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# Phylogeny of the Caecidae (Caenogastropoda)

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With 13 plates, 24 text-figures, and 1 table

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## Abstract

Caecidae have undergone an evolution from normally coiled Caenogastropoda of the rissooidean relation to uncoiled inhabitants of the niches between sediment particles and within algal thickets. The history of the minute (below 5 mm) Caecidae began in the Paleogene of New Zealand with the appearance of a straight uncoiled teleoconch emerging from a caenogastropod with vitrinellid shell characters. Still during the Eocene, development from *Strebloceras* continued into two directions, one leading to *Caecum* with subgenera (Caecinae), and the other to *Parastrophia* and relation (Pedumicrinae). Evolution in the Caecinae resulted in a continuously more planispiral coiling of the protoconch and the repeated shedding of earlier ontogenetic portions of the shell. During the Oligocene more strongly ornamented subgenera developed. Evolution in the Pedumicrinae resulted in the transformation of the adult character of uncoiled shell into the ontogenetic stage of the pelagic larva. Here such a protoconch usually remains attached to the teleoconch. Strongly ornamented Pedumincrinae of the type of *Parastrophia* (*Watsonia*) living in the northern Australian shallow sea have since started to coil the postlarval shell again. Within the genus *Ctiloceras* the protoconch still retains the morphology of that of *Parastrophia,* but in the newly erected genus *Ponderoceras* spiralization has by heterochrony reached the larval shell, but still an umbilical aperture remains. In the species of the Caecinae most larvae developed planispiral shell coiling since adults ceased to construct a trochispiral shell. When the adult shell within the species of *Strebloceras* in the Pedumicrinae began to coil again, the protoconch remained unchanged, reflecting the ancestral condition. However, in one genus, *Ponderoceras* gen. nov., even this feature is neoteneously becoming spiral again.

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## Zusammenfassung

Die Geschichte der kleinwüchsigen Caecidae begann im älteren Eozän Neuseelands. Schon während des mittleren Eozäns hatten sich die zwei vornehmlichen auch heute noch existierenden Gruppierungen der Caecinae und Pedumicrinae herausgebildet. Im frühen Tertiär entrollte sich die Adultschale des möglicherweise den Vitrinelliden verwandten Vorfahren aus dem Verwandtschaftskreis der kleinwüchsigen, marinen, Rissooidea, und es entstand so die Gattung *Strebloceras*. Hieraus entwickelten sich dann zum einen wenig skulptierte Arten der Gattung *Caecum* (Caecinae) und zum anderen die Verwandten von *Parastrophia* (Pedumicrinae). In der Phylogenese der Caecinae wurde der Protoconch flacher, die juvenile Schale wurde abgeworfen, und es entstanden allmählich auch Untergattungen mit kräftigerer Skulptur. Bei den Pedumicrinae verlagerte sich das adulte Merkmal der Schalenentrollung auf den larvalen Abschnitt der Ontogenese, und das frühontogenetische Gehäuse blieb zumeist mit dem Teleoconch verbunden. Von kräftig skulptierten Pedumicrinae des Types *Parastrophia* (*Watsonia*) entwickelten sich seither im nordaustralischen Raum die Gattung *Ctiloceras*, die durch einen sekundär eingerollten Teleoconch charakterisiert ist. Der Protoconch von *Ctiloceras* gleicht dabei noch weitgehend dem von *Parastrophia*. Die hier neu beschriebene Gattung *Ponderoceras* zeigt eine erneute Einkrümmung der Larvalschale.

Die Caecidae durchliefen eine Evolution zu schlanken gestreckten Sandlücken- und Algenfilzbewohnern. Dadurch konnte sich auch die Larvalschale in ihrer Gestalt verändern, indem sie teils abflachte, teils sich die Streckung des Teleoconches möglicherweise durch Neotenie auf die Larvalschale ontogenetisch vorverlagerte. Als die Streckung des Teleoconches durch sekundäre Einrollung wieder rückgängig gemacht wurde, blieb der Protoconch weitgehend unbeeinflußt, mit Ausnahme von *Ponderoceras* gen. nov. wo das Larvalgehäuse zur Spirale zurückkehrt.

# 1. Introduction

The Caecidae are Caenogastropoda that can be traced to the base of the Tertiary with the oldest representative known from the Early Eocene of New Zealand (Beu & Maxwell 1990). Thirteen species are known from the Middle and Late Eocene of the Paris Basin (Gougerot & Le Renard 1981). The uncoiling of the shell within the individual ontogeny distinguishes the Caecidae and differs from most other Caenogastropoda. The embryonic part of the protoconch is always dextrally coiled. The teleoconch, in contrast, has become almost straight. In one subunit this tendency of uncoiled shell has secondarily been reversed, and individuals return to the spiral coil after metamorphosis from larval life (Iredale & Laseron 1957). According to Thiele (1931) and Wenz (1938) Caecidae are related to the Cerithioidea. However, the shape of the radula and anatomy suggest that some Rissooidea, probably the Vitrinellidae, may be the sister group of the Caecidae (Moore 1962). Cerithioidea and Risooidea are representatives of the Palaeo-Caenogastropoda (Bandel 1993) and encompass several subunits of still extant snails of which little is actually known (Ponder 1988, 1994, Houbrick 1988). The connection of the Caecidae with the Vitrinellidae representing a family of the Rissooidea still appears to be the most likely one (Moore 1962).

In the diagnosis of the Caecidae two characters of the shell are of importance. Firstly the early shell part is often discarded during later life and secondly the teleoconch is uncoiled and forms a weakly curving tube with slow increase in whorl diameter. These two characters are found within the Caecinae and describe the genus *Caecum* rather well. Here the coiled protoconch is succeeded by an uncoiled tube-like shell with little increase in shell diameter. As soon as the shell has increased in length so much that the soft body of the animal can be withdrawn from the early ontogenetic shell, the apical portion is closed off by a septum and discarded. The resulting elephant tusk-like shell is characteristic for the group, but fills only one of the types of morphologies realized by the members of the Caecidae. Within the Pedumicrinae the shell begins uncoiling from the spiral earlier in ontogeny than is the case in Caecinae. Around the genus *Ctiloceras* the shell coils again at a later stage of ontogeny after it had uncoiled (IREDALE & LASERON 1957).

## 2. Habitat and mode of life

The tiny tusk-shaped Caecinae are abundant in shallow-water grass beds or around coral reefs. Some live on the open sand bottom of the shallow continental shelf. Here they move through the uppermost layers of soft marine sediment or crawl about among algal thickets feeding on detritus and minute algae and other organisms. About 10 species live in the Caribbean Sea (ABBOTT 1974), usually in all littoral zones below the tidal regime (BANDEL & WEDLER 1987). Eight species of *Caecum* were discovered in St. Croix in the Virgin Islands by MOORE (1972). There are two perhaps three species in the Canal and North Sea, *Caecum glabrum* (MONTAGU, 1803), *C. amoricum* FOLIN, 1869 and *C. imperforatum* (KANMACHER, 1798). They are rarely dredged from sandy bottoms (GÖTZE 1938, FRETTER & GRAHAM 1962). In the Mediterranean Sea *Caecum glabrum* and relation prefer the areas covered with sea grass, and *C. imperforatum* (= *trachea*) lives within soft sediment, preferably sand in the deeper littoral zone and the shallow sea (ARNAUD & POIZAT 1979, 1981, PANETTA 1980). Like their Atlantic relation they mainly feed on diatoms. In the tropical Indo-Pacific with the Red Sea, Cebu in the Philippines, as well as in the Great Barrier reef of Australia *Caecum* is found in the lagoons and near reefs within shallow water environments. It occurs less commonly than in the Caribbean Sea. At Lizard Island the smooth *Caecum* (*Fartulum*) *glabellum* lives on algal thickets in shallow water, another resembling *Caecum* (*Caecum*) *vertebrale* is more rarely found in the same type of environment on reef rubble. From the littoral waters of Hong Kong HUGHES (1983a,b) described seven species, and here they seem to be as common as in the Caribbean Sea near Santa Marta. *Caecum digitulum* of the shore of New Zealand lives within the tidal zone on pebbles (MORTON 1976). Individuals here utilize the film of water that remains between rocks and algal covers to remain active even at low tide grazing diatoms. In the Bermuda area *Caecum* (*Elephantulum*) cf. *troglodyta* is common among mangrove roots in a lake near Ferry Point that is connected to the sea by caves. Here it lives among filamentous algae. *Parastrophia* lives in muddy and protected coastal bays like that of Hodeida in the Red Sea of Jemen, or the Limpski Fjord at Istria in the Adriatic Sea.

The small shell of the Caecidae is often washed from the shore and from the shallow water environments, and it may be deposited in much deeper environments which are not the actual living place of the animals. Such transport is a general feature found among small gastropod shells (BANDEL 1991) and should be taken into consideration when literature data indicate deep water living localities. Such reports should be evaluated critically.

## 3. Features of the radula

The radula has a quite independent character, and is adapted to the mode of life as collector of minute particles. The median tooth and usually also lateral tooth are reduced in size and may even have lost their functionality altogether. Bandel (1984) described the radulae of *Caecum (Elephantulum) imbricatum* (*C.* cf. *floridanum*), *Caecum* (*Fartulum*) *antillarum* and *Caecum* (*Meioceras*) *cornucopiae* (*C.* cf. *nebulosum*). The central tooth of *C.* (*M.*) *cornucopiae* is angular and has a prominent central cusp on its cutting edge. The central tooth of *C.*(*F.*) *antillarum* is more slender than that of *C.* (*C.*) *imbricatum* and is higher than wide. Both have minute cusps on their cutting edge and are so small that they are of little use during radula function. *Caecum* (*Brochina*) *glabrum* from the Mediterranean Sea at Banyuls-Sur-Mer has a similar central tooth (Pl.1, Fig.1) to that of *C.*(*F.*) *antillarum* with even basal platform and rounded cutting edge with median cusps only slightly larger than the 5-6 continuously smaller flanking cusps. Hughes (1983b) described the teeth of *C.* (*C.*) *vertebrale* and *C.* (*F.*) *glabellum* from Hong Kong which also have similar central teeth.

The lateral tooth of *C.* (*B.*) *glabrum* is about as high as wide (Pl.1, Fig.2) and like that of the Caribbean *C.*(*F.*) *antillarum* has a long lateral flexible extension that is attached to the basal membrane. In all the radulae that were studied from the Caribbean Sea and the Mediterranean Sea as well as those studied by Hughes (1983b) from Hong Kong, both marginal teeth have changed into rakes combing in particles. The inner of these marginal teeth is prominent and has many comb-like cusps. It is the main scythe shaped tool for raking in food particles like diatoms. The outer marginal tooth is as high as the inner one, but much more slender with a dented spoon-like end. Lateral teeth may or may not be still active in food gathering, but those of *Caecum* (*Brochina*) *digitulum* from New Zealand are still quite large (Morton 1976). The pair of inner marginal teeth in all caecid radulae are the most active during the feeding process and sweep in food particles when the radula is pulled over the odontophore. The outer marginal teeth prevent sideways loss of collected particles (Pl.1, Figs.3,4).

The radula of the caecids does not closely resemble that of the Rissoidae or the Hydrobiidae (see Bandel 1984) especially regarding the shape of the central teeth. However, this should be the case if a closer relation exists as was assumed by Marcus & Marcus (1963). Götze (1938) who studied C. (*B.*) *glabrum* indicated a relation of the Caecidae to *Hipponix* and species of *Cerithium*. This view can not be supported. On the other hand Moore's (1966) assumption that Vitrinellidae like *Cyclostremiscus* may represent the next relatives of the Caecidae was not supported by Bieler & Mikkelsen (1988). Thus, the caecid radula produces evidence for an independent evolution of this group that has started about 50 Million years ago. In general appearance the radula resembles those of quite a number of species of the Littorinimorpha and Cerithiimorpha, but not with any specific group among these.

The radula of the vitrinellid species *Cyclostremiscus beaui* (Fischer, 1857) and *Circulus texanus* (Moore, 1965) described by Bieler & Mikkelsen (1988) has central and lateral teeth bearing resemblance with such found among the rissoine genera *Zebina* H. & A. Adams, 1854 and *Rissoa* Freminville, 1814 (Bandel 1984). These teeth are much larger in relation to those found in *Caecum*. While the lateral teeth are of similar shape, the central tooth of *Caecum* is much reduced in size, and there are neither cusps on the basal membrane nor are there extended posterior corners as among the Rissoidae and the Vitrinellidae. In regard to the marginal teeth similarities are present between Caecidae on one side and Vitrinellidae on the other. Similar features are also found in the Tornidae Sacco, 1896 (Ponder 1994), Vanikoroidae Gray, 1845 (Waren & Bouchet 1988) and other groups of the Rissooidea (Draper 1978).

## 4. Morphology of the soft body

When moving over or through sediment the small gastropods pull the straight shell continuously or in jerks. The retractor muscle is attached to the shell at the ventral and concave side of the shell in a position just before the begin of the visceral mass, so that pulling itself into the shell will leave the visceral mass uncompressed. The concave side lies on the lower surface in the active animal itself (Text-figs.1, 2). The foot is quite small and carries the relatively large operculum that seals the round aperture perfectly right at the margin of the shell. It closely resembles the operculum of the vitrinellids with its concentric and multispiral construction. The ciliated tentacles of the head resemble those found in the Vitrinellidae like *Parviturboides* (see Moore 1962), *Cyclostremiscus* and *Circulus* (see Bieler & Mikkelsen 1988). Like the Vitrinellidae and most other Rissooidea the Caecidae have a penis (in contrast to most Cerithioidea). Moore (1962) indicated a relation between Caecidae and Vitrinellidae based on similarities of the general appearance of the soft parts. Bieler & Mikkelsen (1988) studied the vitrinellids *Cyclstremiscus* and *Circulus* anatomically and found pallial tentacles that differ from the metapodial tentacles of the Tornidae and Vanikoroidae (see also Ponder 1994). The Caecidae have no pallial tentacles. Bieler & Mikkelsen (1988) noted no closer relation between Vitrinellidae and Caecidae except in the sense that both represent groups that belong to the superfamily Rissooidea. Marcus & Marcus (1963) have also placed the Caecidae in the Rissooidea and suggested a closer affinity to the Hydrobiidae.

The digestive system of *Caecum digitulum* has been studied by Morton (1976). He found the esophagus to be a simple tube and the stomach to be eqipped with the large gelatinous mass of the crystalline style, which is characteristic to many herbivorous gastropods.

## 5. Systematic descriptions

### Family Caecidae Gray, 1850

Description: Group of marine lower Caenogastropoda with small species that have a coiled embryonic shell and in the following shell - either larval or begin of teleoconch - uncoils with the the option of spiral coiling again at later stages .

### Subfamily Streblocerinae nov.

Diagnosis: The protoconch is trochispirally coiled and remains connected to the uncoiled teleoconch.

### Genus *Strebloceras* Carpenter, 1858

Type-species: According to Cossmann (1896) *Caecum edwardsi* Deshayes, 1864 from the Oligocene of France, and according to Gougerot & Le Renard (1981) *Strebloceras lituus* Deshayes, 1861 from the Eocene of the Paris Basin.

Description: The protoconch is trochospirally coiled, and the teleoconch is uncoiled forming a slightly curving tube with slowly increasing diameter. Protoconch and teleoconch remain together during the whole life-time.

Remarks: The oldest known caecid is from the early Eocene of New Zealand (Beu & Maxwell1991, Pl.55, Figs.h,j) (Text-fig.3). The protoconch consists of about two whorls, and the teleoconch curves gently being almost straight and forming a slowly expanding tube of circular cross section that lacks sculpture aside from growth lines. Cossmann (1888) mentioned several species of *Strebloceras* from the Eocene of the Paris Basin and the Oligocene of France. *Strebloceras lituus* Deshayes, 1861 occurs in the Eocene of the Paris Basin (Deshayes 1866, Pl.26, Fig.5). In the figured specimen the protoconch is well visible and resembles that illustrated here (Pl.1, Figs.6, 7). Morellet & Morellet (1943) and Gougerot & Le Renard (1981) suggested that *Strebloceras lituus* represents the same species as *S. edwardsii*, so that this species occurred from the Eocene to the Oligocene in the warm shallow Euopean sea.

*Strebloceras* differs from other Caecidae by retaining the protoconch instead of shedding it during development of the teleoconch (Pl.1, Figs.5,6,7). *Strebloceras edwardsii* from the Aquitaine (RGM 228,494, Leiden) resembles the older *Strebloceras* n. sp. from New Zealand (Beu & Maxwell 1991), but is more slender. The embryonic shell consists of somewhat less than one whorl, measures only about 0,08 mm across and it is succeeded by one and a half larval whorls, all of which are smooth (Pl.1, Fig.5). The onset of fine growth increments marks the time of hatching from the egg capsule. The larval shell measures about 0,3 mm across and is coiled to a dextral trochospiral.

According to (Thiele 1931) the protoconch of a modern species of *Strebloceras* from Hawaii remains in contact with the teleoconch, and according to Wenz (1939, Figs.1950,1952) it consists of three whorls. The latter author described *Strebloceras* to have bilateral symmetrical shape, which, however, is not correct. Iredale & Laseron (1957) considered *Strebloceras* to belong to the same subfamily as *Parastrophia*, the Pedumicrinae Iredale & Laseron, 1957 (= Parastrophiinae Hinoide & Habe, 1978). However, this placement makes little sense as is discussed later. *Strebloceras subannulatum* Folin, 1879 from Hawaii in the holotype collection of the British Museum of Natural History in London is very similar to the specimens from the Eocene and Oligocene of Europe (own observ.).

### Subfamily Caecinae Gray, 1850

Description: This subfamily consists of *Caecum* and subgenera. During ontogeny the shell uncoils, and early shell portions are dropped off.

### Genus *Caecum* Fleming, 1817

Type-species: *Dentalium imperforatum* Kanmacher, 1798 (= *trachea* Montagu, 1803) from Europe, Mediterranean Sea and Atlantic to southern England (Pl.2, Fig.3).

Description: The shell of the teleoconch is a small, slightly curved tube ornamented only with growth lines, numerous ring-like collabral lirae and/or axial ribs. The posterior end of the tube is closed by a conical septum. The protoconch is trochospirally or planispirally coiled. Uncoiling of the shell begins after metamorphosis.

*Caecum* begins postembryonic life as free swimming veliger bearing a spiral shell of more than one whorl, or it hatches from the egg as crawling young with a spiral shell of about one whorl. When *Caecum* begins its benthic existence the teleoconch grows in form of a simple slightly curved tube. As the animal grows, it forms an internal septum, and the spiral apex (protoconch) along with the earliest portion of the teleoconch is dropped off. The shell is dissolved to form a ring-like furrow just apical of the position of the septum, so that its apical portion usually falls off soon after the septum has been secreted. As growth continues another septum is formed at the rear of the snail, and another posterior shell portion is dropped off. Several (up to 6) of such stages are present, and their number is specific to the species. The septum is usually armed with a spike or a mucro.

### Subgenus *Brochina* GRAY, 1837

Type-species: *Dentalium glabrum* MONTAGU, 1803 from the European Atlantic.

Description: The teleoconch is slender, smooth, marked only by inconspicuous growth rings and sometimes by very delicate longitudinal striae. It forms a slightly curving cylindical tube with slow increase in width and simple circular aperture.

Remarks: *Caecum (Brochina) erroneum* L. & J. MORELLET, 1943 from the Lutetian (Mid-Eocene) of the Paris Basin is characterized by having an apertural collar in all the different growth sections formed during the ontogeny of one individual (Pl.2, Fig.2, text-fig.11). GOUGEROT & LE RENARD (1981) described several of these ontogenetic stages, but as separate and distinct species. The protoconch of *C. erroneum* consists of 1.7 whorls, and is planispirally coiled. There was a planktotrophic larval phase of similar duration as is found in the modern *C. (Brochina) glabrum* or *C. (Fartulum) glabellum* (Pl.2, Figs.1,3). A short portion of the teleoconch remains attached to the protoconch when the first part is discarded. The second portion is about 1.5 mm long with rim-like varix at the apertural end. The third section measures about 1.8 to 2 mm in length and has the same curvature and similar slow increase in shell diameter. Then the next septum forms just in front of its apertural rim, and the following section is about 2 mm long. The next stage measures about 3-5 mm in length (Pl.2, Fig.2), and may represent the last one. The whole shell therefore consists of an about 9 to 10 mm long tube with 5 pieces forming three quarters of a complete whorl that has planispiral orientation and very slow increase in shell width (Text-fig.11). The shape of the septum is similar at all stages. It usually carries a tubercle on the convex side that appears to be a little more pointed in the younger stages than in the later ones.

*Caecum (Brochina) schulzei* GOERGES, 1952 from the Late Oligocene (Chattian) of Kassel in central Germany has an almost planispiral protoconch with 1.7 whorls and a diameter of 0.38 mm (Pl.5, Fig.7). A short piece of the teleoconch remains attached to it while it is breaking off (Pl.3, Fig.7). Here a thickened rim is found only in the last of the four parts that form the whole planispirally coiled shell. The second portion of the evenly curving tube is about 1.2 mm long, the third almost 2 mm long and the fourth measures about 2.2 mm in length. The apex is closed with a convexly rounded septum. The Oligocene species closely resembles *Caecum (Brochina) digitulum* HEDLEY, 1904 from New Zealand which has a slightly trochospirally coiled protoconch of 2.3 whorls measuring 0.42 mm in diameter (Pl.2, Fig.7). In ths species 3 to 5 stages of growth occur with the last measuring about 3 mm in length and about 0.5 mm in width. The septum in the second portion is angular with highest point near the convex shell side (Text-fig.7).

*C.* (*B.*) *glabrum* (MONTAGU, 1803) from the North Sea, the Mediterranean Sea (Pl.2, Fig.3), and the Canary Islands (Lanzarote) has a pointed mucro on its septum in the second and third growth stage, while the last one closely resembles that of *C.* (*B.*) *schultzei* from the Oligocene and *C.* (*B.*) *digitulum* from the other side of the world. Since the septum morphology shows some variability the similarities are even greater. In European waters *C.* (*B.*) *glabrum* has a smooth shell and a bulging operculum and grows to about 2 mm length. Such shells have been called *Caecum subannulatum* FOLIN, 1869 and *C. auriculatum* FOLIN, 1867 by PORTA et al. (1993, Pl.3, Figs.1-9). The protoconch of *C.* (*B.*) *glabrum* from the Golf of Lion near Banyul-Sur-Mer very closely resembles that of the Oligocene species in having one and three quarters of whorls which are smooth, slightly trochospirally coiled with a diameter of about 0.35 mm (Pl.2, Fig.3). *Caecum vitreum* CARPENTER, 1858 from Teneriffa may represent the same species as *C.* (*B.*) *glabrum* according to what can be seen in the type collection at the British Museum of Natural History in London.

*Caecum* (*Brochina*) *vestitum* FOLIN, 1870 from the Caribbean Sea near Santa Marta and the subfossil reef sediments near Cartagena (Galerazamba) is also quite similar to the three species from Europe, New Zealand and the Oligocene, all showing very slow increase in shell width. Some individuals have a very fine pattern of longitudinal lirae (Pl.3, Fig.5). Most of the slender and cylindrical shells are smooth, and the last fully grown stage has some incised collabral furrows near its anterior end forming a slight varix. There are at least four stages in the ontogeny of this species and the last one is 2 to 2.5 mm long.

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Fig.1: *Caecum troglodyta* from Bermuda carries the shell stretched right behind its foot.

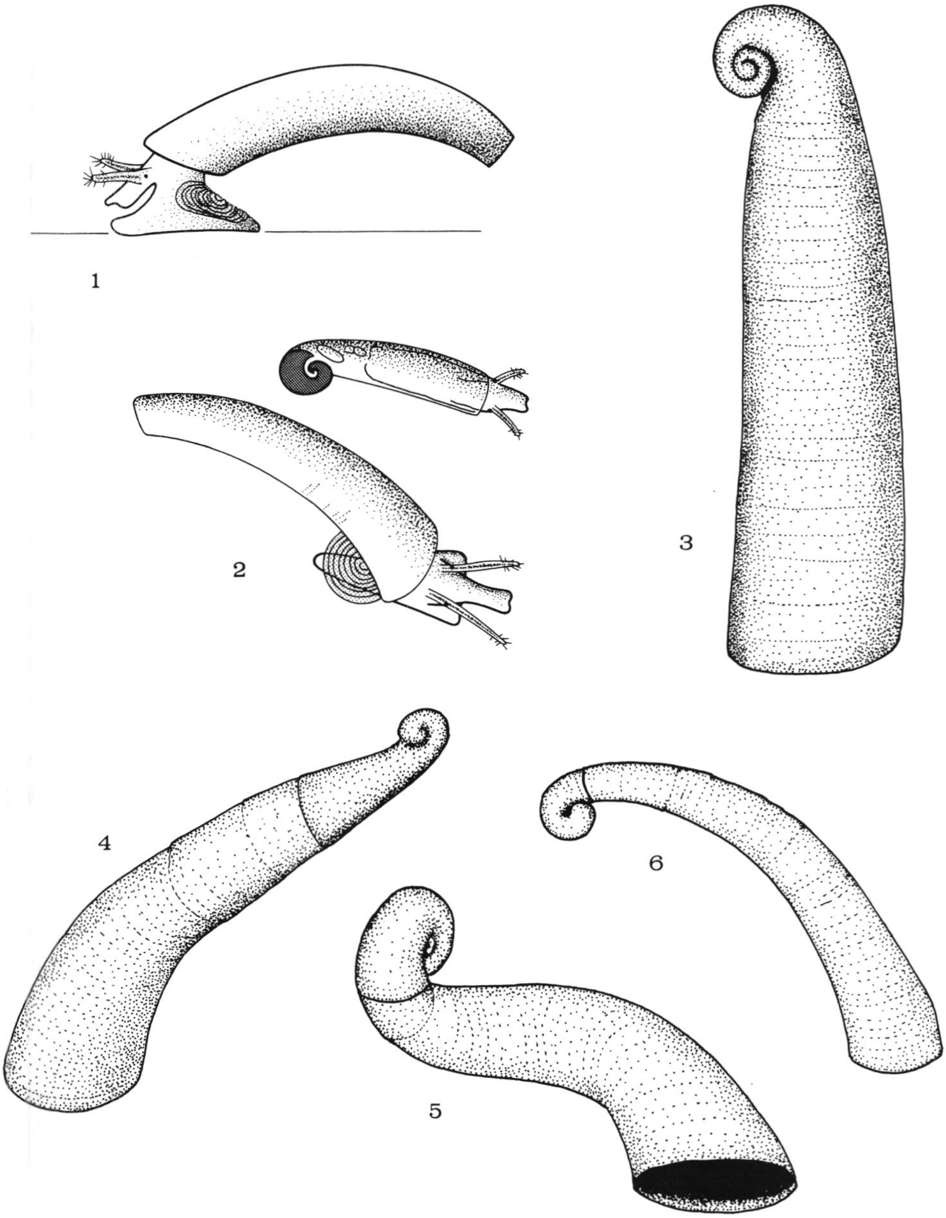
Fig.2: *Caecum gracile* from Lizard Island in the Barrier Reef pulls the shell that is usually fallen to one side when adult and carried it above the foot holding it up when young.

Fig.3: The shell of *Strebloceras* sp. from the early Eocene of New Zealand ( redrawn from BEU & MAXWELL 1991) has a coiled protoconch that remains connected to the uncoiled teleoconch.

Fig. 4: Sketch of *Parastrophia* from the Oligocene of Kassel, with 0.9 mm long protoconch.

Fig.5: The first portion of the teleoconch of *Caecum* (*Meioceras*) *nitidum* from the Caribbean Sea has an almost planispirally coiled protoconch of 0.3 mm width and helically twisted juvenile teleoconch.

Fig.6: The first shell portion of *Caecum* (*Elephantulum*) *troglodyta* from Bermuda is ornamented only by growth lines and may remain intact for great length (here 3 mm). Embrionic shell is here succeeded by teloconch directly.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### Subgenus *Fartulum* CARPENTER, 1857

Type-species: *Caecum laeve* C.D. ADAMS, 1852 from the Pacific Panama (Fig.1962 in WENZ 1938).

Description: The teleoconch is slender, smooth, marked only by inconspicuous growth rings and forms a slightly curving cylindrical tube with oblique round aperture facing to one side. In one of the growth stages there is a more rapid increase in shell width as usual.

Remarks: From the Caribbean Sea *Caecum (Fartulum) antillarum* CARPENTER, 1858, which may be identical with *C. (F.) ryssoticum* FOLIN, 1867 (ABBOTT 1974) has a low trochospiral protoconch that consists of two whorls and measures about 0.35 mm across (Pl.2, Fig.6). The juvenile teleoconch attached to it forms an evenly and weakly curving tube of almost 2 mm length which fractures at least once to discard the protoconch along with a more or less extended portion of the early teleoconch. The septum consists of an inclined plug with angular mucro on the convex side. The increase in shell width was also noted on the specimens of the type material of *Meioceras cornucopiae* CARPENTER, 1859 preserved in the type collection of the British Museum of Natural History in London.

In the next shell section there is a rapid increase in shell width (Pl.3, Fig.4). Here the shell usually breaks off and the final and adult shell is closed by an evenly convex plug with low triangular outline and flattened mucro. The third and last shell portion is glassy white, cylindrical with tapering section in the posterior end and a thickening around the aperture that twists to a very oblique position (Pl.3, Fig.6). This last shell twist is characteristic to the final portion of the total shell which, with all three or four sections connected, consists of about two thirds of a planispiral coil (Text-fig.8). The intermediate and second stage resembles a shell described under the name *Caecum subvolutum* FOLIN by MOORE (1972, Fig.4) from St Croix, US Virgin Islands. From the type collection at the British Museum of Natural History in London *Meioceras cornubaris* CARPENTER, 1858 from the Antilles and *Meioceras bitumidum* FOLIN, 1869 from the West Indies closely resemble the last stage.

As in *C.(Caecum) pulchellum*, (see above) different growth stages show differences which might be mistaken to characterize different species. The last stage of *C. (F.) antillarum* is similar to more slender forms of *C. (Meioceras) nitidum*, but differ because there is no pattern of coloration that consists of white zigzag marks, and in earlier portions there is no trochospiral twist.

A *Caecum (Fartulum)* species from Lizard Island in the Australian Barrier Reef (Pl.3, Fig.1) and Port Sudan in the Red Sea (Pl.3, Fig.3) resembles *C. (F.) glabellum* (CARPENTER, 1868) when fully grown and *C. (F.) variegatum* FOLIN, 1869 from Hong Kong when juvenile, as described by HUGHES (1983a Fig.1A,C) (Pl.2, Figs.1,4). The Australian individuals were observed while living. The animals crawl through algal thickets on a short very mobile and ciliated foot (Text-fig.2). While juvenile animals hold their shell up when crawling, the adults pull the shell in short jerks behind. The tentacles of the head have several short rigid sensory cilia and the snout is broad with the teeth of the relatively large radula exposed now and then to pick up food particles. The shell is dissolved right behind the position in which a new septum is formed. The apical portion of the shell is thus attached only by the thin periostracal cover, and it soon falls off. The almost planispiral protoconch of 0.3 mm in diameter and 1.5 whorls, continues in a weakly curving, about 1 mm long tube with slight increase in shell diameter (Pl.2, Fig.1). The larval shell is ornamented by fine somewhat irregularly arranged spiral lirae (Pl.2, Fig.5). The protoconch forms a right angle with the coiling plane of the teleoconch. With formation of the first evenly convex septum an up to 2 mm long tube of similar shape as the first teleoconch forms. It is ornamented by annular growth increments and some weak longitudinal lirae. In the next shell section of up to 2 mm length there is a rapid increase in shell width (Pl.2, Fig.4). It breaks off from the second portion when the last, fourth part of the shell is formed. Here the septum is convex, but a little higher at the convex side of the shell tube. At the aperture the up to 2.8 mm long last gently curved shell portion decreases in width and is slightly twisted inwards (Pl.3, Fig.1). The shell is smooth with very faint longitudinal striae and shows a coloration pattern of zigzag marks of gray on white background. If all four parts were attached to each other, the tube of the shell would have a length of 8 mm and would form three fourth of a planispiral coil, with the protoconch deviating from it by 90° (Tex-fig.9). A larger last stage (4 mm long) could belong to *C. (F.) glabellum* and was collected among rocks covered by algae in the reef lagoon of Port Sudan, Red Sea (Pl.3, Fig.3).

*C. (F.) glabellum* resembles *C. (F.) antillarum* in general shape and *C. (F.) cornucopiae* probably is the same species as the later.

### Subgenus *Meioceras* CARPENTER, 1858

Type-species: *Caecum nitidum* CARPENTER, 1858 from the Caribbean Sea.

Description: The shell is narrow at the posterior end, wider in the middle, and contracts near the aperture. The stage of growth succeeding the protoconch occurs in a widely open spiral.

Remarks: *Caecum (Meioceras) nitidum* is rather common in the shallow sea near Santa Marta (Colombia) and especially among brown algae attached to the rocky shore. The juvenile shell retains a vestige of the ancient spiral coiling of the ancestors (Pl.5, Figs.3,4,5) (Text-fig.5). The stage after this twisted portion curves weakly in one plane. The protoconch consists of one and three-quarter whorls in planispiral coiling and measures 0.3 mm in maximum diameter (Pl.5, Figs.5,6). The initial one mm of the teleoconch forms a loosely coiled trochospiral. The first discarded apical shell consists of the protoconch and a piece of the teleoconch attached to it (Pl.5, Fig.5). The second portion is two to three mm long and partly twisted to a spiral (Pl.5, Figs.3,4). The third and last stage of growth reaches a maximum length of 2.8 mm (Pl.5, Fig.2; Text-fig.10). Its coloration consists of mottlings of chalky white on glassy translucent background, which in some individuals may also be light brown. On the other hand, there are many individuals of this species with smaller shells, some even less than 2 mm long.

Similar smaller and larger final stages were attributed by MOORE (1972, Figs 10,11) to *Caecum (F.) cornucopiae* and *C. (M.) nitidum* from St- Croix, US Virgin Islands. A 2.1 mm long specimen shows a strong growth recession (Pl.5, Fig.1), which indicates that even individuals with adult morphology may still continue to grow and discard the vacated shell as soon as a new septum has been formed. Segments formed during this process are not uncommon in the sand drift. The juvenile second stage has a plane septum with a pointed small tubercle near the convex shell side, while the adult third stage has a septum with a rounded inclined plug connected to a solid tubercle. All three pieces of the shell fitted together form an about a 5-6 mm long tube (Text-fig.10).

Moore (1975) stated that four species of *Caecum* (*Meioceras*) are found in the Western Atlantic of which only *Caecum* (*Meioceras*) *nitidum* Stimpson, 1851 has the second stage shaped like a cow´s horn. The type material of this species at the Britisch Museum of Natural Histoy in London has only fully grown last stages, which agree with *C.* (*M.*) *nitidum* as found in Santa Marta. A very similar, if not identical species from the „Antilles" called *Meioceras deshayesii* Folin, 1869 has among the type material a young stage with a trochospiral twist. According to Abbott (1974) there are numerous species names available for similar *C.* (*Meioceras*) varieties or species from the Caribbean Sea and the Western Atlantic. It is unknown which of these represent independent species, or if they are variations of one or a few species. The stages of *C.* (*M.*) *nitidum* from Santa

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Fig.7: *Caecum* (*Brochina*) *digitulum* from New Zealand forms four stages of growth which reassembled form a planispirally openly coiled shell with very regular slow increase in whorl diameter and with the last formed apertural rim thickened.The shell tube is about 9 mm long.

Fig. 8: The total shell of *Caecum* (*Fartulum*) *antillarum* from the Caribbean Sea consists of four stages of growth and forms an open planispiral coil with a rapid width increase in the third stage and a slight inward twist at the end of the fourth and last stage.The whole shell tube is about 9 mm long.

Fig.9: The total shell of *Caecum* (*Fartulum*) *glabellum* from the Barrier Reef lagoon is about 8 mm long and has the protoconch forming a right angle with the open spiral of the teleoconch. The later form less than one whorl with a rapid increase in width just before that last part and a decrease in width near the adult aperture.

Fig.10: *Caecum* (*Meioceras*) *nitidum* from the Caribbean Sea consists of three growth stages with total length of 5-6 mm, of which the first shows an open spiral twist and the third a decreased apertural width.

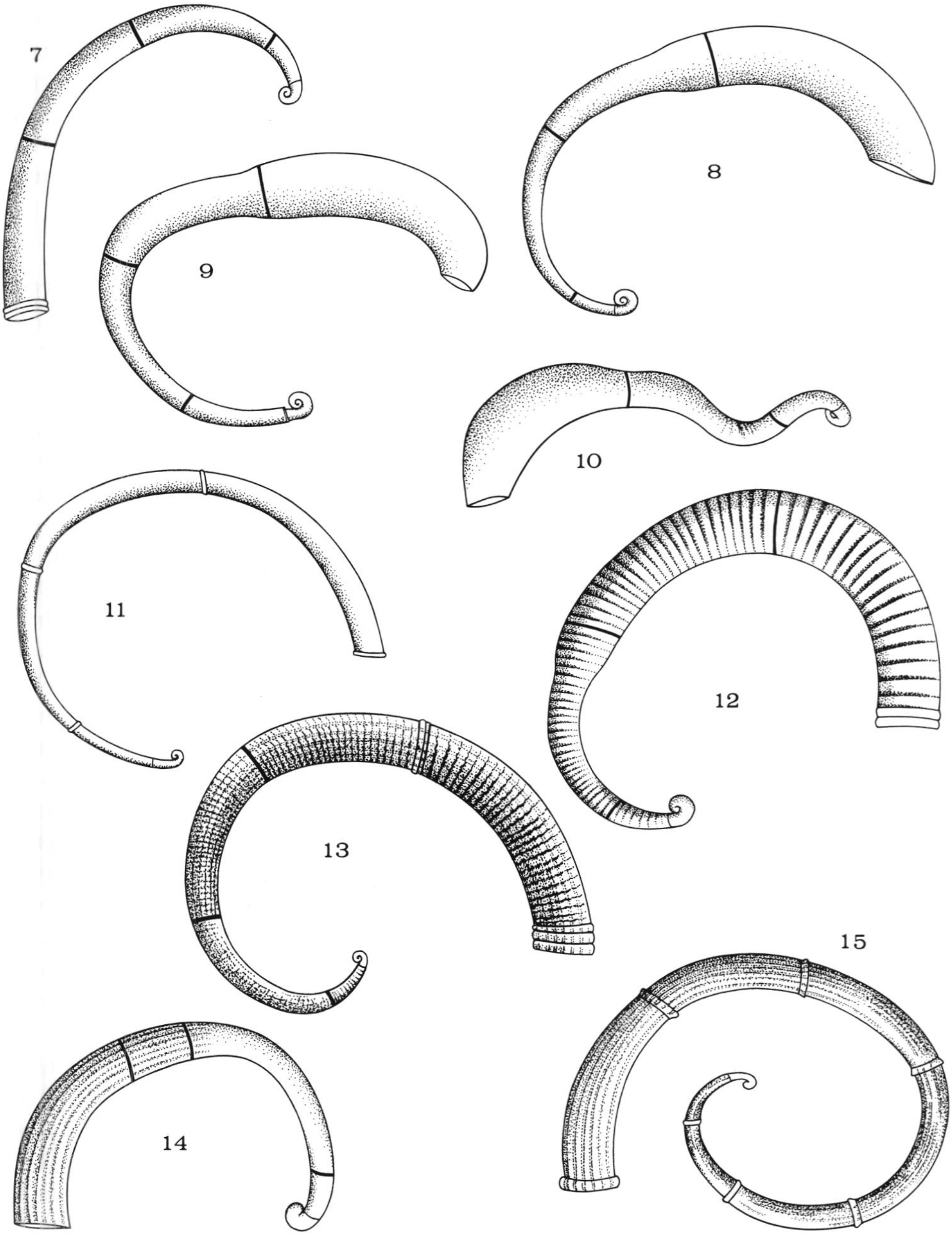
Fig.11: *Caecum* (*Brochina*) *erroneum* from Eocene of Paris Basin forms five stages of growth which reassembled form a planispirally openly coiled shell with regular increase in whorl diameter and with apertural rims of most stages thickened. The tube is about 10 mm long.

Fig.12: Four parts can be assembled to represent the whole shell of *Caecum* (*Caecum*) *pulchellum* from the Caribbean Sea, with a rapid increase in shell diameter in the second growth stage. All parts assembled form a 7 mm long tube.

Fig.13: The five portions of *Caecum* (*Elephantulum*) *imbricatum* from the Caribbean Sea near Santa Marta assembled form an 8-11 mm long openly coiled tube.

Fig.14: *Caecum* (*Elephantulum*) *troglodyta* hatches crawling from its egg-case and may or may not fracture into irregular portions when it moves among roots and algae in marine ponds in Bermuda. The protoconch is simple and has no larval shell, and the early teleoconch is ornamented only by growth lines. All parts assembled form as 7-8 mm long tube, while the early part is about 1.5 mm long.

Fig.15: All eight segments of *Caecum* (*Bambusum*) *plicatum* from the Caribbean Sea near Santa Marta assembled and fitted to each other form a regular open spiral with almost 20 mm long tube-shell.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Marta and their variations call for caution and suggest that there may perhaps only be this one species.

*Caecum* (*Meioceras*) *nitidum* from Santa Marta resembles *Caecum* (*Fartulum*) *glabellum* from Lizard Island due to the white color pattern, a twist between protoconch and early teleoconch shell and the decreased shell width near the final aperture. It differs by being more bulbous in the centre of its final portion, having the spiral twist in the early teleoconch and falling only into three segments during ontogeny. Regarding the final stage, *C.* (*M.*) *nitidum* resembles *Caecum* (*Fartulum*) *antillarum* while the early stages differ.

### Subgenus *Caecum* (*Caecum*) FLEMING, 1813

Type-species: *Dentalium imperforatum* KANMACHER, 1813 from European seas.

Description: The shell is a small slightly curved tube with an ornament consisting of numerous ring-like collabral ribs which are crossed by very fine longitudinal lirae. The apertural end is round, and the apical end is closed by a convex septum (Pl.6, Fig.8).

Remarks: The Caribbean *C.* (*Caecum*) *pulchellum* STIMPSON, 1851 produces usually five separate shell portions with the last one about 2.5 mm long and provided with 19 to 20 axial rings. The change in sculpture that occurs within the ontogeny can be a source of confusion. *C.* (*C.*) *pulchellum* from the Caribbean Sea near Santa Marta, Colombia and from Curacao has a smooth protoconch with 1.7 whorls and diameter of 0.35 mm. It has a simple round aperture. The teleoconch follows with prominent axial ribs and a fine dense pattern of longitudinal lirae. It grows to a slightly curved tube-like shell of about 1.5 mm length, until the first septum is secreted. Just posterior of it the protoconch along with a first section of the juvenile teleoconch breaks off. The first septum has a hooked denticle situated near the convex side of the shell. The blunt tube thus formed has a length of 1.2 to 1.5 mm and is ornamented with 25 to 35 axial rings and very fine longitudinal lirae. Further growth of the tube is connected with a sudden increase in width and a change in ornamentation (Pl.6, Figs.1,4,6). Quite often the new septum forms right at the site of tube transformation, but commonly a septum is secreted a little way posterior of it, and later again anterior of it after the new ornamental type is well established. This type of tube with ornament of about 22- 24 prominent axial rings crossed by very fine longitudinal striation (Pl.7, Fig.2) is about 2 mm long (Pl.6, Fig.3). The septum is recessed, and the mucro is a short sharp spike. With further growth the ornament changes again, but this change and septum position are usually correlated to each other. The increase in tube diameter remains stable. The last stage grows to about 2.5 mm length, has a thickened ring that enforces the aperture, and is ornamented by 18 to 20 smooth axial rings (Pl.6, Fig.2; Pl.7, Fig.1). Its septum lies at the apical end and has a massive triangular mucro. Thus three growth stages of *C.* (*C.*) *pulchellum* usually show no transitions of ornament in their shell. They thus differ in regard to size (1.5 mm; 2 mm; 2.5 mm), in ornamention (longitudinal liration on weak axial rings; stronger axial rings with very fine longitudinal liration; strong axial rings on smooth or almost smooth background), in the number of axial rings (25-30; 22- 24; 19-20) and the shape of the septum (sharply hooked spike, sharp spike, triangular solid mucro). All three growth stages produced by the same individual during its life time have often been considered to represent different species. With the protoconch portion and the transition from a narrow to a wide tube there are usually 5 different shell portions which altogether would form an about 7 mm long tube (Text-fig.12).

MOORE (1972, Fig.7) named a very similar shell from St. Croix, Virgin Islands *Caecum regulare* CARPENTER, 1858. The mucro of the septum is weaker than that of *C. imperforatum* from Europe. Very close to the latter, perhaps even representing the same species, is the western Atlantic *Caecum* (*Caecum*) *textile* FOLIN, 1867 which could be collected south of Cape Hatteras off shore of Cape Fear at the US East-Coast near North Carolina. Specimens from off shore Savannah in Georgia have almost smooth shells with little else than growth lines and a septum characterised by a high, pointed spine on the convex side of the shell, which closely resembles that seen in *C.* (*C.*) *imperforatum* from the seagrass and „coralligen" facies near Banyuls-Sur-Mer in the Mediterranean Sea. *Odontidium rugolosum* PHILIPPI, 1836 from the Greek Mediterranean preserved in the holotype collection of the British Museum of Natural History in London probably also represents this species.

ABBOTT (1974) mentioned that *Caecum bipartitum* FOLIN, 1870 found in the Gulf of Mexico seems to be a variety of *Caecum pulchellum* with axial rings of ornament disappearing on the anterior part of the shell. This seems to be the same feature of the *Caecum* (*Caecum*) *imperforatum* / *C.* (*C.*) *textile* group as found off shore of Georgia (own observations) or the Caribbean Sea (MOORE 1972, Figs.8,9). Totally smooth forms have been placed in *Caecum carolinianum* DALL, 1892, which were common in off shore samples from North and South Carolina, US-Eastcoast. MOORE (1972, Figs.3,5) called the later *Caecum lineicinctum* FOLIN.

In the Indopacific *Caecum vertebrale* HEDLEY, 1899 as described by HUGHES (1983a) is similar to *C.* (*C.*) *pulchellum* and individuals that could belong to this species were observed at Aqaba and Port Sudan in the Red Sea, and at Cebu (Philippines). Regarding the Pacific *Caecum* (*C.*) *vertebrale* from Hong Kong HUGHES (1983a) suggested that perhaps this species could be connected with *Caecum gracile* CARPENTER, 1858 and *Caecum maculatum* HABE, 1963 and, thus, with forms with a different number of ornament rings. She suggested that allowence should be made for changes in shell characteristics that occur at individual ages of one animal. It is even conceivable that *Caecum attenuatum* FOLIN, 1879 represents the earliest teleoconch section of *C.* (*C.*) *vertebrale* from Hong Kong described by HUGHES (1983a). This is a plausible assumption and should be considered when new species are described. It seems that *Caecum* (*Caecum*) *gracile* CARPENTER, 1858 may represent a species with a geographically very extended occurrence ranging from the Red Sea to the Coral Sea and perhaps even further in the Indo-Pacific.

*C.* (*C.*) *gracile* was studied while being alive among algal covered rubble in the reefs of the Great Barrier Reef area at Lizard Island (Queensland, Australia) and similar environment in the Red Sea near Port Sudan (Pl.6, Fig.5). The shell falls to the side when the animals crawls, but movement is continuous even though the foot is rather short. The proboscis continuously probes the sediment particles while collecting food from them and among the algal filaments through which the animal moves. Feeding and digestion is continuous so there is a steady stream of solid round faecal pellets being formed, similar in shape to those produced by *Caecum* (*Fartulum*) *antillarum* (BANDEL 1974, Fig.7 G). Specimens of *C.* (*C.*) *gracile* from Cebu show similar transitional phases from a dense rib pattern in the early shell portion to more widely spaced ribs as were found in *C.* (*C.*) *pulchellum*. The protoconch consists of two whorls, is planispirally coiled and measures

0.34 mm across (Pl.6,Fig.9).The embryonic shell has a groove and ridge ornament and measures 0.07 mm across.

### Subgenus *Elephantulum* CARPENTER, 1857

Type-species: *C. abnormale* CARPENTER, 1857.

Description: A *Caecum* with ornament that consists of longitudinal ribs as well as collabral elements.

Remarks: *Caecum (Elephantulum) imbricatum* CARPENTER, 1858 from the Caribbean Sea near Santa Marta, Columbia lives commonly on sandy bottom in reef and sea grass environments, in water depth of about 2 to 15 m. Its protoconch has one and three quarters whorls of almost planispiral coiling mode, measuring 0.3 mm in diameter and having a round and simple aperture (Pl.7, Figs.7,8). The slightly curving tube of the teleoconch attached to it has an ornament of transverse collabral rings. Later about ten longitudinal ribs appear, which in the first 0.5 mm of teleoconch are indistinct and have a slightly spiral orientation (Pl.7, Fig.7). A transition from an ornament with annular ribs dominating to a collabral groove sculpture occurs at about 1 mm of teleoconch length. The apical shell portion of about 0.6 mm length is discarded when the first septum with a strong and pointed mucro has been formed. The next, up to 3 mm long third stage, has 10 to 12 sharply crested longitudinal ribs (Pl.8, Fig.5). They form tubercles when crossing the collabral elements (Pl.7, Fig.3). In the following over 3 mm large fourth distinct section of the shell, the ornament remains similar to that of stage three (Pl.8, Fig.6). Near the aperture several deep collabral grooves appear. In the last up to 4 mm long stage of *C. (E.) imbricatum* ribs split and multiply so that there may be more than 20 of them present near the margin (Pl.7, Figs.4,5,6). The whole shell with all four to five parts connected consists of an about 8 to 11 mm long tube with open planispiral coiling. In the last segment a deep collabral groove connected to two strong ridges indicate the end of growth (Pl.7, Fig.6, Text-fig.13). All three to four complete tube-like stages have a similarly formed pointed septal mucro while apertural thickenings occur only in the last two stages. The final stage also differs from the two intermediate ones by having an ornament with more longitudinal ribs. In this respect, as well as regarding the shape of the septal spine which is more slender. *C. (E.) imbricatum* differs from *C. (E.) cooperi* S. SMITH, 1860 from the coastal Atlantic off shore area of the Carolinas and Georgia. *C. (E.) cooperi* in general shape resembles *C. (E.) tortile* DALL, 1892 from about the same area. However, in these species ornamentation of longitudinal ribs is less developed, and the mucro is more solid and triangular in shape. Both grow to larger size than is found in *C. (E.) imbricatum* from Santa Marta.

ABBOTT (1974) mentioned even more species from the Western North Atlantic and the Caribbean Sea that fit into the morphological range of these three species. One of them is living in Bermuda and has been named *Caecum troglodyta* by MOOLENBEEK et al (1989). This species is common among mangrove roots in a sea water lake near Ferry Point, where it lives among filamentous algae. Here individuals carry their up to 3 mm long shell free from the ground when crawling. Aquarium held individuals multiplied even in artificial sea water seeded with algae from the Bermudan locality since they develop directly without pelagic larvae. The young hatch and crawl from their egg mass with a 0.3 mm large shell of one whorl (Pl.4, Fig.6). The weakly curving early teleoconch of about 2 mm length has no ornament with exception of growth lines. It may coil almost planispiral

(Pl.4, Fig.5), but more commonly in an open trochospiral way so that the axis of coiling in regard to the protoconch deviates by about 90°. The teleoconch is coiled planispirally and the ornament changes to longitudinally ribbed. About 15 ribs form a regular pattern and have a rounded crest. During ontogeny at least five septa are included into the tube-like shell, but not all are connected to a fracture of the shell even though the shell is usually thinned, often cracked behind each septum. While the septum in the first stages has a pointed mucro, that of later stages has a triangular solid shelf. The hypothetical complete shell would form an about 7-8 mm long tube that is arranged in a widely open half whorl (Text-fig.14).

### Subgenus *Bambusum* OLSSON & HARBISON, 1954

Type-species: *C. cornellum* DALL, 1892 from the Pliocene of Florida (OLSSON & HARBISON 1954, Pl. 45, Fig.5)

Description: The adult shell is relatively large, curved with little or no taper, and its apertural end is thickened by a stout collar with a sharp or coarsely serrated edge. The sculpture consists of longitudinal and circular riblets. The posterior plug (closing septum) is flattened or a cap-like plate with a short excentric mucro.

Remarks: Individuals of *Caecum (Bambusum) plicatum* CARPENTER, 1858 from muddy and sandy bottoms in about 15 m depth near Santa Marta as well as from subfossil reef deposits of Galerazamba near Cartagena, Colombia, measure about 5 mm in length in their final growth stage. The shell is ornamented by 12 to 25 longitudinal ridges crossed by fine collabral lirae which may form a delicate pattern between ridges or may be very indistinct (Pl.8, Figs.1,4). When there is a twist to the right at the end of one growth stage of *C. (B.) plicatum*, the longitudinal ribs curve to the right (Pl.8, Fig.7). A tendency throughout the growth of this species for such a twist is seen in the position of the tubercular spine on the septum, which is displaced toward the upper side on its position near the convex shell flank (Pl.8, Fig.2). An inclined course of the longitudinal ribs here and there is also an indication of relicts of the trochospiral twist that is present during the growth of the tube shell. A complete ontogeny consists of at least 7-8 individual fragments which all end with a varix at their aperture, with exception of the first one holding the protoconch. This rim-like thickening is crenulated and especially thick in the last stage (Pl.8, Figs.1,3,4). The whole shell tube with all fragments connected could well be 20 mm long (Text-fig.15). The third or fourth stage measures about 2.5 mm length and could represent *Caecum plicatum* in ABBOTT's (1974) key. ABBOTT (1974) called a form with apertural twist as the illustrated (Pl.8, Fig.7) *Caecum cycloferum* FOLIN, 1867. ABBOTT (1974) and WARMKE & ABBOTT (1961) named similar shells *Caecum clava* FOLIN, 1867 which perhaps belongs to this species.

Thus *C. (Bambusum)* differs from *C. (Elephantulum)* by having a widened apertural portion (varix) in all complete growth stages. Also the excentric mucro found in the individual sections is characteristic of *C. (Bambusum)* while varices in all stages resembles the condition found in the Lutetian fossil *C. (Brochina) erroneum*.

### Subfamily Pedumicrinae IREDALE & LASERON ,1957

Description: The subfamily holds the genus *Parastrophia* with its two subgenera *Parastrophia* and *Watsonia* and the genera *Ctiloceras* and *Ponderoceras* gen nov.. The chief characteristic of the Pedumicrinae is that the protoconch is not discarded and that the larval shell is uncoiled.

Remarks: MOORE (1975) expressed the opinon that Pedumicrinae are characterized by having the coiled portion of the protoconch retained, which is correct, but it should be added that the protoconch has an uncoiled portion which contrasts to the Caecinae that have not uncoiled portion of their larval shell. IREDALE & LASERON (1957) established a new genus *Pedumicra* within their new subfamily Pedumicrinae. MOORE (1975) considered the separation of *Pedumicra* from *Parastrophia* to be unnecessary. Pedumicrinae IREDALE & LASERON, 1957 could be substituted by Parastrophiinae, a taxon proposed by HINOIDE & HABE (1978) since *Pedumicra* IREDALE & LASERON, 1957 represents a synonym of *Parastrophia*. This independent subfamily of the Caecidae encompasses the two genera *Parastrophia* and *Watsonia* as suggested by IREDALE & LASERON (1957), but is also understood to hold *Ctiloceras* and relation. Ctiloceratinae IREDALE & LASERON, 1957 were formed to accommodate caecid-like shells which unlike *Caecum* retain the protoconch throughout life, and in which the adult animal becomes secondarily coiled in contrast to the uncoiled teleoconch of *Caecum*. Here they are interpreted as offsprings of *Parastrophia*-like ancestors and placed regardingly.

### Genus *Parastrophia* FOLIN, 1869

Type-species: *P. cornucopiae* FOLIN, 1869 from the Pacific as recently described by HUGHES (1983a Fig.1k; Pl.1E) from Hong Kong.

Description: The genus holds species with teleoconches that consist of a slightly curved to openly spiral tube with round aperture. The early ontogenetic shell remains usually attached to the teleoconch. The coiled embryonic shell is succeeded by the larval shell that uncoils and forms a more or less curved planispiral tube. The protoconch is separated from the teleoconch by a varix.

### Subgenus *Parastrophia* (*Parastrophia*) FOLIN, 1869

Description: The teleoconch is gently curving like that of *Strebloceras*, but the protoconch consists of a coiled embryonic shell and a smooth uncoiled larval shell of the same morphology as the teleoconch. The latter has a sculpture of fine longitudinal lines crossed by growth increments.

Remarks: According to HUGHES (1983a, Pl.1E) *Parastrophia* (*Parastrophia*) *cornucopiae* FOLIN, 1869 is represented by an up to 4 mm long and up to 0,8 mm wide shell that has an about 0,5 mm long protoconch. Its coiled part consists of 1-1.5 whorls which are succeeded by a slightly curved larval part that ends in a varix. The teleoconch surface is sculptured by fine longitudinal lines and growth increments. *P.* (*Parastrophia*) *cornucopiae* from Hong Kong fits with the descriptions of THIELE (1925) and FOLIN (1869) and it can also be applied to describe *P.* (*P.*) *cygnicollis* from Australia and *P.* (*P.*) *asturiana*.

*Parastrophia* (*Parastrophia*) sp. from the Chattian stage of the Oligocene near Kassel (Glimmerode) has a 0.9 mm long protoconch attached to the teleoconch that may have a slight spiral twist in it (Pl.3, Fig.8; Pl.10, Figs.3,6), resembling modern *P.* (*Parastrophia*). LOZOUET (1986, Fig. 61 B,C) noted the similarity of the Oligocene P. (*Parastrophia*) from Peyrère in southern France with about 0,6 mm long protoconch (Pl.10, Fig.7) with *P.* (*P.*) *asturiana* living in the Mediterranean Sea. A very similar species from subfossil deposits off-shore Valencia was called *Parastrophia garganica* MONCHARMONT-ZEI, 1954 by PORTA et al (1993, Pl.3, Fig.9). The modern Mediterranenan *Parastrophia (P.) mediterranea* (COSTA, 1861), which probably is identcal with *P.(P.) folini* also from the Mediterranean, according to GOUGEROT & LE RENARD (1984) can be synonimized with *P.(P.) asturiana* from the Atlantic.

*P. (P.) asturiana* FOLIN, 1869 from the Eastern Atlantic has a larval shell that measures 0,5 mm. It closely resembles *P. (P.) corniculum* MORELLET & MORELLET, 1943 from the Eocene of France (GOUGEROT & LE RENARD 1984). *P. (Parastrophia) cygnicollis* (HEDLEY, 1904) from Australia (Pl. 9, Fig. 6; Pl. 10, Fig. 4) was studied from New South Wales (Port Stephen, Australian Museum No. C19640 ) and the Capricorn Islands (Australian Museum No. C 162396). These specimens have an embryonic shell of about 0.09 mm in diameter and a larval shell that is 0.5 mm long ending in a smooth varix. *Parastrophia challengeri* FOLIN, 1879 from Cape York off North Australia may be this species, but its holotype in the collection of the British Museum of Natural History in London consists only of a few shell fragments that can no longer serve for comparison.

The protoconch of *P. challengeri* is just the same as that noted in *P. (P.) asturiana* from off shore St. Jean de Luz in the eastern Atlantic (Pl.10, Figs.2,5) (British Museum Nr. 172-20). *Parastrophia (P.) filum* MERVILL, 1906 from the Gulf of Oman preserved in the holotype collection of the British Museum of Natural History in London is also very similar, but has an incomplete protoconch which can no longer be measured. A fossil shell from Turkey with 0.8 mm long larval shell (Pl.9, Fig.9) intermediates between modern species living in the Mediterranean sea and elsewhere and the Oligocene form that lived in the shallow sea near Kassel (northern Germany) (Text-fig.4). From strictly conchyological point of view *Parastrophia (Parastrophia) cornucopiae* can not be separated from other modern species living in the Atlantic and Pacific Oceans as well as in the Mediterranean Sea. Fossil species that have lived from Eocene times in the Paris Basin, and from Oligocene times in several shallow seas that covered Europe differ from the Extant species by having a larger protoconch. The small veliger hatched with a 0.09 mm large embryonic shell and remained in the plankton for a long period of time, growing a shell of up to 0.9 mm length in the Oligocene of northern Germany (Pl.10, Fig.3), of 0.8 mm length at the same time in Turkey (Pl.9, Fig.9) and 0.6 mm length in southern France (Pl.10, Fig.7), while modern representatives stop growth of the larval shell with about 0.5 mm length (Pl.10, Figs.1,4,5). Differences in the coiling mode of the teleoconch may also vary to some degree as is also noted in other species of the Caecidae.

*P. (P.) queenslandica* (IREDALE & LASERON, 1957) from the Hope Islands (Australia) has a more rudimentary embryonic shell resembling a bulb when seen from the side (Pl.9, Fig.7). This embryonic shell is much larger (0.28 mm) (Pl.10, Fig.8) than that seen in *P. (P.) cornucopiae* from Recent and fossil occurrences (0.09 mm) and indicates that embryos developed from larger eggs than is the case in the latter. IREDALE & LASERON (1957) distinguished *P. (P.) queenslandica* from *P. (P.) cygnicollis* by the finer, more narrow end of the protoconch. But there is also *Parastrophia challengeri* FOLIN, 1879 that was described from specimen collected near Cape York. HINOIDE & HABE (1978) described a new species *Parastrophia japonica* as connected to a protoconch with small coiled apex, about 0,7 mm in length and terminating with a varix. They remarked that their new species from Japan differs from *Parastrophia cygnicollis* (HEDLEY, 1904) from Australia by having a larger and longer shell and from *P. (P.) queenslandica* (IREDALE & LASERON, 1957) by its larger coiled apex. The latter is possibly not the case and both species may be the same. A simplified embryonic shell can easily be mistaken to be not coiled at all as is reported from the fossil *Thecopsella* MUNIER CHALMAS from the Eocene of the Paris Basin. Here the embryonic portion of the protoconch is supposedly of oval outline while the larval shell is like that of *Parastrophia* (LOUZOUET 1986). The fossils described from the European Lutetian may quite well have an embryonic shell like that of *P.* (*Parastrophia*) *queenslandica* and GOUGEROT & LE RENARD (1981) correctly doubted the existence of a separate genus *Thecopsella* of which JANSSEN (1978) reported an occurrence in the Oligocene deposits of Kassel. COSSMANN (1912) attributed a similar shell with simple apex from the Eocene to *Euchilotheca* FISCHER, 1882. It had originally been described as *Vaginella succincta* DEFRANCE and placed with the pteropods. According to his figure *Euchilotheca* could well represent a juvenile scaphopod with the early ontogenetic shell still not dissolved as figured by ENGESER et al (1993). If *Thecopsella* is a *Parastrophia* with a similar development as seen in modern *P.* (*P.*) *queeenslandica* both forms with small and large eggs have a history ranging back to the Eocene.

A cork screw shaped spire is developed in a species from Hong Kong that was described with the name *Fartulum* sp. by HUGHES (1983a Pl.1B). This *Fartulum* sp. from Hong Kong can be attributed to the genus *Parastrophia* (*Parastrophia*) in respect to the characteristic larval shell ending in a varix, while there is an open spiral twist of almost one whorl present in that portion of the shell that was formed after metamorphosis from the larva. Later on the teleoconch follows straight course as is the case in *Parastrophia* (*P.*) *asturiana(=cornucopiae)*. Thus *Parastrophia* from Hong Kong displays the same type of reminiscence of original and ancestral spiral coiling resembling a cow´s horn as is found in *Caecum* (*Meioceras*) *nitidum* from the Caribbean Sea near Santa Marta. Due to the similarities of the protoconch of *Pedumicra* (= *Parastrophia*) to the adult shell of *Meioceras* (= *Caecum* (*Meioceras*)) from the Caribbean Sea IREDALE & LASERON (1957) suggested to place the latter into the Pedumicrinae. The differences of the protoconch found in *Parastrophia* on one side and *Caecum* (*Meioceras*) on the other side clearly advise not to follow that suggestion, as was also suggested by MOORE (1975).

### Subgenus *Watsonia* FOLIN, 1879

Type-species: *W. elegans* FOLIN, 1879 from the Wednesday Island, Cape York, Queensland Australia.

Description: *P.* (*Watsonia*) resembles *P.* (*Parastrophia*) but its teleoconch is sculptured with collabral ribs.

*Parastrophia* (*Watsonia*) *elegans* (FOLIN, 1880) that is the same species described as *Gladioceras armorum* IREDALE & LASERON,1957 (Australian Museum No.C27502). It has a protoconch very similar to that of *P.* (*Parastrophia*). The protoconch is 0.65 mm long, and the initial embryonic portion measures 0.09 mm in maximum diameter with sculpture of ridge and groove pattern (Pl.4, Fig.2). The smooth larval shell ends in a crenulated varix (Pl.9, Fig.2). The teleoconch is ornamented by fine collabral ribs connected to very fine longitudinal striae (Pl.9, Fig.5). The matured shell is regularly conical, slightly curved and the aperture is round and oblique and usually thickened (Pl.9, Fig.1). A specimen of this species from Cebu (Philippines) is longer (3.2 mm) (Pl.9, Fig.3), but has the same type of protoconch as found in the 2.1 mm long Australian species from Hope Island. Here it seems that the fully grown individual with enlarged apertural rim continued to grow (Pl.9, Fig.4) and thickened the shell in comparison to the specimen from Australia.

IREDALE & LASERON (1957, Pl.2, Figs 34, 35) created a new genus *Gladioceras* based on *G. armorum* IREDALE & LASERON,1957, a species with *Watsonia* - like adult shell and a protoconch as found in *Parastrophia* (=*Pedumicra*). MOORE (1975) noted that FOLIN (1880) had badly illustrated a fractured shell with only the anterior part of the teleoconch preserved and the apertural thickening present when creating the genus *Watsonia*. The syntype of *Watsonia elegans* FOLIN, 1879 from Cape York preserved in the collection at the British Museum of Natural History in London represents a shell without the protoconch and a teleoconch as the one described and illustrated here. *Gladioceras* IREDALE & LASERON, 1957 is based on a more complete specimen that is identical with *Watsonia elegans* FOLIN, 1879. The subgenus *Watsonia* is unknown from the European Eocene and Oligocene and seems to represent an Indopacific form, probably evolved later than the subgenus *Parastrophia*.

### Genus *Ctiloceras* WATSON, 1886

Type-species: *C. cyclicum* WATSON, 1886 from Queensland in Australia.

Diagnosis: The matured whorl leaves a large umbilical aperture. The larval shell resembles that of *Parastrophia* while the teleoconch is lowly trochospirally coiled.

### Subgenus *Ctiloceras* WATSON, 1886

Description: A *Ctiloceras* with sculpture of transversal (axial) ribs which surround the whorls.

Remarks: In *C.* (*Ctiloceras*) *cyclicum* WATSON, 1886 from Darwin (North Australia, No. C162397 Australian Museum) the dextral shell rests with its circular aperture against the trompet shaped larval part of the protoconch (Pl.11, Figs.5-7). The embryonic shell measures about 0.09 mm across and consists of smooth three quarters of a whorl. The onset of the larval shell is marked by a decrease in whorl diameter and the begin of growth increments. After a first half whorl the larval shell becomes almost straight until reaching a length of 0.6 mm. In this course the diameter increases from 0.06 mm to almost 0.2 mm and the final margin forms a regularly crenulated rim of a varix. The larval shell is ornamented by fine longitudinal lines of tuberculate lirae that end in the apertural varix. The begin of adult ornament is abrupt. It consists of lamellar and continuous axial ribs and a very delicate pattern of fine spiral lirae in undulating course crossing these ribs. The shell reaches only about 0.9 mm in size, and its teleoconch forms an even coil with regular increase in shell width. The aperture is circular and slightly inclined to the axis of coiling.

### Subgenus *Torresella* IREDALE & LASERON, 1957

Type-species: *Ctiloceras striatum* HEDLEY, 1902 from near Cape Grenville, Queensland, Australia.

Diagnosis: A *Ctiloceras* with spiral lirae as sculpture.

Remarks: *Ctiloceras* (*Torresella*) *striatum* HEDLEY,1902 from Darwin in North Australia (Australian Museum No. C162398) is ornamented by numerous spiral lirae crossed by growth lines and irregular collabral ribs (Pl.13, Figs.1,2,3). The dextral shell with its circular aperture carries the protoconch that rests with the early half of the trumpet shaped larval part on the teleoconch whorl. The embryonic shell measures about 0.1 mm across and consists of three quarters of a whorl. The onset of the larval shell is detectable by the appearance of growth lines. After a first half whorl the larval shell becomes almost straight until reaching a length of 0.5 mm. In this course the diameter increases from 0.08 mm to almost 0.12 mm, and the final margin forms a varix with raised margin. The twist into the spirally coiled teleoconch begins in the very final portion of the larval shell. The begin of adult ornament is abrupt, and it consists of numerous spiral lirae of undulating outline that are arranged on the smooth background of the shell. Collabral ribs feature the first whorl of the teleoconch and disappear in the last half of the shell. The whorl is well rounded, and its diameter increases quite slowly. The aperture is circular, and the 1.6 mm large shell is almost planispirally coiled with apex and umbilicus in depressions of similar dimensions.

### Subgenus *Transcopia* Iredale & Laseron, 1957

Type-species: *Ctiloceras clathrata* Hedley, 1902 from Torres Strait, Australia.

Description: A *Ctiloceras* with ornament of several strong spiral ribs crossed by transverse ribs creating a clathrate scupture.

Remarks: In *C.* (*Transcopia*) *clathrata* from Darwin in northern Australia (Australian Museum No. C162394) the dextral shell with its circular aperture carries the protoconch that rests with the late portion of the trumpet shaped larval part on the teleoconch whorl (Pl.11, Figs.1-4). The embryonic shell measures about 0.1 mm across and consists of three quarters of a whorl with a network ornament of grooves and ridges in its initial part. The onset of the larval shell is indistinct, but clearly detectable with the begin of growth lines. After a first half whorl the larval shell has almost straight course until reaching a length of 0.7 mm. In this course the diameter increases from 0.07 mm to almost 0.24 mm, and the final larval aperture forms a varix with pitted margin and keeled inner side. The twist into the spirally coiled teleoconch begins in the final portion of the larval shell. Ornament of the larval shell is present on its apertural portion and consists of longitudinal lirae that end in the varix (Pl.11, Figs.2,4). The begin of adult ornament is abrupt, and it consists of about eleven spiral keels. Axial ribs in collabral arrangement feature the apical and umbilical side of the whorl and end on the lateral side. The whorl is well rounded, and the aperture is circular. The shell reaches only about 1 mm in size, and its teleoconch forms an even coil with regular increase in shell width.

### Subgenus *Carinoceras* Iredale & Laseron, 1957

Type-species: *Carinoceras bicarinata* Iredale & Laseron, 1957 from the shallow sea in Queensland and the Northern Territories in Australia.

Description: A *Ctiloceras* with sculpture of two prominent spiral keels fine spiral lirae and axial ribs that end at the keels.

Remarks: In *C.* (*Carinoceras*) *bicarinata* from Darwin in the Northern Territories of Australia (Australian Museum No. 162313) and from Port Hedland (Australian Museum No. C162315) the dextral shell with its circular aperture carries the embryonic shell and the early portion of the trumpet shaped larval part of the protoconch (Pl.12, Figs.1-6). The embryonic shell measures about 0.1 mm across and consists of smooth three quarters of a whorl. The onset of the larval shell is rather indistinct. After a first half whorl the larval shell becomes almost straight until reaching a length of 0.57 mm (Pl.12, Fig.2). In this course diameter increases from 0.08 mm to almost 0.16 mm and the final margin forms a regular and smoothly rounded rim of a varix. The twist into the spirally coiled teleoconch occurs in the final portion of the larval shell (Text-fig.20). The ornament of the larval shell consists of indistinct growth increments and longitudinal lines. The begin of adult ornamention is abrupt and it consists of two marginal spiral keels. Axial ribs present on the apical flank and on the base end in the spiral keels as well as on the inner umbilical flank. Spiral lirae ornament the whole teleoconch. The shell reaches only about 1.5 mm in size of which the teleoconch forms an even coil with regular increase in whorl diameter. The aperture is circular and slightly inclined to the axis of coiling.

IREDALE & LASERON (1957) described another species that is even more strongly keeled than *Ctiloceras* (*Carinoceras*) and connected to a protoconch like that in *Ctiloceras* as *Jayella compressa* IREDALE& LASERON, 1957. They considered it to represent another genus of their family Ctiloceratidae.

### Genus *Ponderoceras* n. gen.

Type-species: *Ctiloceras annulatum* IREDALE & LASERON, 1957 from Queensland, Australia.

Derivatio nominis: Named for Dr. WINSTON F. PONDER, the curator of the malakological section at the Australian Museum in Sydney.

Diagnosis: A teleoconch like *Ctiloceras* with a larval shell that is strongly curved in the line of the later matured coiling.

Type locality: Van Dieman´s Inlet, Queensland. Additional material studied comes from the Gulf of Carpenteria (Australian Museum No. C162399).

Description: *Ponderoceras annulatum* (IREDALE & LASERON, 1957) is ornamented with about 16 spiral ribs which are crossed by discontinuous transverse ribs creating a clathrate sculpture in the first whorl of the teleoconch (Pl.13, Figs.4-7). The second whorl bears evenly spaced axial ribs in collabral arrangement. The dextral shell with its circular aperture carries the protoconch attached to the whorl of the teleoconch on its outer flank, while there is an umbilical opening on its inner flank. The larval part of the protoconch is less strongly coiled than the embryonic shell that measures about 0.1 mm across and consists of three quarters of a whorl. The onset of the larval shell is indistinct, but clearly detectable with the begin of growth lines. After a first half whorl the larval shell detaches from the initial whorl but remains in spiral arrangment ending in a varix with smooth rim in front of it (Pl.13, Figs.5,7). The spirally coiled teleoconch is continuous with the larval shell and its inner flank touches the protoconch after half a whorl (Text-fig.21). The larval shell is smooth and increases in width from about 0.09 mm at the end of the embryonic shell to almost 0.2 mm at the varix of the pediveliger. The onset of spiral lirae on the teleoconch is abrupt. The shell reaches about 2.5 mm in size with two well rounded teleoconch whorls terminating in a circular aperture. The apical portion is flattened, and the umbilical part is wide.

Remarks: According to IREDALE & LASERON (1957) *Ponderoceras annulatum* is the largest of the species described by these authors in their family Ctiloceratidae and reaches a size of 3 mm. IREDALE & LASERON (1957 Pl.2, Figs.24,25) coined *Enigmerces* as another genus of the Ctiloceratinae. It is of turbinate shell morphology and has an umbilical opening smaller than in *Ctiloceras,* but wider than in *Ponderoceras*. The protoconch is described as small and strongly curved and according to their figure could be transitional in its mode of coiling between the two genera of the Ctiloceratidae.

## 6. Development of the shell

### 6.1. Ontogeny of *Caecum*

CARPENTER (1858) and DE FOLIN (1877) noted three stages of shell ontogeny to occur within the life cycle of *Caecum*. The first consisting in the spiral protoconch constructed by the embryo and the larva, the second is that of the juvenile with straight shell that is still connected to the protoconch, and the third is that of a tube-like adult with the protoconch and juvenile shell discarded. From the above stated data it is evident that his view is to simplistic.

*Caecum (Fartulum) antillarum* develops in spherical egg capsules of less than 1mm in diameter which are camouflaged by a cover of small particles glued to their sticky

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Fig.16: The veliger larva of *Parastrophia* seen from the side and juvenile right after metamorphosis as observed in the Red Sea near Hodeida. The shell is about 0.5 mm long.

Fig.17: The veliger larva of *Parastrophia* as in text-fig.16 seen from above while swimming.

Fig.18: The veliger of *Caecum (Fartulum) glabellum* from the Great Barrier Reef swims with two large lobes of the velum (lower part) and crawls on a narrow foot right after metorphosis (upper part).

Fig.19: Protoconch and early part of teleoconch attached to each other in the first shell portion of *Caecum antillarum*. The protoconch is helicospirally coiled.

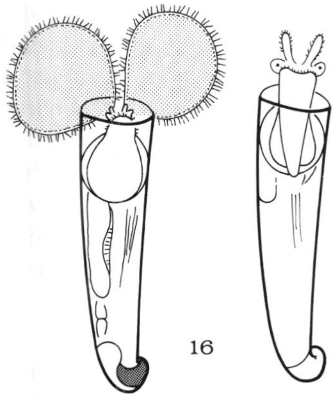
Fig.20: The about 0.6 mm long protoconch of *C. (Carinoceras) bicarinata* from Darwin in the Northern Territories of Australia resembles closely that of *Parastrophia.*

Fig.21: The shell of *Ponderoceras annulatum* from the northeastern Australian sea measures about 2.5 mm across and has an openly coiled larval shell.

Fig.22: Protoconch (about 0.3 mm wide) and sketch of teleoconch (about 1.7 mm wide) of *Parviturboides* sp. from the Indopacific Ocean near Satonda (Indonesia) with inclined lirae as larval ornament.

Fig.23: Protoconch (about 0.5 mm wide) and sketch of teleoconch (about 3.5 mm wide) of *Cyclostemiscus beauii* (FISCHER, 1857) from Santa Marta (Colombia) with inclined lirae as ornament of the larval shell.

Fig.24: Protoconch (about 0.4 mm wide) and sketch of teleoconch (about 1.3 mm wide) of *Teinostoma megstoma* (C.B. ADAMS, 1850) from Santa Marta (Colombia) with simple spiral lirae as ornament of the larval shell.



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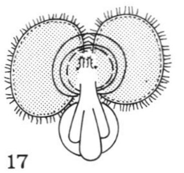

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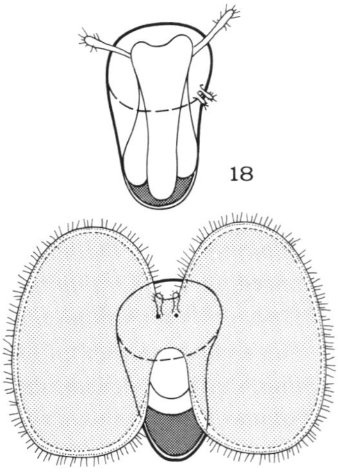

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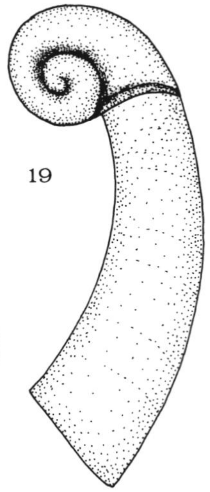

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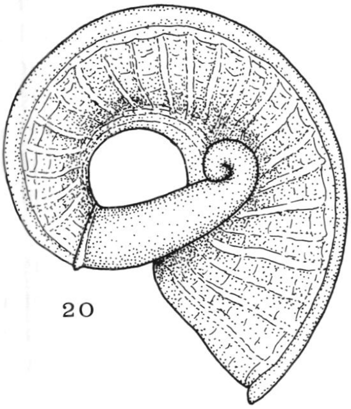

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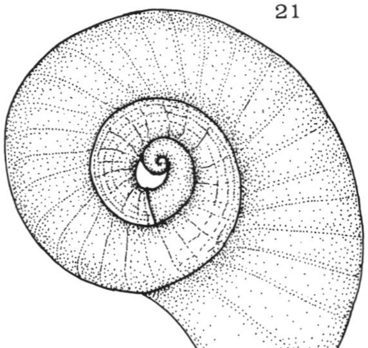

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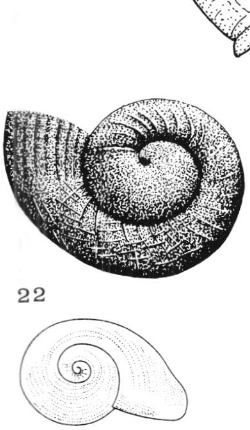

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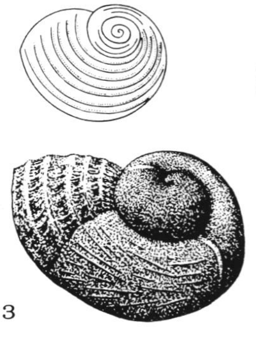

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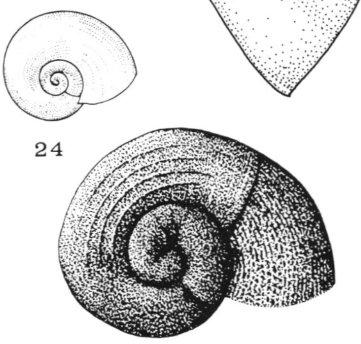

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outer surface. The opaque egg-case holds one embryo that is surrounded by an extra spherical egg cover of about 0.3 mm width. The uncleaved egg measures about 0.1 mm size right after deposition (BANDEL 1976). GÖTZE (1938) observed similar spherical egg-cases in *Caecum (Brochina) glabrum* from the North Sea also holding a single egg that hatches as a veliger having a shell of about 0.1 mm in diameter. In contrast *Caecum glabellum* from Japan hatches as crawling young with a 0.58 mm large shell (AMIO 1963). This species is probably a different one to *C. (F.) glabellum* from Hong Kong and Lizard Island in the Great Barrier Reef, since that species has a planktotrophic larva (Pl.2, Fig.5). In species without free larval stage the embryonic shell is larger and has less whorls. *Caecum (Elephantulum) troglodyta* from the mangrove ponds at Ferry Point in Bermuda hatches crawling with a 0.35 mm large shell (Pl.4, Fig.6) . *Caecum caverna* also hatches not as swimming veliger but crawls from its egg mass (AARTSEN 1977). A *Caecum (Brochina)* sp. from Madeira from the British Museum collection, which had been determined as *C. (B.) glabrum*, also hatched as crawling young with 0.25 mm large embryonic shell (Pl.4, Fig.4).

The embryonic shell of all Caecinae is almost planispirally coiled (BANDEL 1975, Pl.3, Figs.8,9,10). A delicate pattern of fine ridges that surround 1-2 micron wide shallow grooves may be present while there are no growth lines, except very close to the aperture (Pl.4, Figs.1,3). The latter mark the time of detachment of the mantle tissue from the shell prior to hatching. *Caecum glabrum* from the North Sea and the Mediterranean Sea (Pl.2, Fig.3) *C. corneum* from Brazil also hatch as planktotrophic veliger (GÖTZE 1938, MARCUS & MARCUS 1963). In cases where young hatch from the egg after metamorphosis is completed the embryonic shell is succeeded directly by the teleoconch without a larval shell present at all. Morphology as well as size also differ from those with planktotrophic development. In this way members of the genus *Caecum* resemble those of most other marine gastropods (BANDEL 1982) (Text-fig.6).

The larval shell in most species is smooth except for very fine growth lines (Pl.5, Figs.6,7). In *Caecum (Fartulum) glabellum* a fine ornament of spiral lirae is present as well (Pl.2, Fig.5) resembling that found in some Vitrinellidae. The aperture is round and simple, in contrast to that of most members of the Cerithioidea and Rissooidea with planktotrophic larva that have an apertural projection (BANDEL 1993). A similar pattern has been described by RICHTER & Thorson (1975) in the case of the Mediterranean *Caecum (C.) imperforatum*. The early ontogenetic shells of this species were also described by HOENSELAAR & HOENSELAAR (1990). Two whorls and planktotrophic development are present in *Caecum (F.) antillarum* (Pl.2, Fig.6), *C. (C.) pulchellum* and *C. (C.) gracile* (Pl.6, Fig.9) from the Caribbean Sea and *C. (F.) digitulum* from off New Zealand (Pl.2, Fig.7). 1,7 whorls and planktotrophic development are noted in *C. (Elephantulum) imbricatum* (Pl. 7, Figs. 7,8) and *C. (M.) nitidum* (Pl.5, Fig.6) from the Caribbean Sea as well as in *C. (B.) glabrum* from the Mediterranean Sea (Pl.2, Fig.3).

The protoconch of *Caecum (Caecum) imbricatum*, *C. (Meioceras) nitidum* and *C. Caecum) pulchellum* is weakly dextral helicoidal, and whorls just touch each other (Text-fig.5). In *C. (Fartulum) antillarum* the protoconch is more clearly helicoidal in shape and whorls overlap more onto each other, but much less as is the case in *Strebloceras* (Pl.1, Fig.5).

The ontogenies of *C. (Brochina) erroneum* and of *C. (Bambusum) plicatum* resemble each other by consisting of 5 to 8 segments all of which with exception of the one that is connected to the protoconch are of similar shape and have an apertural rim or varix (Text-figs.11,15). Increase in whorl dimension is steady and slow. The two species differ in ornamentation, which places one into the smooth subgenus *Brochina* and the other in the longitudinally ribbed subgenus *Bambusum*. *C.* (*Brochina*) *glabrum*, and *C.* (*Brochina*) *digitulum* consist of fewer segments (about 4). They have no varices but also very regular increase in shell width (Text-fig.7). Segments have a rather similar increase in size, except for the first one with the protoconch attached to it. *C.* (*Elephantulum*) *imbricatum* intermediates between the two cases, having regular increase in shell width, about 5 segments and varices only in the last two segments (Text-fig.13).

All these cases differ from those of *C.* (*Caecum*) *pulchellum* and *C.* (*C.*) *gracile* by having a regular increase in shell width throughout the growth of the planispirally and openly coiled shell. In the two species of *C.* (*Caecum*), in contrast, the second or third segment has a section of rapid increase in shell width along with change in ornamention (Text-fig.12). Such a sculptural change is also seen in *Caecum* (*Elephantulum*) *troglodyta*, but here without rapid increase in whorl diameter. *C.* (*Fartulum*) *glabellum*, *C.* (*F.*) *antillarum* and *C.* (*Meioceras*) *nitidum* demonstrate a reduction in the number of segments formed during one ontogeny (Text-figs.8,9,10). In the last of these there is also a trochospiral twist, which can be found in others as well, but not as strongly expressed. In *C.* (*Bambusum*) *plicatum* such trochospiral influences produce a twist in the aperture now and then resulting in a characteristic apertural swelling connected to a curving rib pattern. In *C.* (*F.*) *glabellum* the trochospiral tendency is seen in the angle between protoconch and teleoconch, and in *C.* (*E.*) *troglodyta* it is expressed individually.

### 6.2 The veliger of *Parastrophia*

Individuals of *Parastrophia* which live near the shore of the coast of Jemen in the Red Sea have the characteristical straight larval shell. From the vessel "METEOR" larvae were caught in August 1987 with a plankton net in the Bay of Hodeida and kept alive in the laboratory until they metamorphosed. The embryonic shell measures about 0.07 mm and is succeeded by a 0.5 mm long larval shell with only a slight curvature and slightly decreasing diameter near the aperture. It resembles, thus, protoconchs as are found in the Mediterranean / Atlantic *P.* (*P.*) *asturiana* and Indo-Pacific *P.* (*P.*) *cornucopia* / *P.* (*P.*) *cygnicollis*. The larva swims with a velum of two equally rounded lobes that pull the animal upwards while the shell hangs down. Tentacles are provided with basal eyes and lie between the velar lobes on the head. The foot with statocysts at its base holds a round operculum on its back that seals the aperture when the animal retracts into its shell. The foot is in a position on the concave side of the protoconch. The shell retractor muscle is attached to the apical end of the shell interior and withdraws the mantle deep into the shell when it contracts. A larval heart pulsates in the „neck“ behind the head and in the mantle cavity, and the adult heart pumps with two chambers in a position near the base of the mantle cavity. Both blood pumps remain active for some time even after metamorphosis and suck blood from the velum and the roof of the mantle cavity to the stomach and visceral mass. A ribbon of cilia moves water from the neck into the posterior end of the mantle cavity and from here along the roof of that cavity, past the anus to its edge at the outer lip. This system remains active also for some time after metamorphosis, since a ctenidium is not present in the early benthic juvenile. During metamorphosis the velum is lost and locomotion is taken over by the densely ciliated foot. Both tentacles of the head produce sensory cilia and the eyes form lenses. The visceral mass withdraws from the embryonic shell, and a first septum forms, sealing that part of the shell from the rest. Since larvae of *Parastrophia* were very common in the bay of Hodeida , but not encountered outside of it in the open Red Sea they probably do not spend much time in the plankton before metamorphosis into the benthic individual (Text-figs.16, 17).

## 7. Fossil Caecidae

The oldest known Caecidae are from the Early Eocen of New Zealand (Beu & Maxwell 1990). Gougerot & Le Renard (1981) report on thirteen species of the genera *Caecum*, *Strebloceras* and *Parastrophia* from the Middle and Late Eocene of the Paris Basin. The different species of the genus *Caecum* in this occurrence resemble each other in general morphology and differ mainly in regard to the shape of septa closing the apex and the presence or absence of a varix. This somewhat doubtful difference was used by Gougerot & Le Renard (1981) to differentiate several species all of which can be placed with *C.* (*Brochina*). *Caecum* (*Brochina*) *glabrum* is considered to be among these species, and shells very close to those from the Mid-Eocene are still found on the extant individuals that live in the shallow Atlantic Ocean and the Mediterranean Sea near the coast of France. From late Eocene deposits (Zinsmeister 1982) reported the presence of Caecidae on the Antarctic Peninsula. With *Parastrophia coniculum* from the Lutetian (Mid-Eocene) a species that closely resembles the modern *P. asturiana* from the Mediterranean and the French Atlantic coastal waters is present (Gougerot & Le Renard 1981).

Janssen (1978) described from the younger Oligocene of Glimmerode near Kassel (northern Germany) four species of Caecidae: *Caecum* (*Brochina*) *schulzei* Görges, 1952 (Görges) 1952, Fig.47-48, Anderson 1960, Pl.9, Figs.2a-d, Tembrock 1965, Pl.7, Figs.18 a-c), *Caecum* (*Brochina*) *glimmerodense* Janssen, 1978 (Janssen 1978, Pl.3, Figs.3-4); *Caecum* (*Meioceras*) *rapidecrescens* Janssen, 1978 (Janssen 1978, Pl.3, Fig.5), and *Thecopsella tenuiannulata* Janssen, 1978 (Janssen 1978, Pl.3, Figs.1-2), which actually represents a member of *Parastrophia*. Louzout (1986) noted five species of Caecidae from the Aquitaine in southern France and stated that eleven species are known from the Oligocene of Europe. Anderson (1960, Pl.9, Figs.2a,b,c,d) illustrated from the Late Oligocene (Chattian) of Kassel *Caecum schulzei* Görges, 1952 (Pl.3, Fig.7), which resembles the modern species *C.* (*B.*) *vestitum* from the Caribbean Sea, *C.* (*B.*) *glabrum* from the North Sea (Pl.2, Fig.3), and *C.* (*B.*) *digitulum* from New Zealand (Pl.2, Fig.7), especially when regarding the teleoconch size, shape, rounded apical septum, and morphology of the protoconch.

Porta et al. (1993) document, that *C.* (*Caecum*) *imperforatum* (=*trachea*) has been living in European Seas for many million of years and has hardly changed since the Eocene. The earliest representatives were described by Cossmann (1919) and Morellet & Morellet (1943) from the Paris Basin. According to Porta et al. (1993, Pl.1, Figs.1-9) the species has also been described from the Oligocene and Miocene of Europe and they illustrate the variability of fine ornament from the Miocene and Pliocene of Spain. In the Oligocene of southwestern France *Caecum* (*Caecum*) is present and was called *C. mineurei* by Lozouet (1986).

*Caecum* is rather poorly represented in the Tertiary of the Gulf coast of the USA. *C. alteratum* MEYER, 1886 comes from the Jackson Group of the Eocene and *C. solitarium* MEYER, 1886 from the Vicksburg Group of the Oligocene (MCNEIL & DOCKERY 1984). The later is very close to the juvenile stages of the modern Caribbean species *C.* (*E.*) *imbricatum*. Later stages of the extant group have longitudinal ribs, which are missing in the fossil species that has a planospiral protoconch of two whorls (MCNEIL & DOCKERY 1984, Pl.42, Fig.15). *C.* (*Meioceras*) is known from the Miocene of Panama and Florida with species very close to the modern *C.* (*M.*) *nitidum* (WOODWARD, 1959).

While since the Oligocene members of the subgenus *C.* (*Fartulum*) and *C.* (*Elephantulum*) apparently have developed in the general area of the Caribbean sea, members of the subgenus *P.* (*Watsonia*) and the genera *Ctiloceras* and *Ponderoceras* have developed in the area between southeastern Asia and northern Australia.

## 8. Summary of systematics of the Caecidae

The phylogeny of the Caecidae has left its imprints on the ontogeny of the species connected to each other within this family of Caenogastropoda. When unraveled it can be illustrated in a cladogram, which is additionally tested by the appearance of taxa in time (Text-fig.25). The caecids appear first in the Early Eocene, gave rise to the Strebloceratinae, and diversified by Eocene into Caecinae and Pedumicrinae.

The earliest known caecid genus *Strebloceras* has a larval shell of low trochospiral shape, similar to those still found among some living caecinid species. *Strebloceras* did not cast off the early part of its shell during later life. Thus, the common, synplesiomorphic feature found among all caecids in the Eocene is the uncoiling of the teleoconch. After larval life the benthic *Strebloceras* secreted an uncoiled shell, which in contrast to Vermetidae was not attached to some substrate. Convergence is noted to uncoiling that occurs among fresh water gastropods belonging to the Planorbidae (*Gyraulus*) and Valvatidae (*Orygoceras*) (RIEDEL 1993, NÜTZEL & BANDEL 1993), but both these groups developed in fresh water and belong to the Heterostropha and are not related to the Caenogastropoda.

Members of the subfamily Caecinae with the only genus *Caecum* discard their early ontogenetic shell and begin to uncoil after metamorphosis. In the subfamily Pedumicrinae the early ontogenetic part of their shell remains attached to the teleoconch. Caecinae and Pedumicrinae have an uncoiled teleoconch. In the genus *Ctiloceras* the larval shell indicates its place among the Pedumicrinae even though the teleoconch is secondarily spirally coiled.

The larvae of the Caecidae recapitulate the type of larval shell found among their ancestors that lived further back in time, probably the Late Cretaceous. It is possible but not sure that stem group caecids had a low spired shell similar to that found among Recent vitrinellids (MOORE 1962). The history of the Vitrinellidae ranges back into the Cretaceous (SOHL 1969, BANDEL 1993, Pl.6, Figs.5,6, DOCKERY 1993, Pl.11, Figs.2-9), and these have the same ornament and general shape in their larval shells (BANDEL 1993). Thus, MOORE´s assumption of vitrinellid relation to the Caecidae is supported by the similarities of the larval shell.

The life cycle of the caecid ancestor resembles that present in many marine lower Caenogastropoda with a normally coiled trochospiral shell. A similar shell ornament and shape as found on the caecid protoconch is developed in the small littorinimorph

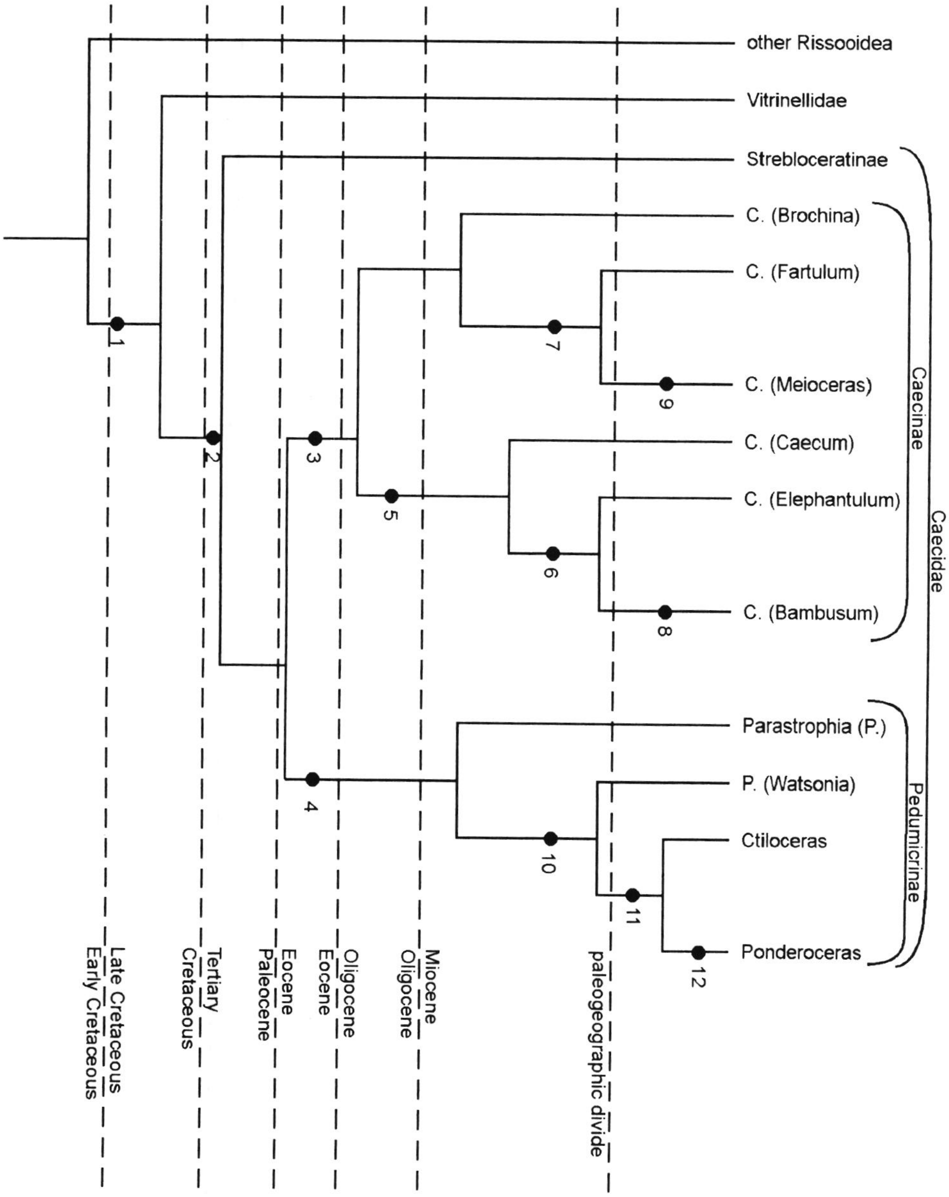

Table 1: Cladogram indicating the relations among Caecidae within the range of their evolution in time. 1 indicates the appearance of larval ornament of inclined spiral lirae. 2 represents the begin of uncoiling of the teleoconch. 3 is the begin of truncation of early ontogenetic shell portions (Caecinae) while 4 represents the uncoiling of the larval shell in the other branch (Pedumicrinae). 5 indicates the appearance of shell annulations which in 6 becomes connected to longitudinal striation in the ornament of the teleoconch. 7 indicates a twist of the aperture at the shell end, and 9 marks a decrease in the width of the aperture in fully grown stages. 10 marks the begin of transversal ribbing of the teleoconch, and in 11 the teleoconch begins to coil spirally, with spiral coiling in 12 also appearing in the larval shell.

Vitrinellidae Bush, 1897 of which Moore (1962) suggested a relation to the Caecidae. Vitrinellidae are probably of rissooidean stock (Bieler & Mikkelsen 1988, Ponder 1988, 1994). Their embryonic shell has a delicate ornamental pattern of shallow grooves surrounded by an irregular net of ridges as is common among lower Caenogastropoda (Pl.4 , Figs.1,2,3). The embryonic shell has the size range of less than 0.1 mm as is usually the case among these lower caenogastropods (Bandel 1975). With this shell the larva hatches to take up planktonic life which lasts a few weeks, as is the case among many marine Littorinimorpha. During this time of planktotrophic life the larval shell is constructed that may bear a fine ornament of continuous or interrupted spiral lirae (Bieler & Mikkelsen 1988, Fig.9) (Text-figs.22, 23, 24).

In many other groups of Littorinimorpha, as defined by Bandel (1992), the larval shell has a quite different ornamentation. The protoconch of the Vitrinellidae, along with the tentacles equipped with terminal bristles, and the horny multispiral concentric operculum may represent plesiomorphic characters, distinguishing the two families Vitrinellidae and Caecidae from the other Rissooidea Gray, 1847 as suggested by Moore (1962).

When the production of a septum that seals off early and no longer used portions of the shell was connected to a dissolution ring posterior to the septum position the early shell was discarded, and the next step in evolution within the Caecidae had proceeded in the *Caecum* direction. This apomorphic character of the Caecinae had developed in the Eocene. The tiny (1 to 3 mm long) animals with tusk-shaped shell since then plow their way through soft sediment, algal thickets and across pebble surfaces and feed on unicellular algae. Since the early ontogenetic shell has been discarded, its shape is almost irrelevant to the growing juvenile and adult. Some species still have lowly trochspiral protoconchs of the type found among the Vitrinellidae, others have planospiral protoconchs. All the early species belong to the subgenus *Brochina* with simple slightly curving apically closed tube-shells forming the fully grown adults. The shell is smooth, and its increase in width minute in respect to its last form.

The subgenus *Caecum* developed later and was clearly present in the Oligocene time (Lozouet 1986, Porta et al 1993). It has since been distributed around the world and is found in all Oceans.

The subgenera *C.* (*Bambusum*) and *C.* (*Elephantulum*) can be found in the western Atlantic, the Caribbean Sea and the Western Pacific, but not in the eastern Indopazific Ocean. This indicates that their origin lay in the Caribbean region and on the American shelf and that they were unable to spread along old Tethyan pathways as had been possible before Oligocene and Eocene times. The same can not be said about *C.* (*Meioceras*), even though it is not very different from *C.* (*Fartulum*) that occurs in all oceans and should have appeared at similar times as *C.* (*Caecum*).

The spiral coiling mode of the ancestor still remains visible, as is seen in *C.* (*Meioceras*) *nitidum* with its horn-like juvenile teleoconch and in *C.* (*Bambusum*) *clava* with its final twist that affects the adult aperture. The strong ornament found in the anulations present in *C.* (*Caecum*) as well as the reticulate pattern seen in *C.* (*Elephantulum*) are best developed in the adult stages and begin slowly in the early teleoconch. They appear late in phylogeny and late in ontogeny and, thus, represent fairly new additions to the characters of the Caecinae.

In the other branch of the caecid diversification in the Eocene the adult character of shell uncoiling that evolves in the adult phase of life has subsequently been transferred to the pelagic larva during ontogeny. This is the Pedumicrinae in which the late ontogenetic uncoiled shell does not separate from the larval shell. Here *P.* (*Parastrophia*) appears early, while the highly ornamented *P.* (*Watsonia*) probably developed from it later. *P.* (*Watsonia*) appears to be restricted to the Pacific Ocean i.c. to south eastern Asia and Australia. On the other hand *Caecum* (*Meioceras*) appears to be characteristic of the Caribbean Sea. This indicates a fairly late evolution of these subgenera belonging to the Pedimicrinae (*Watsonia*) on one hand and the Caecinae (*Meioceras*) on the other hand.

The uncoiling in the larval shell in the *Ctiloceras* offshoot of the Pedumicrinae was succeeded by a coiled teleoconch. In the *Ctiloceras* branch the original adult character has, thus, disappeared, while the larvae are more conservative and retain the shape of their ancestors. This is a principle which conditions the occurrence of ancient adult features and which make larvae valuable for considerations of phylogeny (Jägersten 1972). Once an adult character has been lost in the adult it cannot appear in the larva. Thus, the uncoiled larval shell of *Ctiloceras* and *Ponderoceras* clearly present evidence of their derival from ancestors within the Pedumicrinae around *Parastrophia* and recapitulate an ancient adult that had a teleoconch like *Strebloceras*. The tendency to coil the shell again at later ontogeny has moved into the larval shell in *Ponderoceras*. This new genus can therefore be derived from an ancestor such as the present genus *Ctiloceras*.

In *Caecum* the shape of the embryonic and larval shell is of little significance to the benthic animal since it is discarded soon after metamorphosis. To a veliger swimming with a ciliary apparatus the morphology of its shell is also of little importance, as soon as evolution had produced an uncoiled adult shell. The shell is here utilized as protective exoskeleton, and its shape is not very relevant in regard to the fitness of the larva. New free paths have, thus, been opened to the morphology of the embryonic and larval shell of caecids.

These free paths in morphology of the larval shell are documented by 1. normally trochospirally coiled larval shells in *Strebloceras* and some species of *Caecum*; 2. planospirally coiled larval shells in most species of *Caecum*; 3. uncoiled larval shells in *Parastrophia* and *Ctiloceras*; and perhaps 4. uncoiled larval and embryonic shell in the *Thecopsella* form of *Parastrophia*. In the peculiar side branch of northern Australian caecids of the genus *Ctiloceras*, the adult shell is coiled again while the larval shell remains uncoiled like in *Parastrophia*. In *Ponderoceras* the trend regarding the larval shell seems to have been reverted again and it is converted into a still open spiral, but evenly curved form (Text-fig.21).

Uncoiling of shell occurs independently in the larval shell and in the adult shell. The despiralization of the larval shell in *Caecum* (*Meioceras*) is not linked to the cow-horn-like open spiralization present in the juvenile shell. A comparable despiralization of the protoconch occurs in *Parastrophia* named „*Fartulum* sp.“ by Hughes (1983a) and is connected to a similar cow-horn-like juvenile teleoconch. On the other hand are the larval shell of *Strebloceras* as well as that of *Caecum* trochospirally coiled, while the teleoconch is a non spiralized tube. In the lineage of the Caecidae the embryonic shell remained conservatively unaffected by despiralization as seems to be a general feature noted among the Caenogastropoda. Therefore the case of *Thecopsella* may represent a mistake in observation or preservation artifact. During ontogenetic development accidental despiralized embryonic shells found on hatching veliger larvae are commonly observed (Bandel 1975), but they seem to end always in early death of these individuals. This is different among the Heterostropha where uncoiled embryonic shells occur in serveral lineages, especially visible in the Pteropoda (Bandel & Hemleben 1995).

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# Plate 1 - 13

## Plate 1

Fig. 1: The central teeth of the radula of *Caecum (Brochina) glabrum* from the Mediterranean Sea near Banyuls-Sur-Mer 3000 times magnified.

Fig. 2: Detail with central, lateral and inner marginal teeth of the radula of *Caecum (Brochina) glabrum* (detail to Fig.3) 3000 times magnified.

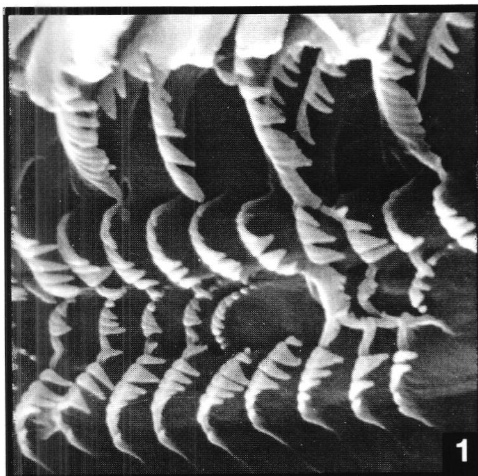
Fig. 3: Anterior part of the radula of *Caecum (Brochina) glabrum* from the Mediterranean Sea near Banyuls-Sur-Mer 1000 times magnified.

Fig. 4: Radula of *Caecum (Brochina) glabrum* from the Mediterranean Sea near Banyuls-Sur-Mer 1000 times magnified.

Fig. 5: The protoconch of *Strebloceras edwardsii* from the Oligocene of the Aquitaine measures 0.3 mm across and is trochospirally coiled (detail Fig.6).

Fig. 6: *Strebloceras edwardsii* with 1.9 mm long shell from the Oligocene of the Aquitaine, France (RGM Nr.228,494, Leiden).

Fig. 7: *Strebloceras edwardsii* in lateral view with slightly curving shell that succeeds the trochospiral protoconch (same as Fig.6).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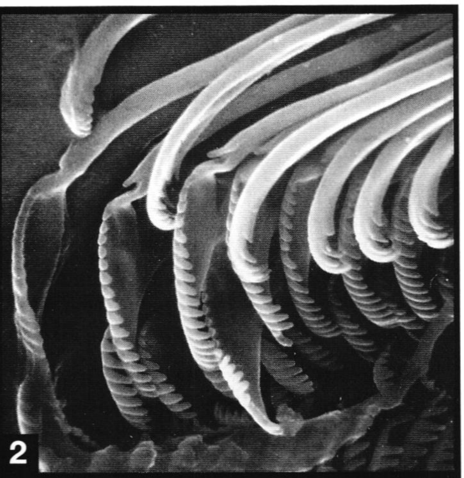
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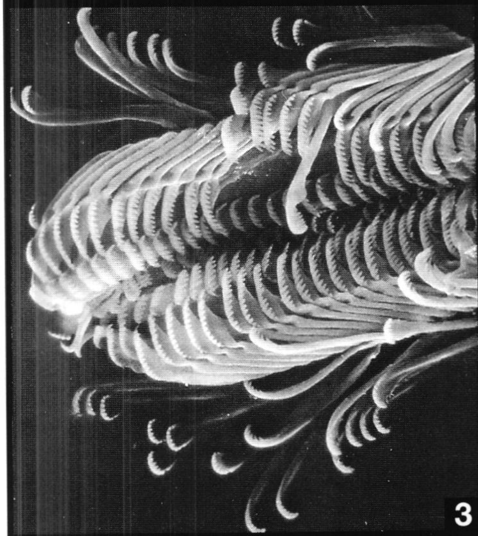
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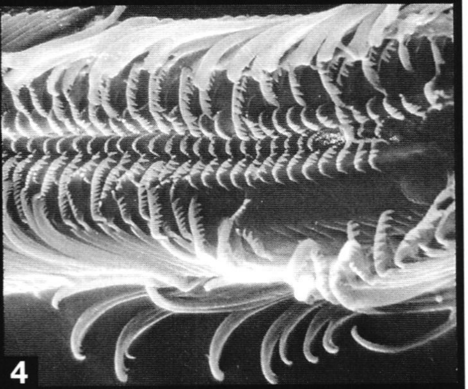
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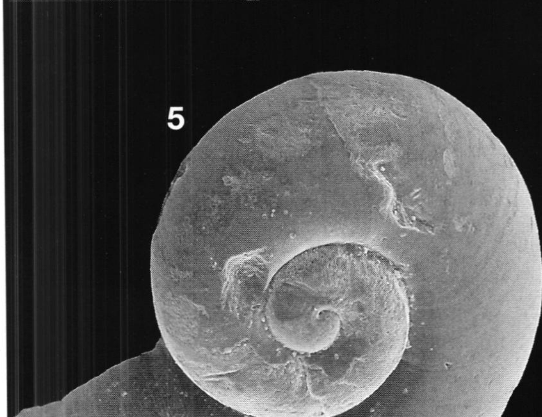
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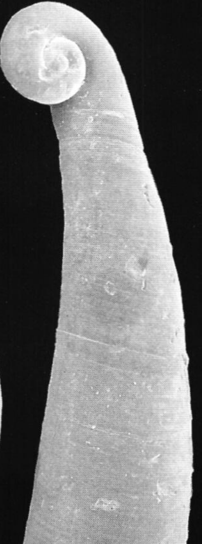
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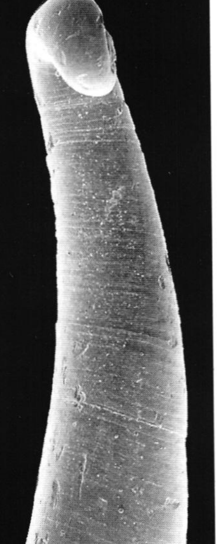
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## Plate 2

Fig. 1: *Caecum (Fartulum) glabellum* from Lizard Island, Queensland, Australia with 1.5 mm long shell. (detail in Fig. 5).

Fig. 2: *Caecum (Brochina) erroneum* with 5 mm long last growth stage from the Mid Eocene (Villiers) of the Paris Basin.

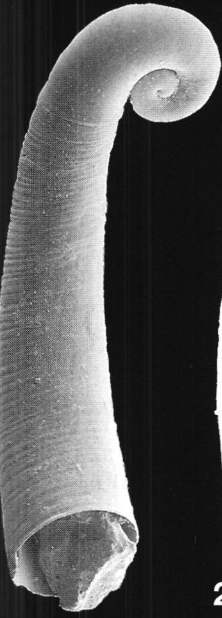
Fig. 3: The protoconch of *Caecum (Brochina) glabrum* from the Mediterranean Sea near Banyuls-Sur-Mer has a slightly trochospiral twist. The shell measures 1.5 mm in length.

Fig. 4: Intermediate growth stage of *Caecum (Fartulum) glabellum* from Lizard Island, Queensland, Australia with sudden increase in width and 2 mm long shell.

Fig. 5: The protoconch of *Caecum (Fartulum) glabellum* from Lizard Island, Queensland, Australia measures 0.34 mm across.

Fig. 6: The low trochospiral protoconch of *Caecum (Fartulum) antillarum* from Villa Concha near Santa Marta, Colombia is attached to the early teleoconch. Length 1.2 mm.

Fig. 7: The protoconch and early teleoconch of *Caecum (Brochina) digitulum* measure 1.1 mm in length. (NZ Museum Nr. M30666) (details in Pl.3, fig.2)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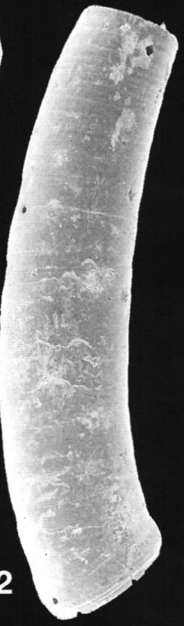
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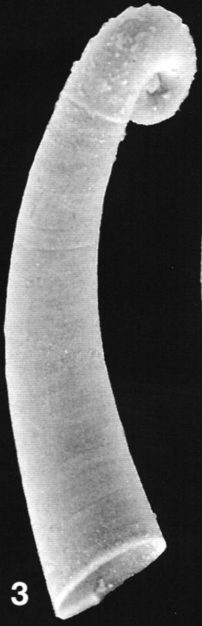
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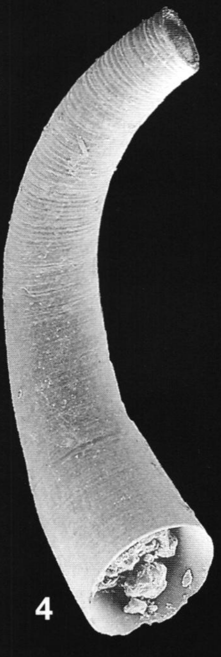
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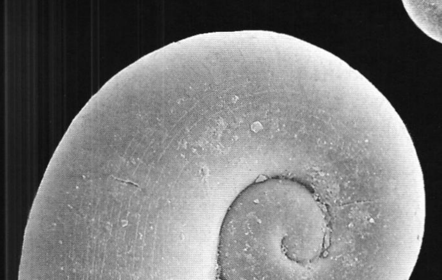
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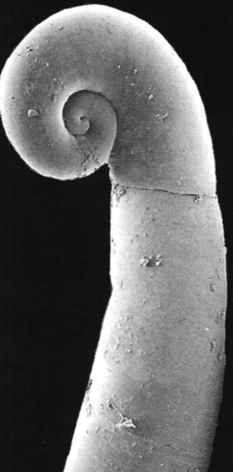
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## Plate 3

Fig. 1: *Caecum (Fartulum) glabellum* from Lizard Island, Queensland, Australia with 1.95 mm long shell.

Fig. 2: *Caecum (Brochina) digitulum* from Middlesex Bank, New Zealand with 2.4 mm long shell (N.Z. Museum, Nr. M.100521)

Fig. 3: *Caecum (Fartulum) glabellum* from the reef lagoon of the Red Sea near Port Sudan with 4 mm long shell.

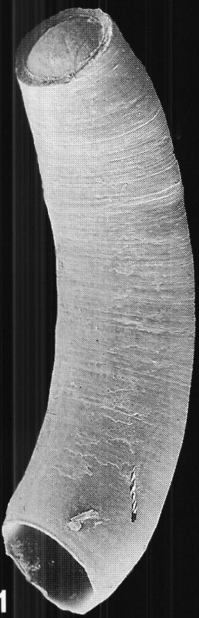
Fig. 4: Growth stage of *Caecum (Fartulum) antillarum* with sudden increase in shell diameter and 1.9 mm long shell.

Fig. 5: Last growth stage of *Caecum (Brochina) vestitum* from Galerazamba near Cartagena, Colombia with 2.7 mm long shell and fine longitudinal striae and apertural rings.

Fig. 6: Fully grown shell of *Caecum (Fartulum) antillarum* from Santa Marta, Colombia with 1.9 mm long shell.

Fig. 7: *Caecum (Brochina) schulzei* from the Oligocene of Kassel with protoconch and early teleoconch. Shell length 0.7 mm.

Fig. 8: The embryonic shell of *Parastrophia* cf. *asturiana* from the Oligocene of Glimmerde (near Kassel) measures 0.09 mm in diameter and shows the onset of the coiled and uncoiled larval shell indicated by the begin of growth lines (detail to Pl.10, Fig.4).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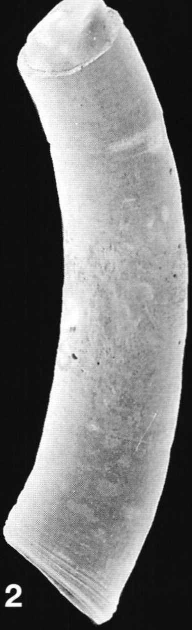
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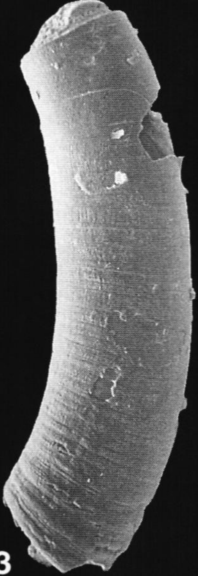
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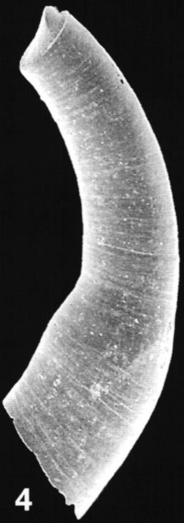
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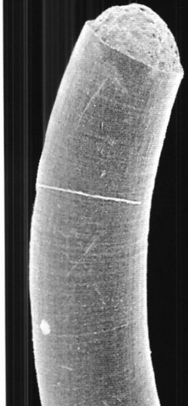
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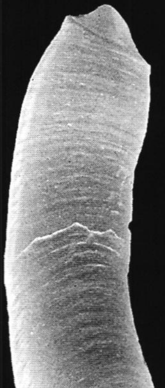
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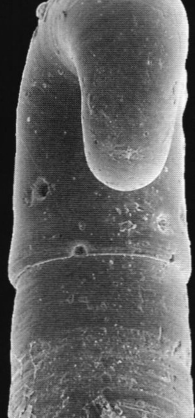
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## Plate 4

Fig. 1: The embryonic shell of *Caecum (Brochina) digitulum* from Waitotura, New Zealand (N.Z. Museum, Nr. M30666) is ornamented, ends with first growthlines and measures 0.9 mm across.

Fig. 2: The embryonic shell of *Parastrophia (Watsonia) elegans* from Hope Island, Australia (detail to Pl.9, Figs.1,2) has pit and ridge ornament, the onset of the larval shell indicated by growth lines and is 0.9 mm in diameter.

Fig. 3: The embryonic shell of *Caecum (Brochina) digitulum* seen from the side with onset of the larval shell (detail to Fig.1).

Fig. 4: *Caecum (Brochina)* sp. from Madeira (British Museum, Nr. 1615) has a non-planktotrophic development and therefore a simplified protoconch of 0.25 mm diameter.

Fig. 5: The juvenile shell of *Caecum (Elephantulum) troglodyta* from the mangrove pond at Ferry Point, Bermuda has a smooth early teleoconch and late appearance of longitudinal ribs. Shell length 2.4 mm.

Fig. 6: The embryonic shell of *Caecum (Elephantulum) troglodyta* from Bermuda measures 0. 3 mm and was formed in non planktotrophic development.

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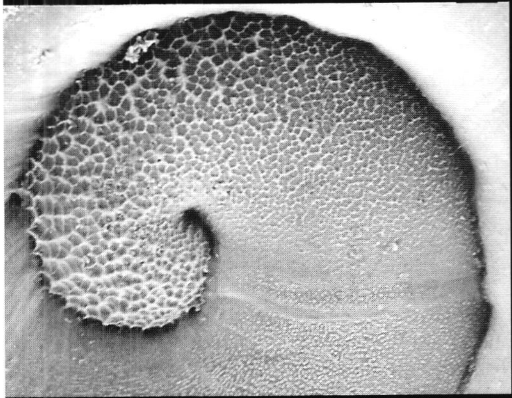

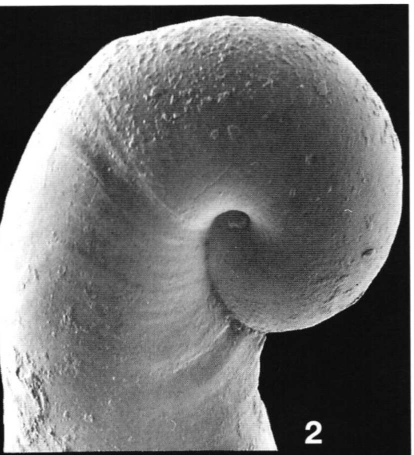

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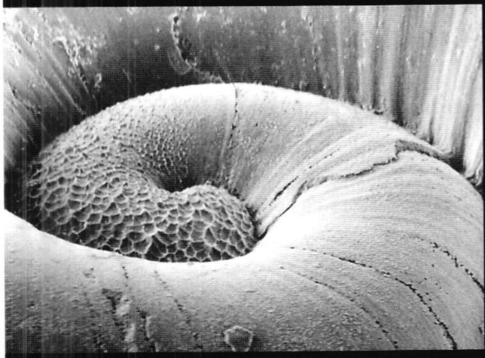

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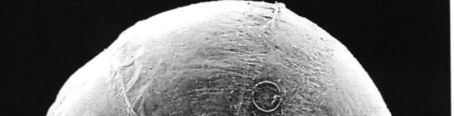

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## Plate 5

Fig. 1: In the adult shell of *Caecum* (*Meioceras*) *nitidum* with 2.3 mm length from Santa Marta, Colombia growth recessions may result in late production of an even larger adult stage.

Fig. 2: Last stage of growth of *Caecum* (*Meioceras*) *nitidum* from Santa Marta, Colombia with 2.5 mm length.

Fig. 3: Intermediate stage of *Caecum* (*Meioceras*) *nitidum* from Santa Marta, Colombia with rapid increase in shell diameter and open trochospiral twist ending. The shell is 2.7 mm long.

Fig. 4: Intermediate stage of *Caecum* (*Meioceras*) *nitidum* from Santa Marta with operculum and 1.3 mm length.

Fig. 5: Earliest section of the shell of *Caecum* (*Meioceras*) *nitidum* from Santa Marta with protoconch attached and 1.6 mm length.

Fig. 6: The larval shell of *Caecum* (*Meioceras*) *nitidum* from Villa Concha near Santa Marta, Colombia is 0.3 mm in diameter.

Fig. 7: The larval shell of *Caecum* (*Brochina*) *schulzei* from the Oligocene of Kassel is of planispiral shape and measures 0.28 mm across.


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## Plate 6

Fig. 1: Transitional stage of *Caecum (Caecum) pulchellum* from Galerazamba near Cartagena, Colombia with sudden widening of the 2.6 mm long shell connected to ornament change near the aperture.

Fig. 2: Last growth stage of *Caecum (Caecum) pulchellum* from Curacao with 2.7 mm long shell.

Fig. 3: The second last stage of *Caecum (Caecum) pulchellum* from Santa Marta, Colombia with 1.9 mm long shell.

Fig. 4: Transitional stage of *Caecum (Caecum) pulchellum* from Galerazamba near Cartagena, Colombia with sudden widening of the 1.2 mm long shell.

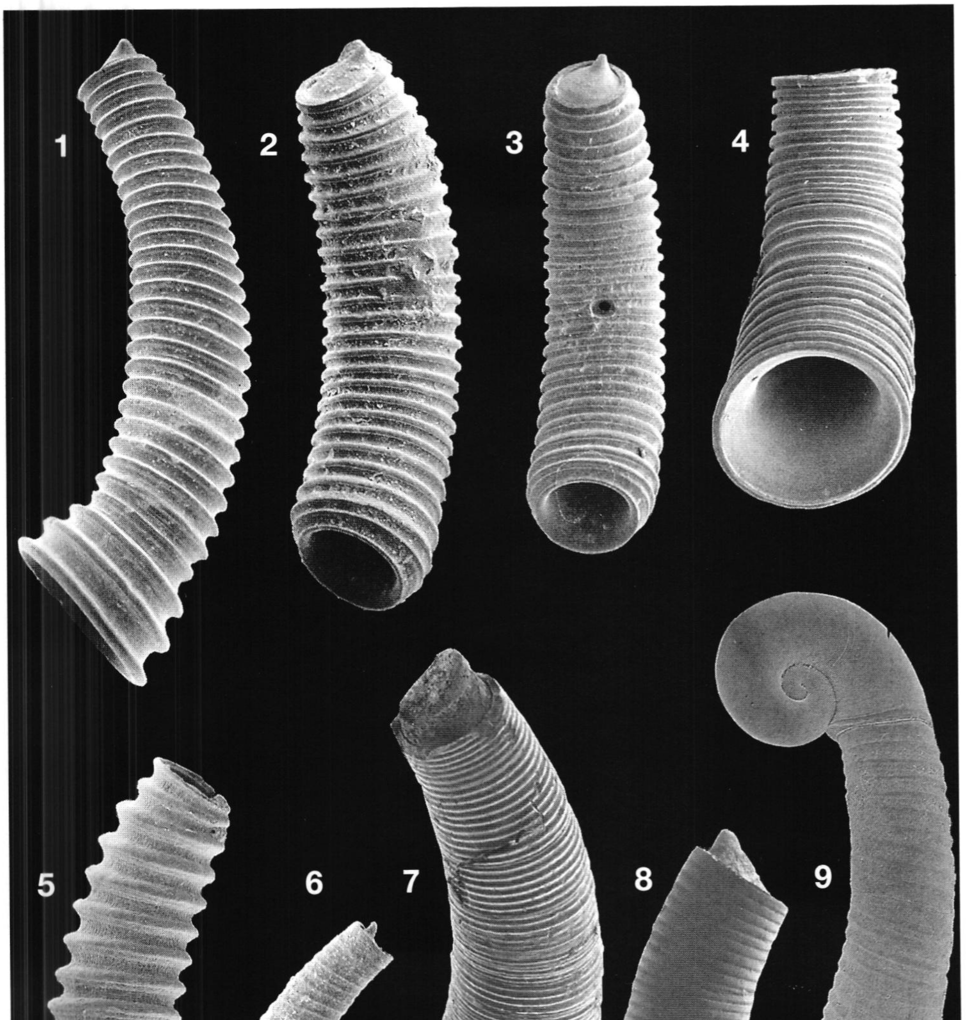
Fig. 5: Late stage of *Caecum (Caecum) gracile* from Port Sudan, Red Sea with 2.1 mm long shell.

Fig. 6: Intermediate stage of *Caecum (Caecum) pulchellum* with change in ornament and diameter from Villa Concha near Santa Marta, Colombia with 1.8 mm long shell.

Fig. 7: Juvenile shell of *Caecum (Caecum) imperforatum* from the Oligocene of the Aquitaine (Peyrére) with 1.6 mm length (RGM PC469-6, Leiden).

Fig. 8: Intermediate shell of *Caecum (Caecum) imperforatum* from Exmouth, southern England with 2.1 mm length. (British Museum Nr. 1858)

Fig. 9: Juvenile shell of *Caecum (Caecum) gracile* from Cebu, Philippines with protoconch and 1.1 mm total length.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## Plate 7

Fig. 1: The last growth stage of *Caecum (Caecum) pulchellum* from Galerazamba near Cartagena (Colombia) has ornament collabral ribs with smooth background. Distance between two ribs is 0.09 mm.

Fig. 2: The second last stage of *Caecum (Caecum) pulchellum* from Santa Marta, Colombia, with rib distance of 0.08 mm and striated background ornament. (Detail to Pl.6, Fig.3).

Fig. 3: The ornament of the second last stage of *Caecum (Elephantulum) imbricatum* from Santa Marta with annulations of 0.05 mm width.

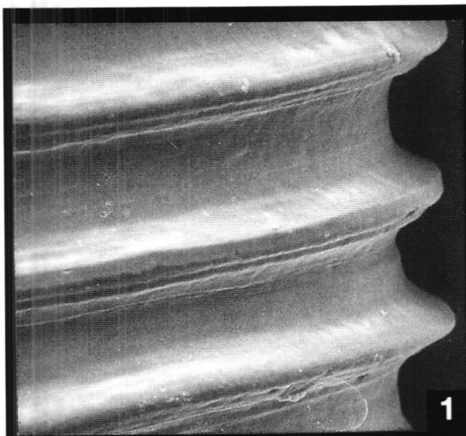
Fig. 4: The ornament of the last stage of *Caecum (Elephantulum) imbricatum* with many longitudinal ribs and furrow like annulations of about 0.2 mm distance to each other.

Fig. 5: Late growth stage of *Caecum (Elephantulum) imbricatum* from Arecifes Bay near Santa Marta, Colombia with 4.3 mm long shell.

Fig. 6: The last growth stage of *Caecum (Elephantulum) imbricatum* from Arecifes Bay near Santa Marta, Colombia with 3.5 mm long shell.

Fig. 7: Protoconch and first teleoconch with ornament of annulation of indistinct longitudinal ribs of *Caecum (Elephantulum) imbricatum* from Villa Concha near Santa Marta, Colombia of 0.7 mm length.

Fig. 8: The protoconch of *Caecum (Elephantulum) imbricatum* from Villa Concha near Santa Marta, Colombia measures 0.3 mm across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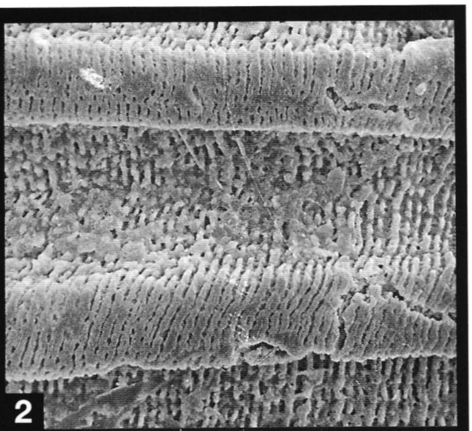
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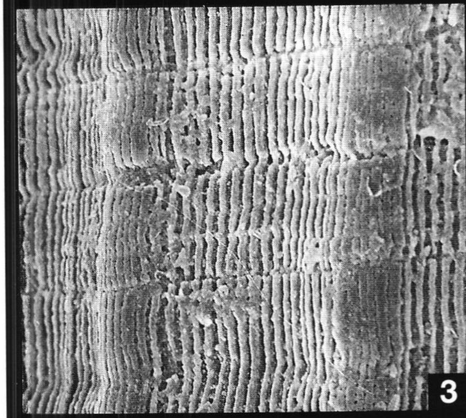
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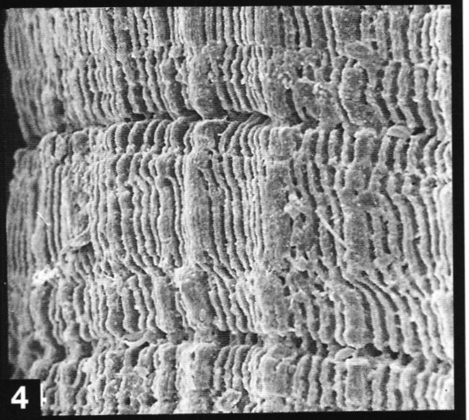
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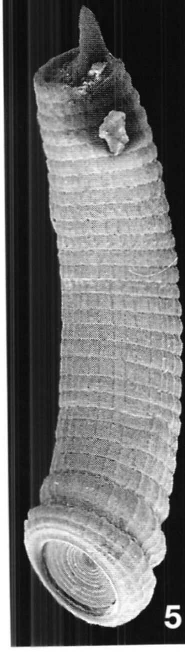
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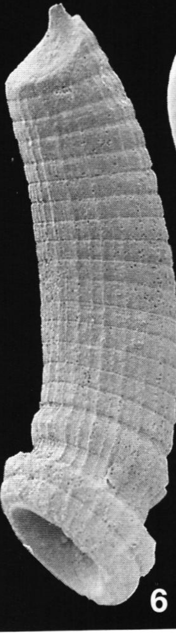
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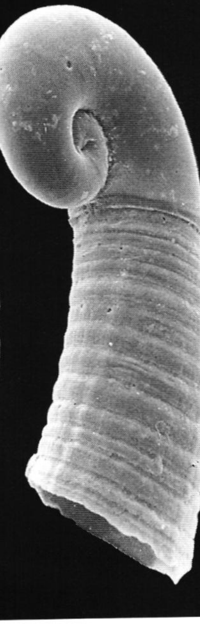
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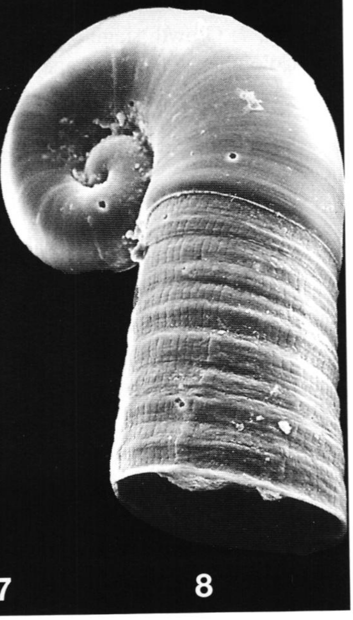
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## Plate 8

Fig. 1: Apertural thickening of *Caecum (Bambusum) plicatum* from Galerazamba near Cartagena, Colombia with 0.8 mm wide aperture.

Fig. 2: Apical end with septum of *Caecum (Bambusum) plicatum* from Galerazamba near Cartagena, Colombia with 0.5 mm width.

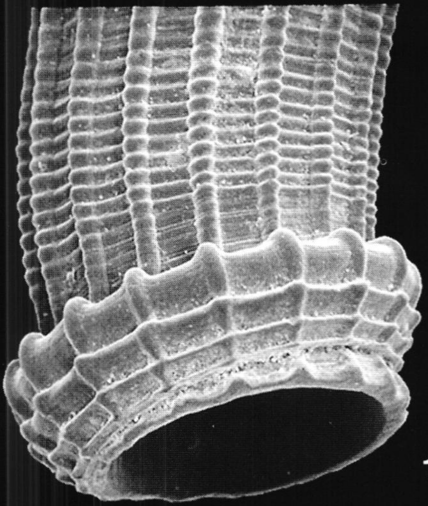
Fig. 3: Intermediate growth stage of *Caecum (Bambusum) plicatum* from Galerazamba near Cartagena, Colombia with 4 mm length.

Fig. 4: Late growth stage of *Caecum (Bambusum) plicatum* from Galerazamba near Cartagena, Colombia with 3.9 mm length.

Fig. 5: Intermediate growth stage of *Caecum (Elephantulum) imbricatum* from Santa Marta, Colombia is 2.4 mm long.

Fig. 6: Late growth stage of *Caecum (Elephantulum) imbricatum* from Arecifes Bay near Santa Marta with 3.1 mm long shell.

Fig. 7: Growth stage of *Caecum (Bambusum) plicatum* from Santa Marta Rodadero, Colombia with twisted aperture and 2.3 mm length.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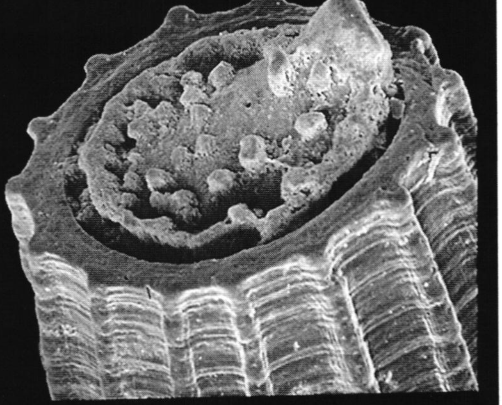
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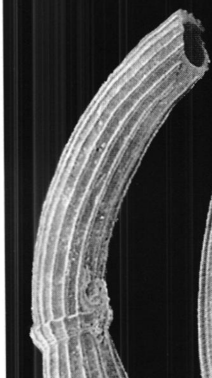
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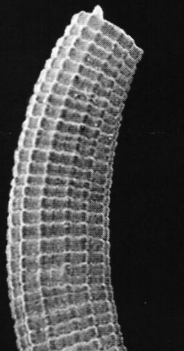
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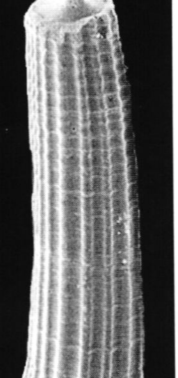
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## Plate 9

Fig. 1: *Parastrophia* (*Watsonia*) *elegans* from Hope Island (Australia) with 2.1 mm long shell (Australian Museum Nr. C27502).

Fig. 2: *Parastrophia* (*Watsonia*) *elegans* in detail to Fig 1 with the 0.65 mm long protoconch that ends in a varix.

Fig. 3: *Parastrophia* (*Watsonia*) *elegans* from Cebu (Philippines) with 3.2 mm long shell and protoconch broken off.

Fig. 4: *Parastrophia* (*Watsonia*) *elegans* in detail to Fig. 3 with the aperture measuring 0.8 mm across and growth increments showing repeated growth of adult shell.

Fig. 5.The ornament of *Parastrophia* (*Watsonia*) *elegans* in detail to Fig. 1.

Fig. 6: *Parastrophia* (*Parastrophia*) *cygnicollis* from Capricorn Island (detail see Pl. 10, Fig.4) with 2.8 mm long shell.

Fig. 7: *Parastrophia* (*Parastrophia*) *queenslandica* with 2.8 mm long shell from Hope Island (Australia) (Australian Museum Nr. C27503).

Fig. 8: *Parastrophia* (*Parastrophia*) *asturiana* from Istria, Adriatic Sea, Mediterranean with 3.3 mm long shell (RGM 224,574, Leiden). (Detail see Pl.10, Fig.1).

Fig. 9: *Parastrophia* (*Parastrophia*) cf. *asturiana* from Turkey with 0.8 mm long protoconch.

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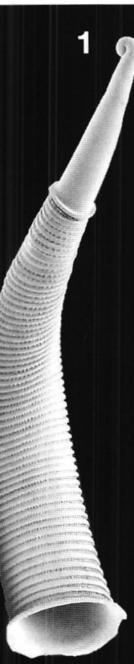

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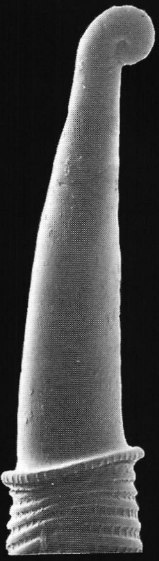

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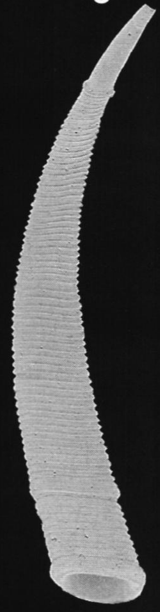

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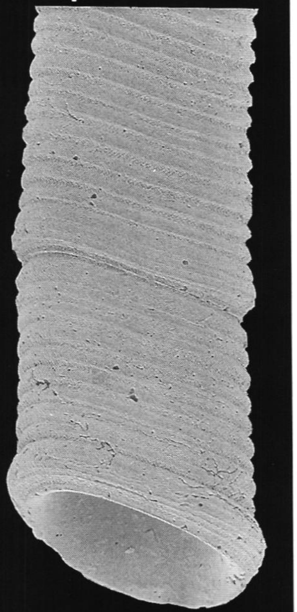

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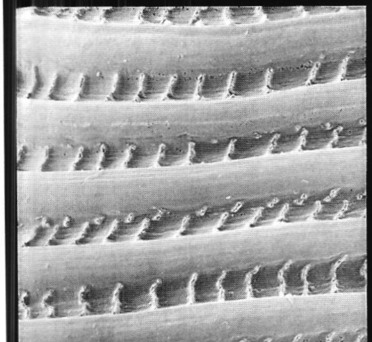

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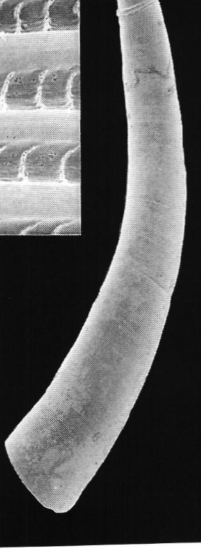

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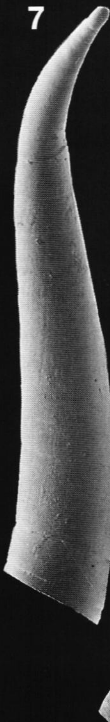

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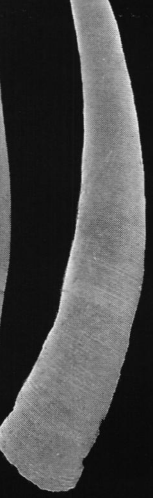

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## Plate 10

Fig. 1: *Parastrophia (Parastrophia) asturiana* from the Adriatic Sea near Istria (RGM 224,574 Leiden). The shell is 3.3 mm long and also illustrated in Pl.9, Fig.8.

Fig. 2: *Parastrophia (Parastrophia) asturiana* from St. Jean de Luz, Biscaya with 3.5 mm long shell. (British Museum Nr. 172-20).

Fig. 3: *Parastrophia (Parastrophia)* cf. *asturiana* from Glimmerode (Chattium, Oligocene of Kassel) with 0.9 mm long larval shell.

Fig. 4: *Parastrophia (Parastrophia)* cygnicollis with o.5 mm long protoconch that ends in a varix from Capricorn Islands in Australia (Austalian Museum Nr. C19640).

Fig. 5: Protoconch of *Parastrophia (Parastrophia) asturiana* (detail to Fig.2) with 0.5 mm long larval part that ends in a varix attached to the teleoconch with ornament of growth lines.

Fig. 6: *Parastrophia (Parastrophia)* cf. *asturiana* from the Oligocene of Glimmerode (Hessen) (same as Fig.3) with varix on the end of the protoconch well developed.

Fig. 7: *Parastrophia (Parastrophia)* cf. *asturiana* from the Oligocene of the Aquitaine (Peyrére) has a 0.6 mm long protoconch.

Fig. 8: The protoconch of *Parastrophia (Parastrophia) queenslandica* (detail to Pl.9, Fig.7) has less than one whorl and measures 0.28 mm in width.

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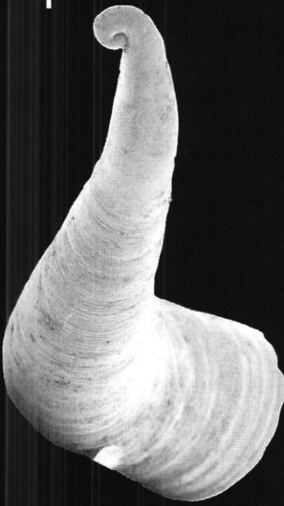

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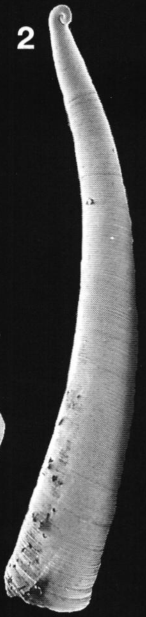

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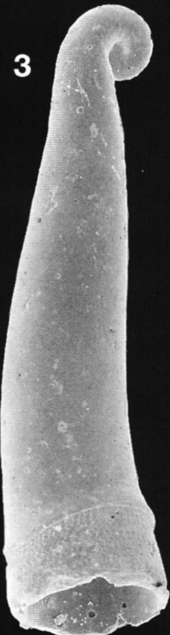

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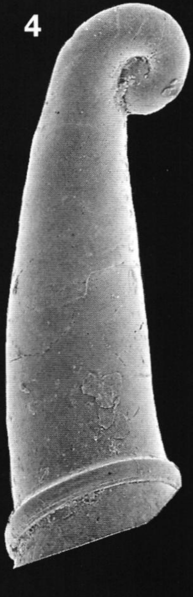

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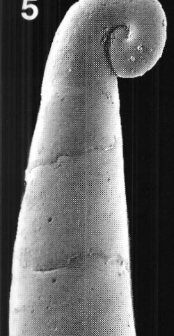

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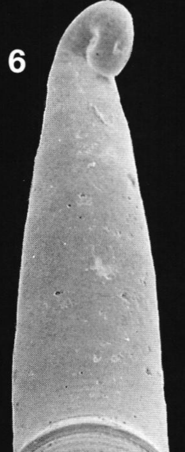

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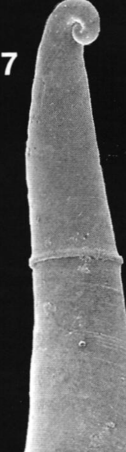

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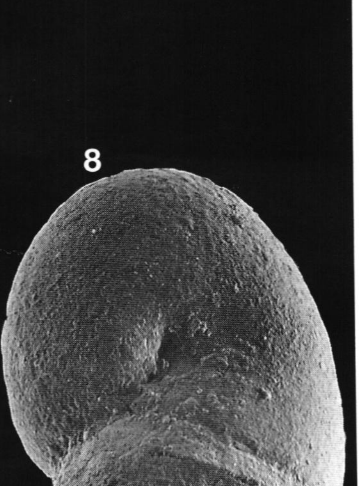


## Plate 11

Fig. 1: *Ctiloceras (Transcopia) clathrata* from Darwin, Northern Territories, Australia with shell measuring about 1 mm across. (Australian Museum Nr. C162394)

Fig. 2: Protoconch of *Ctiloceras (Transcopia) clathrata* in detail to Fig.1.

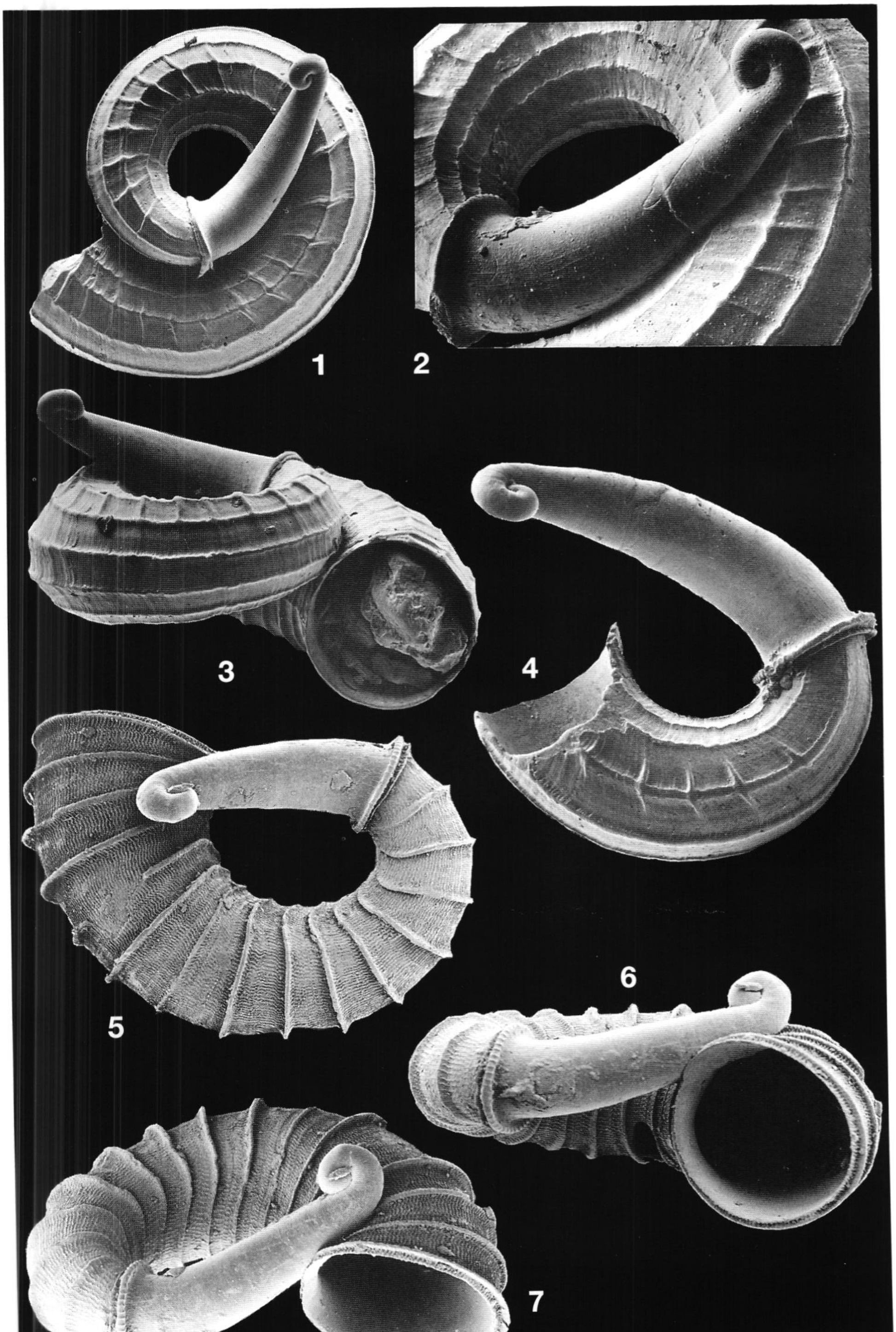
Fig. 3: Apical view of *Ctiloceras (Transcopia) clathrata* from Darwin, Northern Territories, Australia with shell measuring 1.1 mm across. (Australian Museum Nr. C162394)

Fig. 4: Protoconch and early teleoconch of *Ctiloceras (Transcopia) clathrata* from Darwin, Northern Territories, Australia with shell measuring 0.7 mm across. (Australian Museum Nr. C162394)

Fig. 5: Apical view of *Ctiloceras (Ctiloceras) cyclicum* from Darwin, Northern Territories, Australia with shell measuring 0.8 mm across. (Australian Museum Nr. C162397)

Fig. 6: Apertural view of *Ctiloceras (Ctiloceras) cyclicum* (same as Fig.5).

Fig. 7: *Ctiloceras (Ctiloceras) cyclicum* like Fig.5.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## Plate 12

Fig. 1: Apical view of *Ctiloceras* (*Carinoceras*) *bicarinata* from Darwin, Northern Territories, Australia with 0.9 mm large shell.

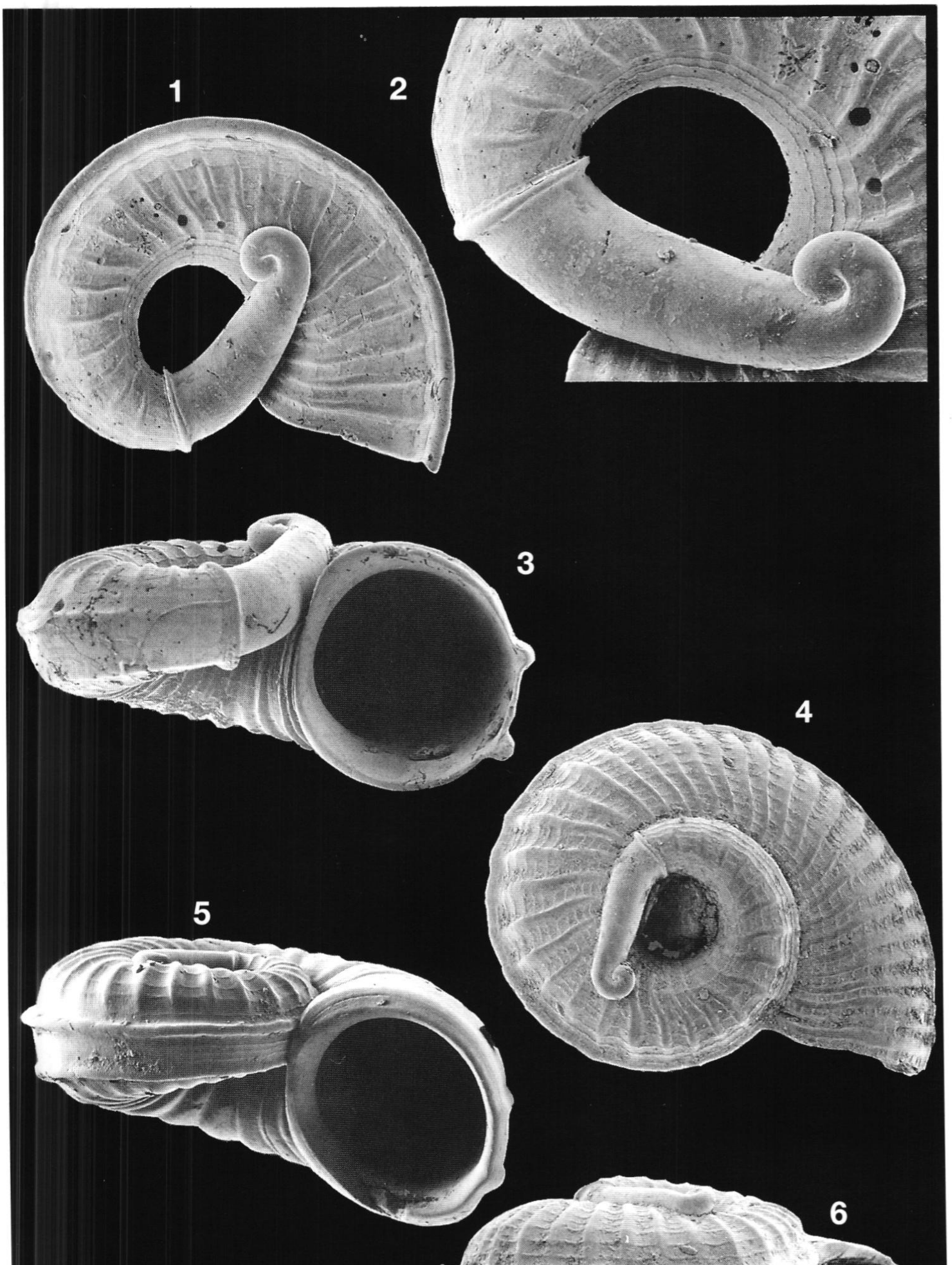
Fig. 2: The protoconch of *Ctiloceras* (*Carinoceras*) *bicarinata* (Detail to Fig.1).

Fig. 3: Apertural view of *Ctiloceras* (Carinoceras) *bicarinata* of the same shell as in Fig.1 (Austalian Museum Nr. C162314)

Fig. 4: Apical view of *Ctiloceras* (*Carinoceras*) *bicarinata* from Port Hedland with 1.5 mm large shell (Australian Museum Nr. C162315).

Fig. 5: Apertural view of *Ctiloceras* (*Carinoceras*) *bicarinata.*

Fig. 6: Apertural view of *Ctiloceras* (*Carinoceras*) *bicarinata* (same as in Fig.4).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## Plate 13

Fig. 1: Apical view of *Ctiloceras* (*Torresella*) *striata* from Darwin, Northern Territories, Australia with 1.6 mm large shell (Australian Museum Nr. C162398)

Fig. 2: Protoconch and early teleoconch of *Ctiloceras* (*Torresella*) *striata* (detail to Fig.1).

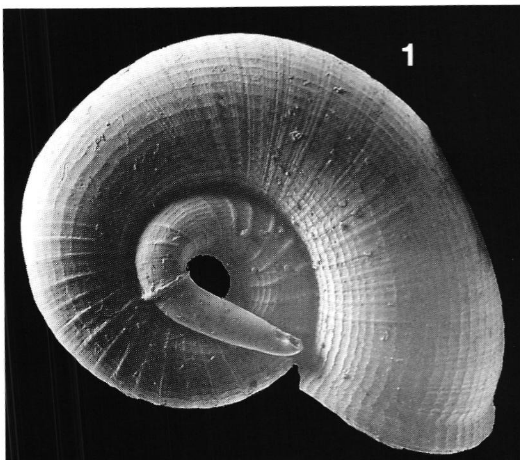
Fig. 3: *Ctiloceras* (*Torresella*) *striata* (same as in Fig.1).

Fig. 4: Apertural view of *Ponderoceras annulatum* from the Gulf of Carpenteria, northern Australia with 2.5 mm large shell.

Fig. 5: The apex of *Ponderoceras annulatum* with protoconch fitted in the teleoconch leaving an umbilical opening. (same shell as in Fig.4).

Fig. 6: Apical view of *Ponderoceras annulatum* from the Gulf of Carpenteria. (same shell as in Fig.4).

Fig. 7: The protoconch of *Ponderoceras annulatum* has openly coiled larval shell and measures 0.2 mm. (detail to Fig.5).



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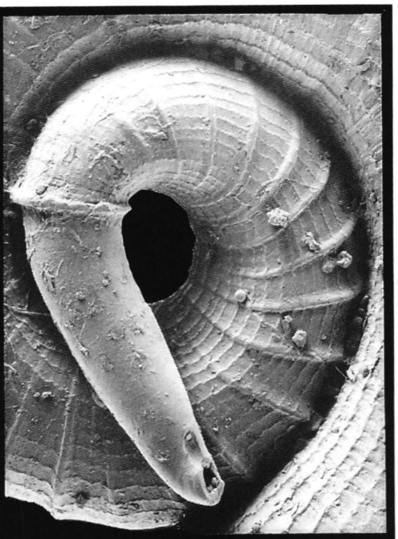

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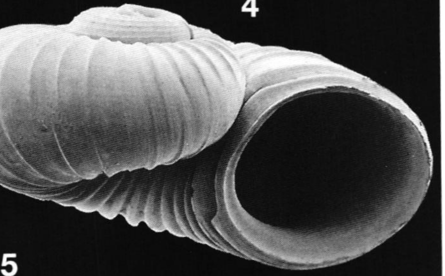

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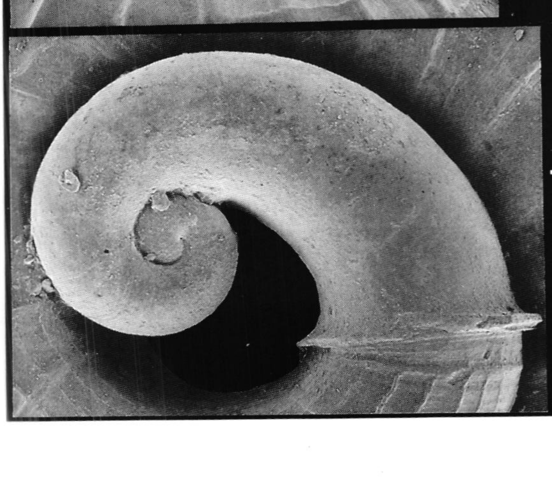

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