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THE VELIGER

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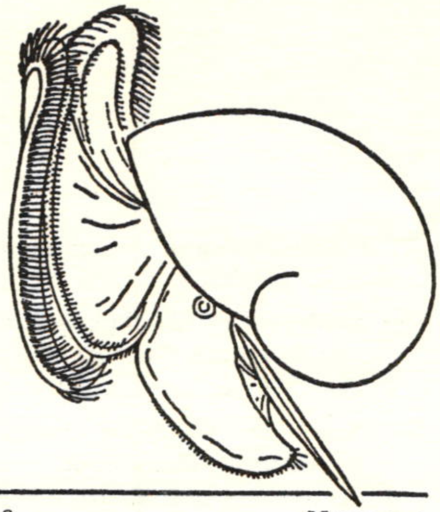

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Note: The various taxa above species are indicated by the use of different type styles as shown by the following examples, and by increasing indentation.

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

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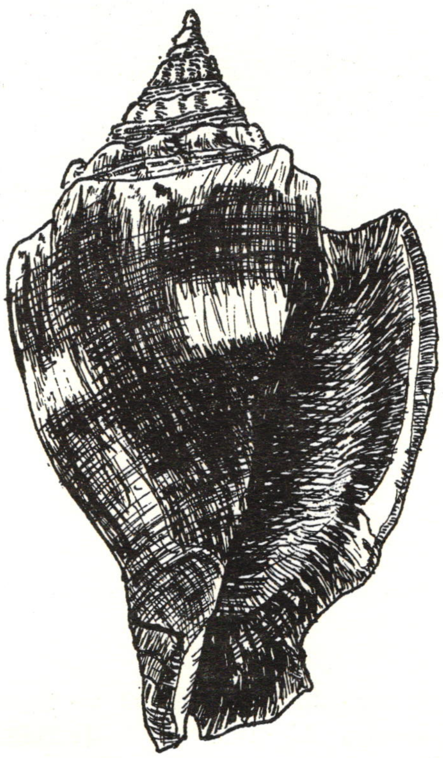

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Observations on Spawn, Embryonic Development and Ecology of Some Caribbean Lower Mesogastropoda

(Mollusca)

BY

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(25 Text figures)

INTRODUCTION

WHILE I WAS WORKING for 18 months (1970 - 1972) as guest of the Instituto Colombo Aleman (ICAL) in Santa Marta on the Caribbean coast of Colombia the spawn of 23 species of Mesogastropods, including one species belonging to the family Pyramidellidae, was collected. Observations on spawning females were carried out in the sea and in the aquaria for most species mentioned here. Additional samples were collected at Curaçao, Netherlands Antilles during a 10 day visit as guest of the Caraibisch Marien Institute (Carmabi) in 1971.

The study was financed by the Deutsche Forschungsgemeinschaft (ER 4/26).

The only fresh water representatives mentioned in this study belong to the family Ampullariidae. They are *Marisa cornuarietis* (Linnaeus, 1758), *Ampullarius monticolus* Vernhout, 1914, and *A. porphyrostomus* Reeve, 1856. The superfamily Cerithiacea includes most of the species mentioned here. Its family Turritellidae is represented by *Turritella variegata* (Linnaeus, 1758); family Architectonicidae with *Architectonica nobilis* Röding, 1798; family Vermetidae with *Petaloconchus mcgintyi* Olsson & Harbison, 1953, and *P. erectus* Dall, 1888; family Caecidae with *Caecum antillarum* Carpenter, 1858; family Planaxidae with *Planaxis nucleus* (Bruguière, 1789); family Modulidae with *Modulus modulus* (Linnaeus, 1758) and *M. carchedonius* (Lamarck, 1822); family Cerithiidae with *Cerithium litteratum* (Born, 1778), *C. atratum* (Born, 1778), *C. lutosum* Menke, 1828 and *Alaba incerta* (d'Orbigny, 1842). The superfamily Epitoniacea is represented by *Epitonium lamellosum* Lamarck, 1822. The superfamily Pyramidellacea includes *Cingula babylonia* C. B. Adams, 1845. *Cheilea equestris* (Linnaeus, 1758) and *Hipponix antiquatus* (Linnaeus, 1767) are included in the superfamily Hipponicacea. The superfamily Calyptraeacea is represented by *Calyptraea centralis* Conrad, 1841; *Crucibulum auricula* (Gmelin, 1791); *Crepidula convexa* Say, 1822; *C. glauca* Say, 1822 and *C. plana* Say, 1822.

The egg capsules of some representatives of the Littorinacea from Santa Marta have been described by BANDEL (1974b) and the discussion of those of some higher Mesogastropoda is at the printer (BANDEL, in press) or has

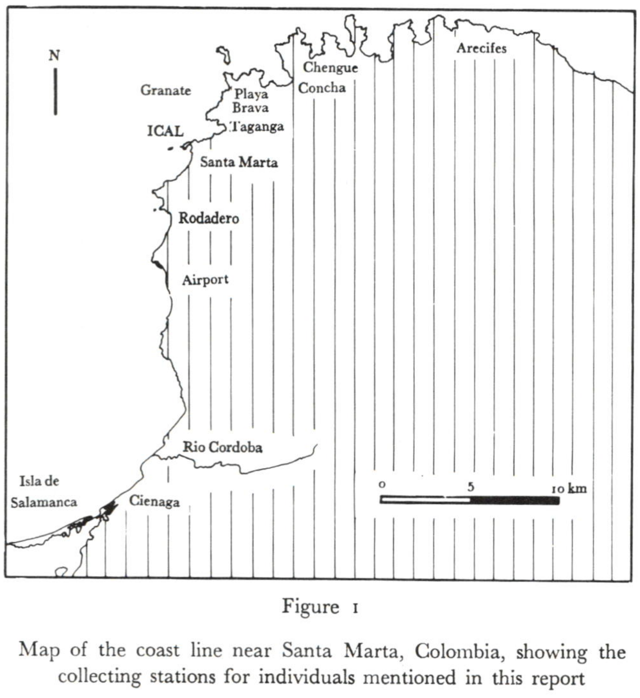


Figure 1

Map of the coast line near Santa Marta, Colombia, showing the collecting stations for individuals mentioned in this report been published (BANDEL, 1973). Most shells of young hatching from egg masses described here are figured and described by BANDEL (1975, in press).

METHODS

Seawater was continuously exchanged during 12 hours of each day in the aquarium, which was sufficient for successful maintenance of most the species discussed. Some aquaria and laboratory space were provided by the former director of ICAL, Dr. R. Kaufmann whom I like to thank here. Fins, snorkel and face-plate were used to collect animals or their spawn in the sea. Diving equipment with compressed air tanks was only rarely needed. Most collecting and observing was carried out by my wife and me. A few egg masses were collected by R. von Cosel (Giessen) and Mr. de Jong (Curaçao) during our stay in Santa Marta and Curaçao and turned over to me. To both I like to express my thanks.

Freshly collected spawn from the sea and freshly deposited spawn from the aquaria were usually kept in glass bowls until embryos hatched, or if the spawn was of larger size, in aquaria with running seawater until hatching started and then transferred into larger bowls. Water in the glass bowls was exchanged every 2 days, which proved to be quite sufficient, as was verified by comparison with like spawn developing under observation in the sea and in aquaria.

Drawings of typical egg-capsules and egg-masses were made, if possible, from freshly deposited spawn. They were made by my wife with the aid of a binocular microscope. Spawn was transported to Bonn in 70% ethanol.

Identifications of the adult spawning animals were made with the aid of publications by WARMKE & ABBOTT (1962) and KAUFMANN & GÖTTING (1970). Members of the genus *Cerithium* were checked and misidentifications corrected by Dr. Richard S. Houbrick, Washington, D. C.

REMARKS ON THE ECOLOGY OF THE ADULT INDIVIDUALS

In a transect beginning on a rocky, wave-swept beach and continuing across a bay with at first sandy, later muddy bottom, to coral growth protecting a lagoon which lies behind it, and beyond it still a closed off lagoon with brackish or saline water, almost all species mentioned in this report could be encountered. This may, in reality, be observed in the Ensenada Chengue north of Santa Marta.

Where waves wash against large rocks and cliffs, populations of *Petaloconchus mcgintyi* are found. Individuals of this species will settle within the narrow intertidal zone (only 20 cm high) of the area at Santa Marta and above it in rock crevices that are often washed-through, and in tide pools in exposed situations. Normally, single individuals or groups of individuals entangled with each other are tightly attached to the rock-surface and extend with their apertures very little above it. Short periods of dryness during low tide or water warmed in tide pools are tolerated without ill effects on the animal. In the bay of Playa Brava, individuals of this species have settled on a beach rock platform in the upper part of the intertidal range. Here in an area where normally heavy surf action is encountered, *P. mcgintyi* individuals form small reef-like bodies of about 5 cm height and 10 cm width. The shells of single individuals within these bodies support each other so that the apertures of all jointly can be extended further above the surface of attachment than seems to be possible to a single individual.

On rocks and pebbles of shingle or pebble beaches in areas with strong wave action as well as beaches with little wave action, *Planaxis nucleus* may be found in great abundance. On days with strong sun radiation, all individuals remain concealed under rocks in wet surroundings. When the sun is obscured, at dawn, or conditions with strong spray prevail, the snails will graze algae on the surface of pebbles and boulders. The population will migrate up and down with the tide, so that they may always be found in greatest density just above the water line or under rocks. Pure rock cliffs are avoided by members of the genus *Planaxis.*

In shallow water just below the lowest tide line or in the lowermost part of the tidal range as well as to about 1 m depth (below the ICAL), cliffs and large rocks on beaches with moderate or little surf may be covered with a dense growth of *Sargassum*-bushes. On the leaves of this alga we usually encounter a rich population of the small *Alaba incerta. Sargassum* is its favoured milieu, but smaller populations of this species may also be found on all algal growths in shallow, well lighted water. In the bays of Chengue and Granate during the season with passat winds, when water is very clear, large bushes of *Sargassum* will grow up from a maximum depth of 10 m to the surface. They form thickets rooted on the bottom of the rocky Granate and the off-shore calcareous slabs broken off the Chengue coral reefs. On each bush of this alga a huge population of *A. incerta* is established within a short time. After a few months' time the wind conditions will change, due to the rainy season, and connected with it,

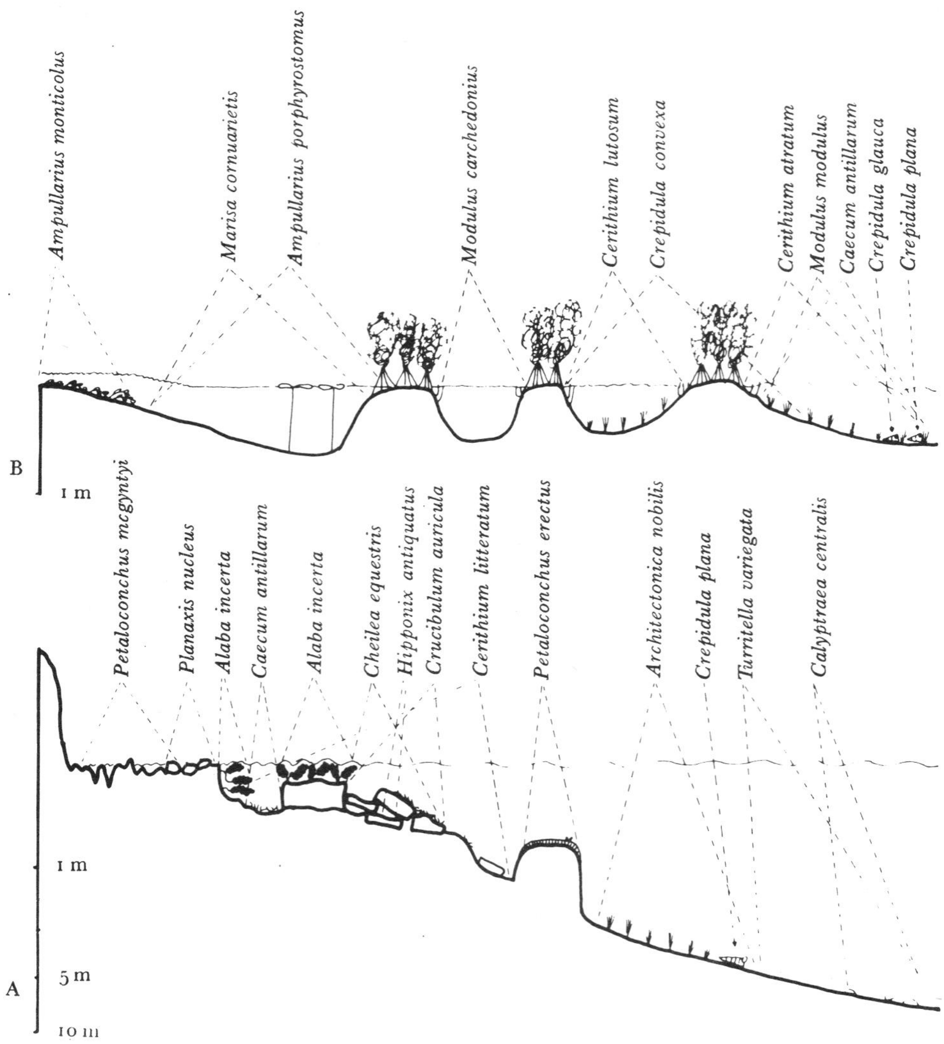


Figure 2

Generalized profiles demonstrating typical habitats of the mesogastropod species of which the spawn is described. From left to right: A) Rocky shore with tidal and splash pools, wave-washed rocks in the intertidal area, rocky drop-off from low water line to water a few decimeters deep, with growths of *Sargassum*, fine filamentous algae forming crusts and overgrowths on pebbles and rocks, large rock extending up to low water line in places with thick growths of *Sargassum*, rubble with open interspaces and algal overgrowth, large rock with coelenterate cover, turtle grass bottom, sandy to muddy bottom. B) River coming from the mountains, ending in fresh water lake, bordered by mangrove swamp, a brackish lagoon, mangrove swamp, fully marine to saline lagoon, beach overgrown by mangrove, fully marine sand bottom with turtle grass.

higher fresh water runoff occurs, so coastal waters will become more turbid. Therefore, light conditions will become unfavourable to the *Sargassum* bushes and they will die. With them the population of this small cerithid will perish, leaving abundant fresh shells on the bottom in an area where no living *Alaba* may be found and the next living population may be encountered some distance away.

At the ICAL below the *Sargassum* belt and between it is situated an area with large rocks. Where surf is not too strong, a thick growth of fine algae will cover the surfaces of the rocks. This cover may be found from a depth of 0.5 m to about 2 m; in the Ensenada Chengue it continues down to about 5 m. In this thicket of filamentous algae many individuals of a few different species of *Caecum* can be encountered, one of them being *C. antillarum*. Algal thickets within the well lighted zone on rocks, gravel, sand, and mud are the favoured living-place for members of this genus around Santa Marta. Only the area of direct wave action is avoided. The animals live on diatoms and other minute organisms which occur in the thickets or on detrital particles that may become entangled in them from water passing through.

This general area is also favoured by *Cerithium litteratum*. Populations often consist of many individuals which settle on rock surfaces in cliff areas, in pebble and boulder zones, and where rocks are strewn into sand and mud surroundings. When rocks are settled, the area with surf action is avoided and individuals will occur in depths with calmer water.

Another large occurrence lies within the lagoonal seagrass environment in association with *Modulus modulus* and *Cerithium atratum*. While *C. litteratum* shows a preference for hard substrates, *C. atratum* prefers soft bottoms. It may be found from the intertidal area in quiet bays and lagoons down to a few meters of depth. Near the former small settlement of Tanganilla, just below the ICAL, especially rich populations of this species are indicators of abundant natural (raw) sewage. Here up to 50 individuals may be counted on 10 cm^2 of gravel beach. But also on deeper bottoms groups of up to 100 individuals usually graze in close contact with each other on the muddy or sandy surface, similar to flocks of sheep. Both members of the genus *Cerithium* feed mainly on detrital material collected continuously on the surface of the sediment.

A somewhat intermediate biotope of rocks on a sandy or muddy bottom is preferred by *Modulus modulus* below the ICAL. But along with both species of *Cerithium*, it is most common on the blades of lagoonal seagrass. Its occurrence lies between 0.2 and 2.0 m of water. Individuals of this species graze algae from rocks and the blade-like leaves of *Thalassia*.

On the surface of flat rocks, under the cover of other rocks with an open system of spaces between them, the sessile *Hipponix antiquatus* is located. It was found in a depth of 0.5 to 2.0 m. Adult individuals have become completely sessile and have secreted a calcareous plate which cements the sole of the foot to the underlying rock surface. Therefore they cannot be removed from the substrate without damage to the tissue of the foot. Individuals of this species rely on filtering seawater as a source for food and consequently prefer open rock cove systems close to areas with strong wave movement, but far enough from strong surf where rocks may be turned over by the force of the waves. Individuals have never been found on the lower sides of rocks and on exposed rock surfaces.

Cheilea equestris, on the other hand, normally uses the lower sides of rocks in depths of 0.4 to 4.0 m of water for attachment, and may be removed easily from its site of attachment without injuring the tissue of the foot. The outer edge of the shell follows the irregularities of the substrate to which the individual clings. This may indicate that the individual will not voluntarily change its location but will remain confined to one spot where it lives by filtering the seawater for food. In addition to the undersides of rocks, bottles and shells of dead or living larger mollusks may be used for attachment by *Cheilea*.

Crucibulum auricula inhabits exactly the same environment as *Cheilea equestris*; but it is also common in deep dredgings (down to 50 m). There it is attached to larger shells and rocks. The animal lives by filter-feeding.

In a depth of 1 to 2 m large boulders are often completely covered by colonial actinians (below the ICAL). From this cover emerge the tube endings of *Petaloconchus erectus*, while the whole shell is otherwise hidden by the coelenterate cover. The gastropod usually forms tightly entangled colonies of a few individuals which live protected from predators by the polyps of the nettling coelenterates, and feed by filtering the seawater.

Sandy bottoms between seagrass are the preferred habitat of *Architectonica nobilis* during the daytime. Individuals of this species are usually hidden in the sand, buried shallowly, strangely with the apical part of the shell pointing into the sand, quite opposite to the usual way in which prosobranchs rest in the substrate. Only rarely may individuals of this species be seen searching for food during daylight, but at dawn or at night most animals become active. They leave their resting place in the sand and crawl over the substrate on a broad sole, the apex now pointing in the normal upward position. Their prey consists of all kinds of soft bodied actinian-type coelenterates which usually are present in large numbers on the blades of seagrass and on rock-surfaces. Large prey individuals are attacked by the gastropod close to the base.

Here *Architectonica* rasps a hole and extends its proboscis into the coelenterate, feeding on it until it dies (up to a few days).

Many larger gastropods carry individuals of *Crepidula convexa* on their shells. The preferred site for attachment was found to be close to the outer lip of the host. In the Ensenada Chengue mostly *Tegula fasciata* (Born, 1778) were used as substrate in the lagoonal seagrass biotopes. In more closed-in lagoonal areas the shells of *Cerithium lutosum* were used for attachment. Close to the airport of Santa Marta, individuals of *C. convexa* were found on *Tegula lividomaculata* C. B. Adams, 1845, *Leucozonia nassa* (Gmelin, 1791) and even on the outside of the siphonal canal of *Fasciolaria tulipa* (Linnaeus, 1758) living on a beachrock bar within and a little below the tide zone. Below the ICAL, in the small bay of Taganilla, *Latirus infundibulum* (Gmelin, 1791) and *Cerithium atratum* were used as substrate. The area of distribution of *Crepidula convexa* is restricted to the tidal zone and the area just below it, but extends into a larger number of habitats from warm, slightly saline lagoons to fairly exposed rock cliffs, from muddy substrates to pebble beaches. Commensalism with the host or usage of the feces of the host does not seem to be of importance to *Crepidula convexa*, for the different prosobranchs used for attachment have widely different requirements of food (Bandel, 1974a). But it can be expected that the inhalant watercurrent of the hosts may be an aid to the slipper shell filtering its food from the water.

While *Crepidula convexa* may only be found associated with the shells of living gastropods, *C. plana*, and more rarely, *C. glauca* are only found associated with shells carried around by hermit crabs. Almost every shell used as shelter by hermit crabs is also inhabited by a few individuals of *C. plana* of different sizes. They are attached close to the inner side of the outer lip of the shell. *Crepidula glauca* was found in the same position in a few shells carried around by hermit crabs in the bay of Chengue. Both species probably can be considered as true commensals with the very active hermit crabs, using both the feeding and defecation of their host as sources of food which is filtered from the water passing their site of attachment. Hermit crabs can roam over large areas, extending from the intertidal zone to depths of 15 m, and therefore the living ranges of both species of *Crepidula* equal that of the crabs.

Dead shells of larger mollusks found on soft substrates in depths greater than 10 m are often used for attachment by *Calyptraea centralis*. This species feeds by filtering seawater for food. It usually has a smooth shell edge.

Cerithium lutosum was found only in the bay of Chengue. It occurs there in huge numbers on the soft bottom and on algae in a slightly saline, shallow lagoon connected to the sea only by a continuously open narrow channel. Another place with abundant individuals may be found in the intertidal zone of a backreef lagoon, where decaying seagrass (*Thalassia*) provides their favored source of food. Diatom covers and all kinds of decaying plant material are used as food by individuals of this species. They prefer water of a higher salinity and higher temperature than found in the open ocean.

Modulus carchedonius also prefers closed off lagoonal environments, but with water of somewhat lower salinity than is found in normal seawater. In the area of Santa Marta, living individuals were encountered only in a sand-locked channel leading into a small artificial harbour of the resort settlement of Santa Marta Rodadero. Into this basin, which exchanges water with the sea only at high tide, a few sewer pipes enter, coming from apartment and hotel buildings. They enrich the water with organic material and add fresh water to it. *Modulus carchedonius* lives here, feeding on algae growing on large debris of plants and wood at the bottom of the channel, which is only about 1.5 m deep. They are also found on rotting wood pilings and rocks covered with algal growths on the sides of this channel which was constructed to connect the harbour with the open sea. In dry periods of the year, the salinity is only slightly lower than that of the open sea, but during rainy times it may drop to about 15‰.

Turritella variegata usually remains immobile for long periods of time, shallowly buried in soft substrates; it is a filter feeder. The high conical shell lies in a horizontal position parallel to and just below the surface of the sediment, but completely hidden. Only 2 holes may be seen in the sediment where the animal lies concealed, one of the inhalant, the other of the exhalant water current. The exit from the mantle cavity is kept open with the siphon extending to the surface of the substrate. The individuals are encountered in large populations with the animals situated closely together in mud of quiet lagoons. Good examples of this are found in the little bay of Taganilla, just below the ICAL, and the larger bay of Taganga, from a depth of 2 m downward. The animal will leave its resting place voluntarily only at the time of spawning, once a year, and crawl to more sandy bottoms or bottoms covered with gravel. Here they can attach their spawn more firmly in and on the substrate than would be possible in the muddy environment. Observations carried out continuously during 18 months on a population of this species in the bay of Taganilla showed no movement of *Turritella* outside of this period. The trails left by the crawling animals returning from spawning are destroyed rapidly by benthonic animals, so nothing reveals the living place of the buried animal on a bottom pierced by numerous openings of all types of filtering and bottom inhabiting animals.

Marisa cornuarietis lives in all larger bodies of fresh water distributed in considerable numbers within the large delta region of the Rio Magdalena and in dead arms of this river. Large populations were encountered in ponds along the road from Barranquilla to Cienaga, if they contained fresh water. Individuals of this species were also observed in large populations in the inland lakes and fresh water lagoons between Barranquilla and Cartagena. The animals were easily maintained in a small concrete outdoor pond within the area of the ICAL. Here they were fed with all sorts of fresh plant material, especially green lettuce. Well fed individuals spawned at regular intervals throughout the year.

Ampullarius monticolus lives in the Rio Cordoba between Santa Marta and Cienaga and was collected below the road bridge from the steep walls of irrigation canals carrying fast flowing clear mountain river water. Individuals of this species prefer shady places but may also be seen crawling on the sandy bottom in creeks with fast flowing water. The animals feed on decaying plant material as well as on fresh plants of many kinds. In the above mentioned pool at the ICAL, they lived on lettuce and remained close to the shore, often exposed partly to the free atmosphere, but always remaining on wet soil.

Ampullarius porphyrostomus lives very much the same way and in the same environment as *Marisa cornuarietis.* The white spawn, clearly visible from some distance, attached to reeds and bushes some distance above the water level, indicates in lagoonal waters and mangrove forests (as in the Cienaga Grande), the dividing line between fresh and brackish water faunas.

A parasitic mode of life is observed in *Cingulina babylonia.* Up to 5 individuals of this species were often found attached to *Bursa cubaniana* (d'Orbigny, 1842). The small pyramidellids (adults only about 2 mm long) sit near the siphonal canal or close to the apertural edge of the outer lip of their host, well protected within the sculptural depressions of the varical ridge and in front of it. They seem to live by sucking body fluids from the mantle edge of *Bursa.* Only in the aquarium were other hosts, such as *Petaloconchus mcgintyi,* attacked. From the sea they were collected only on *Bursa cubaniana.*

DESCRIPTION OF THE SPAWN

1. *Marisa cornuarietis* (Linnaeus, 1758)

(Figures 3A, 3B)

The undersides of leaves of water plants floating at the surface of the water are the favoured places where members of the species *Marisa cornuarietis* attach their egg

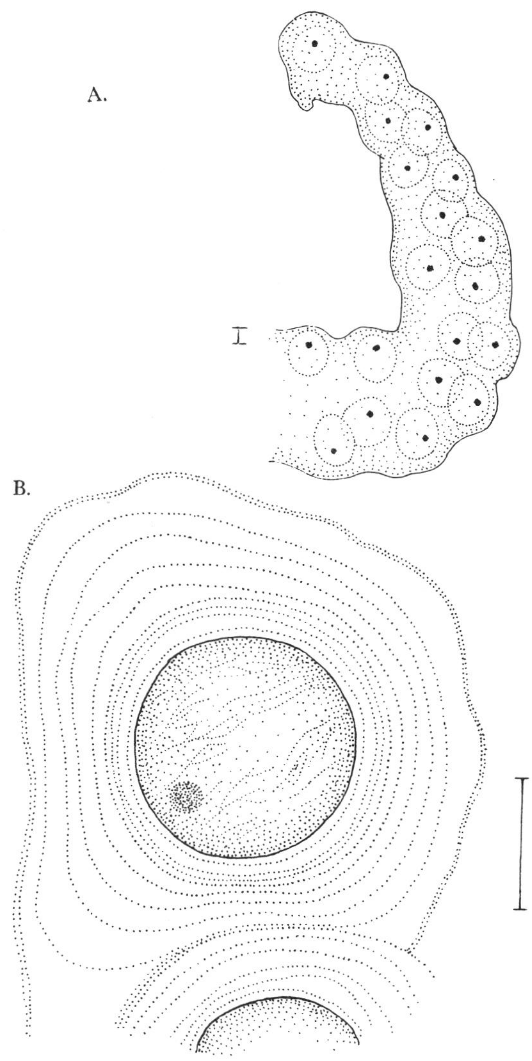


Figure 3

Gelatinous egg mass of *Marisa cornuarietis*

A – half of the whole egg mass B – single egg capsule
(scale 1 mm)

masses. Also all kinds of hard substances extending out of the bottom sediment of a pool or lake may be used for oviposition. In the small, artificial pool of the ICAL egg masses were attached to buoyant plastic sheets floating on the surface of the water.

Each gelatinous spawn mass contains about 80 eggs. Each egg, immediately after oviposition, lies within a 2.5 mm wide capsule. With advanced development the capsules expand until after 8 - 9 days they measure 4.5 mm in diameter, shortly before the young will hatch. Each round, clear capsule contains several thin, spherical inner layers so that it has the appearance of being concentrically striped. The center of it is taken up by a round, opaque inner body containing one egg. The capsules themselves are held by a long, oval to kidney-shaped gelatinous mass which is up to 6 cm long and 2 cm wide. The opaque inner capsular mass is slowly devoured by the developing embryo. Also the concentric inner lines disappear one by one with continued growth of the embryo until the outer capsular sphere is filled by it. At hatching, the young are miniature adults in morphology of the shell and the soft parts of the animal.

2. *Ampullarius monticolus* Vernhout, 1914
(Figure 4)

The animals maintained in the small artificial pool near the ICAL spawned at different times of the year, depositing their egg masses in the shade of plants about 5 cm above the water level. With the aid of her foot the female digs a small depression into the wet soil and deposits into it about 80 capsules. The more or less rounded egg mass extending over the rim of the depression consists of spherical capsules fused to each other by a mucoid substance where they touch, without deforming each other. Each capsule contains one egg that develops into a crawling young.

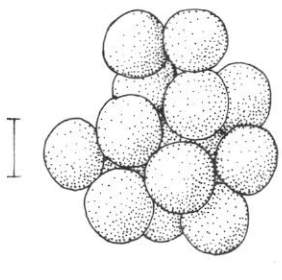


Figure 4

Some egg capsules of the spawn of *Ampullarius monticulus* (scale 1 mm)

The egg mass, when freshly secreted, is soft and opaque-whitish. Within hours, each egg capsule hardens as the gelatinous material dries. Therefore the color changes to white. This color is caused by finely distributed calcium carbonate crystals found in the mucoid cover of each capsule. The egg mass, within a short time, becomes a durable shelter to the developing embryos. Each egg capsule measures 1 mm in diameter and holds one egg that will develop until the crawling young, with the help of its radula, chews its way into the open.

3. *Ampullarius porphyrostomus* Reeve, 1856
(Figure 5)

Females ready to spawn leave the water during times without sun exposure, and crawl up a stem of a bush or tree or any other solid object extending at least 10 cm above the surface of the water. Here, 10 to 40 cm above water the spawn will be secreted.

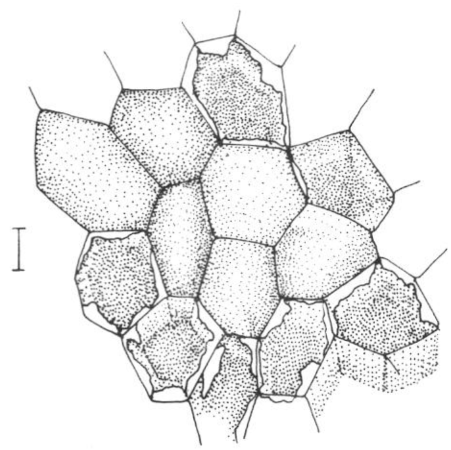


Figure 5

Some egg capsules of an *Ampullarius porphyrostomus* spawn which was broken open (scale 1 mm)

Freshly formed egg masses are soft and will harden after some hours of exposure to the air. The pinkish opaque color changes to a slightly pinkish-white. Dry, developing spawn dissociates into single, unattached, gelatinous capsules if soaked in water.

About 120 - 150 capsules attached to each other form the oval egg mass (about 2.5 cm long and up to 2 cm wide) surrounding the branch of a mangrove bush or some stem of a water plant. Egg masses not secreted around a thin stem are of more irregular shape but still retain their oval outline. At the outside of the egg mass walls of capsules are well rounded, while those of the inner ones deform each other, thus exhibiting a more or less regular hexagonal outline in capsular section. The material of the walls consists of mucous substance containing small crystals of calcium carbonate.

In each 3 mm wide egg capsule one embryo develops within 14 days into a crawling adult-like young. The young eat the entire interior walls of the egg mass before hatching. They then fall, lumped together, through a hole at the bottom part of the now hollow egg mass into the water below. As fast growth and numerous fecal pellets shed by the young show (BANDEL, 1974a) the egg mass walls serve as food for the hatching young.

4. *Turritella variegata* (Linnaeus, 1758)
(Figure 6)

In the months of December to February 1970-1971 and 1971-1972, spawning females were collected in the bay of Taganilla just below the ICAL. Most egg masses were found here at the edge of the area where the adult animals normally live hidden in the mud at a depth of about 1.5 m. Here the fine mud grades into sand with pebbles. This constitutes the preferred substrate for spawning. Here egg masses can be anchored securely to pebbles hidden within the sediment.

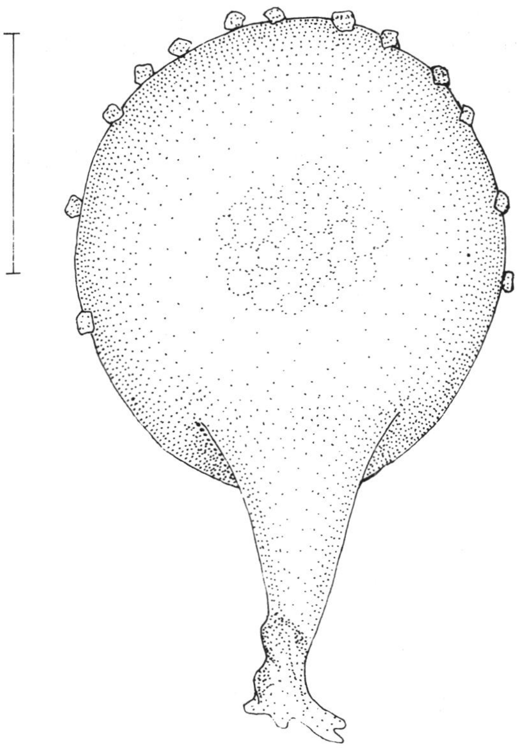


Figure 6

Single egg capsule of the egg mass of *Turritella variegata* (scale 1 mm)

The egg mass, shaped like a bunch of grapes, consists of 200 to 300 round capsules. Each ootheca consists of a clear, colorless, durable, shiny, spherical inner capsule which is surrounded by a mucoid sticky, soft outer capsule. This opaque outer hull extends into a trunk-like protrusion which is fused with other such protrusions of other capsules at its end, thus forming bundles which again are fixed to an inner elastic ribbon common to all. This long internal ribbon extends into the sediment and is there fixed to a larger particle. The diameter of the inner capsule makes up about $\frac{1}{3}$ of the whole capsule diameter of $1\frac{1}{2}$ to 2 mm. The lower oothecae of one spawn mass are closer to the sediment and usually covered completely by unsorted particles. The uppermost and last produced capsules sometimes lack this agglutination and clearly display their interior. The inner round capsule holds 16 to 18 yellowish eggs which, at the beginning of their development, form a lump in the center. After about 5 days of development veligers are actively swimming around in the interior of the capsule and after 16 to 18 days veliconcha will hatch that can swim as well as crawl. After 2 to 3 days veliconcha held in a glass bowl had completed their metamorphosis and were able to crawl only.

5. *Architectonica nobilis* Röding, 1798
(Figures 7A, 7B)

In the area of occurrence of adults of this species their gelatinous egg masses may be found at all times of the year, anchored in the sand. Animals maintained in the aquarium spawned frequently if fed well with actinians.

The spawn consists of up to 50 cm long and 3 - 4 mm thick, gelatinous massive tubes, round in cross section. These are looped in such a way that every 5 to 10 cm of tube they are connected with a gelatinous anchor extending into the substrate. Thus, a spawn mass in place looks like a number of independent loops, even though it actually consists only of one long, soft, continuous tube. Within the tube the capsules are arranged in irregular spiral lines. Each of the shiny, spherical, durable capsules contains one greenish egg or embryo and is connected to the next by a string. One millimeter of egg tube contains about 300 capsules. Therefore, an average 10 cm long spawn tube of one female contains about 30 000 embryos.

After 5 to 8 days of development the spawn dissolves and liberates small veligers.

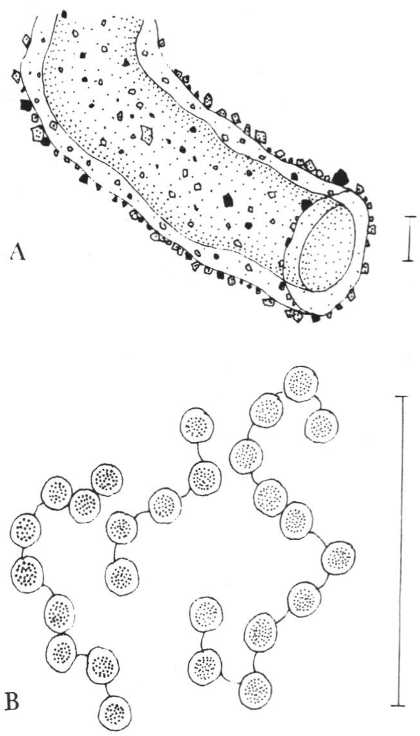


Figure 7

Gelatinous egg mass of *Architectonica nobilis*

A) Part of the gelatinous egg ribbon
B) Isolated egg-case string from the jelly-mass
(scale 1 mm)

6. *Petaloconchus mcgintyi* Olsson & Harbison, 1953
(Figure 8)

At all times of the year females collected from their habitat could be found containing egg capsules.

The capsules are fixed to the interior of the shell-tube of the egg-producing female about 1 cm behind the apertural edge. The 80 to 100 embryos within each capsule found with one female usually show different stages of development. Capsules have been produced successively with long time-intervals between each other. The colorless ootheca shows a round shape and oval diameter, is 1.5 mm long and 1.1 mm wide, fixed singly by a 0.3 mm long peduncle, round in cross section, to the inner wall of the female's shell. All embryos leave the capsule as veligers through an irregular rupture of the wall.

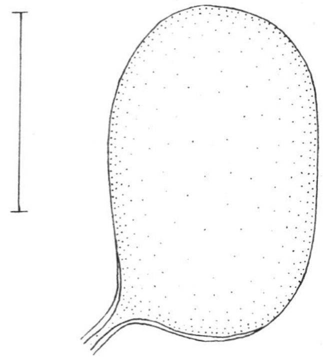


Figure 8

Ootheca of *Petaloconchus mcgintyi*
(scale 1 mm)

7. *Petaloconchus erectus* Dall, 1888
(Figure 9)

Animals collected at their habitat with chisel and hammer will often expel all their egg capsules. Normally, these capsules are attached to the interior of the shell of the female just as described for *Petaloconchus mcgintyi*. If embryos of one egg capsule are ready to hatch, the female will transport it to the apertural edge where the very brittle capsules usually rupture, as was observed on females maintained in the aquarium.

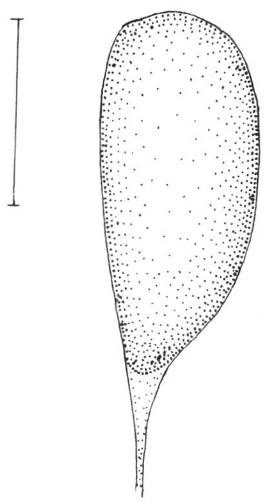


Figure 9

Ootheca of *Petaloconchus erectus*
(scale 1 mm)

Each colorless, transparent capsule has a round egg-like shape and a short peduncle, which is round in section. Of the over 100 eggs originally present only 12 to 20 will develop, while all others serve as nurse eggs. The whitish veliconcha finally hatching carry a shell with $2\frac{1}{2}$ whorls and remain only a short time swimming until completion of metamorphosis.

8. *Caecum antillarum* Carpenter, 1858
(Figure 10)

Due to their small size, eggs were only observed in the laboratory. Animals maintained in a small bowl with seawater would at all times of the year produce round, spherical capsules, 0.1 mm wide, which are camouflaged

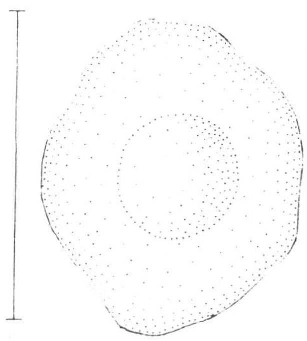


Figure 10

Egg capsule of *Caecum antillarum*
(scale 1 mm)

by a cover of fecal pellets and other small agglutinated particles. The opaque egg case holds one white embryo within an extra, spherical egg cover. Shortly before hatching the wall of the inner egg cover ruptures and the embryo grows until it fills the whole interior of the egg case. It hatches as a small veliger.

9. *Planaxis nucleus* (Bruguière, 1789)

At all seasons of the year some of the females freshly collected from the shore shed veligers if kept for a few hours in a bowl of standing seawater. The veligers carry a small, soft shell with one whorl. Females brood their spawn within the mantle cavity in a special brood pouch until the embryos are ready to hatch.

10. *Modulus modulus* (Linnaeus, 1758)
(Figures 11A, 11B)

Egg ribbons of *Modulus modulus* could be found throughout the entire year, attached to the lower side of rocks within the habitat of adult populations. Animals living in the aquarium spawned at all seasons of the year if fed well.

A female needs about 1 to $1\frac{1}{2}$ hours to produce one spawn mass. The gelatinous egg ribbon leaves the mantle cavity of the female as a wide belt and is attached to the substrate by a narrow side with the help of the snout and the foot. Before attaching an egg mass, the female cleans the substrate thoroughly with bites of the radula. The egg mass consists of a bilaterally compressed hollow tube

(on facing page →)

Figure 11

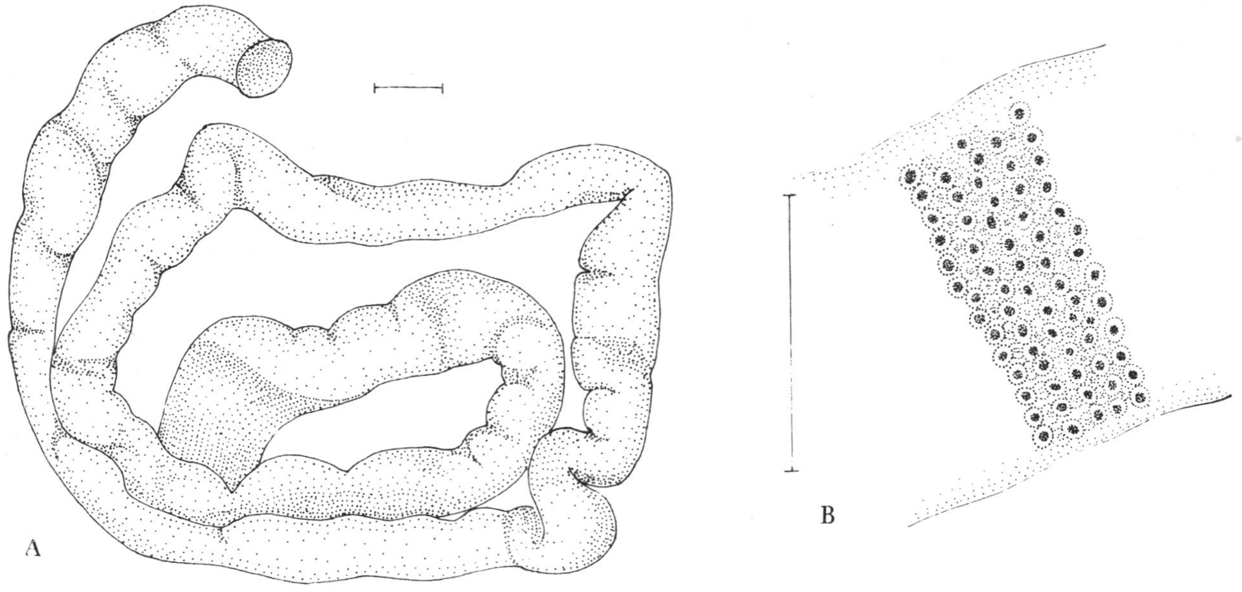
Gelatinous egg mass of *Modulus modulus*

A) View of the whole coiled egg mass
B) Seen from the side of a transparent egg ribbon, free of agglutinations
(scale 1 mm)

that is fixed to the substrate by its narrowest side. The egg ribbon measures between 3 and 6 cm in length. It is arranged into an irregular spiral. The surface of the mass is covered with detrital particles stuck to its gluey outside. Between the outer and inner wall of the tube, the egg capsules are arranged in rows giving a striped appearance to the entire egg mass. Each capsule contains one greenish egg. Actually the arrangement of capsules is spiral in such a way that the single loops touch each other and are compressed. The turning point of each loop is either hidden by the cover of agglutinated material near the attachment or indistinctly visible through the opaque surface. One millimeter of spawn contains 300 to 500 embryos and the whole egg mass contains a maximum of 30 000 embryos. After 5 to 6 days of development a small veliger hatches. Just before hatching the whole egg mass acquires a soft gelatinous appearance. The egg capsules dissolve and the veligers swim into the hollow center of the tube. From here they find their way to the open sea through the open ends of the tube or through a rupture.

11. *Modulus carchedonius* (Lamarck, 1822)
(Figures 12A, 12B)

In the habitat of this species, wood, rock, and palm leaves serve for attachment of the egg ribbons. Freshly



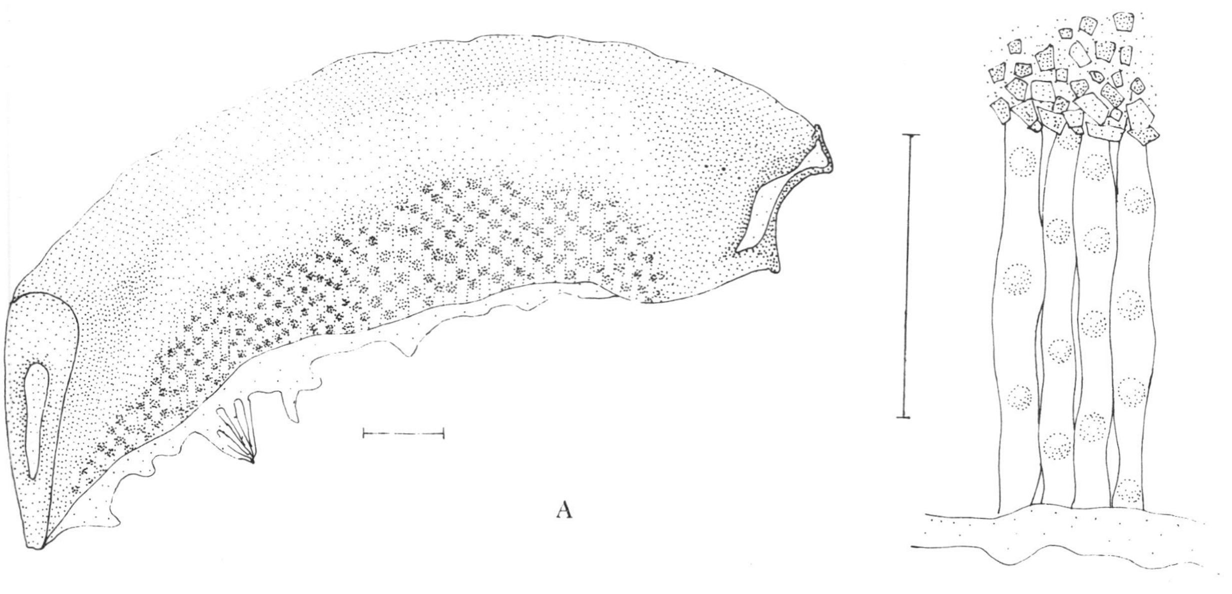


Figure 12

Gelatinous egg mass of *Modulus carchedonius*

A) View of the entire crescent shaped egg mass
B) Lower, lateral part of the egg mass showing the tubes containing eggs
(scale 1 mm)

collected animals spawned in the aquarium, using the walls as place for attachment of their egg mass. Animals maintained in the aquarium for some time did not spawn again, but at the yacht harbour of Rodadero spawn was found at all times of the year.

The egg mass consists of a bilaterally compressed hollow tube that is attached to the substrate by its narrowest side and is halfmoon shaped. It is 1½ to 2 cm long, 3 to 4 mm high and 0.7 to 1½ mm thick. The upper part of the ribbon is often agglutinated with detrital particles, the basal part of it is generally free of them, clear, transparent and shows vertical thin tubes containing greenish eggs in loose distribution. One millimeter of egg ribbon holds about 12 vertical tubes with 15 embryos each. Within the gelatinous walls of an egg mass the tubes form part of one continuous spiral tube with each whorl of the spiral touching the next. One egg mass contains about 7000 embryos which hatch as veligers after 5 to 6 days. The inner tubes of the egg mass dissolve, liberating the veligers into the inner cavity of the tube formed by the outer walls of the egg mass. The veligers find their way into the open sea by the open ends of the hollow mass.

12. *Cerithium lutosum* Menke, 1828
(Figures 13A, 13B)

Spawn of this species was found at all seasons of the year attached to sectors of *Halimeda*, blades of *Thalassia*, and other hard substrates in the lagoonal habitat preferred by the adults. Freshly collected individuals and those held in the aquarium over a long period of time will frequently produce egg masses attached to the walls of the aquarium.

An egg mass consists of a gelatinous ribbon which is arranged into tight loops touching each other and fused together at the contact points. Within this ribbon very delicate, roundish to rectangular capsules are seen; they contain spherical, durable, shiny egg capsules. These capsules are distributed in alternating rows, one above the other, and each contains a yellowish-white embryo. Some egg masses show ribbons with loops containing 4 intermediate capsules, others up to 10. The looped mass can have a spiral appearance or it can be arranged into packets close to each other or overlapping each other, thus forming a mass like a shallow staircase. Each ribbon is 0.6 mm wide and the total egg mass contains 400 to 1000 embryos. The development lasts 18 days; after that, small adult-like snails hatch.

13. *Cerithium litteratum* (Born, 1778)
(Figure 14)

Animals were found spawning at all seasons of the year, both in the sea and in the aquarium. The place for at-

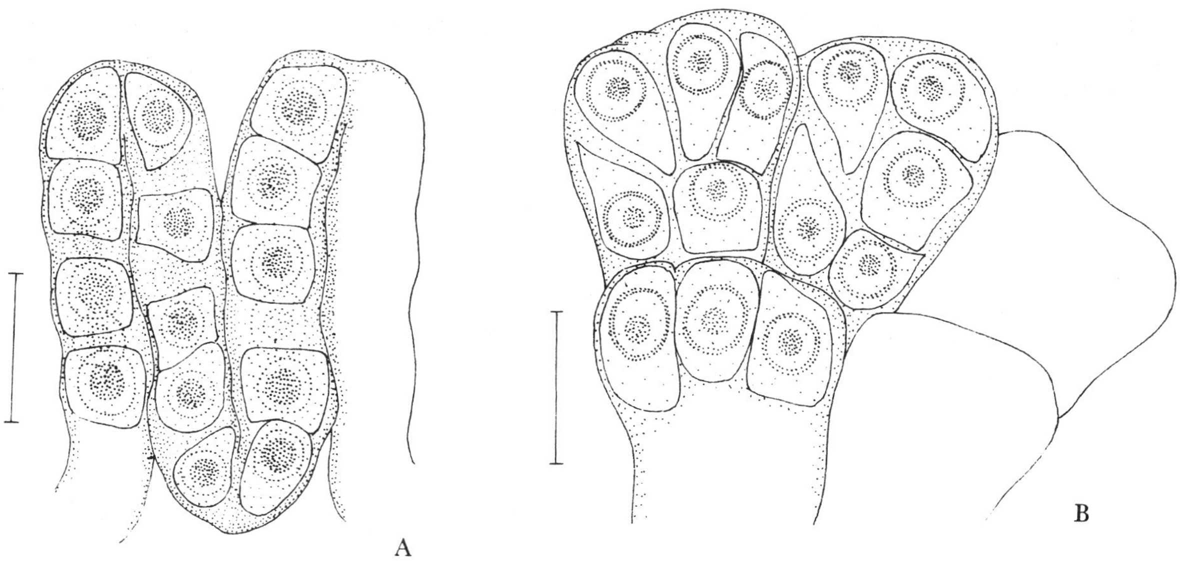


Figure 13

Gelatinous egg mass of *Cerithium lutosum*

A) Loops of simple meandering egg mass
B) Loops of egg mass agglutinated to a shallow, staircase-like compact mass
(scale 1 mm)

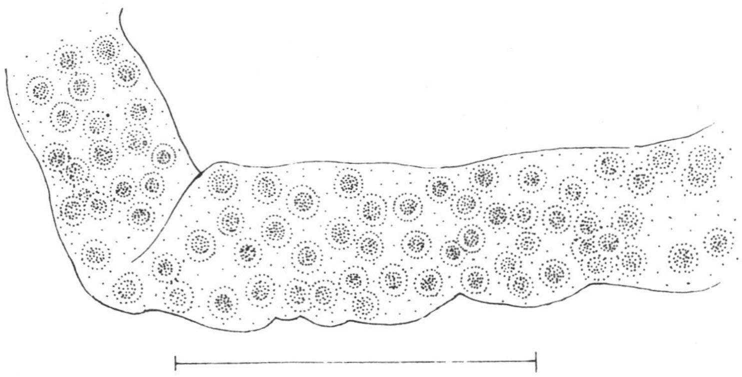


Figure 14

Fraction of the egg ribbon of *Cerithium litteratum* (scale 1 mm)

tachment of the egg mass is cleaned by the female with bites of the radula while the egg tube is being secreted. Each egg tube is very narrow (about ½ mm), contains about 40 eggs per millimeter, and is twisted into loops and irregular knots, forming an egg mass ribbon which in itself is irregularly coiled and a few centimeters (up to 10 cm) long. Each yellowish-white egg is surrounded by a spherical egg capsule. Its development within the capsule lasts 3 to 4 days; then a clear, transparent veliger will hatch.

14. *Cerithium atratum* (Born, 1778)

(Figure 15)

Spawn of *Cerithium atratum* can be found in the sea and in an aquarium at all times of the year; the spawn is attached to any hard substrate in the areas where the adult population lives. The female cleans the place used for oviposition very carefully with bites of the radula. While the egg ribbon is produced from the mantle cavity, the head moves from side to side, cleaning the substrate before pushing the egg ribbon against it with the foot.

The egg tube is extremely thin; it is entangled into an irregular mass, forming a loosely coiled, undulating ribbon, a few centimeters long, attached to the substrate. The actual egg tube is much longer and would, if uncoiled, measure a few meters in length. One millimeter of egg tube contains about 50 whitish embryos, each surrounded by its own spherical egg capsule. The tube measures about 0.3 mm in width and disintegrates completely after 4 days of development, liberating small veligers.

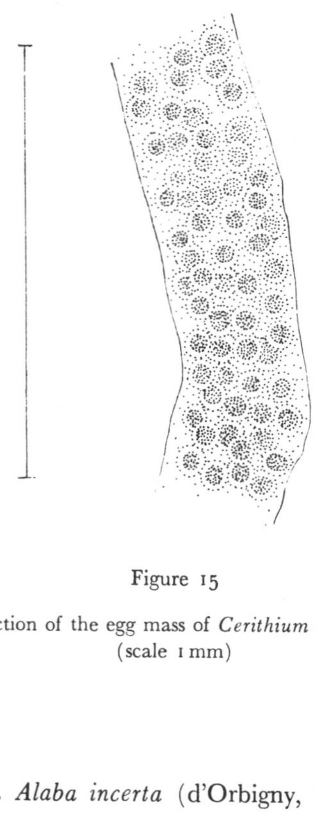


Figure 15

Fraction of the egg mass of *Cerithium atratum* (scale 1 mm)

15. *Alaba incerta* (d'Orbigny, 1842)

(Figures 16A, 16B)

The spawn of *Alaba incerta* can be found fixed to the leaves of *Sargassum* at all seasons of the year, but it is especially common in the seasons of clear water when *Sargassum* growth is at its maximum. Animals maintained in aquaria or bowls of seawater will spawn easily

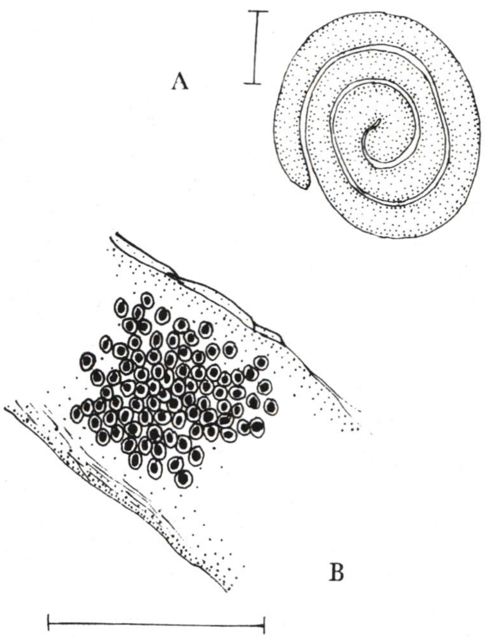


Figure 16

Gelatinous egg mass of *Alaba incerta*

A) Whole coil of the egg ribbon
B) Portion of the egg ribbon showing egg cases
(scale 1 mm)

right after having been collected in the sea or if fed well with filamentous algae.

The egg mass consists of a tight spiral ribbon; it measures in its entirety about 4 mm in diameter. Each coil of this ribbon, for the most part, touches the next and forms thus a solid sheet. Sometimes coils are arranged in a somewhat rectangular shape with rounded corners. The ribbon measures up to 1 mm in width and is quite low, providing space for only about 2 - 3 layers of capsules in its central portion. Each capsule contains one white egg and will dissolve after 4 - 5 days of development, liberating a colorless veliger. Within the egg ribbon the capsules are tightly packed in the central region, while near the outer wall a rim without eggs is seen, if the coiling in the egg mass is not tight. If, as is usual, this rim is fastened to the rim of an earlier whorl capsule, free rims overlap and are very difficult to detect.

A female requires 90 minutes to produce a 2 cm long ribbon which contains about 1000 eggs.

16. *Epitonium lamellosum* Lamarck, 1822

(Figure 17)

The egg mass produced by a member of this species was collected by Mr. de Jong in 1971 in shallow water at the shore of Curaçao. A very similar egg mass was collected among stones in the lower intertidal area of Fuerteventura (Canary Islands) in June 1972 by myself. Within this general ecology the only members of the genus *Epitonium* are *E. lamellosum* at both widely separated locations.

The general shape of the egg mass is similar to that of *Turritella variegata*. Single round, sand-agglutinated capsules form an egg mass resembling a bunch of grapes. The capsules from Curaçao are up to 2 mm wide, those from

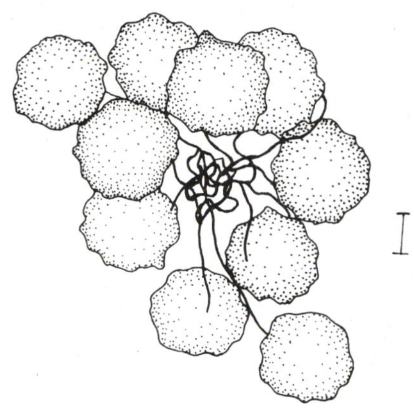


Figure 17

Some egg cases from the egg mass of *Epitonium lamellosum*
(scale 1 mm)

the Canary Islands only up to $1\frac{1}{2}$ mm. Each egg mass consists of about 120 capsules, each of which holds 150 to 200 yellowish, small eggs. The capsular hull is tightly agglutinated with sediment particles of different dimensions without apparent pattern. Within the egg mass 3 to 12 capsules may be counted in one transversal section and the entire mass forms a longish oval or ribbon-like structure that is attached to a stone with one of its narrow ends. The first capsules secreted are attached to a hard substrate each by 4 - 5 elastic, clear threads. The neighboring capsules within the egg mass are attached to a median bundle of threads in a similar manner.

Development of the eggs was not observed, but judging from the embryonic and larval shell preserved on many individuals, a veliger must hatch that will live for a long time in the plankton.

17. *Cingulina babylonia* C. B. Adams, 1845 (Figure 18)

Spawn of *Cingulina babylonia* was found attached to the outer apertural edge of the outer lip of *Bursa cubaniana*. Here depressions between the varical ridge and the apertural edge are filled with the gelatinous egg masses. Individuals maintained in glass bowls together with *Bursa* fastened egg masses not only to the shell of their hosts, but also to the glass walls.

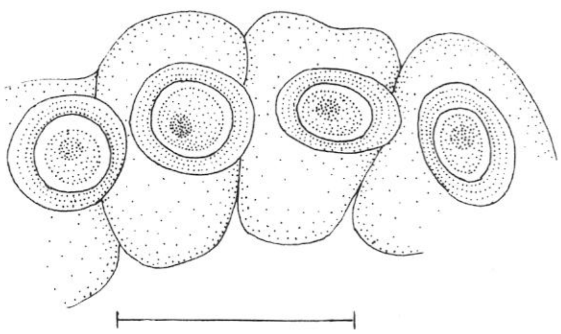


Figure 18

Some egg capsules from the spawn of *Cingulum babylonia* (scale 1 mm)

Egg capsules are enclosed in a thick, gelatinous cover combined into a gelatinous ribbon which in a spiral or looping course forms a continuous layer. Each gelatinous cover is about 1 mm thick and contains a capsule within it that has transparent, colorless, delicately striped walls. Within this capsule the oval egg capsule with smooth, solid, transparent walls is seen containing one egg. The yellowish-brown egg develops into a colorless, crawling, adult-like snail with a white shell, hatching after 18 - 21 days. The egg mass produced by one female contains 11 to 31 eggs.

18. *Calyptraea centralis* Conrad, 1841 (Figure 19)

From the muddy bottom off-shore of Santa Marta airport, individuals of *Calyptraea centralis* were brought up from a depth of about 10 m (14 October 1971), some of which were brooding females. The animals were attached to empty bivalve shells.

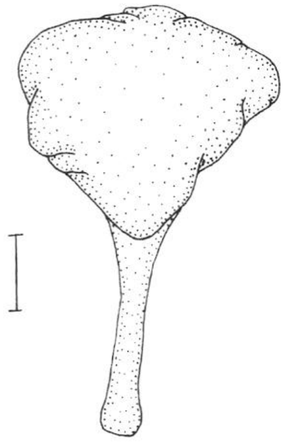


Figure 19

Ootheca of *Calyptraea centralis* (scale 1 mm)

Up to 15 capsules were affixed to the bivalve shell at one spot where all of their peduncles were fused. The female brooded above this bundle, holding it in the shelter of its cup-shell. Each capsule is of triangular outline, somewhat compressed, and has a long thin peduncle attached to the narrowest end of it. This peduncle is about 2 mm long, while the capsule measures 3 mm in length and $2\frac{1}{2}$ mm in width. Capsular walls are transparent, thin and colorless, providing free view of the 120 white embryos that will hatch through the ruptured walls as veligers after more than 5 days development.

19. *Crucibulum auricula* (Gmelin, 1791)

Among animals collected attached to shells of living adult *Strombus gigas* in the bay of Arecifes one contained 5 egg capsules. They were protected by the shell of the mother and attached to the *Strombus* shell at one point common to all.

The capsules are formed very much like those of *Calyptraea centralis*, except that they have a somewhat more irregular shape of the capsular sac. The walls are extremely thin, colorless, transparent. Ten to 12 yellowish eggs all develop into veliconcha possessing a functional foot and a large velum. Capsular dimensions are: height 4 mm; width 3 mm; the foot is 2 mm long.

20. *Crepidula convexa* Say, 1822

(Figure 20)

Larger females usually carried on their shell or right beside it a smaller male. About half of all females examined carried egg capsules in the shelter of their slipper-like shell; this held true at any time of the year.

The egg mass consists of a bundle of 11 to 50 capsules attached to the substrate at one spot where all their peduncles are fused together. The peduncle at its location of attachment to the capsule is somewhat bilaterally compressed and its sides continue into 2 thin lamellae a little way onto the narrow sides of the capsular walls. The transparent, colorless, thin-walled, sac-like capsules contain at first bright orange eggs which are agglutinated to the inner capsular walls so that the center of the capsule remains free of them. Later, the embryos take up the entire interior and change their color to bright yellow. Shortly before hatching a final color-change toward a greyish brown is observed. The embryo, moving about rapidly in the interior of the capsule, deforms its walls when bouncing into them. After at least 12 days of development the walls rupture and 2 to 28 embryos are liberated as veligers. The number of eggs per capsule and the size of the capsules are related to the size of the female producing them. Small females produce small capsules with few eggs, larger females large capsules with many eggs. The capsules are up to 1 mm long, 0.9 mm wide and are attached by a peduncle which is up to $1\frac{1}{3}$ mm long.

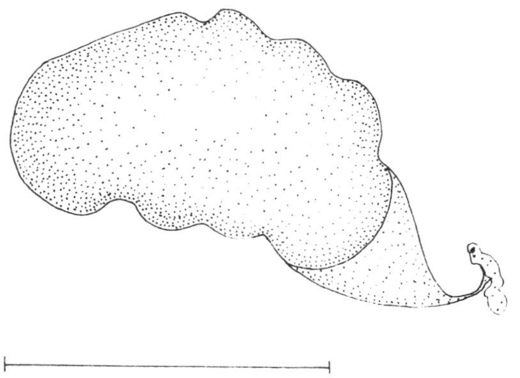


Figure 20

Ootheca of *Crepidula convexa*
(scale 1 mm)

21. *Crepidula glauca* Say, 1822

(Figure 21)

Spawn connected to a female was collected only once, on June 1971 in the bay of Chengue. The female was attached near the aperture on the inner wall of a shell of *Strombus gigas* inhabited by a hermit crab.

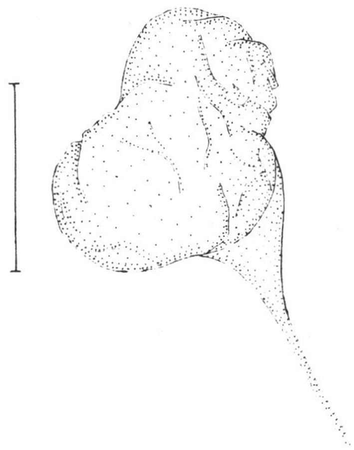


Figure 21

Ootheca of *Crepidula glauca*
(scale 1 mm)

Capsules are united to a bundle of 25, all attached at the same spot on the substrate. Here all peduncles are fused. The female, brooding the egg mass, protects it with the slipper-like shell. Each capsule has a sac-like appearance, an irregular folded outer wall which continuously changes shape as the embryos bounce into it. It has a cellophane-like luster and is completely colorless and transparent. The peduncle is thin, bilaterally compressed, and quite wide at its attachment to the capsule. Each capsule measures $1\frac{1}{2}$ mm in width and height and has a 1 to $1\frac{1}{2}$ mm long peduncle. Embryos at the beginning of development have a strong, yolk-like yellow color which later in development changes to a greyish opaque. Only 7 to 9 large eggs, rich with yolk, are present and develop into veliconcha. These hatch through a rupture of the wall, are able to swim and crawl, and have a slipper-like shell. They can crawl upright on the substrate, or under the water surface hanging down, or swim in a wide spiral.

22. *Crepidula plana* Say, 1822

(Figure 22)

Females of this species, holding egg capsules in the protection of their shell, were collected at all times of the year. Almost every shell of a larger gastropod occupied by a hermit crab contained also individuals of *Crepidula plana*. The smaller males are always attached beside the larger females and not on top of them as often noted for *C. convexa*.

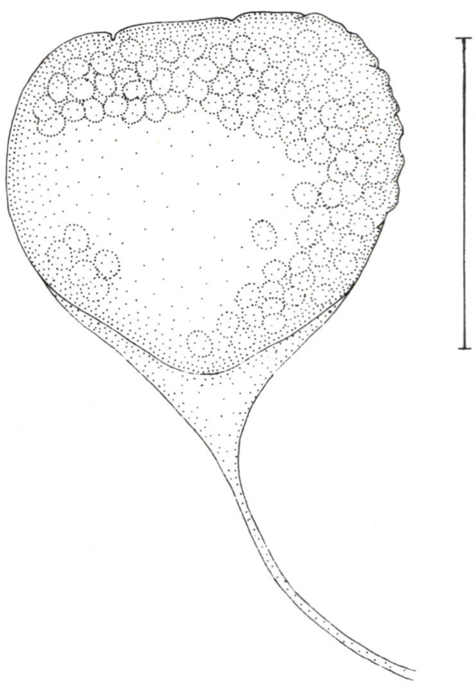


Figure 22

Ootheca of *Crepidula plana*
(scale 1 mm)

Fourteen to 24 kidney-shaped capsules on long slender peduncles are fused with their peduncles at the spot of attachment to the substrate protected by the slipper shell of the female. Capsules are transparent, colorless and bilaterally somewhat compressed. Two lamellae running down the narrow sides continue into the slender peduncle. Capsular walls are extremely delicate and often rupture if taken out of the water. About 80 white eggs fill not all of their interior at first. Later, embryos fill all of it and at last are so tightly packed that the shape of the capsule becomes spherical. The capsules are $1\frac{1}{2}$ mm long, up to 1 mm thick and have peduncles up to $2\frac{1}{2}$ mm long. The capsule walls rupture after at least 11 days of development to release veligers. In some capsules not all eggs developed but rather disintegrated into small yolk granules. These were then consumed by the other developing embryos. Thus it happened that in some cases of 80 eggs only about 25 developed and hatched as veligers.

23. *Cheilea equestris* (Linnaeus, 1758)

(Figure 23)

Capsule secretion could be observed in females of *Cheilea equestris* attached to the glass wall of the aquarium. Capsules appeared at intervals of 7 to 10 minutes and were manipulated by the snout of the snail towards their point of attachment. A single spawn was completed with 7 capsules and the female brooded on it for 9 days until the young hatched. During all this time she continued feeding. About half of the females collected in the sea at various seasons of the year had egg capsules with them.

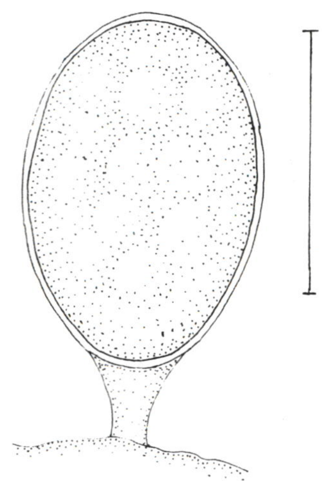


Figure 23

Ootheca of *Cheilea equestris*
(scale 1 mm)

The oval, sac-like capsules are attached by their peduncle to the tissue of the female. Each capsule, up to 1.7 mm high and $1\frac{1}{2}$ mm wide is round in section and holds 17 - 28 white embryos. The peduncle is up to 2 mm long and quite narrow. At first, the embryos form a lump in the interior of the capsule, later, after they have changed color to a brownish yellow, they swim within the capsule, filling it completely. Hatching of simple veligers occurs through a rupture of the walls.

24. *Hipponix antiquatus* (Linnaeus, 1758)

(Figure 24)

Spawn of *Hipponix antiquatus* was found at all times of the year attached to the females collected in the area.

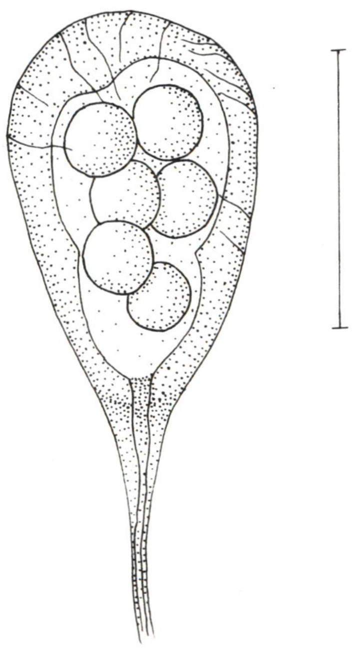


Figure 24

Ootheca of *Hipponix antiquatus* (scale 1 mm)

Each capsule consists of a transparent, colorless, pear-shaped sac which extends at its narrow end into a thin peduncle. The peduncles of one egg mass are united at a common base and are therewith attached to the tissue of the female within the mantle cavity. One spawn mass consists of about 5 capsules which are $1\frac{1}{2}$ mm long, round in cross section, and are about 1 mm wide. The peduncle of them is longer than they are themselves. Every capsule contains 6 - 8 embryos which are white at first and leave much free space. They later change color to yellow and fill the internal space completely. After about 14 days the young hatch, crawling through the ruptured wall and carrying a helicoid shell which has not as yet become patelliform as that of the adults.

DISCUSSION

Within the superfamilies Valvatacea, Cerithiacea, Pyramidellacea and Calyptraeacea and Hipponicacea a variety of egg mass shapes can be noted. Two major types can be differentiated, the first with gelatinous egg masses and the second with cuticular egg capsules. Within the first type 10, and within the second 3 morphological groups can be distinguished. In these groups most known egg mass morphologies of lower mesogastropod superfamilies can be included.

1. Group of *Planaxis nucleus*

In the group of *Planaxis nucleus* all eggs are retained in a brood pouch of the female until the young are ready to hatch. *Planaxis nucleus* and *P. lineatus* (Da Costa, 1778) from the Caribbean Sea and *P. sulcatus* (Born, 1778) from New Caledonia (Risbec, 1935) hatch as small veligers while *P. sulcatus* from the Persian gulf, feeding on nurse eggs during embryonic development, hatch as crawling young (Thorson, 1940).

In lower mesogastropods, *Littorina saxatilis* Olivi, 1792 also retains its eggs in a brood pouch until crawling young hatch, here without feeding on nurse eggs (Thorson, 1946; Fretter & Graham, 1962; Bandel, 1974), while some other littorinids from the tropics have veligers emerge from the brood pouch of the female (Bandel, 1974b). *Potamopyrgus jenkinsi* Smith, 1889 and *P. antipodarum* Gray, 1843, both hydrobiid species, reproduce parthenogenetically, also retaining the eggs in round egg capsules within a brood pouch until crawling young are hatching (Thorson, 1946; Winterbourne, 1970, 1972; own observations).

2. Group of *Caecum antillarum*

Members of the group of *Caecum antillarum* produce spawn consisting of a single egg capsule surrounded by mucous material agglutinated with all sorts of detrital particles. Egg cases of this kind are found in other members of the genus *Caecum* (Götze, 1938; Lebour, 1937; Marcus & Marcus, 1963; Thorson, 1946). Similar eggs are formed by a number of small mesogastropods and were described from members of the genus *Littoridina* (Marcus & Marcus, *op. cit.*), *Assiminea* (Marcus &

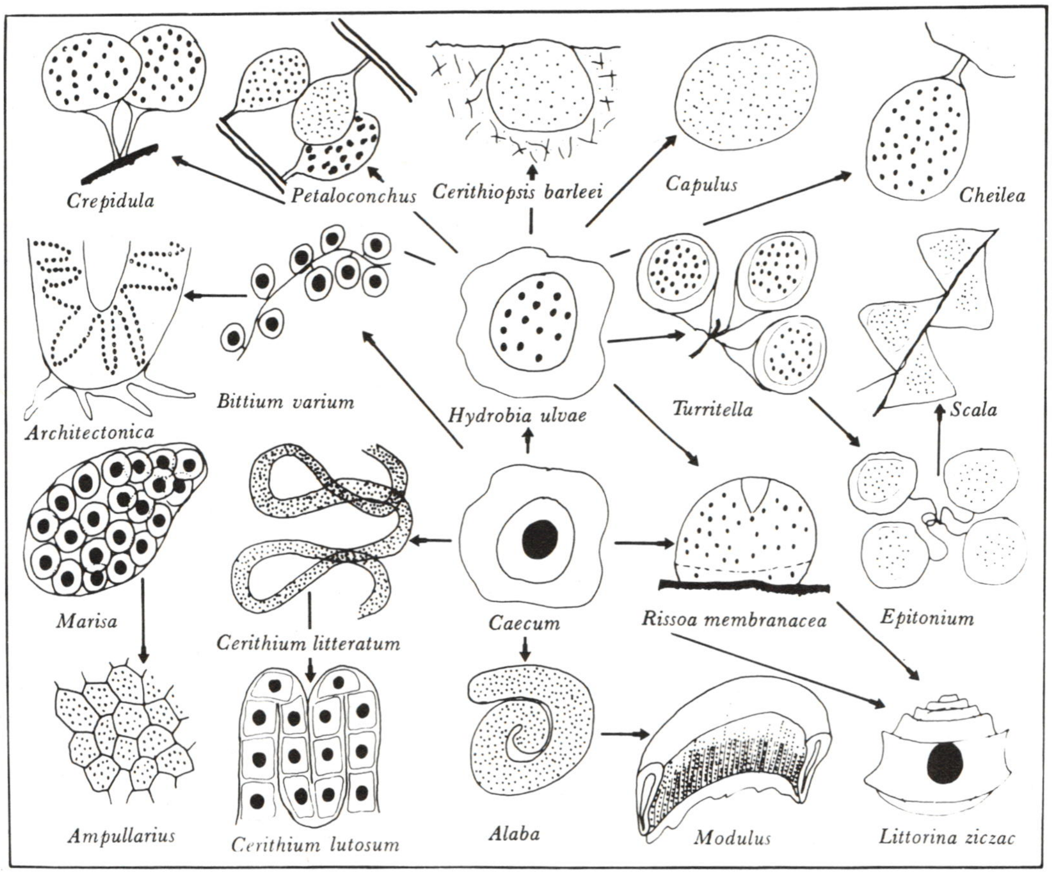


Figure 25

Generalized diagram showing shapes and possible relationships between morphological groups of spawn of lower mesogastropods.

Marcus, *op. cit.*; Sander, 1967), *Hydrobia* (Ankel, 1936; Benthem Jutting, 1922, 1933; Thorson. *op. cit.*), *Skeneopsis* (Linke, 1933; Fretter, 1948) and *Homalogyra* (Fretter, *op. cit.*) from the superfamily Rissoacea, and *Fagotia* (Ankel, 1928) from the family Melanidae. *Hydrobia ulvae* Pennant, 1777 (Thorson, 1946; see there for more literature) produces capsules of similar shape but containing 3 - 25 eggs each. Egg capsules of *Fagotia* show a small extension of the gelatinous mucus hull which could connect the capsules of this group with those of the group of *Turritella variegata*.

3. Group of *Marisa cornuarietis*

Spawn produced by *Marisa cornuarietis* is of very simple shape. It consists of a gelatinous matrix into which are embedded one or more layers of egg cases, each containing one egg. The outline of the egg mass may be oval to kidney-shaped, may be formed like a long ribbon, or like a short rounded mass.

This type of spawn can be produced by members of quite different superfamilies in the mesogastropoda. Besides in the Ampullariacea, as here in the genus *Marisa*, it may be found in the genus *Valvata* (Lamy, 1928) of the Valvatidae, the genera *Lacuna* and *Littorina* (*L. obtusata*) of the Littorinacea (Bandel, 1974b, see there for more literature), and the genus *Triphora* (Lebour, 1933, 1937) of the Cerithiacea. Within the genus *Cerithium* we encounter egg masses of 3 different groups of spawn morphologies noted here. *Cerithium rupestre* Risso, 1826 from the Mediterranean Sea, *C. gemmulatum* Hombron & Jacquinot (Risbec, 1935) from New Caledonia, and *C.*

lutosum (HOUBRICK, 1973) from Florida produce spawn belonging to this group, while *C. lutosum* from Santa Marta produces meandering spawn ribbons, and other species of this genus secrete filamentous egg masses.

4. Group of *Cerithium lutosum*

Egg masses in the group of *Cerithium lutosum* consist of gelatinous egg ribbons arranged into regular loops containing single egg capsules. Each embryo hatches as a crawling young. Surprisingly, spawn of *C. lutosum* (identifications of material made by R. S. Houbrick, Washington, D. C.) from Santa Marta is very similar to that of *C. muscarum* Say, 1832 from Florida and rather different from *C. lutosum* spawn from there (HOUBRICK, 1973, 1974). The small egg mass of the pyramidellid *Cingulina babylonia* differs from this general type of spawn only in possessing oval egg capsules.

5. Group of *Turritella variegata*

The spawn in the group of *Turritella variegata* consists of single egg capsules containing a number of embryos. These egg capsules are surrounded by a mucus cover which is agglutinated with sediment particles. The whole egg mass consists of numerous capsules. In the case of *Turritella variegata* and *T. communis* (LEBOUR, 1933, 1937; THORSON, 1946) they exhibit a peduncle on each egg capsule uniting the capsules to bundles which, through an elastic ribbon, are connected to each other, giving the egg mass an appearance resembling a bunch of grapes. This elastic ribbon also anchors the mass to the substrate.

Scala clathrus Linnaeus, 1758 (VESTERGAARD, 1935) produces spawn related to that of *Turritella* in its shape. Here single agglutinated egg capsules are attached directly to a common central ribbon anchoring the whole egg mass to the substrate. In *Epitonium lamellosum* the round agglutinated egg capsules also form bundles but attachment of each capsule to the median string is achieved by a number of clear threads instead of one peduncle as in *Turritella*. The general appearance of the entire egg mass of *Epitonium* very much resembles that of *Turritella*.

6. Group of *Ampullarius porphyrostomus*

Ampullarius porphyrostomus and *A. monticolus* secrete soft egg masses which in a short time harden into stiff, durable structures. Strauch (in a talk given in the fall of 1973) was able to show that the walls of each capsule of *Ampullarius* include, in addition to organic mucoid material, calcium carbonate which crystallizes in the shape of small cuboid calcite crystals. The mucoid material dries within a short time when both species have deposited their egg masses outside of the water. This material provides a hard shelter as protection of the developing embryo. Except for the calcite crystals, the egg mass very much resembles that of *Marisa cornuarietis*, which produces spawn attached below the water surface. If the spawn of *Ampullarius* is dropped into water it becomes gelatinous due to the softening of the dried mucoid material and will disintegrate within a short time until all egg cases are unattached to each other.

Other members of the genus *Ampullarius* produce the same type of spawn as do *A. porphyrostomus* and *A. monticolus* (LAMY, 1928).

7. Group of *Cerithium litteratum*

Small narrow tubes irregularly coiled into egg ribbons attached in a regular or irregular manner to hard substrates and with small veligers hatching have been described from a large number of species of *Cerithium*; *C. litteratum* from Florida produces the same type of spawn as found in Santa Marta (D'ASARO, 1970); *C. atratum* from Brasil (MARCUS & MARCUS, 1964) and from Florida (HOUBRICK, 1974) also produce spawn like those of Santa Marta. Egg masses of other members of the genus *Cerithium* from the western Atlantic belonging in this group are described in detail by HOUBRICK (*op. cit.*) who also discusses earlier descriptions of other authors.

The spawn of the genera *Clava* (OSTERGAARD, 1950), *Proclava* (AMIO, 1963), *Cerithidea* (AMIO, *op. cit.*) and *Cerithium* (NATARAJAN, 1958; WOLFSON, 1969) from the Pacific belong in this group. *Cerithium vulgatum* Bruguière, 1789 from the Mediterranean Sea and from the Canary Islands produce spawn quite like that of *C. litteratum* as my own observations indicated and as briefly described by THIRIOT-QUIÉVREUX (1969).

8. Group of *Alaba incerta*

The group of *Alaba incerta* is characterized by flattened, rounded gelatinous egg ribbons attached firmly in spirals to the hard substrate. Each of the numerous eggs is surrounded by a separate spherical egg case. The young hatch as small veligers. LEBOUR (1936) described the flat, slimy spiral coils of *Bittium reticulatum* (Da Costa, 1778) from England. Spawn produced by individuals of this species from the Canary Islands and the Mediterranean Sea look just like that (own observations) and just like that of *Alaba incerta*. Other authors have seen and described the spawn of *B. reticulatum* also (MEYER & MÖBIUS, 1892; LO BIANCO, 1888; ANKEL, 1936; THORSON, 1946; FRETTER & GRAHAM, 1962). Perhaps the spawn of *Litiopa melanostoma* Rang, 1829 described by LEBOUR (1945) as a flat gelatinous mass of round appearance is actually a coil with the spiral whorls touching each other with their rims, thus giving the appearance of one continuous mass. The same holds true for the spawn of *Australaba* which is described by HABE (1960) as a narrow gelatinous spiral coiled 4 times clockwise and is figured by AMIO (1963) as, in outline, a round egg mass without spiral appearance.

9. Group of *Modulus modulus*

Egg masses of *Modulus modulus* and *M. carchedonius* are characterized by consisting of a tube formed by a gelatinous sheet containing eggs arranged in rows. The hatching young of both species from Santa Marta are small veligers. LEBOUR (1945) found veligers hatching from spawn produced by *M. modulus* from Bermuda; these veligers were close to the conclusion of their metamorphosis. Here only 40 eggs are observed in one mass and veligers will remain inside the egg mass until they have secreted a shell with $2\frac{1}{2}$ whorls.

The type of spawn described here, consisting of a hollow tube, is so far only known from the 2 species mentioned.

10. Group of *Architectonica nobilis*

In this group, producing soft tube-like looped egg masses consisting of egg cases connected to each other by a thread and incorporated in a gelatinous mass, so far only *Architectonica nobilis* can be included. No similar egg mass anchored with additional mucoid roots in soft bottom is as yet known from prosobranchs. *Heliacus* produces an U-shaped jelly mass attached with mucous threads to *Zoanthiniaria* colonies (ROBERTSON, 1967). Egg cases connected to each other by a thread are produced by another architectonicid, *Philippia radiata* Röding, 1798 which attaches its gelatinous egg mass to the umbilicus of its own shell (ROBERTSON, 1970). In addition to spawn from architectonicids, such connections between egg capsules were described from the pyramidellid *Brachystomia* (RASMUSSEN, 1944, 1951; THORSON, 1946) and the marine pulmonates *Siphonaria* (VOSS, 1959) and *Trimusculus* (HAVEN, 1973).

11. Group of *Petaloconchus mcgintyi*

The shape of the capsules of the group of *Petaloconchus mcgintyi* and that of the following 2 groups is quite similar and only their modes of attachment differentiate them clearly one from the other. Members of this group produce capsules that are attached singly with their peduncles to the inside shell of the tube of the female. One spawn mass within the shell of the mother animal usually consists of quite a number of capsules showing different degrees of development each.

Besides in *Petaloconchus erectus* and *P. mcgintyi*, such spawn exists also in the vermetid genera *Lemintina* (LAMY, 1928), *Serpulorbis* (HABE, 1953), and *Bivona* (own observation). Development of the embryos varies from hatching as veligers, as veliconcha, or as crawling young.

12. Group of *Crepidula convexa*

The group of spawn morphologies similar to that of *Crepidula convexa* is characterized by simple capsules attached by one common base, where all peduncles of one egg mass are fused. Its location of attachment is on the substrate under the slipper shell of the female. Spawn of one egg mass is of about the same age and produced in one continuous spawning act. Quite a number of species is known to have egg capsules of this type. They belong to the genera *Calyptraea, Crepidula, Crucibulum* and *Amalthea.* The latter genus includes species with this type of capsules (HABE, 1953) and species where the capsules are attached to the tissue of the female (THORSON, 1940) as is typical for the group of *Cheilea equestris* (see next group). Perhaps this indicates some confusion within the genus *Amalthea* which seems to include species belonging partly to the Calyptraeacea and partly to the Hipponicacea.

Development of embryos within the capsules of this group, known from the literature, reflects the same situation as was found for the Caribbean species. In addition to *Crucibulum* from Santa Marta with veliconcha hatching, Persian Gulf members of this genus hatch as veligers (THORSON, 1940). Representative of *Calyptraea* from Santa Marta and the Persian Gulf (THORSON, *op. cit.*) hatch as veligers, while the European species hatch crawling (FRETTER & GRAHAM, 1962). Many members of the genus *Crepidula* (COE, 1949; HABE, 1953; THORSON, *op. cit.*) hatch as veligers while just as many hatch as veliconcha or crawling young (COE, *op. cit.*; DEHNEL, 1955; KNUDSEN, 1950; MORITZ, 1939; WERNER, 1955).

13. Group of *Cheilea equestris*

Capsules in the group of *Cheilea equestris* are attached to the tissue of the female. Other than that the shape of the capsules is quite the same as was seen in the 2 preceding groups. Each spawn consists of a number of capsules produced in one spawning act. As mentioned before, the genus *Amalthea* includes species with egg masses belonging to the group of *Crepidula convexa* and to the present group. Besides that, only members of the genera *Cheilea* and *Hipponix* (CERNOHORSKY, 1968; LAWS, 1970; RISBEC, 1935) produce spawn of this type. From spawn of the genera *Amalthea* (THORSON, 1940), *Hipponix* (CERNOHORSKY, *op. cit.*) and *Cheilea* veligers hatch, while in other members of the genus *Hipponix* (LAWS, *op. cit.*; THORSON, *op. cit.*) crawling young leave their egg capsules.

With 4 additional groups the spawn morphologies of lower mesogastropods known from the literature could be completed. Many members of the genera *Littorina, Nodilittorina, Echininus* and *Tectarius* of the Littorinidae produce pelagic egg capsules (BANDEL, 1974b; see there for additional literature). They would comprise the first of the 4 additional groups.

Shallow cupolas or hemispheres of transparent capsules attached to all kinds of substrates are produced by many species of the Rissoacea (LEBOUR, 1936, 1937; FRETTER, 1948; FRETTER & GRAHAM, 1962; and others). Here some contain only one egg, others many. Connections to capsule shape as found in the group of *Caecum antillarum* with one egg per capsule or like those of *Hydrobia ulvae* with many eggs per capsule are close, and intergrading forms are known.

The third additional group could be seen represented by the spawn of *Bittium varium* (Pfeiffer, 1840) described by MARCUS & MARCUS (1962). Here egg capsules are connected to each other by a thread common to all from which threads branch off holding a capsule each at their ends.

The fourth and last additional group may be seen in the unattached sausage-like capsules of *Capulus hungaricus* (Linnaeus, 1758) which are held, one per female at one time, in a fold of the propodium of the mother under the protective cover of the limpet-shell (LO BIANCO, 1888; ANKEL, 1937; THORSON, 1946; FRETTER & GRAHAM, 1962). These capsules, in contrast to those of the groups of *Petaloconchus mcgintyi, Crepidula convexa* and *Cheilea equestris* do not have peduncles.

The morphology of spawn and egg capsules in higher Mesogastropoda (BANDEL, 1975, in press), with the exception of those of the Strombacea, is quite different from almost all groups mentioned here, with the exception of the cupola-shaped capsules of the Rissoacea which are encountered in similar shape in many quite unrelated taxonomic of the Neogastropoda as well (BANDEL, in press).

Some species of the Archaeogastropoda belonging to the superfamilies Pleurotomariacea, Patellacea and Trochacea, as indicated by my own observations, produce egg masses resembling those of many of the groups here differentiated, consisting of gelatinous spiral or looping ribbons or strings. The same holds true for opisthobranch egg masses (HURST, 1967; see there for more literature; own observations). Especially spawns consisting of gelatinous ribbons and strings and also of sac-like shapes are common in different representatives of the opisthobranchs. Marine pulmonates (HAVEN, 1973; VOSS, 1959), as well as many aquatic freshwater pulmonates produce spawn similar to that described in the group of *Marisa cornuarietis.*

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