

## Character of a microgastropod fauna from a carbonate sand of Cebu (Philippines).

KLAUS BANDEL<sup>\*)</sup>

with 36 Textfigures and 8 Plates

### Contents

Introduction . . . . .	442
1. Subclass Archaeogastropoda . . . . .	443
2. Subclass Neritomorpha . . . . .	445
3. Subclass Caenogastropoda, order Ctenoglossa . . . . .	446
4. Subclass Caenogastropoda, orders Cerithiimorpha, Littorinimorpha and Strombimorpha . . . . .	448
5. Subclass Caenogastropoda, order Neomesogastropoda . . . . .	453
6. Subclass Caenogastropoda, order Neogastropoda . . . . .	457
7. Subclass Heterostropha . . . . .	460
8. Pelagic gastropods . . . . .	463
9. Conclusions . . . . .	467
Acknowledgment . . . . .	468
References . . . . .	468

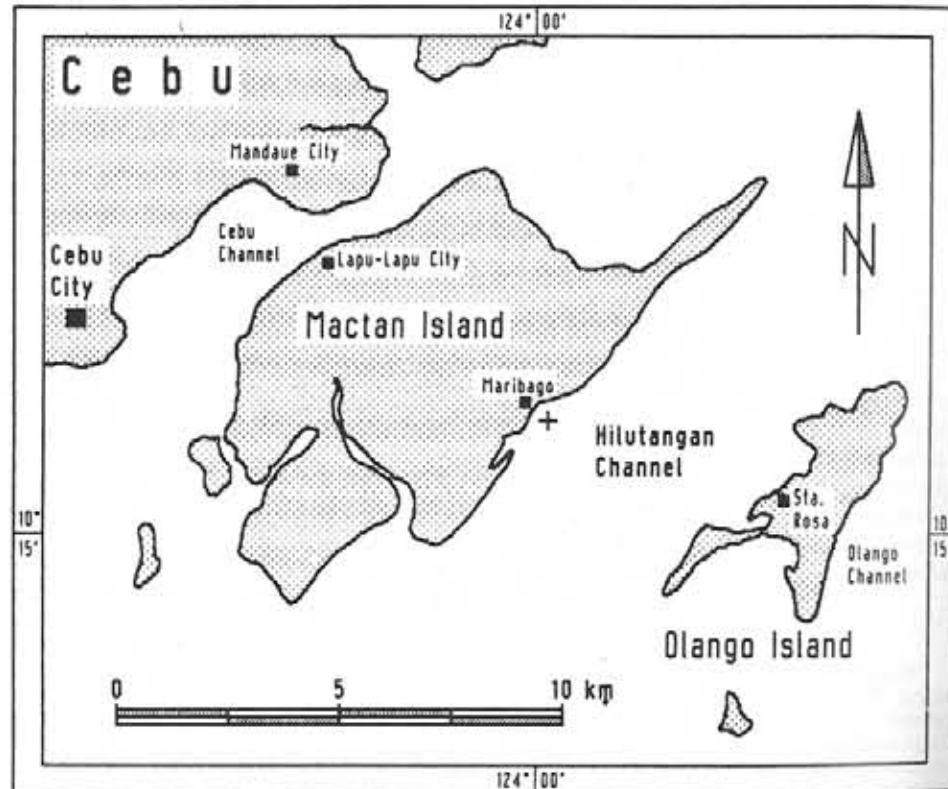
### Abstract

Small shells of gastropods are common in marine calcareous sands of tropical Cebu Island. They commonly represent juvenile shells of larger adults but also many outgrown individuals of small-sized species. The morphology and sculpture of the first whorls is often sufficient to determine a species. It places a shell into one of the four subclasses Archaeogastropoda, Neritomorpha, Caenogastropoda or Heterostropha. Usually a certain order and superfamily can be determined as well. Only rarely a shell is not characteristic. Gastropod species and groups of species characterize quite well the environment in which they live. Most of the species found in the studied sample provide evidence for a specific shallow water environment occurring nearby ranging from the shore, across lagoons into the reef and its slope. Many species of the gastropods from Cebu had relatives in the European Paleogene. Ecologic characterization of the modern fauna will thus enable more reliable paleoecologic interpretation of fossil sediments. The analysis of the composition of the dead shells within a given sample of calcareous sand can give clear indication about the area of origin of the shells and thus the source of the analysed sediment. The method can be greatly improved when the biology of the species living in the shallow sea near Cebu, Philippines is better known.

<sup>\*)</sup> Author's Address: Prof. Dr. KLAUS BANDEL, Geologisch-Paläontologisches Institut und Museum, Universität Hamburg, Bundesstraße 55, D-2000 Hamburg 13.

### Zusammenfassung

Kleine Gastropodenschalen sind im Kalksand vor der Küste Cebus sehr häufig. Sie bestehen zum Teil aus den Jugendstadien größerer bis sehr großer Arten und zum Teil aus Gehäusen kleinwüchsiger, ausgewachsener Arten. Schon die ersten Windungen ermöglichen oftmals die Bestimmung einer Art, meist die genaue Zuordnung zu einer taxonomischen Gruppe, und nur selten kann keine Ansprache erfolgen. Damit läßt die Schnecken-totfauna einer einzigen Kalksandprobe (im untersuchten Fall etwa 500 g. Trockengewicht) eine Aussage über die in der Nähe lebenden Gastropoden zu. Da viele Gastropodengruppen charakteristische Lebensbereiche besiedeln und typische Gewohnheiten besitzen, ermöglicht die Analyse Aussagen über in der Nähe der Fundstelle anzutreffende Milieus. Bei besserer Kenntnis der Lebensweise einiger Arten wäre eine noch viel genauere Aussage leicht möglich. Da in den Philippinen zahlreiche Arten leben, die im älteren Tertiär Europas Verwandte besaßen, könnten diese ökologischen Befunde in der geologischen Ausdeutung genutzt werden. Bei heutigen Sedimenten erlauben sie die Ermittlung der Herkunft der untersuchten Sedimentpartikel.



Textfigure 1: Location map of the studied sample. Illustration by P. BUCHSEL.

### Introduction

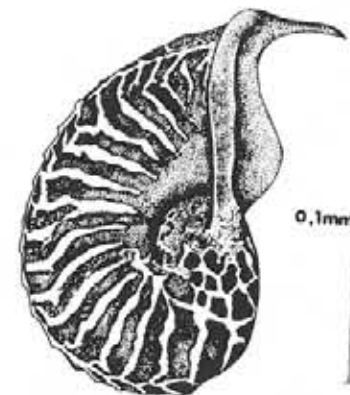
A sample of sandy sediment with about 500 gr. weight had been taken from 80 m depth at the slope into Hilutangan Channel off shore from Mactan Island near Cebu City during a survey carried out by the working group HILLMER-SCHOLZ (1990). From this sample gastropods were selected until it became evident that most characteristic representatives had been encountered (with about 5000 individuals). All are smaller than a few mm and larger than 0,2 mm and consisted of a large number of species. Determinations of these on a rough taxonomic scale resulted in the classification of systematic groups with usually similar ecologic requirements and a similar functional morphology. They represent species and groups that originally lived within very different environ-

ments and have been deposited together in the substrate found on the slope of Hilutangan Channel. In this study a coarse characterization of these groups is undertaken and the mode of their differentiation with the help of the earliest whorls of the shell is demonstrated. It is hoped that the study results in the begin of a more thorough analysis of the gastropods from the sea near Cebu.

### Systematic Descriptions

#### 1. Subclass Archaeogastropoda

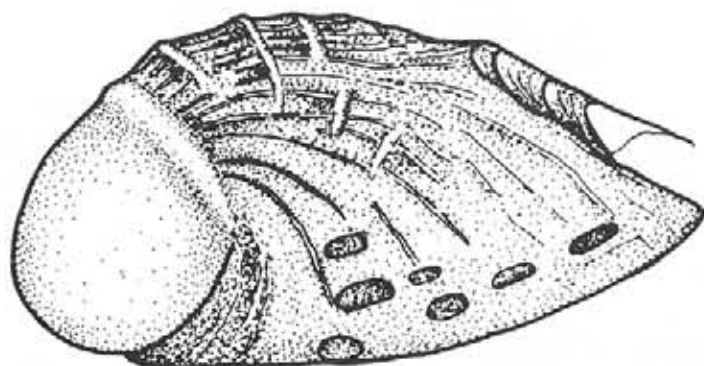
Members of the Archaeogastropoda can be recognized by their first whorl in well preserved juvenile shells (textfig. 2, pl. 2, figs. 1-6). In contrast to all other Gastropoda the embryonic whorl is never succeeded by a larval shell. At first the embryonic shell is not mineralized and of bilateral symmetrical shape. Before benthic life begins and after the body has become torted the shell is deformed by muscular action and the apical and the ventral side of the embryonic shell are usually deformed (Bandel 1982) (pl. 2, figs. 1-6).



Textfigure 2: The embryonic shell of *Scissurella* from the Mediterranean Sea shows the deformed sculpture on the inner side near to the fold, a marginal thickening of the aperture added to the shell after deformation and a small addition in front of it added from the swimming veliger. Shell diameter about 0,15 mm.

Most of the recognized Archaeogastropoda live on hard substrates from which they rake, bite and scrape their food with the help of their radula. Only species of the Umbroniidae like the figured ones with rounded whorls (pl. 1, fig. 3; pl. 2, fig. 8) represented by numerous shells, live within the sand, can bury quite well. They may live near the location of the bottom sample. As Hickmann (1985) demonstrated, species of the Umbroniidae feed by filtering food from the seawater that is pumped across the feather-like gill by the action of cilia.

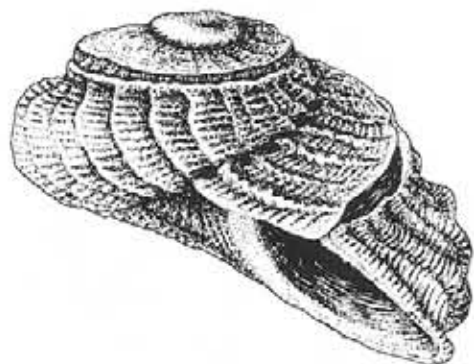
Several typically conical shells of the limpet-like Patellogastropoda belong to the Acmaeidae as well as the Patellidae (pl. 1, fig. 8). Their usually battered condition indicates that they have been transported to the site on the slopes of the channel from nearshore areas. Here they graze algae from hard bottom substrate. Key-hole limpets of the Fissurelloidea are less common and presented by emarginulid forms with anterior fissure (textfig. 3) and fissurellid forms with a central orifice. Species of fissurellids either feed on algae within the tidal zone and in well illuminated environments or on crust forming animals like sponges, bryozoans and tunicates and occur wherever their prey may live.



Textfigure 3: The juvenile shell of *Emarginula* demonstrates the embryonic shell, the following juvenile shell without slit and the later juvenile shell with slit. Size of shell about 0,7 mm.

When animals are collected alive their fecal pellets tell what they have been feeding on and they can then faithfully be assigned to a certain type of environment (BANDEL 1976a).

The small, thin shelled, slit bearing Scissurellidae are common in the sand, well preserved and belong to several species (textfig. 4; pl. 2, fig. 7). Species belonging to this group are common in the deep water environment (pl. 2, fig. 7) and also in the reef rubble and algal thickets growing within the reef (textfig. 4). Here they collect minute food particles from the substrate on algae and secondary hardgrounds. The specific living environment is usually unknown for most species but is probably species specific. Deep water species are restricted to that environment and do not live in shallow water and the littoral species do not occur below this zone. The scissurellid shell is light and thin so that it is easily transported by currents over long distance.



Textfigure 4: A shallow water scissurellid of the type that lives on reef rubble covered by algae around Cebu. Size of shell about 1,5 mm.

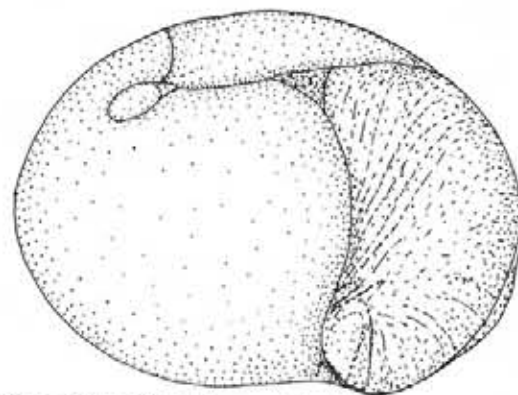
Juvenile shells of *Astraea/Turbo* - relation with flat apex (pl. 1, figs. 6, 7, 9), of *Tricolia* - relation with littoriniform shell and smooth shiny surface, of *Trochus* - relation with dark lines and spiral ribs (pl. 2, fig. 3), of liotiinid relation (*Liotia* etc.) with fenestrate shell ornament have probably come from the shallow water. Here the reefs and shallow limestone flats and connected limestone slabs and algal growths are the most likely living environment for most species.

Within the area of the taken sample the ear-shaped members of the Stomatellinae (pl. 1, fig. 5; pl. 2, fig. 1) are to be expected to be found alive, as well as a cyclostrematid occurring in all sizes and shows little corrosion (pl. 1, fig. 1; pl. 2, fig. 4). A little species of the Solariellinae also may have lived in these sands (pl. 1, fig. 2) since its relatives are common on substrates in deep water where they hunt animal prey. Extremely small trochiform archaeogastropods are found within the Skeneidae (pl. 1, fig. 4; pl. 2, figs. 2, 11) and may live on sunken wood (MARSHALL 1988) but also on shallow water algal mats like the liotiinid *Cyclostrema*.

In general the archaeogastropod fauna of the vicinity of the analysed sample is very diversified. Most species here represented by juvenile shells live on hard substrates within the reef slopes and on its top as well as in the coastal area. The smaller forms are characteristic to a wide range of substrates. All will be very useful for as ecological marker species in their specific environment (BANDEL & WEDLER 1987).

## 2. Subclass Neritomorpha

The veligers of Neritoidea differ from those of all other gastropods by dissolving the internal walls of their shells. The visceral mass and pallial cavity thus occupy very much of the whole cup-like space of the area behind the aperture. In addition the shape of the larval shell is characteristically coiled in such a way that successive whorls cover each other to a large extent (textfig. 5; pl. 2, figs. 9, 10). In the analysed sample the shells of pediveligers ready to metamorphose are very common and of different sizes. Their construction, their smooth surface and their almost spherical shape is very similar to each other so that different species could only be differentiated from each other by their size (textfig. 5). Planktonic stages of the Neritomorpha are abundant in the sea near the source of the studied sediment but pediveligers could not successfully settle here and metamorphose. The light shells of freshly settled veliger may also have been transported to the slope of the channel.



Textfigure 5: Pediveliger shell of a neritomorph with aperture closed by the operculum. Size of the shell about 0,4 mm.

Neritomorpha of the genus *Nerita* and related forms live within the intertidal area on hard substrates along the whole shore of the Indo Pacific Ocean and most shores of tropical seas. Individuals scrape algae and other encrusting plants from hard surfaces of rock and coral debris aided by the mineralized teeth of their radula. All species of the littoral Neritidae related to the genus

*Nerita* produce cupola shaped egg capsules (BANDEL 1982) which are attached to rocks and camouflaged and protected by additions of Calcium-carbonate spheres to the top of each egg capsule. Such capsules should be very common along the rocky shores with the tidal area and in tidal rock pools of the coast of Cebu.

The small neritid *Smaragdia viridis* lives on and from the leaves of the turtle grass and should be common in the shallow lagoons of Mactan Island. Here the greenish, well camouflaged egg capsules are also present from which planktotrophic veliger hatch that stay in the plankton for several months (SCHELTEMA 1971, BANDEL 1982). On seagrass also representatives of the limpet-like Phenacolepadidae are to be expected, but little is known about their ecological requirements.

Larval shells probably also belong to different species of the Neritidae living in large numbers of individuals within the estuaries and moving up the fresh water streams. Their larvae after hatching from the egg capsule also enter the sea and have a more or less extended planktotrophic stage before they enter again the brackish water environment to metamorphose and settle only here. *Septaria* (pl. 2, fig. 9, 10) has been washed from estuarine environment.

### 3. Subclass Caenogastropoda, order Ctenoglossa

The Ctenoglossa are represented by numerous species and individuals of the Triphoroidea, a fair number of species of the Eulimoidea and some representatives of the Janthinoidea.

a) Most or all members of the Triphoroidea parasitize on sponges. A large number of species of the characteristically sinistrally coiled Triphoridae and the dextral Cerithiopsidae occur in the Indian Ocean and a fair share of them is represented in the studied sample. Wherever sponges have settled near the beach, within the lagoon, at the reef and in water of greater depth triphorids live on and in them feeding on their tissue and from the suspended material collected by the sponge. The different species of triphorids have species specific sponge hosts so that they reflect biozones of sponge growth.

The veliger of Triphoroidea hatch from the egg mass that is hidden within the sponge. It is usually provided with a highly sculptured embryonic shell of about one whorl (pl. 5, fig. 1). The veliger larvae of most tropical species remain in the Plankton for a long time often amounting to several months. During pelagic life velum bases fit into two lobes of the outer lip of the aperture of the shell and between these the outer lip projects characteristically (textfig. 6). The



Textfigure 6: Fully grown veliger shell of *Triphora*. Shell about 0,4 mm high.

sinistral larval shell of most Triphoridae is slender turritiform and highly ornamented by spiral and axial ribs (pl. 5, fig. 1). Mediterranean larvae have been presented by (RICHTER & THORSON 1975). Adult shells with a similar sculpture to Triphoridae but dextral coiling are found in the related Cerithiopsidae (pl. 5, figs. 2, 3, 4). Their larval shell may be less ornamented but otherwise are of similar shape (BANDEL 1991) (textfig. 7).



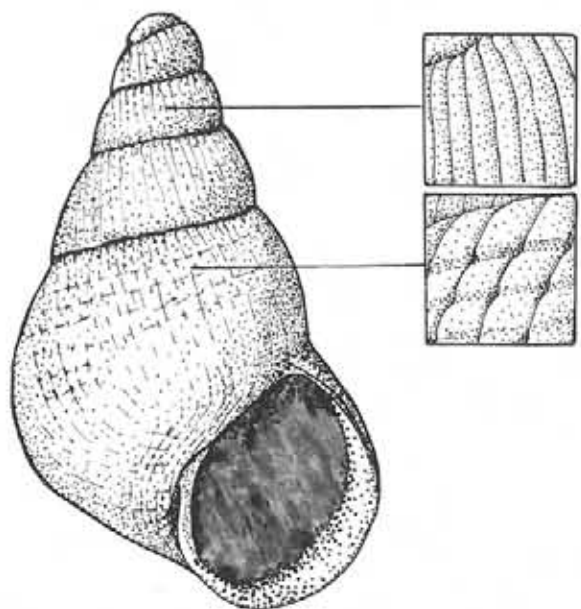
Textfigure 7: Fully grown veliger shell of *Cerithiopsis*. Shell about 0,6 mm high.

b) Species of the Epitoniidae usually live by sucking body liquid and feeding on body tissue from benthic coelenterates. Species of small body size live closely associated to one host, while species of larger body size move from prey to prey. Epitoniid species are found in the shallow lagoon and reef environment to greater depth. Their presence is not so much correlated to depth zonation but to the presence of hosts. One encountered species has whorls that are detached from each other (pl. 5, figs. 6, 8), and most probably lives within its anthozoan host protected by its body walls and the poisonous netting cells. This may also be the case in some of the small species of the group which are encountered here (pl. 5, figs. 8, 10, 11). The ecology of only a few species is known well (ROBERTSON 1983).

Veligers hatch from egg masses consisting of grape-like capsules on bundles of strings attached to some hard substrate (BANDEL 1976b). From each capsule 150 to 200 small veligers hatch with a shell of a little less than one whorl (BANDEL 1975). They stay in the plankton for a long time growing characteristically ornamented shells (ROBERTSON 1971) (textfig. 8; pl. 5, fig. 6). Only rarely these are provided with a projection of the outer lip (BANDEL 1991a) and mostly the aperture is simple. Fully grown larval shells with fine axial striae are fairly common in the sample while larger shells are rare and usually fragmented.

c) Eulimidae like *Hoplopteron* are represented by at least four species and may be regarded as intermediating to the Epitoniidae. One representative is relatively common and present with shells of all stages of growth (pl. 5, fig. 7). It may well live near the location of the sample on the slope of Hilutangan Channel. It would be very interesting to learn something about its mode of life of which very little is known.

The actual Eulimidae are parasites on and in echinoderms. Their shells are usually slender, sometimes curiously curved (pl. 5, fig. 5), and all have a highly polished surface. The larval shell usually grades into the teleoconch without



Textfigure 8: Shell of pediveliger of *Epitonium* with details of the fine sculpture. Shell about 0,7 mm high.

much change in shape and sculpture. Several species are present giving evidence of a diverse and rich fauna of echinoderms in the vicinity of the location of the sample. Most species are host specific (WAREN 1988) and could characterize the echinoderms that live in the area if we knew which species belongs to which host.

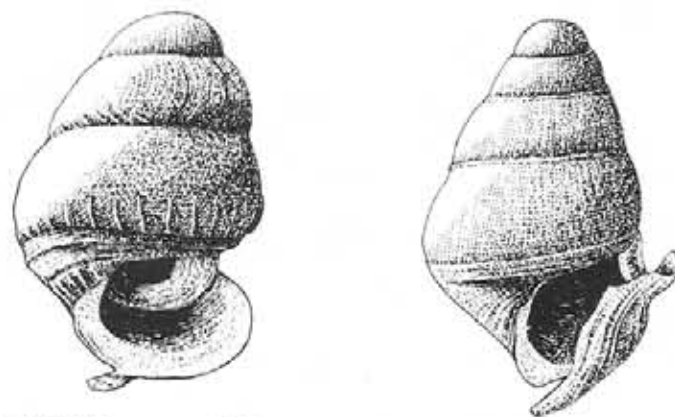
#### 4. Subclass Caenogastropoda, orders Cerithiimorpha, Littorinimorpha and Strombimorpha

Representatives of the Cerithioidea, Rissoidea and Littorinoidea produce quite a variety of fairly different shapes of adult shells within a large range of sizes but regarding their larval shells show similarities. It is usually of conical shape, about as wide as high and consists of several sculptured whorls. They are smaller than those of the Neomesogastropoda and Neogastropoda and shorter and less slender than those of the Ctenoglossa. The portion that is produced during the planktotrophic stage is commonly provided with a strong projection of the apertural lip (textfigs. 9A, 9B).

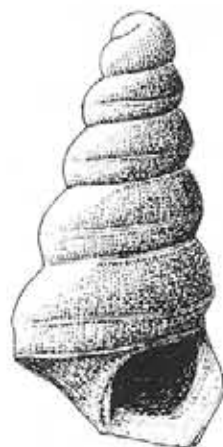
##### a) Cerithiimorpha

The shell of the Turritellidae is slender, many-whorled and the larval portion smooth or provided with one median keel of the whorl (textfig. 10A). Adult individuals usually hide within the sand and acquire their food by filtering it from the water with their gill. They live wherever enough suspension is carried across a sandy bottom below wave base with sufficient sediment stability.

The Cerithioidea are represented by a variety of different species that lived in a number of environments and have been transported into the bottom sediments of the channel. Larger forms of the relation of *Cerithium* rake small algae and plant fragments from sediment surfaces and from interstices of sand (pl. 3, fig. 11). They thus move in flocks across of through sandy bottom or move



Textfigure 9: A and B represent fully grown larval shells of Cerithiimorpha or Rissoidea with large projection of the outer lip as caught from the Plankton in the Indopacific. Height of shells about 0,4 mm.



Textfigure 10: A. Pediveliger shells of *A Turritella* with about 0,4 mm height

through dense algal thickets covering hard substrates in the well illuminated zone below the tidal range. Small species belonging to this group in the relation to the genera *Bittium*, *Alabina*, *Styliferina* and *Diastoma* live within algal thickets and may be present in extraordinary numbers within a well vegetated zone at one time of the year and in the absence of such growths at other times of the year be rather rare (pl. 3, figs. 5, 12; pl. 4, figs. 1, 2, 8; pl. 5, figs. 9, 15). This explains their common occurrence in the sediment, into which most probably they have been transported from more shallow living place. A probable member of the genus *Obtortio* owns a larval shell (pl. 3, fig. 12; pl. 4, fig. 8) which is very similar to forms found in Triassic and Carboniferous faunas (BANDEL 1991a).

*Modulus* has an unusually short conical shell for a representative of the Cerithioidea (pl. 4, fig. 6). Only juvenile shells are present and these have been washed in from intertidal and very shallow subtidal hard substrates, where the members of this genus live. Similar turbinat small shells are present in the *Sansonia* relation (textfig. 14) represented with three species (pl. 4, figs. 3, 5). The larval shell resembles that of Cerithioidea (pl. 5, fig. 14) but the thickened apertural margin clearly sets the adult shell apart from any other group and

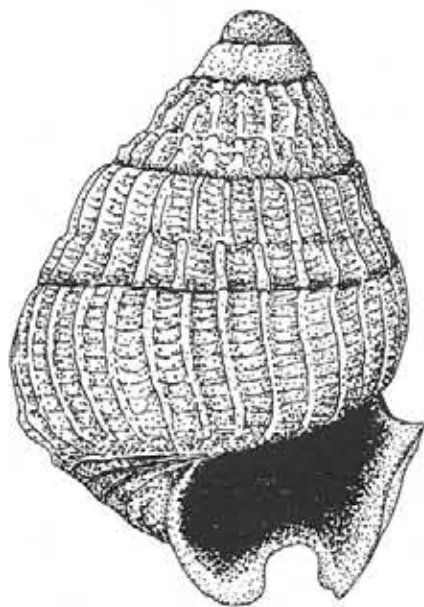


Textfigure 14: The shell of *Sansonia* is about 1,2 mm high.

allows to trace them into the past to at least Upper Cretaceous time. Their environmental requirements as well as their living place are unknown.

*Scaliola* is easily recognized with sand grains agglutinated in its shell. This small cerithioid is very common and may live near the sampling place but also in more shallow water among the reefs and lagoons (BANDEL & EL NAKHAL 1991). It is well camouflaged on the sandy bottom by grains agglutinated to its shell.

Litiopid Cerithioidea are found on intertidal algal growths as well as on drifting algae. The shells seen here with moderate number may have dropped down from such floats which seasonally are common, or they may have been washed in from the shore (textfig. 10B).



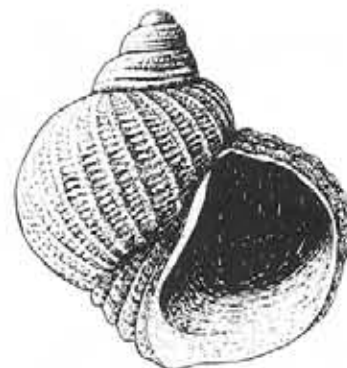
Textfigure 10: *B Alaba* with about 0,3 mm height.

#### b) Littorinimorpha and Strombimorpha

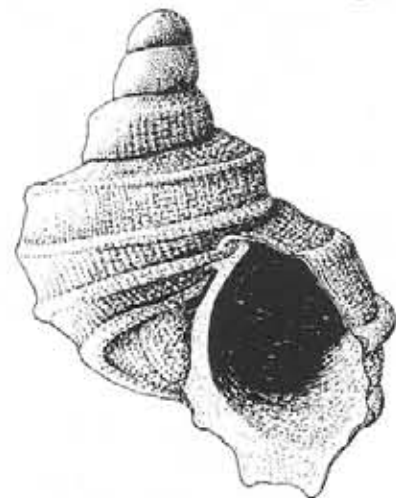
Shells of Littorinidae have not been recognized even though representatives of this group surely live in great numbers within the tidal area of the shore. Among the litter of bushes and trees found in shady places in the sublittoral environment reached by the sea only at extremely high tides or storms *Truncatella* is living. It has a light shell and in contrast to the littorinids has been washed into the channel (pl. 5, figs. 12, 13).

A number of species of the Rissoidea are present. Among these a few species of the *Alvania*-type with few spiral and radial ribs (pl. 3, figs. 6, 8), of the *Rissoina*-type with axial ribs (pl. 3, fig. 4) and of *Barleeia*-type with smooth shell (pl. 3, fig. 10) are present with many individuals. Most of these most probably live in shallow, well illuminated water within algal growths and have been transported down slope.

Vitrinellids with almost planspirally coiled small shell represent a specialized group that live as commensals of endobenthic worms of different types. Species of the genera *Cyclostremiscus*, *Scissilabra* (pl. 3, fig. 9) and *Circulus* (pl. 3, fig. 7) could be recognized, other species are present. The more highly coiled *Macromphalus*, *Vanikoro* and *Fossarella* with small auriform shell (textfigs. 11, 12) are not related to the Vitrinellidae as can easily be gathered



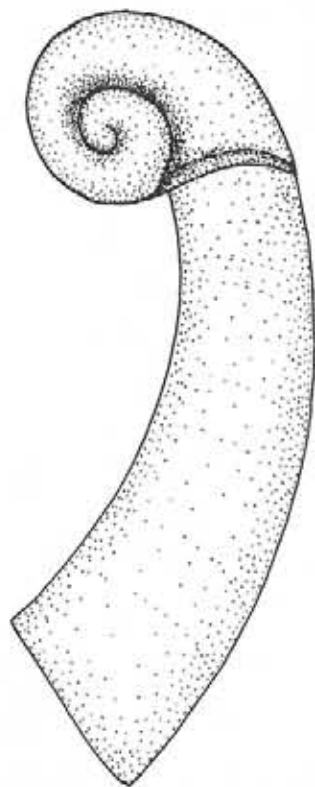
Textfigure 11: The shell of *Vanikoro* is very different in its early ontogenetic portion of the embryonic and larval shell from the teleoconch. Total height about 1,5 mm.



Textfigure 12: *Fossarella* from Cebu is a member of the Vanikoridae. Height about 1 mm.

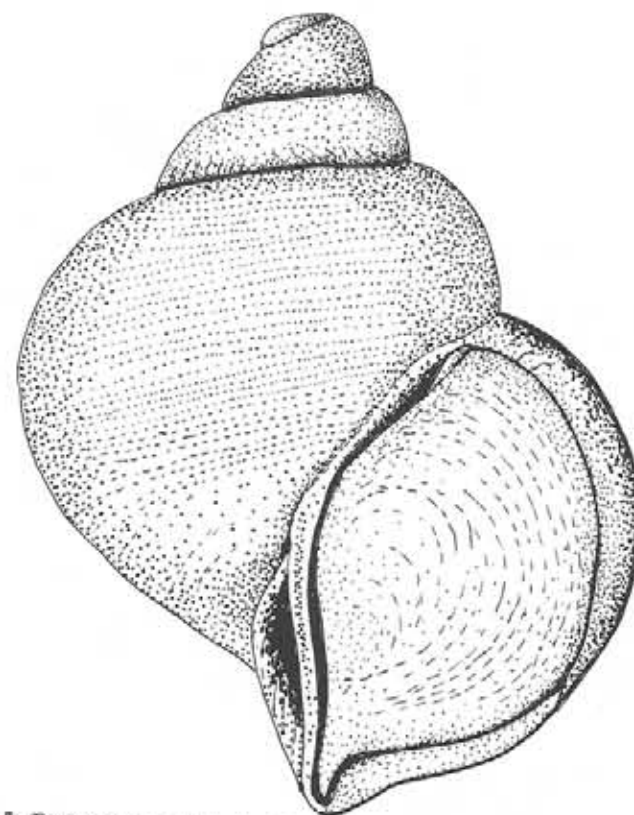
from the morphology and sculpture of its larval shell. They resemble members of the Vanikoridae in this regard. Individuals of Vanikoridae (textfigs. 11, 12; pl. 4, fig. 4) may live within crevices of reef-rock and other hard substrate like their Mediterranean relatives (WARÉN & BOUCHET 1988).

A specialized group of minute gastropods with secondarily uncoiled shells is represented by the Caecidae (pl. 3, figs. 1, 2). These may have a coiled larval shell in the *Caecum* relation (textfig. 13; pl. 3, fig. 1) and only a coiled embryonic shell and straight larval shell in the *Strebloceras* (pl. 3, fig. 2a) relation, both of which are common in the sample. The juvenile shell is usually shed when the animal is fully grown and the apical end of the elephant tusk-like shell is formed by a septum (pl. 3, fig. 2). The small animals move through algal thickets and the soft surface layers of the sediment in the search for food, consisting of diatoms and similar small particles. *Caecum* and relatives live in shallow water, while the living environment of *Parastrophia* and *Strebloceras* is still unknown (BANDEL 1991c).



Textfigure 13: The larval shell of *Caecum* is coiled, while the teleoconch is uncoiled. Size about 1 mm.

The Stromboidea form a conspicuous group of large to moderately sized gastropods that live in the shallow tropical sea and here collect plant materials as food. Their juvenile shells are best recognized by their larval shells found uncommonly in the sampled sediment (textfig. 15). Xenophoridae are present as well and recognized by the broad larval shell and the juveniles that start to agglutinate sediment particles right after metamorphosis (PONDER, 1984).



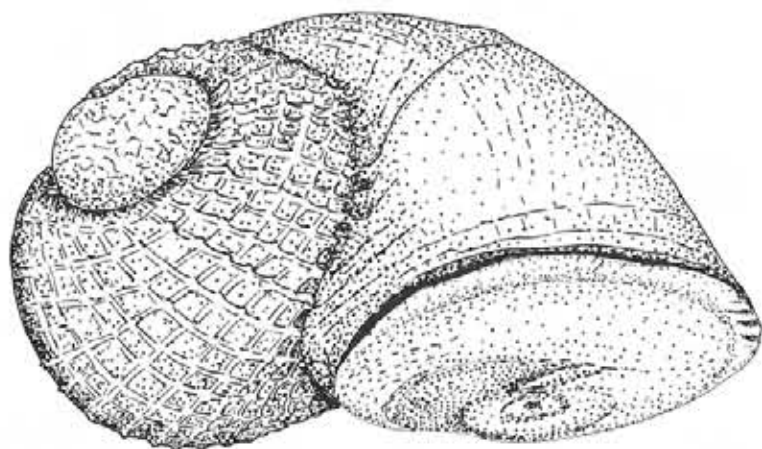
Textfigure 15: Pediveliger shell of a *Strombus* with aperture closed by the operculum. Shell about 0,4 mm high.

##### 5. Subclass Caenogastropoda, order Neomesogastropoda

Members of the Neomesogastropoda BANDEL, 1991b usually have especially large larval shells. Within them the Calyptraeidae, Naticoidea, Cypraeoidea, Tonnoidea and the Echinospira group are united. Each group has a characteristic larval shell as well as a special mode of life. Similar larval shells as found in this group have been noted on teleoconchs of species that are more similar to Littorinimorpha (pl. 3, fig. 3). These species would surely be very interesting to study alive.

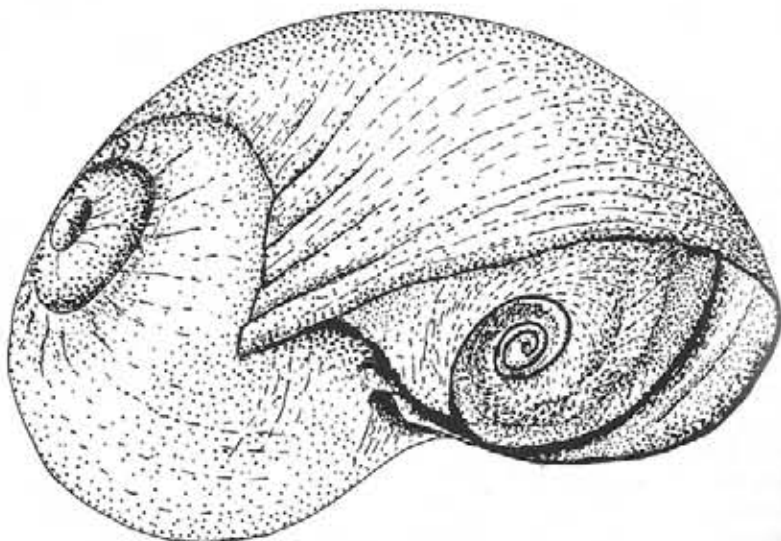
a) The Calyptraeidae for example are present with some juvenile limpet shells of *Cheilea* (pl. 4, fig. 7) and *Crepidula* relation as well as even more fully grown larval shells (textfig. 16). The larvae of the *Cheilea-Hipponix* type can stay in the plankton for quite a long time that may amount to several months. The metamorphosed animal grows into a limpet that is attached to moving substrate like a larger gastropod or the home of a hermit crab or other stable substrate and filters food from the sea water. Larvae of the Hipponicidae differ from those of the Calyptraeidae in shape and can help to differentiate these two groups of limpets. Calyptraeidae hatch late in their ontogeny and stay in the plankton for less time. The shell is almost planspirally coiled and has less than two whorls, while that of the Hipponicidae is of rounded outline and has more than two whorls (pl. 4, fig. 7).

b) Naticoidea with members of genera like *Natica*, *Mamilla* and *Polinices* are found in sandy bottoms below low water in the whole tropical Indian Ocean.



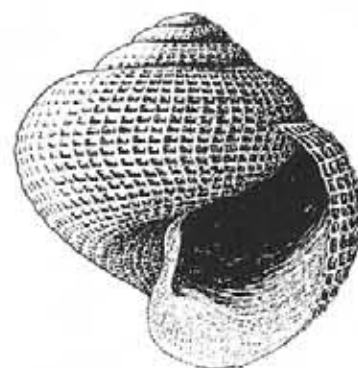
Textfigure 16: The larval shell of *Hipponix conicus* from Indopacific plankton with operculum in place is about 0,5 mm wide.

Naticidae do not only rest but also move within the sediment and here hunt prey that consists predominantly of bivalves but also other shelled organisms like ostracods, tube-worms or scaphopods. Victims are opened by a hole which is drilled through the shell, and such shells are common in the sample. From characteristic egg collars (BANDEL 1976c, THORSON 1946) planktotrophic veligers commonly hatch with about 0.2 mm large shell (BANDEL 1975). The larva may remain for many weeks, and in some cases several months, in the open sea and carries a rather large shiny-smooth shell suspended below a large four lobed velum (textfig. 17). The shell margin of the pediveliger is smooth and straight providing no indication for the presence of the tube-like siphuncle that is formed by the folded mantle. Fully grown larval shells are common while more solidly calcified juvenile shells are rare.

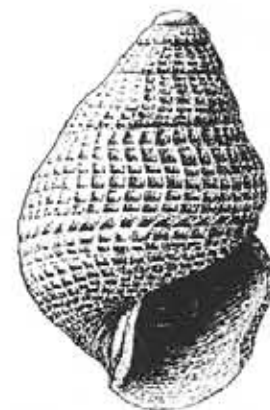


Textfigure 17: Naticid larval shell of about 0,6 mm width with the operculum closing the aperture.

c) The Cypraeoidea are present with members of Cypraeidae and Ovulidae. A number of species of the common genus *Cypraea* live in the shallow lagoons and among the reefs and debris in the reef. Here they usually remain hidden on the underside of boulders and rocks. They feed on crust formig colonial animals. The last whorl of the adult shell covers all early whorls including the embryonic and larval shell. Many species brood their egg masses. I have observed *C. nebrites* and *C. arabica* from the Red Sea at Port Sudan to brood their egg masses until veliger hatched. The larvae remain in the plankton for a long time until their larvae settle and metamorphose. Their shell is sculptured by axial and spiral ribs forming a regular pattern (textfigs. 18, 19). Larval shells of several species are present and some have started to produce the juvenile shell. Larger and heavier juvenile and adult shells were not encountered and have probably remained in their shallow living environment.



Textfigure 18: The larval shell of a *Cypraea* is highly sculptured and about 0,6 mm high.

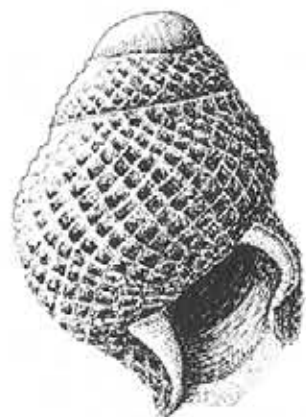


Textfigure 19: Cypraeid larval shells have similar reticulate sculpture but different dimensions and shapes. Height about 0,5 mm.

The shells of Ovulidae are of similar shape as those of *Cypraea*. Ovulidae also cover their shiny but usually unicoloured shell with muscular mantle that has colourful patterns. They feed on coelenterates, preferrably the colonies of gorgonarian octocorals. Their skeletal spicules compose much of the studied calcareous sand. Small species of ovulids like those of the genera *Simnia* and *Primovula* feed on the polyps of gorgonarian colonies, while larger individuals like *Ovula* and *Cyphoma* eat the flesh of these anthozoans along with much of



the calcareous skeleton. Several species of Ovulidae are represented with their larval shells that can be recognized due to the characteristic pattern formed by inclined ribs crossing each other (textfig. 20). From egg capsules attached to branches of their prey veligers hatch (BANDEL, 1973) with shells covered by a pattern of grooves and ridges (BANDEL, 1975). Shells of veligers have been described and figured from *Pedicularia* by ROBERTSON (1971) and from *Simnia* by THIRIOT-QUIEVREUX (1972) and RICHTER & THORSON (1975).



Textfigure 20: Larval shell of an ovulid with the pattern of oblique ribs. High of shell about 0,6 mm.

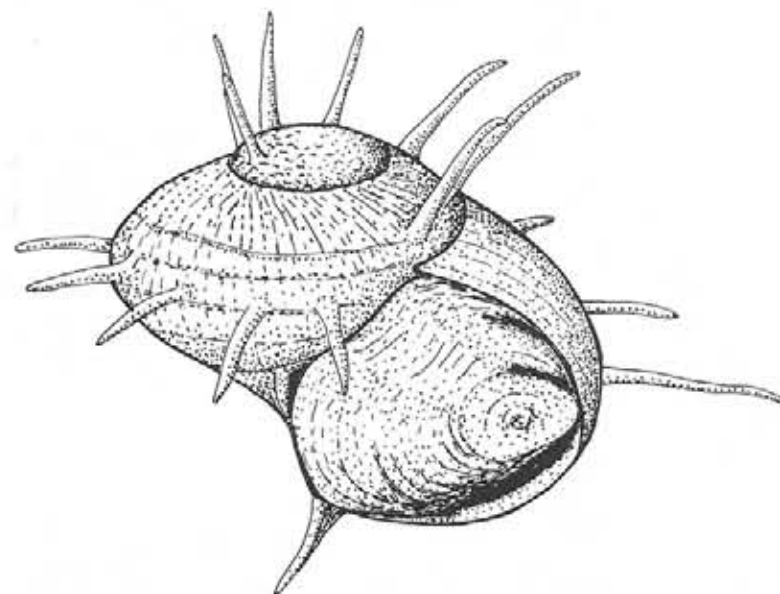
d) Tonnoidea of the the genera *Cymatium*, *Charonia*, *Bursa*, *Malea*, *Casmaria* and *Tonna* can be encountered within lagoons and reefs of all tropical Indopacific areas. They feed on a variety of animals. *Charonia* hunts echinoderms like sea urchins, starfish and holothurians on hard substrates as well as on sandy bottoms. *Malea* digs in fine sand for irregular sea urchins. *Tonna* hunts holothurians on sandy bottoms. *Bursa* and *Cymatium* hunt other gastropods and worms.

Members of the genera *Cymatium*, *Bursa* and *Charonia* brood their spawn (BANDEL 1975, 1976c) until young hatch and are released into the plankton. Egg masses of *Tonna* and *Distorsio* lie on sandy bottom in a similar way as found in the Naticidae. Like the attached egg masses of *Cypraecassis*, *Cassis* and *Phalium* these egg cases are left behind after oviposition and are not brooded. Larvae remain in the plankton for an extended time of up to a year (SCHELTEMA 1971) and construct conspicuous shells (BANDEL 1981).

The most characteristic organ of larger tonnoid veligers is the trunk-like extension of the mantle margin with which the whole former shell can be covered by an additional layer of periostracum with each newly formed whorl (BANDEL 1991c). In many cases the early shell shows a different sculpture than the later shell because early sculptured whorls become covered and the cover itself may be spinous or carinate (textfig. 21). A few of these veliger shells of predominantly organic composition were found.

e) The members of the -Echinospira group are a diverse lot (BANDEL 1991c) of which some members of the *Erato* and *Trivia* relation were found (pl. 4, fig. 9) as well as a small trochiform member of the *Lippistes* relation of the Trichotropidae (pl. 4, fig. 10). The larvae of these diverse forms of which the first two feed on tunicates, and the last probably filters food from the water are characterized by the presence of a gelatinous cover that is usually lost at or after

metamorphosis. This cover coats a normally coiled shell in the Triviidae (pl. 4, fig. 9), a planspirally coiled shell in the Trichotropidae (pl. 4, fig. 10) and Capulidae and an openly coiled shell in the Lamellariidae. In the later case the larval shell is not mineralized and pulled into a coil with whorls touching each other only after metamorphosis, which results in strong folds (pl. 4, fig. 11).



Textfigure 21: Tonnoidean larval shell with large periostracal spines that corrode easily. Size about 0,7 mm.

#### 6. Subclass Caenogastropoda, order Neogastropoda

Many species of the Neogastropoda have conspicuous adults with large shell that are easily detected by snorkel or scuba diving. Almost all neogastropods are carnivorous and hunt prey consisting of different animals as various worms, molluscs, coelenterates, bryozoans and even fish and carrion. The shells found in the studied sample to a large extent belong to juvenile or larval neogastropods and only a few small sized species actually live on the slope between reef and channel bottom like a columbellid (pl. 6, fig. 1), a marginellid and several turrids (pl. 6, figs. 6, 7). In many neogastropod species the phase of the planktotrophic larva has been abolished for an intracapsular development. Here yolk or nurse eggs serve as food of the embryos and a miniature young hatches from the egg mass. But the encountered shells of this group rarely show the characteristic large embryonic shells of species with intracapsular development. One example is the little marginellid mentioned earlier, which plows through the sand nearby in the hunt of its prey.

Most shells of neogastropods have been transported to the channel slope from a more shallow environment, and the washed in shells are small, light and represent the early whorls of larger species with planktotrophic development. Within several of the larger groups it is possible to recognize characteristic larval shells, while others still are quite badly known.

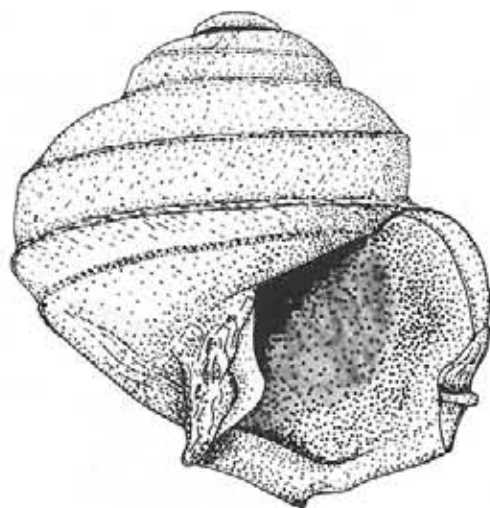
a) A number of Muricidae live in the reef zone and close to it, only very few live away from it in deeper water. Many species have a development without free larvae, others like members of the genera *Nassa*, *Drupa*, *Morula* and

*Coralliophila* produce egg capsules from which veligers with a well ornamented shell hatch (BANDEL, 1975). *Coralliophila* retains egg capsules in its mantle cavity until the veligers hatch and are released into the plankton (BANDEL, 1976f) (textfig. 22). The Coralliophilidae usually live as parasites on and in coelenterates feeding on their tissue. Several juvenile shells are present (pl. 6, fig. 11). The other muricids are carnivorous prey searching species feeding on molluscs as well as different types of worms which they often reach by way of a drilled hole similar to the naticids. Their larval shells are less conspicuous as those of the highly sculptured coralliophilids (pl. 6, figs. 10, 13).



Textfigure 22: The larval shell of a coralliophilid neogastropod is almost 0,9 mm high and strongly sculptured.

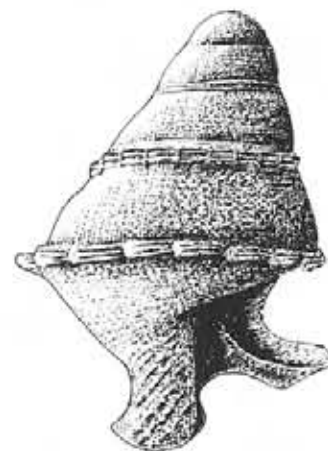
b) Nassariidae and similar buccinid Neogastropoda have a low conical veliger shell with a single or double spiral carina and a strong projection of the outer lip of the aperture (textfig. 23; pl. 6, fig. 12). The adults live in a variety of environments from shallow to deep water usually by actively hunting down animal prey but also by utilizing all kinds of carrion. Here they deposit their characteristic egg



Textfigure 23: Fully grown pediveliger shell of a nassariid neogastropod with two spiral keels measures about 0,6 mm in height.

capsules from which small veligers may hatch (BANDEL 1976g). The different species prefer different depths within the littoral zones and below these and are also characteristic in their requirements of substrates, so that they could be useful ecological indicators (BANDEL & WEDLER 1987). It seems that many of their species can be recognized by the morphology of their larval shell as well as by that of the adult shell.

Members of the Mitridae, Fasciolaridae and other groups of the Muricoidea are present and have to be savely recognized by studying their larval characters (textfigs. 24, 25, pl. 6, figs. 5, 9). Cancellariidae are also present. They represent an independant parasitic group of neogastropods that suck blood from sharks and rays and body liquid from a number of benthic animals. Nothing much is known regarding the life habits of this interesting group but its larval shell clearly differentiated it from other neogastropods. Its apical portion is almost flat and it resembles shell found in some tonnoidean genera.



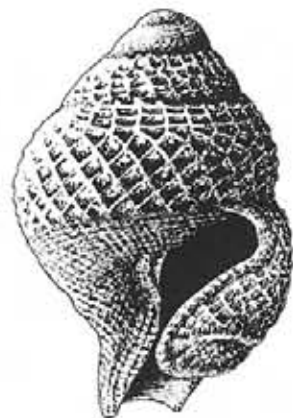
Textfigure 24: Pediveliger shell of a neogastropod probably of fasciolarid relation with large apertural projection and a size of about 0,6 mm.



Textfigure 25: Pediveliger shell of neogastropod with probable columbellid relation and a height of about 1 mm.

c) Turridae live in a variety of environments, most commonly in soft sediment of deeper more quiet water. Here they hunt worm-like prey which is poisoned and immobilized before it is swallowed as a whole. The veligers

belonging to some members of this group can be recognized by two features. Firstly the larval shell is often highly sculptured by axial and spiral ribs (textfig. 26; pl. 6, figs. 6, 7) similar as shown by THIRIOT-QUIÉVREUX (1969, 1971) and BABIO & THIRIOT-QUIÉVREUX (1974) from Mediterranean and Atlantic species and secondly the veliger of some turrid species when disturbed does not retract into its shell but folds the velum onto and around the shell (own observations in the Red Sea, Meteor cruise 5/5, 1987).



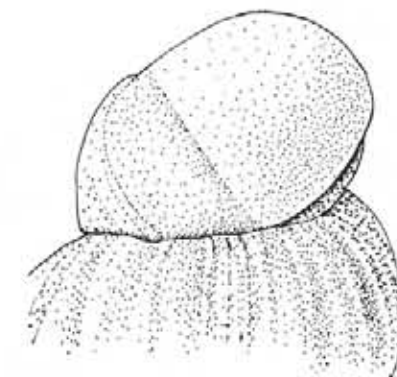
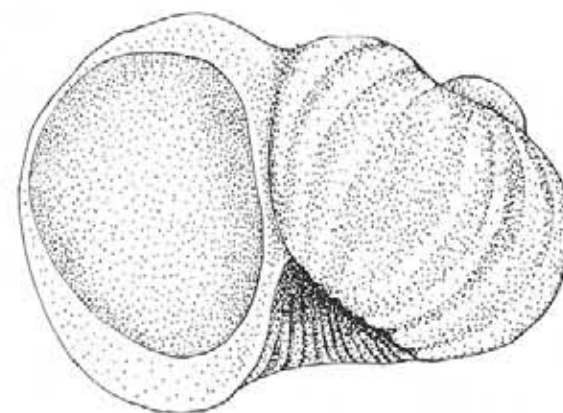
Textfigure 26: Many turrid species have highly sculptured shells with strong apertural projections like this one that is about 0,6 mm high and can be differentiated from similarly sculptured ovulid veligers by the sculpture of the embryonic shell.

From shallow water juvenile shells of members of the genus *Conus* have been washed in. *Conus* and *Terebra* are probably found with numerous species in the reefs and lagoons where their characteristic egg masses are attached to the underside of stones (BANDEL, 1976h). Their postnuclear shell is quite heavy so it was not transported off their lagoonal or reefal living site.

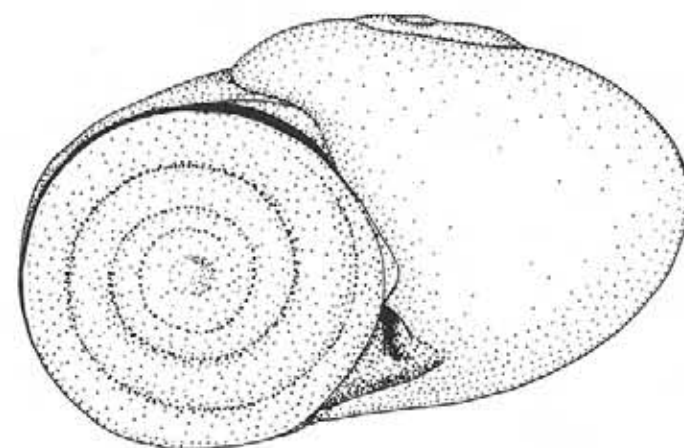
### 7. Subclass Heterostropha

The unifying conchological character common to all Heterostropha is represented by the early whorls of the shell. These coil sinistrally while the adult shell coils dextrally (pl. 8, fig. 7). The switch over from left to right mode of shell coiling usually occurs in the transition from pelagic to benthic life when the pediveliger is fully grown (textfig. 27).

a) The shelly fauna of the floor of the channel holds corroded juvenile shells of Architectonicidae. They have the characteristic switch in the mode of coiling of their shell in transition from the larval to the adult shell without a change in the position of the axis of coiling (pl. 8, fig. 7). While the adult shell is low, conical and dextral, the larval shell is a low sinistral trochospire (textfig. 28). Architectonicidae live on coelenterates, either actively searching for them or living on or even within them. The large *Architectonica* feeds on sea anemones by piercing the base of the polyp with its proboscis and sucking the tissue of the coelenterate until it collapses and dies (BANDEL 1976b, BANDEL & WEDLER 1987) while the small *Heliacus* lives within *Zoanthinaria* without damaging its host much (ROBERTSON 1967). A fair number of species of architectonicids are present in and near the reef and its lagoon but they don't seem to be common in the deeper water near the sampled area. The same is the case for the genus *Mathilda* which was only encountered by one juvenile shell (pl. 8, fig. 12). While architectonicids



Textfigure 27: The twist from left to right coiling characterizes all Heterostropha like this pyramidellid. The shell in the upper figure is about 0,5 mm wide, that of the lower about 0,5 mm high.



Textfigure 28: Fully grown veliger shell of architectonicid species ready to metamorphose with operculum closing the aperture. Width about 0,6 mm.

have a low, almost planspirally coiled shell, the shell of *Mathilda* is turritiform and similar to that of many cerithiids with which mathildids are easily mistaken when the heterostrophic shell is disregarded (pl. 8, fig. 12).

b) Distantly related to Architectonicidae are the minute representatives of the Omalogyridae and the Orbitestellidae (BANDEL 1988, PONDER 1991). *Ammonicera* is the smallest fully grown gastropod present in the fauna (about 0.5 mm in diameter) (pl. 7, fig. 4, 9), and its brown shell differs from the slightly larger white keeled shell of *Orbitestella* (about 1 mm in diameter) (pl. 7, fig. 5, 8). Both species with planspirally coiled shell have probably become washed in from algal thickets that grow in the littoral zone. Here they probably live by piercing cells with the teeth of their radula and suck the sap from them. Shells from species that are known from the Eocene of Europe very closely resemble some forms (pl. 7, figs. 1, 2, 7, 10) and their sinistral larval shell clearly states their systematic place near Orbitestellidae or Conirostridae (PONDER, 1991 a, b), even though nothing more is known about them.

c) Most members of the Pyramidellidae have slender, many whorled shells that mostly are of small size. But some are shorter, or even almost planspirally coiled (pl. 7, fig. 3, 6) (ROBERTSON 1973). They usually represent ectoparasites living on large sessile worms and molluscs, some even on arthropods sucking their body liquid. A large number of species, all of which are badly known, live in the Indian Ocean in all fully marine environments from the beach to great depth. A fair selection of species is present in the studied sample probably washed together by currents from the many different ecological zones present here. The specific mode of life and kind of host of all encountered species is still unknown. Two groups can be differentiated. The *Ebala* (pl. 8, fig. 1) relations go back into Paleozoic times. The very slender minute, and thin shells are present in Mesozoic sediments since Triassic St. Cassian Formation (BANDEL 1991c). The group of the *Pyramidella*-*Odostomia* relation shells are more solid, larger and show a variety of shapes (BABIO & THIRIOT-QUIERVREUX 1975) and seem to have their origin in the Cretaceous.

d) While the *Ebala* protoconch is similar to that of the modern pyramidellids, that of *Murchisonella* and related members of the Aclididae (pl. 8, figs. 5, 11) can be conneted to the Carboniferous genus *Donaldina* (YOO 1988) of the Palaeozoic Streptacididae. Another species (pl. 8, figs. 6, 10) is more similar to the Triassic Tofanellidae (BANDEL 1988, 1991c). The animal or *Murchisonella* is also differently organized than Pyramidellidae and Eulimididae as own observations on living individuals from the lagoons of Lizard Island in the Australian Barrier Reef indicated (1991).

e) Tectibranchiate opisthobranchs (Cephalaspidea, Architectibranchia) of genera like *Acteon*, *Ringicula*, *Acteocina*, *Retusa*, *Cylichna*, *Bulla*, *Atys* (pl. 8, figs. 2, 3, 4) and others live in soft substrates as well as along algal tufts in shallow water as well as deep water. Some are carnivorous others hunt prey like foraminifera, small bivalves and gastropods etc. Regarding their larval stage they are very similar to the parasitic pyramidellids, even though later shell is quite different (BABIO & THIRIOT-QUIERVREUX 1975). Due to a rapid increase in whorl height during the early benthic life sinistral whorls become covered by later dextral whorls and in some species they totally disappear below later whorls (pl. 8, fig. 4).

Egg masses are gelatinous ribbons from which small veligers hatch (BANDEL 1976e). These grow into more or less large pediveligers which are rather conspicuous since the last whorl of the larval shell twists to about 90 degrees in regard to the trochospirally left-coiled earlier whorls. Due to it the mantle cavity

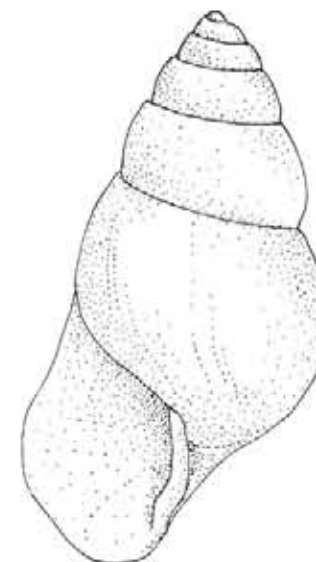
is also rotated by 90 degrees and fixed in this new position when metamorphosis occurs and the formerly left coil is continued as right coil.

f) A special group of opisthobranch species united in the Julioidea of the Sacoglossa is characterized by the presence of a bivalved shell (pl. 8, fig. 9). They live on green algae in rather shallow water and obtain their food by piercing the algal cells and sucking cell liquid. The shells thus must have become transported to the sampled site from shallow lagoonal waters. A limpet-like shell covered by body tissue is found in notaspidean opisthobranchs like *Pleurobranchus* (pl. 8, fig. 8) which feed on sponges.

## 8. Pelagic gastropods

Three types of fully pelagic gastropods, members of the Pteropoda, Heteropoda and *Janthina* are associated with the calcareous sand and shell debris found on the bottom of the channel.

a) The most common shell remains are those of the Pteropoda. Here several species of the sinistally coiled *Limacina* are easily recognized (textfig. 29). The

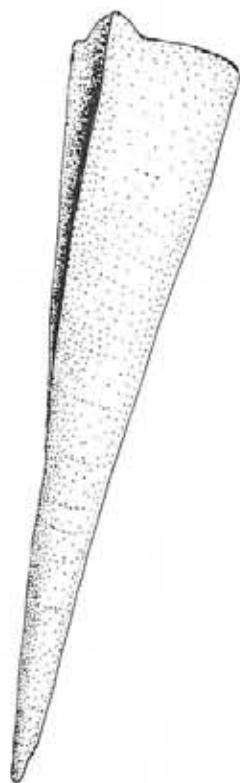


Textfigure 29. The fully grown shell of *Limacina bulimoides* is about 2 mm high.

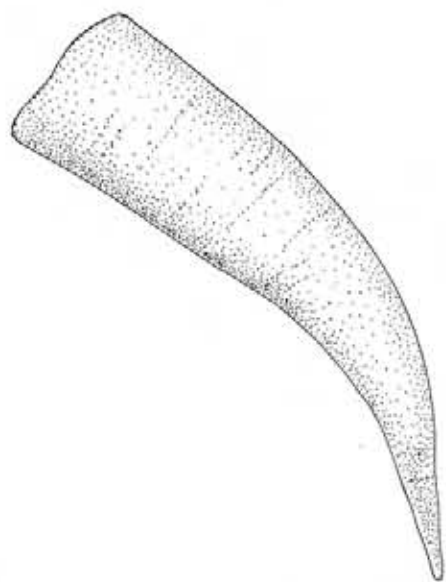
straight uncoiled shells of *Styliolina* and *Creseis* (textfigs. 30, 31) as well as of juvenile *Diacria* and *Clio* (textfig. 32) are common. Larger box like shells of adult *Diacria* and mostly fragmented *Cavolinia* are also found (textfig. 33). The pteropods catch planktonic organisms by a mucus float on which they drift passively through the sea and from which they feed (GILMER & HARBISON 1986).

b) The second common pelagic group is represented by shells of Heteropoda. Especially common are the veliger shells of members of the Carinariidae and veligers and further grown shells of the Atlantidae with their keeled, transparent, planspiral adult shell (textfigs. 34, 35). Heteropods actively pursue animal prey in the plankton.

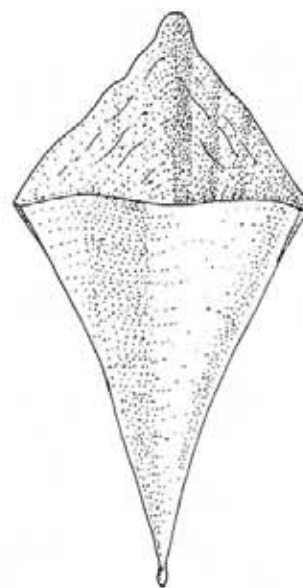
c) More rare are veliger shells of the Janthinidae. After metamorphosis they drift hanging on a self-fabricated bubble raft and hunt pelagic coelenterates.



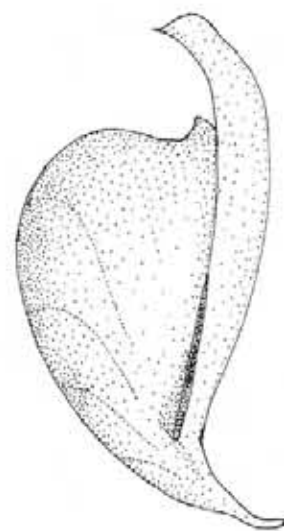
Textfigure 30: *Styliola subula* is a pteropod with straight shell of about 5 mm length.



Textfigure 31: *Creseis virgula* shells may curve like this one, or also be straight. Shell about 5 mm long.



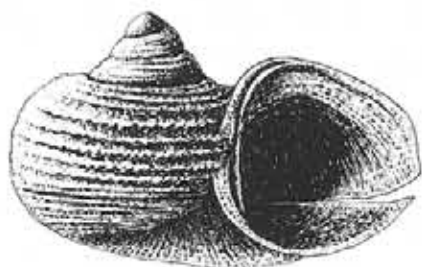
Textfigure 32: *Clio pyramidata* has a conical about 10 mm long shell with bulbous protoconch.



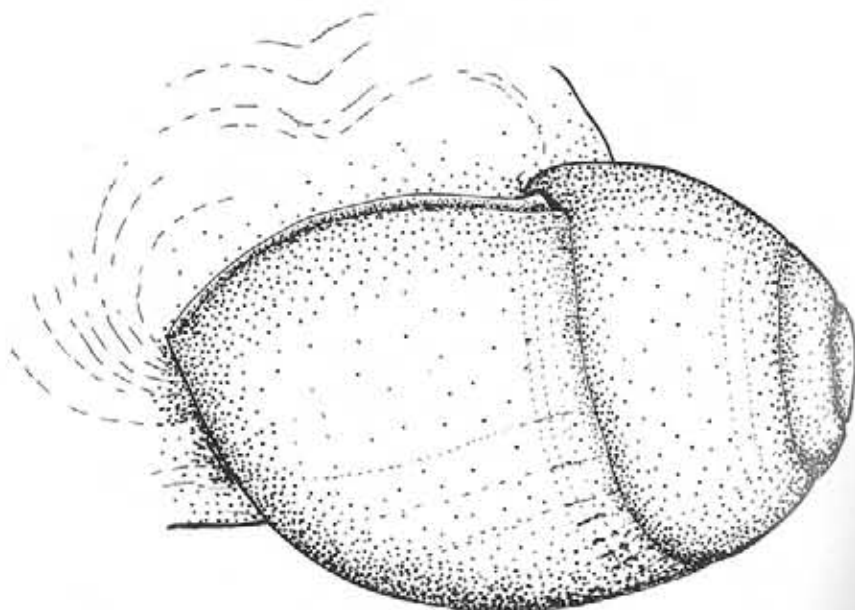
Textfigure 33. *Cavolinia uncinata* shells of box-like character are very unusual among gastropoda. Shell about 7 mm long.



Textfigure 34: The larval shell of an *Atlanta* ready to metamorphose resembles that of some Cerithiimorpha. Shell about 0,7 mm high.



Textfigure 35: After metamorphosis the shell of *Atlanta* becomes planspirally coiled and forms a slit.



Textfigure 36: The larval shell of *Janthina* is similar to that of the Epitoniidae. Larval shell about 0,5 mm high.

## 9. Conclusions:

Gastropod shells are a very common constituent in the sediment of the channel. In their systematic composition they reflect the rich ecological differentiation of the surrounding marine environments from which shells have been transported to the location of the sampled spot on the slope of the channel. Eight larger groups of gastropods can easily be differentiated and these can again be split into many recognizable subunits. Species of most subunits with few exceptions could be determined more closely when the fauna is studied in more detail. Several of the larger groups represented in subunits belong to animals that represent a specific way of life as herbivore, filter feeder, carnivore, commensal or parasite. Only in a few groups, for example the fissurellids, the way in which food is reached is varied. Most groups of related species have limited requirement in regard to their living place. The Triphoroidea for example live on and in sponges, the ovulids on octocorallian corals, the littorinids within the littoral environment. Some prefer a hard substrate for attachment like the Patellogastropoda and Calyptraoidea or the presence of well sorted sand to move through like the naticids, etc. When such environmental and ecological needs of a species are known, the species can be used as environmental indicator (BANDEL & WEDLER 1987).

Most of the species that have here been studied are provided with a pelagic phase occurring within their ontogeny. A true larval phase as is characterized by the presence of a larval shell is never found within the Archaeogastropoda but very common among the other species. In most cases this larval shell shows species specific features, as soon as a certain larval shell of a species can be connected to its teleoconch. In quite a number of the represented species, we can recognize a larva of a benthic gastropod caught far out in the ocean and determine it to species level. It will then be possible to make intelligent guesses about its place of origin. This way oceanic currents can be traced in their path through the sea by the characteristic larvae that they have picked up on their way.

The ocean around Cebu can be considered to belong to that part of the world where most species of gastropods are living and this fauna is taxonomically the most diversified. In this fauna there are quite a number of taxa that have a long history that ranges back through Neogene times into the Paleogene when there still was a connection with the Tethys Ocean and to the shallow shelf seas that covered parts of Europe. A number of species from the modern Philippian sea can be related to species found especially in the Eocene of France, as for example *Scaliola* (BANDEL & EL NAKHAL, 1991). Several other species and species groups can be traced back in time much further, as is the case in the acolidid *Murchisonella*, the cerithoid *Obtortio* and the small heterostrophic species of the *Orbitestella* relation. The modern fauna can thus help in the interpretation of the fossil fauna, its systematic relations as well as its ecological requirements.

Gastropods are useful ecological indicator once they have been studied well enough. The analysed sample presents ample evidence for the deposition of species of very different environments in one and the same place where they have not lived. As soon as ecological requirements of a number of key species are known the depositional history of a sediment of the area can be untangled. The results will also be a very helpful tool in the interpretation of fossil deposits.

### Acknowledgment

The studied sample has been collected within the scope of the German Research Council (DFG) project H. 273/3-1 by Dr. Gero Hillmer and Dr. Joachim Scholz aided by the staff members of the marine biological section of the University of San Carlos (Cebu City, Philippines). The plates have been assembled and the gastropods have been photographed by Angela Engelhardt (Hamburg); the drawings were made by Gerarda Van Spaendonk-Bandel and D. Lewandowski (Hamburg). To all these persons and institutions I am grateful as well as to the other members of the Geologisch-Paläontologisches Institut of the University of Hamburg who were involved in one or the other way.

### References

- BABIO, C. R. & THIRIOT-QUIEVREUX, C. 1974: Gastéropodes de la région de Roscoff. Etude particulière de la protoconque. *Cahiers de Biologie Marine*, 15: 531-549.
- BABIO, C. R. & THIRIOT-QUIEVREUX, C. 1975: Pyramidellidae, Philinidae et Retusidae de la région de Roscoff. Etude particulière de la protoconque de quelques espèces. *Cahiers de Biologie Marine*, 16: 83-96.
- BANDEL, K. 1973: Notes on *Cypraea cinerea* GMELIN and *Cyphoma gibbosum* (LINNAEUS) from the Caribbean Sea, and description of their spawn. - *Veliger* 15: 335-337.
- BANDEL, K. 1975: Embryonalgehäuse karibischer Meso- und Neogastropoden (Mollusca). - Akademie der Wissenschaften und der Literatur (Mainz), Abhandlungen der mathematisch naturwissenschaftlichen Klasse Jahrgang 1975, 1: 1-133; Wiesbaden.
- BANDEL, K. 1976a: Faecal pellets of Amphineura and Prosobranchia (Mollusca) from the Caribbean Coast of Columbia, South America. - *Senckenbergiana Maritima* 6: 1-31.
- BANDEL, K. 1976b: Observations on spawn, embryonic development and ecology of some Caribbean lower Mesogastropoda. - *The Veliger* 18: 249-271.
- BANDEL, K. 1976c: Die Gelege karibischer Vertreter aus den Überfamilien Stromabacea, Naticacea und Tonnacea (Mesogastropoda, Mollusca). *Mitteilungen des Instituts Colombo-Aleman Investigaciones Cientificas, Santa Marta (Kolumbien)*, 8: 105-139, Giessen.
- BANDEL, K. 1976d: Observations on spawn, embryonic development and ecology of some Caribbean higher Neogastropoda (Mollusca). - *Veliger*, 19: 176-193.
- BANDEL, K. 1976e: Egg masses of 27 Caribbean opisthobranchs from Santa Marta, Columbia. - *Studies on Neotropical Fauna and Environment* 11: 87-118.
- BANDEL, K. 1976f: Morphologie der Gelege und ökologische Beobachtungen an Muriciden (Gastropoda) aus der südlichen Karibischen See. - *Verhandlungen der Naturforschenden Gesellschaft Basel* 85: 1-32.
- BANDEL, K. 1976g: Morphologie der Gelege und ökologische Beobachtungen an Buccinaceen (Gastropoda) aus der südlichen Karibischen See. - *Bonner zoologische Beiträge* 27: 98-133.
- BANDEL, K. 1976h: Spawning, development and ecology of some higher Neogastropoda from the Caribbean Sea of Colombia (South America). - *The Veliger* 19: 176-193.
- BANDEL, K. 1981: Struktur der Molluskenschale im Hinblick auf ihre Funktion. - *Paläontologische Kursbücher*, 1: 25-48, München.
- BANDEL, K. 1982: Morphologie und Bildung der frühontogenetischen Gehäuse bei conchiferen Mollusken. *Facies* 7: 1-198.
- BANDEL, K. 1988a: Repräsentieren die Euomphaloidea eine natürliche Einheit der Gastropoden? - *Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg* 67: 1-33.
- BANDEL, K. 1988b: Early ontogenetic shell and shell structure as aid to unravel gastropod phylogeny and evolution. - In: *Prosobranch Phylogeny* (PONDER, W. F. ed.). Proceedings of a Symposium held at the 9th International Malacological Congress, Edinburgh Scotland, *Malacological Review, Supplement* 4, 267-272; Ann Arbor/Mich.
- BANDEL, K. 1991a: Über triassische „Loxonematoidea“ und ihre Beziehungen zu rezenten und paläozoischen Schnecken. - *Paläontologische Zeitschrift* 65: 239-268.
- BANDEL, K. 1991b: Major groups of gastropods from Mesozoic times. - *The Fossil Record* 2, in prep.
- BANDEL, K. 1991c: Ontogenetic changes reflected in the morphology of the molluscan shell. - In: *Constructional Morphology and Evolution*, SCHMIDT-KITTLER, N. & VOGEL, K. eds. Springer Verlag, Berlin, 211-230.
- BANDEL, K. & EL-NAKHAL, H. A. 1991: The history and relationship of *Scaliola*, a gastropod that cements particles to its shell. - *Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg*, in prep.
- BANDEL, K. & WEDLER, E. 1987: Hydroid, Amphineuran and Gastropod Zonation in the Littoral of the Caribbean Sea, Columbia. - *Senckenbergiana Maritima*, 19: 1-129.
- GILMER, R. W. & HARBISON, G. R. 1986: Morphology and field behavior of pteropod molluscs: feeding methods in the families Cavoliniidae, Limacinidae and Peracalidae (Gastropoda: Thecosomata). - *Marine Biology* 91: 47-57.
- HICKMAN, C. S. 1985: Gastropod morphology and function. - In: *Mollusks, notes for a short course organized by D. J. BOTTJER, C. S. HICKMAN, P. D. WARD, ed. T. W. Broadhead*. University of Tennessee Department of Geological Science, *Studies in Geology* 13: 138-156.
- MARSHALL, B. A. 1988: Skeneidae, Vitrinellidae, and Orbitestellidae (Mollusca: Gastropoda) associated with biogenic substrata from bathyal depth of New Zealand and New South Wales. - *Journal of Natural History* 22: 949-1004.
- PONDER, W. F. 1984: Xenophoridae of the world. - *Australian Museum Memoir* 17: 1-126.
- PONDER, W. F. 1990: The anatomy and relationships of a marine valvatoidean (Gastropoda: Heterobranchia). - *Journal of Molluscan Studies*, 56: 533-555.
- RICHTER, G. & THORSON, G. 1975: Pelagische Prosobranchier-Larven des Golfes von Neapel. - *Ophelia* 13: 109-185.
- ROBERTSON, R. 1967: *Heliacus* (Gastropoda: Architectonicidae) symbiotic with Zoanthinaria (Coelenterata). - *Science* 156: 246-248.
- ROBERTSON, R. 1971: Scanning electron microscopy of planktonic larval marine gastropod shells. - *The Veliger* 14: 1-12, Berkeley.
- ROBERTSON, R. 1973: *Cyclostremella*: a planispiral pyramidellid. - *The Nautilus*, 87: 88.
- ROBERTSON, R. 1983: Observations on the life history of the wendletrap *Epitonium albidum* in the West Indies. - *Am. malacol. Bull.* 1: 1-12.
- SCHELTEMA, R. S. 1971: Larval dispersal as a means of genetic exchange between geographically separated populations of shallow-water benthic marine gastropods. - *Biological Bulletin*, 140: 284-322.
- THIRIOT-QUIEVREUX, C. 1969: Caractéristiques morphologiques des Véligères planctoniques de gastéropodes de la région de Banyuls-sur-Mer. - *Vie et Milieu, sér. B*: 20: 333-366.
- THIRIOT-QUIEVREUX, C. 1971: Les véligères planctoniques de prosobranches de la région de Banyuls-sur-Mer (Méditerranée occidentale): phylogénie et métamorphose. - in D. J. CRISP (ed). *Fourth Eur. Mar. Biol. Symp.* Cambridge Univ. Press (1971) 222-225.
- THORSON, G. 1946: Reproduction and larval development of Danish marine bottom invertebrates. - *Meddel. Komm. Havundersoeg., Ser. Plankton* 4, 1-523, Kopenhagen.
- WARÉN, A. & BOUCHET, P. 1988: A new species of Vanikoridae from the western Mediterranean, with remarks on the northeast Atlantic species of the family. - *Boll. Malacologico (Milano)*, 24: 73-100.
- YOO, E. K. 1988: Early Carboniferous Mollusca from Gundy, Upper Hunter, New South Wales. - *Records of the Australian Museum* 40: 233-264.

**Plate 1**

Figure 1: The almost fully grown cyclostrematid archaeogastropod with the embryonic shell shown in pl. 2, fig. 4 is only 1,3 mm wide.

Figure 2: The almost fully grown solariellid trochoidean archaeogastropod lives on sandy bottom and is 2,7 mm high.

Figure 3: This umboniid trochoidean archeogastropod lives within sand and has an almost smooth shell with minute spiral pattern. Width 2 mm.

Figure 4: The almost planspirally coiled shell of a skeneid archaeogastropod does not grow to much more size than the 1 mm width.

Figure 5: Whorls increase rapidly in diameter in this 0,8 mm wide juvenile stomatellid trochoidean archaeogastropod with the embryonic shell shown in detail in pl. 2, fig. 1.

Figure 6: The astraeid trochoidean archaeogastropod with a flat apex and sculptured embryonic shell with even fold and apertural thickening is 1,4 mm wide.

Figure 7: The astraeid trochoidean archaeogastropod with gutterlike marginal spines and flat apex measures about 1,8 mm in width.

Figure 8: The apical view of a 1,5 mm wide patellomorph gastropod shows the characteristic embryonic shell of the archaeogastropods with slight deformation on the sides.

Figure 9: A juvenile turbinid trochoidean with 1 mm high shell has an embryonic shell that is figured in detail in pl. 2, fig. 6.

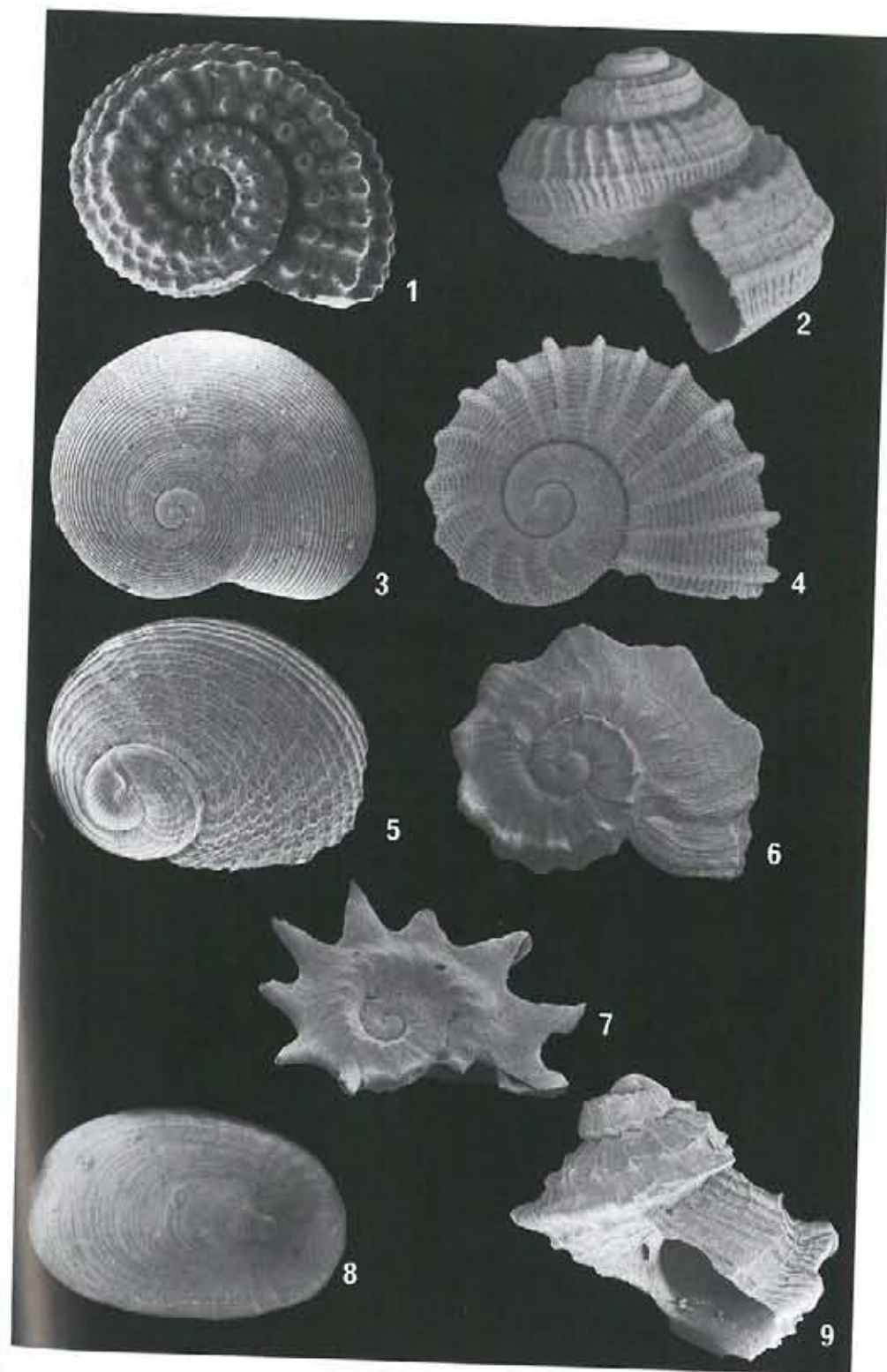




Plate 2

- Figure 1: The embryonic shell of the stomatellid gastropod (detail to pl. 1, fig. 5) is highly sculptured and shows the distortions of the lateral folds and apertural rim. Width 0,16 mm.
- Figure 2: The detail to fig. 11 of the embryonic shell of a skeneid indicates that the embryo has been swimming in the sea and formed a sinuous pattern of the apertural lip before it settled to benthic life. Width of embryonic shell 0,22 mm.
- Figure 3: The 0,33 mm wide embryonic shell of a trochid archaeogastropod demonstrates the presence of teleoconch right after embryonic shell as is characteristic to all archaeogastropods.
- Figure 4: The embryonic shell of the cyclostrematid shown in pl. 1, fig. 1 has the sculptural pattern of the originally symmetrical organic shell distorted due to the subsequent deformation into a helical shell. Width of embryonic shell 0,18 mm.
- Figure 5: The 0,25 mm wide embryonic shell of the umboniid in fig. 8 shows even spiral ribs.
- Figure 6: The detail to pl. 1, fig. 9 of an astraeid shows the 0,18 mm wide embryonic shell with lateral folds and distorted sculptural patterns.
- Figure 7: The slit bearing scissurellid archaeogastropod is one of several species found. Height 1,8 mm.
- Figure 8: The juvenile umboniid trochoidean archaeogastropod differs in teleoconch pater and morphology from the embryonic shell. Width 1,2 mm.
- Figure 9: The neritimorph limpet *Septaria* FERRUSAC, 1807 is 2,6 mm wide and was propably washed out of an estuary.
- Figure 10: The 0,5 mm wide larval shell of *Septaria* (detail to fig. 9) is characteristic to neritimorph larvae in beeing tightly coiled and having the inner walls dissolved.
- Figure 11: The minute (0,9 mm high) skeneid archaeogastropod is fully grown and lives among algae. Its embryonic shell is illustrated in fig. 2.

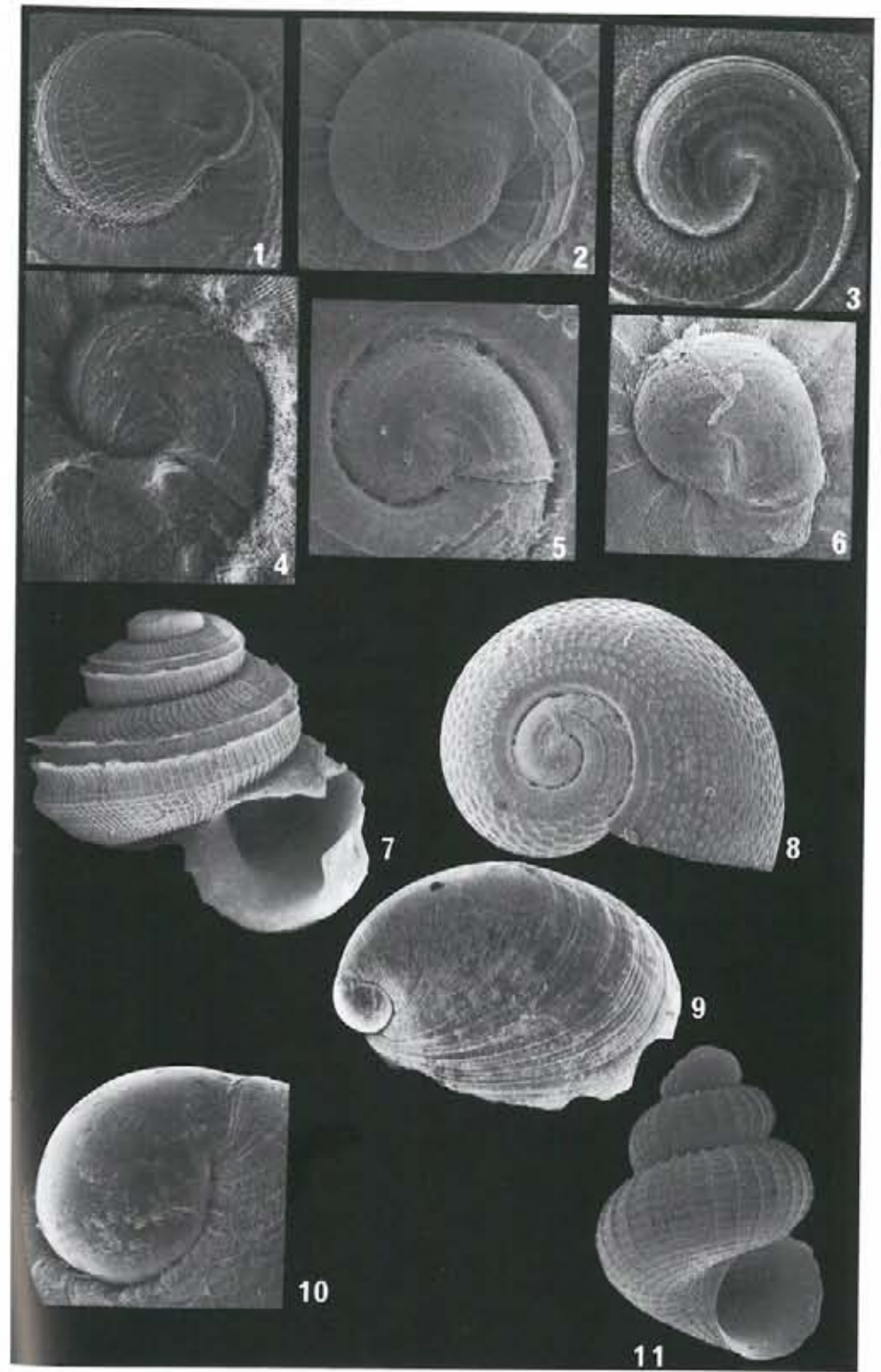


Plate 3

Figure 1: The larval shell of *Caecum* is planspirally coiled while the teleoconch becomes a straight tusk-like tube. 1 mm length.

Figure 2: The adult *Caecum* FLEMING, 1817 has cast of the early coiled shell portion. Shell 1,7 mm long. Below 1.

Figure 2a: *Parastrophia* DE FOLIN, 1869 has a coiled embryonic shell (broken off) and straight larval shell that borders the sculptured teleoconch with an apertural thickening. Shell 3,2 mm long.

Figure 3: The undetermined species has a simple caenogastropod teleoconch with a neomesogastropod-like larval shell. The shell is slightly larger than 1 mm.

Figure 4: The 3 mm high shell of *Rissoina* ORBIGNY, 1865 has a characteristically sculptured larval shell that can be found in the plankton far from the coast.

Figure 5: The 2 mm high shell has a teleoconch resembling that of a epitoniid while the larval shell is similar to that of *Bittium* GRAY, 1847 indicating its systematic place within the Cerithioidea.

Figure 6: The rissoid *Alvania* RISSO, 1826 is present with several species (see fig. 8). Height 1,2 mm.

Figure 7: The almost planspirally coiled vitrinellids like *Circulus* JEFFREYS, 1826 have a smooth trochiform larval shell. Width 1,6 mm.

Figure 8: *Alvania* RISSO, 1826 has a short larval shell with a striated embryonic shell as is commonly found among rissoids. Height 1 mm.

Figure 9: The highly sculptured *Scissilabra* BARTSCH, 1907 represents one of the several members of the commensal vitrinellids. Width 1,3 mm.

Figure 10: The almost smooth teleoconch of *Barleeia* CLARK, 1853 is connected to a typical rissoid larval shell similar to that of *Alvania* (figs. 6, 8) with large projection of the outer lip. Height 5 mm.

Figure 11: The 1 mm high shell of a juvenile cerithiid has a characteristic larval shell commonly found in species related to *Cerithium* BRUGUIÈRE, 1789.

Figure 12: *Obtortio* HEDLEY, 1899 represents a small cerithioid herbivore gastropod with sculptured larval shell (pl. 4, fig. 8). height 0,9 mm.



Plate 4

Figure 1: The apex of the cerithiid *Plesiotrochus* shown in fig. 2 represents the almost smooth larval shell and its typical large larval hook on the outer lip. Width of the larval shell 0,35 mm.

Figure 2: The cerithiid *Plesiotrochus* of about 1 mm height carries a larval shell of *Bittium*-like character and lives among algae in the shallow reef and lagoon.

Figure 3: *Sansonia* JOUSSEAUME, 1892 has basically unchanged in shell shape lived since oldest Paleocene (Danian) times. Height 1,3 mm.

Figure 4: *Vanikoro* QUOY and GAIMARD, 1832 is easily recognized with its highly sculptured larval shell that has a strong projection of the apertural lip and the sculpture of the teleoconch that is almost fully grown and 1,1 mm high.

Figure 5: *Mecoliota* HEDLEY, 1899 with characteristic larval shell (pl. 5, fig. 14) is related to *Sansonia*. Width 1,4 mm.

Figure 6: The 1 mm high juvenile shell of *Modulus* GRAY, 1842 carries a large larval shell with spiral ornamentation.

Figure 7: *Cheilea* MODEER, 1793 is a limpet that has a long-term planktotrophic larva. Width 2,5 mm.

Figure 8: The larval shell of *Obtortio* (detail to pl. 3, fig. 12) has a shape and pattern that is known from Carboniferous and Mesozoic fossils (BANDEL 1991 a). Larval shell is 0,2 mm high.

Figure 9: The larval shell of *Trivia* BRODERIP, 1837 is 1,2 mm high and quite different from the cowrie shell of the adult. It had been included within a gelatinous scaphoconcha of an echinospira larva as long as the veliger was afloat.

Figure 10: The 1 mm wide larval shell of *Lippistes* MONTFORT, 1810 is almost planspirally coiled and in shape resembles the scaphoconcha of *Lamellaria* (see fig. 11 for actual shell), while the teleoconch is trochospirally coiled.

Figure 11: The openly coiled internal shell of the echinospira larva of *Lamellaria* MONTAGU, 1815 becomes deformed and folded during metamorphosis and before it is calcified, while the teleoconch is limpet like and formed below the mantle cover. Width 1,2 mm.

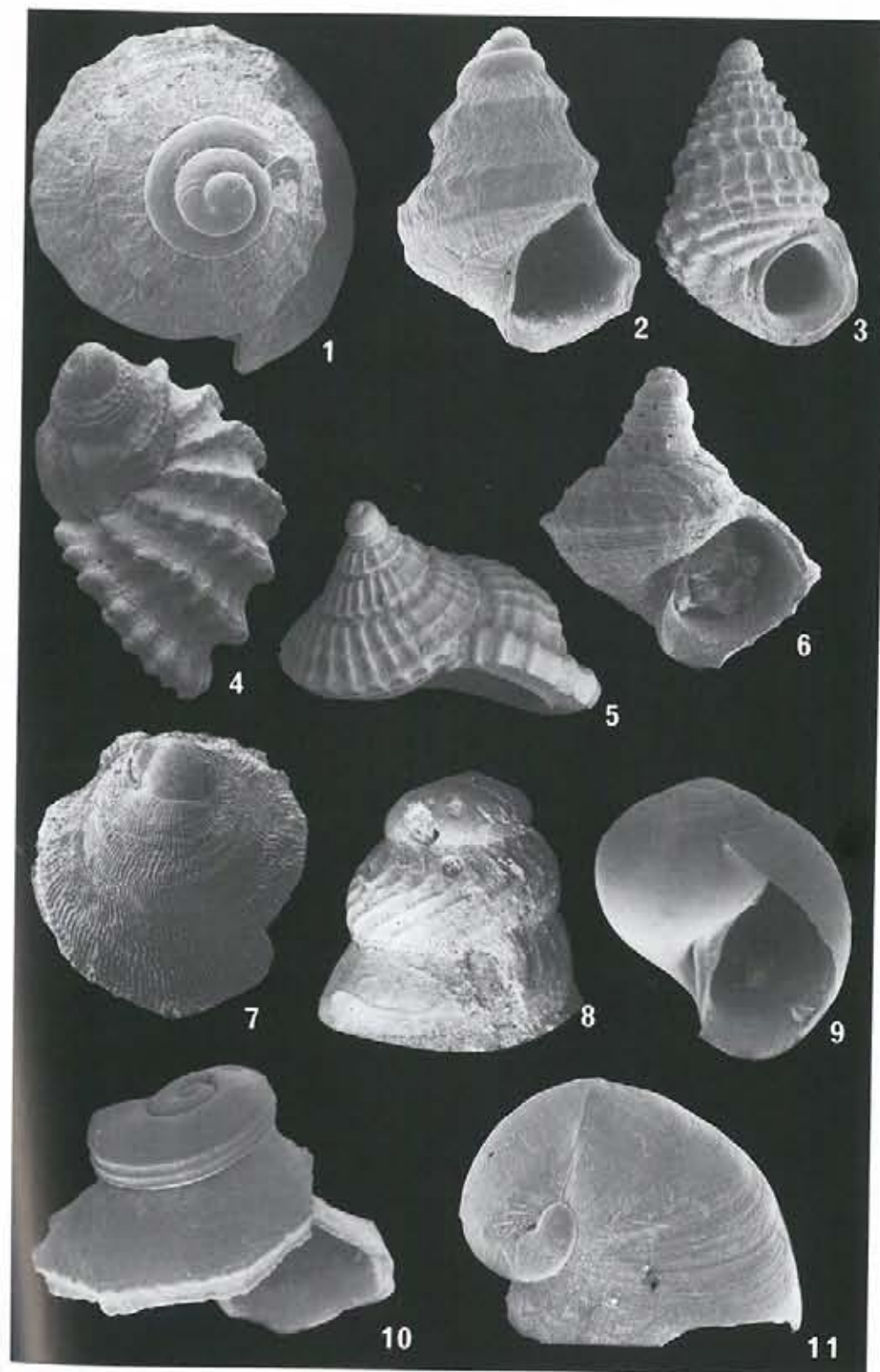


Plate 5

Figure 1: The sinistral juvenile shell of *Triphora* BLAINWILLE, 1828 with 1,2 mm height shows the strongly sculptured larval shell.

Figure 2: The 1,2 mm high shell of a juvenile member of the Cerithiopsidae is sculptured by a pattern of axial ribs.

Figure 3: The larval shell on a member of the Cerithiopsidae is almost smooth as is noticed within related forms through time up to the Triassic (BANDEL, 1991 a). Height 0,7 mm.

Figure 4: There are many different species of the Triphoroidea present that can often be separated from each other by the sculpture of their larval shell as is documented by comparing figs. 1-4. Height 1 mm.

Figure 5: *Melanella* BOWDICH, 1822 represents a typical eulimid shell with smooth teleoconch that differs only little from the smooth larval shell. Height 3 mm.

Figure 6: The apical view of the *Epitonium* shown in fig. 8 demonstrates the sculpture of the larval shell by delicate axial lines only. Width of larval shell 0,4 mm.

Figure 7: *Hoplopteron* P. FISCHER, 1876 with about 3 mm long, fully grown shell has a larval shell that in morphology intermediates between Eulimidae and Epitoniidae.

Figure 8: The juvenile epitoniid has the characteristic larval shell of the group connected to a teleoconch that is loosely coiled. Height 1 mm.

Figure 9: *Styliferina* A. ADAMS, 1860 is a very common little cerithioid that lives among algae in the shallow water. Height 1,4 mm.

Figure 10: The 2 mm high epitoniid gastropod has a highly sculptured teleoconch and almost smooth larval shell.

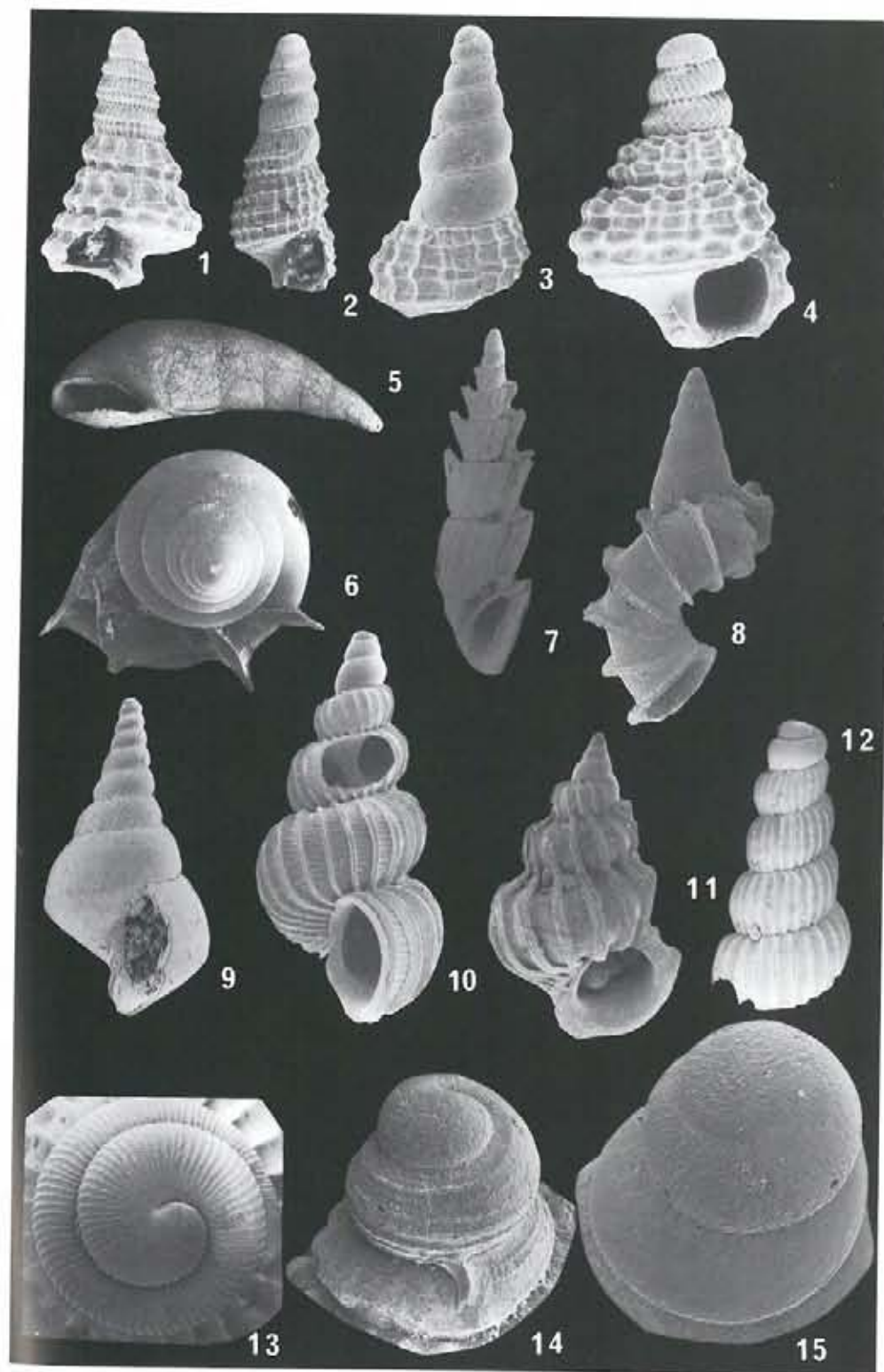
Figure 11: *Epitonium* RÖDING, 1798 and relation are present with a number of species (figs. 6, 8, 10) easily recognized by their larval shell. Height 3 mm.

Figure 12: *Truncatella* RISSO, 1826 has been washed in from the shore. Height 3 mm.

Figure 13: The embryonic shell of *Truncatella* (fig. 12) is 0,7 mm wide, highly sculptured and carried by a young that crawls from the egg mass.

Figure 14: The larval shell of *Mecoliota* is sculptured by spiral carinae and owns a large hook of the outer lip. It resembles shells as found among the Cerithiimorpha. Height of larval shell 0,27 mm.

Figure 15: The about 0,11 mm wide embryonic shell of *Styliferina* (fig. 9) shows a sculpture, while the larval shell is smooth and merges in shape with the teleoconch.



**Plate 6**

Figure 1: Juvenile shell of columbellid neogastropod with 1,1 mm high larval shell with little sculpture aside from growth lines.

Figure 2: The just metamorphosed pediveliger shell of a toxoglossan neogastropod is about 1 mm high.

Figure 3: This neogastropod veliger reaches almost a size of 2 mm in the plankton before it changes to benthic life.

Figure 4: Turrid neogastropod veligers have many different types of larval shells which in this 2,5 mm high juvenile shell is smooth.

Figure 5: The 1,4 mm high neogastropod has just started its benthic life and the change in sculpture from the veliger shell to the teleoconch is drastic.

Figure 6: The 1,7 mm high shell of a turrid neogastropod has a larval shell with reticulate sculptural pattern quite different from the sculpture of the teleoconch.

Figure 7: Turrid gastropods of several different genera and many species live in the littoral zone as well as deep water near Cebu. This one is a juvenile of 2,2 mm height.

Figure 8: The shell of fig. 7 seen from above demonstrates the highly ornamented embryonic shell that differs from the larval shell and both are differently sculptured than the adult shell.

Figure 9: The shell of fig. 5 seen in apical view.

Figure 10: The 1,6 mm high shell of a juvenile muricid neogastropod shows a characteristic larval shell ornament, which is seen in more detail in fig. 13.

Figure 11: Apex of a coralliophilid neogastropod with highly sculptured embryonic and larval shell that ends in a large apertural projection. Height 1,2 mm.

Figure 12: Apex of a nassariid neogastropod with a conical larval shell featured by spiral keels and a large apertural projection. Height 1,6 mm.

Figure 13: Apical detail to fig. 10.

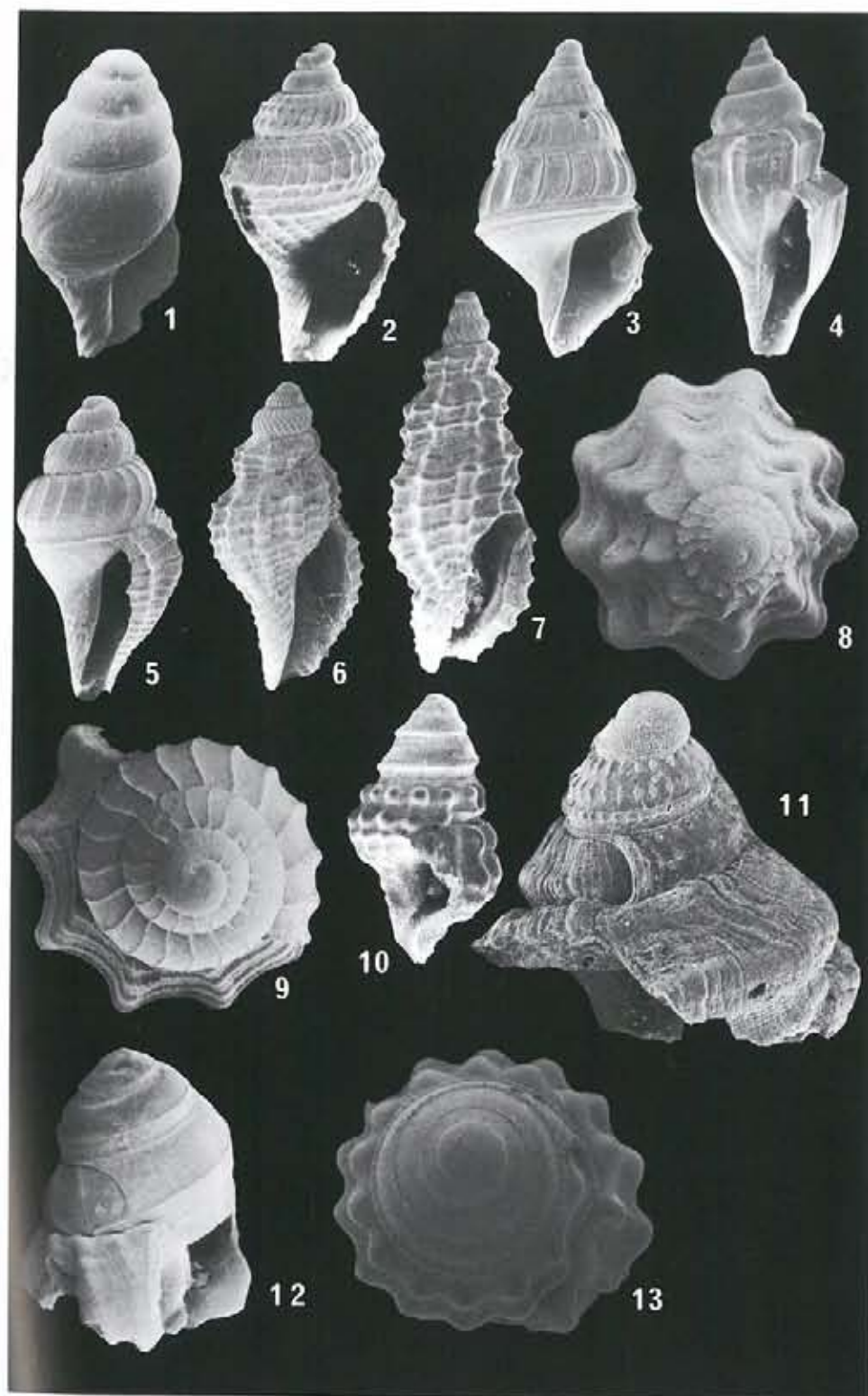


Plate 7

Figure 1: The gastropod with small (less than 1 mm wide) heterostrophic shell (fig. 10) is little known and may have relatives among the modern Orbitestellidae, but is common in the fauna of the European marine Eocene.

Figure 2: The minute (1,2 mm wide) heterostrophic shell (fig. 7) may belong to a member of the Conirostridae and also has relatives in the European Tertiary fauna.

Figure 3: The almost planspirally coiled *Cyclostremella* BUSH, 1897 with regular sinistral larval shell (fig. 6) represents a member of the large group of the pyramidellids. This little parasite has grown to 0,8 mm size.

Figure 4: *Ammonicera* VAYSSIERE, 1893 measures only 0,5 mm in width in its fully grown shell with a characteristically wrinkled protoconch (fig. 9).

Figure 5: *Orbitestella* IREDAL, 1917 with its 0,8 mm wide, fully grown shell lives among algae in shallow water and its sinistral protoconch is shown in fig. 8.

Figure 6: The detail to fig. 3 shows the smooth whorls of the sinistral, 0,2 mm wide larval shell of *Cyclostremella*.

Figure 7: The detail to fig. 2 shows the sinistral, 0,16 mm wide larval shell.

Figure 8: The detail to fig. 5 illustrates the reticulate sculpture of the embryonic shell and the pattern of folds on the sinistral, 0,16 mm wide larval shell of *Orbitestella*.

Figure 9: The detail to fig. 4 shows the planspiral embryonic shell of *Ammonicera* with 0,16 mm width.

Figure 10: The detail to fig. 1 shows the 0,2 mm wide, sinistral larval shell that is rather similar to that of *Orbitestella* (fig. 8).

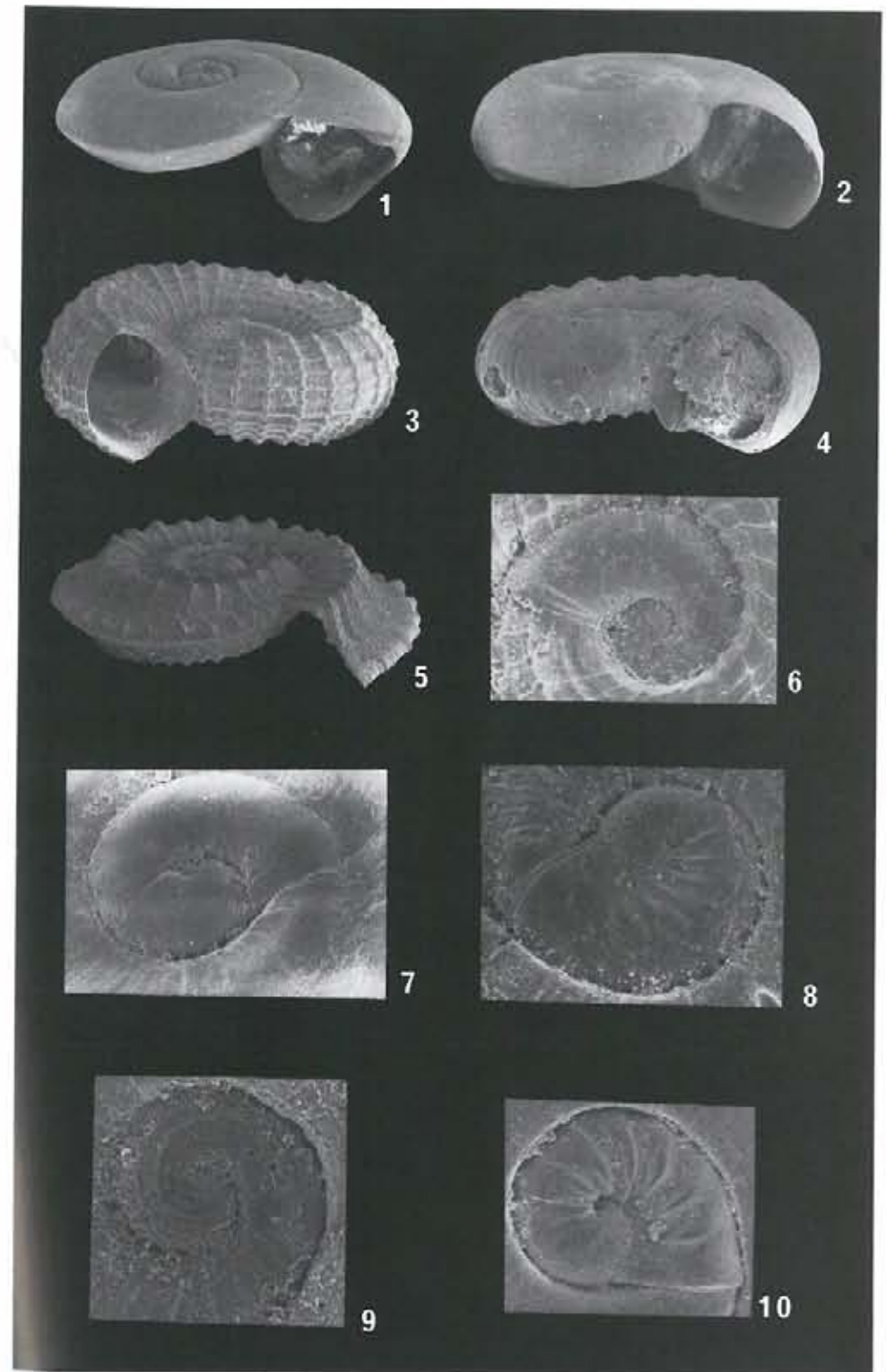


Plate 8

Figure 1: The small shell (1,2 mm high) of *Ebala* LEACH, 1847 with a sinistral protoconch forming a right angle with the teleoconch represents a pyramidellid of a group that can be traced in time to the Triassic.

Figure 2: In the cephalaspidean opisthobranchs like *Retusa* T. BROWN, 1827 most of the sinistral protoconch is covered by the dextral shell. Height 1 mm.

Figure 3: The cephalaspidean opisthobranch *Acteocina* GRAY, 1847 demonstrated the sinistral larval shell that forms an angle of 90° with the teleoconch. This 2,5 mm high shell represents a type of gastropod that can be traced into the Carboniferous.

Figure 4: In many cephalaspidean shells as in *Atys* MONTFORT, 1810 the teleoconch totally covers the sinistral protoconch. Height 1,2 mm.

Figure 5: *Murchisonella* MORCH, 1875 represents a shallow water acclidid with a sinistral protoconch (fig. 11) and a dextral shell with subsutural sinus of a type that can be traced through time to the Carboniferous Donaldinidae. Height of shell 0,8 mm.

Figure 6: An undetermined pyramidellid species has a very unusual larval shell (fig. 10) that reminds of the Triassic Tofanellidae. Height of shell 1,2 mm.

Figure 7: In *Architectonica* RÖDING, 1798 the large sinistral larval shell is smooth and to it the sculptured first whorl of the dextral teleoconch is added. Width of shell 1,5 mm.

Figure 8: The internal shell of *Pleurobranchus* CUVIER, 1804 has a sinistral larval shell that is partly covered by the limpet-like thin oblong teleoconch. Shell 2,3 mm long.

Figure 9: Internal view of a shell of the bivalved *Julia* GOULD, 1862 that lived in shallow water sucking sap from green algae. Width of shell 2 mm.

Figure 10: Detail of the protoconch of the undetermined pyramidellid demonstrates the tofanellid twist from sinistral first whorl into the dextral right shell within the larval shell. The larval shell is almost 0,3 mm wide.

Figure 11: The larval shell of *Murchisonella* is sinistral and very closely resembles that of the Carboniferous *Donaldina* (Yoo 1988, figs. 71, 109). Smooth larval shell 0,2 mm wide.

Figure 12: The larval shell of *Mathilda* SEMPER, 1865 resembles that of *Architectonica*, while the teleoconch is turritiform. Height 1,3 mm.

