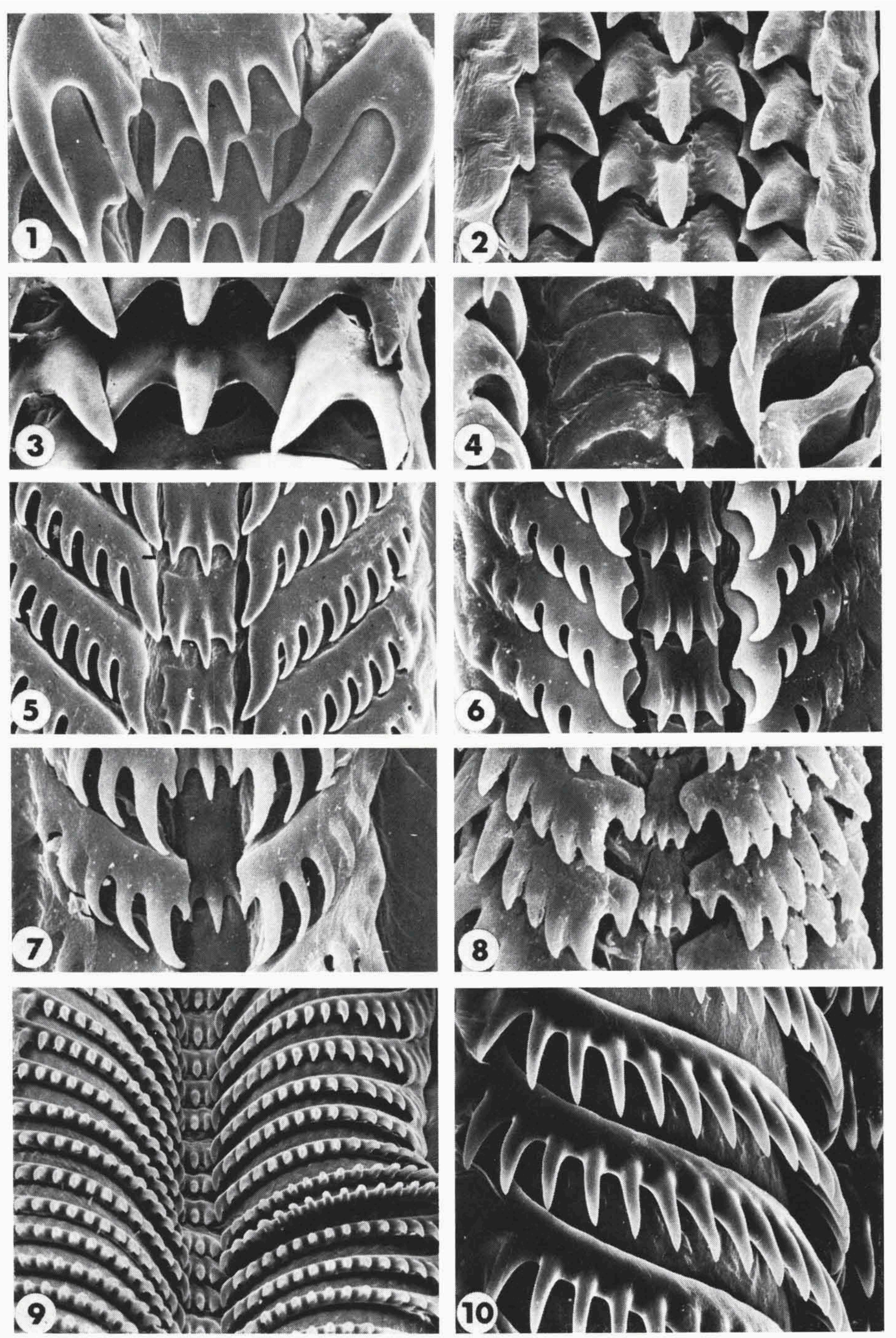


Fig. 1. *Melongena melongena*; × 170. — Fig. 2. *Vasum capitellum*; × 170. — Fig. 3. *Vasum muricatum*, × 100. — Fig. 4. *Turbinella angulata*; × 440. — Fig. 5. *Leucozonia nassa*; × 190. — Fig. 6. *Leucozonia ocellata*; × 330. — Fig. 7. *Latirus infundibulum*; × 330. — Fig. 8. *Latirus angulatus*; × 330. — Fig. 9. *Fasciolaria tulipa*; × 82. — Fig. 10. *Fasciolaria tulipa*, lateral teeth; × 200.

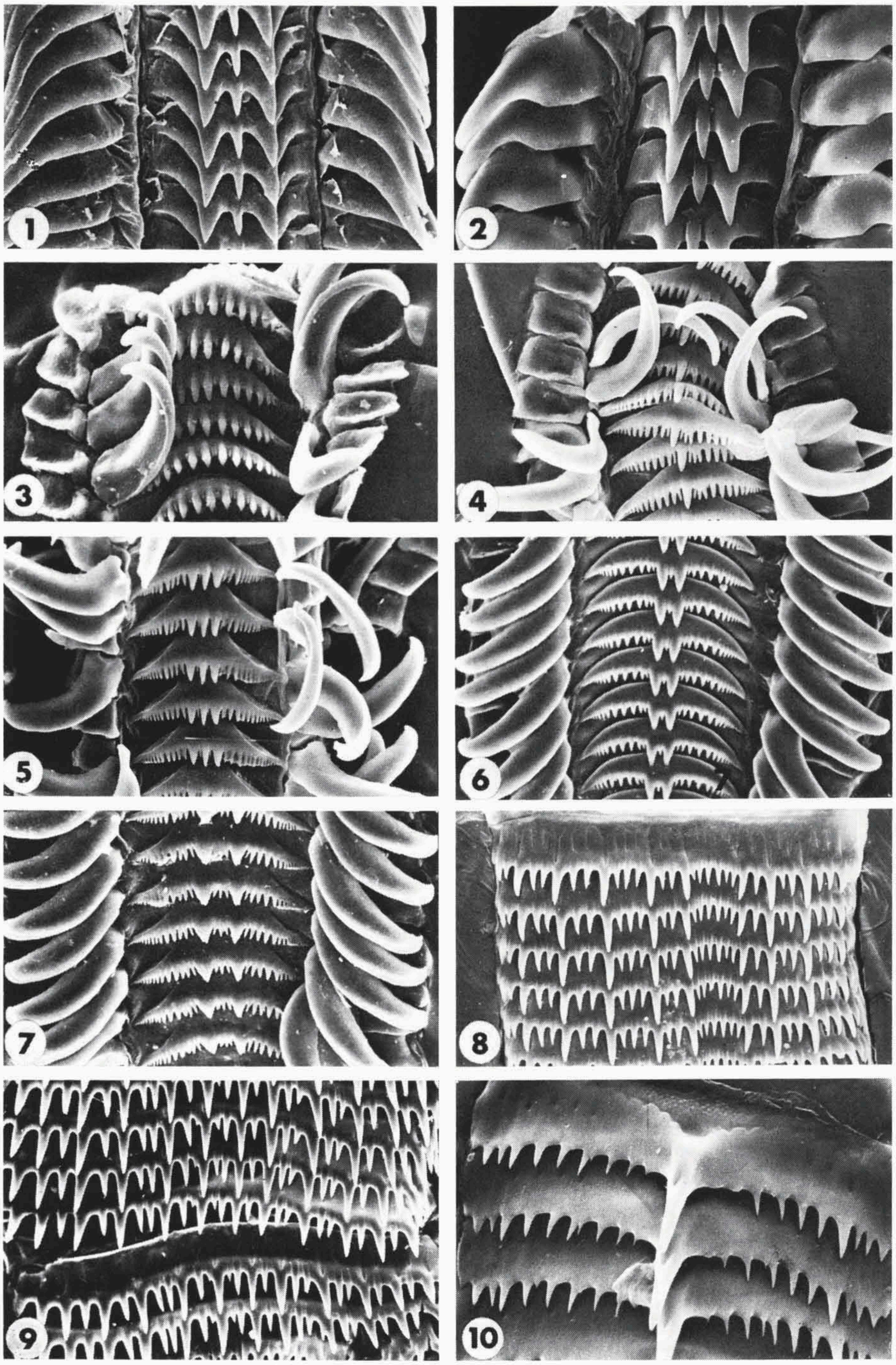


Fig. 1. *Oliva reticularis*; × 214. — Fig. 2. *Jaspidella jaspidea*; × 295. — Fig. 3. *Olivella dealbata*; × 245. — Fig. 4. *Olivella adelae*; × 190. — Fig. 5. *Olivella petiolita*; × 164. — Figs. 6-7. *Olivella nivea*; 6, × 80; 7, × 180. — Fig. 8. *Prunum marginatum*; × 140. — Fig. 9. *Prunum prunum*; × 92. — Fig. 10. *Hyalina avena*; × 260.

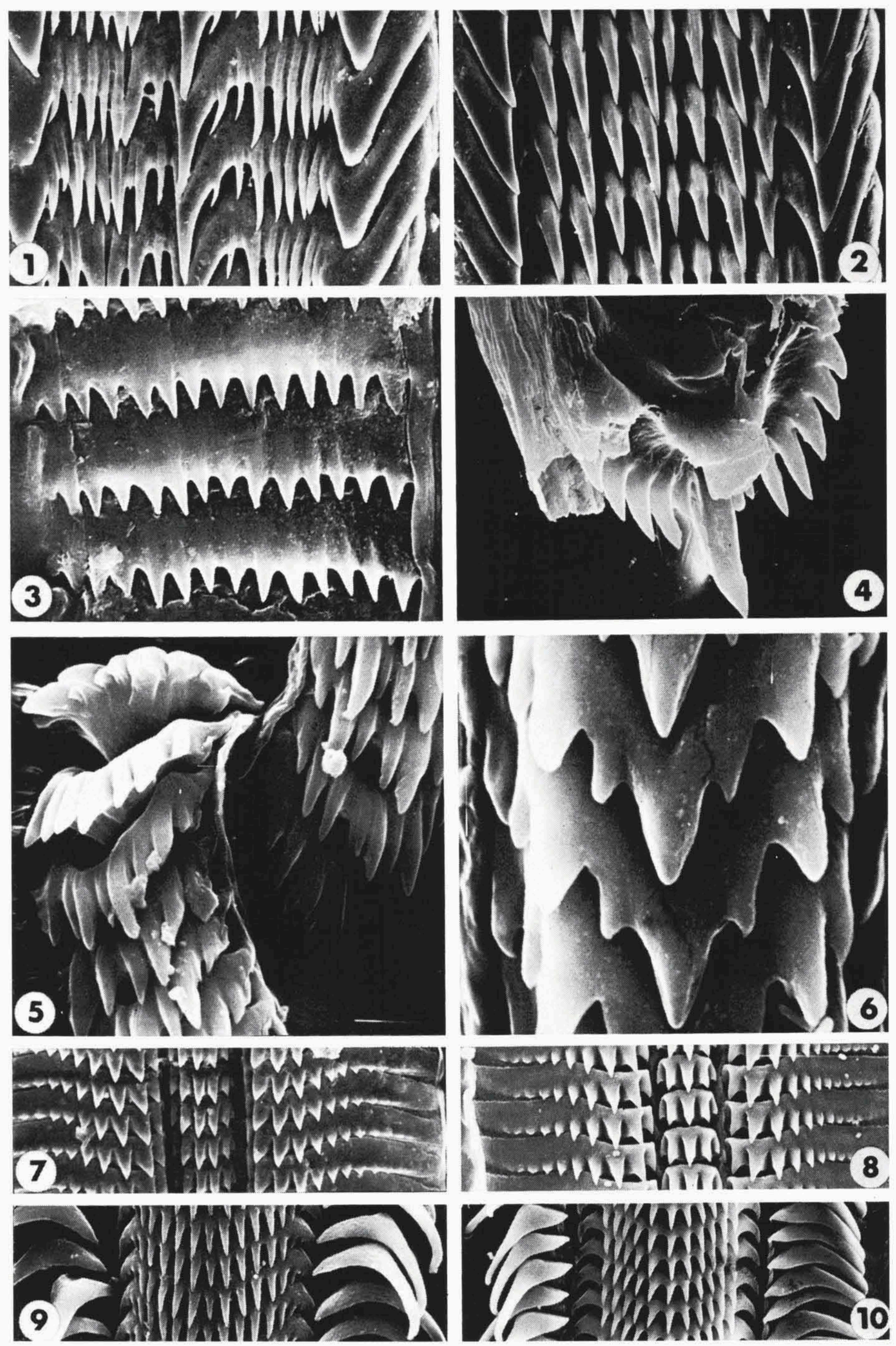


Fig. 1. *Voluta virescens*; × 295. — Fig. 2. *Voluta musica*; × 152. — Fig. 3. *Hyalina lactea*; × 985. — Fig. 4. *Persicula interruptolineata*; × 500. — Fig. 5. *Persicula pulcherrima*; × 1460. — Fig. 6. *Marginella lavalleana*; × 2600. — Figs. 7-8. *Mitra nodulosa*; 7, large form; × 116; 8, small form; × 172. — Fig. 9. *Vexillum dermestinum*; × 226. — Fig. 10. *Vexillum puella*; × 370.

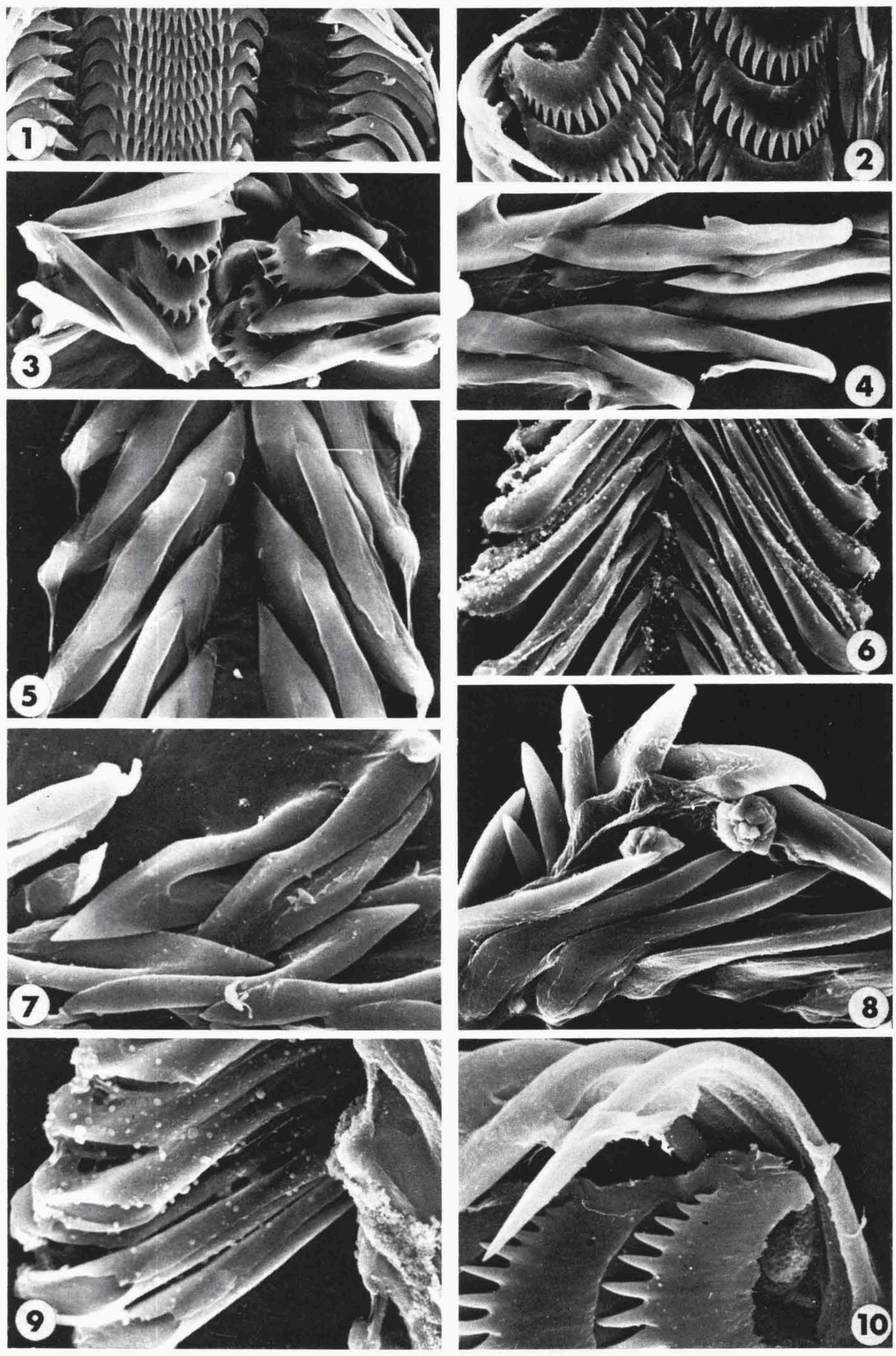
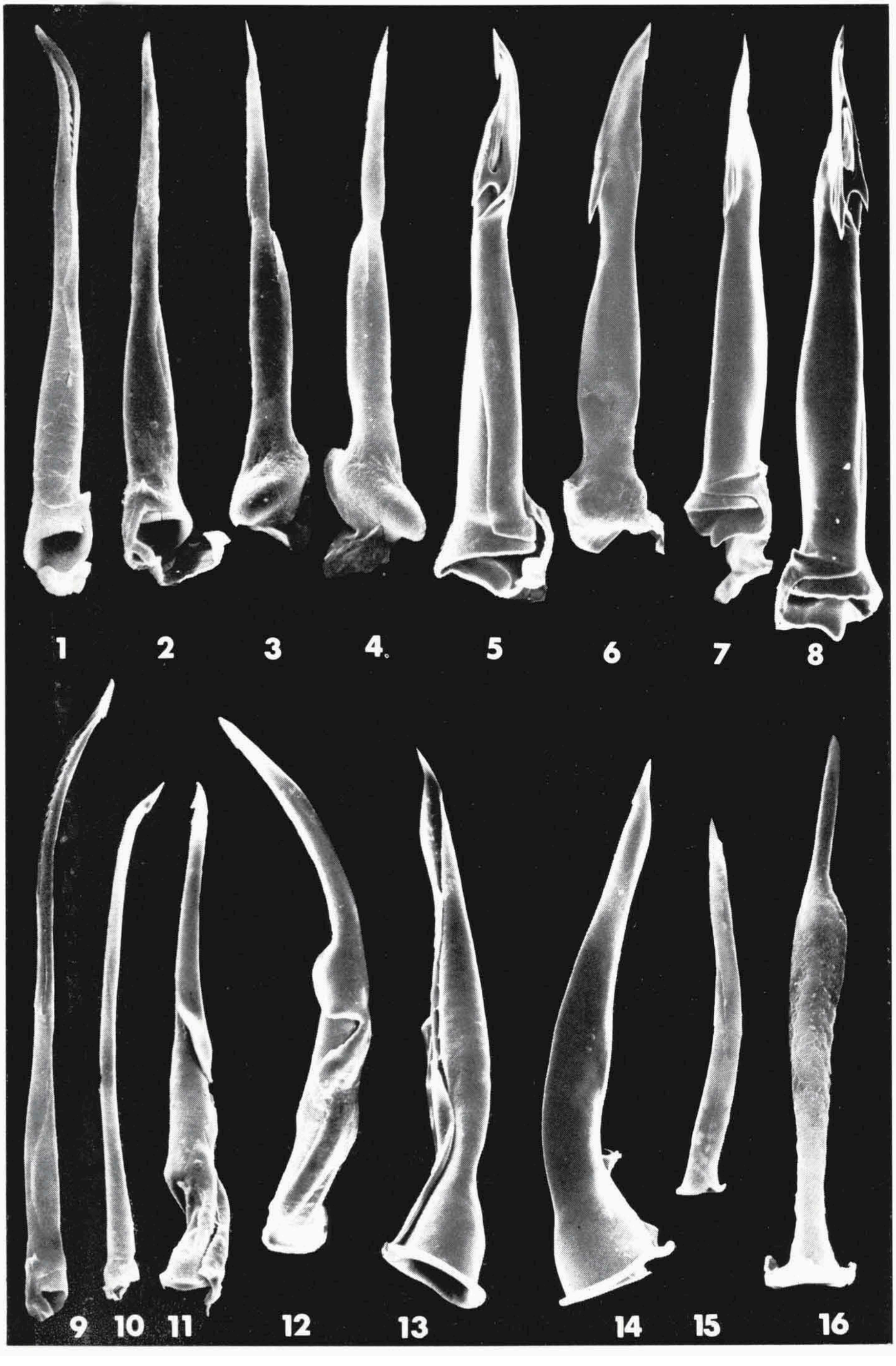


Fig. 1. *Vexillum hendersoni*; × 226. — Fig. 2. *Crassispira* sp.; × 245. — Fig. 3. *Drillia* sp. (2); × 225. — Fig. 4. *Drillia* sp. (1); × 380. — Fig. 5. *Crassispira albomaculata*; × 690. — Fig. 6. *Crassispira leucocyma*; × 214. — Fig. 7. *Polystira albida*; × 480. — Fig. 8. *Drillia solida*; × 362. — Fig. 9. *Crassispira leucocyma*, open ends of teeth; × 370. — Fig. 10. *Crassispira* sp., marginal teeth; × 570.



Figs. 1-2. *Conus mus*; 1, × 128; 2, × 150. — Figs. 3-4. *Conus jaspideus pygmaeus*; 3, × 175; 4, × 175. — Figs. 5-6. *Conus regius*; 5, × 45; 6, × 59. — Figs. 7-8. *Conus testudinarius*; 7, × 36; 8, × 46. — Figs. 9-10. *Conus spurius phlogopus*; 9, × 101; 10, × 55. — Figs. 11-12. *Terebra taurinus*; 11, × 85; 12, × 88. — Figs. 13-14. *Terebra cinerea*; 13, × 111; 14, × 108. — Fig. 15. *Terebra protexta*; × 230. — Fig. 16. *Terebra* sp.; × 625.

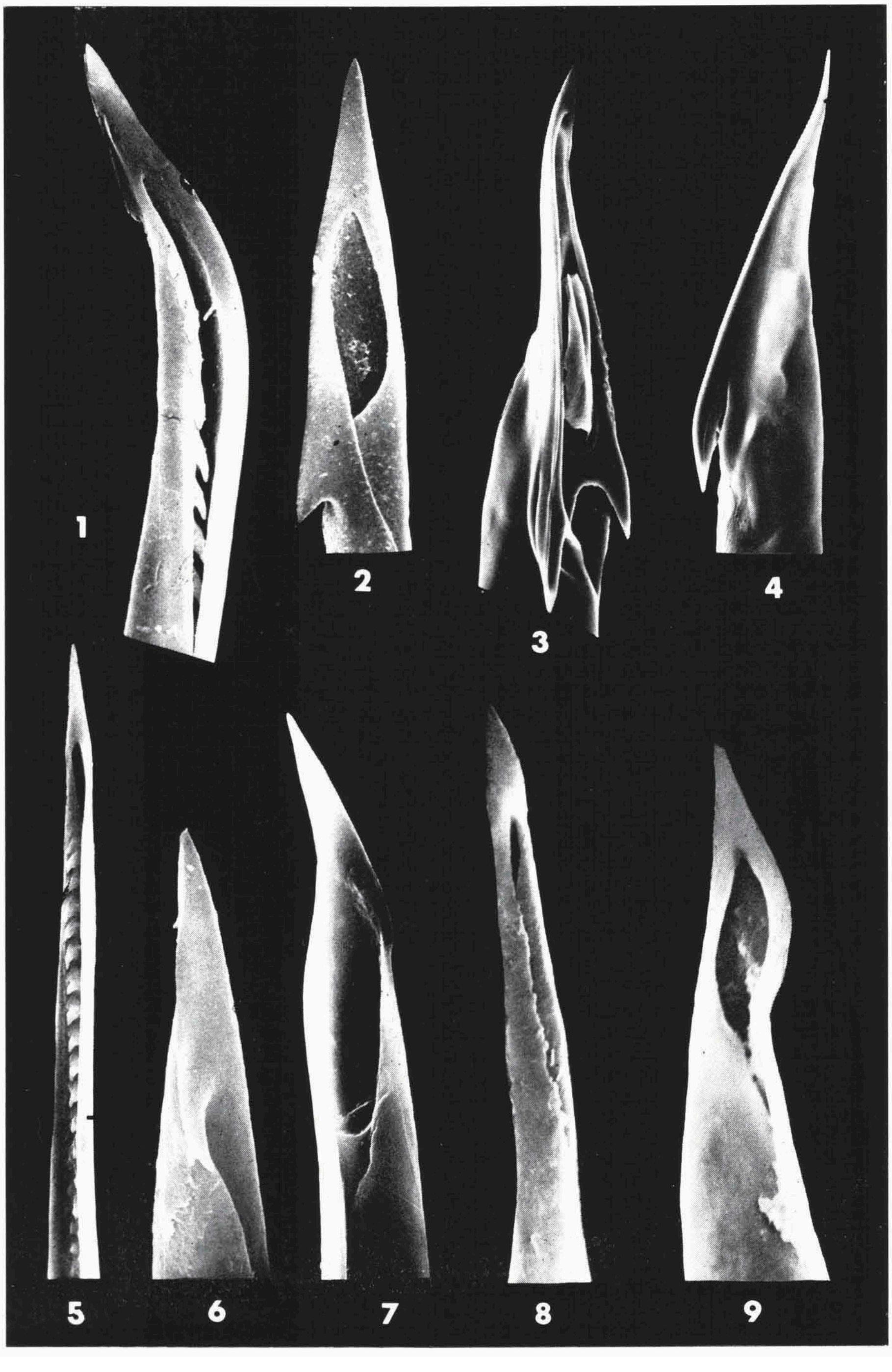


Fig. 1. *Conus mus*, apex of tooth; × 580. — Fig. 2. *Conus jaspideus pygmaeus*, apex of tooth; × 930. — Fig. 3. *Conus testudinarius*, apex of tooth; × 115. — Fig. 4. *Conus regius*, apex of tooth; × 117. — Fig. 5. *Conus spurius phlogopus*, apex of tooth; × 300. — Fig. 6. *Terebra taurinus*, apex of tooth; × 785. — Fig. 7. *Terebra cinerea*, apex of tooth; × 500. — Fig. 8. *Terebra* sp., apex of tooth; × 2500. — Fig. 9. *Terebra protexta*, apex of tooth; × 1500.