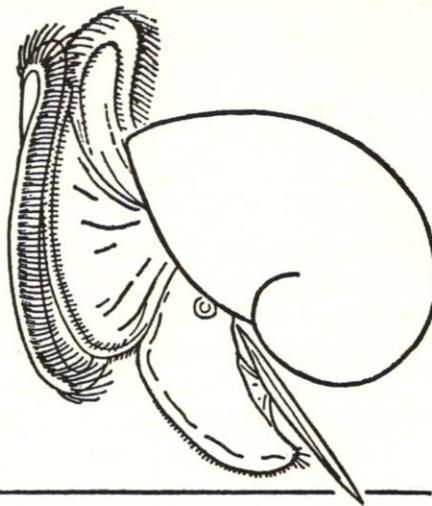


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ORDER, Suborder, **DIVISION**, Subdivision, **SECTION**,
SUPERFAMILY, FAMILY, Subfamily, *Genus*, (*Subgenus*)
New Taxa

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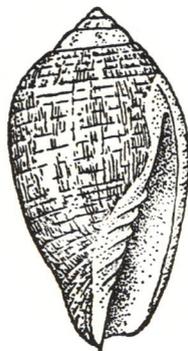
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Spawning and Development of Some Columbelloidea from the Caribbean Sea of Colombia (South America)

BY

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(15 Text figures)

INTRODUCTION

THE EGG CAPSULES OF THE COLUMBELLIDAE show a great variety of shapes as is evident from the descriptions of their spawn by THORSON (1940), BACCI (1942), FRANK (1941), KNUDSEN (1950), LÉBOUR (1945), MARCUS & MARCUS (1962), SCHELTEMA (1963), and D'ASARO (1970). The spawn of 10 species of Columbelloidea from Santa Marta (Colombia) also demonstrates this; 9 of these are described here for the first time.

This study was supported by the Deutsche Forschungsgemeinschaft, which made possible a stay of 18 months at the Instituto Colombo Aleman (ICAL) in Santa Marta, Colombia. Identification of the egg-laying females was accomplished with the aid of publications by WARMKE & ABBOTT (1961), MARCUS & MARCUS (1962), and KAUFMANN & GÖTTING (1970). Dr. R. Tucker Abbott verified the identifications on material sent to him.

METHODS

Spawn was collected in the sea near the ICAL with the help of fins, mask and snorkel, and in some cases with aqua-lung-diving equipment. Animals and spawn were collected from fall 1970 to spring 1972. Most egg cases described here were produced by animals held in aquaria with sea water running 12 hours a day. In some cases the way of capsule production could be observed on the glass and plastic walls of the aquaria. Freshly spawned egg masses were marked or taken out of the aquaria and then observed in glass dishes filled with sea water that was renewed every 2 days. The drawings of the capsules were made, immediately after spawning, by my wife with the aid of a binocular microscope. Capsular dimensions were determined on fresh oothecae containing living embryos. The spawn was observed in the laboratory of the ICAL at a room temperature of 25 - 27° C until the young

hatched. The time for development in the glass dishes was more or less the same as that in the aquaria and in the sea.

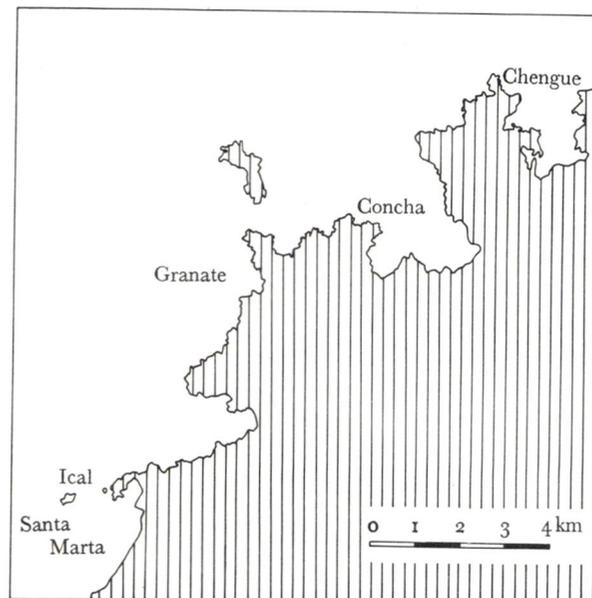


Figure 1

Map of the coast-line near Santa Marta, Colombia, showing the collecting stations for the individuals mentioned in this report.

LIVING PLACE IN THE SEA

Columbella mercatoria (Linnaeus, 1758) was found all around Santa Marta under coral rubble in water of 0 to 2 m depth in the reef zone, in the shallow lagoon behind it and in areas with extensive lawns of turtlegrass. Also commonly *C. mercatoria* was found on large bushes of *Sargassum* rooted near exposed rocky cliffs or coral reefs.

Anachis pulchella (Blainville, 1829) is restricted in its occurrence to lagoons behind coral reefs and was found attached to the underside of coral rubble behind reefs in Chengue Bay, north of Santa Marta, and also under flat stones in the extensive turtlegrass flats behind the coral reefs and thickets in this bay. Here, members of this species are the only representatives of the genus *Anachis*. In the reefstructure its occurrence overlaps that of *Anachis* sp.

Anachis sp. lives in depths from 0.2 to 1.5 m of water and is commonly found in all pebble and rubble zones where the rocks are overgrown by an algal crust. This species was found on and under stones near the Santa Marta airport, right below the ICAL, and in all bays north of Santa Marta up to Ensenada Arcifes. In areas, where rocks have a sandy bottom between them, *A. brasiliana* (v. Martens 1897) and *A. sparsa* (Reeve, 1859) join *A. sp.* in depths between 0.2 and 1.5 m of water. The latter sometimes can be found on *Sargassum* plants rooted in and just below the low water line together with *Nitidella laevigata* (Linnaeus, 1758), *N. nitida* (Lamarck, 1822), and *Mitrella argus* (Orbigny, 1842). *Nitidella laevigata* eats the leaves of *Sargassum* and clings so strongly to the plant that when the collector tears it off, the leaf is torn off also. If rocks and boulders are densely overgrown by algae just below the tidal zone, this species will also be found on them. *Nitidella nitida* mostly settles on the lower stems of *Sargassum* bushes close to the attachment to the rocky

substrate. More commonly it is found on the underside of rocks between 0.1 and 1 m depth of water. It prefers rubble beaches without sand or mud between the rocks, where it lives in large groups. The activity of this animal generally takes place at night.

Mitrella argus (Orbigny, 1842) is not as common as the 2 species mentioned previously, but is regularly found under rocks in depths up to 1 m and on all parts of *Sargassum* plants where it eats small animals attached to the plant. Underneath pebbles and rocks in the zone between low water and 0.5 m depth of water *Mitrella ocellata* (Gmelin, 1791) is common, especially where no sand or mud is present between the rocks. In deeper water it is gradually replaced by *Nitidella nitida*.

Anachis obesa (C. B. Adams, 1845) feeds on hydroids and is found on the lower sides of rocks with hydroid colonies, on algae and turtle grass if they are used as substrates by hydroids. They can be found on hard objects lying on sandy or muddy bottoms; for example, on egg collars of naticids. *Anachis obesa* occurs in depths between 0.5 and 5 m of water.

LIFE IN AQUARIA

All 10 species have been kept in aquaria for some time, and, with the exception of *Anachis pulchella*, all have successfully been brought to copulation and spawning. *Co-*

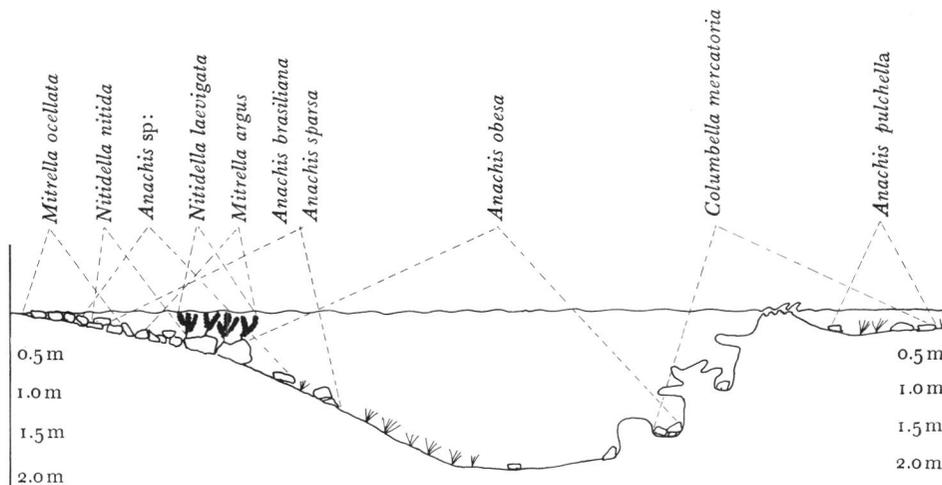


Figure 2

Generalized profile demonstrating typical habitats of 10 columbellid species of which the spawn is described. From left to right: rocky shore, rubble below low water, single large rocks with *Sargassum*-growth on them, turtle grass bottom, muddy to sandy bottom, coral reef, coral reef lagoon with turtle grass and coral rubble.

lumbella mercatoria can be fed with algae, especially with fine green filamentous ones; it also eats fish meat if near it, but does not go long ways to find it. *Nitidella laevigata* can be fed with *Sargassum* plants and will consume them completely with the exception of the stem and the larger veins in the leaves. It can grab leaves, holding them with the posterior part of its foot to the substrate and searching with quick motion with the anterior part of the foot for a new hold. *Nitidella laevigata* crawls some distance to eat flesh, extending its redbrown proboscis deep into it. *Mitrella argus* and *Anachis obesa* eat hydroids but also feed on fresh pieces of clam and fishmeat. All the others can easily be fed on fresh fishmeat. If fed well, all species can be held in great numbers in one aquarium with circulating sea water. *Mitrella argus*, *A. obesa*, and *N. nitida* have been observed reaching food through free water on their own mucus secreted by the foot. *Nitidella nitida* secretes mucus ribbons that are very durable, so that one ribbon, over 10cm long, fixed to the shell of an individual making rapid escape motions, did not break.

EGG CAPSULES

Columbella mercatoria (Linnaeus, 1758)

(Figure 3)

In the Ensenada Granate north of Santa Marta, in water up to 1 m in depth, the egg capsules of *Columbella mercatoria* were found on stems and leaves of *Sargassum* plants which were also the habitat of the adults. In the Ensenada Chengue, capsules were also fixed to smooth spots on the

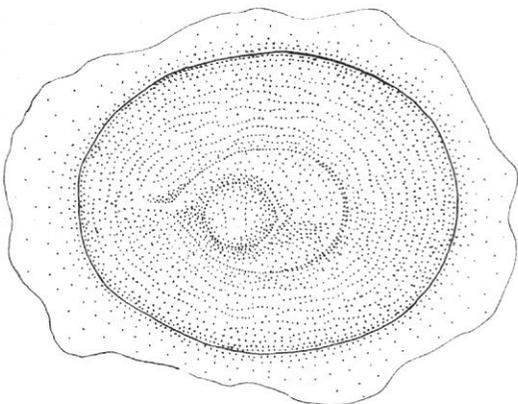


Figure 3

Ootheca of *Columbella mercatoria* seen from above (scale: 1 mm)

underside of rocks in lagoons with lawns of turtlegrass behind reefs. In the bay of Santa Marta, spawn was found fixed to the shell of a living *Vasum muricatum* (Born, 1778) at Isla Moro.

In the aquaria, the glass or plastic walls are usually used for oviposition. When fed well in aquaria, animals spawn at all times of the year, one female generally producing 2 to 6 capsules in one egg mass. Communal spawning was not observed. The capsules in one egg mass are attached individually to the substrate in loose groups to the aquarium panes, or in rows to *Sargassum* stems. The capsules are oval at the base, and the basal membrane extends in an irregular rim somewhat beyond the capsule walls. The cupola-shaped ootheca slopes to one side from the central escape aperture and from the other side more steeply from a projection on the apical plate. A suture divides the capsule in 2 halves. It crosses the opaque membrane of the escape aperture along its long axis, is enlarged into a ridge ending in the apical projection, and is only faintly discernible on the sides of the cupola. The sides of the ootheca have delicate transversal and radial wrinkles. The membrane of the escape aperture shows delicate transverse wrinkles. The opaque, translucent oothecae are 2 mm high, 3 mm long, and 2.5 mm wide. One capsule contains 16 to 27 green eggs that fill only $\frac{1}{4}$ of the lumen of the capsule. In development, 4 to 8 embryos devour all others and fill the entire lumen before hatching. After 33 days the membrane of the escape aperture dissolves and miniature snails crawl out.

Anachis pulchella (Blainville, 1829)

(Figure 4)

The spawn of *Anachis pulchella*, produced by freshly collected animals from the Ensenada Chengue, has only been found once (17th October 1971). The capsules were glued to the pane of the aquarium in a group of 6 without pattern in their arrangement. The ootheca is oval at the base, forming a cupola above an adhesion disk that extends beyond the capsule walls. The dome is divided into a lower and an upper part, separated from each other by one or a few concentric ridges. The lower part of the capsule is sculptured with a large number of radial wrinkles that end in the last $\frac{1}{3}$ of the rim of the adhesion disk at the lower part and at the lower edge of the concentric ridges at the upper part. The upper section of the capsule is characterized by a large escape aperture which is closed by an opaque membrane, in contrast to all other parts of the capsule, which are transparent and colorless. The long axis of the membrane of the escape aperture is followed by a suture that continues, reinforced by a ridge, down at

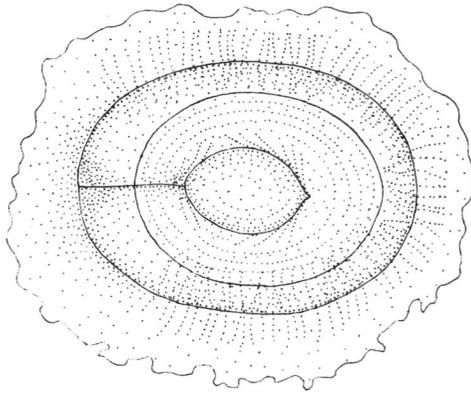


Figure 4

Ootheca of *Anachis pulchella* seen from above (scale: 1 mm)

one side of the capsule and is not visible on the other side in most oothecae. The membrane is delicately striped like a section of an onion, the stripes running into that point where the suture meets the rim of the escape aperture. From these points small wrinkles originate, crossing some of the weaker concentric ridges in the upper section of the capsule and ending there. The oothecae are about 2 mm long and 1.5 mm wide. They contain 2 to 9 (average 4) yellowish-white embryos at the beginning of their development which fill only very little of the lumen of the capsule. Later on the embryos fill the entire lumen. After 29 days of development the membrane of the escape aperture is dissolved and all embryos hatch as crawling miniature snails with a transparent shell showing 2 brown spots at the edge of the aperture and a brown line just above the sutural canal.

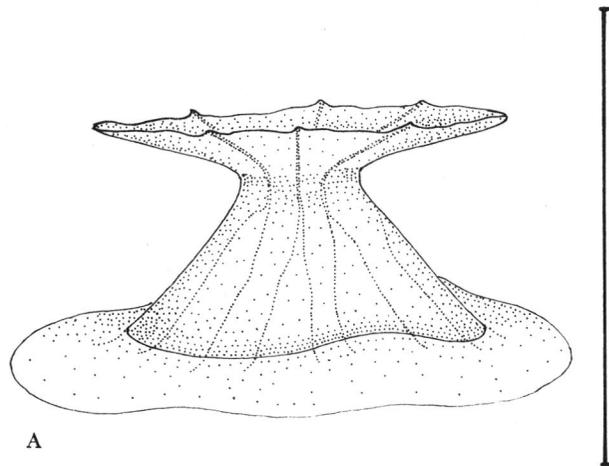
Anachis brasiliiana (v. Martens, 1897)

(Figures 5A, 5B, 5C)

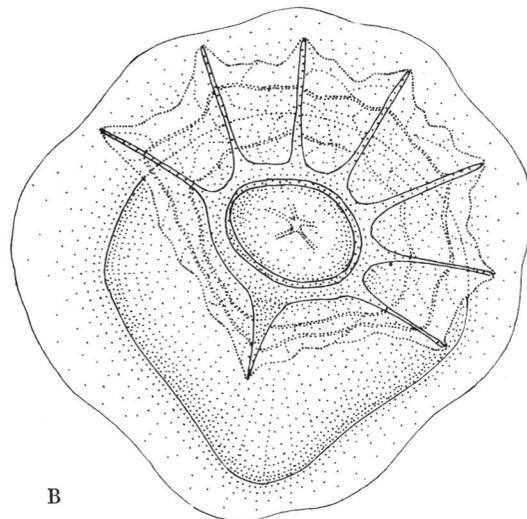
Anachis brasiliiana attaches its spawn at all times of the year to hard substrates, wherever many adults can be found.

Animals, kept in aquaria, spawn if fed well. The capsules are glued to the glass and plastic panes of an aquarium in masses of 40 to 60 capsules by one female. Usually one spawning female attracts other females, so that large communal egg masses are produced. A single egg mass shows a pattern of orientation of the oothecae in rows ex-

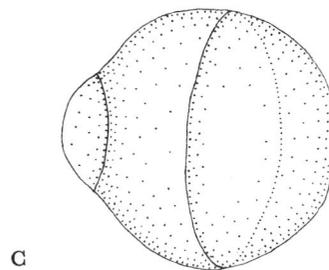
hibiting a hexagonal pattern if seen from above and a scaly pattern if viewed from below.



A



B



C

Figure 5

Ootheca of *Anachis brasiliiana*

A: seen from the side; B: seen from above
C: before final shaping in the pedal gland (scale: 1 mm)

The mode of formation and attachment of capsules to the transparent panes of the aquaria was observed. To prepare for the later attachment of the entire egg mass, the female cleans the locality with her extended proboscis and bites off all kinds of growth from the substrate with her radula. After having cleaned an area sufficiently large, the female rests for some time, sitting without motion in one spot.

Then the first soft capsule is transported by ciliary movement in a fold to the frontal part of the foot's sole and is sucked here into the pedal gland. This still soft capsule, coming from the capsule gland, is spherical. It is divided into 2 halves by a suture separating one smooth hemisphere from another carrying a round escape aperture in its centre, which is closed by a convexly arching membrane.

After the capsule disappears into the pedal gland, the entrance to the gland is pressed against the spot of fixation of the capsule, and the capsule itself is milled and strongly moved about inside the gland for about 1 to 1½ minutes, until the disk of attachment becomes clearly visible. The female then rests, motionless, for 1 to 1½ minutes on the capsule. After 2 to 3 minutes the female leaves the now hardened capsule, shaped into its final form, by detaching the pedal gland from it and moving on with a searching motion of the frontal part of the foot. After about a minute of searching the female stops with opening of the pedal gland at the location for attachment of the next capsule. Then this capsule is passed from the oviduct to the pedal gland along a groove situated in the right anterior portion of the foot, formed temporarily for this purpose. The whole time needed for capsule formation amounts to about 4 minutes, so that the egg mass produced by one female requires about 3 to 4 hours. Fully formed capsules are fixed to the substrate with a flat round adhesion disk. One side of the disk is fixed in an arch to the substrate, the other side overlaps the capsular sides and the rims of the adhesion disks of the row of capsules produced earlier. This gives the scaly appearance of the egg mass seen from below (through the transparent panes of the aquarium). The walls of the capsule rise from the adhesion disk. They are supported by 16 ribs, 2 each joining at the upper part of the walls and continuing as 8 ribs, reinforcing a collar around the escape aperture. This collar has 2 unequal halves, one having 7 ribs and the other only 1. All collars in one egg mass point in the same direction so that the halves with the 7 supporting ribs point toward that part of the egg mass formed in the previous instance. The collar carries 2 concentric ridges connecting the stiffening ribs with each other. The lid of the escape aperture bears a 5- to 7-rayed fold in its centre. Each transparent ootheca, 0.7 - 0.8 mm wide and

0.4 - 0.5 mm high, contains 4 to 15 embryos (average 10). After 11 to 13 days the white eggs have developed into veligers with a simple velum and a transparent shell with a brownish siphonal canal; they hatch through the open escape aperture after dissolution of the membrane.

Anachis sparsa (Reeve, 1859)

(Figure 6)

Anachis sparsa spawn was found at different times of the year on the underside of rocks in about 50 cm of water below the stairs near the pumping station of the ICAL. Sometimes capsules were found fixed to the leaves of *Sargassum* plants rooted on the rocks.

A well fed population of *Anachis sparsa* copulates and spawns at all times of the year in the aquaria. One female produces up to 60 capsules in one egg mass on the glass or plastic walls of the aquaria. Usually a spawning female attracts other females, as well as males, of the same species. The males copulate with spawning and non-spawning females. The newly arrived females also begin producing egg masses, so that at one time large patches of egg masses are produced at different spots in the aquarium, containing many hundreds of capsules. The capsules are arranged in irregular rows, and the rims of the adhesion disks usually fuse with each other. The walls of the cone-shaped capsule rise from the round adhesion disk and end in a projecting edge, forming a collar around the concave mem-

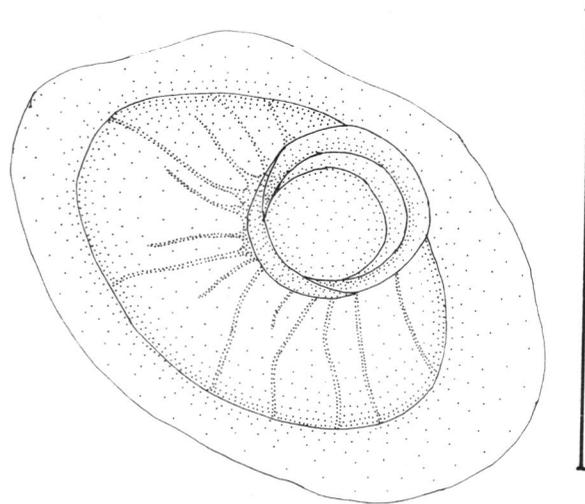


Figure 6

Ootheca of *Anachis sparsa* seen from above (scale: 1 mm)

brane of the escape aperture. The collar is a little inclined in relation to the plane of the adhesion disk so that all collars of one honeycomb-shaped egg mass point in the same direction. The sides of the capsules are re-inforced by 20 to 25 somewhat irregular radial ridges. The transparent, colorless oothecae measure about 1 mm in diameter, if more ovoid 1.2×1 mm, and are 1 mm high. The 10 to 25 (average 17) embryos lie loosely on the bottom of the lumen of the capsule at the beginning of development and later fill the entire interior. At first they are white; at hatching, after 11 to 13 days of development, they are veligers with a large two-lobed rectangular velum and a transparent shell with a brown siphonal canal. The small foot carries an operculum that cannot close the aperture.

Anachis obesa (C. B. Adams, 1845)

(Figures 7A, 7B)

In the sea, capsules of *Anachis obesa* have only been found on the stalks of hydroids, arranged in a row of one capsule behind the other. Well fed animals produce at all times of the year large communal egg masses fixed to the walls of

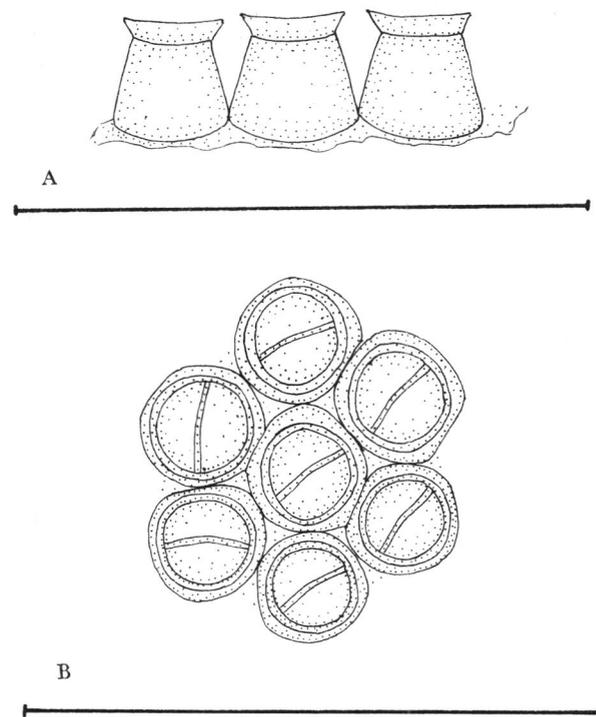


Figure 7

Ootheca of *Anachis obesa*

A: seen from the side; B: seen from above (scale: 1 mm)

the aquarium. One female secretes between 45 and 100 capsules in one egg mass, but communal egg masses sometimes contain more than 1000 capsules. Usually one spawning female induces spawning in other females so that up to 8 females may be observed spawning at the same time, adding to the communal egg mass.

The capsules in one egg mass are arranged close to each other so that the basal membranes of all capsules are fused to each other with their rims. The bases of the cone-shaped oothecae are often touching and deforming each other, thus producing a hexagonal pattern of the egg mass if viewed from above. The weakly conical cylinders end in a short collar surrounding the escape aperture. The membrane of the escape aperture is crossed by a lamellar transverse ridge. The transparent, colorless capsules measure only 0.2 - 0.25 mm in diameter and height, and each capsule contains only one embryo. After 6 days of development the white egg, with much space in the lumen of the capsule, has grown into a transparent veliger filling the whole capsule. At hatching, the edge of the round lid of the escape aperture dissolves and the lid is turned into a vertical position, with the median ridge acting as a hinge. The hatching veliger has a round, bilobed velum and a transparent shell with a yellowish-brown tint at the edge of the aperture.

Anachis sp.

(Figure 8)

Spawn of *Anachis* sp. is found at all seasons of the year at the localities where adults of this species are common. The capsules are fixed to the underside of rocks, rarely to leaves of *Sargassum* plants rooted on the rocks. Well fed animals spawn at all times of the year, fixing the capsules to the glass or plastic walls of the aquaria.

The rectangular, brick-shaped oothecae are arranged in a row consisting of from 2 to 11 capsules, with an average of 4 capsules. The longer sides of the oothecae in a row are fused with each other and slope vertically at the end of the adhesion membrane. The upper plate of the rectangular capsule is surrounded by a ridge that extends out into a plate overlapping the next capsule at one of the corners. These projections of the rim from the apical plate point in the same direction in one row of capsules. An escape aperture is not present. The whole upper plate is covered by a tegmentum made of tubercles, bristles and ridges. At hatching a roundish hole somewhere in the apical plate opens due to dissolution originating from the interior of the capsule. No chewing activities of the developing larvae from the inside at the apical plate can be observed. The opaque capsules are 1.5 mm long, 1 mm

to 8 capsules, are fixed to the glass and plastic walls and to the inside of plastic hoses. Usually the capsules of one egg mass are not arranged in a specific pattern, but mostly in groups and rows of 2 or 3 capsules close together so that the basal membranes of neighbors are fused at the rim. The capsules are flask-shaped and oval or round in cross section at the base. The round adhesion disk is smooth and transparent. The opaque sides of the capsule are covered with a reticular pattern of ridges, which at the crossing points of the ridges are drawn out into vertical small pointed projections. The oval escape aperture is closed by a transparent membrane that is sculptured with a large number of very fine transverse wrinkles. The

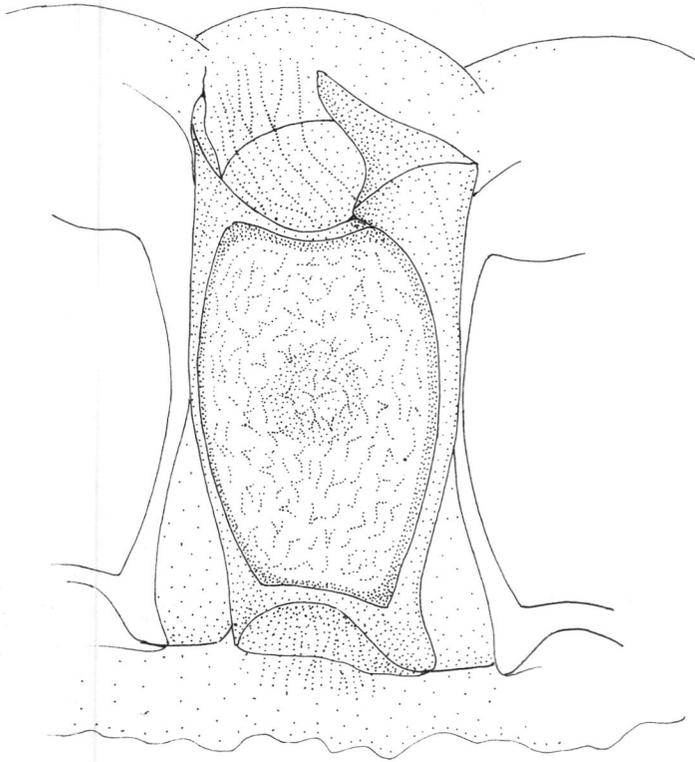


Figure 8

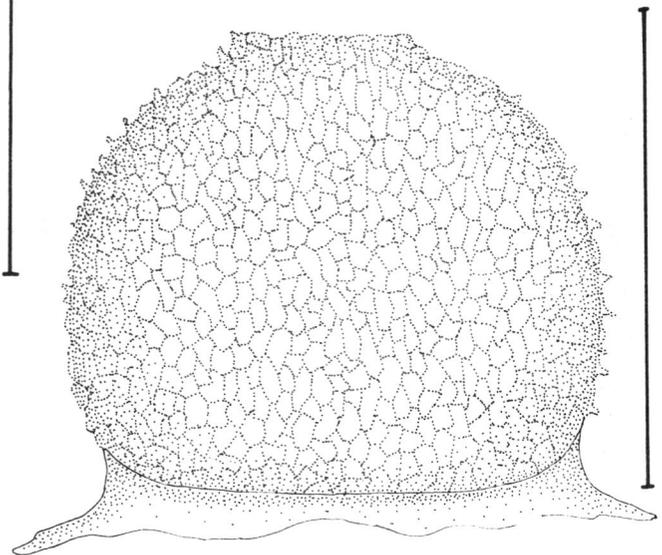
Ootheca of *Anachis* sp. seen from above (scale: 1 mm)

wide and 0.7 mm high. Each capsule contains one, rarely 2 white eggs filling only a small portion of the lumen. In later stages of development, the embryo fills much of the interior. After 26 days of development a fully differentiated little snail with a transparent, light brown shell crawls through the irregular dissolution hole of the apical plate.

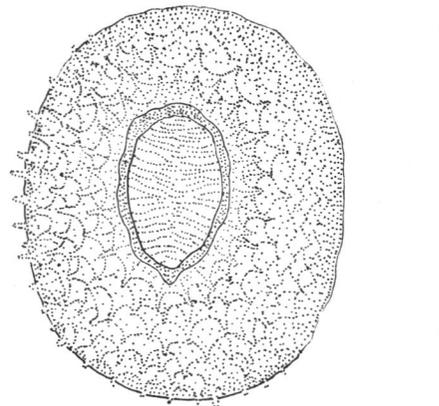
Nitidella nitida (Lamarck, 1822)

(Figures 9A, 9B)

Fixed to the lower part of *Sargassum* plants rooted on the rocks just below low water level, below the ICAL, capsules produced by *Nitidella nitida* are common on stems and leaves. Spawn can also be found at all times of the year on the underside of rocks in areas where adults of this species are common. Sometimes as many as 58 capsules of different ages can be found in communal egg masses. In the aquarium, egg masses of one female, consisting of 3



A



B

Figure 9

Ootheca of *Nitidella nitida*
A: seen from the side; B: seen from above (scale: 1 mm)

capsules measure 1.25 mm in diameter and are of about the same height. Each capsule contains 6 to 10 white embryos with much free space in the interior at first. After 29 to 30 days of development the embryos, now completely filling the lumen of the capsule, are ready to hatch. The membrane of the escape aperture dissolves completely and miniature, fully developed snails with yellowish-white body and opaque shell crawl out.

Nitidella laevigata (Linnaeus, 1758)

(Figures 10A, 10B)

Nitidella laevigata spawn was found at all times of the year on *Sargassum* plants growing on rocks below the ICAL. Usually the leaves of *Sargassum* were used for affixing the capsules, rarely the stem or other thallose algae. Occasionally egg masses were found on the undersides of rocks just below low water level at the ICAL and behind a small *Porites* reef in a few decimeters of water in the bay of Villa Concha.

Animals kept in aquaria usually produce spawn only shortly after collection in the sea and rarely after longer times of life in the aquarium. Spawn is then fixed to *Sargassum* leaves and, if none are available, to the walls of the aquarium. Spawn of one female consists of 3 to 26 capsules (average 12). Communal spawning of more than 1 female at one time has never been observed. The capsules are always arranged in rows of 2 or 3 lines in such a way that the capsules of the second line are fixed beside the interstices of the first line. The collars surrounding the escape aperture are all bent into the same direction in one egg mass. The rims of the basal membranes of the capsules in one egg mass are fused to each other. Usually one egg mass covers most of the upper or lower surface of one *Sargassum* leaf and egg masses fixed to other substrates reflect the size and shape of a *Sargassum* leaf.

The cylindrical capsule is fixed to the smooth, transparent basal membrane at an angle, varying from capsule to capsule, and most strongly inclined at the edges of the egg mass. The apical plate forms a sharp edge with the sides of the capsule, and ridges crossing it are drawn out into projections. The round escape aperture lies in the middle of the apical plate and is closed by a transparent membrane. The membrane is sculptured with rows of 5 to 8 furrows. The escape aperture is surrounded by a high collar which is bent on one side toward the escape aperture and on the other side away from it. The collar is supported by 25 to 30 ribs which continue across the apical plate and over the edge down to the middle of the side walls of the capsule. Each rib ends in 2 points at the edge of the collar, one pointing toward the inside

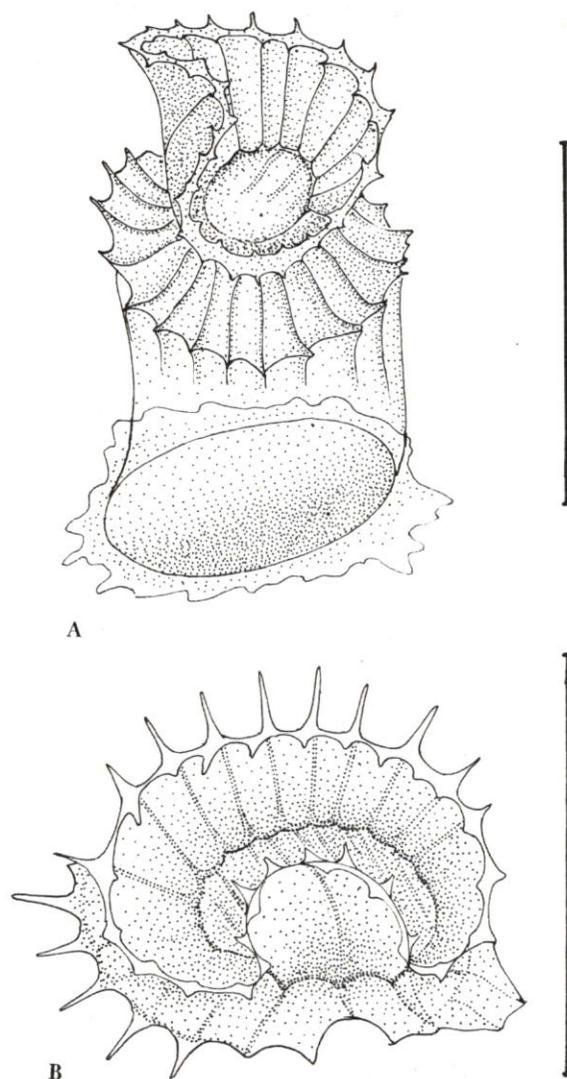


Figure 10

Ootheca of *Nitidella laevigata*

A: seen from the side; B: seen from above (scale: 1 mm)

and the other toward the outside of the collar.

Each opaque capsule contains between 15 and 30 white embryos with much empty space in the lumen immediately after secretion. After 13 days the membrane of the escape aperture dissolves, setting free veligers with a rounded 2-lobed velum, a transparent shell with a brownish siphonal canal, and a small operculum that cannot close the aperture.

Mitrella ocellata (Gmelin, 1791)

(Figures 11A, 11B)

Capsules can be found, attached to the undersides of rocks in the areas where *Mitrella ocellata* adults are common, at all times of the year. The lower parts of *Sargassum* plants rooted on rocks near low water level are often used for oviposition.

In the aquarium, spawning females usually prefer empty clam shells to the aquarium walls. One egg mass contains 1 to 6 irregularly arranged capsules, only rarely fixed to the substrate so close to each other that the disks of attachment are fused with one another at the rim. The irregular oval basal membrane extends only in a narrow

rim beyond the capsule walls. The smooth capsule is dome-shaped, one side sloping more rapidly than the other. The large oval escape aperture is closed with a transparent membrane and surrounded by a smooth lamellar collar. The escape aperture is somewhat shifted from the centre of the capsule cupola along the long axis toward the strongly sloping side. The collar continues on the more gently sloping side, almost down to the base of the capsule and is here higher than at the upper side, at the edge of the escape aperture. The whitish opaque capsule is up to 1.5 mm long, 0.8 mm wide, and 0.7 mm high. Capsules contain 11 to 27 white embryos (average 17) and there is much space in the lumen when the capsules are freshly secreted. All embryos undergo development and hatch after 13 to 14 days as veligers, showing a 2-lobed round velum, a transparent shell with a brown siphonal canal, and an operculum that cannot close the aperture.

Mitrella argus (Orbigny, 1842)

(Figure 12)

Single capsules of *Mitrella argus* can be found at all times of the year glued to leaves of *Sargassum* plants rooted on rocks at the ICAL just below the intertidal zone. In the aquarium capsules are produced when the animals are fed well. Only single capsules are fixed to the leaves of *Sargassum* or to the plastic panes. The egg masses sometimes consist of loose groups of capsules with no pat-

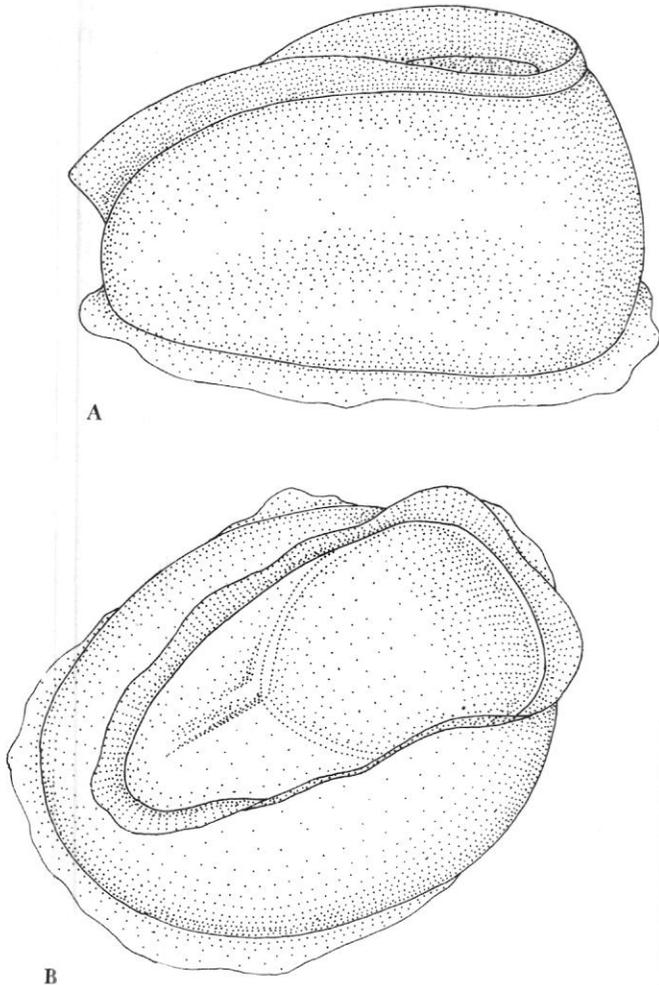


Figure 11

Ootheca of *Mitrella ocellata*

A: seen from the side; B: seen from above (scale: 1 mm)

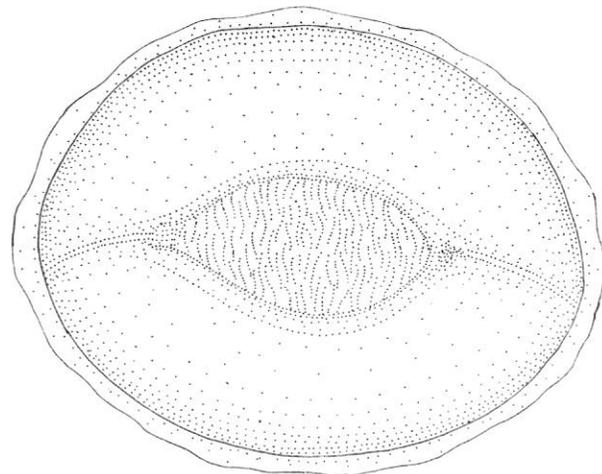


Figure 12

Ootheca of *Mitrella argus* seen from above (scale: 1 mm)

tern of arrangement and with different stages of embryonic development.

The capsules have the shape of a shallow dome on a broad, irregularly rounded disk of adhesion which only extends in a narrow rim beyond the capsule walls. The walls are smooth and in the cupola a large spindle-shaped escape aperture is situated, closed by a clear membrane with delicate transverse furrows. From the pointed sides of the escape aperture, ridges run down the sides of the capsule to the basal membrane. The ootheca measures about 1 mm in diameter, is about 0.25 mm high and contains 12 to 16 white eggs which occupy only a small fraction of the lumen of the capsule at the beginning of their development. Later, the embryos fill the entire lumen of the capsule and are freed after more than 6 days of development by dissolution of the membrane of the escape aperture. The hatching veliger has a simple rounded 2-lobed velum and a transparent shell with a reddish-brown siphonal canal.

DISCUSSION

According to the literature and my own material 6 morphological groups of columbellid egg capsules can be distinguished.

1. Group of *Mitrella argus*

The simplest shape of egg capsules is found in *Mitrella argus*, resembling the unformed soft capsules leaving the capsule gland. The transformation consists only of hardening the membranes and fixation to the substrate with the aid of a round adhesion disk by the pedal gland. Similar capsules are widely observed in other families of Neogastropoda but have so far not been described from Columbelloidea. Egg cases of members of the genera *Bedequina* (AMIO, 1963), *Trophon* (THORSON, 1940, 1946), *Risomurex* and *Drupa* (own observations) in the family Muricidae, *Fusus* (FIORONI & PORTMANN, 1968) in the family Buccinidae, *Tritia* (AMIO, 1963) in the family Nassariidae, *Mitra* (FRANC, 1942), *Pusia* (own observations) in the family Mitridae, and *Drillia*, *Bela* and *Philbertia* (THORSON, 1946) in the family Turridae are of the same general shape.

2. Group of *Anachis sparsa*

The next, more complicated shape of columbellid capsules is characterized by a collar surrounding the escape aperture. This collar may be smooth and simple and the capsules unsculptured as in *Anachis sparsa*, *A. avara* (Say, 1822) (SCHELTEMA, 1969), and here all embryos develop

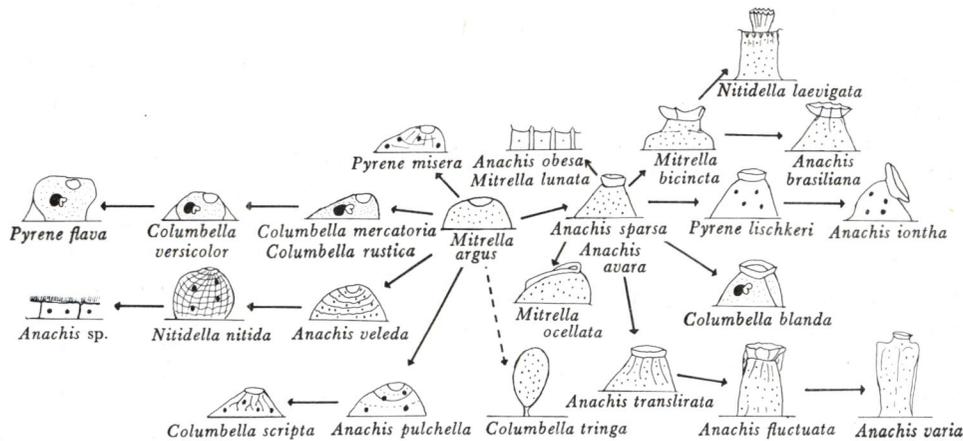


Figure 13

Diagram showing hypothetical links between capsules of different shapes and with different embryonic development within the columbellids. Capsules with small dots represent those with veligers hatching, capsules with large dots those with all embryos hatching as small crawling snails, and capsules with one big embryo and many small dots represent directly developing embryos consuming nurse eggs.

and hatch as veliger larvae. The same general shape of capsules is observed in *Anachis translirata* (Ravenel, 1861) (SCHELTEMA, *op. cit.*), *A. fluctuata* (Sowerby, 1832) and *A. varia* (Sowerby, 1832) (D'ASARO, 1970). Here also all eggs develop into veliger larvae, but the capsules are laterally sculptured by wrinkles and ridges and the capsules of the latter 2 species are more columnar than those of the others.

Simple capsules with large collars around the escape aperture are produced by *Pyrene lischkei* (Smith, 1879) (AMIO, 1963) and *Anachis iontha* (Ravenel, 1861) (PERRY & SCHWENGEL, 1955). But here the young hatch as crawling miniature snails without having fed on nurse eggs.

Similar capsules are figured and described as unidentified spawn by LEBOUR (1945) from Bermuda. The capsules were attached to hydroid stems (LEBOUR, *op. cit.*, text fig. 33) and related to *Columbella*; larval development is direct. *Columbella blanda* (Sowerby, 1844) (THORSON, 1940) differs from the last described capsule shapes in having nurse eggs.

The small columbellids *Anachis obesa* and *Mitrella lunata* (Say, 1826) (MARCUS & MARCUS, 1962) produce large egg masses with small capsules each containing only one egg that develops into a planktotrophic veliger larva.

The collar surrounding the escape aperture of *Mitrella ocellata* extends almost to the base of the sides of the capsule with one of its ends and is farther down on the side. Here the eggs develop into veliger larvae.

Mitrella bicincta (Gould, 1860) (AMIO, 1963), *Anachis brasiliensis*, and *Nitidella laevigata* capsules are characterized by a more complexly shaped collar around the escape aperture. The oothecae of *A. brasiliensis* from Santa Marta show close relationship to oothecae of this species from Brazil, as described and figured by MARCUS & MARCUS, 1962. The Brazilian capsules show a collar with radial symmetry and 10 stiffening ribs, while the capsules from Santa Marta have only 8 stiffening ribs arranged in a bilaterally symmetrical collar. Also the number of capsules in Brazilian egg masses is (with 10) much lower than that of the Colombian with up to 60 capsules shed by one female.

3. Group of *Columbella mercatoria*

In this group dome shaped capsules are combined with an asymmetrically located escape aperture. *Pyrene misera* (Sowerby, 1844) (AMIO, 1963) produces egg masses which hold eggs developing into crawling miniature snails before hatching without feeding on nurse eggs. All other members of this group have nurse eggs. *Columbella mercatoria* and *C. rustica* (Linnaeus, 1758) (FRANC, 1941) (own observations) have bilaterally symmetrical capsules, while those of *C. versicolor* (Sowerby, 1832) and *Pyrene*

flava (Bruguière) (PETIT & RISBEC, 1929) become more irregular.

4. Group of *Nitidella nitida*

Egg capsules with radial symmetry and sculptured sides are produced by *Nitidella nitida*, *Anachis pulchella*, *A. veleda* (Duclos, 1846) (MARCUS & MARCUS, 1962) and *Columbella scripta* (Linnaeus, 1758) (THORSON, 1940). The sculpture of the sides is radial in *C. scripta* and concentric in *A. veleda* and *A. pulchella*. *Nitidella nitida* has both directions in the sculpture, producing ridges and at the crosspoints additional spines. Only *A. veleda* has veliger larvae hatching; all others produce eggs from which young miniature snails hatch without feeding on nurse eggs in the capsule.

5. Group of *Anachis* sp.

Rows of brick-shaped egg capsules of *Anachis* sp. are the only representatives of this group. Here only 1 or 2 embryos in each capsule undergo direct development.

6. Group of *Columbella tringa*

Capsules of *Columbella tringa* (Laurent) (PETIT & RISBEC, 1929, fig. 4) are of oval shape, standing on a peduncle.

Description of *Anachis* sp.

(Figures 14 and 15)

Shell: Height up to 10mm, width 3.7mm, total of whorls 8, protoconch 2½ - 3 whorls, smooth. Junction of protoconch with teleoconch indistinct. Teleoconch with distinct ribs, strongest near body whorl. Body whorl with 12 - 13 rounded ribs as broad as their interspaces. Suture smooth or undulated by tips of ribs. Spiral cords strong and crossing ribs. Distinct cord on penultimate whorl (5), body whorl (8 - 10) and basal ones (10) on the anterior-most part of body whorl. Aperture medium wide, sigma shaped. Interior of outer lip with 6 - 8 denticles, the first 3 (adapical ones) thickest. Interior of inner lip with 4 - 5 strong teeth. Columellar callus raised into a smooth little lip at its edge. Periostracum thin, transparent, on living specimens often polished off. Color of dry shell variable from light orange, dark purplish brown to black. Living snails show more dull brownish to black colors. Some specimens uniformly colored, others variegated with white.

Operculum: Light yellow, translucent, concentric, rounded in front and pointed behind, broadest behind



Figure 14

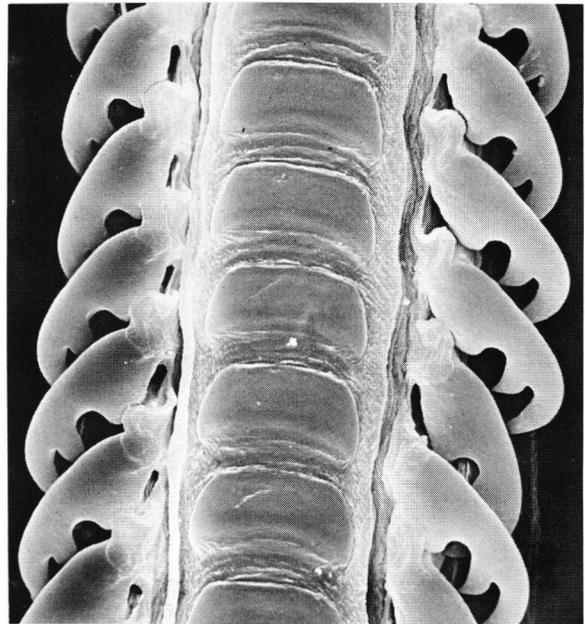
Shell of *Anachis* sp. (scale: 1 mm)

Figure 15

Radula of *Anachis* sp. (magnification $\times 660$)

its middle. Nucleus terminal, projecting very slightly beyond opercular lobe. From the nucleus a broadening cord curves to the rounded side, perpendicular to the growth lines. Operculum up to 1 mm long, with up to 8 thick growth lines, with about 8 thin lines between each 2 of them.

Soft Parts: Siphon opaque with white and brown spots; proboscis, head-foot irregularly striped and dotted with black and dark brown; sole of foot yellowish opaque with white spots at the rim; large eyes at the base of the tentacles; tentacles opaque with internal white spots and 2 black to dark brown external rings.

Radula: Central tooth plate broad, rounded at the edges; lateral teeth with 3 cusps, the first broad and rounded, the second and third narrow and pointed.

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