

Classification of fossil and Recent Calyptraeidea (Caenogastropoda) with a discussion on neomesogastropod phylogeny

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Abstract: The somewhat confusing story of the systematic placement of the caenogastropod families Hipponicidae and Calyptraeidae is briefly reviewed. It is shown that the two families can be arranged in the same superfamily, which is in contrast to all former major classifications. The genera *Cheilea*, *Hipponix*, *Neojanacus* and *Thylacus* compose the Hipponicidae. *Neojanacus* usually has been attributed to the Capulidae. The Calyptraeidae include the genera *Calyptraea*, *Crucibulum* and *Crepidula*. They can be separated from the Hipponicidae with the aid of the radula and a different early ontogeny, i.e., the formation of the protoconchs. New data on Recent and fossil species of the families are presented and used to construct a phylogenetic tree of the Calyptraeidea on generic level. The relationship of the Calyptraeidea to the other families of the Neomesogastropoda Bandel, 1991 is discussed and the connecting key characters are presented. The Calyptraeidea originate from the same, probably Mid Cretaceous, unknown stem group as the other superfamilies of the Neomesogastropoda. A higher classification of the order Neomesogastropoda with the introduction of the new suborders Simrothina and Troschelina is presented.

Zusammenfassung: Die verworrene Geschichte der systematischen Stellung der Hipponicidae und Calyptraeidae wird kurz besprochen. Während in den bekannten früheren Klassifikationen die beiden Familien immer in verschiedene Überfamilien gestellt wurden, wird hier belegt, daß Hipponicidae und Calyptraeidae enger zusammengehören. Die Familie Hipponicidae setzt sich aus den Gattungen *Cheilea*, *Hipponix*, *Neojanacus* und *Thylacus* zusammen. *Neojanacus* wurde zuvor gewöhnlich den Capulidae angegliedert. Die Gattungen *Calyptraea*, *Crucibulum* und *Crepidula* konstituieren die Calyptraeidae. Diese Familie läßt sich von den Hipponicidae hauptsächlich mit Hilfe der Daten zu Radula und Ontogeneseablauf abgrenzen, insbesondere spielt die Bildung der frühontogenetischen Schale eine Rolle. Rezente und fossile Arten beider Familien wurden untersucht und die neuen Daten benutzt um die Phylogenie der Calyptraeidea auf Gattungsniveau zu rekonstruieren. Die Verwandtschaft der Calyptraeidea zu den anderen Familien der Neomesogastropoda Bandel, 1991 wird diskutiert und Apomorphien werden herausgestellt. Die Calyptraeidea haben ihren Ursprung in einer unbekanntem Stammgruppe, die wahrscheinlich in der mittleren Kreidezeit lebte und die auch die Vorfahrenfamilien der Neomesogastropoda beinhaltet. Die höheren Taxa der Ordnung Neomesogastropoda werden klassifiziert und die beiden neuen Unterordnungen Simrothina und Troschelina eingeführt.

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Introduction

The main intention is here to present an outline of calyptraeidean phylogeny and not a detailed classification on species level. The classification that will be introduced includes the Hipponicidae and Calyptraeidae in a single superfamily Calyptraeidea, which is in contrast to all commonly known systematic arrangements. Some of the better known classification schemes on family level are briefly reviewed to avoid taxonomic confusion. The attribution or validation

of genera is discussed in the systematic part of this paper.

Thiele (1929) presented two superfamilies holding seven families: **Calyptraeacea** with Trichotropidae, ?Anaplocamidae, Capulidae and Calyptraeidae; **Amaltheacea** with Fossaridae, Vani-koridae and Amaltheidae.

Wenz (1938-1944) adopted this family classification but changed Amaltheidae Dall, 1889 to Hipponicidae Troschel, 1861, which is the older name and therefore has priority. Wenz used the superfamily name Hipponicoidea and did not

recognize that Vanikoridae Gray, 1840 is the oldest family name.

Taylor and Sohl (1962) introduced a classification in which the ?Anaplocamidae has been removed and the Xenophoridae placed within the Calyptraeidea. A.o. Keen (1971) fully adopted this classification.

Abbott (1974) considered a different taxonomy and family arrangement: **Crepidulacea** with Trichotropidae, Crepidulidae and Xenophoridae; **Hipponicacea** with Fossaridae, Vanikoridae, Hipponicidae and Capulidae. The important difference to former classifications is the attribution of the Capulidae to the Hipponicacea. Moreover, Abbott (1974) confused the priority of Crepidulidae Fleming, 1822 (and Crepidulacea), which is a younger synonym of Calyptraeidae Lamarck, 1809.

Gollkov and Starobogatov (1975) proposed the following classification: **Calyptraeidea** with Trichotropidae, Capulidae, Calyptraeidae, Xenophoridae, Lyocyclidae and Lamelliphoridae; **Vanicoidea** with Fossaridae, Vanicoroidae, Hipponicidae.

Ponder and Warén (1988) synonymized Lyocyclidae with Vanikoridae and attributed the Lamelliphoridae to the superfamily Xenophoroidea. The Fossaridae were placed in the Cerithioidea. The Trichotropidae and the Capulidae are considered to be closely related and form a single family. Ponder and Warén introduced the following scheme: Calyptraeidea with Calyptraeidae and Capulidae; Vanicoidea with Vanikoridae and Hipponicidae.

The somewhat confusing history of classification schemes is strongly correlated to the interpretation of radula morphology. The differentiation of Hipponicidae and Calyptraeidae on one hand and the close position of Capulidae and Calyptraeidae on the other can be traced to the radula studies of Troschel (1856-1863). He considered the Hipponicidae with wider central and lateral teeth quite different from Calyptraeidae and Capulidae with more narrow teeth. But Troschel (1856-63) did not notice the intermediate character of the radula of *Hipponix conicus* (Schumacher, 1817) as was noted by Bandel (1984).

Cernohorsky (1968) expressed the opinion that a close relation exists between members of the genera *Hipponix* and *Calyptraea*. This suggestion was confirmed by Bandel (1976, 1984), based on studies concerned with spawn and radula morphology. According to Risbec (1955) the Hipponicidae are not closely related to the Fossaridae (see Ponder & Warén, 1988) and Vanikoridae. On the other hand Graham (1954) and Fretter & Graham (1962) stated the distinction

of the Capulidae, which have an echinospira larva, from the Calyptraeidae with a different early ontogenetic strategy. Fretter & Graham (1962) suggested a close relation of Capulidae to the operculate Trichotropidae (see Ponder & Warén, 1988) and put both families in a more-or-less informal group Echinospiracea, jointly with the other echinospira-larvae bearing groups, which are Triviidae Troschel, 1863 and Lamellariidae Orbigny, 1841. These considerations are supported by our own results (Bandel et al, 1993).

Regarding fossil representatives of the Calyptraeidea, Clench & Aguayo (1943) and Ponder (1983) suggest a connection of Jurassic gastropods resembling *Trochita* Schumacher, 1817 with the Xenophoridae. Members of the genus *Xenophora* Fischer, 1807 are present in the Upper Cretaceous (Sohl, 1960; Dockery, 1993) and show the same characteristic features which occur in modern species. Ponder & Warén (1988) propose that the Jurassic genera *Jurassiphorus* Cossmann, 1915 and *Lamelliphorus* Cossmann, 1915 represent ancestors both to the Calyptraeidea as well as to the Xenophoroidea. The Upper Triassic *Jurassiphorus triadicus* Haas, 1953 from Peru is probably related to *Rolandomphalus* Bandel, 1993, which, however, is a member of the Vetigastropoda (Archaeogastropoda) (Bandel, 1994).

Data on the early ontogenetic shell of a number of Recent, Tertiary and Upper Cretaceous species are provided. In addition to the morphology of the protoconchs observations on the early ontogeny of several calyptraeoids are presented. A new scheme of classification of the group of neomesogastropod limpets is proposed that tries to incorporate data on the ontogeny and shell morphology of modern species with that of fossil species. The phylogeny of the Calyptraeidea is then discussed in context of the other superfamilies of the Neomesogastropoda Bandel, 1991. This outline of neomesogastropod phylogeny is presented in the summary and conclusions chapter.

Methods and materials

The origin of material is indicated in the systematic part. Small shells and the radulae were mounted on stubs, coated with gold and examined using a scanning electron microscope (CamScan). Larger specimens were photographed with a reflex camera (Leica), with or without the aid of a light microscope.

Systematic part

Subclass Caenogastropoda Cox, 1959

Order Neomesogastropoda Bandel, 1991

Suborder Troschelina nov.

Superfamily Calyptraeoida Lamarck, 1809

Characteristics: the shell of the suspension feeding taenioglossan limpets is cap-shaped with the outer lip being joined and circling around the whole base. The shell rests on hard substrate. Its inner lip lies above the basal rim, is transformed, reduced in size or may be totally absent. The operculum is usually lost during the ontogeny, commonly when limpet life style has begun but may also be totally abolished. The plesiomorphic protoconch is large, about as wide as high, has rounded whorls and a straight outer lip of the aperture. Its sculpture resembles that of larval shells of basal representatives of the other Neomesogastropoda superfamilies (see below).

Lecithotrophic development changes the original shell morphology and sculpture up to the total disappearance of the larval shell in cases where metamorphosing (pediveligers) or already metamorphosed juveniles hatch from the egg. Egg capsules are attached below the maternal shell and the spawn is brooded.

Family Hipponicidae Troschel, 1861

Characteristics: the conical limpets are provided with or without internal shell walls. The protoconch of those species with a larval shell of the planktotrophic veliger is rounded and composed of several ornamented whorls with spiral ridges and axial ribs that may produce a pattern of rectangles. With more yolk available to the developing embryo, the number of whorls decreases and the sculpture is reduced or changed. In case a pediveliger or a crawling young hatches, only an embryonic shell is formed, which, however, may be highly sculptured but also almost smooth. Individuals after metamorphosis to benthic life attach themselves solidly to the substrate and the foot commonly produces a calcareous attachment plate or etches itself into the calcareous attachment surface. Egg capsules are attached to the parental individual.

Genus *Thylacus* Conrad, 1860

Type: *Thylacus cretaceus* Conrad, 1860 from the Upper Cretaceous of the SE-USA.

Generic description: the limpet-like, elongate shell has only short, fragmentary, marginal lamellae as remnants of the inner lip (shelf) and a horseshoe-shaped muscle scar. The protoconch is large, lies in the posterior position of the shell and belongs to a planktotrophic veliger.

Thylacus cretaceus Conrad, 1860

Pl.1, figs.1-5

Material: from Upper Campanian Coffee Sand (Mississippi) and Lower Maastrichtian Coon Creek (Tennessee), collected in collaboration with D.T. Dockery (Geological Survey, Jackson).

Description: the naticoid protoconch consists of three whorls with a diameter and a height of about 1.1 mm. The embryonic shell measures about 130 µm across and shows the typical groove-ridge pattern. The larval whorls are set with numerous spiral striae which are more prominent on the lower flank of the whorls. The striae are crossed by distinct growth lines which on the last protoconch whorl indicate a sinusigera aperture. The upper flank of the first larval whorl shows remains of axial ribs.

The teleoconch expands to assume limpet-shape. The juvenile teleoconch has an umbilical spiral shelf (inner lip). When fully developed the muscle support is horse-shoe-shaped and the inner shelf is absent.

Remarks: Wade (1926), Sohl (1960) and Dockery (1993) described this species rather well. The larval shell is illustrated by Dockery (1993) and Bandel (1993). According to Sohl (1960) and Dockery (1993) *Thylacus cretaceus* lived as an attached form on the columella of gastropods where it was found (Dockery) or the shape of the shell with a sinuous apertural lip indicates this living habit (Sohl).

Thylacus was interpreted to represent a member of the Capulidae by Sohl (1960), but its larval shell clearly places it with the modern Calyptraeoida (Dockery, 1993) like *Cheilea* or *Hipponix*. *Hipponix* Defrance, 1819 is reported from the Upper Cretaceous of Ripley Formation (U.S. Gulf Coast), but this needs confirmation. The teleoconch of *Thylacus* resembles that of modern *Neojanacus* Suter, 1907 and like it lived on the inside of shells that might also have been carried around by hermit crabs (see *Neojanacus perplexus*). With *Calyptraea* connects the shell of the freshly metamorphosed individual that has a spiral shelf, while it is lost during later life.

Thylacus squamaeformis (Lamarck, 1802)

Pl.1, figs.6-8; Pl.2, figs.1-3

Material: from the Lutetian (Eocene) of Southampton, British Museum (London); and the Lutetian of Damery/France, Natural History Museum Leiden (Netherlands), RGM 220.606.

Description: the naticoid protoconch consists of nearly 3 whorls after which the shell expands to assume limpet-shape. The teleoconch of the newly metamorphosed individual has an umbilical spiral inner lip, while when the shell is fully developed

the muscle support is horseshoe-shaped and the inner shelf is absent. The embryonic shell measures 0.15 mm in diameter and is separated by a strong growth increment from the onset of the larval shell, which measures about 0.6 mm in diameter and is about as high as wide. The larval whorls bear faint spiral striae which partly form a cancellated pattern when crossed by distinct growth lines. The spiral striae may be disintegrated to rows of tubercles.

Remarks: a similar protoconch as described here is present on a Miocene species (Pl. 2, figs.4-5) from Siebenbürgen (Romania) from the collection of the Natural History Museum in Vienna.

Genus *Neojanacus* Suter, 1907

Type: *Neojanacus perplexus* Sliter, 1907 from New Zealand.

Generic description: the teleoconch is similar to that of *Crepidula* but without a desk. The adults live on gastropod shells carried by hermit crabs. The radula differs from that of other Calyptraeidea in having the number of teeth per row reduced.

Remarks: according to Beu & Maxwell (1990) *Neojanacus* belongs to the Capulidae along with the genera *Malluvium* and *Capulus* Montfort, 1810. Vaught (1989) places *Neojanacus* in the same family but together with *Krebsia* Mörch, 1877 and *Capulus*.

Neojanacus perplexus Suter, 1907

Pl.2, figs.6-8; Pl.3 figs.1-,4

Material: from the Tasman Sea, 280-540 m water depth; National Museum of New Zealand (Wellington), M. 35032 and M. 52543.

Description: the teleoconch is very variable in shape but usually extremely flattened and about crescent-shaped. The length amounts to about 2 cm. The calcareous shell is white, covered by a brownish periostracum. The interior of the shell shows a horseshoe-shaped muscle scar. There are no remains of a columella. The protoconch consists of about one and a half whorls amounting to a maximum diameter of 0.6 mm and a height of 1.5 mm. The first half whorl shows several distinct irregular growth increments. Regular growth lines can be recognized first at the transition to the second whorl.

The animal shows a comparatively small head with a distinct neck and a long muscular snout. The tentacles taper regularly and bear minute eyes. The radula is reduced in size as well as in number of teeth per row. The total length of the radula is about 350 µm, the width is 50 µm. The outer marginals are absent, reducing the number of teeth per row to five. The central teeth are about 30 µm wide and 10 µm high, having the

general shape of a *Hipponix* central tooth. The laterals and marginals are claw-like and very small compared to the central teeth.

Remarks: the teleoconch of *Neojanacus perplexus* is most similar to species of *Thylacus*, which is a fossil genus. The protoconch clearly indicates non-planktotrophic development. According to Dell (1956) the embryos metamorphose within the capsule, hatching as minute limpets. Two limpets measuring 1.2 mm across were found sticking to the maternal visceral mass. The shells of these embryos are very thin and show remains of the egg capsule wall on their surface. The egg capsules possibly had been attached to the soft body of the adult. The information on the soft body of *Neojanacus perplexus* was gained from the remains of a dried animal and therefore is incomplete. However, the radula could be fully extracted. Dell (1956) figured a radula without marginal teeth, which is in contrast to our findings. Dell (1956) did not have the possibility to use an electron microscope. The marginal teeth are very close to the laterals and therefore can hardly be seen with the aid of a light microscope.

Genus *Hipponix* DeFrance, 1819

Type: *Patella cornucopiae* Lamarck, 1803 from the Eocene of the Paris Basin.

Generic description: the cap-like shell has no internal shelf and shows a horseshoe-shaped muscle scar. The protoconch of species with a planktotrophic larva is of rounded shape and has up to 3.5 whorls. In non-planktotrophic development the embryonic shell usually measures only 1.2-1.5 whorls with about the same size of 0.5-1.0 mm across. The embryonic shell is commonly covered by irregular groove-ridge pattern and the larval shell may be sculptured by spiral lirae crossed by axial ribs, in the first larval whorl forming a reticulate pattern. Sculptural elements on embryonic and larval shell may also be missing.

Remarks: *Sabia* Gray, 1839 (type: *Amalthea conica* Schumacher, 1817) from the Indopacific Ocean is considered to belong to *Hipponix*, as well as *Antisabia* Iredale, 1937 (type: *Hipponyx foliaceus* Quoy & Gaimard, 1835) from the Caribbean Sea. *H. foliaceus* may actually be synonymous with *Hipponix antiquatus*. *Malluvium* Melvill, 1906 (type: *Capulus lissus* E.A. Smith, 1894) from the Bay of Bengales is also considered to represent *Hipponix* (compare Vaught, 1989). This coincides with Thiele (1929) who pointed out that *Malluvium* and also *Sabia* are synonyms of *Amalthea*. The name *Amalthea* had been preoccupied and therefore *Hipponix* has to be used. However, Wenz (1938-44) and subsequent authors preferred the name *Sabia*. Abbott (1974) considered *Malluvium* to represent a genus of the Hipponicidae, Beu & Maxwell (1990) placed

Malluvium in the Capulidae jointly with *Neojanacus* and *Capulus*.

Thiele (1929) also included *Amathina tricarinata* (Linné, 1758) within *Amalthea* (= *Hipponix*), a species which, however, does not even represent a neomesogastropod but rather a pyramidellacean limpet that lives parasitic on sea stars (Ponder, 1987; Herbert, 1991)

Hipponix cornucopius (Lamarck, 1803)

Pl.3, figs.5-8

Material: from the Lutetian (Eocene) of Damery/France, Natural History Museum in Leiden (Netherlands), RGM 220.604.

Description: a juvenile shell could be examined measuring 6 mm in length, 4.5 mm in width and 2.5 mm in height. These are the same proportions as in fully grown shells, which, however, are five to ten times larger than the juvenile. The teleoconch is limpet-like and set with coarse strong growth increments and spiral ribs. The aperture is oval. An attachment plate was not found but usually occurs in this species (Wenz, 1938-1944). The plate and the interior of the shell show horseshoe-shaped muscle scars. The protoconch consists of one and a quarter whorls measuring 1 mm across. The initial part of it is wrinkled, while the final half whorl of the protoconch is smooth except for growth lines. The transition from the wrinkled to the smooth part is irregularly constricted.

Remarks: the protoconch of *H. cornucopius* clearly indicates non-planktotrophic development. The gastropod probably fed on nurse eggs which can be interpreted from the wrinkled shell. Feeding on nurse eggs usually means that the embryos have to stretch their still organic shell to get the possibility to incorporate these large portions of food. When having digested the food the shell is shrunk to the normal size and consequently wrinkles may appear. *H. cornucopius* is the type species for that genus and thus the teleoconch characters are diagnostic also for modern species. The protoconch type, however, is not described from Recent members of the Hipponicidae but can only be used for taxonomy on species level.

Hipponix conicus (Schumacher, 1817)

Pl.4, fig.1; Text-Fig.1

Material: teleoconchs from Port Sudan (Red Sea); larval shells from Red-Sea-cruise of Research Vessel Meteor (1987).

Description: the cap-like teleoconch has no internal shelf and a horseshoe-shaped muscle scar. The foot is attached to the substrate by a cemented plate. The teleoconch has a pointed apex near the posterior margin. Radiating ribs of variable breadth separated by narrow interstices form the sculpture.



Text-Fig. 1: Juvenile *Hipponix conicus* from the Seychelles. Largest dimension = 2.1 mm.

The shell margin may be irregular, conforming to the shape of the substrate.

The limpet is found attached to living gastropods within the lagoons (near Stiakin), the reef lagoon and the shallow reef flats like for example to *Strombus* Linné, 1758, *Pleuroploca* Fischer, 1884 and *Trochus* Linné, 1758. The females brood the spawn consisting of about 15 stalked egg capsules, which are attached as a bundle to the soft body. Within each of the transparent capsules about 120-150 yellow eggs all develop and hatch as veligers.

The protoconch consists of 2.3 whorls measuring about 0.5 mm in diameter. The shape is naticoid with round simple aperture and regular rapid increase in whorl diameter. The embryonic shell measures 0.12-0.15 mm across, consists of almost one whorl and is sculptured by a fine groove and ridge pattern that ends abruptly with first onset of growth lines. The first whorl of the larval shell is sculptured by a pattern of about equal spiral and axial ribs forming a network of rectangles. In ontogenetically later parts of the larval shell axial ribs disappear and spiral elements remain, but as low sculpture. The aperture is closed by a spirally colled operculum of a size that fits perfectly into the apertural margin. The pediveliger swims with two large rounded velar lobes, the shell below with apex pointing down and the foot with the operculum held vertically behind.

Remarks: *Hipponix australis* (Lamarck, 1819) from South Australia described by Knudsen (1991) resembles *H. conicus* closely, when regarding the teleoconch. It lives attached to living gastropods and broods its spawn under the shelter of its shell. The small male lives associated to the larger female and usually changes sex when growing to larger size. The egg capsules of *H. australis* each contain 17 to 67 eggs, which are large enough to develop into crawling young before they hatch with a shell of almost 1 mm in diameter (Knudsen,

1991). The simple brownish protoconch of 1.3 to 1.5 whorls is set with spiral lirae on the base and distinct growth lines on the wider end.

A similar mode of development was noted by Habe (1953) who recognized *Hipponix conicus* from Japanese waters. In these reports the crawling young hatch with a shell of about 1 mm across, sculptured by about 20 spiral ridges. In contrast Taylor (1975) observed in *Hipponix conicus* a protoconch of about 0.5 mm in diameter set with a reticulate sculpture, as is the case in the form from Port Sudan, which was described here. Finally, Cernohorsky (1968) noted for *H. conicus* from Fiji that veligers hatch with a shell measuring 120 to 130 μm . Moreover, Cernohorsky (1972) treated *H. australis* as a synonym to *H. conicus*.

These contradicting data on ontogenetic strategies indicate that there are at least two species with the teleoconch morphology of *Hipponix conicus*, one with non-planktotrophic and one with planktotrophic development (see Matsunaga, 1964; Laws, 1971).

Hipponix antiquatus (Linné, 1767)

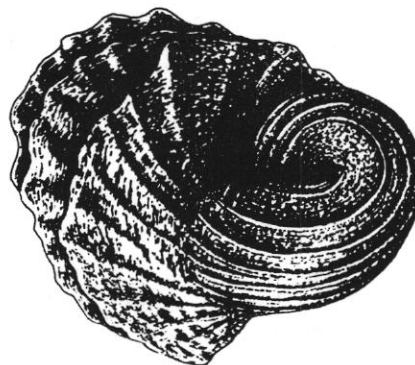
Pl.4, figs.2-3; Text-Fig.2

Material: from the Caribbean Sea near Santa Marta (Colombia), Yucatán; and the Bahamas, Smithsonian Museum (Washington).

Description: the curved apex is situated near the centre or on one end of the heavy, cap-shaped, obliquely conical shell and projects backwardly. The teleoconch sculpture consists of irregular growth lines, radial costellae and prominent axial sculpture of rugose ribs, which are crossed by incised lines. The muscle scar inside the shell is horseshoe-shaped. The foot is attached with a carbonate plate, like a very similar species from California described by Yonge (1953, 1960). The individuals of this species are usually attached to hard substrate within the littoral zone, preferably below rocks. Coral thickets are settled as well as rocky shore.

The egg capsules were attached to the female and consist of pear-shaped sacs containing 5-8 embryos each. The embryos all develop feeding on liquid yolk contained within the capsule and hatch as crawling juveniles after 12-14 days development. The protoconch was described by Bandel (1975a), measuring 0.5 mm across, of helicoid shape, which has not yet become patelliform (Bandel, 1976).

A specimen from the Bahamas has a very well preserved embryonic shell that was formed by individuals without planktotrophic phase. The same could be observed on specimens living in the seagrass flats of the Yucatán Peninsula (collected by Hüssner, Tübingen). Here the embryonic shell



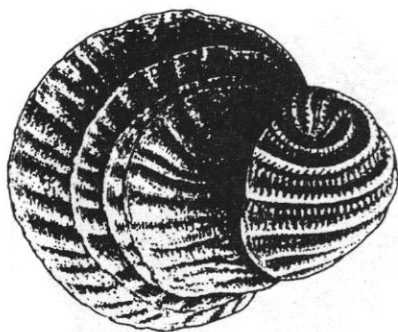
Text-Fig. 2: Juvenile *Hipponix antiquatus* from the Caribbean (Yucatán). Largest dimension = 0.85 mm.

consists of 1.2-1.5 whorls with a diameter of 0.6mm. The sculpture consists of 10 to 25 spiral ribs formed by more-or-less fused tubercles. These protoconch ribs continue into ribs on the juvenile teleoconch. The aperture is drop-shaped and as wide as high.

Remarks: a species labeled *Hipponix foliaceus* (Quoy & Gaimard, 1835) from Tuamoru in the Pacific (housed in the Natural History Museum at Vienna) has an embryonic shell covered by 7-8 strong spiral ribs and measuring 0.65 mm across. These raised and coarse spiral features of the sculpture are crossed by fine collabral lamellae (Text-Fig.3). The spiral elements of the protoconch are continuous into the spiral ribs present on the early teleoconch.

A species named *Hipponix minor* Garret, 1853 collected from Hermes Reef in Hawaii (same collection in Vienna) has a flat limpet-like teleoconch with strong growth increments and weak dense spiral ribbing. The protoconch consists of 1.2 whorls with a diameter of about 0.5 mm and has no sculpture except for growth lines (Pl.4, fig.8). This specimen looks very similar to a juvenile shell (Pl.4, figs.4-7) from the Kermadec Islands (Australian Museum, C 162442). Both shells indicate an early ontogeny with crawling young hatching and may come from representatives of the same species, however, living in different portions of the Pacific Ocean.

A *Hipponix* (Pl.4, figs.9-11) from Tonga (Australian Museum, C 162444) could be examined which in contrast has an embryonic shell closely resembling that of *Hipponix antiquatus*.



Text-Fig 3: Juvenile *Hipponix foliaceus* from the Pacific (Tuamoru). Largest dimension = 1.3 mm

Hipponix benthophilus (Dall, 1889)

Pl.5, figs.1-2

Material: from off Sambo Reef in Florida, in 270 m depth, Smithsonian Museum, USNM 436865

Description: the cap-shaped shell with 1.5 to 2 whorls has a hooked-over apex at the posterior end. A thick shelly platform is secreted upon which the animal sits. The narrow shell is smoothish except for irregular growth lines and very fine numerous spiral cords. The shelly platform is shaped oval to circular and is attached to the spines of large cidaroid sea urchins. The muscle scar is horseshoe-shaped.

The protoconch consists of 1.2 to 1.4 whorls with 0.7 mm width. The only sculptural elements consist of growth lamellae beginning on the embryonic shell beyond the initial cap that is with 0.2 mm about as wide as high.

Remarks: Abbott (1974) called this species *Capulus incurvatus* (Gmelin, 1791) but it clearly represents a member of *Hipponix*. According to Abbott (1974) *Capulus intortus* (Lamarck, 1822) is merely a variety of *Capulus incurvatus*. This explains why the radula of *Hipponix intortus* studied by Barnard (1963) resembles that of *Cheilea equestris* as was noted by Bandel (1984).

Also included in *Hipponix* can be the genera *Cochlear* Mörch, 1877 and *Pilosabia* Iredale, 1929, which were not included in the account of Wenz (1938-44). *Rothpletzia* Simonelli, 1890 is a fossil form from the Miocene and probably also represents a member of *Hipponix*. Its characteristic calcareous plate forms a low asymmetrical cone similar to a rudist. In *Rothpletzia* the basal cone secreted by the foot is commonly larger than the actual cap-like shell.

Hipponix sp.

Pl.5, figs.6-7

Material: from the Red Sea; Natural Museum in Vienna

Description: a small limpet with the general shell features of the genus *Hipponix*. It has a protoconch which intermediates in shape between *Hipponix benthophilus* and *H. conicus*. The naticoid protoconch consists of 1.7 whorls. The embryonic shell is about 0.25 mm wide and clearly demarcated from the larval shell which is about 0.6 mm high and wide. The embryonic shell shows the characteristic groove and ridge pattern found in *Hipponix* species that have a planktotrophic veliger. The larval whorl appears smooth but bears a rather indistinct delicate pattern of spiral striae and growth lines. The aperture is simple and of circular shape. The limpet shell begins with onset of the first teleoconch whorl, which is featured by distinct growth lines as main sculptural element. The fully grown teleoconch is cap-like, coiled to such a degree that the apex with the protoconch points downward.

Hipponix sp.

Pl.5, figs.3-5,8

Material: from Papua (Australian Museum, C 162443), Dampier (Australian Museum, C 162445) and Indonesia (near Satonda).

Description: the teleoconch is smooth and has the general shape of *Hipponix benthophilus*. The helicoid larval shell with 2.5 whorls is over 0.6 mm high, 0.45 mm wide and similar to that of Miocene *Cheilea* sp.. The embryonic shell measures 0.18 mm across and is coarsely set with grooves surrounded by ridges. The embryonic sculpture ends abruptly with the onset of the larval shell. Axial lines feature the larval shell, which are at first developed as ribs later as indistinct pattern and the growth lines become the more dominant element.

Genus *Cheilea* Modeer, 1793

Type: *Patella equestris* Linné, 1758 from the Indopacific Ocean (Philippines).

Generic description: the shell is irregularly conical or cyrtocoid, sculptured by irregular commarginal and radial ribs. The apex lies a bit excentric towards the posterior. The cap-shaped shell has an internal cup support that is attached only at the base and has one third of it neatly cut out. It is similar to that of *Crucibulum*, but in place of the open cone there is a plate curved into a half-cone widely open in front like a shoehorn.

Remarks: Thiele (1929) placed *Cheilea* together with *Amalthea* (= *Hipponix*) within the Amaltheidae (= Hipponicidae). Here it is also placed by Vaught (1989) together with *Hipponix*,

Malluvium and *Sabia*. Abbott (1974) preferred the subfamily Calyptraeinae with genera like *Calyptraea*, *Crucibulum* and *Crepidatella* being part of the family Crepidulidae, Beu & Maxwell (1990) preferred the family name Calyptraeidae and here *Cheilea* is seen in the relation of *Crepidula*, *Sigapatellia* and *Zegalerus*. The morphology of the protoconch clearly supports Thiele's and Vaught's placements.

Cheilea equestris (Linné, 1758)

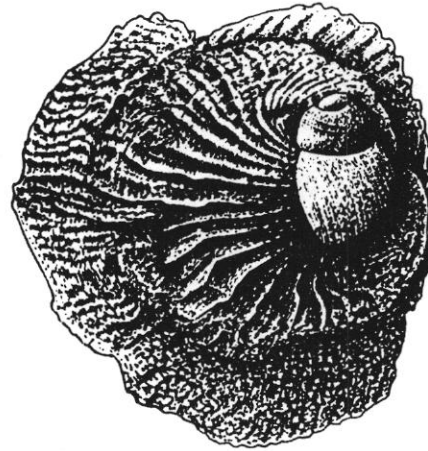
Pl.6, fig.1; Text-Fig.4

Material: from the Caribbean Sea near Santa Marta (Colombia)

Description: the adult individuals of this species preferably inhabit dead solid objects within the littoral zone where waves produce constant currents on the surface as well as on the undersides of the substrate (Bandel & Wedler, 1987). The cap-shaped shell has an internal, delicate, deep cup, which has its anterior third neatly sliced away. The base of the cup is attached near the centre of the inside of the shell but slightly off in the direction in which the apex of the shell points. The exterior has small axial corrugations or tiny cords.

The embryonic shell (compare Bandel, 1975a) is of neritiform shape with a rapid increase in whorl diameter and measures 0.34 mm across. Its sculpture consists of a network of grooves surrounded by acute ridges, which grade into 14 spiral ridges near to the aperture. The embryonic conch may be closed by a spirally coiled operculum.

The spawn consists of stalked egg capsules attached to the maternal soft body. The eggs are brooded in the shelter of the female shell and after 9 days of development 17-28 veligers hatch (Bandel, 1976). Freshly hatched veligers have a bilobated velum, the foot bears an operculum and is not used for crawling. This planktotrophic larva remains free-swimming until it has grown to 2.2 whorls, amounting to a height of 0.65 mm and a width of about 0.5 mm. The increase in whorl diameter is rapid. The aperture of the naticoid larval shell is about circular. The groove sculpture of the embryonic shell continues onto the first half larval whorl and then disappears. Spiral lirae feature this first half whorl and become less prominent during larval ontogeny. The late larval shell sculpture consists mainly of spiral periostacal lamellae, which after metamorphosis are easily corroded. Thus pediveliger shells appear spirally ornamented, however, the larval part of the apex of the juvenile appears to be sculptured by growth lines only.



Text-Fig. 4: *Cheilea equestris* from the Caribbean (Colombia). Largest dimension = 2 mm.

Cheilea cicatricosa (Reeve, 1858)

Pl.6, fig.2

Material: teleoconchs from Port Sudan (Red Sea), larval shells from the Red-Sea-cruise of the Research Vessel Meteor (1987).

Description: the fairly large limpet is found attached to coral rubble and larger debris within the reef and in the lagoon just behind the reef. Within the lagoon it occurs in spots with coarse sand and usually is attached to the underside of slabs resting on the sand. A smooth basal plate for attachment is formed with the aid of the foot.

The larvae that were caught in the plankton of the Red Sea have a shell consisting of 3.5 whorls when in the pediveliger phase. The embryonic shell is quite distinct from the larval shell and measures about 0.15 mm across. Its sculptural pattern consists of fine grooves surrounded by ridges forming an irregular network. The embryonic shell up to its aperture consists of primary shell (Bandel, 1982) and therefore has no growth lines. On the first whorl of the larval shell axial ribs on the upper whorl flank and spiral ribs on the lower flank and base form characteristic sculpture. The spiral elements are continuous onto the second larval whorl up to the apertural margin of the pediveliger. The spiral sculpture of the protoconch does not continue to the teleoconch.

Remarks: a similar species (Pl.6, fig.3) is present in the Red Sea where a fully grown larval shell of almost the same sculptural pattern can be recognized, however, there is one larval whorl less.

A *Cheilea* from the lagoons of Lizard Island (Queensland, Australia) with non-planktotrophic development has an embryonic shell ornamented with rectangles (Pl.6, fig.7). This pattern is usually

reduced in species, which have lost the planktotrophic phase in their ontogeny.

Cheilea sp.

Material: from the Miocene of Antwerp (Belgium); Natural History Museum in Leiden (Netherlands), RGM 117.241.

Description: The teleoconch is limpet-shaped and coarsely set with radial costae. The protoconch consists of little more than three whorls amounting to a height of 0.75 mm and a width of 0.8 mm. The embryonic shell measures 0.17 mm across. The larval shell appears smooth aside from short, subsutural, axial costae that end on the flank and are present on the first larval whorl. On the later larval shell only growth lines can be recognized.

Remarks: a very close similarity of this fossil species from the Miocene of western Europe to a modern species *Cheilea* sp. (Pl.6, figs.4-6) from New South Wales (Australian Museum, C 162449) can be stated. Teleoconchs and protoconchs are nearly alike.

Family Calyptraeidae Lamarck, 1809

Characteristics: the limpet-like, cap-shaped shell of circular to oval outline carries an internal lamina or shelf (inner lip) which may be spiral, flat or conical. To it the shell muscles are attached. The embryonic and larval shell of the planktotrophic veliger either have fine spiral lirae or rows of tubercles or are smooth. The protoconch and juvenile teleoconch are widely conical, almost planispirally coiled. The coiling becomes less prominent in the late whorls of the teleoconch.

Egg capsules are attached to the hard substrate below the shelter of the shell of the mother.

The members of this group are ciliary feeders and have a crystalline style in the stomach. They are protandrous hermaphrodites. In *Crepidula* and *Calyptraea* a wide mantle cavity lies above the attached foot, the gill is greatly enlarged with long, rod-shaped filaments extending obliquely across the cavity from the left to the right. The gill thus forms a divide between a leftward and ventral inhalant chamber and a dorsal exhalant chamber towards the right. Lateral cilia carry water between the gill filaments from one compartment to the other. Fine particles are collected between filaments and transported by cilia to the tips of the filaments where they are incorporated into a mucous food string, which is carried forward to the head. It issues from the mantle cavity in a groove behind the right tentacle where the short, cleft proboscis can reach back and pull off portions of the food string using the tiny radula.

In comprehensive studies Werner (1951, 1953) analyzed the feeding methods of the

Calyptraeidae, based on detailed data on *Crepidula fornicata*. Bandel (1984) noted that the Caribbean representatives of the Calyptraeidae and Hippo- nicidae feed in the same way. Usually the radula is only used to pick up the particles which have been caught by the mucus-ciliary filter system.

The genera can be conchologically differentiated by the shape of the columella. In *Calyptraea* it remains coiled, in *Crucibulum* it becomes cup like and forms a septal flat deck in *Crepidula*.

Genus *Calyptraea* Lamarck, 1799

Type: *Patella chinensis* Linné, 1758 from the Mediterranean Sea.

Generic description: the shell is conical with more-or-less central apex. The spiral sutures are more-or-less distinct and the sculpture consists of spiral ribs and growth lines. The basal aperture is almost circular and there is an internal spiral labrum which has a twisted columellar border. The whole shelf is oblique and the aperture narrow. The protoconch consists of less than two whorls, being wider than high, and has become almost smooth.

Remarks: Thiele (1929) attributed the following subgenera to the genus *Calyptraea*: *Trochatella* (= *Trochita*), *Sigapatella*, *Clypeola*, *Bicatillus*, *Crucibulum* and *Calyptraea*. Wenz (1938-1944) added *Spirogalerus* and *Calyptropsis*. With exception of *Crucibulum* and *Bicatillus* all these taxa are quite similar to each other and are here considered to be species of the genus *Calyptraea*. Subgenus *Trochita* Schumacher, 1817 (= *Trochatella* Lesson, 1830; type: *Patella trochiformis*; Gmelin) from the South American Pacific Ocean is very similar to the subgenus *Sigapatella* Lesson, 1830 (type: *S. novaezelandiae* Lesson, 1830) from New Zealand. The apex of the shell of *Sigapatella* lies in excentric position and there is no radial ornament but otherwise it is like *Trochita*. Vaught (1989) considers *Trochita* to represent a subgenus to *Calyptraea*, while *Clypeola* Gray, 1867 (= *Zegalerus* Finlay, 1927; type *Clypeola tenuis* Gray, 1867) and *Bicatillus* are thought to represent subgenera of *Sigapatella*. *Spirogalerus* Finlay & Marwick, 1937 (type: *S. lamellaria* Finlay & Marwick, 1937) from the Paleocene of New Zealand is considered by Beu & Maxwell (1990) to represent a subgenus to *Sigapatella*.

Calyptraea chinensis (Linne, 1758)

Material: from the Mediterranean Sea near Banyuls-sur-Mer and the Atlantic Ocean near Roscoff.

Description: in the Mediterranean Sea adult individuals of *C. chinensis* are found on rocks and shell debris in water from 15 m onward to greater depth. The teleoconchs have a conical outline

measuring about 2 cm in diameter. The growth increments are the dominating sculptural elements. The apex lies nearly central and is pointed.

The egg capsules account to about 11 and are attached to the substrate under the shelter of the shell. Each capsule measures about 1.2 mm in length, 1 mm in width and 0.6 mm in breadth. About 7-9 eggs per capsule all develop into embryos that hatch as veliconcha. The embryonic shell of the newly hatched veliger is already limpet-like in shape and measures 0.9 to 1.0 mm in maximum diameter. The initial shell portion may be well rounded or somewhat pointed and measures up to 0.14 mm in width. Fine wrinkles and growth lines are present in the first half whorl of the protoconch, later growth lines are conspicuous. The embryo hatches with 1.5 whorls and is able to swim for some time before settling.

The development of *C. chinensis* embryos from the Atlantic Ocean (Marine Station of Roscoff, August 1991) could be studied in more detail. 10 to 15 egg capsules are attached by their stalks to the substrate in the shelter of the parental shell. 6 to 12 yolk-rich eggs are contained within each egg capsule. As usual the cleavage leads to the formation of a cell ball and to gastrulation. The first organs clearly visible are the bulge of the anlage of the foot and the more narrow bulges of the velum. The embryo is very dense and cells are yolk-filled. The anlagen of the organs increase rapidly in size due to liquid that is pumped into them. During this embryogenetic phase the anlage of the mantle makes its first appearance. Connected to the growing pallial tissue the first tiny shell is secreted. It increases in size quite slowly, compared to the growth of the soft body. The velum and foot expand balloon-like giving the intracapsular veliger a shape that differs very much from a free swimming planktrophic form. The soft body is still much larger than the lumen of the shell when the mantle margin detaches from the shell margin. The larval heart can be recognized to pulsate in the neck region which lies outside the shell lumen. The foot does not secrete an operculum.

The pallial cavity remains small for a long time, which is correlated to the embryo feeding on liquid yolk from the egg capsule. In the stage of about one whorl of the shell much of the soft body still lies outside the shell. The visceral mass is densely filled with yolk. The mouth of the embryo is widely open and the anterior portion of the digestive tube is distinct while the intestine is scarcely visible. The velum has two lobes set with numerous cilia keeping the embryo in constant rotation. The head bulges but the anlagen of the tentacles as well as eyes on their bases have developed. Thus this intracapsular stage reflects the ontogenetic phase of a comparable late free-swimming veliger.

During the next stage of development the cilia on the velum increase in length, the head decreases in size and becomes denser. The tentacles significantly have grown in length. The pallial cavity has deepened and in addition to the larval heart the adult heart can be recognized to be situated between stomach and the base of the pallial cavity. The adult heart beats two times faster than the larval equivalent. The posterior portion of the digestive system forms a distinct tube crossing over in the roof of the pallial cavity.

The pediveliger stage demonstrates a large well functioning velum and a wide pallial cavity which is dominated by a large gill. The embryos all went through metamorphosis before they hatched as minute gastropods leaving parental care. The outer lip of the shell is not completely closed around the spire, but the general shape of the shell is already close to a limpet. The gill is well developed to create strong water current into the pallial cavity and to filter suspension from the sea water.

The radula of the adult is characterized by the nearly quadrangular central tooth which has a straight or slightly concave anterior front and posterior edge and convex margins. The basal platform has two narrow marginal ridges that end in pointed basal denticles. The triangular cutting edge with 7 to 13 pointed cusps rises above a narrow frontal rim. A gap separates the central tooth from the angular lateral tooth, which is about as wide as high. Its cutting edge is vertical and occupies the inner two thirds with 9-12 cusps on the outer and 3-5 on the inner flanks. The outer margin ends in a rounded anterior, and angular, somewhat extended, posterior corner. The posterior edge is straight, the anterior front concave and the inner margin convex with the platform shovel-like, with raised margins. Marginal teeth are slender and claw-like, with a central supporting ridge having a bulbous base on the inner pair that ends in a denticle at the cutting edge where also the sharp margins end in denticles. The outer pair is less supported by ridges but of similar length that amounts to 5 times its width. The teeth appear to be unworn.

Remarks: the unusual in the early ontogeny is the total absence of an operculum, a feature which is rarely found among marine gastropods. *Calyptrea chinensis* from Southwest England was found to have direct development by Lebour (1936), which is supported by the description provided here. The differences in development to the Mediterranean *C. chinensis* could be correlated to seasonal changes of environmental conditions, which could cause (e.g.) different egg sizes.

Lebour (1936) found the animals as single individuals, the females remaining in one spot. The small male is temporarily associated with the

larger female and actively moves. When it grows it switches to female sex and remains in its place, but retains the ability to move. Troschel (1863) already noted the variability of the cusp number on the teeth of the radula in *Calyptraea chinensis*.

According to Janssen (1984) *C. chinensis* is common in the Neogene deposits of Central Europe and the North Sea Basin since the Oligocene and closely related to the Middle Oligocene *C. striatella* Nyst, 1845. *Calyptraea "deformis"* from the Helvetian kept in the collection of the Natural History Museum in Vienna is also extremely similar to modern *C. chinensis*. The protoconch of this fossil from the Miocene measures about 0.6 mm across and consists of only a little more than 1 whorl.

Calyptraea novaezelandia Lesson, 1830

Material: collected in the intertidal zone at Otago Harbour near Portobello Marine Station (Southern Island New Zealand) and from Castle Rock and Flat Point (Northern Island New Zealand).

Description: the convex and circular limpet has a small spiral coil. A thick periostracum is lamellose and rugged edged. The anterior of the shell is white. *Calyptraea novaezelandia* is common in the intertidal area of Otago Harbour. Individuals are found on the underside of rocks within the low water zone. The animals are found single and are more-or-less sessile, but for copulation must migrate to each other.

The spawn consists of 10 to 15 capsules, each holding about 50-70 eggs. The first organs which are clearly visible in the embryogeny are the anlage of the foot and that of the velum, which both are bulgy. In this phase the embryo is very dense and cells are yolk-filled.

The next stages of development can be distinguished from those of *C. chinensis*. In *C. novaezelandia* the velum and features of the head (like tentacles and eyes) appear very early in the embryogeny and are already present before the thin shell is secreted by the mantle. The intracapsular veliger feeds on liquid yolk contained within the egg capsule and simultaneously digests the egg yolk, until the embryo has reached about three times the size of an uncleaved egg. The shell has remained attached to the mantle and is still connected to the tissue when the pallial cavity deepens and the main structures of the digestive system can be clearly recognized. The foot houses two large statocysts and bears a thin, elastic operculum.

Shortly before the embryos hatch the mantle detaches from the shell margin. The velum is rimmed with yellow pigment, the pallial cavity is well developed. The adult heart is periodically functional, while the larval heart pulsates continuously. The visceral mass is differentiated to

a large stomach, still empty connected to the intestine, and the digestive gland that still contains a fair amount of yellow yolk granules. After hatching the yolk is needed by the free-swimming veliger until it is established in the plankton and can switch to planktotrophic feeding strategy.

Calyptraea sp.

Pl.6, figs.8-10; Pl.7, fig.7

Material: specimen from the Lutetian (Eocene) of Southampton (England); British Museum (London).

Description: the teleoconch closely resembles that of *Calyptraea tenuis* from New Zealand, while the protoconch is closer to that of *Calyptraea centralis*.

The protoconch measures 0.6-0.7 mm in diameter and consists of 1.7 whorls. The embryonic shell measures 0.18 mm across and its transition into the larval shell is well documented by dense growth lines that can be recognized after the first whorl.

Calyptraea centralis (Conrad, 1841)

Material: from the Caribbean Sea near Santa Marta (Colombia).

Description: the teleoconch is cap-shaped, white in colour and about 1 cm in diameter. The embryonic shell (see Bandel, 1975a) accounts to 1.2 whorls measuring 0.15-0.2 mm across. The initial whorl consists of primary shell (see Bandel, 1982) sculptured with delicate spirally arranged tubercles. The later portion of the embryonic shell is smooth except for dense growth lines. The veligers hatching from the egg capsule are planktotrophic. During larval life they secrete another half whorl of shell set with fine spiral lirae. The protoconch finally consists of about 1.7 whorls and measures 0.6 mm across. The spiral lirae of the larval part are continuous to spiral threads sculpturing the early teleoconch.

Remarks: the larval part of the protoconch is a characteristic feature to distinguish *Calyptraea centralis* conchologically from *C. novaezelandia* and *C. chinensis* where pediveligers or crawling juveniles hatch. The protoconch of *C. centralis* resembles that of *C. pellucida* Reeve, 1859 from the Persian Gulf, which, however, according to Thorson (1940) has a smooth embryonic shell.

Calyptraea lybica (Quaas, 1902)

Pl.7, figs.2-3

Material: the shells originate from the Upper Maastrichtian deposits of the Ammonite Hills (*Exogyra overwegi* beds) in the western desert of Egypt ('Sand Sea', Barthel & Hermann-Degen, 1981), west of Dakhla Oasis.

Description: the shell is spirally coiled, of conical shape and a little wider than high. The apex lies in

the centre and is rounded. The whorls are separated externally by a depressed spiral suture. With four whorls the shell is about 12 mm wide and 10 mm high. The base is concave with the margin forming a flange. The labrum forms a flat spiral shelf like that of modern *Calyptraea*. The sculpture of the shell consists of spiral and/or oblique costellae which may be broken up by growth increments.

Calyptraea tenuis (Gray, 1867)

Pl.7, figs.4-5

Material: from New Zealand (Otago Harbour) and from Australia (Sydney Harbour).

Description: the teleoconch is spirally coiled, the aperture is almost circular. The dominating sculptural elements are spiral ribs, which, due to the rapid increase of whorl diameter, appear to run oblique. The spiral elements are crossed by distinct growth lines. The protoconch is smooth and amounts to 1.5 whorls which coil almost planispiral.

Remarks: *Calyptraea tenuis* has a shell shape and sculpture rather similar to Cretaceous as well as to Eocene representatives of this genus. In comparison to the Cretaceous species the modern species is smaller (up to 8 mm wide), has less whorls (3) and a more rapid increase in whorl dimensions (height about 5 mm). However, when regarding the general morphology and i.e. the early ontogenetic shell it can be considered to be a close relative to the Maastrichtian fossil from Egypt.

Calyptraea has been described from Upper Cretaceous occurrences at different places in Europe (Wenz, 1938-44). Quaas (1902: *Galerus libycus*) described and figured *Calyptraea libyca*. Unfortunately the original material of Quaas was lost during World War II, but it is assumed that the new material collected by Barthel (see Barthel & Hermann-Degen, 1981) at about the same locality holds the same species as were collected in the last century.

Genus *Crepidula* Lamarck, 1799

Type: *Patella fornicata* Linné, 1758 from the Atlantic Ocean.

Generic description: the limpet-like shell has a coiled apex situated at the posterior end. An interior shelly platform covers the posterior portion of the soft body. The dorsal midline of the shell follows a right spiral.

Remarks: the genus was reviewed and analyzed by Hoagland (1977) and she noted that *Crepidula* cannot easily be split into several sections because of shell convergence. There are at least 40 valid species of *Crepidula* worldwide of which about 10 are known only as fossils (Hoagland, 1977). *Maoricrypta* and *Zeacrypta* (both Finlay, 1927)

from New Zealand are younger synonyms of *Crepidula*. According to Thiele (1929) *Sandalium* Schumacher, 1817 is fixed for a neritoidean gastropod but is regarded a subgenus to *Crepidula* by Hoagland (1977). Abbott (1974) uses *Bostrycapulus* Olssori & Harbison, 1953 (instead of *Sandalium*) with the type *Patella aculeata* Gmelin, 1791, from the central American Pacific Ocean and the Caribbean Sea.

Thiele (1929) considered the following subgenera: *Dispotaeta*, *Crepidula*, *Crepipatella*, *Garnotia*, *Maoricrypta*, *Siphopatella*, *Zeacrypta* and *Janacus*. *Crepipatella* Lesson, 1830 (type: *Crepidula dilatata* Lamarck, 1822) is a slipper shell that is similar to *Crepidula* but differs in having the deck not attached on one side. *Dispotaeta* Say, 1829 (type: *Calyptraea striata* Say, 1824) from the American Atlantic Ocean has a not quite marginal apex, the septal lamella descends from the apex and the left side is strongly curved. *Siphopatella* Lesson, 1830, which according to Vaught (1989) represents a subgenus to *Crepidula* has a rather flat shell of oval outline and a spiral marginal apex. The septum is medially compressed into a funnel and concave on the left.

Crepidula fornicata (Linné, 1758)

Material: from the North Sea (Oosterschelde).

Description: the internal shelf extends over the posterior half on the inside of the shell. The internal shelf is concave and its edge is almost straight, sinuate or waved in two places.

Individuals usually stack on top of one another. In *Crepidula fornicata* the pediveliger settles on a female, commonly permanently. The animals form chains of up to 13 individuals, the small males on top, animals changing sex in the middle and females at the base. The females spawn balloon-shaped egg capsules which are attached by a short stalk onto the substrate under the maternal shell. The egg capsules number up to 70 in one spawn and each contains 100 to 250 eggs.

The embryogenies that could be observed lasted about four weeks. After gastrulation mouth, foot and shell gland make their appearance at about the same time. The shell produced by the mantle tissue increases in size slowly compared to the embryo which has much yolk available and grows more rapidly. The velum has already become bilobated before the primary shell progresses in growth. Statocysts have been developed. The digestive system then is completed, being utilized to feed on liquid yolk held within the egg capsule. The pallial cavity has formed but is still situated in front and outside of the shell as is the anus and the larval heart. When the shell becomes proportional to the size of the embryo the mantle detaches from its margin. The pallial cavity has moved inside the shell. The intestine has grown in length crossing

over the roof of the pallial cavity to the anus near the shell margin. Still it takes some time before the shell muscle becomes functional and the animal can withdraw into its shell and seal it with the operculum that has been secreted. The functionality is reached shortly before the veligers hatch. The veligers feed via a food groove on which microscopic phytoplankton is transported to the mouth (Werner, 1955; Fretter & Montgomery, 1968).

The embryonic shell consists of little more than one whorl (Fretter & Pilkington, 1971; Bandel, 1975b) measuring about 0.25 mm across. The initial whorl is set with delicate spiral rows of tubercles, ending with and demarcating the onset of the larval shell. After metamorphosis to benthic life the maximum size of the larval shell can be measured. The diameter is 0.55 mm, 1.5 larval whorls have been built. The larval part of the protoconch is smooth except for growth lines.

Settling occurs when the outer lip of the shell has enlarged so much that it is almost continuous. The early juvenile thus becomes a limpet right after metamorphosis (Bandel, 1975b).

The radula of the adult animal has quadrangular central teeth which are a bit wider than long. The front of a central tooth is shorter than the base with straight margins. The triangular cutting edge ends in rounded anterior corners and consists of a dominant vertically orientated main cusp accompanied by 2-4 smaller marginal cusps located right at the front. The lateral teeth are of rectangular outline and twice as wide as long. The triangular cutting edge with 3-6 denticles on the inner flank and 7-13 denticles on the outer flank, rises vertically at the front taking up about the inner half of the width of the tooth and continues to the outer edge as upturned ridge. The short inner edge is straight like the long posterior edge that ends in a handle-like extension of the outer posterior corner. The basal platform is enforced by a ridge that is continuous from the inner posterior corner to a central denticle, leaving a deep gutter like concavity on the outer side, into which the marginal teeth are fitted when the radula is folded. The marginal teeth are slender, 5-6 times longer than wide and claw-like with the inner pair supported by strong stalk ridges with rounded bulbous base and apical cutting edge of 6-9 denticles on the inner and 3-5 on the outer side. The outer pair appears a little more slender and stalks are more flattened with a cutting edge of 3-5 denticles. The radula teeth are quite similar to those of *Calyptraea* and also to *Capulus*, as has been noted by Troschel (1863) and Bandel (1984).

Remarks: according to Werner (1948) this species was observed in the North Sea first in the year 1931 having been introduced from the U.S. eastcoast. A lose relative to modern *C. fornicata*

lived in the North Sea Basin during the Miocene. According to Janssen (1984) *C. crepidula* (Linné, 1766) has a very similar protoconch to *C. fornicata*. Hoagland (1977) considered *C. crepidula* to represent fossils of the modern *Crepidula unguiformis* Lamarck, 1822.

Crepidula convexa Say, 1822

Material: from the Caribbean Sea near Santa Marta (Colombia).

Description: in shallow water the individuals sit attached to other living gastropods of a wide variety like *Tegula* Lesson, 1835, *Cerithium* Bruguière, 1789, *Batillaria* Benson, 1842, *Latirus* Montfort, 1810, *Leucozonia* Gray, 1847, etc., and also enter lagoonal environments with slightly raised salinity.

Egg capsules contain each up to 20 eggs. The embryogeny lasts about 12 days after which planktotrophic veligers hatch. The embryonic shell of 1.3 almost planispiral whorls measures 0.32 mm across (Bandel, 1975a).

Crepidula costata Sowerby, 1824

Material: near Portobello Marine Laboratory (Otago Peninsular, New Zealand).

Description: a species with large, evenly concave septum and a larva like that of *Crepidula fornicata*. Like *C. convexa* it attaches to hard substrates, especially to the outside of shells, commonly to gastropods moving about within the littoral zone. The species can be recognized by its sculpture of strong spiral ribs. It lives in New Zealand waters since the Oligocene.

Remarks: this species represents the type of *Maoricrypta* Finlay, 1927, which, however, is here recognized as a synonym to *Crepidula*.

Crepidula glauca Say, 1822

Pl.7, fig.6

Material: from Chengue Bay near Santa Marta (Colombia).

Description: this species can be found within the shells of *Strombus pugilis* Linné, 1758 that were carried around by hermit crabs.

The protoconch of *C. glauca* consists of the embryonic shell (see Bandel 1975a) measuring 0.5 mm across, which at hatching is already surrounded by the first limpet shell of the outer lip fused around the inner lip. The earliest portion of the embryonic shell is wrinkled and demonstrates a very rapid increase in shell diameter.

The pediveliger develops from rather large eggs of which about 9 are contained within each egg capsule. Even though already limpets, the young hatch as pediveligers, which swim for a short time with the aid of the bilobated velum. The

veligers may use their foot in case hard substrates are close to the water surface.

Remarks: a close relative may be *C. protea* d'Orbigny, 1841 from southern Brasil which lives very much the same way (Hoagland, 1984). However, members of that species have planktotrophic veligers which hatch out with a shell size of 0.15 mm in diameter and thus is much smaller than in *C. glauca*.

Crepidula plana Say, 1822

Pl.7, figs.7-8

Material: from the Caribbean Sea near Santa Marta (Colombia)

Description: the animals bear a white shell and live attached to the interior of large gastropod shells that are carried around by hermit crabs. *C. plana* occurs in the intertidal zone down to depths of more than 10 m.

In some capsules of the spawn not all eggs develop but disintegrated into small yolk granules which are consumed by the developing embryos (Bandel, 1976). Thus it occurred that of 80 eggs only 25 developed and hatched as veligers.

The protoconch resembles that of *C. convexa* when regarding the hatching veliger, which is equipped with a planispiral embryonic shell set with fine spiral rows of tubercles (Bandel, 1975a).

Remarks: Hoagland (1984) noted that *Crepidula plana* from the northern regions of the American Atlantic coast produces veligers, but pediveligers at the southern coasts. The same was also noted in regard to *Crepidula convexa*.

These tendencies can certainly not be confirmed with Caribbean species from Santa Marta. Hoagland (1984) noted differences between the electrophoretical patterns of the northern and southern specimens, possibly indicating that there are two different species, which may also account for the Caribbean forms described here.

Crepidula monoxyla (Lesson, 1830)

Material: from off Otago (Southern Island New Zealand) in about 100 m depth.

Description: *C. monoxyla* is common attached to the inside shells of gastropods carried by hermit crabs in about 100 m deep water. The male is found on the shell of the larger female. The male switches to female sex when growing larger. *Crepidula monoxyla* represents the type to *Zeacrypta* Finlay, 1927, which, however, is recognized here as a synonym to *Crepidula*. *C. monoxyla* has a flat to concave white shell like in *Crepidula glauca* and *C. plana*.

The egg capsules of *Crepidula monoxyla* contain 100 to 150 yellow eggs of which only one or a few develop. The embryogeny resembles that

of the here described *Calyptrea novaezelandia*. However, the small non-operculate limpets metamorphose inside the egg capsule. They feed on large nurse eggs (0.15 mm across), devouring them all before hatching as over 1 mm large limpets.

Remarks: the mode of hatching has also been described by Pilkington (1974).

Genus Crucibulum Schumacher, 1817

Type: *Patella auricula* Gmelin, 1791.

Generic description: the cap-shaped shell has a complete cup-like supporting cone which is attached by its base or along one side and open downwards. The ornament consists of radial striae or costellae and the shell margin reflects the attachment surface.

Remarks: *Bicatillus* Swainson, 1840 (type: *Crepidula extintorium* Lamarck, 1799) from the Chinese Sea is similar but the inner cone is reduced to a lamina of its attachment. The shell is otherwise similar to that of *Crucibulum*.

Crucibulum auriculum (Gmelin, 1791)

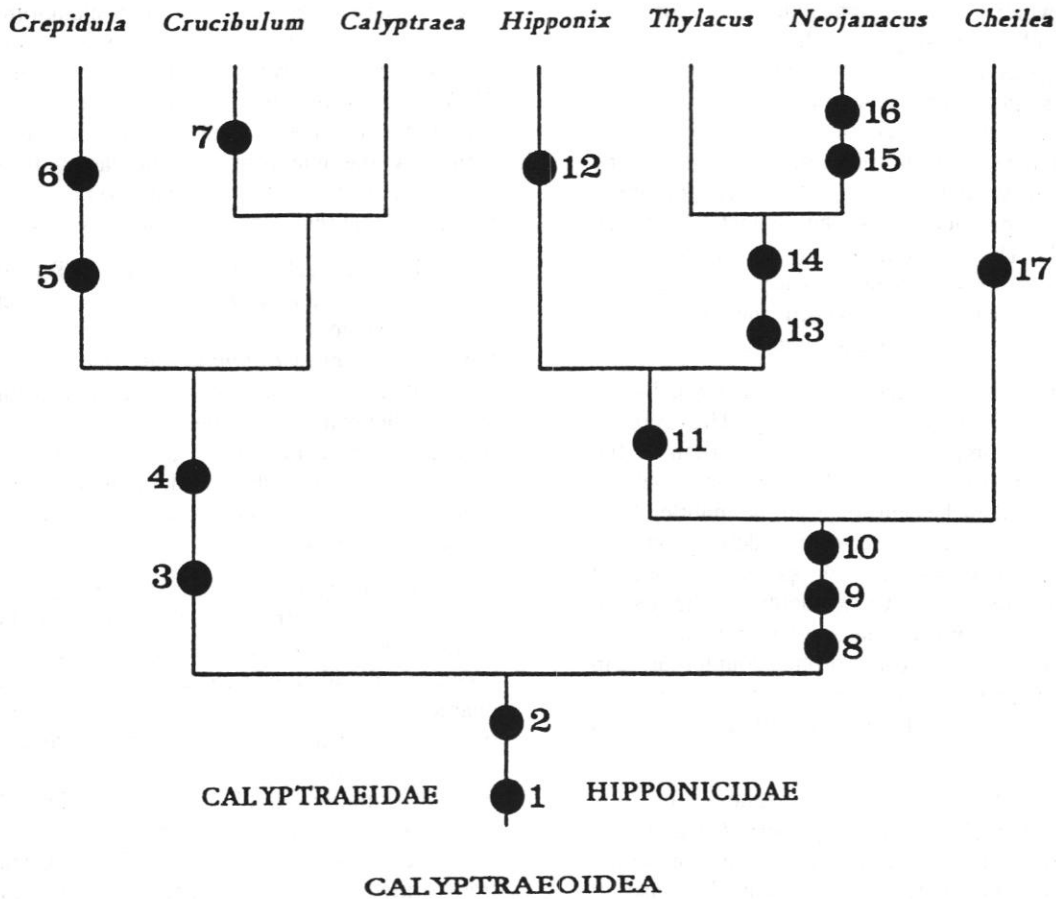
Pl.7, figs.9-10

Material: from the Caribbean Sea near Santa Marta (Colombia).

Description: two different types have been found, which are considered to be varieties. One variety has a low shell cone of white and reddish brown colour. It is found under stones and also on shells of living *Strombus gigas* Linné, 1758. The second variety has a comparatively higher shell and can be found attached to other shells, especially to living *Latirus infundibulum* (Gmelin, 1791) (Muri-coidea). Individuals of this species are especially common on dead shells assembled on muddy surfaces or fine sand in a water depth of 5 to 20 m.

Crucibulum auriculum has a cap-shaped shell with a circular base and a central apex. The spiral diaphragm is a shelly cup attached to the inside of the shell near its centre. Its free edge is thickened. The animal has a foot that is reddish white. The head bears two lamellar processes running to the neck. The females spawn up to 15 egg capsules which each hold about 120 eggs (Bandel, 1976).

About 5 egg capsules are attached to the *Strombus* shell in the shelter of the maternal *C. auriculum* shell. Each capsule contains 10 to 12 eggs that develop into a veliconcha having a functional foot and a large velum. The protoconch consists only of the embryonic shell which amounts to little more than one whorl measuring about 1 mm across. The protoconch is set with 25 periostracal ribs (Bandel, 1975a), which, however, are easily worn off when the juvenile limpet moves in his habitat. Consequently the remaining sculpture consists of growth lines only.



Text-Fig. 5: Phylogeny of the **Calyptraeoida**; numbers indicating apomorphic characters: **1**: teleoconch limpet-shaped; breeding stalked egg capsules; **3**: retardation of shell embryogeny; **4**: no proboscis, filter-feeding obligatory; **5**: teleoconch with slipper limpet shape; **6**: columella reduced to flat deck; **7**: columella reduced to cone; **8**: central radular teeth widened; **9**: columella reduced; **10**: egg capsules attached to soft body; **11**: horseshoe-shaped muscle scar; **12**: columella totally reduced; **13**: teleoconch with slipper limpet shape; **14**: attached to the inside of gastropod shells; **15**: columella totally reduced; **16**: radular teeth per row reduced to five; **17**: teleoconch projecting on upper flank on last protoconch whorl.

The growth lines of the embryonic shell begin already shortly after the formation of the initial shell cap reflecting the very early detachment of the mantle from the shell margin.

Remarks: Thorson (1940) described the embryonic shell of *Crucibulum scutellatum* (Wood, 1828) from the Persian Gulf. It is not ornamented and was attached to a pelagic veliger.

Summary and Conclusions

In the systematic part of this study the genera *Crepidula*, *Crucibulum* and *Calyptraea* compose the family Calyptraeidae while *Hipponix*, *Cheilea*, *Thylacus* and *Neojanacus* are placed in the Hipponicidae (Text-Fig.5). *Thylacus* is a fossil genus, which is only known from the Upper Cretaceous and the Eocene. *Neojanacus* had been attributed to the Capulidae (e.g. Beu & Maxwell, 1990), however, the central radular teeth and the

shape of the head are similar to those of hipponicid genera. Moreover, it must be assumed that the egg capsules of *Neojanacus* are attached to the soft body, which is a synapomorphy for the Hipponicidae (Text-Fig.5). In the Calyptraeidae the egg capsules are attached to hard substrate. A second shared derived character of hipponicid genera is the wide central radula tooth. The Calyptraeidae show the plesiomorphic radula type with a narrow central tooth. A third synapomorphy for the Hipponicidae is the reduction of the columella. This happens also in the Calyptraeidae (Text-Fig.5), however, not already when the two families branch off but within the family. I.e. *Calyptraea* has a complete columella.

The Calyptraeidae are characterized by the retardation of the shell embryogeny. The embryos incorporate comparatively more yolk than is the case in the Hipponicidae. The primary shell of calyptraeids detaches earlier from the mantle. Thus the embryonic shell is covered widely by growth lines, which is in contrast to hipponicids. A second synapomorphy for the Calyptraeidae is the loss of the proboscis and connected to that obligatory filter-feeding. The plesiomorphic counterpart can be recognized in the Hipponicidae where a proboscis is present and the filter-feeding is facultative.

Classifying the four genera of the Hipponicidae (Text-Fig.5), *Hipponix*, *Thylacus* and *Neojanacus* are united by having a horseshoe-shaped muscle scar, which is not the case in *Cheilea*. The columella of *Cheilea* is less reduced compared to the other genera, showing the plesiomorphic condition within the family. Species of *Cheilea* share at least one apomorphy: the teleoconch projects on the upper flank of the early part of the last protoconch whorl. The three genera with a horseshoe-shaped muscle scar can be differentiated by the total loss of the columella in *Hipponix*, while *Thylacus* shows remains of this shell portion. The columella is also totally lost in *Neojanacus*, however, this genus is closely related to *Thylacus*. *Neojanacus* and *Thylacus* both live or lived attached to the columellar region of gastropod shells carried around by hermit crabs (analogous to some *Crepidula*). The teleoconch of the two genera thus usually has slipper limpet shape. *Neojanacus* has the radular teeth per row reduced to five. This character of course is not useful to separate *Neojanacus* from *Thylacus* as the radula of a fossil species usually is not preserved. The early ontogeny of *Neojanacus* differs from that of

Thylacus in being non-planktotrophic. It is generally known that in many caenogastropod genera different developmental patterns may occur. Thus planktotrophic or non-planktotrophic development cannot be used to define taxa higher than species. The weak arguments to distinguish *Thylacus* from *Neojanacus* are the remains of the columella in juveniles of the former and the extremely flat teleoconch in the latter. It seems quite possible that further research on the two taxa may show that they represent a single genus.

In the calyptraeid branch (Text-Fig.5) *Calyptraea* is characterized only by plesiomorphies which indicates that this genus represents the family stem-line. *Crucibulum* and *Calyptraea* are also united by a plesiomorphy: the conical limpet-shaped teleoconch. *Crucibulum* with its columella reduced to a cone shows an apomorphy. The *Crepidula* branch is characterized by the columella transformed to a flat deck and the slipper limpet shape of the teleoconch.

The Hipponicidae and Calyptraeidae can be united to the Calyptraeioidea (Text-Figs.5-6) by two shared derived characters: the limpet shape and the breeding of stalked egg capsules. An evaluation of characters of course means to look at the outgroups. The adelphotaxon of the Calyptraeioidea is the Capuloidea Fleming, 1822 with the two families Capulidae and Trichotropidae Gray, 1850. The presence of an echinospira-larva unites these two families (Text-Fig.6). The Capulidae transformed to limpet shape and developed a pseudoproboscis while the Trichotropidae show only plesiomorphic characters. The larval whorls of echinospira bearing veligers usually show an open suture (Text-Fig.7), which is a useful tool to unravel the convergence of certain hipponicid and capulid teleoconchs.

The Calyptraeioidea share with the Capuloidea the facultative filter-feeding and connected to that a modified gill. Proposing that the Calyptraeioidea is the adelphotaxon of the Capuloidea means that the echinospira-larva in the Capuloidea and Lamellarioidea d'Orbigny, 1841 has developed convergently. It will be shown here that the two superfamilies belong to the same order, however, to two different evolutionary lines that probably branched off in the Mid Cretaceous, shortly after rise of the still unknown neomesogastropod stem group.

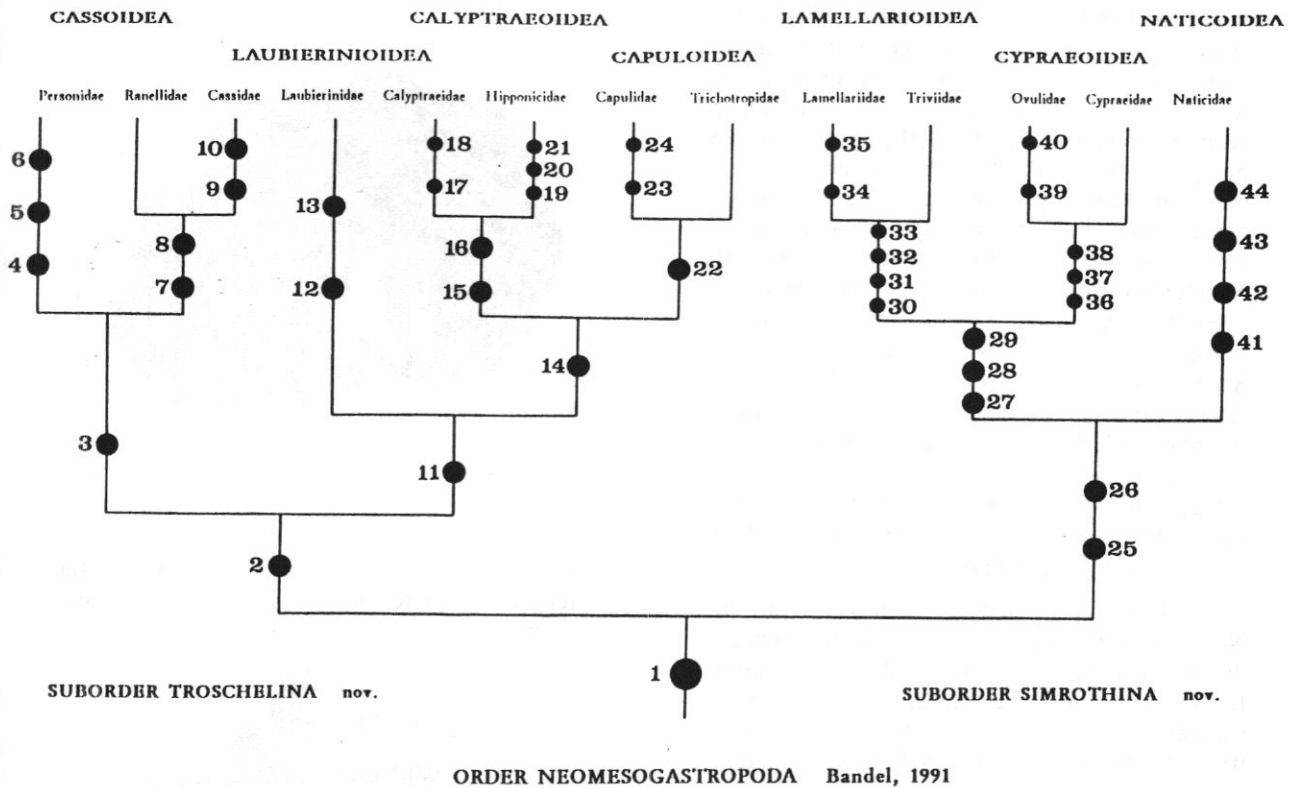


Fig. 6: Phylogeny of the **Neomesogastropoda**; numbers indicating apomorphic characters: **1**: large globular protoconch composed of large embryonic whorl sculptured with groove-ridge pattern, and of larval whorls coarsely covered by rectangles; **2**: pleurembolic proboscis; **3**: larval pallial tentacle; **4**: teleoconch whorls distorted; **5**: groove-ridge pattern of embryonic shell lost; **6**: proboscis extremely long and coiled when retracted; **7**: large (accessory) salivary glands; **8**: preying on echinoderms; **9**: salivary glands extremely enlarged; **10**: food specialization on certain echinoderms; **11**: consecutive hermaphroditism; **12**: monopectinate osphradium; **13**: protoconch much enlarged; **14**: facultative filter-feeding; **15**: teleoconch limpet-shaped; **16**: breeding stalked egg-capsules; **17**: retardation of shell embryogeny; **18**: no proboscis, filter-feeding obligatory; **19**: central radular teeth widened; **20**: columella reduced; **21**: egg capsules attached to soft body; **22**: echinospira; **23**: teleoconch limpet-shaped; **24**: pseudoproboscis; **25**: naticoid teleoconch; **26**: pedial ganglia with anterior lump; **27**: teleoconch involut; **28**: mantle may cover the shell; **29**: operculum lost in adult; **30**: echinospira; **31**: seminal duct closed; **32**: feeding on tunicates; **33**: egg capsules embedded in tunicate tissue; **34**: teleoconch ear-shaped; **35**: jaws united; **36**: triradiate osphradium; **37**: pedal ganglia elongated; **38**: sinusigera protoconch; **39**: larval whorls set with rhombs; **40**: marginal radular teeth serrated; **41**: accessory boring organ; **42**: inflatable foot may cover shell; **43**: egg mass collar-shaped; **44**: sculpture of larval whorls reduced.

The order Neomesogastropoda was coined by Bandel (1991a) and will be differentiated here in more detail. The Neomesogastropoda besides the Calyptraeidea, Capuloidea and Lamellarioidea includes the Cassoidea Latreille, 1825; Laubierinioidea Warén & Bouchet, 1990; Cypraeoidea Rafinesque, 1815 and Naticoidea Forbes, 1838 (Text-Fig.6).

The first neomesogastropod was omnivorous (possibly carnivorous), had a taenioglossan radula, a proboscis, a large leaflet bipectinate osphradium, separate sexes, an open seminal duct, a simple egg mass, a yolk-rich embryogenesis, a long-term

veliger, a dextrally coiled teleoconch without significant varices (e.g. similar as in *Trichotropus migrans* Dall, 1881), an operculum, etc. However, all these characters are plesiomorphies. The feature which allows to attribute a taxon to the Neomesogastropoda is the protoconch. The embryonic shell shows a groove-ridge pattern (Pl.5, fig.5), which can also be found in many other caenogastropod groups, e.g. in many cerithioideans. However, the embryonic shell of neomesogastropods is significantly larger compared to these (see Bandel, 1975a). Large embryonic shells occur also in the Neogastropoda, however, not having the groove-ridge pattern. The

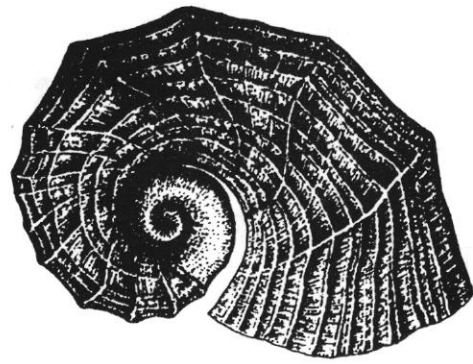
larval shell of the neomesogastropod stock is also comparatively large with a diameter of at least 0.5 mm, but usually much larger. The characteristic feature of the larval whorls is the cancellated sculptural pattern (Pl.8, figs.2,9), which is formed by spiral and axial ribs. This pattern may also occur in some Cancellarioidea. These, however, never show the groove-ridge pattern on the embryonic shell. The basic condition within the Neomesogastropoda is a larval shell which is coarsely cancellated on all whorls and the transition to the teleoconch is scarcely demarcated. Such a protoconch was described by Schröder (1992) from the Aptian/Albian of Lower Saxony (Northern Germany). Moreover, Riedel (1992) showed for the Cassoidea that the evolution of the protoconch within that superfamily must have started with similar type as here described to be basic for neomesogastropod.

The two main branches of the Neomesogastropoda can already be differentiated by the teleoconch. While the evolutionary line that leads to the Cassoidea, Laubierinoidea, Calyptraeidea and Capuloidea starts with a trichotropoid adult shell, which is later more-or-less modified, the branch with Lamellarioidea, Cypraeoidea and Naticoidea shows the apomorphic condition, starting with a teleoconch similar to that of *Natica*. A second synapomorphy for this branch is the shape of the pedal ganglia that show an anterior lump (Thiele, 1929). The members of the three superfamilies are also characterized by a synplesiomorphy: the proboscis is acrembolic. The pleurembolic proboscis type can be found in the other branch and has to be considered to represent the apomorphic condition.

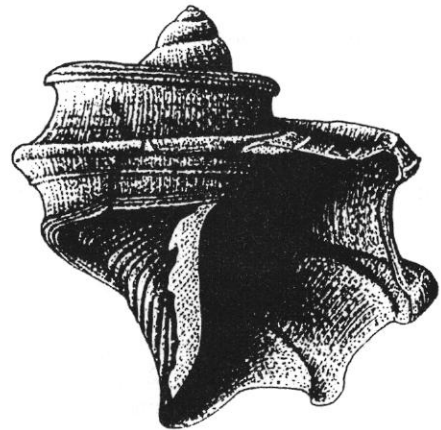
Basing on the considerations that there are two main neomesogastropod branches, which possibly already split off in the Mid Cretaceous, two new suborders are introduced here:

Troschelina, with the superfamilies Cassoidea, Laubierinoidea, Calyptraeidea and Capuloidea; derivatio nominis: in honour to the German malacologist F.H. Troschel.

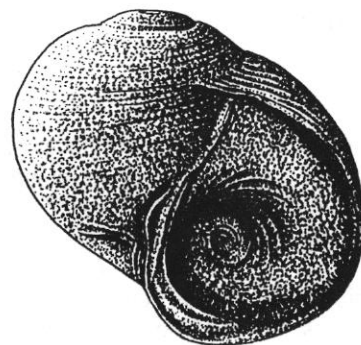
Simrothina, with the superfamilies Naticoidea, Cypraeoidea and Lamellarioidea; derivatio nominis: in honour to the German malacologist H. Simroth.



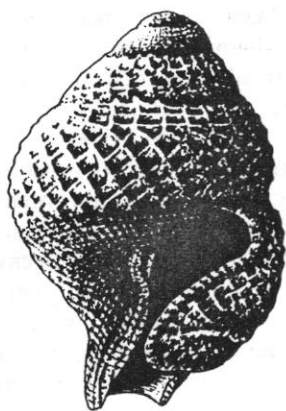
Text-Fig. 7: Juvenile *Capulus* sp. From the Oligocene of Eyre (France). Largest dimension = 2.5 mm.



Text-Fig. 8: *Akibumia orientalis* (Laubierinoidea) from the northern Pacific (Japan). Largest dimension = 1 cm.



Text-Fig. 9: Larval shell of a *Natica* from the Red Sea showing remains of spiral sculpture. Largest dimension = 1.5 mm



Text-Fig. 10: Ovulid larval shell from the Red Sea showing the characteristic pattern of rhombs and a sinusigera aperture. Largest dimension = 0.75 mm.

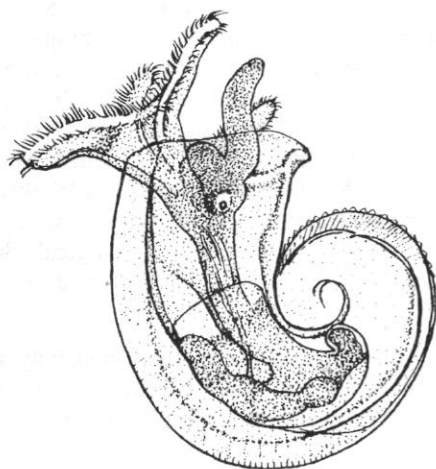


Fig. 11 a: Veliger of *Lamellaria* sp. From the red Sea with echinospira. Largest dimension = 2 mm.

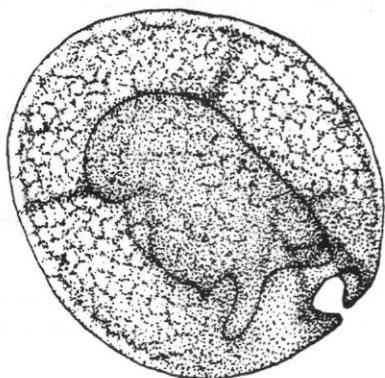


Fig. 11 b: Same individual (as in 11 a) a few days later and freshly metamorphosed, with the mantle covering the shell. Largest dimension = 1.5 mm.

Within the Trochelina subord. nov. the Cassoidea have developed a larval pallial tentacle, which allows the veliger to secrete and fix additional periostracum sculptural elements (for details see Bandel et al., 1994). The phylogeny of the Cassoidea will be published elsewhere (see also Riedel, 1994), however, a few apomorphies of the families are presented. The teleoconch of the Personidae Gray, 1854 is distorted, the groove-ridge pattern of the embryonic shell is lost and the proboscis is extremely long. The Ranellidae Gray, 1854 (Pl.8, fig.1,2) and the Cassidae (Pl.8, fig.3) share the possession of large (accessory) salivary glands and both include echinoderms in their diet. In the Cassidae the salivary glands are extremely enlarged and the taxa are specialized to feed on certain echinoderms.

The Laubierinioidea (Pl.8, fig.4; Text-Fig.8) originally had been attributed by Warén and Bouchet (1990) to the Cassoidea. The knowledge of this group is very incomplete, however, the Laubierinioidea do not share any derived character with the Cassoidea, Warén and Bouchet (1990) propose that the salivary glands of *Laubierina* and allies are typical as for cassoideans. However, Riedel (1992) showed that there is no typical complex of salivary glands uniting the Cassoidea. Moreover, the pallial larval tentacle which is a synapomorphy of the Cassoidea is not known from the Laubierinioidea. On the other hand the members of the latter are probably protandrous hermaphrodites (Warén & Bouchet, 1990) which is not known from cassooids but unites the Laubierinioidea with the Calyptraeioidea and Capuloidea. The species of the Laubierinioidea have a monopectinate osphradium (Warén & Bouchet, 1990), which is also not known from the Cassoidea. An evolutionary tendency to reduce the osphradium can be recognized in members of the Calyptraeioidea or Capuloidea. The enlargement of laubierinioid protoconchs is interpreted to have developed convergently in the Cassoidea, i.e. in the Ranellidae.

The superfamilies of the new suborder Simrothina each can be defined by apomorphies very well. The Naticoidea have an accessory boring organ, the foot is specialized to cover the conch, the egg mass is collar-shaped and the cancellation of the protoconch is reduced to spiral lirae or a few axial ribs (Text-Fig.9). The Lamellarioidea and Cypraeoidea commonly share that the teleoconch is involut, the mantle may cover the shell and the operculum is lost in the adult. The members of the two families of the Cypraeoidea have triradiate osphradia, the pedal ganglia are elongated and the veliger forms a sinusigera aperture (Pl.8, figs.9-10; Text-Fig.10). The sinusigera type is known from many gastropod taxa and usually cannot be used to characterize taxa higher than the species level. However, the protoconchs of Ovulidae Fleming,

1822 and Cypraeidae generally show the sinusigera aperture and the loss of this feature has to be interpreted as apomorphic within the Cypraeoidea. Gosliner & Liltved (1985) doubted that the elongation of the pedal ganglia is a useful character to differentiate the nervous system of the Cypraeoidea from that of the Triviidae Troschel, 1863. Gosliner & Liltved (1985) found also spherical pedal ganglia in some Cypraeidae as is usual for Triviidae. However, the spherical pedal ganglia occur in cypraeids where the concentration of ganglia (cephalization) is significantly higher than in comparable species of the same family (see Gosliner & Liltved, 1985). Thus we interpret the spherical condition of pedal ganglia to be a derived character within the Cypraeoidea. The species of Cypraeidae still show a larval shell that is completely and coarsely covered by a cancellated pattern (Pl.8, fig.9), which is similar to the basic neomesogastropod type. In contrast the Ovulidae have changed their larval sculpture to a pattern of rhombs (Pl.8, fig.10; Text-Fig.10) (compare Bandel, 1991b, 1992). A second apomorphy of the Ovulidae is the modification of the radula, i.e. the serration of the marginals.

The Triviidae and the Lamellariidae compose the superfamily Lamellarioidea. The synapomorphies are the echinospira larva and connected to this the reduction of the cancellated pattern of the larval shell, the closed seminal duct, feeding on tunicates and the egg capsules embedded in the tissue of tunicates. The echinospira is helicoid in the Triviidae and discoidal in the Lamellariidae (Text-Fig.11). It is unknown which type is apomorphic. The Lamellariidae show derived characters with the jaws united and the secondarily ear-shaped teleoconch.

The formation of an echinospira larva in the early ontogeny is interpreted by some authors (e.g. Warén & Bouchet, 1991) to represent a synapomorphy which unites the Capuloidea with the Lamellarioidea. However, as has also been shown here, there is a close relation between Capuloidea and Calyptroidea on one hand (compare Graham, 1954) and Lamellarioidea and Cypraeoidea on the other hand (compare Gosliner & Liltved, 1985). Uniting these two branches to the suborder Echinospirida Fretter & Graham, 1962, would include the loss of the echinospira larva in the Calyptroidea and/or in the Cypraeoidea. However, in both taxa there are planktotrophic species which have a cancellated protoconch. In contrast, the larval sculpture is reduced in case an echinospira is formed. Thus it must be assumed that Calyptroidea and Cypraeoidea or precursors of both do not have and never had an echinospira in their ontogeny. Consequently the echinospira larva has developed independently two times in the phylogeny of the Neomesogastropoda.

It has been shown that anatomical and conchological characters can be correlated very well when using all ontogenetic stages (embryonic, larval, juvenile and adult shell) of a gastropod shell. There are no taxa among the Neomesogastropoda where all features of the different ontogenetic shells have been developed convergently. Thus fossil shells (if well preserved) can be used to trace back the phylogeny of higher as well as of lower taxa of this gastropod order quite safely. The stem group of the Neomesogastropoda is unknown, which, however, has to do with the very incomplete knowledge of Lower Cretaceous gastropod faunas.

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Plate 1

Fig. 1: juvenile *Thylacus cretaceus* from the Upper Cretaceous of the SE-USA. Scale bar = 1 mm.

Fig. 2: apical view of protoconch of same specimen as in fig. 1. Scale bar = 0.5 mm.

Fig. 3: magnification of embryonic whorl revealing the groove-ridge pattern; same specimen as in figs 1-2. Scale bar = 50 μ m.

Fig. 4: another specimen of *Thylacus cretaceus* with more distinct spiral lirae on the larval whorls. Scale bar = 1 mm.

Fig. 5: magnification of same specimen as in fig. 4 showing remains of a cancellated sculpture on the lower flank of the terminal protoconch whorl. Scale bar = 0.2 mm.

Fig. 6: *Thylacus squamaeformis* from the Lutetian of Daméry (France). Scale bar = 2 mm.

Fig. 7: magnification of protoconch of same specimen as in fig. 6. Scale bar = 0.5 mm.

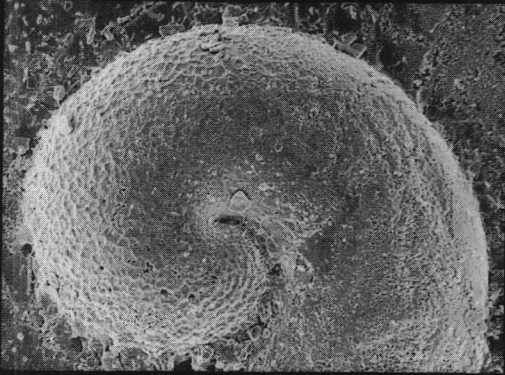
Fig. 8: teleoconch of *Athleta* sp. (Neogastropoda) from the Lutetian of Southampton (U.K.) with several *Thylacus squamaeformis* attached to. Scale bar = 2 cm.



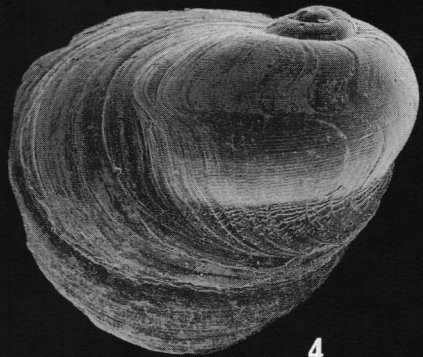
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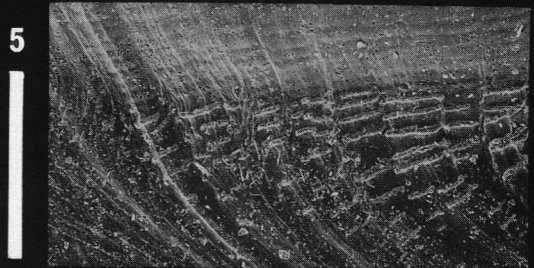
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Plate 2

- Fig. 1: another specimen of *Thylacus squamaeformis* from the Lutetian of Daméry. The interior shell shows part of horseshoe-shaped muscle scar. Scale bar = 1 mm.
- Fig. 2: lateral view of apical whorls of same specimen as in fig. 1 showing the transition from the naticoid protoconch to the limpet-shaped teleoconch. Scale bar = 0.5 mm.
- Fig. 3: apical view of protoconch of same specimen as in figs. 1-2. Scale bar = 0.3 mm.
- Fig. 4: specimen from the Miocene of Romania that may represent a species of *Thylacus*. Scale bar = 1 mm.
- Fig. 5: magnification of protoconch of same specimen as in fig. 4. Scale bar = 0.2 mm.
- Fig. 6: apical view of anterior half of teleoconch of *Neojanacus perlexus* (from New Zealand) with smoothish protoconch on left hand. The shell is largely covered by the organic periostracum. Scale bar = 5 mm.
- Fig. 7: lateral (from the anterior) view of protoconch and teleoconch of same specimen as in fig. 6. Scale bar = 1 mm.
- Fig. 8: magnification of protoconch of same specimen as in figs. 6-7. Scale bar = 1 mm.



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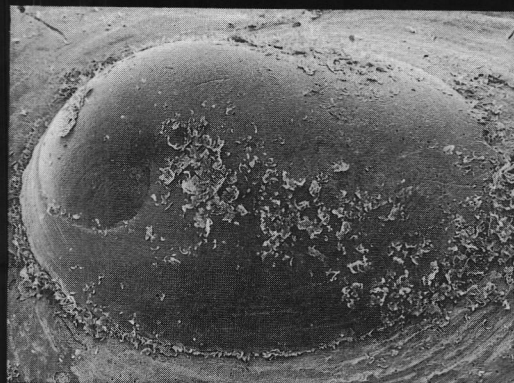
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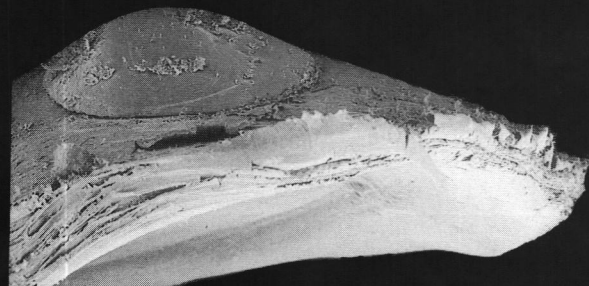
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Plate 3

Fig. 1: radular teeth of *Neojanacus perplexus* in semi-lateral view. Scale bar = 50 μ m.

Fig. 2: same radula as in fig. 1 but in different view. Scale bar = 50 μ m.

Fig. 3: same radula as in figs. 1-2; magnification of a lateral tooth. Scale bar = 20 μ m.

Fig. 4: same radula as in figs. 1-3; magnification of a half-row of teeth. Scale bar = 20 μ m.

Fig. 5: juvenile shell of *Hipponix cornucopius*, the type species of *Hipponix* from the Lutetian of Daméry (France). Scale bar = 2 mm.

Fig. 6: same specimen as in fig. 5; lateral view of protoconch. Scale bar = 0.5 mm.

Fig. 7: same specimen as in figs. 5-6; apical view of protoconch. Scale bar = 0.5 mm.

Fig. 8: same specimen as in figs. 5-7; magnification of initial whorl revealing wrinkles of the shell. Scale bar = 0.1 mm.

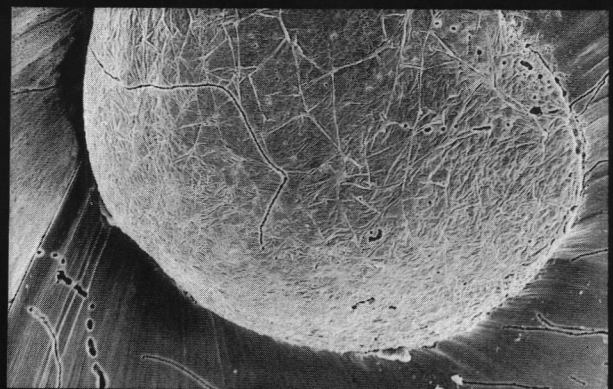
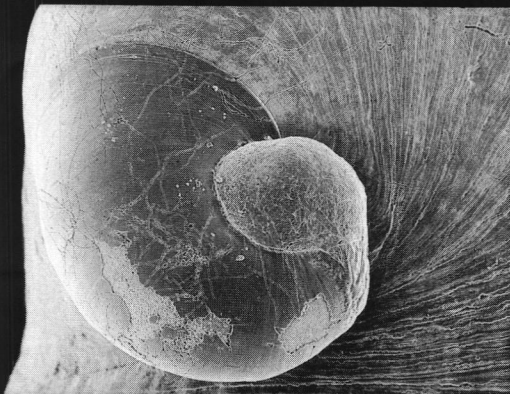
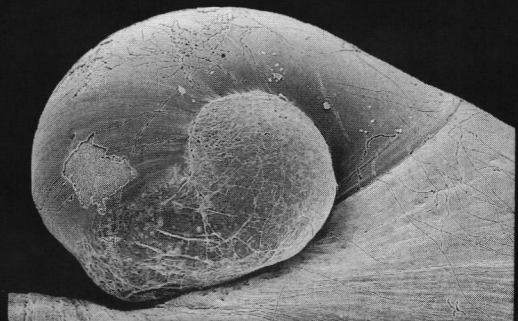
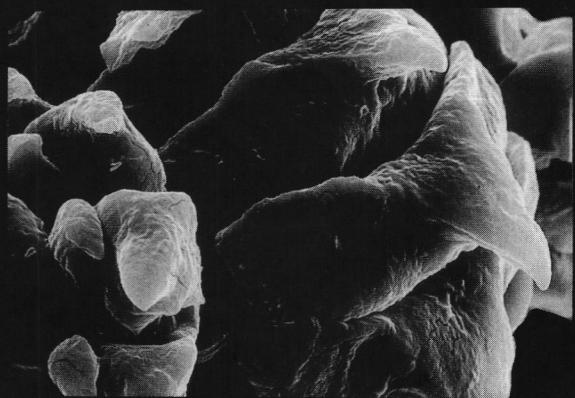
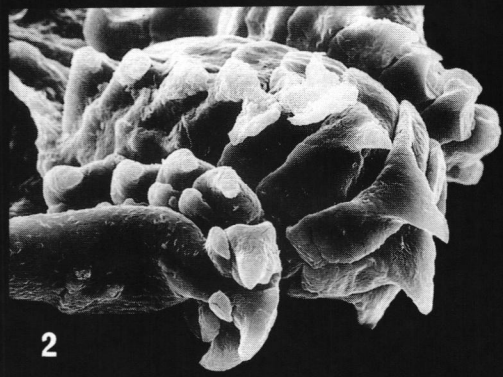
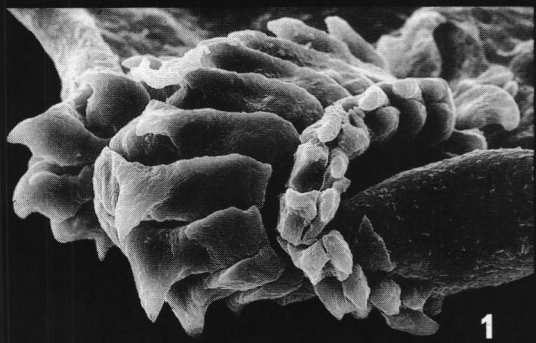


Plate 4

Fig. 1: larval shell of *Hipponix conicus* from the Red Sea. Scale bar = 0.2 mm.

Fig. 2: *Hipponix antiquatus* from the bahamas. Scale bar = 2 mm.

Fig. 3: same specimen as in fig. 2; magnification of the protoconch. Scale bar = 0.3 mm.

Fig. 4: lateral view of *Hipponix* sp. From the kermadec Islands. Scale bar = 0.5 mm.

Fig. 5: same specimen as in fig. 4 in apical view. Scale bar = 0.5 mm.

Fig. 6: same specimen as in fig. 4-5; apertural view. Scale bar = 1 mm.

Fig. 7: same specimen as in figs. 4-6; magnification of protoconch. Scale bar = 0.3 mm.

Fig. 8: apex of *Hipponix minor* from the pacific (Hawaii). Scale bar = 0.5 mm.

Fig. 9: a species of *Hipponix* from the pacific (Tonga). The interior shell shows the horseshoe-shaped muscle-scar. Scale bar = 1 mm.

Fig. 10: same specimen as in fig. 9 in apical view. Scale bar = 0.5 mm.

Fig. 11: same specimen as in figs 9-10; magnification of the protoconch. Scale bar = 0.5 mm.

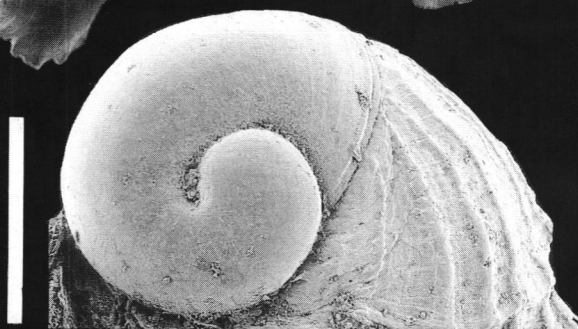
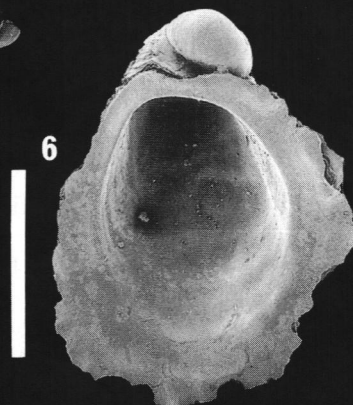
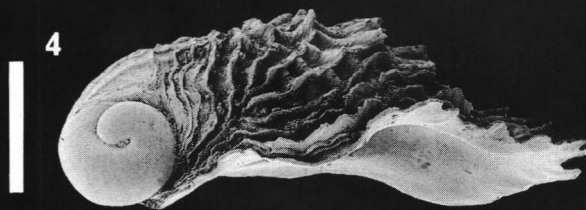
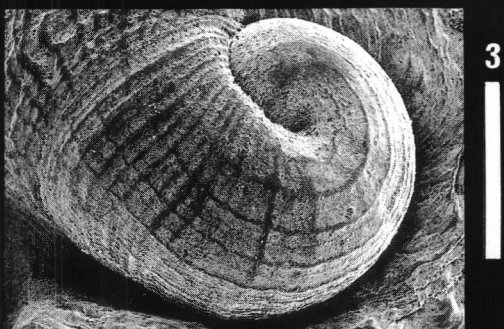
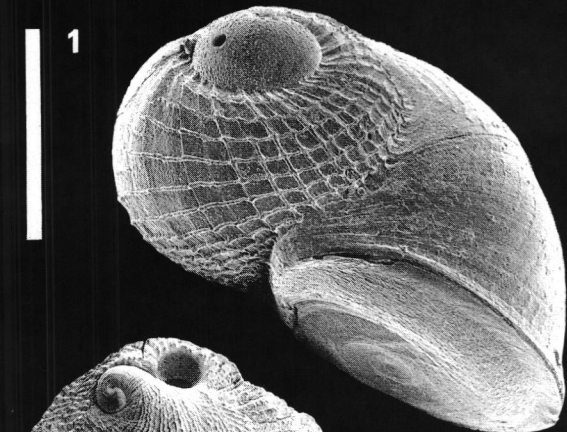


Plate 5

Fig. 1: *Hipponix benthophilus* from the east coast of the USA (Florida). Scale bar = 1 mm.

Fig. 2: same specimen as in fig. 1; magnification of the protoconch. Scale bar = 0.3 mm.

Fig. 3: a species of *Hipponix* from the Pacific (Papua). Scale bar = 1 mm.

Fig. 4: same specimen as in fig. 3; lateral view of the protoconch. Scale bar = 0.3 mm

Fig. 5: same specimen as in figs. 3-4; magnification of embryonic whorl and transition to larval shell revealing the embryonic groove-ridge pattern and remains of a cancellated sculpture on initial larval whorl. Scale bar = 0.1 mm.

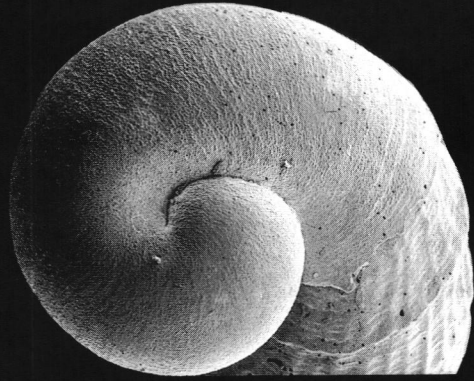
Fig. 6: a species of *Hipponix* from the Red Sea. Scale bar = 1 mm.

Fig. 7: same specimen as in fig. 6; magnification of the protoconch. Scale bar = 0.3 mm.

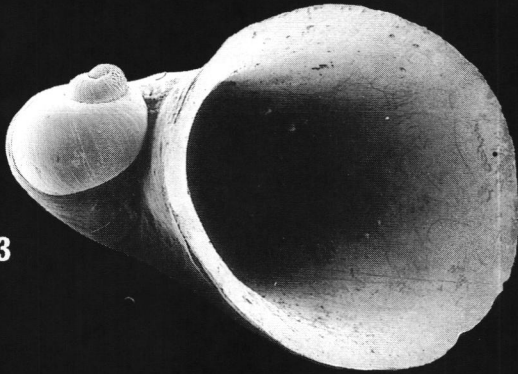
Fig. 8: a species of *Hipponix* from the Pacific (Dampier). Scale bar = 0.5 mm.



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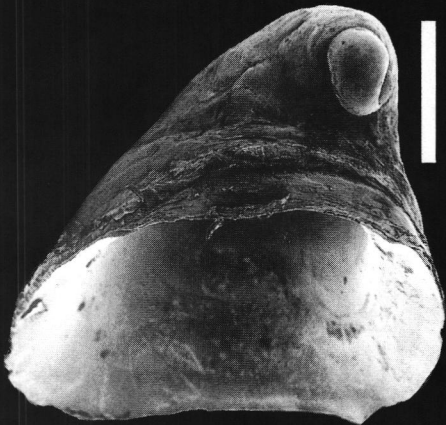
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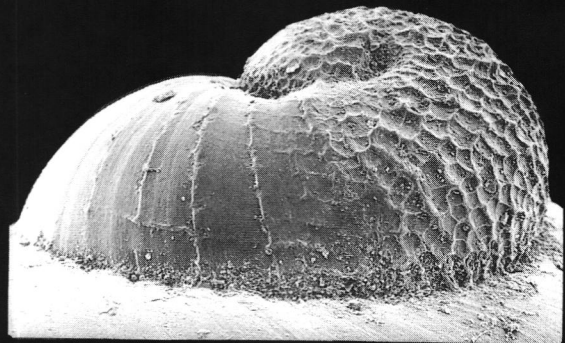
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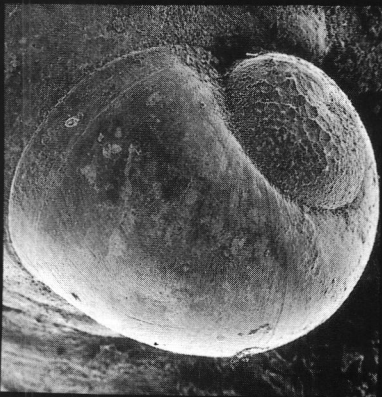
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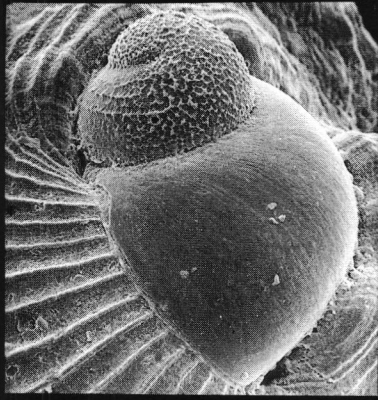


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Plate 6

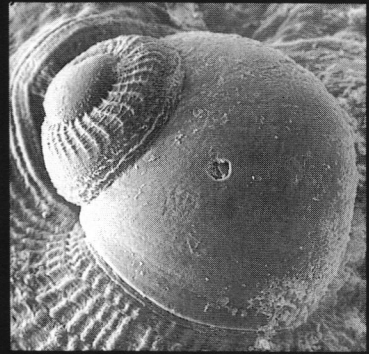
- Fig. 1: lateral view of protoconch of *Cheilea equestris* from the Caribbean (Colombia). Scale bar = 0.3 mm.
- Fig. 2: apical portion of shell of *Cheilea cicatrosa* from the Red Sea. Scale bar = 1 mm.
- Fig. 3: lateral view of protoconch of *Cheilea* sp. from the Red Sea. Scale bar = 0.4 mm.
- Fig. 4: a species of *Cheilea* from the southern Pacific (NSW, Australia) in semi-apertural view. Scale bar = 0.5 mm.
- Fig. 5: same specimen as in fig. 4 in lateral view. Scale bar = 0.5 mm.
- Fig. 6: same specimen as in figs. 4-5; magnification of protoconch. Scale bar = 0.3 mm.
- Fig. 7: cancellated apical whorl of a non-planktotrophic *Cheilea* sp. From the Pacific (Lizard Island). Scale bar = 0.3 mm.
- Fig. 8: juvenile *Calyptraea* sp. From the Lutetian of Southampton (U.K.) in lateral view. Scale bar = 1 mm.
- Fig. 9: same specimen as in fig. 8; magnification of protoconch. Scale bar = 0.5 mm.
- Fig. 10 a larger specimen of same species as in figs. 8-9 in apertural view. Scale bar = 2 mm.



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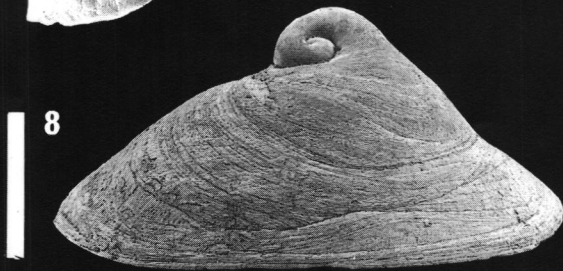
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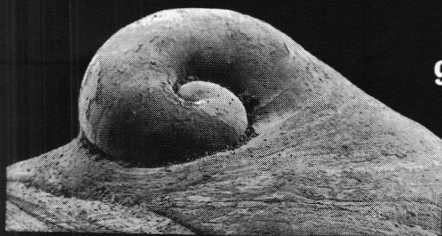
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Plate 7

- Fig. 1: *Calyptraea* sp. From the Lutetian of Southampton (U.K.) showing the transition from juvenile to adult ornamentation. Scale bar = 2 mm.
- Fig. 2: *Calyptraea lybica* from the Upper Cretaceous of Egypt (Western Desert) in apical view. Scale bar = 1 cm.
- Fig. 3: same specimen as in fig. 2 in lateral view. Scale bar = 1 cm.
- Fig. 4: *Calyptraea tenuis* from off Otago (New Zealand). Scale bar = 1 mm.
- Fig. 5: same specimen as in fig. 4; magnification of protoconch. Scale bar = 0.3 mm.
- Fig. 6: early juvenile of *Crepidula glauca* from the Caribbean (Colombia). Scale bar = 0.5 mm.
- Fig. 7: juvenile of *Crepidula plana* from the Caribbean (Colombia). Scale bar = 2 mm.
- Fig. 8: same specimen as in fig. 7; magnification of the protoconch. Scale bar = 1 mm.
- Fig. 9: juvenile *Crucibulum auriculum* from the Caribbean (Colombia). Scale bar = 1 mm.
- Fig. 10: same specimen as in fig. 9; magnification of the protoconch. Scale bar = 0.5 mm.

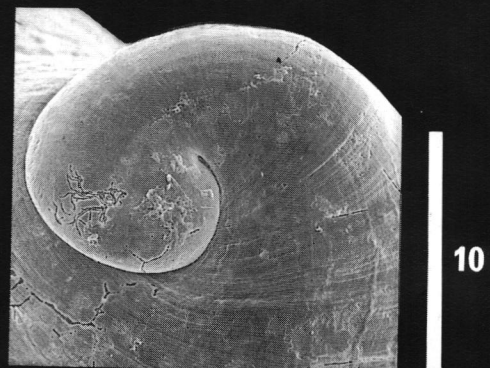
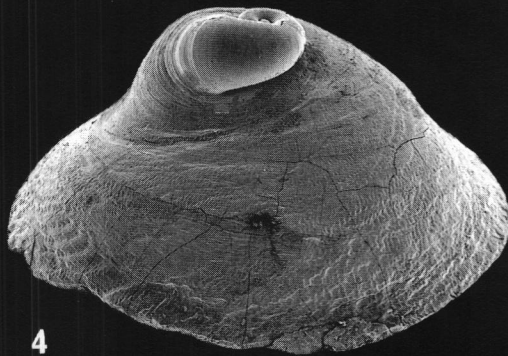
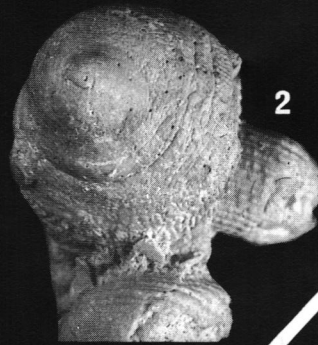
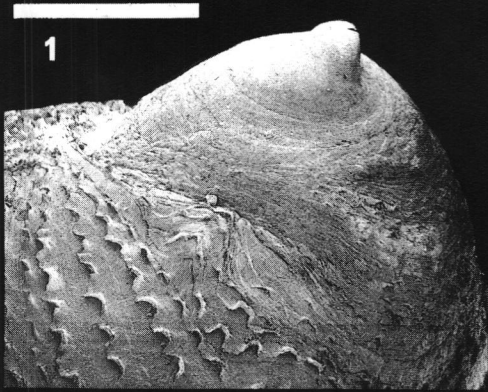
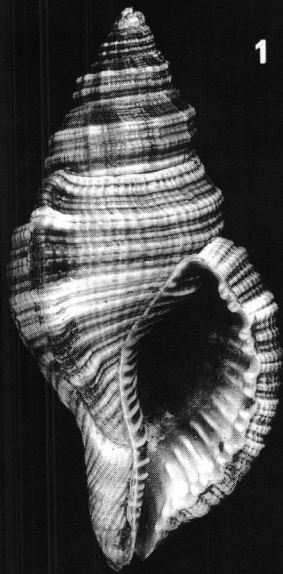
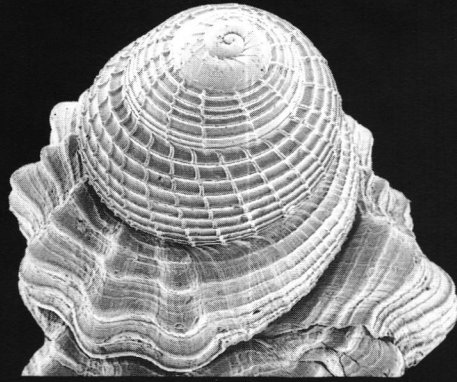


Plate 8

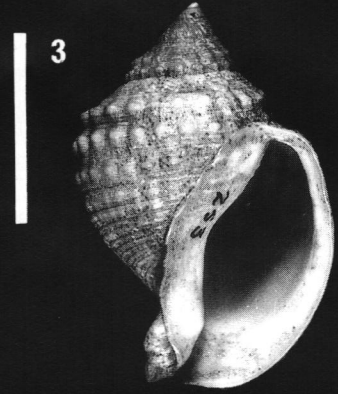
- Fig. 1: *Cymatium pileare* from the Caribbean shows typical conchological characters of the Ranellidae. Scale bar = 2 cm.
- Fig. 2: *Sassia delafossei* (Ranellidae) from the Eocene of the Paris Basin shows coarsely cancellated larval whorls. Scale bar = 1 mm.
- Fig. 3: *Galeodea triganceae* (Cassidae) from New Zealand waters shows a teleoconch which represents a more-or-less basal type within the Cassoidea. Scale bar = 2 cm.
- Fig. 4: apical whorls of *Akibumia orientalis* (Laubierinioidea) from the Pacific, with transition of protoconch to teleoconch. Scale bar = 2 mm.
- Fig. 5: the larval whorls of *Trichotropis* sp. From the southern pacific show a reduced cancellation. Scale bar = 1 mm.
- Fig. 6: the trichotropid *Zelippistes benhami* from the southern pacific with ist teleoconch connects with the limpet-shaped capulidae. Scale bar = 2 mm.
- Fig. 7: same specimen as in fig. 6; enlargement of the protoconch which shows remains of rectangles on the terminal larval whorl. Scale bar = 0.5 mm.
- Fig. 8: apical view of protoconch of *Torellia* sp. From the Weddell Sea (Antarctica) showing faint cancellation on larval whorl. Scalebar = 0.5 mm.
- Fig. 9: larval shell of *Cypraea* sp. From the Red Sea, with characteristic pattern of rectangles on larval whorls and a sinusigera aperture. Scale bar = 1 mm.
- Fig. 10: juvenile *Pedicularia* sp. (Ovulidae) from the southern Pacific, with characteristic pattern of rhombs on larval whorls and a sinusigera aperture. The teleoconch becomes involut. Scale bar = 1 mm.
- Fig. 11: apex of *Marseniopsis* sp. (Lamellariidae) from the Weddell Sea (Antarctica) showing distinct spiral ornamentation. Scale bar = 0.5 mm.
- Fig. 12: the early ontogenetic shell of *Lamellaria* sp. (Japan) shows the characteristic deformation which is correlated to the presence of an echinospira during larval life. Scale bar = 0.5 mm.



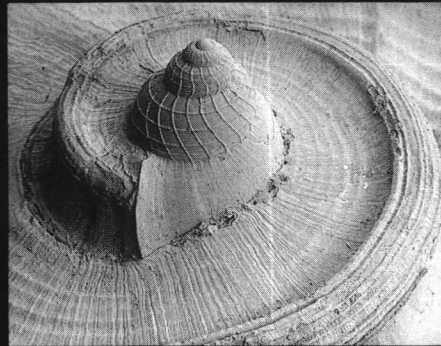
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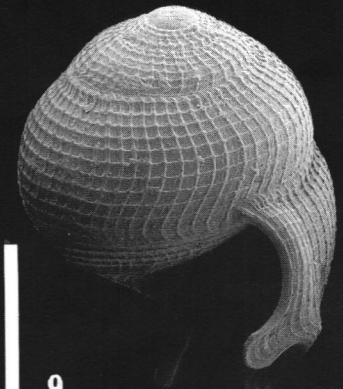
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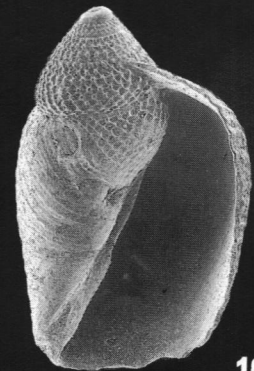
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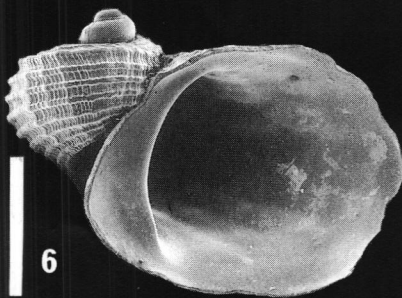
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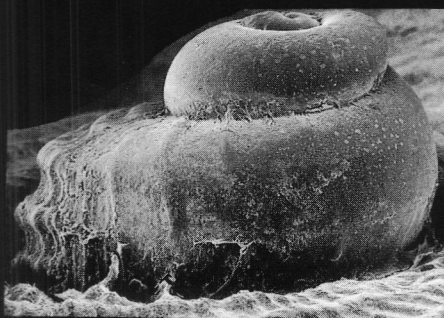
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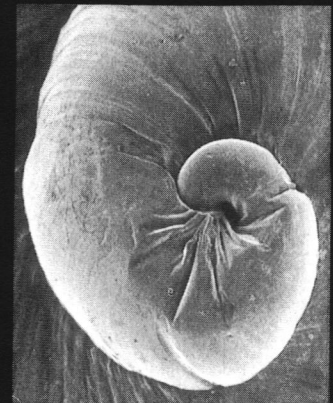
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