

Systematic value of the larval shell of fossil and modern Vanikoridae, Pickworthiidae and the genus *Fossarus* (Caenogastropoda, Mollusca).

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Abstract: The larval shells of *Vanikoro*, *Macromphalus*, and *Megalomphalus* are similar to each other. The convergent genus *Fossarus*, in contrast, is related to the Cerithioidea, especially to the family Planaxidae which is evidenced by the protoconch. *Iselica* is not related but a member of the Heterostropha. The Vanikoridae and Pickworthiidae, documented since Paleocene times, and the Miocene to Recent genus *Fossarus* apparently have ancestors among the Triassic Caenogastropoda and here those with strongly sculptured barrel-shaped to conical larval shells. Regarding their larval shell the Vanikoridae and Pickworthiidae are neither related to the Hipponicidae, nor to the Capulidae, which have an Echinospira-larva, both representing members of the Neomesogastropoda. There's a possible relation to the main groups of the basic Caenogastropoda, especially to the Littorinidae within the Littorinimorpha to which they share many characters of the protoconch. Comparison to Triassic Prostyliferidae is carried out. The new genus *Gania* and the new species *Macromphalus stantoni*, *Vanikoro satonda*, *Constantia acutocostata* (Vanikoridae), *Gania carinata*, *Sansonia hedegaardi*, *Sansonia hilutangensis*, *Sansonia cebuana* and *Mecoliota philippina* (Pickworthiidae) are introduced.

Zusammenfassung: Die Larvalschalen der Gattungen *Vanikoro*, *Macromphalus* und *Megalomphalus* sind einander sehr ähnlich. Die gehäusekonvergente Gattung *Fossarus* dagegen erweist sich aufgrund protoconchmorphologischer Daten als den Cerithioidea, insbesondere der Familie Planaxidae zugehörig. *Iselica* ist nicht verwandt, sondern ein Vertreter der Heterostropha. Die seit dem Paläozän nachgewiesenen Familien Vanikoridae und Pickworthiidae, sowie die seit dem Miozän bekannte Gattung *Fossarus* scheinen Vorfahren unter triassischen Caenogastropoda mit stark skulptierten tonnenförmigen bis konischen Protoconchen zu haben. Die Vanikoridae und Pickworthiidae zeigen jedoch weder Beziehungen zu den Hipponicidae, noch zu den Capulidae mit Echinospira-Larve, beides Vertreter der Neomesogastropoda. Eine mögliche nähere Verwandtschaft könnte zu den Hauptgruppen der basalen Caenogastropoda, insbesondere zu den Littorinidae innerhalb der Littorinimorpha bestehen, denen sie hinsichtlich der Protoconchmorphologie sehr ähnlich sind. Ein Vergleich zu triassischen Prostyliferidae wird dargestellt. Die neue Gattung *Gania* und die neuen Arten *Macromphalus stantoni*, *Vanikoro satonda*, *Constantia acutocostata* (Vanikoridae), *Gania carinata*, *Sansonia hedegaardi*, *Sansonia hilutangensis*, *Sansonia cebuana* und *Mecoliota philippina* (Pickworthiidae) werden beschrieben.

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Introduction

Troschel (1856-1863) had examined the radula of *Fossarus Philippi*, 1841 and noted its distinct shape warranting own family status to the Fossaridae. Thiele (1929) included within this family the genera *Megalomphalus* Brusina, 1871, *Couthouyia* A. Adams, 1860 (including subgenera *Zeradina* and *Radinista*), *Fossarella* Thiele, 1925 and *Fossarus*. Thiele (1929) included Fossaridae and Vanikoridae with the group of limpets Amaltheidae in the superfamily Amaltheacea. The members within this superfamily are considered to own a radula with similar morphology of the teeth and a tendency to form a cap-like shell. Thiele

(1929) separated the Vanikoridae according to their sculpture and characteristic features of the radula from the other two units of his superfamily. Wenz (1939) accepted Thiele's suggestions but changed the terms Amaltheacea into Hipponicea and Vanikoridae into Vanikoroidae. Wenz (1939) included the Triassic *Palaeonarica* in the Fossaridae and also *Lacunaria* Conrad, 1866 from the Eocene.

Gougerot & Le Renard (1981) found among 27 species of Vanikoridae from the Eocene of the Paris Basin transitional forms connecting the genera *Vanikoro* Quoy & Gaimard, 1832, *Lacunaria*, *Macromphalus* Wood, 1842 and

Cymenorhytis Cossmann, 1888. Warén & Bouchet (1988) assembled data on modern representatives of the Vanikoridae especially dealing with the genera *Vanikoro*, *Macromphalus* and *Megalomphalus* with some notes on their anatomy and ecology and a description of their radula. Ponder (1980) had noted that *Fossarus* has a brood pouch above the head as is found among the Planaxidae and Thiaridae (both Cerithioidea) and Warén & Bouchet (1988) noted as further difference between *Fossarus* and members of the Vanikoridae that *Macromphalus* has a penis and large epipodial flaps on each side of the foot which are not present in *Fossarus*.

According to Houbrick (1990) the genus *Fossarus* has close affinity to the Planaxidae, especially to the genus *Supplanaxis* Thiele, 1929. This systematic placement is based on detailed anatomical studies on *Fossarus ambiguus* (Linné, 1758) from the Azores. The morphology of the protoconch supports this placement. Houbrick (1990) suggested that fossarids comprise a subfamily, Fossarinae, within the Planaxidae.

Sansonia Jousseau, 1892 and relation have been included in the Adeorbidae of the Rissooidea in Thiele's (1929) classification. Here it is found with *Mecoliotia* Hedley, 1899, *Pickworthia* Iredale, 1917 and *Reynellona* Iredale, 1917 together with genera like *Cochliolepis* Stimpson, 1858, *Adeorbis* S. Wood, 1842, *Vitrinella* C.B. Adams, 1850, *Microthyca* A. Adams, 1863 and *Moerchiella* Thiele, 1937. Wenz (1939) called this family Tornidae including also genera like *Episcynia* Mörch, 1875 which has been found to be a member of the Heterostropha (Bandel 1996). Vaught (1989) considered *Sansonia* with the subgenera *Mecoliotia*, *Microlotia*, *Pickworthia* and *Reynellona* to be a member of the Vitrinellidae together with genera like *Vitrinella*, *Circulus* Jeffreys, 1865, *Teinostoma* H. & A. Adams, 1853 and others. This classification of *Sansonia* was suggested by Ponder (1985). Ponder & Warén (1988) suggested an independent family status of *Sansonia* within the family Pickworthiidae Iredale, 1917. *Urceolabrum* Wade, 1916 from the Upper Cretaceous Coffee-Sand-Formation of Mississippi/USA had been considered to represent an achaegastropod of the Turbinidae by Wenz (1939). Sohl (1960) accepted this place in the system, but Dockery (1993) found a larval shell which clearly indicates that it actually is a caenogastropod and suggested a connection to

modern *Sansonia*. A similar switch back and forth in the system had occurred with *Microlotia* Böttger, 1901 from the Rissoinae (Wenz 1939) into the genus *Sansonia* (Ponder 1985) within the Pickworthiidae.

Fossil and Recent shells belonging to the above mentioned groups and genera have been studied and allow to trace them back into time to the Early Tertiary. This suggests a perhaps longer lasting independent history of some of these lineages and the data are presented here. The history of the different groups within the Cerithiimorpha and Littorinimorpha (Metamesogastropoda Bandel, 1991) is by no way obvious as yet, and this study may add some data to this puzzle of gastropod evolution. Type-material is deposited under 3760-3773 at the GPluM, Hamburg.

Results

Genus *Fossarus* Philippi, 1841

Warén & Bouchet (1988) studied the radula of *Fossarus* and noted differences to that of *Macromphalus* and *Megalomphalus* which proved to be similar to that of *Vanikoro*. Thus they concluded that *Fossarus* on one side and *Vanikoro* and relation on the other side are not close to each other. *Fossarus* in addition has no penis, no epipodial lappets, no special feature of the foot serving for attachment to the substrate and also differs in regard to the operculum construction. Warén & Bouchet (1988) thus supported a systematic connection that had been suggested by Ponder (1980) that *Fossarus* and *Planaxis* Lamarck, 1822 both with brood pouch above their head, are related. This placement has later been confirmed by Houbrick (1990) who suggested subfamily status of the Fossarinae within the Planaxidae on the base of anatomical studies on *Fossarus ambiguus* from the Azores.

The type species of the genus *Fossarus*, *Turbo ambigua* Linné, 1766, lives in the Mediterranean Sea and the northeastern Atlantic. Its adult shell was figured well by Sabelli & Spada (1977) and the larval shell has been illustrated by Warén & Bouchet (1988) and Houbrick (1990). The western Atlantic species *F. orbigny* Fischer, 1864 is anatomically identical and considered conspecific (Houbrick 1990). The shell of this Caribbean form was studied from Yucatan as well as from a subfossil occurrence of a reef

and its debris in Columbia near Cartagena (Galerazamba) (Pl. 1, figs. 1, 4).

Description: The white teleoconch consists of 2 to 2.5 whorls and the shell is about 1.5 mm high. The protoconch measuring 0.21 mm in height is of quite different shape and of translucent brown coloration as had already been noted by Abbott (1974). The embryonic shell is almost smooth, well rounded and measures only 0.08 mm in width. Its transition into the larval shell after completion of about three quarters of a whorl is marked by the onset of axial ribs that dominate the first larval whorl. About 20 of these are present here and they are sinuous reflecting the position of a sinus in the subsutural outer lip of the veliger shell. In the second larval whorl spiral ridges that had appeared during the course of the first larval whorl become as strong as the axial ribs, thus forming a reticulate pattern with them. The distance between these spiral cords is unequal. Two cords on the base of the subsutural lobe that forms the top of the apertural projection are close to each other and form a ribbon-like band. The change from the larval shell into the teleoconch is drastic and occurs with a little more than three whorls completed. The larval shell of the pediveliger is provided with a long projection of the apertural lip as is commonly found among the planktotrophic veligers of Cerithioidea (Bandel 1993). The fully grown shell consists of two or a little more postlarval whorls which are sculptured by acute spiral ribs. Three of these ribs are more prominent others between them are smaller. The number of ribs increases with the number of whorls. The base is covered by strong ribs and the umbilicus is partly covered by the thickened inner lip.

Remarks: The larval shell of *Fossarus orbigny* in all features of the sculptural pattern and of the dimensions is like that figured by Warén & Bouchet (1988, Fig. 2) from the Mediterranean *F. ambiguus*. This supports the consideration of identity of species on both sides of the Atlantic Ocean based on anatomical data by Houbrick (1990). Jung (1975, Figs. 13-16) figured the larval shell of a *Bittium* sp. that looks just like the shell of a pediveliger of *Fossarus*. In this Pleistocene material from deep water sediment samples of the Caribbean Sea the embryonic shell is better preserved as in the studied specimen and shows a fine pitted surface. It looks very similar to the embryonic shells as found among other marine Cerithioidea (especially Planaxidae) hatching as planktotrophic larvae

and also has the same dimensions (Bandel 1975: Pl. 4, Figs. 1-12).

According to Warén & Bouchet (1988) *Fossarus ambiguus* lives in small cavities among encrusting coralline algae just below the intertidal zone along rocky shores of the Mediterranean Sea. The Caribbean individuals are also representatives of the shallow water fauna and probably lived in similar environment connected to coral debris and reef encrusting organisms.

Gardner (1947) figured two species of *Fossarus* from the Miocene of southeast USA. One is *Fossarus floridus* Gardner, 1947 that probably represents a member of the genus *Iselica* (see below). The other, *Fossarus chipolanus* (Dall, 1892) according to Gardner (1947, Pl. 57, Fig. 29) is supposed to have a small and smooth protoconch. Most probably it has been corroded. *F. chipolanus* fits into the general shape of the Mediterranean and Caribbean *Fossarus*. Like these the strongly shouldered whorls of the teleoconch are featured in its first whorl by four strong spiral ridges on the flanks which are crossed by well developed growth lines. The umbilicus in juvenile shell is quite wide while it becomes narrow and slit-like when the shell is fully grown.

Comparison with larval shells of modern and fossil Cerithioidea: Planaxidae

Houbrick (1987) described the larval shells of the Planaxidae *Hinea brasiliensis* (Lamarck, 1822), *Angiola lineata* (da Costa, 1778) and *A. lineolata* Gould, 1851, *Supplanaxis nucleus* (Bruguière, 1789) and *Planaxis sulcatus* (Born, 1780). The protoconch of *Angiola lineata* from the Caribbean coast of Columbia shows the characteristic features. It is 0.24 mm high and consists of three whorls. The embryonic shell consists of three quarters of a whorl measuring about 0.08 mm across. It is succeeded by one half whorl with fine axial ribs. After that three spiral ribs appear which are crossed by axial ribs of about the same width and height. At the crossing points small nodes form giving the appearance of a string of pearls. The spiral ribs are continuous into the apertural projection of the pediveliger shell. This projection of the outer lip forms right after hatching from the egg but reaches largest size when the veliger shell is fully grown (in the pediveliger stage). The transition into the teleoconch is abrupt as is the end of free swimming larval life and the

change into the milieu of the algal grazer living on pebbles within the intertidal zone (Bandel & Wedler 1887). The protoconch of *Angiola lineolata* from Rarotonga (Cook-Islands) (Pl.1, figs. 2, 7, 8) is very similar and differs in consisting of 3.5 whorls reaching a height of 0.26-0.27 mm. The embryonic shell takes about one whorl measuring 0.1 mm in diameter. The protoconchs of the genus *Angiola* in all essential features regarding the size and sculpture are very similar to that of *Fossarus*. The protoconchs of the genera *Hinea*, *Planaxis* and *Supplanaxis* differ in the weaker axial element of the sculpture.

Fossil Planaxidae from deposits of the northwestern Pyrenees and of central Texas from Eocene strata can be compared:

A species from the Claibornian of Brazos River near College Station in Texas is present by pediveligers with slightly more than four whorls and juvenile shells (Pl.1, fig. 5). The sculpture of the larval shell consists of seven spiral ribs of which only the two upper ones do not become covered by the following whorls. The uppermost spiral rib is continuous into the upper rim of the apertural projection of the outer lip. The spiral keels are crossed by axial ribs forming a reticulate pattern. The larval projection appears on the first larval shell succeeding the three quarters of a whorl of the embryonic shell with 0.1 mm width. The fully grown larval shell is almost 0.6 mm high and 0.35 mm wide.

The larval shell of planaxids from the Lutetian of Gan (southwest France) (Pl.1, figs. 3, 6) consisting of three and one quarter whorls is about 0.3 mm wide and 0.4 mm high. Its sculptural pattern is very similar to the one from the Claibornian and the difference lies in the size of the shell. The early whorls of the teleoconch are similar to a shell described as *Planaxis fischeri* de Raincourt, 1884. It has later been assigned to the genus *Hinea* by Lozouet & Maestrati (1993). This placement is problematic because the specimen figured (1993: Pl.3, fig.1) is more like that of a recent *Angiola* with a strong spiral sculpture in the early teleoconch-whorls. Another figured specimen from Sao Tomé (Western Africa) (1993: Pl.3, fig.2) determined as *Hinea* cf. *lineata* in all essential features corresponds to *Angiola lineata* (see Houbrick 1987: fig. 14) and is not like the smooth more slender shell of the genus *Hinea* with a peculiar South Pacific distribution. The type of *Hinea*, *H.*

brasiliiana, as figured by Houbrick (1987: fig. 10) has a protoconch with only weak axial sculptural element.

Comparison of the radula of *Fossarus* with that of the Planaxidae and Thiaridae:

The comparison of the radulae of *Fossarus ambiguus* from the Mediterranean Sea (Warén & Bouchet 1988: Fig. 11-13) with those of *Planaxis* from the Caribbean and the Red Sea (Bandel 1984: Fig. 57-59, Taf. 2, Fig. 5-8) confirmed the great similarity between them. The rachidian tooth bears one median denticle accompanied by smaller denticles. The base shows a pair of small denticles. The two laterals are about four times wider than high and consist of handle-like extensions of the outer posterior corner bearing more denticles in the case of *Fossarus*. The two pairs of inner and outer marginals form long bilaterally flattened sheets with paw-like apices with several narrowed acute cusps. A comparison with the radula of the genus *Stenomelania* (Thiaridae) also proves some similarities (Bandel et al. 1997: Fig. 6 a-f): The round shaped laterals show a long lateral extension of the broad basal plate. They bear a long pointed major cusp on their inner sides. The two pairs of marginals are elongated with paw-like apices. The rachidian tooth bears one median main denticle, in contrast to the Planaxidae there are no basal denticles.

Discussion: The radula, protoconch-morphology and anatomical data (Ponder 1980, Warén & Bouchet 1988, Houbrick 1990) support the former hypothesis that the genus *Fossarus* is no higher systematic unit at family level but is closely related to the Planaxidae, representing a subfamily of this taxon as Houbrick (1990) had suggested.

Abbott (1974) included the genus *Iselica* within the Fossaridae even though Thiele (1929) and Wenz (1939) had placed it with the Pyramidellidae. About *Iselica* Dall, 1918 with the type *I. anomala* C.B. Adams, 1850 that lives in the Caribbean Sea, it can be stated that it resembles "*Fossarus*" *floridus* Gardner, 1947 from the Miocene of Florida. Gardner's description of the protoconch indicates that it is heterostrophic. Keen (1971) placed the genus *Iselica* with the Pyramidellidae where it has been placed by Thiele (1929: 233) and Wenz (1939: 849) as subgenus of *Phasianema* S. Wood, 1842.

Family Vanikoridae Gray, 1840

Description: According to Warén & Bouchet (1988) the shell is small to medium sized (2-20 mm), depressed to rissoiform, usually with a large and wide umbilicus, smooth or sculptured. The foot carries epipodial folds. The operculum consists of rapidly enlarging whorls. The taenioglossate radula has long marginal teeth with comb-like head portion, shovel-like lateral teeth with one densely dented cusp and drawn out outer corner. The central tooth has a concave smooth base without basal cusps and a triangular upturned cutting edge with one main cusp accompanied by many denticles.

The protoconch is not like that characterized by Warén & Bouchet (1988) when species are included that have a planktotrophic larva. With regard to this planktotrophic larva their diagnosis is not quite correct and must be changed. Only in non-planktotrophic ontogenetic development the shell may be smooth and has no or only a poorly developed sinusigera notch as Warén & Bouchet (1988) stated. The shell of the planktotrophic veliger in contrast is sculptured by spiral ribs and ridges, is of littoriniform shape and has a projection of the apertural lip (sinusigera notch).

Remarks: The oldest known representatives of the Vanikoridae may be among the Paleocene genus *Vanikoropsis* Meek, 1876 with the type-species *V. tuomegana* (Meek & Hayden, 1857) from Nebraska. Kollmann & Peel (1983: 65, figs. 131, 132 & 133) figured *Vanikoropsis skoui* Rosenkrantz, 1970, *Vanikoropsis* sp. 1 and sp. 2 from the Paleocene of Nûgssuaq Peninsula, West Greenland, which could belong to the Vanikoridae regarding the teleoconch but lack preserved protoconchs.

Within the family Vanikoridae also the genera *Vanikoro*, *Megalomphalus*, *Dialytostoma*, *Macromphalus*, *Micromphalina*, *Constantia*, *Talassia* and *Fossarella* are included.

Genus *Vanikoro* Quoy & Gaimard, 1832

The type to the genus is *Sigaretus cancellatus* Chemnitz, 1829 from Vanikoro Island in the Indonesian Archipelago in the Indopacific Ocean.

Thiele (1931) and Wenz (1939) only placed members of the genus *Vanikoro* into the family Vanikoridae. According to the revision of Warén & Bouchet (1988) most members of

the Fossaridae that were placed here in the classifications of Thiele and Wenz with the exception of the genus *Fossarus* should be transferred into the Vanikoridae.

The difference between the type, *Vanikoro cancellata*, and *V. semiplicata* Issel, 1869 from Aqaba/Red Sea lies in the more depressed shell of the latter. *Vanikoro semiplicata* lives within the coral debris in the shallow water of the Gulf of Aqaba. The shell is characterized by rapidly increasing diameter of the whorls and a teleoconch-sculpture of strong axial ribs crossed by finer spiral lines. The 0.26 mm high protoconch is barrel-shaped. The embryonic shell measures 0.1 mm across and takes three-fourth whorls ornamented by a strong groove-ridge pattern. The two following whorls built during a planktotrophic larval stage bear five zigzag-like spiral ribs crossed by very fine axial threads. The protoconch is terminated by a strong sinusigera which is thickened in the upper half of the whorl.

Species *Vanikoro satondae* n. sp.

(Pl. 2, figs. 1, 5)

Material: The holotype, GPIuM 3760, is present.

Derivatio nominis: After the type locality Satonda/Indonesia, Indopacific Ocean.

Locus typicus: Shallow sea at Satonda/Indonesia.

Diagnosis: The shell is up to 1.1 mm high. The sculpture of the teleoconch consists of prosocline axial ribs crossed by finer spiral lines. The aperture is angular in shape and a narrow umbilicus is present. The protoconch consists of an embryonic shell ornamented by a groove-ridge pattern and the larval shell sculptured by five spiral keels.

Description: The teleoconch is terminated after 1.5 whorls. It is up to 1.1 mm high and ornamented by dense prosocline axial ribs (about 30 on the first teleoconch-whorl) crossed by numerous very fine spiral lines. They are not thickened in crosspoints with the axial ribs. The aperture is angular. The umbilicus is narrow. The protoconch of 2.6 whorls is up to 0.27 mm high. The initial cap is about 0.04 mm wide. The embryonic shell measures 0.13 mm across. It is inflated and sculptured by a groove-ridge pattern. The larval shell is characterized by five spiral keels. The uppermost two are zigzag-like and tuberculated. The lower three are crossed by

very fine axial threads. The protoconch is terminated by a short sinus of the outer lip.

Differences: *Vanikoro satondae* n. sp. resembles *V. semiplicata* from the Red Sea. In contrast to that the protoconch-dimensions of the former are slightly larger consisting of half a whorl less. The axial ribs in *V. satondae* are of greater number. They are weaker and not pronounced when crossed by the spiral lines.

Species *Vanikoro oxychone* Mörch, 1877

Description: Shells from the sediment of the bay of Villa Concha near Santa Marta at the Caribbean coast of Columbia are present with well preserved embryonic and larval whorls. The sculpture of the teleoconch is similar to that of *V. semiplicata* but it is weaker. The shell is fully grown after 1,5 teleoconch whorls are terminated.

The protoconch is 0.16 mm high. The embryonic sculpture consists of a strong groove-ridge pattern. Spiral lines (7-8) on the larval whorls crossed by fine axial threads are forming an irregular reticulate pattern. The sinusigera is short.

Differences: In contrast to *V. satondae* n. sp. the protoconch is considerably smaller and consists of one whorl less. The sculpture of the larval shell consists of several more spiral lines. The sinusigera notch is shorter and mediates to forms with holostome pediveliger-aperture like in *Talassia tenuisculpta* and *T. coriacea* or *Macromphalus abylenis* (Warén & Bouchet 1988, Fig. 40-42).

Species *Vanikoro ligata blainvilliana* Recluz,
1869

(Pl. 2, fig. 6)

Material: The investigated shell is from the collection of the Naturhistorical Museum of Vienna (Collection Edlaner, 30740). It has been collected in New Caledonia.

Description: The shell is nearly globular and the last whorl embraces the preceding ones rather completely measuring about 5 mm in diameter. In contrast the 0.3 mm high protoconch of two whorls is slender and high-spired. The non-spiral initial cap measures about 0.09 mm in width and the embryonal shell which consists of about three-fourth whorls reaches a maximal diameter of 0.16 mm. It is sculptured by an irregular groove-ridge pattern. The larval shell bears seven

spiral keels with finer threads intercalated. The upper two keels are often disintegrated into rows of nodules. The protoconch is terminated by a well developed sinusigera.

Differences: *V. ligata blainvilliana* differs from *V. semiplicata*, *V. cancellata* and *V. satondae* n. sp. by its larger protoconch and by bearing two spiral keels more on its larval shell. It differs from *V. oxychone* by its considerably larger dimensions of the protoconch, by having the uppermost spiral keels of the larval shell dissolved into rows of nodules, and by having a well developed large sinusigera notch.

Genus *Megalomphalus* Brusina, 1871

Subgenus *Megalomphalus*

Type to the genus is *Stomatina azona* Brusina, 1864 from the Adriatic Sea (Mediterranean Sea). Warén & Bouchet (1988) discussed the type species of *Megalomphalus* in detail and Gougerot & Le Renard (1981) figured some fossil species from the Eocene of the Paris Basin and supplied a key for them.

Description: The shell is as wide as high or wider than high with rounded whorls. It is sculptured with sharp collabral axial ribs or growth lines crossed by very fine spiral lines. The umbilicus is open and wide and the aperture is inclined. In case of planktotrophic larval development the larval shell is sculptured with fine spiral lines.

Differences: *Megalomphalus* (*Megalomphalus*) differs from the subgenus *Macromphalina* by a protoconch that is not inclined and from *Vanikoro* by its inclined aperture, the wide umbilicus and the very weak sculpture of the protoconch. The teleoconchs of *Macromphalus*, *Micromphalina* and *Constantia* in contrast to that of *Megalomphalus* are higher than wide. In *Dialytostoma* the last whorl is detached from the spire.

Species: *Megalomphalus* (*M.*) *azonus*
(Brusina, 1864)

(Pl.2, fig. 2)

Description: *Megalomphalus* from Le Puyet has an early ontogenetic shell that is attached in upright position on the teleoconch representing only one juvenile whorl. The early shell is not differentiated into embryonic and larval portion and represents the embryonic whorl. With it the young either

hatched as crawling miniature adult or as pediveliger. The 0.13 mm wide first whorl begins with a 0.05 mm wide initial shell cup. At its end growth lines begin which cover the embryonic shell up to its simple end after 1.5 whorls. It resembles the better preserved embryonic shell of *Megalomphalus* (*M.*) *decussatus* (Cossmann, 1888) from Pontleroy (Pl. 2, figs. 3, 7).

Remarks: Material from Pliocene clays of Le Puyet near Nice at the French Riviera is similar to the illustrations of Warén & Bouchet (1988, Fig. 30-33). What Thiele (1929) described as *Megalomphalus* (*M.*) *azonus* does not fit as well as his illustration. The illustration of Sabelli & Spada (1977, Fig. 1) also does not show the same species but looks like *M. (M.) disciformis* with a more depressed shell illustrated by Warén & Bouchet (1988, Figs. 33-34). The modern *Megalomphalus* (*M.*) *azonus* studied by Warén & Bouchet (1988, Fig. 43) hatches after a yolk-rich embryogeny with a shell covered by spiral ridges as is found in a similar pattern in *M. (M.) floridanus* (Moore, 1965). *Megalomphalus* (*M.*) sp. from the Miocene of Antwerpen (Material from the RMNH, Leiden) (Pl. 2, figs. 4, 8, 9) is characterized by a teleoconch measuring 1.3 mm in length. The protoconch consists of 2.25 whorls reaching a height of 0.3 mm. The maximal diameter of the first whorl measures up to 0.13 mm. The initial cap measures about 0.05 mm in width. The smooth embryonic shell takes a little less than one whorl. The thickened rim of the aperture of the embryo represents the moment of hatching and the larval shell is characterized by the onset of six spiral threads. The vanikorid larval shell is terminated by a projection of the outer lip of the pediveligers aperture.

Differences: The Pliocene species *Megalomphalus* (*M.*) *azonus* differs from *M. (M.) decussatus* by its less depressed teleoconch and from *Megalomphalus* (*M.*) sp. from the Miocene of Antwerpen by its direct mode of early ontogeny without differentiation of an embryonic and larval shell.

Subgenus *Macromphalina* (Cossmann, 1888)

The type species of the genus is *Sigaretus problematicus* Deshayes, 1864 as described by Gougerot & Le Renard (1981) from the Eocene of the Paris Basin.

Description: The depressed auriform shell has a wide umbilicus and an ovate, inclined,

widened aperture. The larval shell has a characteristic shape with fine spiral lines as sculpture and lies inclined, partly covered by the first whorl of the teleoconch on the side opposite to the aperture. Otherwise characters are those of the Vanikoridae.

Differences: *Megalomphalus* (*Macromphalina*) differs from the subgenus *Megalomphalus* by its inclined protoconch that is partly covered by the first whorl of the teleoconch. It differs from *Vanikoro* by its inclined aperture, the wide umbilicus and the protoconch with very weak sculpture. The shells of *Macromphalus*, *Micromphalina*, *Constantia* and *Dialytostoma* in contrast are higher than wide. The last whorl of the latter is detached from the spire.

Species *Megalomphalus* (*Macromphalina*) cf. *bouryi* (Dautzenberg, 1912)

(Pl. 3, figs. 1, 9)

Material: Shells are present from a subfossil coral debris of Galerazamba near Cartagena at the Caribbean coast of Columbia.

Description: The 1 mm high depressed shell consists of 1.6 adult whorls. The sculpture consists of a regular pattern of axial and spiral ribs with domination of the axial element. The axis of the 0.3 mm high protoconch is inclined. It takes two whorls, more than one whorl built during a planktonic veliger stage. The larval shell is sculptured by very fine spiral lines and terminated by a sinusigera which is thickened in its upper half.

Differences: The species is very similar to *M. bouryi* (Dautzenberg, 1912) from Senegal and Angola as described by Adam & Knudsen (1969: Fig. 30) which is characterized by a depressed shell not higher than 4 mm with a wide umbilicus and an inclined larval shell of 2.5 to 3 whorls. It differs from *Megalomphalus* (*Megalomphalus*) *azonus* by its indirect mode of early ontogeny and its inclined protoconch partly covered by the first whorl of the teleoconch.

Genus *Dialytostoma* Cossmann, 1888

Description: The shell is like that of *Macromphalus* but with the last whorl detached from the spire.

Remarks: The modern species united in the genus *Radinista* Finlay, 1927 have a shell that in all essential features is like that of the fossil *Fossarus fischeri* de Laubrière, 1881 from the

Eocene of the Paris Basin that represents the type to *Dialytostoma*. The generic definition relies on the data presented by Gougerot & Le Renard (1981).

Genus *Macromphalus* S.V. Woods, 1842

Description: The shell is higher than wide, otherwise like that of *Megalomphalus*.

Remarks: The type species *Macromphalus reticulatus* S.V. Wood, 1842 from the Pliocene British Crag Formation has such a similar shell with the type to the living *Couthouyia* A. Adams, 1860 that Warén and Bouchet (1988, figs. 26, 27) consider them synonyms.

Differences: *Macromphalus* is just like *Dialytostoma* with exception of the last formed whorl of the adult shell that remains in contact with the spire, while it detaches from it in *Dialytostoma*. *Macromphalus* differs from *Megalomphalus* by a shell that is higher than wide and from *Vanikoro* by its inclined aperture, the wide umbilicus and the protoconch with very fine sculpture.

Species *Macromphalus stantoni* n. sp.
(Pl. 3, figs. 4, 7)

Material: The holotype, GPIuM 3761, and two paratypes, GPIuM 3762 and 3763 are present.

Derivatio nominis: Named after Robert Stanton, a colleague in A & M University of Texas who knows the type locality and demonstrated it to one of us (K.B.).

Locus typicus: Brazos River, near College Station/Texas.

Stratum typicum: Claibornian Brazos River-Formation, Eocene.

Diagnosis: The 1.2 mm high teleoconch consists of one whorl sculptured by axial ribs crossed by finer spiral lines. The aperture is oval-shaped and an open umbilicus is present. The early ontogeny was characterized by a planktotrophic larva. The larval shell bears weak spiral lines.

Description: The teleoconch of the 1.2 mm high and less than 1 mm wide specimen consist of only one whorl that increases rapidly in diameter and bears an open umbilicus. Its sculpture consists of about 20 narrow axial ribs which are crossed by numerous densely arranged weaker spiral lines forming a regular pattern. The embryonic shell begins with a 0.07 mm wide initial cap. The onset of the larval shell is indicated by the

begin of growth lines. The larval shell consists of three whorls and is almost 0.5 mm high and 0.3 mm wide. The rounded whorls have a very delicate pattern of 6-7 spiral lines crossed by dense growth lines that follow the sinuated outline of the apertural lip. The apertural projection of the pediveliger was pronounced with the central projection of the outer lip forming a broad saddle.

Differences: A similar form is *Macromphalus* aff. *roberti* (De Morgan, 1915) as described by Janssen (1984; pl. 52, fig. 4)) from the Miocene of West Germany and the east Netherlands. It also has a fairly large larval shell with 2.5 whorls, but in addition two postlarval whorls. *Macromphalus abylenis* Warén & Bouchet, 1988 from the Mediterranean Sea near Marocco has a similar teleoconch sculpture but hatches as pediveliger or crawling young. Its embryonic shell is covered by fine spiral lines and consists only of a little more than one whorl with larger dimensions as in *M. stantoni* n. sp. and *M. aff. roberti*. Aside from the growth lines there are fine spiral threads as in the protoconch of *Vanikoro oxychone*, but the 6-7 spiral lines are very weak. *Macromphalus stantoni* n. sp. mediates between the types of the genera *Macromphalus* and *Megalomphalus* as described by Warén & Bouchet (1988, figs. 26-34). The wide umbilicus is very similar to that of *Megalomphalus azonus* but the whorls are slightly higher, rather as high as in *Macromphalus reticulatus*. The sculpture is also similar to that of the latter. The difference lies in the larval shell. It documents that *Macromphalus stantoni* n. sp. is characterized by a long planktonic veliger stage while *Megalomphalus azonus* hatched as crawling young. In the case of *Macromphalus reticulatus* the early ontogenetic shell is unknown but the Recent species *M. abylenis* Warén & Bouchet (1988, fig. 42) is characterized by veligers with short time in the plankton building a larval shell of less than one whorl.

Remarks: Cossmann (1891) mentioned the fossil genera *Micreschara* Cossmann, 1888 und *Lacunaria* Conrad, 1866. Cossmann's type *Micreschara citharella* and the genus *Lacunaria* from the French Eocene fit well with the type of *Macromphalus* and can be considered as congeneric.

Genus *Micromphalina* Cossmann, 1888

The type species is *Lacuna elegans* Deshayes, 1864 from the Eocene of the Paris Basin.

Description: The shell is small and turreted with rounded whorls which are sculptured by sinuate fine axial ribs or growth lines crossed by fine spiral striae or fine low ribs. The larval shell is of the vanikorid type with spiral sculptural pattern. All sculpture is lost in the early whorls in case no planktotrophic larva developed. The ovate aperture has a pointed upper end, the inner lip twists upwards and accompanies the slit like narrow umbilicus.

Differences: The genus *Micromphalina* can be distinguished from *Vanikoro*, *Megalomphalus*, *Macromphalus* and *Dialytostoma* by its rissoiform shell. In contrast to *Constantia* the sculpture of the teleoconch is less prominent and the aperture is oval, has a pointed upper end and the inner lip twists upwards accompanying the umbilicus.

Micromphalina sp. from Upper Oligocene marls of Peyrère, Southern France (Pl. 3, figs. 2, 8) is characterized by a slender up to 1.4 mm high shell that consists of 2.75 slightly rounded teleoconch-whorls. The sculpture of the teleoconch consists of densely arranged sinuous axial ribs crossed by numerous fine spiral threads. The ovate aperture with pointed upper edge takes less than one half of the shells height. A narrow, slit like umbilicus is present. The 0.3 mm high protoconch consists of 2.25 whorls. The embryonic part of about one whorl is sculptured by a strong groove-ridge pattern and measures 0.016 mm across. The typical vanikorid larval shell is sculptured by seven spiral ribs with irregularly intercalated fine axial threads. It is terminated by a slight sinus.

Differences: *Micromphalina* sp. differs from the type, *M. elegans*, by having less shouldered whorls and an aperture taking less than one half of the shells height. It differs from *Constantia* A. Adams, 1860 by having a less pronounced axial sculpture and an ovate aperture.

Remarks: *Zeradina* Finlay, 1927 in all essential features resembles the type to the genus *Micromphalina*, *Lacuna elegans* Deshayes, 1864 from the Eocene of the Paris Basin. *Zeradina* from New Zealand is very similar with regard to the shape and sculpture of the teleoconch. The smooth inflated embryonic shell of one whorl indicates a direct mode of development. *Nilsia* Finlay, 1927 is

convergent with regard to the teleoconch but the spiral sculpture of its embryonic shell closely resembles that of the Indo-Pacific *Rissoina*-relation.

Genus *Constantia* A. Adams, 1860

Description: The genus *Constantia* with the type-species *C. elegans* A. Adams, 1860 from the Strait of Korea (figured by Warén & Bouchet 1988: 87, fig. 35) is characterized by a tall rissoiform shell having a strong reticulate sculpture with straight axial ribs. The aperture is rounded. A narrow slit-like umbilicus is present.

Differences: The tall rissoiform shell distinguishes *Constantia* from the genera *Vanikoro*, *Megalomphalus*, *Macromphalus* and *Dialytostoma*. It differs from *Micromphalina* by the prominent sculpture of the teleoconch and by the well rounded aperture.

Species *Constantia acutocostata* n. sp.

(Pl. 3, figs. 3, 6)

Material: The holotype, GPIuM 3764 is present.

Derivatio nominis: After the sharp axial ribs sculpturing the teleoconch-whorls.

Locus typicus: Slope of Hilutangan Chanal, Cebu/Philippines.

Diagnosis: The small shell is turreted with rounded whorls. The sculpture of the teleoconch consists of sharp axial ribs crossed by fine spiral lines forming a reticulate pattern. The protoconch consists of an inflated embryonic part and a larval shell sculptured by very fine spiral lines.

Description: The up to 1.4 mm high turreted shell consists of 2.5 rounded teleoconch-whorls sculptured with nine sharp axial ribs on the first teleoconch-whorl. These are crossed by numerous fine spiral lines forming a reticulate pattern. The aperture is rounded, the umbilicus narrow. The protoconch consists of 3.5 rounded whorls reaching a height of 0.32 mm. The initial cap measures 0.05 mm in width. The inflated embryonic shell of one whorl is smooth and measures 0.13 mm in diameter. The larval shell is characterized by the onset of six very fine spiral lines. It is terminated by a well developed sinusigera notch.

Differences: This species differs from the type, *C. elegans*, by having stronger developed axial ribs which dominate

considerably over the spiral element. Another difference lies in the smaller size of *C. acutocostata* n. sp.. The protoconch of the species representing a planktotrophic veliger stage is of typical vanikorid sculpture especially close to that of *Macromphalus* and *Micromphalina*. The latter is also similar regarding the shape of the teleoconch but differs in its less pronounced axial sculpture and in its ovate aperture.

Genus *Fossarella* Thiele, 1925

Description: The very small shell is depressed. The teleoconch is sculptured by acute spiral keels. The base is ribbed. A wide umbilicus is present. The protoconch is barrel-shaped, sculptured with very fine spiral lines.

Differences: *Fossarella* differs from *Vanikoro*, *Megalomphalus*, *Macromphalus*, *Micromphalina* and *Constantia* by the sculpture of the teleoconch only exhibiting a spiral element. It differs from the convergent genus *Fossarus* (Planaxidae) by the protoconch with very fine spiral lines lacking any axial sculpture.

Species *Fossarella pacifica* Thiele, 1925

(Pl. 3, fig. 5)

This species has been described from the Samoa Islands by Thiele (1925). It also lives in the Indopacific near Satonda/Indonesia and at Cebu/Philippines as described below.

Description: *F. pacifica* is very similar to *Fossarus orbignyi* (Fossarinae, Planaxidae) in regard to the dimensions, shape and sculpture of the teleoconch. The 0.3 mm high protoconch of *Fossarella pacifica* takes 2.75 whorls. The embryonic part of 0.75 whorls is smooth and measures about 0.1 mm in diameter. The larval shell is sculptured with ten fine spiral lines. It is terminated by a well developed sinus.

Differences: The teleoconch in all essential features resembles that of *Fossarus orbignyi* (Planaxidae). The difference lies in the morphology of the protoconch. The early ontogenetic shell is very similar to those of the genera *Macromphalina* and *Megalomphalus* and documents that *Fossarella* is closely related to these genera and belongs to the Vanikoridae.

Family Pickworthiidae Iredale, 1917

This family was considered a questionable representative of the Rissooidea by Ponder & Warén (1988) and seen as own family together with the Reynellonidae Iredale, 1917 by Ponder (1985). It can be distinguished by the unique obliquely attached protoconch and holds the genera *Sansonia*, *Mecoliota* and *Gania* n. g..

Genus *Sansonia* Jousseau, 1892

The type of the genus is *Iphitus tuberculatus* Watson, 1886 from the Caribbean Sea.

Description: The shell is smaller than 2 mm, turbinate with a high spire and flattened whorls. The outer lip of the fully grown individual is thickened and forms a strong varix. The larval shell is barrel shaped, sculptured by spiral lines and ends with a large apertural projection.

Difference: *Sansonia* differs from *Mecoliota* by having a more slender teleoconch with a narrow umbilicus and an apical angle less than 60°. It differs from *Gania* n. g. by having a regular sculpture of the teleoconch with axial and spiral elements.

Species *Sansonia tuberculata* (Watson, 1886)

(Pl. 4, figs. 1, 5)

Material: The investigated specimen have been collected by Hans Martin Hüssner (1989) in a shallow sea bed of Cozumel Island in Yucatan, Mexico and extracted from the sediment by O. Lehnert (1990) and characterized with regard to the accompanied fauna.

Description: The generic diagnosis applies. The shell is about 1.5 mm high and the apical angle measures about 52°. There are 5.5 postlarval whorls each bearing two rows of rounded beads and a narrow suprasutural beaded keel. The base of the shell is flattened with a row of beads bordering a narrow umbilicus. The round aperture has a thickened lip. The 2.5 whorls of the protoconch are well rounded and thus quite different from the flat whorls of the teleoconch. The protoconch is 0.16 mm high and 0.13 mm wide. The embryonic shell has a 0.07 mm wide initial cap and consists of three quarters of a whorl with 0.11 mm width. Fine spiral lines sometimes consisting of an alignment of nodes are continuous up to the thickened margin of the pediveliger shell. The

outer lip of the fully grown larval shell bears a large apertural projection that is wider at its end than at its base and thus usually fractured in the shell.

Differences: *S. tuberculata* differs from *S. kenneyi* and from *S. cebuana* n. sp. by having a smaller protoconch and by bearing one spiral line less on its larval shell. It differs from *S. hilutangensis* n. sp. by bearing five spiral ribs less on its larval shell and from *S. hedegaardi* n. sp. by the smaller dimensions of its protoconch and by bearing one spiral keel more on its larval shell.

Remarks: Abbott (1974, Fig. 414) considered it unwise of Thiele (1929) to group *Sansonia* with the Adeorbidae instead of the Trochoidea and here near to the genera *Liotia* Gray, 1847 and *Arene* H. and A. Adams, 1854. Wenz (1939, Fig. 1833) placed the genus in the Tornidae, in which relation it is still seen by Ponder & Warén (1988). Ponder (1985) suggested a possible relation with the Vitrinellidae.

Comparison: The convergent species *Iphitus* (= *Iphitella*) *tuberculatus* Jeffreys, 1883 lives in the deep northern Atlantic Ocean (about 1000 m depth) and owns a very characteristically sculptured larval shell. The about 3 mm high shell carries the slightly inclined 0.42 mm high larval shell with axial ribs and fine spiral striae between these (Bouchet 1977, Pl. 1; Bouchet & Warén 1979, Fig. 1-3). The embryonic shell is about 0.16 mm wide and is covered by a fine pattern of grooves. While the larval shell very much resembles that of some epitoniids or the fossil Protorculidae (Bandel, 1991), the adult shell resembles that of *Sansonia tuberculata*, but is thinner. According to Thiele (1929) *Iphitus* (= *Iphitella* Thiele, 1925) represents a questionable member of the Littorinidae. According to the larval shell it is a member of the Ptenoglossa and here near to the Epitoniidae as was also suggested by Bouchet & Warén (1979).

Species *Sansonia hilutangensis* n. sp.

(Pl. 4, figs. 2, 7)

Material: The holotype, GPIuM 3765 and one paratype, GPIuM 3766, are present.

Derivatio nominis: After the type locality, Hilutangan Chanal.

Locus typicus: Shallow sea at the coast of Hilutangan Chanal near Cebu/Philippines.

Diagnosis: The shell is up to 1.3 mm high. The sculpture of the teleoconch consists of three spiral keels with the median keel pronounced. They are crossed by orthocone axial ribs. The aperture is thickened and a narrow umbilicus is present. The protoconch is obliquely attached. The larval shell is sculptured with 10 spiral rows of tubercles and tuberculate spiral keels. It is terminated by a strong projection of the pediveligers outer lip.

Description: The shell is up to 1.3 mm high and consists of 3.5 teleoconch whorls. The teleoconch whorls each bear three spiral keels, one at the top and at the base of the whorls and one stronger median keel. They are crossed by more than 20 orthocone axial ribs forming a regular reticulate pattern. The base is ornamented by three spiral ribs and has a narrow umbilicus. The aperture is thickened. The protoconch is with about 5° obliquely attached and consists of 2.25 whorls reaching a height of 0.2 mm. The initial cap measures 0.05 mm in width. The smooth embryonic shell takes about 0.75 whorls measuring 0.1 mm in diameter. It is terminated by a thickened rim. The larval shell is sculptured with ten spiral rows of tubercles and tuberculate spiral keels. The protoconch is terminated by a strong projection of the pediveligers outer lip which is nearly vertical in course and thickened in its upper half. The lower portion is thinner and commonly fractured.

Differences: This species is very similar to the closely related *S. kenneyi* from the Oligocene of Peyrère with regard to the sculpture of the teleoconch but differs in protoconch-morphology. There are more and weaker axial ribs sculpturing the protoconch of *Sansonia hilutangensis* n. sp. and in contrast to the Oligocene species they bear tubercles. *S. hilutangensis* n. sp. differs from *S. cebuana* n. sp. by a protoconch that owns 0.75 whorls less and in the absence of short axial ribs on the larval shell.

Species *Sansonia cebuana* n. sp.

(Pl. 4, figs. 3, 6)

Material: The holotype, GPIuM 3767 is present.

Derivatio nominis: After the type locality Cebu/Philippines.

Locus typicus: Shallow coastal sea of Cebu/Philippines near Argao River.

Diagnosis: For description of the teleoconch see *S. hilutangensis* n. sp.. The protoconch consists of three whorls. The embryonic shell is smooth and terminated by a thickened rim. The larval shell is sculptured with six spiral tuberculated ribs. The uppermost two rows of tubercles are modified to short prosocline axial ribs. The protoconch is terminated by a strong sinusigera notch.

Description: The teleoconch with 1.3 mm high and 3.5 whorls closely resembles that of *S. hilutangensis* n. sp.. The protoconch consists of three whorls reaching a height of 0.24 mm. The initial cap is 0.03 mm wide. The embryonic shell takes about three quarters of a whorl and measures 0.08 mm in maximal diameter. It is smooth and terminated by a thickened rim. The larval shell is sculptured with six strong spiral tuberculated keels. The uppermost two keels are most prominent. The tubercles on these keels are modified to very short prosocline axial ribs. The larval shell is terminated by a strong sinusigera notch taking about a quarter of a whorl. It is thickened in its upper half and thinner and projected at the base.

Differences: This species closely resembles the Oligocene *S. kenneyi* and the Recent *S. hilutangensis* n. sp.. It differs from *S. kenneyi* by having half a protoconch-whorl more and by tubercles on the spiral keels sculpturing the larval shell. It differs from *S. hilutangensis* n. sp. in having a protoconch that owns 0.75 whorls more. The larval shell bears only six spiral ribs and the tuberculate sculpture on these ribs is more prominent in *S. cebuana* n. sp. forming short axial ribs on the uppermost two keels.

Species *Sansonia kenneyi* (Ladd, 1966)

(Pl. 5, figs. 1, 4)

Material: An individual from the collection of the Museum of Natural History (Leiden) could be studied by courtesy of Arie Janssen. It comes from the Upper Oligocene of Peyrère in the Aquitaine in France. This species has been described by Lozouet (1986, fig. 58 D-E).

Description: The shell is only 1 mm high and consists of a bit more than three teleoconch whorls forming an apical angle of about 55°. The sculpture is close to that of *S. tuberculata* but differs regarding the base. Here three spiral ridges are present as well as a ridge surrounding the narrow umbilicus. The whorls

are not quite as flat as in *S. tuberculata* and the spiral rows of beads are crossed by axial ribs forming a reticulate pattern with triangular nodes. The larval shell is 0.21 mm wide and a little higher and ends with a very large apertural projection amounting to almost a quarter of a whorl. The sculpture consists of six coarse spiral ridges which feature the last larval whorl, while the whorl succeeding the 0.08 mm wide embryonic shell is covered by sinuous growth lines.

Differences: *S. kenneyi* differs from the type, *S. tuberculata*, in the larger dimensions of its protoconch and in bearing one spiral keel more on its larval shell. It differs from *S. hilutangensis* n. sp. and *S. cebuana* n. sp. in lacking tubercles and axial threads on its larval shell. The protoconch of *S. hedegaardi* n. sp. is larger and bears two spiral ribs less on its larval shell.

Remarks: Lozouet (1986) noted the occurrence of *S. kenneyi* in the shallow littoral facies just as is the case in the modern forms as well. It seems to have survived in European waters in Italy until the Pliocene where Raffi & Taviani (1985) observed it as *Sansonia italica*, which represents a member of *Sansonia kenneyi* according to Lozouet. The species has actually been described from the Lower Miocene of Bikini Island (Ladd 1966).

Species *Sansonia hedegaardi* n. sp.

(Pl. 5, figs. 2, 5)

Material: The holotype, GPIuM 3768 and one paratype, GPIuM 3769 are present.

Derivatio nominis: After Claus Hedegaard who provided us material from the Danian of Faxe/Denmark.

Locus typicus et stratum typicum: Mid Danian bryozoan marls of Faxe quarry / Denmark.

Diagnosis: The shell reached a height of 1.5 mm. The teleoconch is sculptured by prosocline axial ribs that are incised below the top. The aperture is thickened and a narrow umbilicus is present. The protoconch is obliquely attached. The sculpture of the larval shell consists of four spiral ribs. The protoconch is terminated by a strong sinusigera.

Description: The up to 1.5 mm high shell consists of 2.5 teleoconch whorls which are sculptured by up to 20 prosocline axial ribs that are incised below the top of the whorls

forming a subsutural row of large tubercles. The base is sculptured by two spiral ribs. The aperture is thickened and a narrow umbilicus is present. The protoconch consists of 2.75 whorls and is obliquely attached to the teleoconch. It is about 0.3 mm high. The initial cap measures 0.04 mm in width. The first whorl takes 0.14 mm in maximal diameter. After one whorl four strong spiral ribs set on. The larval shell is terminated by a strong projection of the outer apertural lip of the pediveliger.

Differences: This species can be differentiated from the type, *S. tuberculata*, by the irregularly incised axial ribs of the teleoconch-sculpture. It is also different in the protoconch-morphology: The protoconch of *S. hedegaardi* n. sp. is higher and it bears only four spiral ribs that are considerably stronger than those in *S. tuberculata*.

Genus *Mecoliotia* Hedley, 1899

Type to the genus is *Mecoliotia halligani* Hedley, 1899 from Pacific Ocean near Funafuti Island.

Description: The shell has an apical angle of over 60° and the sculpture consists of spiral and axial ribs which at crosspoints are raised into nodes. The umbilicus is wide. Otherwise like *Sansonia*.

Differences: *Mecoliotia* differs from *Sansonia* by having a wider teleoconch and a wider umbilicus.

Species *Mecoliotia philippina* n. sp.
(Pl. 4, figs. 4, 8)

Material: The holotype, GPIuM 3770, is present.

Derivatio nominis: After the area of distribution.

Locus typicus: Slope of Hilutangan Chanal near Cebu/Philippines.

Diagnosis: The shell reaches a height of 1.4 mm with an apical angle of about 80°. The sculpture of the teleoconch consists of spiral keels crossed by orthocone axial ribs. The protoconch consists of an smooth and inflated embryonic part and a larval shell that is sculptured by spiral keels and rows of tubercles. The protoconch is terminated by a short sinusigera.

Description: The up to 1.4 mm high shell consists of 3.5 teleoconch whorls and has an apical angle of about 80°. The sculpture of the

teleoconch at first consists of two spiral keels crossed by about 20 orthocone axial ribs forming a regular ladder-like pattern. Later the number of spiral keels increases to six, the number of axial ribs to about 30. The base is sculptured by smooth spiral keels. The protoconch of 2.25 whorls is about 0.25 mm high. The initial cap measures 0.05 mm in width and the smooth embryonic shell of one whorl is slightly inflated. It measures 0.13 mm in diameter. A weak rim terminates the embryonic shell and documents the stage of development at hatching time. The following larval shell is characterized by a sculpture of six spiral keels with intercalated rows of tubercles. A short sinusigera notch tickened in its upper half terminates the larval shell.

Differences: In contrast to the type, *M. halligani*, the sculpture of *M. philippina* n. sp. is not characterized by prominent nodes in the crosspoint of spiral and axial elements. There is another only badly preserved form from Cebu with very strong median keel which may represent another species of *Mecoliotia*.

Genus *Gania* n. g.

Derivatio nominis: after the type locality Gan in SW France

Type of the genus is *Gania carinata* n. sp.

Diagnosis: The up to 0.8 mm high shell is sculptured with orthocone growth lines and strong spiral keels with fine rows of granules intercalated. The aperture is drop-shaped and not thickened. A narrow umbilicus is present. The protoconch is obliquely attached and sculptured with strong spiral keels.

Difference: *Gania* n. g. differs from the genera *Sansonia* and *Mecoliotia* by lacking any axial sculpture except from growth lines.

Species *Gania carinata* n. g. n. sp.
(Pl. 5, figs. 3, 6)

Material: The holotype, GPIuM 3771 and two paratypes, GPIuM 3772 and 3773, are present.

Derivatio nominis: After the strong carinate spiral sculpture.

Locus typicus et stratum typicum: Lutetian (Eocene) marls of Gan/Aquitaine (SW France).

Description: The shell is up to 0.8 mm high and consists of 2.25 slightly rounded adult whorls. The whorls of the teleoconch are sculptured by up to five strong spiral keels

with fine granulated spiral rows intercalated. Very fine orthocline growth lines are present. The aperture is drop-shaped and not thickened. The inner lip slightly twists upwards. The parietal edge is pointed. A narrow umbilicus is present. The with 5° obliquely attached protoconch consists of 2.75 whorls and is 0.24 mm high. The embryonal whorl measures 0.1 mm in diameter. The initial cap is 0.46 mm wide. The first whorl is smooth. The larval shell is documented by the onset of five strong spiral keels with the uppermost two being most prominent. The protoconch is terminated by a strong sinusigera notch with a thickened upper part.

Differences: *Gania carinata* n. g. n. sp. closely resembles *S. kenneyi* regarding the oblique arrangement and the sculpture of the protoconch. The protoconch of the former is slightly larger and the teleoconch lacks any axial sculpture. Thus the Eocene *Gania* could well be a member of the Pickworthiidae.

Possible relations of Vanikoridae and Pickworthiidae to modern and Mesozoic species:

The Pickworthiidae now can be traced back into the Early Tertiary (Danian, Paleocene). The Danian species *Sansonia hedegaardi* n. sp. has all characters regarding the protoconch and teleoconch of a typical *Sansonia*. *Gania* n. g. from the Lutetian (Eocene) of Gan (Southern France) lacks the axial element of sculpture but closely resembles the Danian and Oligocene to Recent species of the genus *Sansonia* regarding the sculpture and dimensions of the protoconch.

Similar protoconch-types were already present in early Mesozoic Prostyliferidae Bandel, 1992. The obliquely attached protoconch of *Prostylifer paludinaris* (Münster, 1841) from the Triassic St. Cassian-Formation of the Alps bears strong tuberculated spiral keels (Bandel 1993, Pl. 6, Fig. 1; 1994, Pl. 4, Fig. 10; this paper Pl. 5, fig. 8). The shape of the outer apertural projection of the pediveliger shell of *P. paludinaris* is also very similar to that found among Paleocene to Recent Pickworthiidae: The upper half of the postlarval hook is thickened and vertically orientated. The oblique attachment of the protoconch is also present in the prostyliferid *Ptychostoma pleurotomoides* (Wissmann, 1841) from the St. Cassian-Formation (Bandel 1993). The difference to modern Pickworthiidae lies in the smooth teleoconch and

dimensions of the protoconch. This is considerably larger in the Prostyliferidae. It takes 0.5 mm in height in *Prostylifer paludinaris* and 1 mm in *Ptychostoma pleurotomoides*. Since teleoconchs are also quite a bit larger (about 10 mm) in the Prostyliferidae and up to 2 mm in the Pickworthiidae the modern group could represent a branch adapted for small size.

The Vanikoridae are documented since the Paleocene. They share characters regarding the protoconch with Heteropoda (Thiriot-Quiévreux 1973), Rissoidae (Thiriot-Quiévreux 1980) and Littorinidae (Bandel & Kadolsky 1982, Reid 1985, 1986, 1989). Within the planktonic Heteropoda the family Atlantidae is very similar to the Vanikoridae regarding the shape, dimensions and sculpture of the protoconch. Especially the protoconchs of *Atlanta turriculata* (D'Orbigny, 1836) (Thiriot-Quiévreux 1973, Fig. 1 i) and *A. fusca* Souleyet, 1852 (Thiriot-Quiévreux 1973, Figs. 1 h, 6 b) fit well. The shape of the protoconchs is turriculate like in the genera *Macromphalus*, *Megalomphalus* and *Fossarella*. The axis is slightly inclined as present in *Megalomphalus* (*Macromphalina*). The difference lies in the slit in the middle of the larval shell in the genus *Atlanta* and in the pitted surface of its embryonic shell. Bandel & Hemleben (1987) demonstrated that Heteropoda have developed prior to the Late Lower Jurassic so that potential ancestors should also be searched for among Triassic or older gastropods.

The zigzag-pattern of spiral sculpture like in the larval shell of the Vanikoridae also occurs in the rissoid genus *Alvania*. But in contrast to *Alvania* the embryonal shell of vanikorids is sculptured with a groove-ridge pattern whereas it is sculptured with spiral lines and rows of tubercles in *Alvania*. A rim between the embryonal and larval shell is always present in this rissoid and it is missing in Vanikoridae. Another difference lies in the shape of the sinusigera which is not thickened in its upper part of the outer lip in *Alvania*.

A spiral sculpture of the larval shell with short axial ribs intercalated as is common in vanikorid genera also occurs in Littorinidae. For example the genera *Littorina* Ferussac, 1822, *Littoraria* Griffith & Pigeon, 1834, *Mainwaringia* Nevill, 1885. and *Nodilittorina* (Martens, 1897)(this paper: Pl. 5, fig. 7) have such patterns (Bandel & Kadolsky 1982, Reid 1989). The difference lies in the embryonic shell that is smooth in the Littorinidae while a

strong groove ridge pattern is present in Vanikoridae. The protoconch is also more depressed conical in shape in Littorinidae. The postlarval hook in Vanikoridae is less thickened and shorter than in Pickworthiidae and Littorinidae.

The close similarity with modern pelagic Heteropoda on one hand and Triassic Prostyliferidae on the other hand indicates a long history of the still little known Vanikoridae and Pickworthiidae, both of which having adapted to cryptic habitats. Similarities with Littorinidae and Rissoidae may also indicate some relations. This whole scenario probably indicates, that these snails belong to old groups which may have had an independent history from other Caenogastropoda since early in the Mesozoic.

Miniaturization has also occurred in the *Fossarus*-branch of the Cerithiimorpha, relation Planaxidae. But the shape of the protoconch faithfully demonstrates the convergence and difference in relation to the Pickworthiidae and Vanikoridae.

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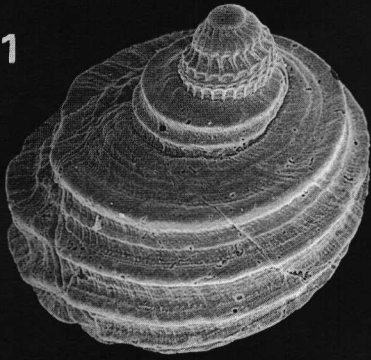
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Plate 1: Planaxidae

- Fig. 1** Shell of *Fossarus ambiguus* (Linné, 1766) from a subfossil occurrence of a reef and its debris from Galerazamba at the Caribbean coast of Columbia measuring 0.74 mm in height.
- Fig. 2** Juvenile specimen of *Angiola lineolata* Gould, 1859 from Rarotonga (Cook Islands). It measures 3.2 mm in height.
- Fig. 3** *Angiola fischeri* (de Raincourt, 1884) from the Lutetian of Gan (SW France) closely resembles its modern relatives. The juvenile specimen measures 1.9 mm in height.
- Fig. 4** The Protoconch of the same specimen as in fig. 1 sculptured by strong spiral and axial ribs measures 0.21 mm in height.
- Fig. 5** The early ontogenetic shell of a planaxid from the Claibornian (Eocene) Brazos-River-Formation near College Station (Texas/USA) is very similar to fossil and modern *Angiola* spp.. It measures 0.6 mm in height.
- Fig. 6** The 0.38 mm high protoconch of the same specimen as in fig. 3 is terminated by a strong sinusigera.
- Figs. 7, 8** Lateral and apical view of the early ontogenetic shell of the same specimen as in fig. 2. The protoconch measures 0.25 mm in height and in maximal diameter.

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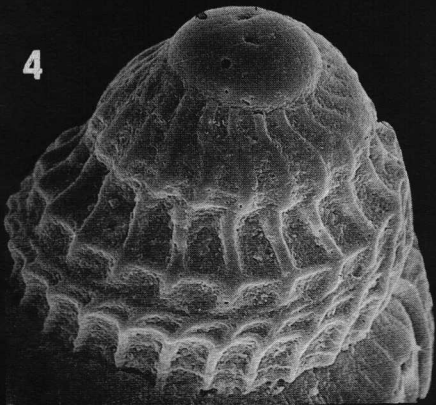
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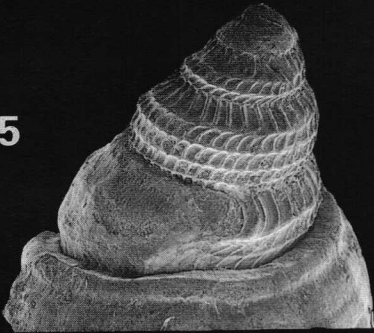
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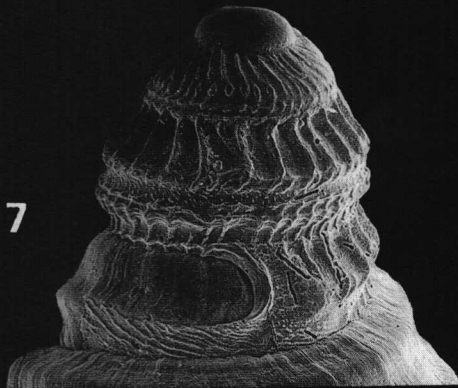
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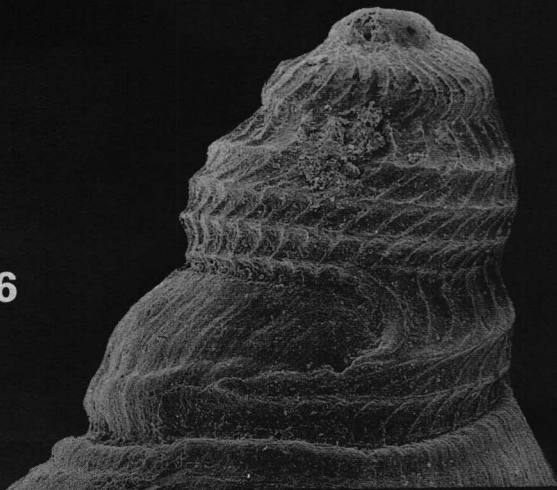
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Plate 2: Vanikoridae

- Fig. 1** The shell of *Vanikoro satonda* n. sp. is sculptured by dense prosocline axial ribs crossed by finer spiral lines. The holotype, GPIuM 3760, measures 1.1 mm in height.
- Fig. 2** *Megalomphalus (Megalomphalus) azonus* (Brusina, 1864) from the Pliocene clay of Le Puyet near Nice (S France) measures 0.94 mm in height.
- Fig. 3** *Megalomphalus (M.) decussatus* (Cossmann, 1888) from the Pliocene of Pontleroy (S France) is characterized by an angular aperture. The figured specimen measures 1.3 mm in height.
- Fig. 4** The shell of *Megalomphalus* sp. from the Miocene of Antwerpen measures 1.3 mm in maximal length.
- Fig. 5** The protoconch of the same specimen as in fig. 1 is sculptured by strong spiral keels crossed by very fine axial threads. It measures 0.27 mm in height.
- Fig. 6** The protoconch of *Vanikoro ligata blainvilliana* Recluz, 1869 from New Caledonia (NHM Vienna, Collection Edlaner, 30740) is terminated by a wide projection of the outer lip of the pediveligers aperture. The protoconch measures 0.3 mm in height.
- Fig. 7** Apical view of the protoconch of the same specimen as in fig. 3. The protoconch documents a lecithotrophic larval development. It measures 0.24 mm in maximal diameter.
- Figs. 8, 9** Lateral and apical view of the protoconch of the same specimen as in fig. 4. The protoconch indicating a planktotrophic larval development measures 0.3 mm in height and in maximal diameter.

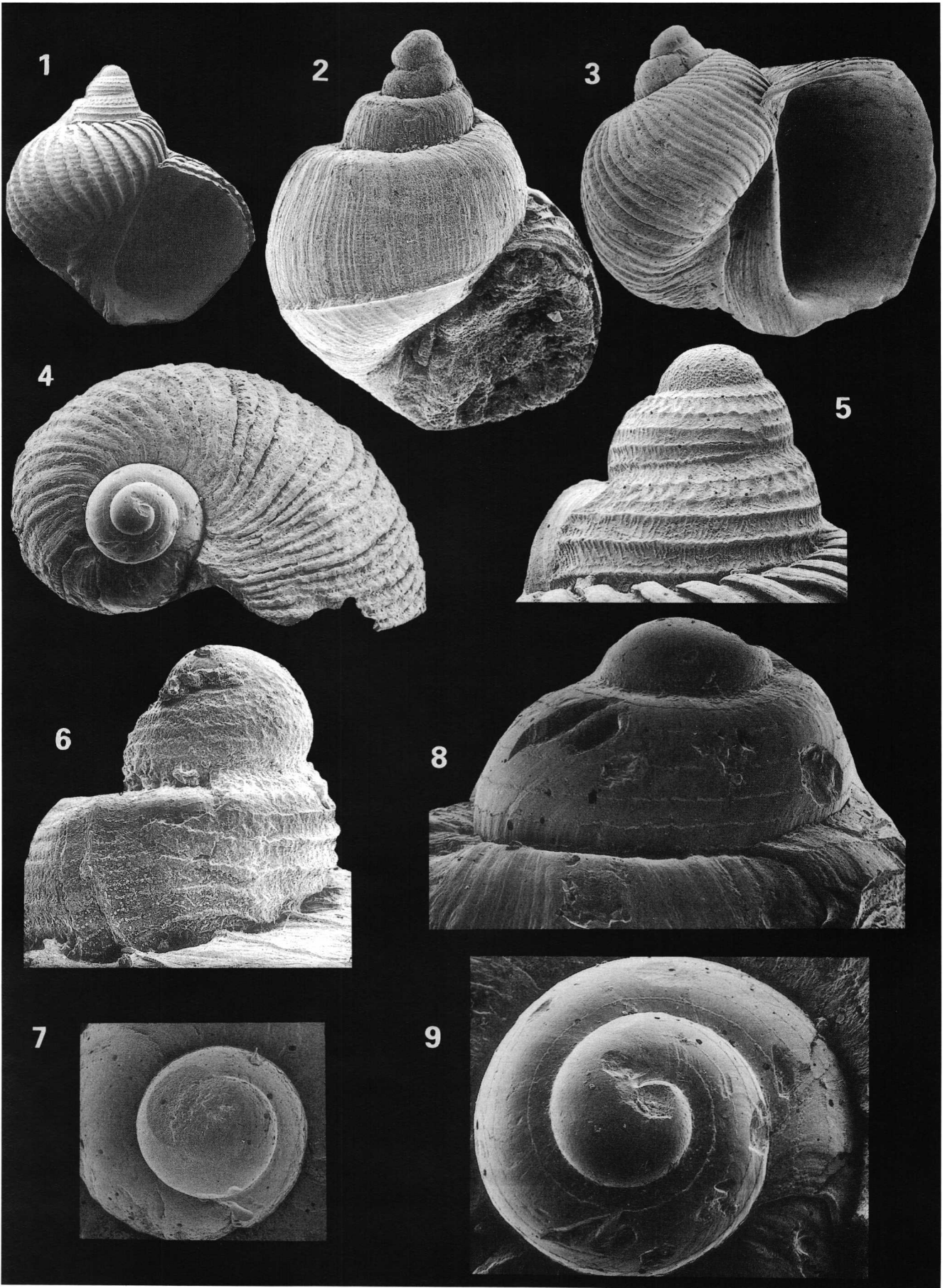


Plate 3: Vanikoridae

- Fig. 1** The shell of *Megalomphalus* (*Macromphalina*) cf. *bouryi* (Dautzenberg, 1912) from a subfossil coral debris of Galerazamba at the Caribbean coast of Columbia measures 1 mm in height.
- Fig. 2** Shell of *Micromphalina* sp. from the Oligocene of Peyrère (SW France). The figured specimen measures 1.4 mm in height.
- Fig. 3** *Constantia acutocostata* n. sp. is characterized by a tall rissoiform teleoconch sculptured by acute spiral ribs. The figured holotype, GPluM 3764, from the slope of Hilutangan Chanal near Cebu (Philippines) measures 1.4 mm in height.
- Fig. 4** *Macromphalus stantoni* n. sp., holotype, GPluM 3761. The shell from the Claibornian (Eocene) Brazos-River-Formation near College Station (Texas/USA) measures 1.2 mm in height.
- Fig. 5** Juvenile specimen of *Fossarella pacifica* Thiele, 1925 from Satonda/Indonesia measuring 0.79 mm in height. The protoconch is sculptured by very fine spiral lines. The teleoconch in contrast bears strong keels.
- Fig. 6** Apikal view of the protoconch of the same specimen as in fig. 3. It measures 0.32 mm in maximal diameter.
- Fig. 7** The vanikorid protoconch of *Macromphalus stantoni* n. sp., paratype, GPluM 3762, measures 0.5 mm in height. The larval shell bears very fine spiral lines.
- Fig. 8** The protoconch of the same specimen as in fig. 2. measures 0.3 mm in height. The embryonic shell is sculptured by a groove-ridge pattern while the larval shell is characterized by spiral keels.
- Fig. 9** The protoconch of the same specimen as in fig. 1 measures 0.3 mm in height. Its axis lies inclined and it is partly covered by the first adult whorl.

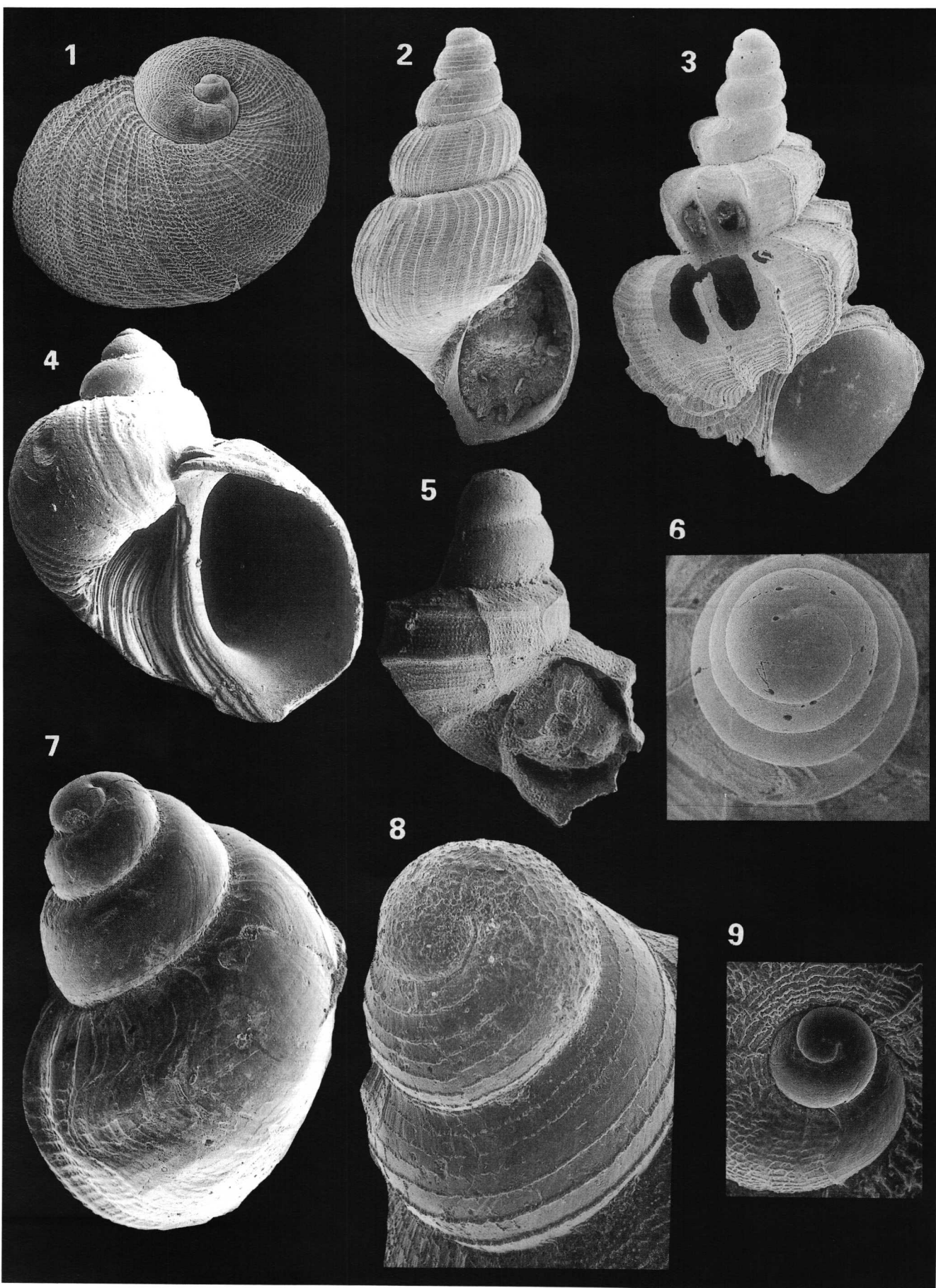


Plate 4: Recent Pickworthiidae

- Fig. 1** Shell of *Sansonia tuberculata* (Watson, 1886) from the shallow sea of Cozumel Island (Yucatan/Mexico), coll. Lehnert. The specimen measures 1.5 mm in height.
- Fig. 2** *Sansonia hilutangensis* n. sp., holotype, GPIuM 3765, from the shallow sea of Hilutangan Chanal near Cebu (Philippines). It measures 1.3 mm in height.
- Fig. 3** *Sansonia cebuana* n. sp., holotype GPIuM 3767, from the shallow coastal sea of Cebu near Argao River (Philippines). It measures 0.9 mm in height.
- Fig. 4** The holotype of *Mecoliota philippina* n. sp., GPIuM 3770, from the slope of Hilutangan Channal (Cebu/Philippines) measures 1.4 mm in height.
- Fig. 5** The protoconch of the same specimen as in fig. 1 measures 0.16 mm in height. The larval shell is terminated by a sinusigera thickened in its upper edge and fractured at the base.
- Fig. 6** The protoconch of the same specimen as in fig. 3 measures 0.4 mm in height. The larval shell is sculptured by strong tuberculated keels.
- Fig. 7** The protoconch of the same specimen as in fig. 2 measures 0.2 mm in height. The larval shell is sculptured by spiral keels and rows of tubercules.
- Fig. 8** Protoconch of the same specimen as in fig. 4. It measures 0.25 mm in height.

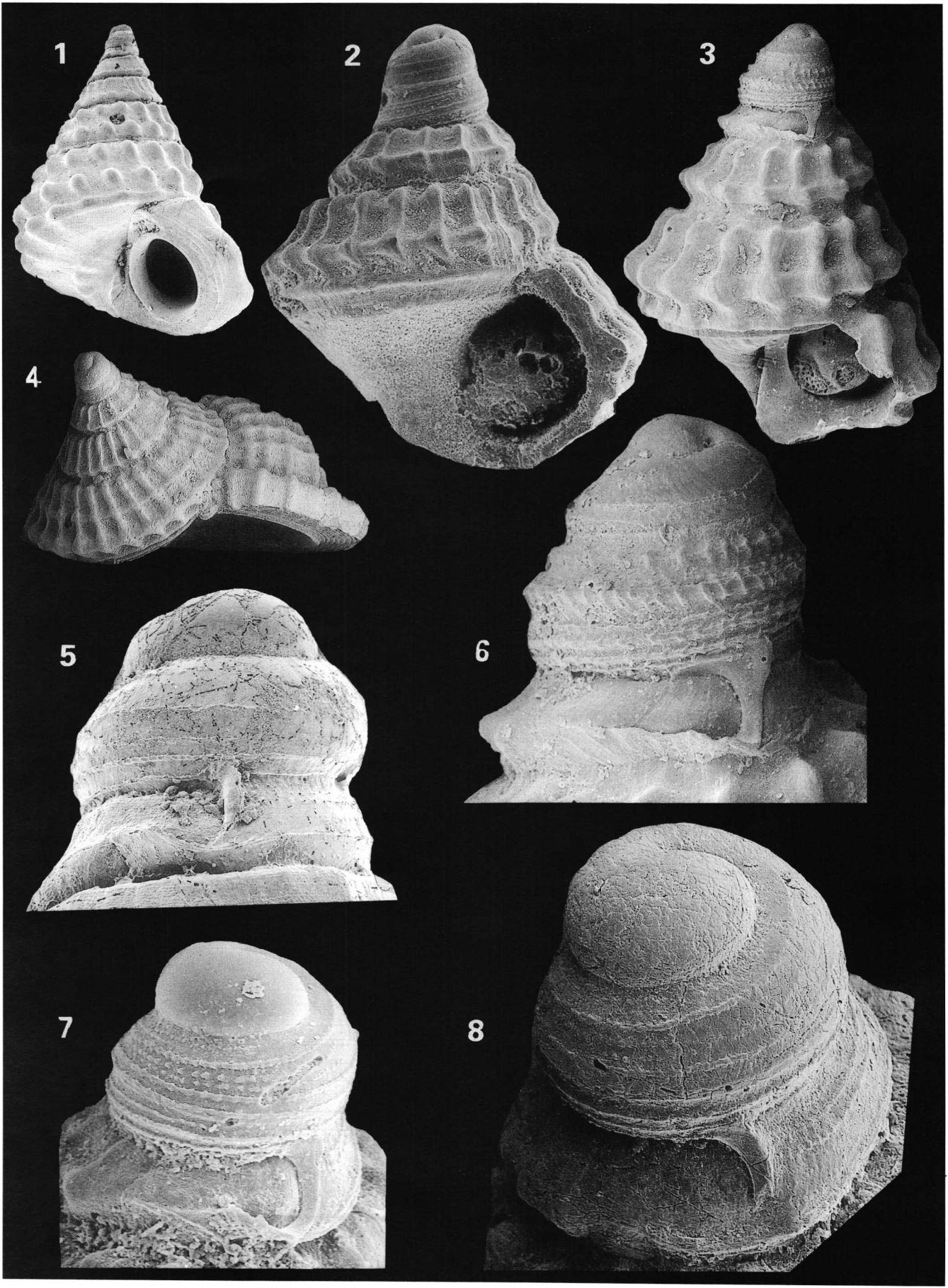


Plate 5: Fossil Pickworthiidae, the genus *Prostylifer* and Recent *Nodilittorina*

- Fig. 1** Shell of *Sansonia kenneyi* (Ladd, 1966) from the Oligocene of Peyrère (SW France), Material from the MNH, Leiden. The figured specimen measures 1 mm in height.
- Fig. 2** Shell of *Sansonia hedegaardi* n. sp., holotype, GPluM 3768, from the Danian of Faxø (Denmark). The specimen measures 1.5 mm in height.
- Fig. 3** *Gania carinata* n. g. n. sp. from the Eocene of Gan (SW France). The figured holotype, GPluM 3771, measures 0.8 mm in height.
- Fig. 4** The protoconch of the same specimen as in fig. 1 measures 0.28 mm in height. The larval shell is terminated by a sinusigera that is thickened in its upper edge and fractured at its base.
- Fig. 5** The Protoconch of *Sansonia hedegaardi* n. sp., paratype, GPluM 3769, measures 0.3 mm in height. It is sculptured by strong spiral keels.
- Fig. 6** The typically pickworthiid protoconch of the same specimen as in fig. 3 measures 0.24 mm in height.
- Fig. 7** The protoconch of *Nodilittorina millegrana* (v. Martens, 1897) from the Red Sea near Port Sudan measures 0.39 mm in height. The sculpture of the larval shell very closely resembles that of fossil and modern Vanikoridae.
- Fig. 8** The obliquely attached protoconch of *Prostylifer paludinaris* (v. Münster, 1841) from the Triassic St. Cassian-Formation of the Alps measures 0.5 mm in height. It is very similar to that of Pickworthiidae.

