

**Families of the Cerithioidea and related superfamilies
(Palaeo-Caenogastropoda; Mollusca) from the Triassic to the Recent characterized by
protoconch morphology – including the description of new taxa**

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Abstract

Morphology and ornament of the larval shell of Caenogastropoda is similar within groups of related species or genera but can not characterize all families that have been distinguished by their anatomy. Among fossil groups recognized to represent families of the Cerithimorpha according to the morphology of their shell, some display close relation to living species, while others are difficult to connect to a modern family. Fossil species of the Caenogastropoda without larval shell as part of the protoconch or with the protoconch not known are usually difficult to place into the taxonomic system due to much convergence in regard to the shape of their teleoconch. The Procerithiidae are interpreted to still exist in the Argyropezinae n. subfam., and have with the Paracerithiinae with relatively large protoconch and three spiral lines, and possibly also the Maturifusidae with very large protoconch distinct fossil groups. Ladinulidae among them *Piazella* n. gen. may connect Procerithiidae with modern Cerithiidae and Planaxidae and their protoconch unites them with the Jurassic Kosmopleurinae and its

Triassic genus *Gusellella* n. gen. Bittiidae can be interpreted as taxon uniting a group of families with small sized Cerithioidea with short and little ornamented protoconch. They may be related to the fossil Probittiinae with *Probittium* n. gen. from Madagascar. Jurassic Maoraxidae with axially and spirally ornamented protoconch may be related to modern Litiopidae, Canterburyellidae with axial ornament of the larval shell could be related with modern Obtortionidae and Triassic Popenellidae. The Zardinellopsidae n. fam. have a characteristic ornament of their larval shell that is also found on the spiny *Cortinellopsis* n. gen. Even though Melanopsidae can be traced far back in time their relation to other Cerithioidea is difficult since no well preserved larval shell is known. Cretaceous Glauconiidae could be related to the Triassic Ladinulidae as well as the modern Telecopiinae. Modern Modulidae have a protoconch resembling that of the Triassic *Modulostylina* n. gen. that is transitional to the Coelostylinidae of the Triassic. The Potamididae, which are in part based on a fossil species and therefore distinguished into Potamidinae and Telecopiinae. Pachymelaniidae can be traced with confidence to the Eocene. The history of the fresh water groups is difficult to trace over long distance of time and for fossils among them the fossil Juramelanatriidae n. fam. are suggested.

Within the units of the Turritellomorpha protoconch morphology presents evidence for convergent evolution within the group. The larval shell of *Turritella* closely resembles that of the tiny Styliiferinidae, and it connects both groups. *Spirotyliiferina* n. gen resembles *Styliiferina* but has quite different protoconch. Paleozoic Murchisonimorpha still have a Triassic representative in *Cheilotomona* and may continue in the Campanilimorpha. Only one species of *Campanile* and few species of *Plesiotrochus* represent a larger unit of which *Metacerithium* and *Sakarahina* n. gen. are interpreted as fossil representatives of related families. The Ampullinidae have only the one surviving species with *Globularia fluctuata* and that has only the embryonic shell, but the protoconch of the family is characteristic in fossil species. Falorininae n. subfam. based on the Triassic *Falorina* n. gen. may connect to *Sakarahina* which connect the Jurassic Ampullospirinae with Cretaceous Pseudamaurinae and Ampullinidae from the Paleogene. Vermetimorpha occur first in the Cretaceous with Vermetinae and Laxispirinae n. subfam. The protoconch of the Dendropomatinae could connect them with the not vermetiform Provannidae, and that of Jurassic *Sakarahellina* n. gen. and modern *Pseudoschwartziella* n. gen. could connect with the *Cerithiovermetus* n. gen. group. In the Siliquariidae, the Stephopominae and Siliquariinae have very different protoconch shape and may have quite and independent history from each other.

Zusammenfassung

Innerhalb verwandter Gruppen von Arten und Gattungen der Caenogastropoda sind Gestalt und Ornament der Larvenschale oft einander ähnlich. Sie können jedoch nicht alle jene Familien der Cerithimorpha voneinander trennen, die auf Grund ihrer Anatomie unterscheidbar sind. Unter den fossilen Gruppen, die auf Grund der Ähnlichkeit ihrer Schale den Status einer Familie erhalten haben, gibt es einige, die noch eng mit heute lebenden Arten verknüpft sind, während bei anderen eine solche Beziehung nicht mehr ohne weiteres ermittelt werden kann. Fossile Arten der Caenogastropoda mit Protoconch ohne Larvenschale oder unbekanntem Protoconch können nur mit großer Unsicherheit in das taxonomische System eingefügt werden, denn Teleoconche sehr unterschiedlicher systematischer Gruppen sind einander oft sehr ähnlich und in ihrer Ausbildung konvergent.

Von den Procerithiidae wird hier angenommen, daß von ihnen heute noch die Argyropezinae n. subfam. leben. Von der Familie haben die Paracerithiinae drei Spiralrippen auf den Windungen der Larvenschale. Möglicherweise gehören auch die Maturifusidae mit großen Protoconchen in die Nähe dieser Gruppierung. Die Ladinulidae mögen über die Procerithiidae mit den heute lebenden Cerithiidae und Planaxidae verbunden sein. Ihr Protoconch verbindet sie mit den jurassischen Kosmopleurinae sowie deren triassischer Gattung *Gusellella* n.gen. Das Taxon Bittiidae kann dahingehend interpretiert werden, daß mit ihm eine Gruppe von Familien kleinwüchsiger Cerithioidea mit kurzem und wenig ornamentiertem Protoconch in Verbindung steht. Möglich ist die Verwandtschaft mit *Probittium* n. gen der Probittiinae n. subfam. aus dem Jura Madagaskars. Jurassische Maoraxidae mit Muster von Axial- und Spiralrippen auf der Larvalschale lassen eine Verwandtschaft mit den modernen Litiopidae möglich erscheinen. Canterburyellidae mit ausschließlich axialen Larvenmustern können mit den heute lebenden Obtortionidae und den triassischen Popenellidae verknüpft sein. Den Zardinellopsidae n. fam. ist eine sehr charakteristische Skulptur der larvalen Windungen zu eigen, wie sie ebenfalls bei *Cortinellopsis* n. gen. zu finden ist. Obwohl sich die Melanopsidae bis in die Kreide zurückverfolgen lassen, ist ihre Verknüpfung mit anderen Gruppen der Cerithioidea nicht möglich, weil keine gut erhaltenen Larvenschalen bekannt sind. Kretazischen Glauconiidae kann man mit triassischen Ladinulidae ebenso wie mit rezenten Telecopiinae in Verbindung bringen. Heutige Modulidae besitzen einen Protoconch, der jenem der triassischen *Modulostylina* n. gen. ähnelt, die ihrerseits mit den Coelostylinidae der Trias in Verbindung stehen könnte. Die Unterfamilien der Potamididae basieren im Falle der Potamidinae auf einer fossilen Art. Hier werden letztere von den Telecopiinae mit rezenter Typusart getrennt. Pachymelaniidae können bis ins Eozän mit einiger Sicherheit zurückverfolgt werden. Die Geschichte jener Gruppen die sich dem Milieu des Süßwassers angepaßt haben, ist schwierig zu rekonstruieren und hier werden als fossile Sammelgruppe die Juramelanatriidae

n. fam. vorgestellt.

Die Gestalt des Protoconches belegt, dass innerhalb der Turritellimorpha konvergente Evolution stattgefunden hat. Die Larvenschale bei *Turritella* ähnelt jener der kleinwüchsigen Styliferinidae und verbindet beide Gruppen miteinander. Die anatomisch ähnliche *Spirostyliferina* n. gen. besitzt einen deutlich von *Styliferina* unterschiedenen Protoconch. Paläozoische Murchisonimorpha haben mit *Cheilotomona* noch einen triassischen Nachläufer und es mag eine Verbindung von ihnen zu den Campanilimorpha geben. Von denen hat nur eine Art der Gattung *Campanile* überlebt und bildet heute zusammen mit mehreren Arten von *Plesiotrochus* die Campaniloidea. Die Gestalt des Protoconches verbindet *Campanile* aus dem Eozän mit dem rezenten *Plesiotrochus* und den mesozoischen *Metacerithium* und *Sakarahina* n. gen. Die Ampullinidae haben mit *Globularia fluctuata* nur eine noch lebende Art ohne charakteristische Merkmale des Protoconches. Doch lassen sich diese an fossilen Arten gut belegen und mit jenen der Campanilimorpha verknüpfen. Falorininae n. subfam., basierend auf der triassischen *Falorina* n. gen., können herangezogen werden, um die jurassische *Sakarahina* der jurassischen Ampullospirinae mit den kretazischen Pseudamaurinae und den alttertiären Ampullininae in Verbindung bringen. Mit Vermetinae und Laxispirinae n. subfam. treten erst in der Kreide die Vermetimorpha in Erscheinung. Der Protoconch der Dendropomatinae ähnelt dem der rezenten und fossilen Provannidae. Andererseits sind die Protoconche der jurassischen *Sakarahellina* n. gen. mit jenen der modernen *Pseudoschwartziella* n. gen. vergleichbar. Sie könnten eine Verbindung zum modernen *Cerithiovermetus* n. gen. herstellen. Innerhalb der Siliquaridae haben die Stephopomatinae und die Siliquariinae so verschiedenartig gestaltete Protoconche, daß daraus auf eine unterschiedliche Entwicklungsgeschichte geschlossen werden darf.

1 Introduction

HOUBRICK (1992) considered the Cerithioidea FLEMING, 1822 to represent an important keystone group for any understanding of higher systematic classification and evolution of the Gastropoda in general. It was recognized that the superfamily Cerithioidea as defined by THIELE (1931) actually holds several groups of gastropods which should be considered superfamilies on their own standing. In reaction to the diversified status of that superfamily also the taxon Cerithimorpha GOLIKOV & STAROBOGATOV, 1975 and the Sorbeoconcha PONDER & LINDBERG, 1997 had been introduced. Cerithioidea as defined by WENZ (1938–1944) range back to the Triassic. Since more than 220 Million years they had their independent evolutionary history from other Caenogastropoda. Cerithimorpha may even have a stem group relation with the Paleozoic Orthonemidae NÜTZEL & BANDEL, 2000 (BANDEL, 2002) (changed to Orthonematidae by BOUCHET & ROCROI, 2005).

Regarding their anatomy members of the superfamily Cerithioidea and of the larger unit Cerithimorpha have males without a penis and fertilization of the female usually is by way of sperm-packages. HOUBRICK carried out much work on members of this group and analyzed many species that belong to living taxa very carefully. Based on these data (HOUBRICK, 1973, 1974, 1975, 1977, 1978, 1979, 1980a–c, 1981a–d, 1984, 1985, 1986, 1987a–b, 1988, 1989, 1990a–b, 1991a–c, 1992a–b), it can be undertaken to try to analyze also fossil representative of the Cerithioidea and their relation.

It was subsequently discovered that several families that had been placed by THIELE (1931) and WENZ (1938) in the Cerithioidea are actually not related to *Cerithium*, such as the Architectonicidae GRAY, 1850 (= Solariidae CARPENTER, 1857), Epitoniidae BERRY, 1910, Cerithiopsidae H. ADAMS & A. ADAMS, 1853, and Triphoridae GRAY, 1847, which since have been placed in orders which have different anatomy (Allogastropoda HASZPRUNAR, 1985 and Ctenoglossa GRAY, 1850 (= Ptenoglossa GRAY, 1850) and different history (NÜTZEL 1998; BANDEL, 2002).

Fossil members of the more basal units with the Caenogastropoda are difficult to be distinguished from each other. It is for example often quite difficult to distinguish a member of the Littorinimorpha GOLIKOV & STAROBOGATOV, 1975 from a member of the Cerithimorpha. The recent members of Littorinimorpha usually have males with a penis and can therefore easily be recognized from Cerithimorpha which have species without such a structure. This distinction is not possible with fossils where anatomical information is missing. The term Palaeo-Caenogastropoda, as introduced by BANDEL (1993), considers this fact. Also many members of the Ctenoglossa (= Ptenoglossa) have a shell shape that closely resembles that of some Cerithioidea. Living species are distinguished by radula, anatomy and sperm shape from the Cerithioidea. Due to the characteristics noted in the shape and ornament of their larval shell it has been possible to trace the history of Ctenoglossa back in time to the Early Carboniferous (BANDEL, 1993, 2002; NÜTZEL, 1998, BANDEL et al., 2002). Here the Cerithioidea and their potential relation are characterized by their larval shell and it is evident that they have evolved parallel to the Ctenoglossa at least since Triassic time.

The Campaniloidea DOUVILLÉ, 1804 which have survived with only two genera and one of them (*Campanile* BAYLE, 1884) with only one species appear to have had many species in the past, and many of them of rather similar shape to Cerithioidea (KIEL et al., 2000). They appear to continue into the Paleozoic with the Orthonematidae NÜTZEL & BANDEL, 2000, which can be traced to the base of the Carboniferous (BANDEL,

2002). In case the Campaniloidea are included in the relation of the Cerithioidea as had been suggested by HOUBRICK (1988), that superfamily would have existed for an extended time also as far back as the base of the Carboniferous, some 330 Million years ago. But, the *Campanile* relation may well represent a distinct evolutionary lineage (Campanilimorpha) that existed parallel to that of the Cerithioidea (Cerithimorpha) since the begin of the Carboniferous. The radula of *Campanile* and *Plesiotrochus* FISCHER, 1878 closely resembles that of the Cerithioidea, but this is also the case in the Viviparidae GRAY, 1847 (order Architaenioglossa).

The Viviparidae represent specialized Caenogastropoda of the fresh water. The family can be traced as independent group at least into the Jurassic (BANDEL, 1991). The Littorinoidea GRAY, 1840 and Rissooidea GRAY, 1840 (Littorinimorpha) with short conical shell undergo special differentiation but can without doubt be recognized only since the Late Jurassic. Before that their stem group representatives can not be distinguished from the other large groups of the Caenogastropoda. Since convergence in shape of the teleoconch represents such a common problem, it has become important to evaluate the shape and ornament of the larval shell. But this character is developed only in species that have a planktotrophic larval stage in the course of their ontogeny. Species with lecithotrophic embryonic development and also such which do not feed while in the plankton have only an embryonic shell. In case of lecithotrophic development it often has simplified shape and ornamental pattern (BANDEL, 1982).

The protoconch with the larval shell as is characteristic of the Caenogastropoda within the general group that belongs to the Cerithioidea differs considerably among the well recognized families of living species. Not only larger units such as Vermetidae, Turritellidae and Campanilidae may be distinguished by their larval shells from the actual units of the Cerithioidea (as in BOUCHET & ROCROI, 2005), but also several families within the Cerithioidea have distinctive shape and ornament. This is documented below and used in the discussion about the relation to the fossil taxa. Some of the differences are sufficient to introduce new taxa, and a few new fossil species and genera are described.

The larval shell also enabled to recognize the *Ampullina* BOWDICH, 1882 relation and distinguish it from the convergent Naticidae GULDING, 1834 (BANDEL, 1999). It has since been documented that one species of this relation still lives with *Globularia* (KASE, 1990; KASE & ISHIKAWA, 2003). Ampullinidae COSSMANN, 1919 and their more ancient relatives may connect to the Campanilimorpha.

The Vermetoidea RAFINESQUE, 1815 with their characteristic teleoconch which leaves the regular coiling mode and becomes more or less irregularly coiled and attached to substrate have been recognized to represent a polyphyletic group. Their presence in the geological record is since the mid-Late Cretaceous. That complex history is well documented in the differences present in shape and ornament of their larval shells. Some of them appear to connect to the *Turritella* LAMARCK, 1799 group, others to Cerithioidea, and some may be relatives to the Provannidae WARÉN & PONDER, 1991 with uncertain connection to other Caenogastropoda. The Turritellimorpha can be traced back further in time (to the Mid-Jurassic) than the Vermetimorpha and here the shape of the protoconch is evidence for the distinction of independent groups since at least the Paleogene. Protoconch shape connects them with the small *Styliferina* which also dates back to at least the Eocene.

2 Classification scheme within the Caenogastropoda

Subclass Caenogastropoda COX, 1959, as emended by BANDEL (2002)

In Caenogastropoda the shell coils unidirectional. Early ontogeny of the species included here has the potential of a planktotrophic larva. The embryonic whorl is always spirally coiled in the same direction as the larval shell and the teleoconch. It represents the shell with which the animal hatches from its egg-capsule. In cases with planktotrophic development most of the embryonic shell has no growth lines. In case of a sinistral protoconch the teleoconch has a sinistral coiling mode as well. In the exceptional cases in which the larval shell and/or the teleoconch are not coiled, the embryonic shell is always coiled. The larval shell has growth lines and is usually distinguished from the teleoconch by an apertural thickening, by change in growth line pattern, general shell shape, and by ornament. The construction of the teleoconch is usually aragonitic with bio-minerals predominantly arranged in crossed lamellar structure. Rarely there is also an external calcitic layer. Species that live on land and in fresh water develop no larval shell and their protoconch is simplified. Marine species that evolved a lecithotrophic ontogeny also simplify their protoconch.

Caenogastropoda include among others the order Cerithimorpha GOLIKOV & STAROBOGATOV, 1975 with many genera and families. Within this somewhat heterogeneous taxon especially the superfamily Cerithioidea FLEMING, 1822 can be traced to the Triassic (BANDEL, 1992). These may be connected to Goniassmitidae NÜTZEL & BANDEL, 2000 and Orthonematidae NÜTZEL & BANDEL, 2000, which can be traced to the base of the Carboniferous (NÜTZEL & BANDEL, 2000; BANDEL, 2002; BANDEL et al., 2002).

Order Palaeo-Caenogastropoda BANDEL, 1993

This order unites large systematic groups of the Caenogastropoda with ancestor having been documented from Triassic times (BANDEL, 1993, 2002). Palaeo-Caenogastropoda hold besides the superfamilies of the Cerithimorpha also such as the Littorinoidea and Rissosoidea (Littorinimorpha, in BOUCHET & ROCROI, 2005). How higher Caenogastropoda such as Meta-Mesogastropoda (Strombimorpha and Heteropoda) (as in BANDEL, 1993) and Latrogastropoda RIEDEL, 2000 (= Neomesogastropoda BANDEL, 1993 and Neogastropoda THIELE, 1929) are related has still not been elucidated. From the stratigraphic point of view Palaeo-Caenogastropoda (Cerithimorpha and Littorinimorpha) have been recognized from the Triassic onward, Strombimorpha (Meta-Mesogastropoda) appear during the Jurassic and Latrogastropoda during the Cretaceous (BANDEL 1997; RIEDEL, 2000).

3 Clade Cerithimorpha

Added to the families mentioned by BOUCHET & ROCROI (2005) are the Finellidae THIELE, 1929 and the Obtortionidae THIELE, 1925 as well as the subfamily Argyropezinae n. subfam. of the Procerithiidae COSSMANN, 1906. Families with only fossil representatives are included, in case their shell resembles reasonably that of living families. These are the Paracerithiinae COSSMANN, 1906, Ladinulidae BANDEL, 1992, Kosmopleurinae GRÜNDEL, 2003, Probitiinae n. subfam., Canterburyellidae BANDEL et al., 2001, Popenellidae BANDEL, 1992, Zardinellopsidae n. fam., Maoraxidae BANDEL et al., 2001, Glauconiidae PCHELINTSEV, 1953, and Jura-melanatriidae n. fam. The Potamididae H. & A. ADAMS, 1854 are seen as unit by BOUCHET & ROCROI (2005), and this family is here split into two parts, one Potamidae based on a fossil species and the other Telescopiinae ALLEN, 1950 based on a living species. The Maturifusidae GRÜNDEL, 2001 resemble some Cerithioidea, but even more the Purpurinidae ZITTEL, 1895 and both together remain quite problematic in their relation.

Superfamily Cerithioidea FLEMING, 1822

Families which are based on genera with living type species are often well known from literature. Problematic are Potamididae and Diastomatidae COSSMANN, 1894, both of which are based on genera with fossil type species from the Paleogene (Tertiary).

The Turritellidae LOVÉN, 1847 are considered here to represent an own superfamily with inclusion of the tiny Styliferinidae BANDEL, 1992 (n. fam.), the Vermetoidea RAFINESQUE, 1815 are also interpreted to belong close to the Cerithioidea, and Campaniloidea DOUVILLÉ, 1804 may well be the sister group to all of them. The terms Campanilimorpha, Vermetimorpha, and Turritellimorpha are applied here to suggest this difference.

Family Cerithiidae FLEMING, 1822 (FÉRUSAC, 1819; BRUGUIÈRE, 1789)

Members of this family frequently are of median size and commonly measure several centimeters in length. The aperture may have flared outer lips and a more or less long and curving canal holding the siphon. The shell is usually elongate conical and ornamented by spiral and axial ribs. The aperture has often a posterior channel. The family is based on *Cerithium* BRUGUIÈRE, 1789 with the type *Cerithium erythraeonense* LAMARCK, 1822 (= *Cerithium nodulosum* BRUGUIÈRE, 1792) from the Red Sea.

The family Cerithiidae consists of about 25 living genera which are united by anatomical characters (HOUBRICK, 1975, 1978, 1988, 1992). Most species live in the shallow sea and collect algae on hard and soft substrates. Many modern species can be traced with few changes to the Miocene and the genera are commonly recognized to the base of the Tertiary. Development is commonly with planktotrophic larva but also in many cases lecithotrophic development occurs. In a recent classification scheme presented by BOUCHET & ROCROI (2005) the Cerithiidae FLEMING, 1822 are with subfamilies Cerithiinae FLEMING 1822, Alabininae DALL, 1927 and Bittiinae COSSMANN, 1906. This is not followed here, due to differences seen in protoconch morphology between the first and the two later subfamilies.

Among the genera described by HOUBRICK (1976, 1985, 1992) *Cerithium* BRUGUIÈRE, 1789, *Rhinoclavis* SWAINSON, 1840, *Clypeomorus* JOUSSEAUME, 1888 and *Royella* IREDALE, 1912 have been recognized on the fringe reef, lagoon and beach in front of the Marine Station at Aqaba. They can also be distinguished by their ecology. *Rhinoclavis* moves within loose sand and coral rubble and also feeds there. *Clypeomorus* lives on the rocky beach within the intertidal zone. *Cerithium* lives among algal mats and on the substrate within the littoral zone, and *Royella* is found on bottom in shallow water with loose sand.

The protoconch of *Cerithium* is relatively short consisting of 2 to 3.5 whorls (pl. 1/1, 6–9). The embryonic whorl

is minutely sculptured by fine ridges and grooves. The larval pattern begins abruptly, with many fine axial ribs on the shoulder and spiral lines or ribs on the rounded sides. Between the spiral lines the space is filled by tubercles or inclined lines. Below the median ribs inclined lines may be present. The rounded base of the larval shell is covered with spiral lines. The aperture has a well rounded and marginally thickened sinus in the shoulder part. The tongue like median projection of the outer lip is quite extensive and ornamented with lines to its margin. The protoconch is about 0.3 mm high and of similar width. Among the different species of *Cerithium* as well as *Rhinoclavis* and *Clypeomorus* from Aqaba (pl. 1/3, 4) the number of whorls of the protoconch differs from 3.5 to 2 whorls, with size, number of whorls and usually also the ornament specific to the species. The ornamental pattern usually is characterized by strongest sculpture in those species with which have most larval whorls.

In case of *Royella* the protoconch consists of 3 whorls, the embryonic one smooth and later with two prominent spiral row of tubercles that border the apertural projection above and below it and are separated from each other by a broad shallow groove. The flattened shoulder has a row of sharp axial ribs which end before reaching the spiral keel. The apertural projection of the fully grown larval shell is large and extends into an angular shape. Its lower portion is covered by the first whorl of the teleoconch (pl. 1/5, 10, 11). The protoconch is about 0.3 mm high in its exposed portion. Ornament and shape of the larval shell is close to that of *Argyropeza*, discussed below.

Cerithium vulgatum from the Mediterranean Sea (RICHTER & THORSON, 1975) has its protoconch with the characteristics of the genus, as is also the case of *Cerithium litteratum* (BORN, 1778) and *Cerithium atratum* (BORN, 1778) from the Caribbean Sea (LEAL, 1990, pl. 6, figs. A, B) (pl. 1/2). Very similar ornamental patterns on the larval shell are present in Cerithiidae from the Eocene of the Paris Basin, from Gant in Hungary (KOWALKE, 1998, pl. 1, figs. 5, 11) as well as from the Brazos River in Texas.

Family Planaxidae GRAY, 1850

The larval shell of the protoconch in size and ornament is very close to that of the Cerithiidae. The family holds two subfamilies of which the Planaxinae are characteristically found in the stony tropical intertidal zone where they feed on crusts of organisms and the minute Fossarinae live attached to stones in shallow water.

Subfamily Planaxinae GRAY, 1850

HOUBRICK (1987) distinguished six genera of the *Planaxis* LAMARCK, 1822 relation, all of which are quite close to the type *Planaxis sulcatus* (BORN, 1780) regarding protoconch, shell shape and mode of life. About 20 species of *Planaxis* are living today and very similar fossil species are known from the Eocene of France as well as from the Brazos River area in Texas (BANDEL & KOWALKE, 1997; KOWALKE, 1998). The protoconch of *Planaxis* (*Supplanaxis*) THIELE, 1929 based on *Planaxis nucleus* (BRUGUIÉRE, 1789) from Santa Marta, Caribbean Sea (pl. 2/1) very closely resembles that of *Planaxis lineolatus* from the Red Sea. *Planaxis* (*Angiola*) DALL, 1926 is based on *Planaxis lineatus* (DA COSTA, 1778) that lives on the same beach on the Caribbean coast (pl. 1/14) as *Planaxis nucleus* but is the smaller of both species. *Planaxis sulcatus* from the Gulf of Aqaba (pl. 2/5, 7, 9) and *Planaxis* (*Angiola*) *lineolatus* (GOULD, 1851) from the same beach but a little further down the shore, have a similar ecology. All four species release their young from a brood pouch.

Veligers released by *Planaxis* (*Supplanaxis*) *nucleus* from the brood pouch have an embryonic shell that measures about 0.1 mm (BANDEL, 1975) and it is similar in the other species studied. The larval shell has a characteristic row of short axial ribs on its shoulder, two spiral lines on the side which continue into the tongue like apertural projection. The protoconch consists of about 3.5 whorls and measures about 0.3 mm in height and width (pl. 2/1). It differs from that of *Planaxis lineatus* in regard to the median spiral ornament that consists of rows of tubercles, while ribs in the later (pl. 1/14). In *Planaxis sulcatus* representing the larger species on the shore at Aqaba the protoconch has only 2.5 whorls (pl. 2/5, 7, 9) and the ornament of the larval shell is more delicate, than in case of smaller *Planaxis lineolatus* (pl. 2/3). The larvae of both species are very common in the plankton of the Gulf of Aqaba.

HOUBRICK (1987, 1988) suggested to group the Planaxidae near the Thiaridae according to the construction of the brood pouch in their neck. But DNA analysis indicated that no closer relation exists between *Planaxis* on one side and the Thiaridae on the other side (unpublished data RALF BISCHOFF).

Subfamily Fossarinae A. ADAMS, 1860

The protoconch has a larval shell with collabral axial ribs transected by two spiral ribs and a median projection

of its outer lip (pl. 2/4). The shell is small and consists of up to three whorls of the teleoconch with conical shape and spiral ornament. The family is based on *Fossarus* PHILIPPI, 1841 with the type *Turbo ambigua* LINNEUS, 1766 from the Mediterranean Sea. *Fossarus ambiguus* lives in small cavities among encrusting coralline algae just below the intertidal zone along rocky shores (WARÉN & BOUCHET, 1988). HOUBRICK (1990) noted that only the very small individuals are males and a change of sex to females occurs when growing in size.

The shell of *Fossarus orbignyi* FISCHER, 1864 is only 1.5 mm high and consists of 2 to 2.5 whorls of the teleoconch. Ornament consists of three keel-like spiral ribs with smaller ribs in the interspaces. The base is covered by strong ribs and the umbilicus is concealed by the inner lip. The protoconch has a smooth embryonic whorl smaller than 0.1 mm. The larval whorls are ornamented by strong collabral ribs crossed by two spiral ribs which trace the margins of the angular apertural projection of the outer larval lip (LEAL, 1990, pl. 6, figs. E, F; BANDEL & KOWALKE, 1997, pl. 1, figs. 1, 4). The protoconch of *Fossarus* from the Gulf of Aqaba and from *Fossarus* at the Caribbean Sea are very similar to each other and also resemble those of *Planaxis* (pl. 2/2, 4).

Family Procerithiidae COSSMANN, 1906

The protoconch has a diagnostic triangular shape with its larval shell with two or three strong spiral keels and added spiral rows of tubercles. The apertural margin of the larval shell is expanded to a large median projection and change to teleoconch ornament is drastic. The family has predominantly species with slender shells consisting of many whorls. Jurassic and Cretaceous Procerithiinae with *Cryptaulax* TATE, 1869 grade with almost no change in shell shape into the Argyropezinae with *Argyropeza* MELVILLE & STANDEN, 1901 living in tropical seas (GRÜNDEL, 1976; GUZHOV, 2004). The Procerithiinae based on a Jurassic type and the modern Argyropezinae resemble in shell shape the Paracerithiinae and to some degree also Maturifusidae, both based on Jurassic types.

Subfamily Procerithiinae COSSMANN, 1906

The characteristic protoconch ornament consists of a row of tubercles below the suture and two spiral keels on the larval shell (GRÜNDEL, 1976, 1997, 1999). The family is based on the genus *Procerithium* COSSMANN, 1902 which probably is quite the same as *Crypaulax* TATE, 1869. *Procerithium* is based on *Procerithium quinquegranosum* COSSMANN, 1902 from the Hettangian of France. The type was restudied by GRÜNDEL (1997, pl. 5, figs. 1–5) and its protoconch is still unknown. According to KAIM (2004) no difference exists between *Procerithium* and *Cryptaulax*. He placed species such as *Procerithium kulickii* SCHRÖDER, 1995 or *Procerithium tricuspis* SCHRÖDER, 1995 as well as *Xystrella armata* described by GRÜNDEL (1997) within *Cryptaulax*. While KAIM (2004) did not note much of a difference between these genera, he recognized the Cretaceous *Schroederium* as proposed by KOWALKE (1998), even though this genus is within the morphological range of the Jurassic species of *Cryptaulax* but also close in shape to modern *Argyropeza*. GRÜNDEL (1976) placed *Cryptaulax* into an own subfamily Cryptaulacinae GRÜNDEL, 1976, which is difficult to uphold when *Cryptaulax* and *Procerithium* are actually based on a very similar perhaps even the same species.

Cryptaulax has a slender teleoconch and its protoconch consists of several rounded whorls in which the larval shell is ornamented by two, often tubercle bearing spiral ribs. The teleoconch is ornamented by axial ribs which may be arranged in an alternating screw-like pattern. They are crossed by two spiral ribs on the first whorl of the teleoconch. Later whorls may have more spiral ribs which form tubercles where they cross the axial ribs. In the juvenile shell the base forms an angle with the sides and it is rounded in the adult shell. The base has commonly three spiral ribs. An anterior notch of the aperture is indistinct in the type to the genus *Cerithium tortile* HÉBERT & EUDES-DESLONGCHAMPS, 1860 (= *Procerithium (Xystrella) protortile* COX, 1969) from the Middle Jurassic of France.

Cryptaulax sakarahensis n. sp.

Holotype: pl. 3/1 in coll. of the Geol.-Pal. Inst. Mus., Hamburg.

Diagnosis: The protoconch consists of 4 to 5 whorls. It is ornamented by three spiral keels and a tubercle bearing subsutural zone. The central keel continues into the lower spiral rib of the teleoconch, while the upper keel ends before reaching the end of the larval shell. The lower keel may be visible just above the suture or may be covered by the succeeding whorls. The ornament of the teleoconch is variable among individuals and consists of sharp axial ribs which begin and end in nodules on the whorls sides. They are crossed by one later more finer spiral ribs.

The species is based on the specimen illustrated in pl. 3/1 and the type material is deposited in the Geological-Paleontological Museum of the University of Hamburg. Its name is according to occurrence just to the West of Sakaraha in Madagascar from Mid Jurassic beds exposed next to the road (locality described by LUGER et al., 1994).

Description: The embryonic shell is smooth, rounded and measures 0.12 mm across. The larval shell has a variable number of whorls and also its ornament is more variable than is usually the case compared with larval shells of modern species of the Cerithiidae, including *Argyropeza*. The first larval whorl may be rounded and covered by tubercles arranged in spiral lines, or two spiral keels begin quite near the end of the embryonic whorl. Actually there are three keels, the lowest of which is commonly covered by the following whorl but may also remain uncovered (pl. 3/4). The keels continue to the last larval whorl. Here the upper keels may totally disappear, but also continue as relict to the margin. The lower keel marks the lower end of the apertural projection of the outer lip. The last larval whorl is flattened and has a median sinus and an anterior tongue-like apertural projection, which is covered largely by the succeeding first whorl of the teleoconch. The protoconch is up to 0.8 mm high, and 0.4 mm wide.

The teleoconch is very similar to a *Cryptaulax* from Europe as described by KAIM (2004), but is quite variable regarding its ornament (pl. 3/2, 5, 6, 7). While the high protoconch distinguishes *Cryptaulax sakarahensis* from other species of that genus known, the teleoconch resembles that of *Cryptaulax armata* (GOLDFUSS, 1843) or *Cryptaulax echinata* (BUCH, 1831) as described by KAIM (2004) from the Jurassic of Poland, but also that of *Schroederium valanginiense* (SCHRÖDER, 1995) from the Early Cretaceous of Poland. *Cryptaulax* (*Neocryptaulax*) GERASIMOV, 1992 and *Cryptaulax* (*Microcerithium*) GUZHOV, 2004 differ from each other by teleoconch ornament, which is less present in the latter (GUZHOV 2004, pl. 2). *Cryptaulax sakarahensis* appears to vary between both subgenera.

Rhabdocolpus COSSMANN, 1906 has an elongate shell with angular whorls. The protoconch consists of 3–5 whorls and their larval whorls are ornamented by two spiral ribs and there may also be a spiral row of tubercles. The teleoconch is initially ornamented by three, later five or more spiral ribs and numerous axial ribs. When crossing each other they form nodes. The axial ribs are straight at first and sinuous later on ending before the convex base. An indistinct anterior notch is at the aperture and its outer lip expands to rounded anterior lobes. The genotype is *Melania scalariformis* DESHAYES 1830–32 from the Middle Jurassic of western France. *Rhabdocolpus kowalkei* BANDEL, GRÜNDEL & MAXWELL, 2000 from the Jurassic of New Zealand has a protoconch with four whorls that is about 0.4 mm high. The teleoconch is slender trochospiral with slow, and later a little more rapid increase in whorl diameter. The axial ribs do not increase in number during shell growth and are oriented to form a screw-like pattern on succeeding whorls (BANDEL 1993, pl. 2, fig. 1; BANDEL et al., 2000, pl.6, figs. 4–6, 8, 10). Similar species from the Russian Jurassic were placed with *Exelissa* by GUZHOV (2004, pl. 4, figs. 3–12). *Rhabdocolpus acodiastrum* GRÜNDEL, 1999 and *Rhabdocolpus kebyensis* GRÜNDEL, 1974 from Jurassic erratic boulders have a protoconch with the characteristic two keels ornamenting the larval shell (GRÜNDEL, 2003, pls. 7 and 8).

Subfamily Paracerithiinae COSSMANN, 1906

The protoconch of *Paracerithium* COSSMANN, 1902 has three spiral lines on the larval shell. The subsutural row of dots and the spiral ribs on the larval shell resembles that of *Argyropeza* but the protoconch may be larger. The subfamily is based on the genus *Paracerithium* from the Jurassic. The teleoconch is characterized by an aperture with anterior notch, conical shell shape and ornament with one or two strong spiral ribs creating a keeled appearance. Smaller spiral lines cover the whorl flanks as well as the base. The few widely spaced axial ribs continue from the suture to the spiral keels on the median whorl, forming nodules with them where they cross. The genotype is *Paracerithium acanthocolpum* COSSMANN 1902 from the Early Jurassic of France.

Paracerithium spinosum BANDEL, GRÜNDEL & MAXWELL, 2002 from the Jurassic of New Zealand has its protoconch ornamented with spiral ribs of which two are strong, with the apical one becoming weaker close to the aperture. It consists of more than three whorls and is about 0.6 mm high. The projection of the aperture of the larval shell is in part covered by the first whorl of the teleoconch, and collabral ribs are present in the last part of the larval shell. Ornament of the teleoconch is characterized by a spine bearing keel. *Paracerithium pacificum* BANDEL, GRÜNDEL & MAXWELL, 2000 from the same locality has its protoconch ornamented by three spiral ribs. It consists of 3.3 rounded whorls, is about 0.35 mm high and 0.3 mm wide. The embryonic whorl measures about 0.1 mm across and appears to be smooth (BANDEL et al., 2000, pl. 5, fig. 5, pl. 6, figs. 1–4, 7, pl. 7, figs. 1–4). Similar species from the Russian Jurassic were placed in the genus *Shurovites* GUZHOV, 2004 with especially *Shurovites unzhensis* GUZHOV, 2004 very closely resembling *Paracerithium pacificum* but with less strong spiral ornament on the larval shell.

Also *Rhynchocerithium* COSSMANN, 1906 based on the Mid Jurassic *Cerithium fusiforme* HEBERT & ETUDES-

DESLONGCHAMPS, 1860 can be included in this subfamily. The genus has a more or less slender protoconch with two to three spiral ribs and a size of over 1 mm in height (GRÜNDEL, 1999, pl. 5, figs. 1–4; 2005, pl. 2, figs. 1, 2). In case of *Cirsocerithium* COSSMANN, 1906 based on *Cerithium subspinosum* DESHAYES, 1842 from the early Cretaceous of France a *Cirsocerithium collignoni* KIEL, 2004 from the Albian of Madagascar has a protoconch with 5.5 whorls that is almost 1 mm high (KIEL, 2006, figs. 3, 11–3, 14). It is larger as within the species of the Procerithiidae and the modern Cerithiidae. The embryonic shell with 0.1 mm in diameter is succeeded by larval whorls with three spiral ribs on a somewhat flattened surface.

Subfamily Argyropezinae n. subfam.

Diagnosis: The subfamily has the characteristics of the genus *Argyropeza* MELVILLE & STANDEN, 1901. The protoconch has a diagnostic larval shell with two strong spiral keels and row of short axial ribs on the shoulder (pl. 3/9, 11, 12). The teleoconch is slender conical in shape with flattened whorls and strong spiral and axial ornament formed nodules where crossing (pl. 3/8, 10). The aperture has a broad anterior notch and the shell is shiny. The type to the genus is *Argyropeza divina* MELVILLE & STANDEN, 1901 from the Indian Ocean, quite similar to the species encountered on sandy bottom in the shallow Gulf of Aqaba. The protoconch of *Argyropeza divina* consists of 3.5 whorls with a long median projection on the outer lip of the larval whorls (HOUBRICK 1980, fig. 21).

Argyropeza differs from *Varicopeza* GRÜNDEL, 1976 by features of the aperture that has an anterior notch and may be accompanied by a varix (pl. 4/1, 2). In case of *Varicopeza* as described by HOUBRICK (1980, 1993) the protoconch has two fine spiral lines (HOUBRICK, 1993, fig. 23C). Actually the larval shell has a similar strong ornament as found in *Argyropeza* (pl. 3/14). GRÜNDEL (1976) interpreted *Varicopeza* and *Argyropeza* to present living species of the Procerithiidae and closely related with *Cryptaulax* TATE, 1869. HOUBRICK (1993) did not agree, but offered no prove for his interpretation, even though he suggested to place both genera with the Bittininae. *Varicopeza pauxilla* (A. ADAMS, 1854) lives in the western Indo Pazific (Philippines to Barrier Reef) (HOUBRICK, 1980).

Species resembling modern *Argyropeza* in shape of the shell including protoconch lived in the Late Cretaceous Ripley Formation of Mississippi (as *Schroederium covickeense* (SOHL, 1964) in KOWALKE (1998, pl. 1, figs. 1, 10) as well as in the Eocene margin of the Tethys Ocean at Hungary (as *Cerithium quadricinctum* DONCIEUX, 1908 in KOWALKE (1998, pl. 1, figs. 4, 9), near Jackson in Mississippi (as *Cerithium* sp. in KOWALKE, 1998, pl. 1, fig. 6, erroneously with locality Texas), (pl. 3/12), and also SW France (as *Cerithium cylindraceum* DESHAYES, 1866 in KOWALKE, 1998, pl. 1, fig. 3).

Family Maturifusidae GRÜNDEL, 2001

The protoconch is large (more than 1 mm high). The larval shell is conical and ornamented by two spiral lines, resembling that of Procerithiidae. The teleoconch is fusiform with rounded whorls and ornament of axial ribs that are crossed over by spiral lines. The aperture is elongated with an anterior canal. The subfamily is based on *Maturifusus* SZABO, 1983 which has the type *Maturifusus densicostatus* SZABO, 1983 from the Jurassic of Hungary without protoconch preserved. It would be difficult to distinguish this genus from *Khetella* BEISSEL, 1977 from the Russian Jurassic as described by GUZHOV (2004) in regard to teleoconch shape. The protoconch was first documented by SCHRÖDER (1995).

The protoconch of *Maturifusus szaboi* SCHRÖDER, 1995 from the mid Jurassic of northwestern Germany has five whorls, is of conical shape, measures 1.4 mm in height and almost the same in width, and ends with a large larval hook on its outer lip (SCHRÖDER, 1995, pl. 4, figs. 17–20). Ornament of the rounded whorls consists only of growth lines. In case of *Maturifusus montagi* GRÜNDEL, 1998 from the Oxfordium of northeastern Germany the protoconch is conical with four to five whorls and a height of almost 1.5 mm (GRÜNDEL, 1998, pl. 7, figs. 5–8; GRÜNDEL, 1999, pl. 7, figs. 1–4). The transition from protoconch ornament to the teleoconch pattern is abrupt. As in *Maturifusus grimmensis* GRÜNDEL, 1999 the larval shell has two keels, the upper of which lies on the corner to a shoulder. In case of *Maturifusus conspicuous* (EICHWALD, 1868) the first larval whorl also has ornament of tubercles and there is a subsutural row of tubercles on all whorls (GUZHOV, 2004, pl. 7, figs. 10–13; GRÜNDEL, 2005, pl. 4, figs. 14–15).

SZABO (1983) related *Maturifusus* with the modern Buccinidae RAFINESQUE, 1815 on one side and on the other with the fossil Purpurinidae ZITTEL, 1895. It could also be connected to the Ladinulidae, which have quite diverse shape of their teleoconch and are united by a protoconch with spiral ornament, but of much smaller size than in the Maturifusinae. KAIM (2004) connected *Maturifusus* with *Astandes* WADE, 1917, a genus based on species from the Ripley Formation of Tennessee. The protoconch of *Astandes* is as large as that of *Maturifusus* but more elongate, and the genus is connected to the Late Cretaceous Pyrifusidae BANDEL, 2000, which may

belong in the stem group of the Latrogastropoda and Neogastropoda (BANDEL & DOCKERY, 2001). GRÜNDEL (2005) did not agree with KAIM (2004) while the same author (GRÜNDEL, 2003) had placed the Maturifusidae into the Latrogastropoda RIEDEL, 2000.

Maturifusidae can be placed only with strong reservations with the Cerithimorpha and Cerithioidea, but they have also not found a comfortable place in relation to any other larger group of Caenogastropoda. Only the Triassic to Jurassic Purpurinidae appear related, but their place in the system of the Caenogastropoda is also in doubt (BANDEL, 1993). Maturifusidae and Purpurinidae can be placed in a superfamily Purpurinoidea ZITTEL, 1895, which would extend the existence of this group from the Triassic to the Cretaceous.

Family Ladinulidae BANDEL, 1992

The protoconch has quite diagnostic larval ornament consisting of a spiral keel that develops in its second whorl on the upper edge of the apertural projection of the outer lip. In addition there are several spiral rows of tubercles. The shape is triangular with rounded embryonic whorl of about 0.1 mm in diameter, and the size of the larval shell is about 0.3 mm in height.

The family is based on Triassic species which have similar protoconch features which can be connected to the Jurassic to recent Procerithiidae as well as to modern Cerithiidae. Among the members of the Ladinulidae the conical shell has flattened whorls and in juvenile stage an angular, later a round shape of their aperture. The ornament of the teleoconch consists of spiral and straight axial ribs. The genera *Ladinula* BANDEL, 1992, *Ampezzoscala* BANDEL, 1992, and *Camposcala* BANDEL, 1992 have the characteristic protoconch of the Ladinulidae (pl. 7/5, 6). *Piazella* n. gen. is newly described with *Piazella subnuda* (KITTL, 1894) (pl. 7/11–13).

Ladinula has a broadly conical shell with umbilicus and spiral ornament in the juvenile shell to which in the later shell axial ribs are added. The genus is based on *Ladinula campana* BANDEL, 1992 from the Late Triassic S. Cassian Formation in the Alps. Its shell has an apical angle of about 45° and is with 7 whorls 1.8 mm high and 1.2 mm wide. The protoconch consists of almost 3 whorls and is 0.3 mm high and almost as wide, with about 0.1 mm wide embryonic whorl. The first larval whorl is ornamented by spiral rows of tubercles, and the second has two spiral keels, one at the top and the other at the base of the long median projection of the outer lip of the aperture. The lower keel comes to lie in the suture of the following whorl. The upper keel continues in a spiral rib on the teleoconch. The first whorls of the teleoconch are ornamented by spiral lines of granules, and from the fifth whorl onward 12 to 15 wide axial ribs are added. Whorl flanks and the base are flattened and the aperture is as wide as high (BANDEL, 1992, pl. 1, figs. 1–5), (pl. 7/9, 10). *Ladinula lima* (as *Tectus lima* by ZARDINI, 1878) is similar (ZARDINI, 1978, pl. 12, figs. 8–11) and may represent a variety.

Ampezzoscala has a shell with high spire and rounded base (pl. 7/8). It is ornamented by few axial ribs crossed by a strong spiral rib forming tubercles at crossing. In addition a dense pattern of fine spiral lines feature the surface (ZARDINI, 1978, pl. 16, figs. 14, 17, 23, 24, pl. 17, figs. 1–3). The protoconch is of rounded triangular shape, and has its larval shell ornamented by several spiral rows of granules and in the second whorl a strong rounded median keel at the edge to its apertural projection. The embryonic whorl measures about 0.1 mm and the larval shell has three whorls and is about 0.3 mm high. The type is *Turritella ornata* MÜNSTER, 1841 from S. Cassian Formation. Its shell has an apical angle of 45–50°, consists of about 13 whorls, is about 14 mm high and 5 mm wide with ornament of 11–14 straight axial ribs. The base has spiral ribs and the aperture is rounded, thickened and detached (BANDEL, 1992, pl. 3, fig. 5–8, pl. 4, figs. 2, 8; 1993, pl. 1, fig. 1; 1994, pl. 3, fig. 2; BANDEL & EL NAKHAL, 1993, pl. 3, figs. 5, 7).

Camposcala has a conical high shell with ornament of straight axial ribs crossed by few spiral ribs forming a pattern of rectangles. The base has spiral ribs and a narrow umbilicus. The type is *Eucycloscala pusilla* ZARDINI, 1978 from the Late Triassic S. Cassian Formation in the Alps. The protoconch has a rounded embryonic whorl of about 0.1 mm in diameter. It is a little more than 0.2 mm high and consists of almost 3 whorls. The larval shell is rounded at first and develops a keel with flat flanks above and below in its second whorl. The ornamented of the late larval shell is by a spiral median keel and ribbons and fine rows of tubercles below the suture, below the keel, and above the suture (pl. 7/5). The keel marks the upper edge of an extended median projection of the apertural outer lip. *Camposcala pusilla* (ZARDINI, 1978) consists of 9 whorls and is about 6 mm high and 3 mm wide with apical angle of about 50°. In early whorls the suture is deep and has triangular shape, later it is shallower. Early whorls of the teleoconch are ornamented by spiral rows of tubercles and later 3–5 spiral ribs crossed by about 10 axial ribs. The aperture is slightly inclined and angular in young shells and round in fully grown ones (ZARDINI, 1978, pl. 16, figs. 4–7; BANDEL, 1992, pl. 3, fig. 3, pl. 4, fig. 1).

Faloriella has a lowly conical, disc-like shell with flattened whorls and a wide conical umbilicus. Two keels with a furrow between them feature the sides. A row of tubercles surround the umbilicus and the base has fine spiral lines. The aperture is angular in juveniles is angular later it is round and oblique. The protoconch resembles that of *Ladinula*. The type is *Faloriella cortinense* BANDEL, 1992 from the Late Triassic S. Cassian Formation in the Alps. The protoconch and the first teleoconch whorls are highly conical, later whorls are low.

The aperture of the adult shell is rounded, thickened and a little detached (ZARDINI, 1978, pl. 9, figs. 3–5; BANDEL, 1992, pl. 2, figs. 3–5, 7).

Genus *Piazella* n. gen.

Diagnosis: The conical shell is smooth with apical angle around 60° in the protoconch as well as in the teleoconch. The whorls are rounded, those of the teleoconch a little less than those of the protoconch. The corner to the base is rounded and distinct. The larval whorls are ornamented by two spiral ridges and a subsutural ribbon of tubercles and have a median apertural projection of the outer lip. Teleoconch whorls have only slightly sinuous growth lines as ornament. The genus is based on *Loxonema (Anoptychia?) subnuda* KITTL, 1894 as documented by ZARDINI (1978, pl. 26, fig. 22), and with less detail by KITTL (1894, pl. 4, figs. 56–57).

Derivatio nominis: Called according to the place of origin in the Prato Piazza (Plätzwiese) that has the locality Alpe di Specie (ZARDINI, 1978). The type of the genus is from the Late Triassic S. Cassian Formation, locality Alpe di Specie.

Piazella subnuda (KITTL, 1894)

The teleoconch resembles that of *Anoptychia subnuda* (KITTL, 1894) in ZARDINI (1978, pl. 26, fig. 22, pl. 29, fig. 4). KITTL (1894) described the shell as conical with convex whorls, smooth and without umbilicus with rounded corner to the base. Growth lines are slightly sinuous and the aperture is rounded. Neither author knew the protoconch of this species from the S. Cassian beds of the locality Specie (pl. 7/11–13).

The protoconch is also of conical shape with three rounded whorls (pl. 7/12–13). It is about 0.3 mm wide and high with the embryonic whorls rounded, smooth and about 0.12 mm wide. Ornament on the first larval whorl consists only of spiral rows of tubercles which in the second larval whorl are arranged as subsutural double row of tubercles, median spiral ridge with tubercles and a smaller ridge with smaller tubercles just above the suture. The main spiral ridge forms the top of the apertural projection which is to a large part covered by the succeeding first whorl of the teleoconch.

Lucmeria GRÜNDEL, 2005 from the Bathonian of France based on *Lucmeria angulosa* GRÜNDEL 2005 has a small conical shell only about 1.5 mm high with simple axial ribs and a protoconch consisting of 4 whorls and about 0.4 mm high with the ornament as found among the *Ladinula* relation (GRÜNDEL, 2005, pl. 2, figs. 3–8). GRÜNDEL placed *Lucmeria* in the family Lucmeriidae GRÜNDEL, 2005 connecting it with the Pickworthiidae IREDALE, 1917.

Subfamily Kosmopleurinae GRÜNDEL, 2003

The teleoconch is slender conical and whorls are axially ribbed with smooth background. The protoconch has ornament of its last larval shell consisting of two strong spiral ribs which are composed of tubercles. The subfamily is based on *Kosmopleura* GRÜNDEL, 2003 from the Early Jurassic of Germany.

GRÜNDEL (2003, pl. 6, figs. 1–6) included the Kosmopleurinae in the Zygopleuridae WENZ, 1938, even though the protoconch has different shape and ornament within the species from that family. The subfamily is transferred to the Ladinulidae, in which teleoconch shapes are quite varied, while the protoconch has the same characteristics. *Kosmopleura* is based on *Kosmopleura hoelderi* GRÜNDEL, 2003 with protoconch consisting of about 4 whorls and about 0.5 mm in height. Ornament is a strong keel on the last larval whorl and a row of tubercles. Ornament of the teleoconch is of strong axial ribs crossed by indistinct and weak spiral lines documented in a granulation of the axial ribs.

Genus *Gusellella* n. gen.

Diagnosis: The teleoconch resembles that of *Zygopleura* KOKEN, 1892 with conical slender shell and ornament of straight axial ribs with simple aperture, while the protoconch is like that of *Ladinula* with three whorls ornamented by rows of tubercles and a median keel on top of the apertural projection in the larval shell (pl. 7/6). The genus is based on *Loxonema haueri* LAUBE, 1868 from the locality Campo at Cortina d'Ampezzo in the Dolomites, S Cassian Formation.

Derivatio nominis: Named after Monte Gusella (2597 m) just to the south of Cortina d'Ampezzo.

Gusellella haueri (LAUBE, 1868)

The apical angle of the teleoconch is about 45° while the protoconch has rounded whorls (pl. 7/6, 14). KITTL (1894, pl. 4, figs. 20–26) described the two species *Loxonema walmstedti* KLIPSTEIN, 1843 and *Loxonema haueri* and noted a difference mainly by their apical angle. The first amounts to 20–30° and the second to 30–45°. Ornament of both species consists of straight axial ribs of which 10 to 15 are present on each whorl. Whorls are wider than high and the aperture is almost as wide as high and simple. The base is almost smooth and has a rounded corner to the sides. Both species have not been described in regard to the shape of their protoconch. *Zygopleura haueri* as described by ZARDINI (1978, pl. 25, fig. 9) fits in regard to the shape and ornament of the teleoconch. *Gusellella haueri* is not a *Loxonema* nor a *Zygopleura* KOKEN, 1892 due to the differences in protoconch morphology and ornament. The protoconch of *Zygopleura* was extensively described by NÜTZEL (1998). It has rounded triangular shape, has more than 4 whorls, is more than 0.7 mm high and has an ornament of the larval shell consisting of short axial ribs below and above the suture, while sides are smooth. *Gusellella haueri* in contrast has the protoconch with three whorls and 0.4 mm in height and 0.35 mm in width (pl. 7/6). Ornament consists of several spiral rows of tubercles in the first rounded larval whorl, a median keel and tubercles concentrated below the suture and below the keel in the second larval whorl. The keel lies at the upper edge of the strong apertural projection with apical sinus thickened in the fully grown larval shell. *Kosmopleura* differs by having a less ornamented larval shell and fewer axial ribs and much more pronounced suture in the teleoconch. Also whorls are unsymmetrical convex, otherwise the Jurassic genus it is similar to the Triassic *Gusellella*.

Family Glauconiidae PCHELINTSEV, 1953 (= Cassiopidae KOLLMANN, 1979)

This group of Cretaceous species with medium sized conical shell with flattened base and umbilicus lived in the coastal swamps of the tropical Tethys Ocean with many species (MENNESSIER, 1984). Their protoconch in shape and ornament of its larval shell resembles that of the Procerithiidae and Ladinulidae (BANDEL, 1993, pl. 1, fig. 2, pl. 2, fig. 3, pl. 4, fig. 6). It is ornamented by two spiral keels and a row of subsutural tubercles. The family is based on *Glauconia* GIEBEL, 1852 which had to be substituted by *Cassiope* COQUAND, 1865 (KOLLMANN, 1979). It is based on *Turritella kefersteini* MÜNSTER, 1844 from the Gosau Cretaceous in the Northern Alps. *Cassiope* has a conical shape, with wavy spiral ribs and rounded aperture. The base is angular and the umbilicus open. Whorls are flattened and ribs may bear tubercles. The outer lip of the aperture is curved so that there is a posterior lobe (CLEEVELEY & MORRIS, 1988). The protoconch of *Cassiope kefersteinii* (MÜNSTER, 1844) from the late Cretaceous of the Gosau in the Northern Alps consists of 3 whorls with the embryonic shell about 0.12 mm wide. Its larval whorls have the characteristic spiral ornament (BANDEL, 1993, pl. 1, fig. 2; KOWALKE & BANDEL, 1996, pl. 5, figs. 5, 6). The operculum found in the aperture of a half grown individual is coiled tightly similar as is the case with living Telescopiinae.

Family Bittiidae COSSMANN, 1906

Within this group consisting of different groups of small sized Cerithioidea the protoconch is rounded, small, and has weak ornament and a large apertural projection of its outer lip. It is not known whether the usually small sized species of the Bittiinae, Dialidae, Alabinae, and Finellidae are more or less closely related to each other. Regarding protoconch shape they resemble each other. The members of this group (subfamilies or families) are characterized by living species and may have the Probittiidae as stem group ranging back for more than 150 Million years.

Subfamily Bittiinae COSSMANN, 1906

The protoconch of *Bittium* GRAY, 1847, *Bittiolium* COSSMANN, 1906, *Cerithidium* MONTEROSATO, 1884 and *Cacozelania* STRAND, 1928 is low trochospiral, has rounded larval whorls with strong median projection of their outer lip of the aperture and either no ornament or fine ornamental patterns, commonly one or several spiral lines, but no keels.

The shell of the species of the Bittiinae only rarely exceed the size of 10 mm. It is turreted, narrowly elongate to pupate with sculpture of axial and spiral ribs or beads. Usually there are 4–5 spiral ribs on the late whorls of the teleoconch. The anterior canal of the aperture may be small or obsolete. Members of this subfamily have been reviewed by HOUBRICK (1993). He distinguished among those that have a larval shell the genera *Bittium* and *Bittiolium* from the Atlantic and Caribbean Sea, the very similar *Cacozelania* from Australia, *Stylidium* DALL, 1907 from the N.E. Pacific in California with spiral ornament dominating, *Lirobittium* BARTSCH, 1911 from

California. HOUBRICK (1993) also included *Argyropeza* and *Varicopeza* which are here interpreted to represent Procerithiidae, as had been suggested by GRÜNDEL (1976).

The shell of *Bittium* is small and elongate with short anterior canal. It is ornamented by 4–5 spiral ribs with many small beads where crossed by axial ribs. The protoconch of *Bittium reticulatum* (DA COSTA, 1778) from the North Atlantic (type to the genus) is smooth and consists of 2.5 rounded whorls with ornament of two weakly developed spiral lines (HOUBRICK, 1977, 1993, fig. 32G). It has a square tongue shaped projection on the outer lip of its aperture.

The Mid-Miocene *Bittium moesiense* JEKELIUS, 1944 from Bulganak on Kertsch Peninsula (Ukraine) has its rounded larval shell covered with ornament of elongate tubercles and fine spiral lines (pl. 5/7, 8). This documents that larval shells of species of the relation may also have a rather complex ornament. Even stronger spiral ribs are found in *Bittium* cf. *impedens* that still lives in the tropical Pacific.

Bittium impedens (HEDLEY, 1899) from the Indo-Pacific has the shell short and stout with wide base reaching 7 mm in length and comprising 8–9 convex whorls (HOUBRICK, 1993). The teleoconch is sculptured with 3–4 major and several minor spiral lines crossed by axial ribs forming beads with them. The body whorl has a prominent varix. The aperture is ovate with short anterior canal. The protoconch consists of 2.5 whorls and its larval whorls bear two spiral lines and subsutural pustules. It resembles that of *Bittium* sp. from the shallow sea near Satonda, Indonesia illustrated in pl. 4/3, 4. The shell of *Bittium impedens* differs from that of the species of Aqaba by having more coarse spiral ribs on the protoconch and less rounded whorls of the teleoconch (HOUBRICK, 1993, fig. 3). Its larval shell has half a whorl less and ornament of it is finer (pl. 4/5, 9–10). When fully grown the larval shell expands on its aperture, and this feature is usually no longer present shortly after metamorphosis.

Cerithidium is based on *Cerithidium submammilatum* RAYEVAL & PONZI, 1854 from the Italian Pleistocene (COSSMANN, 1906). *Cerithidium perparvulum* (WATSON, 1886) from Japan according to HASEGAWA (1998, figs. 33, 34) has a protoconch that resembles *Bittium* from Aqaba (HASEGAWA, 1998, figs. 10, 27). *Bittium* holds *Bittium varium* (PFEIFFER, 1840) from the Caribbean Sea (pl. 5/9–10). Its embryonic shell has a pattern of fine grooves and ridges (BANDEL 1975). The protoconch consist of 3 whorls, is about 0.3 mm high and its larval portion has a fine rib on the top of the apertural projection of the outer lip, and fine tubercles on the shoulder below the suture (HOUBRICK, 1993, fig. 10). The fossil species determined as *Bittium quadricinctum* (DONCIEUX, 1908) from the mid Eocene of Gant in Hungary has an about 1 cm high shell (STRAUSZ 1953, pl. 4, figs. 4–5) According to the illustration of its protoconch by KOWALKE (1998, pl. 1, figs. 4, 9) this species belongs into the relation of *Argyropeza* and is no member of the Bittiinae.

Similar is also *Cacozelania granaria* (KIENER, 1842) from the sea grass environment of Lizard Island in the Australian Great Barrier Reef. Here the protoconch has 2.5 whorls, is almost 0.3 mm high and its ornament is only a spiral line at the top of the apertural projection on the larval shell (KOWALKE, 1998, pl. 2, fig. 13). HOUBRICK (1993, fig. 18F) documented that the spiral ornament is restricted to the very last part of the larval shell. He noted that *Cacozelania* is restricted to the eastern part of Indo-Pacific. The fossil *Semibittium* COSSMANN, 1896 based on *Bittium cancellatum* LAMARCK (WENZ, 1938–44, fig. 2190) from the mid-Eocene of Damery in France has a protoconch consisting of more than three whorls and rounded larval shell with only a line at the top of the large median apertural projection of its outer lip (KOWALKE, 1998, pl. 2, fig. 14).

Subfamily Finellinae THIELE, 1931

The protoconch has a relatively large larval shell with evenly rounded first two whorls and later a strong spiral line at the upper margin of the apertural hook and further lines on the base. *Finella* ADAMS, 1860 is based on *Finella pupoides* ADAMS, 1860, which lives in the Indo-West Pacific from Japan to the Red Sea (HASEGAWA, 1998). Its protoconch is described as consisting of about two whorls and is terminated by a strong varix, forming a notch in the upper half of the whorl (PONDER, 1994, pl. 1, figs. E, G). The outer lip of the aperture has a strong projection.

Finella from the Gulf of Aqaba has the shell with 8 whorls of which more than three belong to the protoconch has evenly rounded whorls (pl. 4/12) The first teleoconch whorls have 4 spiral cords, in the second 5 and with the next whorls these cords change into spiral grooves well separated from each other by smooth higher interspaces. Axial elements are only by growth lines which intersect the grooves to form a wavy pattern with them. The aperture has semicircular shape with a slightly truncated anterior end. The columella is narrow and curved. The larval shells from Aqaba document that the species close to *Finella pupoides* living in the Gulf of Aqaba has more spiral lines on the base, which becomes covered by the following whorl (pl. 5/2). Also the protoconch consists of more than one whorl more than the specimen from Hong Kong (PONDER, 1994). A different species from near Satonda, Indonesia has its protoconch consisting of three whorls and ornament of additional granules and spiral lines on the larval apertural protrusion (pl. 5/5, 6).

Subfamily Alabininae DALL, 1927

The protoconch has a smooth larval shell of low shape and with rounded whorls. The embryonic whorl is delicately ornamented by grooves and ridges and measures about 0.1 mm across (BANDEL 1975, pl. 3, fig. 12, pl. 4, figs. 8, 9), (pl. 4/11, 13). The subfamily is based on the genus *Alabina* DALL, 1902 from the tropical Atlantic. The protoconch of *Alabina cerithioides* DALL, 1889 consists of three whorls and is more than 0.3 mm high. Its larval whorls have a large apertural hook on the outer lip and are quite smooth with exception of a fine spiral line on the upper side of the median projection. The margin of the final subsutural sinus of the fully grown larval shell is thickened (pl. 4/13) and KOWALKE (1998, pl. 3/9).

According to HOUBRICK (1980) *Alabina* is closely related to *Bittium*, and it had been placed as subgenus into *Bittium* by THIELE (1931). *Alabina* from the Caribbean Sea is anatomical distinct from *Finella* (PONDER, 1994). The radula of *Alabina cerithioides* (= *Finella dubia*) from the Colombian Coast differs strongly from that of *Finella pupoides* especially in regard to the central and lateral teeth (BANDEL, 1984). The shell of *Alabina* resembles that of *Finella*.

Finella from near Satonda in the Indonesian archipelago has a similarly shaped protoconch to that from the Red Sea but with an additional third whorl (pl. 5/5, 6). Regarding ornament there is no spiral line at the corner to the larval projection and the lower part of the larval shell has granules on its surface.

Subfamily Dialinae KAY, 1979

The protoconch of *Diala* has fine spiral lines and dots as ornament. The fossil *Aurelianella* COSSMANN, 1893 from the mid-Eocene with similar teleoconch has the area between the spiral lines covered by tubercles. The family is based on the genus *Diala* A. ADAMS, 1861 with type *Diala varia* A. ADAMS, 1861. It has a small shell, usually 5–7 mm or less in length with a high conical spiral teleoconch consisting of several whorls.

In case of *Diala* from the Gulf of Aqaba sculpture consists only of spiral elements. The aperture is simple and lacks the anterior canal (pl. 5/1). The species is common among shallow sea grass and on stones covered by algae near the base of the intertidal area and below it. The small foot has no tentacles, and carries the large operculum that may seal the aperture tightly. The teleoconch consists of 7 whorls without the protoconch. The protoconch consists of about 2.5 well rounded whorls which end with an expanded and angular apertural projection of the outer lip. It has a smooth embryonic whorl that is 0.13 mm wide. The protoconch is exposed on the teleoconch with 0.22 mm in height while it is actually 0.26 mm high. On the larval shell the upper edge of the apertural projection is accompanied by a spiral rib. Another two ribs lie at its lower margin and become covered by the succeeding whorl. The anterior margin of the aperture is thickened and upturned. The projection of the outer lip is flattened and forms a large and expanded median lobe that has two deep bays on each side to hold the two velar lobes (pl. 4/6, 7, 8). The larva when swimming carries the pink shell with the velum of lobes of different size, the smaller lobe is held in front and the larger lobe lies above the shell.

Dialinae can be distinguished from other small-sized cerithioid taxa by their often brightly spotted shells that lacks axial ribbing and an anterior notch in its drop-like aperture (HEALY & WELLS, 1998). WENZ (1941, fig. 2181) included here also the Litiopidae (*Alaba* and *Litiopa*) which have since been recognized as quite distinct and different, also regarding their ornamented larval shell. PONDER (1991) found that *Diala* differs from *Finella* and *Scaliola* by having a paucispiral operculum with eccentric nucleus, posterior flaps at the operculum, some differences in the anatomy of the head and in the shape of the central teeth of the radula. HEALY (1986) noted very different paraspermatozoa. *Diala* has no epipodial tentacles (LUQUE et al., 1988) which distinguishes from the Litiopidae. PONDER & DE KEYZER (1992) noted in Australian waters 6 species of *Diala*, and of these three species to occur widespread in the Indo West Pacific. A species from near Satonda, Indonesia has a shell somewhat intermediate between *Finella* and *Diala* (pl. 5/3, 4). Here the protoconch is almost smooth with well rounded whorls and strong apertural projection in the larval shell.

Subfamily Diastomatinae COSSMANN, 1894

The protoconch of the only known recent *Diastoma melanoides* (REEVE, 1849) reflects a lecithotrophic development (HOUBRICK, 1981, fig. 11) resulting in a simple smooth shape that consists only of an embryonic whorl. The type to *Diastoma* DESHAYES, 1850 based on *Diastoma costellata* (LAMARCK 1804) from the Eocene of the Paris Basin (WENZ, 1938–1944, fig. 2169) has a larval shell with three whorls and its protoconch is up to 0.5 mm in height. It has a strong apertural median projection of its outer lip and two weak spiral lines on the rounded whorls (pl. 5/11–12). The protoconch of *Aneurychilus* COSSMANN, 1889 of the same age is similar in shape and ornament.

The long turreted teleoconch with flattened late whorls and ovate aperture has a subsutural notch (in its final

aperture) and broad base in the modern species from Australia. The inner lip may have a weak median oblique fold. But the genus *Diastoma* is based on the fossil species without fold on the inner lip. *Diastoma melanoides* has the radula and reproductive system typical for Cerithioidea. HOUBRICK (1981) considered *Diastoma* as only living representative of an extinct Tethyan group with many fossil species (COSSMANN, 1906) and appearance not before the K/T break (by assumption) but from the Paleocene onward (again assumed). WENZ (1941) included here with *Diastoma* also *Obtortio*, *Scaliola*, *Alabina* and *Finella*, all of which have since been placed in different families. Regarding protoconch morphology *Obtortio* has quite different ornament of its larval shell. The classification of *Diastoma costellata* from the Eocene of the Paris Basin together with *Diastoma melanoides* from sandy sea bottoms at southern Australia is based on assumed relation. *Diastoma costellata* or *Diastoma roncanum* (BRONGNIART) as described by STRAUSZ (1953, pl. 3, figs. 8–13 from the mid Eocene of Gant in Hungary from Gant have the protoconch preserved (pl. 5/12). It consists of more than three rounded whorls arranged in high conical shape. The larval whorls have two weak spirals as ornament and end in a strong apertural projection of the apertural outer lip. The teleoconch is slender with many whorls, which in the juvenile shell are rounded, later become flattened. Ornament consists axial ribs crossed by fine spiral lines forming a regular net.

Aneurychilus COSSMANN, 1889 based on *Cerithium secale* DESHAYES, 1864 from the mid-Eocene of France was placed near *Diastoma* by WENZ (1938–1944, fig. 2174). This small species from the locality Damery in the Paris Basin has the protoconch with more than three whorls of similar shape as *Diastoma costellata*. The teleoconch consists of a few rounded whorls and rounded aperture. Its ornament consists of about 5 spiral ribs crossed by weaker axial ribs forming tubercles with each other.

The specific taxonomic place of the numerous species of Cerithioidea from the European Eocene still needs to be evaluated in more detail. Their place among the different units that have been created to classify the modern species and genera is still debatable.

Subfamily Probittinae n. subfam.

Diagnosis: In the small and slender shell late whorls of the teleoconch decrease in width. The spire is high and the body whorl small. The aperture is small, ovate and provided with short anterior canal. Ornament in first teleoconch whorls is dominated by two spirals crossed by strong axial ribs and in later the sculpture is of broad axial ribs is overridden by narrow spiral ribs. Axial elements are present as swollen beads below the suture and on the apertural spirals. The conical protoconch consists of rounded whorls which have as only ornament a corner on the last whorl of the larval shell that forms the upper edge of the projection of the outer lip of the aperture. The family is based on *Probittium* n. gen. with the type *Probittium madegascariensis* n. sp. that resembles *Exelissa* PIETTE, 1860 as characterized by GRÜNDEL (1990) and documented with *Exelissa distans* COSSMANN, 1913 by KAIM (2004, fig.31).

Exelissa is based on *Exelissa strangulata* (ARCHIAC, 1840) from the Mid Jurassic of France with pupoid shell (WENZ, 1938). GUZHOV (2004) based on the genus *Exelissa* the Exelissinae with different shapes of teleoconch united by having an anterior apertural groove and a protoconch with strong spiral ornament. *Exelissa multinodosa* GRÜNDEL, 1990 which resembles the type to the genus, in contrast, has a relatively short protoconch with 2.5–3 rounded whorls without distinct spiral lines or ribs. The only spiral sculpture consists of a line on the last part of the larval whorl indicating the upper edge of the apertural projection. The teleoconch is elongate oval with pointed apex. Ornament consists of axial and spiral ribs which form nodules where they cross each other. The axial ribs may be aligned from whorl to whorl with a twist from left to right. The base is rounded and the aperture small and rounded (GRÜNDEL 1997, pl. 4, figs. 12–13).

GRÜNDEL (1999) described further species from the Jurassic of Germany. But *Exelissa* as interpreted by GUZHOV (2004) closely resembles *Rhabdocolpus* as for example described by BANDEL et al. (2000). The Exelissinae GUZHOV, 2004 as defined by GUZHOV (2004) would thus contain the genus *Rhabdocolpus* and therefore quite different gastropods which resemble species of the Procerithiidae.

Teleoconch shape of the *Cerithium quinarium* TRAUNSCHOLD, 1866 that is taken as typical for the genus *Exelissa* by GUZHOV (2004, pl. 4, figs. 3–12) closely resembles that of *Maoraxis kieli* BANDEL et al., 2000 from New Zealand, while protoconch of both species differ strongly from each other. That of the Russian species has strong spiral keels on its larval shell as found in the Procerithiidae, that of the species from New Zealand has a more elongate larval shell with a pattern of collabral axial ribs crossed by spiral ribs on rounded whorls. The teleoconch in both species with so different protoconch is characterized by angular outline due to few strong axial folds which are continuous across individual whorls crossed by smaller spiral ribs. But this similarity of the teleoconch is interpreted as convergence in accordance to the many different shapes seen in the teleoconch of species of the modern Cerithiinae while their protoconchs all have the same characters.

Genus *Probittium* n. gen.

Diagnosis: The genus is based on *Probittium madegascariensis* and its diagnosis is according to that of that species (pl. 5/13).

Regarding shape and ornament of the larval shell as well as the shape of the teleoconch *Exelissa* differs strongly from *Cryptaulax-Procerithium*. Due to their shape Probittiidae (with *Exelissa* as described by GRÜNDEL, 2003, not as characterized by GUZHOV, 2004, who also created the family Exelissidae) resemble modern representatives of the Bittiidae more than those of the Procerithiidae, Procerithiinae.

Probittium madegascariensis n. sp.

Holotype: pl. 5/13 in coll. of the Geol.-Pal. Inst. Mus., Hamburg.

Diagnosis: The fully grown shell is about 2 mm in height with about 8 whorls, of which the first 2.5 belong to the protoconch. The body whorl is narrower than the whorl before and its aperture has a broad apertural notch. The protoconch has a smooth and rounded larval shell. The first two whorls of the teleoconch are ornamented by two spiral ribs crossed by 7–8 axial ribs which are not aligned on successive whorls. The later whorls are dominated by spiral ribs and axial ribs are best developed below the suture. The base is rounded and covered by spiral ribs (pl. 5/13).

Derivatio nominis: After the place of origin in Madagascar.

Description: The protoconch is about 0.2 mm high and is smooth with exception of a line forming the upper border of the apertural projection of the outer lip on the last whorl of the larval shell. The rounded embryonic whorl is about 0.12 mm in diameter. The first whorl of the teleoconch is ornamented with two spiral ribs and within the next two whorls about 8 axial ribs on each whorl appear and increase in strength. In the third whorl of the teleoconch an additional spiral rib is added and axial ribs become less apparent but do not increase in number.

Locality: on road from Sakaraha to Toleara just outside of Sakaraha Mid-Jurassic, SW Madagascar, locality described by LUGER et al. (1994).

Exelissa has, according to COSSMANN (1913), pupoid shape with pyramid-like pointed spire and apical angle of 25 to 30°. The whorls are weakly convex and the final whorl is shorter than the spire. More than 10 whorls are separated by weak sutures and ornamented by seven strong axial ribs which are crossed by four spiral ones, some more of these are present on the rounded base. The type species has been studied and described again by GRÜNDEL (1997, pl. 4, figs. 12–13). Its protoconch is unknown, but GRÜNDEL (1999, 2003) noted in other species of *Exelissa* a smooth protoconch with 2.5–3 rounded whorls which have a line on the last part of the larval whorl indicating the upper edge of the apertural projection. Teleoconch growth is allometric with increase in shell width becoming less after about four whorls of the teleoconch have been formed and width decreases in the last two whorls. Shell shape is thus elongate oval with pointed apex. Ornament consists of axial and spiral ribs which may form nodules where they cross each other. In case of the type to the genus axial ribs are aligned from whorl to whorl with a twist from left to right (according to GRÜNDEL, not in the description of COSSMANN). The base is rounded and the aperture small and rounded.

HUDLESTON (1882, pl. 6) discussed similar species from the mid-Jurassic of Yorkshire in England as members of the genus *Chemnitzia* ORBIGNY, 1839 that is based on a species living in the Mediterranean Sea which belongs to the Pyramidellidae (WENZ, 1938, fig. 2553). GRÜNDEL (1999) discussed several species of *Exelissa* from the Jurassic of Germany. Accordingly the protoconch of *Exelissa multinodosa* GRÜNDEL, 1990 is quite similar to that of *Probittium madegascariensis*. Regarding ornament and shape of the protoconch *Exelissa* differs strongly from *Cryptaulax-Procerithium*. It should not be included in the Procerithiidae, if interpretation is based on what can be noted among modern representatives of the Cerithimorpha. Here different larger taxa can well be recognized by their larval shells. GUZHOV (2004) proposed the family Exelissidae with relatively different teleoconch shapes all ending with a groove-like anterior notch bearing aperture and with protoconch with strongly ornamented larval shell.

Exelissa binodosa GRÜNDEL, 1990 from the Mid Jurassic of North Europe has more straight axial ribs and less variable ornament on the different whorls of the teleoconch. The same is the case for *Exelissa multinodosa* GRÜNDEL, 1990 which has a shorter but otherwise very similar protoconch as in case of *Probittium madegascariensis*. Compared with *Exilissa distans* COSSMANN, 1913 as described by KAIM (2004, fig. 32) from

the Late Jurassic of Poland the early ornament of the teleoconch is similar to that of *Probittium madegascariensis*, while later ornament is dominated by spiral ribs, in contrast to the ornament of rectangles in the later.

Inclusion of Probittiidae into the Bittiinae COSSMANN, 1906, Finellidae THIELE, 1931, Diastomatidae COSSMANN, 1894 or Dialidae KAY, 1979 with living species can not be carried out, due to their similarity regarding protoconch shape and ornament, and resemblance regarding size and organization of the teleoconch with all these. *Probittium* is very similar to *Exelissia* PIETTE, 1860 as in WENZ (1938–1944) and GRÜNDEL (1990) (not to the Exelissidae GUZHOV, 2004) and both could be ancestral to one or several of these modern systematic units (families) of the Cerithioidea.

In comparison with *Tomaszoviella* KAIM, 2001 a general shape of the teleoconch can be noted as well as a similar protoconch bearing a spiral line on the top of the apertural projection in the last whorl of the larval shell. This species from the Valanginium is a little smaller in having only four whorl of the teleoconch and KAIM (2004) related it to the Bittiidae among the living species. This interpretation can be supported and the genus may be connected with *Probittium/Exelissa* from the Jurassic and *Popenella* from the Triassic.

Family Scaliolidae JOUSSEAUME, 1912

The protoconch is relatively high with larval whorls rounded and smooth or with spiral lines and provided with very prominent apertural projection of the outer lip (pl. 6, figs. 7, 8). The family is based on *Scaliola* ADAMS, 1860 which is distinguished by agglutinating sand to the outside of its teleoconch during growth (pl. 6, fig. 6). *Scaliola* has been in existence since the Eocene with *Scaliola jansseni* BANDEL & EL NAKHAL, 1993 from the Paris Basin that resembles living *Scaliola bella* A. ADAMS, 1860 in regard to its conical protoconch as well as the agglutinated grains to the teleoconch (BANDEL 1993, pl. 1, fig. 5; BANDEL & EL NAKHAL, 1993, pl. 2, figs. 3, 8). From the Maastrichtian Ripley Formation of the USA a somewhat problematic species is described by BANDEL & EL NAKHAL (1993, Text-fig. 5, pl. 2, fig. 6).

The protoconch of *Scaliola* from the Gulf of Aqaba is smooth and consists of more than three rounded whorls (pl. 6/7, 8). The embryonic whorl measures about 0.1 mm in diameter and is almost smooth. The larval shell has a median projection of its outer lip. This lip is thickened and upturned when the shell of the veliger larva is fully formed and about 0.3 mm high. The succeeding teleoconch consisting of 4 to 6 whorls and is densely covered by grains of sand, which are agglutinated to the shell (pl. 6/6). The fifth or sixth whorl may detach so that the apertural margin is circular and the umbilicus open.

The larval projection of a species of *Scaliola* from near Satonda in the Indonesian archipelago is very large and the protoconch more slender than that from Aqaba. It has, in addition, also spiral lines on its larval shell (pl. 6/9). HEALY & WELLS (1998) noted resemblance of euspermatozoa of *Scaliola* and *Finella* with each other and with those of some Potamididae but not with *Bittium*. PONDER (1994) included *Scaliola* and *Finella* in the Scaliolidae due to the similarity in regard to the ultrastructure of their spermatozoa (HEALY, 1982). The protoconch of *Finella* is a little shorter as that of *Scaliola*, and has a spiral line as ornament of its larval shell while it is smooth in *Scaliola bella*. But spiral ornament is also present in the *Scaliola* sp. from the Indonesian sea. Here the protoconch has even more whorls and is relatively longer. *Finella* and *Scaliola* differ also in regard to the construction of their operculum (PONDER, 1994).

Family Obtortionidae THIELE, 1925

The shell of *Obtortio* HEDLEY, 1899 is a little more than 3 mm high and differs from that of the similar *Finella* by the presence of axial ribs (WILSON, 1994). The protoconch has a diagnostic ornament on its larval shell consisting of sinuous collabral ribs (pl. 6/3, 5). The teleoconch has spiral lines, later a pattern of fine cancellation, with 14 elevated spiral cords on the body whorl (pl. 6/4). The genus *Obtortio* is based on *Rissoa pyrrhacme* MELVILL & STANDEN (illustrated by WENZ, 1938–1944, fig. 2171; THIELE 1931). Both authors noted that *Obtortio* has a protoconch that consists of several whorls and is ornament of axial ribs. Such a protoconch with sinuous axial ornament was documented by BANDEL (1991, pl. 3, fig. 12, pl. 4, fig. 8) from Cebu (Philippines) and BANDEL (1993, pl. 2, figs. 2, 4) from the Great Barrier Reef, Australia. It has been placed with *Finella rufocincta* according to HASEGAWA (1998, fig. 20). He described the shell as turreted and elongate and ornamented with spiral sculpture to which same axial elements are added forming a reticulate ornament with each other (HASEGAWA, 1998, fig. 13, 18–20). But species of *Finella* are distinct from those of *Obtortio* by having a clearly different ornamental pattern of their larval shell. *Finella* has a smooth larval shell that may have some fine spiral lines, while there is the characteristic pattern of collabral ribs present in *Obtortio*.

The protoconch has a smooth and rounded embryonic whorl with about 0.1 mm in diameter. The characteristic ornamental pattern of the larval shell begins in the first larval whorl. About 20 collabral ribs are on one larval

whorl. The sinus below the suture increases with growth of the larval shell. In the last part of it ribs are detached and only found on the very long tongue like apertural projection while the sinus is actually a deep slit with straight margins formed by the median hook and the suture. The posterior edge of this slit in the fully grown larval shell is upturned and thickened. The ornament of the teleoconch begins after the sinus is filled with increments of growth and the upper edge of the larval hook continues in a spiral rib (pl. 6/3, 5).

Confusion arose from KAY (1979) who suggested that *Finella* ADAMS, 1860 has been based on the same type as *Obtortio* HEDLEY, 1899 as assumed by THIELE (1931). HOUBRICK (1993) had regarded this taxon to be unresolved. THIELE (1931) included in the Finellidae not only *Finella* but also *Cerithidium* MONTEROSATO, 1884 and suggested *Obtortio* to represent a subgenus. But, in contrast, THIELE (1925) had treated *Obtortio* as characteristic genus to the Obtortionidae THIELE, 1925. PONDER & WARÉN (1988) had interpreted the Obtortionidae to be a synonym to the Finellidae. PONDER (1994) included *Scaliola* and *Finella* in the same family. According to Southern Synthesis (HEALY & WELLS, 1998) *Obtortio* is *Finella*, and has the same type as *Finella*. To make the confusion complete, WENZ (1938–1944, fig. 2171) considered *Obtortio* as genus, but suggested to include *Alabina* as subgenus to it. He placed them in the Diastomidae (Diastomatidae) considering Finellidae and Alabinidae to be synonyms. According to WILSON (1994) *Obtortio* has several species in the Australian fauna but he did not illustrate them.

Obtortio and the Obtortionidae can be defined by the ornament of the larval shell, *Scaliola* and Scaliolidae by the agglutination of sand to the teleoconch, while the distinction of *Alabina* and *Finella* by features of their shell is more problematic.

Family Canterburyellidae BANDEL, GRÜNDEL & MAXWELL, 2001

The larval shell of the protoconch is ornamented by sinuous axial ribs and the teleoconch is of *Rissoa*-like shape. The family is based on the genus *Canterburyella* BANDEL, GRÜNDEL & MAXWELL, 2001 from the Jurassic of New Zealand.

The genus *Canterburyella* is based on *Canterburyella pacifica* BANDEL, GRÜNDEL & MAXWELL, 2001 from the Jurassic of New Zealand. Its slender shell is ornamented by broad axial ribs which in the juvenile teleoconch end at the edge to the rounded margin to the base, in the adult are continuous across the rounded conical base. The adult shell with 8 whorls has a thickened and expanding apertural margin. The slender protoconch is about 0.5 mm high and consists of 3.5 whorls. The embryonic shell measures about 0.12 mm. The larval shell is ornamented by numerous axial ribs (about 40 per whorl) which curve forwards into the apertural projection of the outer lip.

The teleoconch of *Canterburyella* resembles that of *Rissocerithium*, but has a shorter apertural notch, *Zebinostoma* CONTI & FISCHER, 1983 has a weaker axial ribs (CONTI & FISCHER, 1981, 1983). GRÜNDEL (1999) placed the very similar *Palaeorissina* GRÜNDEL, 1999 in the Rissoidae, Rissoininae, but later in the Paleorissinae. *Colina* H. & A. ADAMS, 1854 belonging to the living Cerithiidae also has a similar shape of its teleoconch (HOUBRICK, 1990). The larval shell in *Canterburyella* resembles that of Obtortionidae among modern species of the Cerithioidea while the teleoconch resembles *Rissoa*-like species. Jurassic species with similar teleoconch shape usually have a smooth larval shell in their protoconch. The later have partly been described to represent Zygopleuriidae and Pommerozygiidae (GRÜNDEL, 1999a), or are considered to represent Truncatelloidea (Rissooidea), Rissoininae by (GRÜNDEL, 1999b) and Palaeorissinae by GRÜNDEL & KOWALKE (2002).

Family Litiopidae GRAY, 1847 (= Family Litiopidae FISCHER, 1885)

Typical genera are *Litiopa* RANG, 1829 and *Alaba* H. & A. ADAMS, 1853 which have quite similar protoconchs (ROBERTSON, 1971; HOUBRICK, 1987, figs. 8, 10; LUQUE et al., 1988; LEAL, 1990, pl. 6, figs. C, D; BANDEL et al., 1997; HEALY & WELLS, 1998, fig. 15, 87C). The body of these is distinguished from most other Cerithioidea by metapodial and propodial tentacles (THIELE, 1931; HOUBRICK, 1987) (but see Styliiferinidae). *Alaba incerta* (ORBIGNY, 1842) prefers to live on the brown algae *Sargassum* on the rocky shore as well as when it is drifting in the *Sargassum*-Sea (BANDEL & WEDLER, 1987). On floats of filamentous algae in the Red Sea *Litiopa melanostoma* RANG, 1829 is common.

The protoconch has diagnostic ornament on the larval whorls consisting of reticulate pattern of axial and spiral ribs. The protoconch of *Litiopa melanostoma* consists of 5 whorls (pl. 6/13). Its embryonic whorl has a beaten pattern of grooves surrounded by irregular fine ridges and is a little less than 0.1 mm wide. The larval shell consists of four whorls and is about 0.6 mm high and 0.4 mm wide. Its whorls are ornamented by 22 to 28 strong axial ribs and a weak spiral cords between them. Ornament begins within the first larval whorl with axial ribs in the apical portion. On the second larval whorl spiral ribs appear, which do not cross over the axial ribs. The axial

ribs carry a node just above the suture and one on the shoulder that is set off from the sides by a corner. The protoconch terminates with a larval hook that expands at its sides and is accompanied by two deep lobes above and below. Repair of the larval shell is common especially next to the projection of the outer lip of the fully grown shell.

Alaba incerta has the larval shell ornamented by axial ribs crossed by finer spiral lines in a regular pattern (pl. 6/11, 12). The embryonic whorl is almost smooth and the larval shell of four whorls is ornamented by strong axial ribs and a weak spiral cord. The protoconch terminates with a strong projection of its outer lip. The teleoconch is small with weak, shallow anterior canal, smooth or weakly sculptured. The radula is close to that of *Cerithium* (BANDEL 1984; HOUBRICK, 1987, 1993), but especially to *Bittiolium varium* (PFEIFFER, 1840) and *Bittium reticulatum* (DA COSTA, 1778).

The Cretaceous *Litiopella* BANDEL & KIEL, 2000 based on *Litiopella schoeningi* BANDEL & KIEL, 2000 from the Campanian of NW Spain has a small shell with high spire with rounded whorls and well developed sutures. The apical angle is about 30°. The protoconch consists of about 4.3 whorls with the first whorl measuring less than 0.1 mm in width and a total height of 0.6 mm. The larval whorls are ornamented by about 20 straight axial ribs on each whorl crossed by fine spiral lines. The transition into the teleoconch is documented by a change of ornament. The whorls of the protoconch as well as the teleoconch are evenly rounded on their sides and sutures are well developed (BANDEL & KIEL, 2000, figs. 6, 7). *Litiopella* resembles *Litiopa*, but differs from it and *Alaba* by its curved axial ribs in the larval shell. The axial to cancellated ornament of the larval shell unites Litiopidae including *Litiopella* with the Provannidae and Dendropominae (see below).

Family Prisciophoridae BANDEL, GRÜNDEL & MAXWELL, 2001 (= ? Brachytrematidae COSSMANN, 1906)

The family consists of species with a teleoconch resembling that of the Procerithiidae or other slender Cerithioidea but regarding the protoconch also the Cerithiopsidae H. & A. ADAMS, 1853. But the protoconch has quite special ornament and is of elongate conical shape. It is large (around 1 mm high) and consists of more than four whorls with characteristic ornament of its larval shell. The smooth embryonic shell measures only about 0.1 mm in diameter, which is small compared with that of most Ptenoglossa. A first whorl of the larval shell is smooth. Later whorls of the larval shell are ornamented by about 20 major axial ribs, and fine spiral lines. The axial ribs twist into apertural direction low on the whorl and this change in direction is almost completely covered by later whorls. A strong apertural tongue-like projection is present in very low position of the outer lip. The teleoconch is ornamented by strong, straight axial ribs and fine spiral ribs. The aperture is elongate and provided with an anterior siphon canal. The family is based on the genus *Prisciophora* SCHRÖDER, 1995 from Aptian-Albian beds of northern Germany, which closely resembles *Cosmocerithium* COSSMANN, 1906 from the Jurassic.

Prisciophora has the type *Prisciophora beyschlagi* (WOLLEMAN, 1903) with its protoconch consisting of 5 whorls and about 1 mm in height (BANDEL, 1993, pl. 3, fig. 3; SCHRÖDER, 1995, pl. 2, figs. 15–18). It is very similar to *Novoselkella* GUZHOV, 2004 from the Jurassic of Russia (GUZHOV, 2004, pl. 12, fig. 6). Also in case of *Prisciophora schroederi* BANDEL, GRÜNDEL & MAXWELL, 2001 that lived during the Jurassic in New Zealand are the first two whorls of the protoconch are rounded and smooth. The third whorl is ornamented with 25 axial ribs which turn forwards near to the suture as in the type to the genus. But in the fourth whorl a median spiral rib appears and axial ribs are more spaced here and in the fifth whorl of protoconch. This is quite similar in some species placed with *Cosmocerithium* by KAIM (2004, figs. 39–42).

Prisciophora schroederi resembles *Brachytrema turbiniformis* MORRIS & LYCETT 1854 from the Middle Jurassic of England and *Brachytrema wrighti* (COTTEAU) as figured by COSSMANN (1906) from France. MORRIS & LYCETT (1854) did not select a genotype to their genus *Brachytrema*, but noted that they knew seven described species and described two new species. Of these *Brachytrema buvignieri* MORRIS & LYCETT, 1854 from the Middle Jurassic of NW France (WENZ, 1938–1944, fig. 2096) had been selected to represent the type of the genus by COSSMANN (1900). As long as no protoconch is known it remains unknown whether Brachytrematidae COSSMANN, 1906 are related to *Prisciophora*. WENZ (1938–1944) also included here as subgenus *Petersia* GEMMELLARO, 1870 from the Jurassic with extended and convex outer lip of the aperture. A similar shape is not noted in *Prisciophora*.

Cosmocerithium COSSMANN, 1906 from the Jurassic of Poland, according to KAIM (2004, figs. 39–42), is the same as *Prisciophora*. Its type is *Cerithium nystii* ARCHIAC, 1843 for the Mid Jurassic of France (WENZ, 1938–1944, fig. 2101) and was newly described by GRÜNDEL (1997, pl. 5, figs. 10–12). The shell of *Cosmocerithium* is much more slender than *Brachytrema* and ornamented by three spiral rows of nodules on the flattened whorls. GUZHOV (2004, pl. 10) placed Jurassic species of *Cosmocerithium* from Russia in the Cerithiopsidae H. & A. ADAMS, 1854 and in relation to *Prisciophora*. The protoconch of two of these is well preserved and documents the characteristics of the family quite well. The teleoconch is slender and ornament consists of axial rows of tubercles formed where up to 8 spiral ribs cross. A form with slender teleoconch and initial portion of the

protoconch not preserved was placed in the genus *Novoselkella* GUZHOV, 2004. GRÜNDEL (2005, pl. 3, figs. 8–13) placed *Novoselkella* in the Ptenoglossa but had also only protoconch preservation without the early part. He confirmed its closeness to *Prisciophora* as well as *Cosmocerithium*.

NÜTZEL (1998) suggested that *Prisciophora* may belong to the Eumetulidae GOLIKOV & STAROBOGATOV, 1975 of the Ptenoglossa, which was accepted by KAIM (2004). One of these had been described as *Vatopsis antiquus* GRÜNDEL, 2001 and *Vatopsis ewae* KAIM, 2004 from the Valanginian of Poland (KAIM, 2004, figs. 37, 38), and it resembles *Prisciophora beyschlagi* regarding the ornament of the protoconch. It is without a median stronger rib in its larval whorls. An even larger protoconch as that of *Prisciophora* was noted in *Trochoturbella* COSSMANN, 1921 by GRÜNDEL (1997, pl. 6, figs. 13–14, pl. 7, fig. 1; 2001) from the Bajocian of France. The shell is here 2.8 mm high and consists of about 5 whorls, most of which belong to the protoconch. Here axial ribs appear first on the second whorl, change from dense arrangement to wider spacing in the third whorl, while later spiral elements appear, perhaps indicating the presence of one whorl of the teleoconch.

When Prisciophoridae are compared to members of the Cerithioidea the size of the protoconch is unusually large and has a smooth second whorl which is usually not present in Cerithiidae. When compared to the Cerithiopsidae H. & A. ADAMS, 1853 its relatively wide conical shape does not fit well, and the embryonic whorl is smaller, but extends over more than one whorl. The size of the protoconch resembles that found in Protorculidae BANDEL, 1991 from the Triassic St. Cassian Formation, but neither its more slender shape nor the details of the ornament agree well with that of *Prisciophora* and *Cosmocerithium*.

Family Popenellidae BANDEL, 1992

The protoconch has diagnostic ornament of collabral ribs that form a median rib at the upper margin of the extended larval apertural projection (pl. 7/2, 3). It consists of three rounded whorls. The small conical shell has ornament of interrupted axial ribs, and the aperture with short siphon (pl. 7/1, 4). Ornament consists of the rounded ribs crossed by very fine spiral lines. Characteristic is the genus *Popenella* BANDEL, 1992.

Popenella is based on *Trachoeucus nodosus* ZARDINI, 1980 from the Late Triassic St. Cassian Formation in the Alps. The protoconch is a little higher than wide and is of rounded triangular shape. It consists of 2.5 whorls, is 0.3 mm high and 0.25 mm wide, with the embryonic whorl about 0.12 mm in width. The larval shell has ornament of a median spiral line which represents the twist forwards of the collabral ribs that retrace the sinuous outline of the apertural outer lip. The lower ribs may have fine spiral lines between them and they end on the fully grown larval shell that has the projection of its outer lip smooth. *Popenella nodosa* (ZARDINI, 1980) consists of 6 whorls of the teleoconch with the protoconch often a little inclined in its top, is 3 mm high and 1.5 mm wide with apical angle of about 35°. Whorls are weakly convex and ornamented by a row of nodules below the suture connected to sinuous axial folds below which end on the corner to the base, and very fine spiral lines. Growth lines reflect the sinuous outline of the outer lip of the aperture which is pointed above and extended into a short siphon below (ZARDINI, 1978, pl. 32, figs. 17, 19; 1980, pl. 6, figs. 2–4, 1985, pl. 5, fig. 5; BANDEL 1992, pl. 8, fig. 6, pl. 9, figs. 2, 7).

Family Zardinellopsidae n. fam.

Diagnosis: The protoconch is triangular conical, higher than wide and ornamented by strong spiral keels, of which the median is the largest and lies at the upper edge of the apertural projection of the outer lip of the larval shell. The lower portion of larval whorls is covered by a net ornament (pl. 8/8, 9). The family is based on *Zardinellopsis misurina* (BANDEL, 1992) from the St. Cassian Formation, locality Misurina, and *Cortinellopsis* also belongs here.

The name is given in honor of the late Rinaldo Zardini from Cortina d'Ampezzo who collected and described many of the fossils from the St. Cassian Formation.

Genus *Zardinellopsis* n. gen.

Diagnosis: The genus is based on *Popenella misurina* BANDEL, 1992 with grain-shaped shell of 5 teleoconch whorls and 3.5 whorls of the protoconch (BANDEL, 1992, pl. 9, figs. 1, 3). The acute egg-shaped, about 2 mm high and 1.2 mm wide shell has a strong rounded fold on the posterior end of its inner lip forming a narrow funnel (pl. 8/9). Ornament on the whorls consists of low axial folds widest just above the suture and fine spiral lines in the center and on the base. Growth lines clearly reflect the sinuous outline of the outer lip of the aperture (BANDEL, 1992, pl. 9, figs. 1, 3, 4). The embryonic shell measures 0.15 mm in diameter, is well rounded and covered by a fine pit and ridge ornament. The larval shell has a subsutural row of tubercles, a flattened to

concave shoulder, a median keel that also forms the upper edge of the apertural projection and below it a network of inclined lines crossing each other (pl. 8/8). The protoconch is about 0.35 mm high and 0.3 mm wide. Its aperture at the begin of the teleoconch is thickened with the upper sinus with upturned margin and the very large median projection is thin. It is largely covered by the first whorl of the teleoconch. The protoconch is often a little inclined on the teleoconch and it has a larger apical angle (pl. 8/8, 9).

Zardinellopsis giauensis (ZARDINI, 1980) has a cigar-shaped shell that is with 11 whorls a little more than 4 mm high and 1 mm wide (ZARDINI, 1978, pl. 32, figs. 18, 20, pl. 41, fig. 11; 1980, pl. 4, fig. 21). Whorls are flattened and sutures are indistinct. Ornament consists of 12 to 15 shallow axial ribs that retrace the wide apertural sinus of the outer lip and are crossed by fine spiral lines which in the center of each whorl are a little coarser. The aperture extends into a short siphon that twists inwards. The protoconch consists of about 3 whorls, is 0.32 mm high and 0.22 mm wide and is ornamented in its larval portion by two spiral ridges, the lower of which forms the upper edge of the apertural projection of the outer lip. In addition there are collabral lines that cross the spiral elements forming a complex net pattern (BANDEL, 1992, pl. 9, figs. 5, 6, pl. 10, figs. 2, 3).

Zardinellopsis zardini (BANDEL, 1992) is a small, 1.3 mm pupa-form shell that consists of 8 whorls of which more than three belong to the protoconch. The concave whorls are separated by distinct sutures and ornament consists only of collabral fine growth lines. The protoconch is 0.26 mm high and 0.22 mm wide and its larval shell is ornamented by a spiral keel that also forms the upper edge of the apertural projection of the outer lip. Below fine collabral lines and inclined ones crossing them are present (BANDEL, 1992, pl. 10, figs. 1, 6).

Genus *Cortinellopsis* n. gen.

Diagnosis: Protoconch resembles that of *Zardinellopsis* and the teleoconch has ornament with spiny collabral lamellae (pl. 8/10–11). The genus is based on *Promathildia aialensis* ZARDINI, 1980 (ZARDINI, 1980, pl. 5, figs. 7–10) from St. Cassian Formation. Its teleoconch has more than 13 whorls when it is 4.2 mm high. The genus is named according to Cortina with its type locality of Campo at Cortina d'Ampezzo.

Cortinellopsis aialensis (ZARDINI, 1980)

The protoconch consists of three whorls and is about 0.3 mm wide and high (pl. 8/10–11). The embryonic whorl measures about 0.1 mm and the larval shell has the characters as in *Zardinellopsis*. The suture is accompanied by a granulated line below it and an additional ridge with grooves and ridges. The median keel that forms the upper edge of the apertural projection is sharp. Below it a net of narrow ridges on smooth ground is developed on the inclined flank. The transition to the teleoconch is abrupt, and ornament here consists of collabral lamellae and fine spiral lines between them. After about half whorl the lamellae increase in width and fuse in the middle to form an irregular noddled edge of each whorl consisting of about 10 lamellae on each whorl. The base is flattened and covers by spiral lines and undulations. The aperture is strongly inclined, provided with a short and deep siphon and is of angular outline.

The teleoconch is elongate conical with more than 13 whorls in an about 4 mm high shell (ZARDINI, 1980, pl. 5, fig. 8).

Family Maoraxidae BANDEL, GRÜNDEL & MAXWELL, 2001

The protoconch is high conical with rounded whorls. Ornament of the larval shell is a pattern of axial ribs with forward twisted base and spiral lines crossing them. The teleoconch resembles that seen in Procerithiidae in shape with few and strong axial ribs transected by spiral lines and with angular whorls (BANDEL et al., 2001, pl. 7, figs. 5–11). The family is based on the genus *Maoraxis* BANDEL, GRÜNDEL & MAXWELL, 2001 from the Jurassic of New Zealand.

Maoraxis is based on *Maoraxis kieli* BANDEL, GRÜNDEL & MAXWELL, 2001 from the Jurassic of New Zealand. The protoconch with about four whorls is about 0.8 mm high. The embryonic whorl measures less than 0.1 mm in diameter. Larval whorls are ornamented by small rectangles with the axial ribs in collabral arrangement. The median projection of its outer lip of the aperture is partly covered by the first whorl of the teleoconch. The slender teleoconch has angular whorls ornamented by about 5 axial ribs crossed by spiral lines. The base is flattened and has spiral lines on the corner to the sides.

The shape of the teleoconch differs from that of the Prisciophoridae but resembles that of some species from the Jurassic of Russia that have been placed with *Exelissa* by GUZHOV (2004, pl. 4, figs. 4–9), while the protoconch resembles a little that of *Prisciophora* in size and ornament, but differs in detail. The first larval whorl is ornamented in *Maoraxis* and the ornamental pattern if formed by spiral and axial ribs of the same size (BANDEL

1993, pl. 7, fig. 3) as occurs also in larval shells among modern Stephopominae, Thiaridae, Litiopidae, and Provannidae.

Family Melanopsidae H. & A. ADAMS, 1854

The larval shell has fine spiral lines as ornament, but mostly it is not developed due to lecithotrophic ontogeny. Only *Zemelanopsis trifasciata* (GRAY, 1843) from New Zealand has planktotrophic larvae. *Melanopsis serchensis* VIDAL, 1874 from the Maastrichtian of the Tresp Basin in northern Spain, has a protoconch that consists of three whorls and 0.2 mm height with the embryonic shell less than 0.1 mm wide (BANDEL, 1993; KOWALKE & BANDEL, 1996). All other Cretaceous species of *Melanopsis* FÉRUSAC, 1807 known like their Tertiary and recent relatives hatched from eggs as crawling young with the embryonic shell of little more than one whorl and 0.2 to 0.4 mm wide (BANDEL & RIEDEL, 1994; BANDEL, 2001). The teleoconch of Melanopsidae is of spindle shape, usually 1–4 cm high, with large last whorl and the aperture depressed egg shaped with anterior channel.

The spawn of *Zemelanopsis* FINLEY, 1927 consists of an egg ribbon that is attached to hard substrates in the estuarine region of rivers in New Zealand. The eggs are contained within round transparent egg capsules and almost fill them. They develop rapidly into a small veliger of almost the same size as the egg and hatches as planktotrophic larva swimming with two velum wings and a foot that holds an operculum large enough to close the shells aperture. *Melanopsis* lives in running water, usually fresh water streams, more rarely also beaches with moving water on large lakes. Only modern *Zemelanopsis* lives in estuaries and may stay in regions with commonly brackish water, but usually individuals also migrate upriver. *Melanopsis serchensis* lived within the estuarine environment as well.

Molecular data indicate that *Melanopsis* is closest to the Telecopiinae of the Potamididae and to the Pachymelaniidae (unpublished data by RALF BISCHOFF). *Melanopsis* and *Esperia* have existed in Europe since the Cretaceous and are known from the Santonian of Hungary (BANDEL & RIEDEL, 1994). Both genera are genetically close to each other, as are the few species of *Melanopsis* from rivers in New Caledonia and *Zemelanopsis*. The antiquity of the genera of the family and the DNA similarities indicate the validity of the family Melanopsidae.

Family Modulidae P. FISCHER 1884

The adult shell has a broadly conical shape, consists of about five to six whorls and is quite solid. It has an umbilicus and a tooth on the anterior inner lip of the aperture. The family is based on *Modulus* with the type *Modulus modiolus* (LINNE, 1758). Specimens of this species from the Caribbean Sea have an elongate conical protoconch with more than three rounded whorls (pl. 8/5, 6). The embryonic whorl is almost smooth with a rounded groove and ridge pattern and about 0.14 mm in width (BANDEL, 1975, pl. 4, figs. 10, 11). In case of *Modulus carchedonius* (LAMARCK, 1822) the embryonic shell is similar. With begin of larval shell three spiral lines appear which are on the median side and lie on the apertural projection. The rounded whorl side above is covered by fine tubercles which are arranged in 3–4 spiral rows. The protoconch is about 0.3 mm high and only a little less wide. The aperture of the larval shell has a thickened margin of the apical sinus of the outer lip and a strongly projecting median hook, that is half hidden by the succeeding whorl.

Modulidae are characterized by their low shells and stalked eyes (HOUBRICK, 1980), and he suggested that the only genus *Modulus* can be traced to the Cretaceous. The family holds only six living species (HOUBRICK, 1980). *Modulus modiolus* from the Caribbean Sea at Santa Marta, Colombia has a planktotrophic larva, while the same or a very similar species from Bermuda and Florida hatches as crawling young from its egg mass (HOUBRICK, 1980; BANDEL, 1975). The protoconch documented from *Modulus modiolus* by LEAL (1990, pl. 6, figs. G, H) has a relatively large first whorl and a second whorl ornamented by strong spiral ribs, and probably also a lecithotrophic development. The shape of the protoconch of *Modulus* from the Pacific at the Philippines is quite similar to that from the Caribbean Sea (BANDEL, 1991, pl. 4, fig. 6; 1993, pl. 2, fig. 5).

From the Eocene of France the genus *Conocerithium* SACCO, 1895 has some species which are a little more slender than *Modulus*, while their larval shell has the same characteristic spiral ornament as found in *Modulus*.

Genus *Modulostylina* n. gen.

Diagnosis: The teleoconch is of *Coelostylina*-like shape with rounded whorls that have a fine pattern of spiral ridges and grooves as ornament. The protoconch is similar to that of *Modulus* and consists of three rounded whorls with 4 spiral lines as ornament of the larval shell that ends in a strong tongue like median apertural

projection of its outer lip (pl. 8, fig. 7). The genus is based on *Coelostylina waageni* KITTL, 1884 as described and illustrated by ZARDINI (1978 pl. 29, fig. 8, pl. 30, fig. 4) and KITTL (1894, pl. 5 figs. 47, 48) from Late Triassic St. Cassian Formation.

Derivatio nominis: free combination partly derived from of *Modulus* and *Coelostylina*.

Modulostylina waageni (KITTL, 1894)

Description: Whorls increase in size quite rapidly and compose a pointed conical shell with rounded sides. Sutures are deep and the base is rounded. The aperture is oval and the last whorl a little higher than the spire. The protoconch was not observed by KITTL (1894) or ZARDINI (1978) and it differs from that of *Coelostylina* in ornament of its larval whorls. *Coelostylina* has tubercles, while *Modulostylina* has spiral ribs of which four are present below a smooth rounded shoulder. The upper of these ends in the lower part of the subsutural sinus of the outer lip, while the next lower ends in the upper margin of the tongue like apertural projection (pl. 8/7).

Comparison with *Coelostylina conica* (MÜNSTER, 1841), also from St Cassian Formation, shows similarities in regard to the shape of the protoconch (pl. 12/10, 11, 12) as to the teleoconch (BANDEL, 1992, pl. 6, fig. 6, pl. 7, figs. 1, 2, 6). The shell consists of 13 whorls and measures about 22 mm in height and is 13 mm width (ZARDINI, 1985, pl. 5, fig. 14). The protoconch that had been studied by BANDEL (1992) was badly preserved and is here described in more detail (pl. 12, figs. 10, 11, 12). The embryonic whorl is smooth, occupies a little more than one whorl, and measures about 0.15 mm. An ornament of spiral stripes composed of more or less fused tubercles is present on the larval whorls. About ten spirals are exposed on the rounded whorls. The protoconch consists of more than three whorls, is 0.5 mm high and a little less in width. The aperture has a thickened margin in the subsutural sinus of the outer lip and a wide median projection that is covered in most part by the first whorl of the teleoconch.

The teleoconch resembles that of a *Ptychostoma* LAUBE, 1868 from the Triassic (ZARDINI, 1978, pl. 23, figs. 1–5) but the protoconch is smaller and has a much finer ornament. *Ptychostoma pleuromoides* (MÜNSTER, 1841) has rows of larger tubercles as ornament of its larval shell. Its protoconch also ends with a strong median elongation of the middle part of the outer lip, and it is larger with four whorls and 1 mm in height and width (BANDEL, 1992, pl. 6, figs. 1–3).

The protoconch of *Coelostylina conica* resembles that of *Modulostylina waageni*, which otherwise can be compared with modern species with protoconch ornament of spiral lines on their larval shell. A larval shell with similar ornament was described by SCHRÖDER (1995, pl. 4, figs. 1, 2) from the Early Cretaceous of Poland. Among living groups for example *Vanikoro semiplicata* (ISSEL, 1869) from the plankton of the Gulf of Aqaba has a larval shell with similar ornament as found in *Coelostylina conica* (compare pl. 2/8, 10 with pl. 12/10, 11, 12).

Family Thiaridae GILL, 1871

The protoconch may have a larval shell with fine pattern of axial and spiral lines crossing each other forming a network of rectangles. Most species of the family and all genera which live in fresh water have no larval shell due to lecithotrophic development and hatch with the embryonic shell as crawling young. Marine larva are found in some species of the genera *Stenomelania* FISCHER, 1885 and *Thiara* RÖDING, 1798 (BANDEL et al., 1997; BANDEL & RIEDEL, 1998). While the embryonic shell is smooth except for terminal growth lines, the larval shell is sculptured by 7–9 spiral lines.

The protoconch ornament of *Stenomelania* and *Thiara* differs from that of *Planaxis*, and also DNA data document their distance from each other (BISCHOFF unpublished data). KÖHLER & GLAUBRECHT (2002) suggested that a brood pouch as found in Planaxidae and Thiaridae may also be found among the Pachychilidae. The assumption of MORRISON (1954) according to which the Planaxidae with brood pouch in their head-foot represent the sea living counterparts of the Thiaridae, as was also assumed by HOUBRICK (1987, 1988, 1990, 1992), is thus not confirmed.

The genera *Melanoides* OLIVIER, 1804, *Tarebia* H. & A. ADAMS, 1854, *Sermyla* H. & A. ADAMS, 1854 from SE Asia, *Balanocochlis* FISCHER, 1885, *Fijidoma* MORRISON, 1952 from the Pacific realm, *Hemisinus* SWAINSON, 1840, *Cubaedomus* THIELE, 1928 from Central America, and *Tanganyicia* CROSSE, 1881 from the Lake Tanganyica in Africa breed young in a brood pouch until they hatch as miniature adult and crawling. Here the embryonic shell has its initial part wrinkled due to shrinking of the organic shell before becoming fixed in shape by a mineral layer. A thickened rim at the end this first part of the embryonic shell indicates the point of hatching from the egg capsule within the brood pouch. After that the shell is calcified in a regular way and a lobed

apertural lip may be present as if produced in planktotrophic veliger. But hatching from the brood pouch occurs much later as miniature adult (BANDEL & RIEDEL, 1998).

The larva of *Senomelania punctata* (LAMARCK, 1822) hatches from the brood pouch and develops in the open sea (BANDEL & RIEDEL, 1998). The protoconch is about 0.28 mm high. The embryonic whorl measures 0.15 mm and is smooth. The larval shell is sculptured by 7–9 spiral lines. Its aperture has a median projection forming a large beak in the outer lip. The juvenile shell has two spiral ridges, which are crossed by axial ribs producing a reticulated pattern. Later secondary keels are intercalated. The life-cycle corresponds with that of species of *Thiara* noted by BANDEL & RIEDEL (1998) from the same river on Cebu Island.

Melanotarebia BANDEL & KOWALKE, 1997 with the type species *Melania distincta* ZITTEL, 1862 from the Mid Eocene of Hungary has its slender, turreted, up to 1 cm high shell usually decollate with about six whorls preserved. The protoconch of two whorls measuring 0.39 mm in diameter is characterized by a wrinkled surface and a prominent projection of the outer lip after two whorls are completed. The development was here as in modern *Melanoidea* and *Tarebia*.

Family Batillariidae THIELE, 1929

Modern species that belong to this family usually have no larval shell and due to lecithotrophic development hatch from egg masses crawling. In case a species from the Eocene can be included in the genus *Pyrazus* MONTFORT, 1810 the protoconch can be characterized (pl. 8/3, 4). Its type *Pyrazus ebeninus* BRUGUIERE, 1792 lives in mangroves in Australia and hatches crawling (HOUBRICK, 1981). *Pyrazus pentagonatus* (SCHLOTHEIM, 1820) as described by SZÖTS (1953, pl. 3, figs. 29, 30) and KECSKEMETI-KÖRMENDY (1972, pl. 14, figs. 1, 4) from the Eocene of Hungary resembles "*Pyrazus*" from the Late Cretaceous of Tresp in northern Spain and Gosau in the northern Alps. The species from the Eocene of Gant in Hungary has been described as *Gantmelania* by KOWALKE (2001) and *Terebralia* by KOWALKE (1998). *Gantmelania pentagonatus* from the mid Eocene of Gant in Hungary is up to 35 mm high and consists of about 20 whorls. The protoconch has the larval shell ornamented by a weak row of tubercles and two weak spiral lines (pl. 8/3, 4). It resembles that of *Terebralia palustris* from Eastern Africa (KOWALKE, 1998, pl. 4, figs. 11, 19; 2001, figs. 3, 5, 6).

Species of the Batillariidae may live in brackish water and the rocky coast (BANDEL & WEDLER, 1987, BEESLEY et al., 1998). WENZ (1938–1944) defined the family according to shell shape, while THIELE (1931) included characters of the radula into the diagnosis. Batillariidae have a central tooth with small teeth on the margin of the basal plate while in Telescopiinae the tooth has a narrow basal plate without teeth (BANDEL, 1984). *Batillaria* BENSON, 1842 is based on *Batillaria zonalis* BRUGUIERE from southern Australia and *Zeacumanthus* FINLAY, 1927 with the type *Zeacumanthus lutulentus* (KIENER, 1841) from New Zealand living in tidal pools (MORTON & MILLER, 1968). *Batillaria* of the Caribbean Sea lives in shallow bays and its young develop within the egg capsule nourished by liquid yolk and hatches with a shell of more than one whorl completed (HOUBRICK, 1991).

Family Potamididae H. & A. ADAMS, 1854

In mangrove swamps of the Indo-West-Pacific characteristic gastropods are of the genera *Telescopium*, *Terebralia* and *Cerithidea*. The medium sized to large snails with 20 to 100 mm long turreted shells reaching 16 cm in length with high spire and commonly strongly sculptures. The aperture has a deep notch at its base. In similar environment at western Africa *Tympanotonus* is found. According to RNA-analysis Potamididae, Pachymelaniidae and Melanopsidae jointly differ from the other Cerithioidea (RALF BISCHOFF, unpublished data). *Potamides* BRONGNIART, 1810 is based on a fossil species that resembles the Mediterranean *Pirenella* (GRAY, 1847). The relationship between *Potamides/Pirenella* on one side and species that live in the mangrove environment on the other side is not at all resolved (STRAUSZ, 1966). It is, therefore, preferable to present the Potamididae with independent subfamilies, as had been suggested by HOUBRICK (1988). The history of these has not been resolved and the genera included may even connect more closely to other groups of the Cerithioidea than to each other.

Potamididae represent the brackish water radiation of the superfamily Cerithioidea and are morphologically similar to the Cerithiidae. THIELE (1931) and WENZ (1938–1944) included in the Potamididae also the Batillariinae which have since been interpreted as independent living in temperate or subtropical areas, while the Potamididae (Telescopiinae) prefer the tropical area. HOUBRICK (1984) suggested that their geological record reaches the Maastrichtian.

Subfamily Potamidinae H. & A. ADAMS, 1854

Potamides BRONGNIART, 1810 is based on *Potamides lamarcki* BRONGNIART, 1810 from the Oligocene of Mid-Europe (WENZ, 1938–1944, fig. 2132). A very similar species from the Mid-Eocene of Damery in the Paris Basin has an almost smooth protoconch with about three rounded whorls (pl. 8/1, 2). Species bearing a planktotrophic larva are considered expired, but species with lecithotrophic development still live with *Pirenella* (GRAY, 1847) based on *Cerithium conica* BLAINVILLE, 1825 from the eastern Mediterranean Sea. The teleoconch is about 20 mm high consisting of more than 10 slightly rounded, dextral whorls. A keel accompanies the suture, axial ribs and rows of nodules are present. The aperture has a rounded outer lip, short anterior canal of the siphon and broad callus on its inner lip. The shell has no umbilicus. The protoconch consists of about one and a half whorls with 0.3 mm in width with simple margin and sinus-like hook on its outer lip. Individuals of this species live in lagoonal surroundings, but also in Birket Qarun in Egypt, far away from the Mediterranean Sea (KOWALKE & BANDEL, 1996, pl. 4, fig. 5). *Pirenella* has a long history that ranges well into the Late Cretaceous (BANDEL & RIEDEL, 1994) and many species in the Neogene of the Paratethys (WENZ, 1942; JEKELIUS, 1944).

The Cretaceous *Pirenella münsteri* (KEFERSTEIN, 1829) has a protoconch with the larval shell ornamented by two spiral keels (KOWALKE & BANDEL, 1996, pl. 4, figs. 2, 6, 7). *Pirenella balatonica* (TAUSCH, 1886) that lived at the Santonian in coastal swamps of the Tethys Ocean has a shell with about 15 whorls and about 19 mm high and 5 mm wide. The increase in diameter is regular in early ontogenetic whorls and decreases on late ontogenetic whorls. Ornament consists of axial ribs or rows of nodules (BANDEL & RIEDEL, 1994, pl. 7, figs. 4–7; pl. 8, figs. 1–6). Here the protoconch is about 0.25 mm wide and consists of only 1.5 whorls ending in a sinus-like hook at the outer lip of its aperture. It most probably hatched crawling, as is the case in modern *Pirenella*.

Subfamily Telescopiinae ALLEN, 1950 (= ? Cerithideinae HOUBRICK, 1988)

Here contained are species which live an amphibious life in mangrove swamps and salt marshes where they graze detritus and micro-algae. HOUBRICK (1984, 1986, 1988, 1991) interpreted the genera *Telecopium* MONTFORT, 1810, *Terebralia* SWAINSON, 1840 and *Cerithidea* SWAINSON, 1840 as monophyletic group within the Cerithioidea. The shell shape and the outline of the outer apertural lip of fully grown individuals is characteristic.

Telecopium is based on *Trochus telescopium* LINNAEUS, 1758 from the Indian Ocean with rather large shell and living associated with mangrove forests tolerating a wide range of salinities. Spawn consists of large gelatinous masses with eggs measuring about 0.12 mm and young hatching about four days after spawning. The larval shells have still not been described. Young shells collected in several SE Asian mangroves always had their protoconch corroded. HOUBRICK (1991) recognized the genus from the Miocene onward from localities in East Africa, Indonesia and the Philippines and interpreted all older fossils included in this genus to actually belonging to the Campanilidae. *Telecopium telescopium* and *Campanile symbolicum* have convergent shell morphologies and fossil representatives of either one will be difficult to distinguish without protoconch preserved.

Cerithidea has the type *Cerithium obtusum* LAMARCK, 1822 from the tropical Indo-Pacific. HOUBRICK (1991) recognized three subgenera all of which live in mangroves and on intertidal flats in the tropical climate world wide. From the eggs held in a jelly string young hatch about three weeks after deposition as crawling young or almost ready for metamorphosis. The protoconch consists of about 1.5 whorls and is smooth and may end with a marginal ring (HOUBRICK, 1994), and there is no larval shell developed.

Terebralia has the type *Strombus palustris* LINNE, 1758 from the tropical Indian Ocean and three living species. HOUBRICK (1991) found the spawn attached to roots of the mangrove trees and from it veligers hatch. The protoconch of *Terebralia palustris* from the Tansanian coast consists of more than 2 whorls with its larval part ornamented by spiral lines (KOWALKE & BANDEL, 1996, pl. 4, figs. 4, 8). Later, they grow to almost 200 mm in length and develop a very heavy shell and often feed on the wax-like leaves of the mangrove trees. *Terebralia sulcata* (BORN, 1778) from the western Pacific (Indonesia and Philippines) has its spawn attached to the roots of mangroves and veligers may hatch (HOUBRICK, 1991). According to HOUBRICK (1991) the genus ranges back in time to the Early Miocene. But actually *Terebralia* lived during the mid Eocene in the environment of the tropical coastal swamp of the Tethys Ocean. *Terebralia subcorvina* (OPPENHEIM, 1894) has a shell that is up to 150 mm long elongate conical with about 20 whorls. The ornament changes during ontogeny. The protoconch consists of two whorls with the embryonic whorl relatively large and well rounded, and the second whorl is ornamented by two spiral lines which accompany the upper margin of the large apertural projection of the outer lip of the aperture (pl. 6/10), very similar as in case of *Terebralia palustris* from modern mangrove forest.

Tympanotonos SCHUMACHER, 1817 has a turreted conical shell with almost quadrangular aperture and straight columellar lip. The outer lip has a hood-like anterior projection. Ornament is variable and changes with growth. It consists of wavy spiral threads with or without nodes and/or spines. The genotype is *Tympanotonos fluviatililis*

SCHUMACHER, 1817, which lives in estuarine environments in West Africa (BROWN, 1980). *Tympanotonus fuscatus* (LINNÉ, 1758) in the mangrove of Cameroon produces spawn in form of a narrow meandering ribbon that is attached to hard substrates. It consists of many small eggs each held within a round egg capsule. From it small larvae hatch (BANDEL & KOWALKE, 1999).

The species of *Tympanotonos* have been described by DOCKERY (1993) from Ripley Formation and Coffee Sand in Mississippi. The sculpture of these shows differences especially regarding the axial nodes of their teleoconch ornament. The protoconch consists of more than three whorls with two strong spiral keels on the larval whorls (BANDEL, 1993, pl. 3, fig. 2). *Tympanotonus diaboli* (BRONGNIART, 1823) is described from the Eocene of Hungary (SZÖTS 1953, pl. 3, fig. 27; KECSKEMETI-KÖRMENDY, 1972, pl. 12, figs. 11, 12, pl. 13, figs. 3, 4). The species with thorn bearing ornament on its shell lived in coastal swamps. The protoconch consists of 1.7 well rounded whorls of the embryonic shell that ends with a strong median projection of the outer lip of its aperture (KOWALKE, 2001, fig. 1, 3-7, as *Tympanotonos calcaratus* (BRONGNIART, 1823)). The upper margin of the lobe and its median portion is ornamented by a fine spiral line and the lower part of the projection lies hidden beneath the next whorl. The succeeding 6 whorls of the teleoconch have a keel in the lower third and a concave upper side and a steep lower flank. Later whorls develop nodes and even later two more spirals appear of which the subsutural one may have the strongest nodes or even spines. Late ornament is quite similar to that of living *Tympanotonus fuscatus*.

Echinobathra COSSMANN, 1906 from the Cretaceous of the Gosau (Northern Alps) in case of *Echinobathra debile* (ZEKELI, 1852) has a protoconch of about 0.4 mm in height with more than three whorls which are quite round. The larval whorls are ornamented by two spiral ribs (KOWALKE & BANDEL, 1996, pl. 3, fig. 29). *Echinobathra stillans* (VIDAL, 1874) from the Maastrichtian of the Tremp Basin in northern Spain has an up to 8 cm high, turritiform shell consisting of about 17 whorls. The sculpture consists of spiral ribs crossed by axial folds. The protoconch consists of almost two smooth rounded whorls of the embryonic shell and the young hatched crawling.

Hadraxon OPPENHEIM, 1892 is based on *Hemisinus csingervallensis* TAUSCH, 1886 from the Campanian of Hungary (BANDEL & RIEDEL, 1994). It is around 10–15 mm high with high, thin shell with about 20 whorls. The ornament consists of a keel at the suture, spiral lines and pronounced axial ribs. The aperture has a thickened inner lip and bears an anterior channel. The protoconch has two whorls representing the wrinkled embryonic shell that is about 0.3 mm across (BANDEL & RIEDEL, 1994, pl. 6, figs. 5–7; pl. 7, figs. 1–3)

Family Pachymelaniidae BANDEL & KOWALKE, 1999

Pachymelania E. SMITH, 1893 from West Africa has marine larvae but lives in estuarine conditions, often fresh water (BANDEL & KOWALKE, 1999). *Pachymelania* has the type *Strombus bryonensis* WOOD, 1818 from tropical West Africa and here two more species are found. The shell is up to 6 cm high with its spire usually decollate. Sculpture is strong and may change during life. The basal margin of the aperture is produced and spout-like (BROWN, 1980). *Pachymelania fusca* (GMELIN, 1791) regarding its shell morphology is convergent to *Melanoides*, but regarding its anatomy it is not a member of the Thiaridae since sexes are separate and females have no brood pouch. Spawn consists of short packages of gelatinous egg mass consisting of round egg capsules in a jelly mass.

Pachymelania aurita (MÜLLER, 1774) has its lower whorls with a single rows of stout tubercles dominating the ornament, upper whorls with ribs and spiral grooves (BROWN, 1980, fig. 53b). It lives in the estuary of Cameroon rivers on open muddy and sandy intertidal flats jointly with *Tympanotonus* and *Pachymelania fusca*. The barrel-shaped protoconch consists of 2.7 to 3 smooth whorls reaching 0.34 mm in height. The embryonic whorl measures 0.11 mm in diameter, and the larval shell has only fine growth lines which reflect the sinuous outline of the outer lip of the aperture. The transition to the teleoconch is from smooth to the appearance of two spiral keels and weak axial ribs (BANDEL & KOWALKE, 1999, fig. 3). *Pachymelania* may live in fresh water for more than a year as was tested in the aquarium at Hamburg.

RNA-analysis carried out by BISCHOFF (unpublished data) indicated that Potamididae, Pachymelaniidae and Melanopsidae jointly differ from the other analyzed Cerithioidea, such as Thiaridae, Paramelaniidae and Pleuroceridae. They were formerly attributed to the Thiaridae (THIELE, 1929; WENZ, 1941; BINDER, 1957; BROWN, 1980) based on radula and operculum which resembles that of *Melanoides*. They are still placed here by BOUCHET & ROCROI (2005). MORRISON (1954) included *Pachymelania* with the Pleuroceridae. The absence of a brood pouch and the deposition of spawn on the muddy ground as well as differences concerning the radula morphology support the evidence for a systematic placement outside of the Thiaridae as does the protoconch with smooth high shell with rounded whorls (BANDEL & KOWALKE, 1999).

4 Fresh water Cerithioidea with protoconch consisting only of the embryonic shell

The families of fresh water Cerithioidea are quite in discussion and the different taxa will be sorted from each other by molecular analysis. It appears as if different units have geographic distribution such as Pleuroceridae P. FISCHER, 1885 in North America, Pachychilidae TROSCHER, 1857 in Middle and South America, Melanatriidae THIELE, 1928 in Madagascar, Potadomidae GILL, 1871, in Africa, Paludomidae STOLICZKA, 1864 in SE Asia, Paramelaniidae in Lake Tanganyika. Some of these, such as Pleuroceridae and Paramelaniidae have already been documented by molecular analysis to represent natural units of interrelated species (BISCHOFF, unpublished data), while others still need to be analyzed in that regard. BOUCHET & ROCROI (2005) split the family Pleuroceridae P. FISCHER, 1885 into the Pleurocerinae P. FISCHER, 1885 and Semisulcospirinae MORRISON, 1852, the similar Pachychilidae P. FISCHER & CROSSE, 1884 from fresh water are mentioned as unit, and the Paludomidae STOLICZKA, 1868 are distinguished into Paludominae, Cleopatrinae PILSBRY & BEQUAERT, 1927 and Hauttecoeriinae BOURGUIGNAT, 1885. Adult shell is often of convergent shape and their young develop from yolk rich eggs and hatch with a protoconch that consists only of the embryonic shell. Fossil representatives will, therefore often remain problematic in regard to their place in the system. Even in case of very similar shell shapes, as for example in case of the Cretaceous Pyrguliferidae DELPEY, 1841 on one side and the very similar Lavigeriidae THIELE, 1925 and Paramelaniidae MOORE, 1898 from Lake Tanganyika on the other side determination of their relation to each other remains problematic. In case of Synchronopsidae BOURGUIGNAT, 1890 from Lake Tanganyika and very similar Pyrgulidae BRUSINA, 1882 from the Paratethys region the resemblance can be resolved, since living representatives of the later exist and can be analyzed.

Family Pachychilidae P. FISCHER & CROSSE, 1892

Pachychilus from Central America is based on *Melania graphium* MORELET from Guatemala. In regard to characters of its radula (specimen from Nicaragua) it resembles *Potadoma* SWAINSON, 1840 from Cameroon (own data). The operculum consists of many spirals with central nucleus. PILSBRY & BEQUAERT (1927) also noted the similarity of *Pachychilus* from Central America with the African *Potadoma*. According to VAN DER SCHALIE (1937) also to *Brotia* H. ADAMS, 1866 from SE Asia is similar. But here more than 100 species of fresh water Cerithioidea are living in rivers and lakes (KÖHLER & GLAUBRECHT 2002), including *Brotia* and *Sulcospira* TROSCHER, 1857. In regard to their shell shape some of them could also be placed with the Thiariidae, and even ontogeny within a brood pouch is similar, but they usually differ by construction of their operculum. *Brotia* has a protoconch with folds and somewhat irregular shape that reflects its later calcification within the brood pouch (BANDEL & RIEDEL, 1998; KÖHLER & GLAUBRECHT, 2001). *Brotia* apparently also lived in the European Paratethys during the Miocene with *Brotia escheri* (BRONGNIART, 1822).

Melanatria BOWDICH, 1822 has the type species *Buccinum flumineum* GMELIN, 1767 from Madagascar. The two living species of this genus are inhabitants of streams (BROWN, 1980). The from the egg mass that is deposited on the ground young hatch with about 0.3 mm large embryonic shell (GROSSMANN, 1967). Fossils resembling *Melanatria* such as *Melanatria stillans* (VIDAL, 1874) have been noted from the Maastrichtian Isona Formation of Northern Spain and differ regarding their aperture that has a short anterior notch (HARBECK, 1989).

Melanatria may be related to the African *Potadoma* and also to *Cleopatra* TROSCHER, 1856. BANDEL (1998) suggested that only the genus *Cleopatra* is essentially an African genus of the Paludominae. Members of the *Cleopatra* group have a concentric operculum with a spiral nucleus. Paludominae may be distinguished from the Paramelaniinae by the shape of their radular teeth. STARMÜHLNER (1974, 1991) described members of the genus *Paludomus* SWAINSON, 1840 with the type *Melania conica* GRAY from India. Here whorls are smooth or ornamented with axial and spiral ribs, quite variable among individuals. The aperture lip is strongly sinuous.

Potadoma has many species in the rivers of western Africa (BROWN, 1980). The type is *Melania freethi* GRAY, 1831 with smooth whorls or ornamented with spiral ribs which are usually near the base of the shell and the operculum with nucleus near the center (in contrast to *Melanoides* and *Pachymelania*, where it is near to the base). From the eggs present in a gelatinous ribbon in a side stream of Mungo River in Cameroun crawling young hatched. The adult has a heavy shell with the lower part of the aperture elongated and spout-like. The population near Edea in the rapids of the Sanaga river has a population with variable shape of individuals with almost smooth and slender shell as in *Potadoma zenkeri* (MARTENS, 1901) to short and triangular as in case of *Potadoma trochiformis* (CLENCH, 1929) (own observations).

Family Pleuroceridae P. FISCHER, 1885

The family Pleuroceridae P. FISCHER, 1885 represent North American Cerithioidea of rivers and are genetically one unit (HOLZNAGEL & LYDEART, 2000), many of which live in the catchment of the Mississippi River.

According to BOGAN (1998) six genera exist in North America with 156 species. They prefer running water with rocky bottom from which they scrape algae. The Coosa River in SE USA had 82 species of three genera resembling *Pleurocera* RAFINESQUE, 1818. PONDER & WARÉN (1988) synonymized the Pachychilidae with the Pleuroceridae and included here also African taxa. BOGAN, PIERSON & HARTFIELD (1996) noted that the Mobile Bay basin in Alabama, Georgia, Mississippi and Tennessee holds the most diverse freshwater gastropod fauna of the world, comparable only to the diversity reported from the Mekong River in Southeast Asia.

Family Paramelaniidae MOORE, 1898 (= THIELE, 1925),
and Paludomidae STOLICZKA, 1868 with Pyrguliferidae DELPEY, 1941

Paramelaniidae are based on *Paramelania* E.A. SMITH, 1881 and live predominantly in Lake Tanganyika. Some of these are very similar to species from the estuarine environment of a Santonian coastal swamp from Hungary. These Pyrguliferinae are based on *Pyrgulifera* MEEK, 1872, and also hold *Szaboella* BANDEL & RIEDEL, 1994. *Pyrgulifera* has the type *Melania humerosa* MEEK, 1860 from the Bear River Formation (Wyoming, USA), but the genus is best known from deposits of Santonian estuary of Hungary (BANDEL & RIEDEL, 1994, pl. 8, figs. 7–9; pl. 9, figs. 1–16; pl. 10, figs. 1–8). Here the about 0.4 mm wide protoconch consists of one and a half whorl that is clearly demarcated by sinuous thickened apertural margin. Adult shells are from about 1–4 cm in height with teleoconch very similar to living species of *Lavigeria* and *Paramelania* from Lake Tanganyika. *Pyrgulifera purbeckiensis* BANDEL, 1991 is recognized to have lived in coastal swamps at the beginning of the Cretaceous period (BANDEL, 1991; 1993, pl. 2, fig. 6). *Pyrgulifera* lived in the uppermost reaches of estuarine areas, mostly in fresh water during the Late Cretaceous of the Northern Alps (KOWALKE & BANDEL, 1996). *Pyrgulifera* survived the Cretaceous-Tertiary faunal crisis and with *Pyrgulifera gradata* (ROLLE, 1858) and still lived in similar environment of fresh water of estuaries in the coastal area of the Eocene of Hungary (KECSKEMETI-KÖRMENDY, 1972). Fossil *Pyrgulifera* has a recognize existence of more than 60 Million years, so that a possible relations of *Lavigeria* with the Cretaceous *Pyrgulifera* as had been suggested by WHITE (1885), TAUSCH (1885), OPPENHEIM (1892), BANDEL & RIEDEL (1994), BANDEL (1999) is plausible.

Convergence or relation between *Lavigeria* and *Pyrgulifera* is paralleled by that between *Chytra kirki* (SMITH, 1880) from Lake Tanganyika (RIEDEL, 1993, pl. 3, figs. 7, 8) and *Szaboella* BANDEL & RIEDEL, 1994 from coastal swamps at the Santonian of Hungary. The 1.3 embryonic whorls also end abruptly in the Cretaceous species, and they have a more gradational transition in the modern *Chytra*, but similar dimensions of about 0.3 mm in maximal diameter. Especially the juvenile shell with its strong keel and much more slender whorls than in the later shell are very similar to each other in *Szaboella* and *Chytra*. They represent either a case of close convergence or they reflect a relation.

The Cerithioidea from Lake Tanganyika are apparently all interrelated and differ genetically from those of other fresh water environments (unpublished molecular data of RALF BISCHOFF, Bremen). This interrelation was determined to exist between the species of *Lavigeria* which are all related to each other, and the genera *Spekia*, *Stormsia*, *Reymondia* and *Paramelania*. All of them are closer related to each other than to any other group of fresh water Cerithioidea. Among them the Lavigeriidae THIELE, 1925 (= Potadomoidinae) include *Lavigeria* BOURGUIGNAT, 1888 from Lake Tanganyika and *Potadomoides* LELOUP, 1953 from rivers next to it (LELOUP, 1953; MANDAHL-BARTH, 1967). *Lavigeria* has several species in Lake Tanganyika. Their solid shells are of medium to large size according to the species involved from 8 to 32 mm high when fully grown. The brood chamber in *Lavigeria nassa* (WOODWARD, 1859) lies in the anterior part of the oviduct (MOORE, 1899). The embryonic shell has ornament of pits and fine ridges surrounding them (RIEDEL, 1993, pl. 2, figs. 9, 10; BANDEL, 1998, pl. 3, fig. F). The species of *Lavigeria* from Kigoma Bay at Lake Tanganyika prefer different substrates some live on rocky bottom and hard substrates, others on and in sandy bottom and others only on large algae or plants.

Paramelania E. SMITH, 1880 from Lake Tanganyika have species with large, solid, ovate to narrowly conic shell with sculpture of axial ribs and spiral cords, very similar to those of *Lavigeria* but always with a holostome aperture with a strong and smooth margin. The concentric operculum, the shape of the teeth of the radula and the reproductive mode differentiate *Paramelania* from *Lavigeria*. *Paramelania damoni* (SMITH, 1881) has the shell consisting of 10 whorls. It is larger than *Paramelania crassigranulata* (SMITH, 1881) that has more evenly nodular ornament. The latter lives on sandy to muddy substrate while the former prefers steep rocky slopes. Spekiinae BANDEL, 1998 include the genera *Bridouxia* BOURGUIGNAT, 1885, *Spekia* BOURGUIGNAT, 1879 and *Stormsia* LELOUP, 1953 from Lake Tanganyika and are characterized by the central tooth of their radula which has a characteristic split (BANDEL, 1998). Molecular data confirmed the close relation to exist between *Stormsia* and *Spekia* (unpublished results of RALF BISCHOFF). *Spekia* based on *Spekia zonata* (WOODWARD, 1859) has a depressed shell with very large last whorl and oblique aperture, its embryonic shell measures 0.35 mm (RIEDEL, 1993, pl.3, fig. 4; BANDEL, 1998), and it lives on larger rocks on the beach and also on aquatic plants. *Stormsia* based on *Stormsia minima* (SMITH, 1908) with small shell with about six whorls is rock-dwelling in the wave

zone of Lake Tanganyika. The protoconch is 0.22 mm diameter of the first whorl (RIEDEL, 1993; BANDEL, 1998). *Bridouxia* based on *Bridouxia giraudi* BOURGUIGNAT, 1885 has a small ovate shell with conical spire, shallow sutures, spiral ornament and a thickened apertural margin. Protoconch distinguishes the species (BANDEL, 1998, pl. 6, figs. C–F, pl. 7, figs. A–C).

Reymondiinae BANDEL, 1998 differ in regard to their central tooth in the radula strongly from that of Spekiinae, Lavigerinae and Paramelaniinae. *Reymondia* BOURGUIGNAT, 1885 is based on *Reymondia horei* (SMITH, 1880) and has a narrow conic shell with smooth whorls and thickened aperture. It is found on the lower side of rocks below the surf zone often together with the smaller *Reymondia pyramidalis* BOURGUIGNAT, 1888. Their embryonic shell resembles that of *Bridouxia*.

The family Syrnolopsidae BOURGUIGNAT, 1890 with the genera *Syrnolopsis* E. SMITH, 1880, *Anceya* BOURGUIGNAT, 1884 and *Martelia* DAUTZENBERGER, 1908 also live exclusively in Tanganyika Lake. The shell of these small species is convergent to living Pyrgulidae from Europe and their fossil counterparts from the Paratethys, but the radula of *Syrnolopsis* resembles that of the Paramelaniinae indicating that the similarity is due to shell convergence. *Anceya* and *Martelia* share the spiral lines on the protoconch, strong fold on the anterior inner lip and axial sculpture elements dominating in the teleoconch, and a concave anterior edge in their central teeth of the radula. *Syrnolopsis* according to BROWN (1980) has three variable species with protoconch having a diameter 0.23 mm (RIEDEL, 1993, fig. 23; pl. 3, fig. 9; BANDEL, 1998, pl. 2, figs. E, F). *Syrnolopsis* lives on soft bottom off the shore and specimen with keeled shell are more common on isolated spots of soft substrate among rocks.

Anceya with *Anceya giraudi* BOURGUIGNAT, 1884 has an about 10 mm long shell that consists of 14 whorls sculptured by axial ribs. The last whorl may form a strong carination near its base and a columellar fold is present (BANDEL, 1998, pl. 1, figs. A, B). The spiral sculpture of the protoconch in *Anceya* is weaker than in *Martelia* with the type species *Martelia tanganyicensis* DAUTZENBERGER, 1908 has an up to 2.3 mm high shell consists of about 7 strongly ribbed whorls. The ribs may fuse at the periphery forming a single carination. The oval aperture has a strong columellar fold. The protoconch has up to 14 fine spiral ridges on the embryonic shell which continue in the reticulated sculpture on the first 2.5 whorls of the teleoconch (RIEDEL, 1993, pl. 4, fig. 1; BANDEL, 1998, pl. 1, figs. C, D).

Family Juramelanatriidae n. fam.

Diagnosis: Cerithiimorpha of the fresh water with only the embryonic shell representing the protoconch. The family is based on *Juramelanatria* BANDEL, 1991 from the Weald facies at the transition from Jurassic to Cretaceous.

The species of this group of Cerithioidea may belong to the stem group of one or several of the modern genera that live in fresh water and have been placed in Pleuroceridae, Melanatriidae or Pachychilidae.

Juramelanatria is based on *Juramelanatria rugosa* (DUNKER, 1843) from the transitional zone between Jurassic and Cretaceous in Central Europe (BANDEL, 1993, pl. 1, fig. 6). The slender, turreted, *Cerithium*-like shell has its aperture with anterior canal that twists to the left. The sculpture consists of coarse axial ribs which begin low on the upper flank and become stronger in the central portion of the whorl. Axial ribs are crossed by numerous spiral ridges. Below the suture the whorl is flattened and may form a shallow groove. The embryonic shell consists of two smooth whorls. It is found in the French and Swiss Jura Mountains and resembles the modern fresh water genus *Melanatria* BOWDICH, 1822. *Juramelanatria rugosa* inhabited brackish or fresh water. Its shell with up to 8 whorls is about 4 mm high and 1.3 mm wide and has an apical angle of 27°. The whorls are separated by shallow sutures and ornamented by about 10 axial ribs and 7 spiral lines. Axial ribs end in the subsutural depression. The base is weakly rounded, bordered by two spiral keels and ornamented by faint spiral lines. The embryonic shell consists of two whorls, is 0.3 mm wide and high and has indistinct transition into the teleoconch (BANDEL, 1991).

Juramelanoides BANDEL, 1991 has a slender, turreted shell that resembles modern *Melanoides* OLIVIER, 1804 with its aperture angular at its lower end and sculpture consisting of spiral ribs. The embryonic shell is rounded, smooth and consists of less than two whorls (BANDEL, 1991). Only the first whorl with diameter of 0.18 mm is smooth and on the second whorl a spiral rib appears. It is based on *Juramelanoides villersense* (DE LORIO, 1865) from the French Jura Mountain. The shell consists of many whorls, and a 3 mm long shell has 8 whorls with rounded flanks and distinct sutures. The apical angle is about 22°. The aperture is rounded and the base has a spiral rib and umbilicus. The sculpture consists of spiral ridges that increase in number with consecutive whorls.

5 Clade Turritellimorpha

The clade is based on the superfamily Turritelloidea LOVÉN, 1847. It includes the Turritellidae and the Vermiculariidae. According to similarities in the characters of protoconch also the tiny Styliferinidae are here included, even though their anatomy and habits of life appear to be quite different from the other two families. Turritellimorpha may have as sister-groups the Vermetimorpha and Cerithimorpha. Earliest members of Turritellimorpha are known from the Middle Jurassic of Madagascar, from the Early Cretaceous of Europe (SCHRÖDER, 1995) and from that time onward with increasing number of species to the Recent.

The Vermiculariinae have been recognized as independent from the Vermetidae sensu WENZ (1938–1944) and closely related to the Turritellidae (MORTON, 1965; KEEN, 1961; HEALY, 1988; HOUBRICK, 1988). It has also been suggested to regard the *Turritella* relation as a superfamily on its own (HOUBRICK, 1988). He suggested that Turritellidae may be more closely related to the Vermetoidea than to the other families of the Cerithioidea. In regard to the morphology of the teeth of the radula BANDEL (1984) documented that no close relations exists between *Turritella communis* RISSO, 1826 and *Vermetus* or *Petalococonchus* of the Vermetidae. Regarding the shape and construction of spermatozoa of *Turritella* a general cerithioidean type with unique paraspermatozoa was noted (HEALY & WELLS, 1998). HEALY (1983, 1986) noted also a similarity with the spermatozoa of the Dialidae, Litiopidae and Siliquariidae, while they differ strongly from those of the Vermetoidea.

Superfamily Turritelloidea Lovén, 1847

The teleoconch usually consists of many whorls, is elongate and ends with a simple, relatively small aperture. The shape of the protoconch within the Turritelloidea is not uniform but so different among species that it appears quite possible that the superfamily may have arisen from different ancestral groups.

Family Turritellidae LOVEN, 1847

The high shell has an elongate spire consisting of numerous whorls and a simple aperture. Their mode of life is suspension feeding predominantly hiding in soft bottom substrates in the shallow marine environment. Due to their mode of life species of the Turritellidae often live close to each other forming large populations. Since they live in the sediment, layers of shells with a large number of individuals of the same species in one bed are common. Turritellidae in a shell coquina are present from mid Jurassic onwards, observed from Bathonian deposits near Sakaraha in SW Madagascar.

The family is based on *Turritella* LAMARCK, 1799 with type from the Indo-Pacific. The Turritellidae have been divided in Turritellinae LOVÉN, 1847, Orectospirinae HABE, 1955, Pareorinae FINLEY & MARWICK, 1937, Protominae MARWICK, 1957, and Vermiculariinae DALL, 1913 according to BOUCHET & ROCROI (2005). In regard to protoconch morphology the differences between these subfamilies have not been evaluated so that tracing them into the past is not possible.

Turritella LAMARCK, 1799 has a slender, turreted-conical shell with numerous whorls, is sculptured with spiral threads or costae and curved growth lines. The aperture is rounded or quadrate and not large. The columella is smooth and concave. The genotype is *Turbo terebra* LINNÉ, 1758 that lives in the tropical Indo-Pacific. *Turritella terebra* (LINNÉ, 1758) as described by WILSON (1993, pl. 14, fig. 13) from Australia occurs in the Indo-West Pacific and may be up to 17 cm long. When the shell is grown the initial shell portion is usually lost, and apparently still not known. Whorls are convex, base is convex and the periphery is rounded. Ornament consists of spiral ribs (about 7 on the last whorls) and lines between them. The outer lip forms a broad sinus with the aperture round.

The shell of a fully grown larva of a *Turritella* close to *Turritella terebra* from the plankton of the Gulf of Aqaba consists of 5.5 rounded whorls and is 0.65 mm high. The bulbous embryonic whorl has a diameter of about 0.1 mm and is smooth (pl. 8/14). After 0.5 whorls of the larval shell fine spiral rows tubercles begin which are concentrated on the lower half of the whorls. On the second whorl two keels are present, one median and the other near the basal suture of the whorls. The larval shell has a narrow tongue-like somewhat angular median extension of the outer lip of its aperture (pl. 8/12, 13). From Aqaba two species have been encountered which are known from their larval shell, which are similar to each other and the juvenile shell that increases rapidly in width in one case (pl. 8/13) and has no such sudden increase in width in the other species (pl. 9/1). Similar larval shells can be noted among several species from the tropical Indo-Pacific (pl. 9/2, 3). A very similar protoconch was also developed in *Turritella* from the Eocene of Gan in SW France (pl. 9/4).

Turritella communis RISSO, 1826 from the eastern Atlantic and *Turritella variegata* (LINNÉ, 1758) from the Caribbean Sea have a comparatively short protoconch. The protoconch of *Turritella communis* from the Mediterranean Sea is about 0.4 mm high and 0.3 mm wide with the embryonic whorl a little less than 0.1 mm in

width. The larval shell has two fine spiral lines as ornament (THIRIOT-QUIEVREUX, 1969; RICHTER & THORSON, 1975). In case of *Turritella variegata* (LINNÉ, 1758) from the Caribbean Sea the larval shell is short, since only a short period is spent as free living larva in the Plankton (BANDEL, 1975, pl. 2, figs. 8, 9). The embryonic whorl is about 0.1 mm wide and smooth and the short larval shell has two spiral ribs. Similar shapes are also encountered from Late Cretaceous members of *Turritella* from the Campanian and Maastrichtian of Mississippi and Tennessee (USA) (SOHL, 1960, pls. 7, 8; 1964). The protoconch of *Turritella trilirata* CONRAD, 1860 and *Turritella quadrilirata* JOHNSON, 1898 from Ripley Formation is rounded and consist of three smooth convex whorls (DOCKERY, 1993, pl. 8, figs. 1, 6, 7, 8). *Turritella* from the Paleocene of Matthews Landing in Alabama has a short protoconch with keel on its larval shell indication the upper edge of the median lobe (pl. 9, figs. 7, 8). The *Turritella* from the Paleocene resembles in regard to its protoconch that of *Turritella communis* and *Turritella variegata* but consists of three whorls and is about 0.3 mm high. The embryonic shell composes the first whorl. The two whorls of the larval shell have collabral lines that reflect the strong lobe present on the outer lip of the larval aperture. Ornament consists of a median spiral rib that ends in the upper edge of the larval lobe in the outer lip and continues in the ornament of the teleoconch. Growth lines pattern changes from strongly sinuous in the larval shell to straight reflecting the shape of the rounded simple outer lip in the teleoconch.

The protoconch of Early Cretaceous *Turritella* is intermediate in shape with slender early whorls and a widened last larval whorl (BANDEL, 1993, pl. 8, fig. 1; SCHRÖDER, 1995, pl. 4, figs. 12–16; KAIM, 2004, fig. 33). The protoconch of *Turritella polonica* (SCHRÖDER, 1995) consists of more than five whorls and has a height of 0.8 mm. The whorls of the larval shell increase in diameter so much that the shape resembles a tear drop and the last whorls of the larval shell is wider than the first whorl of the teleoconch.

ALLMON (1988) suggested that in *Turritella* the embryonic shell (protoconch I) is not distinct from the larval shell (protoconch II). Also the larval shell supposedly has no apertural projection of the outer lip in its transition to the teleoconch (HEALY & WELLS, 1998). This was suggested to represent a difference to other members of the Cerithioidea, but it is obviously a mistake in observation and does not actually apply to the *Turritella* relation. The protoconch described in this way belongs to a species with lecithotrophic development and no larval stage, but it does not characterize all Turritellidae.

Turritella tokodensis STRAUSZ, 1966 from the Eocene of Dudar in Hungary has a protoconch with only two whorls, but with fine ornament of spiral lines on its larval whorl. It is about 0.4 mm high and ends with a strong triangular extension of the outer lip of the aperture. Transition from the protoconch to the teleoconch is marked by the curving margin of the larval shell and by sudden appearance of two spiral ribs on the teleoconch (pl. 9, figs. 5, 6). The ornament of the larval shell is quite unusual to other species of *Turritella*.

Family Vermiculariidae DALL, 1913

In *Vermicularia* FAUSTINO, 1928 protoconch morphology resembles that seen in *Turritella communis* from Europe or *Turritella variegata* from the Caribbean Sea (BANDEL, 1993, pl. 8, fig. 3). Juvenile individuals of *Vermicularia* move on soft substrates in lagoons and the shallow sea of Bermuda and when the seventh or eighth whorls of their shell is completed they usually contact with a hard substrates and attach to it similar as Vermetidae do right after metamorphosis. If no such attachment is encountered a more or less regular open spiral coil continues to be secreted. Attached individuals live by filtering food from the water as is the case in *Turritella* (BANDEL & KOWALKE, 1997; KOWALKE, 1998, pl. 7, figs. 1, 2). *Vermicularia pellucida* from Panama feeds in much the same way (HUGHES, 1985). BIELER & HADFIELD (1990) observed that *Vermicularia spirata* (PHILIPPI, 1836) from the Florida Keys lives mainly embedded in a white sponge. They observed that small males are free living, and when they become attached and undergo sex reversal and change to females.

In specimen from Yucatan the protoconch consists of 2.5 whorls with a height of about 0.7 mm. The first whorl measures 0.33 mm across. After 1.5 smooth embryonic whorls the onset of a strong median keel may documented the beginning of a short larval stage. Another spiral keel is present near the suture or just below it. In this case the second keel may only be seen in pediveliger-shells. The outer lip of the protoconch is sinuous.

Family Styliiferinidae BANDEL, 1992

Diagnosis: The family is based on the genus *Styliiferina* A. ADAMS, 1860 with smooth fusiform teleoconch and a slender protoconch with characteristic larval shell. It closely resembles that of the type of *Turritella* with its Pacific species around the genotype, consists of about 5 whorls and is slender with strong apertural tongue-like projection of the outer lip. The animal has three pairs of epipodial tentacles (KOSUGE, 1964; BANDEL, 1992).

The closest Cerithioidea regarding the presence of epipodial tentacles is the Litiopidae, but *Alaba* and *Litiopa* differ strongly in regard to their comparatively short and strongly ornamented protoconch. Included in the family is also a small species with two epipodial tentacles from Lizard Island, Great Barrier Reef, Australia, here

described as *Spirostyliferina lizardensis*.

Styliferina has a smooth elongate shell with rounded to inflated whorls. The protoconch is smooth consists of relatively many whorls, is elongate in shape and has a strong projection on the outer lip of its larval shell. The genus is based on *Styliferina goniochila* (A. ADAMS, 1860) that appears to be common over wide regions of the tropical Indo-Pacific. It has been recorded from Hawaii (TAYLOR, 1975) to Eilat (DEKKER & ORLIN, 2000), from Australia to the Philippines (BANDEL, 1991, pl. 5, fig. 9) and Japan (OKUTANI, 2000). Its smooth spindle shaped teleoconch is connected to a long slender protoconch with more than 5 whorls (pl. 10/1, 2). The whorls of the teleoconch are smooth and may have a weak spiral pattern (pl. 9/12). *Styliferina goniochila* is found among algae in the lagoon and on drifting green algae, as they occur commonly in the Red Sea at the time when dust is blown in from the surrounding deserts.

Fully grown larvae with larval shell completed are commonly encountered in the plankton of the Gulf of Aqaba. The slender shell resembles that of *Turritella* from the same plankton samples but in contrast to these has a smooth larval shell. The veliger larvae are very similar with large lobe of the velum held above the shell and the small lobe in front of it. The embryonic whorl has a fine beaten pattern of grooves surrounded by ridges. It measures a little less than 0.1 mm in diameter. With begin of the larval shell this pattern ends and growth lines give evidence of a deep sinus below the suture and an elongate rounded lobe on the outer lip of the aperture. This lobe is present throughout larval life and the growth of the four larval whorls (pl. 10/2). With begin of the teleoconch the sinus above and below the median lobe is closed and further growth reflects the simple outline of the aperture. Also relative height of whorls decreases and the shell becomes wider in the about 6 whorls of the teleoconch.

Styliferina guttulina (SZÖTS, 1953) that had been determined as *Eulimella guttulina* SZÖTS by KECSKEMÉTI-KÖRMENDY (1980, pl. 18, figs. 10–12) is a small smooth species from the Hungarian Eocene. This species is close to modern *Styliferina* and lived in the very shallow water near the shore in Tethys of Gant. It closely resembles a *Styliferina bouryi* (COSSMANN, 1888) as known from the Eocene of the Paris Basin and is more slender than the modern species from the Gulf of Aqaba. In the species from Hungary the protoconch has four whorls and a large projection of the outer lip of the aperture with weak spiral line indicating its upper edge. It measures less than 0.3 mm in height (pl. 9/9, 10).

THIELE (1929) suggested *Styliferina* to represent a synonym to *Diala*, and that opinion was repeated by WENZ (1938). KOSUGE (1964) observed the tentacles on the foot but described *Styliferina goniochila* as member of the genus *Diala*. He noted that the protoconch is paucispiral, which can not be supported for the species from Aqaba. HOUBRICK (1987) suggested *Styliferina* to be a synonym to *Alaba*, and also PONDER (1985) placed it in the Litiopidae due to the presence of foot tentacles in the genus. The shape and ornament of the protoconch places *Styliferina* neither with the Litiopidae as also suggested nor with the *Diala* relation. To include them in the Cerithiidae as suggested by WARÉN (1984) is not plausible due to the same reason.

Genus *Spirostyliferina* n. gen.

Diagnosis: The small species has anatomical features as found in *Styliferina*, with two epipodial tentacles next to the operculum and transparent shell with body shining through with its green, yellow and white pigment dots. The foot is ciliated and split in front into two parts with the mouth between them and it ends rounded with three long sensing cilia extending. The tentacles of the head have eyes as their outer base and also end club like with sensing cilia extending. The shell consists of a conical protoconch with three rounded whorls and a teleoconch with less than one rapidly expanding whorl. The aperture is rounded and detached from the shell and the base is rounded and has a narrow umbilicus. The genus is based on *Spirostyliferina lizardensis* from the shallow sea grass environment next to Lizard Island in the Australian Great Barrier Reef (pl. 9/13–14).

Derivatio nominis: This small snail with similar habits and organization of its body as seen in *Styliferina* is ornamented on its teleoconch by spiral lines- thus *Spirostyliferina*, and it was found next to Lizard Island, and thus *lizardensis*.

Spirostyliferina lizardensis n. sp.

Holotype: pl. 9/13, 14 in coll. of the Geol.-Pal. Inst. Mus., Hamburg.

Diagnosis: As genus with unusual protoconch of a first rounded and high embryonic shell that has ornament of strong wrinkles and measures about 0.1 mm in diameter. The following two whorls are smooth with simple straight, apertural margin and simple collabral growth lines. All whorls of the protoconch are well rounded and the height and width is about 0.4 mm (pl. 9/14). The teleoconch has ornament of spiral lines of which some are

straight most have zigzag pattern. Most of them continue to the margin of the aperture, some end before it (pl. 9/13).

Description: As in diagnosis. The whole shell is less than one mm high with the protoconch taking more than one third of total height. All whorls are evenly rounded, as is the base and the aperture. The spiral lines are on the whole body whorl and there are more than 20 present from suture to umbilicus.

The specimen illustrated in pl. 9/13–14 represents the holotype, deposited in the collection of the Geologisch-Paläontologisches Institut and Museum of the University of Hamburg.

Regarding protoconch morphology *Styliferina* is quite different to *Spirostyliferina*. The similarity is due to the organization of the body that is visible on the active animal. The larval shell of *Spirostyliferina* has no lobe on its outer lip and is more widely conical than that of *Styliferina*. Thus *Spirostyliferina* could also be related with *Alaba* / *Litiopa* regarding the organization of the body but not regarding shell shape. As the Litiopidae, but also as *Styliferina*, it produces mucus threads on which it can retrace its way rapidly and by which it can attach and climb about among algae. Sea grass is its habitat, as is the case in *Styliferina* in the lagoon next to Lizard Island.

6 Clade Murchisonimorpha

According to HOUBRICK (1981) and HASZPRUNAR (1988) the anatomy of *Campanile symbolicum* IREDALE, 1917 unites characters of the Caenogastropoda and of the Allogastropoda HASZPRUNAR, 1985. *Campanile* FISCHER, 1884 has an own type of osphradium (HASZPRUNAR, 1988) as well as parasperm morphology that differs from that of other Caenogastropoda (HEALY, 1986). Its radula is typical for Caenogastropoda, and not very different from that of *Plesiotrochus* FISCHER, 1878. THIELE (1928) and WENZ (1938) regarded *Campanile* and *Plesiotrochus* as related to each other and that relation may connect them to the Orthonematidae (= Orthonemidae) of the Late Paleozoic (BANDEL, 2002). Campaniloidea and the Orthonematoidea may form an own clade of the Caenogastropoda that is as ancient as the Ctenoglossa and the Allogastropoda. Many of its Paleozoic representatives had been placed with *Murchisonia* ARCHIAC & VERNEUIL, 1841 and also the last Triassic representative described below, so that the hypothetical order uniting *Campanile* and *Plesiotrochus* with *Orthonema* MEEK & WORTHEN, 1862, and *Cheilotomona* STRAND, 1928 is here determined as “Murchisonimorpha”.

Superfamily Orthonematoidea NÜTZEL & BANDEL, 2000 (= Orthonematoidea)

The superfamily as defined by BANDEL (2002) encompasses species with murchisoniform, turritelliform, and turbiniform shell with slit (Goniasmatidae NÜTZEL & BANDEL, 2000) or without slit or sinus in the outer lip of their aperture (Orthonematidae NÜTZEL & BANDEL, 2000). The protoconch is smooth, rounded trochospiral. It is distinguished from the teleoconch by change in the pattern of growth lines and commonly it has a curving apertural thickening at the end of its larval shell. Often a spiral line marks the upper edge of the apertural lobe of the larval shell. The protoconch consists of up to three whorls. The first whorls of the teleoconch have no slit, later a more or less deep sinus or slit of the outer lip may develop.

While the outer lip of the teleoconch of the Goniasmatidae has a slit or sinus, that of the Orthonematidae is more or less straight (NÜTZEL & BANDEL, 2000). BANDEL (2002) noted that in the genus *Stegocoelia* DONALD, 1889 with its many species the character of a slit, sinus or straight apertural lip became difficult to assess. He found the Goniasmatidae to merge with the Orthonematidae. The later taxon was preferred since it is based on the genus *Orthonema* that had been proposed earlier than the genus *Goniasma* TOMLIN, 1930 and, in addition, is connected to a well recognized genotype.

Family Orthonematidae NÜTZEL & BANDEL, 2001 (as Orthonemidae)

The shell has a high spire with slit, distinct sinus, weak sinus or no sinus in the outer lip of the aperture of a part of the teleoconch. This indentation on the outer lip may result in a selenizone or a more or less sinuous growth line pattern. But growth lines may also be straight. The ornament of the teleoconch may consist of spiral ribs. The protoconch comprises up to three whorls and its larval shell has a well developed apertural lobe. Its position is low on the outer lip and its upper edge may bear a spiral rib (NÜTZEL & BANDEL, 2000, figs. 1, 4, 5; BANDEL, 2002, BANDEL et al., 2002, pls. 8–12). The family is based on the genus *Orthonema* from the Carboniferous of eastern North America.

Among the Carboniferous and Permian species of this group the genera *Orthonema* MEEK & WORTHEN, 1862,

Goniasma TOMLIN, 1930, *Stegocoelia* DONALD, 1889 have species with spiral ornament. A slit usually appears later on the juvenile teleoconch of *Goniasma*, in the teleoconch of *Stegocoelia* there is usually only a sinus, and the apertural margin of several species of *Orthonema* is simple and straight, but in others a deep sinus may develop late.

The protoconch of *Orthonema* consists of two to three whorls with 0.25 to 0.30 mm in height. The embryonic whorls measures about 0.15 mm in diameter and is smooth or has hammer-blow pattern. The larval shell is sculptured with minute granules on smooth background and a spiral line marks the upper edge of the lobe of the outer lip of the aperture. The protoconch of *Stegocoelia* is found in YOO (1988, figs. 71, 79) and BANDEL et al., (2002, figs. 95, 98, 100) and has the same features as that of *Orthonema*.

The Triassic genus *Cheilotomona* STRAND, 1928 is based on *Cheilotoma blumi* (MÜNSTER, 1841) from the St. Cassian Formation of the Dolomites. It is of Late Triassic age belonging to the Lower Carnian stage (BIZZARINI et al., 1986) and here the Cordevol (URLICHS, 1994). In *Cheilotomona* (pro *Cheilotoma* KOKEN, 1889 according to KNIGHT et al., 1960, I 293) the first 5–8 whorls have a strong axial ornament. A median keel is situated almost in the center of each whorl crossed by collabral ribs with nodes next to the suture. A furrow lies above the keel in the first whorls of the teleoconch, later a ledge. In later whorls one or two additional spiral ridges appear and axial elements are less distinct. A narrow lobe appears below the keel representing a short slit in the middle of the outer lip. In fully grown shell that slit lies in central position and the selenizone created by it has a keel in its middle (KOKEN, 1889, fig. 22; ZARDINI, 1978, pl. 6, fig. 11), (pl. 6/2). The aperture forms a gutter-like siphon with a double rim in front. The protoconch is simple, rounded and smooth (KOKEN, 1889, fig. 24), (pl. 6/1) and its diameter is about 0.2 mm.

In case of *Cheilotomona acuta* (MÜNSTER, 1842) the protoconch is about 0.2 mm wide and separated from the teleoconch by dense growth lines. The juvenile shell is rounded for about 1.7 whorls and with the end of the second whorl two strong spiral keels appear. In the third whorl the keel lies in central position and it becomes nodular (pl. 6/2). Only in the seventh whorl a deep slit appears in the outer lip of the aperture, behind which in following whorls a selenizone develops. In this seventh whorl *Cheilotomona acuta* actually changes into *Cheilotomona blumi*.

KITTL (1891) was of the opinion that *Murchisonia* and *Cheilotomona* are so similar to each other that they have to be regarded as representing the same genus. The Paleozoic Murchisoniidae KOKEN, 1896 based on *Murchisonia* with type from the Devonian contain species which closely resemble *Cheilotomona*. FRÝDA & MANDA (1997) found a typical protoconch as is characteristic to the Archaeogastropoda in Devonian species of the genus *Murchisonia* ARCHIAC & VERNEUIL, 1841 from Bohemia, with the protoconch of its type species from the middle Devonian of western Germany still unknown (HEIDELBERGER 2000). The similarity of the shell in *Murchisonia* and *Cheilotomona* is due to convergence. The shell of *Cheilotomona blumi-acuta* consists of aragonitic material in crossed lamellar structure. If it were found in Paleozoic deposits it could be placed with the genus *Goniasma*. *Cheilotomona* represent the last known member of the Orthonematidae.

7 Clade Campanilimorpha

While the teleoconch is a quite different size and shape among the families here included, the protoconch, when connected to a larval shell, consists of rounded whorls and is about as wide as high. The larval shell ornament is of fine tubercles on smooth background and the sinuous apertural margin is expanded when fully grown.

In this group that may be a part of the Murchisonimorpha, the superfamily Campaniloidea with the two families with living species Campanilidae and Plesiotrochidae are united with some families consisting of fossil species such as the Settsassiidae and Metacerithiidae.

HOUBRICK (1981), HEALY (1986, 1993), and HASZPRUNAR (1988) confirmed WENZ (1938) who united *Campanile* and *Plesiotrochus* FISCHER, 1878 among a few other doubtful genera in the subfamily Campanilinae DOUVILLE, 1904. But this taxon was later recognized to have superfamily status independent of that of the Cerithioidea. BOUCHET & ROCROI (2005) included here Campanilidae, Plesiotrochidae as well as Ampullinidae COSSMANN, 1919 and Trypanaxidae GOUGEROT & LE RENARD, 1987. Modern *Campanile* as analyzed by HOUBRICK (1981) and *Plesiotrochus* as characterized by HEALY (1993) may have developed from the Orthonematidae (BANDEL, 2002; BANDEL et al., 2002). Ampullinidae are here considered a separate superfamily the Ampullinoidea.

Superfamily Campaniloidea DOUVILLÉ, 1904

The only species *Campanile symbolicum* still living has lecithotrophic development and thus only a simple embryonic shell. It lives at the rocky shore in Western Australia, is 24 cm long and has up to 30 whorls. A weak keel lies on the base and a row of low nodules ornaments the juvenile shell. The protoconch consists only of a

simple embryonic shell with rounded whorls. The aperture is narrow and angular with anterior canal of the siphon. The protoconch of *Campanile houbrieki* KIEL & PERRILLAT, 2000 from the Late Cretaceous of Mexico has a larval shell quite similar to that found in *Plesiotrochus*. The protoconch is smooth and round, consists of two convex whorls with about 3.5 mm in height and width, and terminates with a strong varix that is flaring in its lower half. The embryonic whorl measures about 0.14 mm across (KIEL et al., 2000). The teleoconch has a single fold on its anterior inner lip, is small and slender and ornamented with two minor spirals below the broad, subsutural belt (KIEL et al., 2000).

Campanile symbolicum was found to be related to *Plesiotrochus* due to similarities in sperm ultrastructure (HEALY, 1986). HEALY (1993) suggested to transfer the Plesiotrochidae HOUBRICK, 1990 to the Campaniloidea. Species of the Cretaceous *Metacerithium* have a protoconch shape like that of modern *Plesiotrochus* and fossil *Campanile*. Also the protoconch of *Sakarahina* from the Jurassic and *Settsassia* from the Triassic is similar. Both are interpreted as possible relatives to the Campanilidae which extends the history of the Campaniloidea back into the late Triassic when also the last member of the Orthonematidae was still living with *Cheilotomona*.

Family Campanilidae DOUVILLÉ, 1904

The genus *Campanile* FISCHER, 1884 is based on *Cerithium giganteum* LAMARCK, 1804 from the Eocene of the Paris Basin in France (HOUBRICK, 1981, 1989). The shell is elongate and turreted, has straight-sided or slightly convex whorls and moderately incised sutures. Growth lines are sinuous and sculpture consists of cords near the suture and nodes that are frequently absent or weak on later whorls. Its body whorl is truncate, the aperture narrow with anterior canal of moderate length. Its inner lip is smooth or has one or more folds. The larval shell (if developed) is smooth and provided with a marginally enforced apertural projection. A species of *Campanile* is preserved with juvenile shell and protoconch from the Eocene of Gan in SW France (pl. 10/10–12). The protoconch is quite similar to that of modern *Plesiotrochus* from Aqaba in shape as well as ornament.

In the tropical shallow sea especially of the Tethys Ocean *Campanile* was apparently common from late Cretaceous time well into the Eocene (JUNG, 1987). From the end of the Eocene onward and the disappearance of the Tethys Ocean, *Campanile* as well as *Plesiotrochus* became restricted to the Pacific region. *Campanile houbrieki* KIEL & PERRILLAT, 2000 from the Maastrichtian of Mexico has a slender shell and a protoconch as found in *Plesiotrochus* and in *Metacerithium ponsi* KIEL & BANDEL, 2000 (KIEL et al., 2000, pls. 1–2).

Family Metacerithiinae COSSMANN, 1906

The small to medium sized shell with high spire has three beaded spiral cords on its whorls. Its base is a little rounded and the anterior canal is straight. On the inner lip of the aperture folds may be present. Species with high spire and ornament of nodules on axial and spiral ribs are included, which have a protoconch as in *Plesiotrochus*. The family is based on *Metacerithium* COSSMANN, 1906 with type from the Early Cretaceous of France. *Metacerithium* differs from *Campanile* by a strong, beaded spiral ridge near the base of the whorls.

The type to *Metacerithium* is *Cerithium trimonile* MICHELIN, 1838 from the Aptian/Albian of England and France. Oblique axial ribs are present on the earliest whorl and a subsutural band appears from the fourth whorl onwards. The ornament then gradually becomes tubercle bearing. Its protoconch is unknown, while that of *Metacerithium ponsi* KIEL & BANDEL, 2000 from the Campanian of northern Spain consists of 2.5 whorls and is smooth and rounded and has the aperture expanded and with sinuous outer lip. It is 0.25 mm high and 0.33 mm wide. The teleoconch has two spiral cords with tubercles (not three as in the type to the genus) and a smooth base. The aperture has a straight columella without plates (KIEL et al., 2000).

A *Metacerithium* aff. *trimoline* MICHELIN, 1838 from the Albian of Mahajanga Basin in Madagascar has a rounded protoconch with 2.5 whorls and about 0.37 mm high. The embryonic whorl measures about 0.11 mm in diameter and has fine dots. Dots are also present on the larval whorls which expand at their final margin with median projection of the outer lip. The teleoconch is elongate consisting of many whorls with ornament of widely spaced axial ribs and fine spiral lines. This species grew to a size of 8 mm (KIEL, 2006).

Metacerithium aff. *trimoline* has a protoconch like that of *Sakarahina* or *Plesiotrochus* with fine dots on the larval shell and a size of about 0.1 mm of the embryonic whorl. In case of *Metacerithium* the teleoconch is elongate and ornamented by ribs, resembling that of *Campanile* sp. from the Eocene of France (pl. 10/10–12). It resembles *Metacerithium ponsi* from the Campanian of Spain (KIEL, 2006). *Dzikella* KAIM, 2004 is similar in respect to the teleoconch. *Dzikella trammeri* KAIM, 2004 from the late Valanginian of Poland resembles *Metacerithium* with its teleoconch having the same pattern of rounded strong axial ribs and weak spiral lines. The difference between both species lies in the number of axial ribs on each whorl, which is a little higher in case of the specimen from Poland. KAIM (2004, fig. 36) described the protoconch as did SCHRÖDER (1995) and

accordingly it resembles that of *Plesiotrochus* as well. *Dzikella* clearly belongs in the relation of *Metacerithium*.

Family Settsassiidae BANDEL, 1992

The protoconch has rounded 2.5 whorls with the larval shell ending with widened lobed margin. The teleoconch is elongate and pointed egg-shaped with rounded whorls which are ornamented by rounded radial ribs. The aperture is about as wide as high and has a short anterior notch (BANDEL, 1992). The family is based on the genus *Settsassia* BANDEL, 1992 from the Late Triassic of the Dolomites of the Alps.

Settsassia with *Settsassia obliquecostata* (MÜNSTER, 1841) has the rounded protoconch (BANDEL, 1993, pl. 4, fig. 2) and elongate teleoconch and *Lacunina* Kittl, 1891 with *Lacunina bronni* (WISSMANN, 1841) also included in the Settsassiidae has a shorter teleoconch with basal angle and a more pointed protoconch. *Settsassia* has a slender shell that consists of numerous rounded whorls with axial ornament on smooth background. The protoconch consists of more than two rounded whorls, is as wide as high and ends with a thickened apertural margin. The type is *Melania obliquecostata* MÜNSTER, 1841 from St. Cassian Formation, Italian Alps (Dolomites). The shell of *Settsassia obliquecostata* (MÜNSTER, 1841) has 13 whorls that measures 14 mm in height and almost 7 mm in width with 12 to 14 axial ribs with slight forward inclination on each whorl. While early whorls are without umbilicus the body whorl detaches and an umbilicus is formed (ZARDINI, 1978, pl. 24, figs. 13, 14, 17, 20–22, pl. 25, figs. 8–9; BANDEL, 1992, pl. 11, figs. 3, 4, 7, pl. 12, figs. 1–2).

The genus *Lacunina* KITTL, 1891 is based on *Turbo bronni* MÜNSTER, 1841 from St. Cassian Formation. It has an egg-shaped shell with conical pointed apex and more or less rounded whorls. Ornament consists of broad rounded axial ribs. The sides form a corner to the base that is weakly convex and has a narrow umbilicus. The aperture is oval with short anterior notch. The shell of *Lacunina bronni* (MÜNSTER, 1841) may have 7 whorls and is 5 mm high and 3 mm wide (ZARDINI, 1978, pl. 14, fig. 17). The protoconch is almost as wide as high with 0.12 mm wide embryonic shell and larval shell ornamented by a row of tubercles below the suture and a median lobe on the outer lip of the outer lip of the aperture (BANDEL, 1992, pl. 12, figs. 3–6; BANDEL, 1993, pl. 5, fig. 6).

Settsassia obliquecostata had a planktotrophic larval stage with rounded shell resembling that of modern *Plesiotrochus* while that of *Lacunina bronni* resembles more that of Triassic *Coelostylina* KITTL, 1894 in regard to the more conical shape, the ornament with a row of tubercles and the not widened apertural margin at its transition to the teleoconch. While the teleoconch with simple rounded axial ribs unites *Lacunina* with *Settsassia*, the protoconch brings *Lacunina* in the vicinity of *Coelostylina*.

Family Plesiotrochidae HOUBRICK, 1990

The protoconch has the larval shell short with rounded smooth whorls and final varix (BANDEL, 1993, pl. 5, fig. 1), (pl. 10/3). It has a small conical to pagoda-like teleoconch that has an angular to ovate aperture with broad anterior siphon notch. The whorls may form short apical ramps, may be flattened or even a little concave. About 7 angular whorls compose the shell with large body whorl. The family is based on the genus *Plesiotrochus* FISCHER, 1878 with several small sized species living in the tropical Indo-Pacific.

HOUBRICK (1990) had noted that *Plesiotrochus* is anatomically distinct from other Cerithioidea, and thus placed the genus in its own family among them, thus confirming WENZ (1938). HEALY (1993) transferred the Plesiotrochidae to the Campaniloidea due to the similarity of the sperma of *Plesiotrochus* with those of *Campanile*. KIEL & BANDEL (2002) extended this similarity to the protoconch morphology noting the fossil species of the Campanilidae had a similar protoconch to that present in modern *Plesiotrochus*. WILSON (1993) described three species of *Plesiotrochus* from Australia, all close to each other in shape. HOUBRICK (1990) suggested that about 11 species live in the Indo-West Pacific.

Plesiotrochus has species with small conical to pagoda-like shell that has an angular aperture with anterior siphon notch. The whorls are stepped and flat to concave. The type species is *Plesiotrochus souverbianus* FISCHER, 1878 from the Red Sea. This species from Aqaba has the smooth embryonic whorl ending in growth increments. The larval shell with smooth background is covered by fine tubercles. It has a corner that may form a spiral rib at the margin of the larval projection of the outer lip of the aperture. The protoconch consists of two whorls and it ends with flaring apertural margin and an apertural projection. The sinus between it and the suture is strongly thickened when the larval shell is fully grown (pl. 10/3). The teleoconch is small, pagoda-like, and consists of 6–7 angular whorls. The body whorl is large and the aperture ovate with anterior canal broad.

Family Trypanaxidae GOUGEROT & LE RENARD, 1987

According to WENZ (1938, fig. 2266) *Trypanaxis* COSSMANN, 1889 is based on a small *Turritella*-shaped species *Trypanaxis umbilicata* (LAMARCK) as type from the mid Eocene of the Paris Basin. He noted that the protoconch is rounded and short, but still placed *Trypanaxis* as subgenus of *Halloysia* (with protoconch unknown) with the Cerithiopsidae. GOUGEROT & LE RENARD (1987) described the genus again and later it was discovered that its protoconch resembles that of *Campanile* and was placed with the Campaniloidea by PACAUD & LE RENARD (1995) and it is listed here by BOUCHET & ROCROI (2005).

Superfamily Ampullinoidea COSSMANN, 1919

Since Early Jurassic time this group with rounded shell is present characterized by *Ampullospira* HARRIS, 1897. Here the genus *Falorina* is described from the Triassic and placed with the Ampullinoidea. The later are convergent in shell shape to some Neritimorpha of the Triassic and especially the Naticoidea from the Late Early Cretaceous onward, but the shape of the protoconch can clearly distinguish these groups from each other and from the Ampullinoidea (BANDEL, 1999). BOUCHET & ROCROI (2005) placed the Ampullinidae with the Campaniloidea, which needs confirmation. Their early appearance at the Triassic indicates independence. SCHRÖDER (1995, pl. 4, figs. 8–11) described some protoconchs connected to juvenile shells, which resemble *Pseudamaura* and related these to *Settsassia* from the Triassic and *Ampullina* from the Eocene (SCHRÖDER, 1995, pl. 4, figs. 5–7). While *Settsassia* has its teleoconch with axial ribs, *Euchrysalis torpediniformis* as described by ZARDINI (1978, pl. 31, fig. 6), here named *Falorina torpediniformis* (ZARDINI, 1978) has weak spiral ornament but also a protoconch as in *Plesiotrochus*. It is here interpreted as intermediating between Ampullinoidea and Campaniloidea, and suggested to represent a relative to *Ampullina* BOWDICH, 1882. Members of the actual Ampullinoidea without Faloriellinae have a well recognized history from the begin of the Jurassic to the Eocene with species common in lagoonal and near-shore environment, and a strong decline afterwards. Only *Globularia* SWAINSON, 1840, and apparently only with a single species, is a still living representative of the superfamily (KASE, 1990). While the living species has only the embryonic whorls as protoconch, the protoconchs of many fossil species are of characteristic type with rounded whorls, shell as wide as high, small embryonic whorl, and larval whorls ending with a sinuous and thickened apertural margin. They were herbivorous, and the only survivor still lives on algae (KASE & ISHIKAWA, 2003).

Family Ampullinidae COSSMANN, 1919

This family holds the Triassic Falorininae, the Jurassic Ampullospirinae, the Cretaceous Pseudamaurinae, the Paleogene Ampullininae and the modern Globulariinae.

Subfamily Falorininae n. subfam.

Diagnosis: The subfamily is as genus *Falorina* with elongate shell with rounded whorls and fine spiral ornament. The aperture is simple as wide as high and the protoconch has rounded whorls. The embryonic shell is about 0.1 mm in diameter and the larval shell about as high as wide with thickened apertural margin when fully grown. Its ornament consists of fine tubercles (pl. 11/1–2).

The subfamily is based on a genus from the Triassic S. Cassian Formation of the Dolomites and it intermediates in shape of its teleoconch between Campaniloidea such as *Settsassia* and Jurassic Ampullospirinae such *Sakarahina* or *Pictavia*, and in shape and ornament of its protoconch with modern *Plesiotrochus*.

Genus *Falorina* n. gen.

Diagnosis: *Falorina torpediniformis* (ZARDINI, 1978) represents the type with the cylindrical shell, that has the apex narrowed and rounded, consists of many whorls. Those of the protoconch are flat in the top of the shell with the embryonic whorl and of rounded as high as wide shape with the larval whorls. The apical margin of the outer lip of the protoconch is a sinus and is thickened and raised (pl. 11/1). The whorls of the teleoconch are wider than high and ornamented by indistinct spiral ribs which form a corner to a narrow shoulder and to the base. The aperture is simple.

Derivatio nominis: Costalaresc is one of the localities of occurrence of the species near the Alpe Faloria of Cortina d'Ampezzo, with the name of the genus derived from it.

Falorina tropediniformis (ZARDINI, 1978)

The elongate shell with rounded apical part has whorl width decreasing in growth and therefore fusiform to cylindrical shape. Sutures are deep and below them a narrow shoulder with spiral rib is developed. Ornament consists of indistinct spiral ridges (pl. 11/2). The corner to the base is rounded at first, later becomes angular and is accompanied by a rib. The aperture is a little angular (ZARDINI, 1978, pl. 32, fig. 6). A shell with 8 whorls of the teleoconch is about 10 mm high, and whorls are broader than high. The protoconch was not known to ZARDINI (1978). It consists of almost three whorls with the embryonic whorl flat in its top. This whorl is smooth and about 0.1 mm in diameter. The larval whorls are rounded and form a protoconch that is a little wider than high, about 0.3 mm in height (pl. 11/1).

The growth lines trace a rounded median lobe of the outer lip. In the fully grown larval shell the margin of the apical sinus of the lip is thickened and upturned. Ornament of the larval whorls consists of granules which form no special pattern and are a little denser in the first larval whorl than in the second.

Subfamily Ampullospirinae COX, 1930

Ampullospira with the type *Ampullospira canaliculata* (MORRIS & LYCETT, 1861) is from the Middle Jurassic of England (HUDDLESTON, 1892; COSSMANN, 1925; BANDEL, 1999). The protoconch consists of about 2.5 smooth whorls with sinuous margin and indication of the end of larval life by a thickened apertural rim (SCHRÖDER, 1995, pl. 4, figs. 8–11; GRÜNDEL, 2003, pl. 14). The embryonic shell is almost planispiral and smooth and about 0.1 mm wide. The larval shell is rounded, naticoid in shape about 0.4 mm high and wide and ends in a thickened rim as found in the Triassic *Settsassia*. The protoconch is also very close to that of *Ampullina* BOWDICH, 1882 from the Eocene, and it does not have the collabral lines as are characteristic to the larval shell *Amaurellina* and *Crommium*.

Pictavia COSSMANN, 1925 with type *Natica pictaviensis* ORBIGNY, 1852 from the Middle Jurassic of France was placed in the Ampullospiridae by GRÜNDEL (2001; 2003, pl. 9, figs. 5–10) and GRÜNDEL & KAIM (2006, figs. 20–21). Species from the Jurassic have a smooth protoconch which can not well be distinguished from the teleoconch and is described as consisting of about three whorls by GRÜNDEL (2003) and two whorls by GRÜNDEL & KAIM (2006). It is similar in shape and size as that known from *Ampullina* of the Paleogene, but that later form has the larval shell well differentiated from the teleoconch by a thickened margin (BANDEL, 1999). *Pictavia* was the inhabitant of coastal swamps so that its ecological requirements did not change much in relation to the Pseudamauridae and the Globulariinae.

Genus *Sakarahina* n. gen.

Diagnosis: The protoconch resembles that of *Plesiotrochus*, while the teleoconch is smooth and with rounded whorls with ornament of interrupted spiral furrows. The protoconch consists of well rounded whorls, is about as wide as high and ornamented by very fine pustules. Its margin with the teleoconch is marked by a strongly thickened outer lip (pl. 10/4–6). The genus is based on *Sakarahina lugeri* n. sp. from the Mid-Jurassic of Sakaraha, SW-Madagascar.

Derivatio nominis: Called after the town of Sakaraha next to the type locality.

The larval shell is like that of *Plesiotrochus* and in *Campanile* and *Metacerithium* from the Cretaceous. It is similar to that of *Metacerithium ponsi* KIEL & BANDEL, 2000 from the Campanian of northern Spain. The teleoconch of *Sakarahina* resembles that of *Pictavia*, but in contrast to it has spiral furrows, while *Pictavia* is smooth (WENZ, 1944, fig. 2924).

Sakarahina lugeri n. sp.

Holotype: specimen illustrated in pl. 10/6. It is deposited in the Geologisch-Paläontologisches Institut of the University of Hamburg.

Type locality: near the road from Sakaraha to Toleara just outside of Sakaraha (LUGER et al 1994).

Diagnosis: As genus. The protoconch is like that of *Plesiostrochus* in shape and ornament of its larval shell and the teleoconch consists of rounded whorls with ornament of incised lines with pits in the shell surface. It is considered of Bajocian age of the southern Morondava Basin, SW Madagascar.

Derivatio nominis: The species received its name in honor of Peter Luger, who discovered the locality.

Description: The characterization of the genus applies to the species. The protoconch consists of 2.5 rounded whorls which end with a rounded and strongly raised margin. The embryonic whorl is smooth and measures about 0.1 mm in width. It is clearly demarcated from the larval shell by a strong increment of growth of straight outline. The larval shell has curving growth lines which reflect the presence of an apertural lobe low down in the outer lip. Very fine pustules cover the surface especially near the suture, but the surface appears smooth in general. The final apertural varix curves slightly reflecting the lobe of the outer lip and to it at that lobe an outer addition may be preserved that enforces the curving shape of the lip (pl. 10/4–6). This added thin shell is often broken. The teleoconch is clearly distinguished and begins with ornament of spiral grooves of which about 20 are present on the first whorl, of which only about 6 remain uncovered when the next whorl is added.

Sakarahina lugeri lived in the shallow sea near the shore of the middle Jurassic of Madagascar. The Jurassic *Pictavia punctura* (BEAN, 1839) according to GRÜNDEL (2001, pl. 4, figs. 10–15) has a similar ornament of its teleoconch with spiral grooves and pits. This species also represents a member of *Sakarahina* and differs from it by the deep suture. The protoconch is of quite similar shape and size, but with its fine ornament not preserved. *Sakarahina punctura* (BEAN, 1839) from northern Germany documents the good exchange of species within the Tethys at Jurassic times from northern shelf seas of Laurasia to such of the Gondwana Continent now at Madagascar.

Subfamily Pseudamaurinae KOWALKE & BANDEL, 1996

The shell is of globular to egg shape with oval aperture. KOWALKE & BANDEL (1996) described members of the Cretaceous Pseudamauridae to have an egg-shaped shell that is quite large and with or without subsutural ramp. The body whorl is large and has a simple aperture. They reconstructed the family based on *Pseudamaura* P. FISCHER, 1885 from the Late Cretaceous of the Gosau (northern Alps) to have had a mode of life as lagoonal inhabitants. They occur in great numbers as do herbivorous animals in contrast to the carnivorous Naticidae to which their shells are convergent.

Pseudamaura with the type *Natica bulbiformis* SOWERBY, 1831 from the Late Cretaceous of the Gosau like *Pseudamaura lyrata* (SOWERBY, 1831) has a simple protoconch of 1.7 whorls and about 0.3 mm width that indicates a crawling young that hatched from spawn (KOWALKE & BANDEL, 1996, pl. 6, figs. 3–6). *Pseudamaura* species from the Ripley Formation of Mississippi and Tennessee (USA) as well as from the Trichinopoly Formation of Tamil Nadu (India) are similar (DOCKERY, 1993, pl. 20, figs. 5–6; BANDEL, 2000). Pseudamauridae would thus include gastropods resembling modern Globulariinae and Paleogene Ampullinidae that lived during the time of the Cretaceous at least from Santonian to Maastrichtian, some 20 Million years.

Subfamily Ampullinae COSSMANN, 1919

The protoconch of *Ampullina* representing the genus on which the Ampullinidae COSSMANN, 1919 are based was found to differ considerably from that of true Naticidae (BANDEL, 1999, pl. 3, figs. 7–8, pl. 4, figs. 1–6). It resembles that of *Amaurellina* FISCHER, 1885 and *Crommium* COSSMANN, 1888 in shape but not in ornament, all of which are typically found in deposits of the Paleogene in similar environment as *Pseudamaura* consisting of deposits of the shallow near coastal sea.

Ampullina represents a large sized, thick, rather globose shell with relatively high spire and stepped whorls and spiral rows of fine pits. Its umbilicus is small and limited by a well defined limb. The aperture is half moon shaped. Its inner lip is covered by a thick callus. The genus is based on *Ampullaria depressa* LAMARCK, 1804 from the middle Eocene of the Paris Basin. The protoconch has an embryonic shell of about 0.1 mm in width and a smooth rounded larval shell ending in a strongly sinuous thickened apertural margin (BANDEL, 1999, pl. 4, fig. 1), (pl. 10/8). The locality from which many specimens can be recovered lies in the grape-yards of Damery near Reims in the eastern Paris Basin. Here the environment was shallow water probably in part with sea grass beds and with some estuarine influence now and then.

Crommium and *Amaurellina* based on species from Damery and the Eocene of Gant and Dudar in Hungary have

a characteristic ornament of their larval shell consisting of sharp collabral lines (BANDEL, 1999, pl. 4, figs. 2, 5) (pl. 10/7, 9). They reflect the sinuous outline of the apertural outer lip. Similar species, but with unknown protoconch, have been described from the American West Coast (MARINCOVICH, 1977) and placed in a number of genera.

Subfamily Globulariinae WENZ, 1941

The subfamily had been suggested by WENZ (1941, fig. 1929) to represent a part of the Naticidae. The taxon is based on the genus *Globularia* that is living in the Philippines and has been studied by KASE (1990) and KASE & ISHIKAWA (2003). According to their analysis *Globularia* differs from the Naticidae anatomically and by features of the radula. It hatches after lecithotrophic development with simple protoconch consisting of only the embryonic shell. *Globularia* (= *Cernina*) *fluctuata* (SOWERBY) appears to be the only surviving representative of this family. They suggested to place *Globularia* in the family Ampullospiridae COX, 1930 based on the Jurassic genus *Ampullospira* HARRIS, 1897. But Ampullinidae COSSMANN, 1918 has priority over Ampullospiridae as well as over Globulariinae WENZ, 1941.

8 Clade Vermetimorpha

It has been made plausible that the *Vermetus*-character of a normally coiled protoconch connected to an irregular and in parts or totally attached teleoconch has probably evolved several times (HEALY, 1988; BANDEL & KOWALKE, 1997). The most ancient species of the clade are known from the Campanian of the Late Cretaceous with *Laxispira* and *Vermetus* (BANDEL & KIEL, 2000), the second with the protoconch as in modern *Vermetus* and the first in shape and ornament of its protoconch closely resembling that of *Tenagodus*.

Superfamily Vermetoidea RAFINESQUE, 1815

Vermetoidea are sessile marine gastropods with a tubular shell that is irregularly coiled and totally or partly cemented to hard substrates. Sessile gastropods with vermiform shells were placed all together in the family Vermetidae RAFINESQUE, 1815 as MÖRCH (1862) had suggested and was adopted by THIELE (1931) and WENZ (1938–1944). These authors placed the Vermetidae into the superfamily Cerithioidea FÉRRUSAC, 1819. WENZ (1938–1944) included into the taxon Vermetidae genera like *Vermetus* DAUDIN, 1800, *Petalococonchus* LEA, 1843, *Stephopoma* MÖRCH, 1860, *Vermicularia* LAMARCK, 1799, *Laxispira* GABB, 1877, *Tenagodus* GUETTARD, 1770, and *Pyxipoma* MÖRCH, 1860.

HEALY (1988) recognized that vermiform caenogastropods belong into two quite separate groups regarding their sperm morphology. PONDER & WARÉN (1988) and BEESLEY et al. (1998), thus, regarded the Vermetidae to represent their own superfamily Vermetoidea with genera like *Vermetus* and *Dendropoma* and being related to the Xenophoridae TROSCHEL, 1852 and Cypraeidae RAFINESQUE, 1815 rather than the Cerithioidea. HEALY (1988), in addition, suggested a closer relation of the Vermetidae to Stromboidea RAFINESQUE, 1815 and Calyptraeoidae LAMARCK, 1809 than to the Cerithioidea, while he regarded Turritellidae and Siliquariidae as representatives of the superfamily Cerithioidea. HOUBRICK (1988), in contrast, included the Vermetidae in the Cerithioidea. BOUCHET & ROCROI (2005) remarked on the problems to place the superfamily and decided to distinguish two groups as distant from each other, placing the Vermetidae among the Neomesogastropoda and the Siliquariidae in the Cerithimorpha (Palaeocaenogastropoda or Sorbeoconcha).

Family Vermetidae RAFINESQUE, 1815

The family holds sessile marine gastropods with a tubular shell that is irregularly coiled and totally or partly cemented to hard substrates. Feeding is by filtering seawater with the gill and is sometimes aided by the production of a mucus net with the foot. In the strict sense as the Vermetidae are seen here, there are three protoconch types found among them, one like that of *Vermetus nielsenii* with a conical shape and rounded whorls (pl. 12/6), and another one like *Petalococonchus* LEA, 1843 with a barrel-like shape (BANDEL & KOWALKE, 1997, pl. 1, fig. 7) (pl. 12/5, 9). A third type has a slender conical larval shell (pl. 11/11) that resembles that of *Pseudoschwartzella* among modern gastropods of not vermiform shape (pl. 11/7) or with shape as *Sakarahella* among Jurassic gastropods (pl. 11/3–5).

Subfamily Vermetinae RAFINESQUE, 1815

The protoconch is conical or barrel-shaped with smooth rounded whorls. Right after metamorphosis the animal attaches to hard substrate cementing its shell to it. The teleoconch is ornamented by more or less regular growth lines and more or less regular longitudinal ribs. The subfamily is based on the genus *Vermetus* DAUDIN, 1800 with type *Vermetus adansoni* DAUDIN, 1800 from the equatorial eastern Atlantic (WENZ, 1938–1944). Individuals of Vermetidae often hatch as free swimming veliger with well developed velar lobes and may swim and feed from phytoplankton as was observed in the Gulf of Aden.

An earliest representative is known from the Campanian (Late Cretaceous) of Torallola in the Tresp Basin, northern Spain (BANDEL & KIEL, 2000, figs. 1–3). *Vermetus nielsenii* BANDEL & KIEL, 2000 has a smooth, trochospiral protoconch that consists of about three whorls. The embryonic shell is about 0.1 mm wide. Two larval whorls have only growth lines which reflect a wide apertural projection on the outer lip of the aperture. The protoconch measures about 0.35 mm in height and in width. The teleoconch is uncoiled with strong irregular growth lines and a keel-like ridge and shell attached to substrate.

Several protoconch shapes can be observed. One is like that of the Campanian species with conical shape and rounded whorls, as documented here from the Caribbean Sea near Cartagena from deposits of a subfossil reef (pl. 12/5). It resembles the species described by BANDEL (1975, pl. 4, figs. 4, 5) as *Petalococonchus mcgintyi* (OLSSON & HARBISON, 1953) from the Caribbean Sea (pl. 12/6). Also the protoconch of *Petalococonchus floridanus* consists of about three rapidly enlarging smooth whorls of hydroboid outline (WOODRING, 1959).

A second is like that of *Petalococonchus* LEA, 1843 with a barrel-like shape (BANDEL & KOWALKE, 1997, pl. 1, fig. 7). *Petalococonchus erectus* (DALL, 1888) has a similar protoconch from the Caribbean Sea at Santa Marta (Columbia) observed hatching from its egg mass by BANDEL (1975, pl. 3, figs. 3, 7). It hatches with barrel-shaped protoconch consisting of 2.5 whorls and almost 0.8 mm in height. At metamorphosis it has grown only little when it became enclosed in the attached teleoconch (pl. 12/5). A protoconch of *Vermetus* sp. from the Island Satonda on the Indonesian Sea is about 0.6 mm high and consists of about 2 smooth whorls. Here the first whorl is bulbous and measures 0.42 mm in diameter and the base has a keel at the corner (pl. 12/9). Probably only a short period is spent by this species swimming after hatching and before metamorphosis occurs. A similar barrel shaped protoconch without the basal keel was noted in case of *Thylaeodus* cf. *rugulosus* (MONTEROSATO, 1878) from the Azores by BIELER (1995, fig. 18). He noted, though, that the young of this species hatch after metamorphosis was concluded.

The reefs in the Gulf of Aqaba have a member of the *Vermetus* group with short barrel-shaped protoconch (pl. 12/4). This larva is not common in the Plankton and consists of almost two whorls forming a 0.33 mm high shell. The embryonic whorl is about 0.2 mm in diameter and covered by a groove and ridge ornament. The larval whorl is rounded and ornamented by spiral rows of fine tubercles and seven spiral lines on the corner and proper of the rounded base. The outer lip of the aperture extends into a wide lobe that is ornamented by inclined lines. The subsutural sinus of the outer lip is thickened and narrow, and the umbilical sinus is wide. The nature of the aperture with thickened margin documents that the larval shell is fully grown, and the larva was ready to settle to benthic life.

Vermetus sp. from the Mediterranean Sea near Banyuls-sur-Mer (Southern France) is very similar in size and shape consisting of about 1.5 whorls. Whorls are sculptured with very fine spiral granulated lines. HADFIELD et al. (1972, fig. 19D) figured the protoconch of *Vermetus alii* from the Hawaiian Islands as consisting of about two whorls and of similar shape to the Mediterranean species. The protoconch of *Petalococonchus keenae* from the Hawaiian Islands consists of 2.5 to 3 cylindrical whorls reaching a height of 0.7 mm (HADFIELD et al., 1972, fig. 19G).

Genus *Cerithiovermetus* n. gen.

Diagnosis: The narrow rounded uncharacteristic shell of this elongate tubular vermetid is connected to the diagnostic protoconch (pl. 11/10–12; pl. 12/1–3). It consists of more than three and up to five rounded whorls of almost the same width as height or is higher than wide. The embryonic whorl has a hammered ornament and the larval shell is ornamented by a subsutural row of tubercles and short irregular ribs on its lower side. The aperture extends in a wide wing-like process of the outer lip that is accompanied by a narrow subsutural sinus and a similar but less deep umbilical sinus. The genus is based on *Cerithiovermetus aqabensis* n. sp from the Gulf of Aqaba, Jordanian coast.

Cerithiovermetus aqabensis n. sp.

Holotype: pl. 12/2 in coll. of the Geol. -Pal. Inst. Mus., Hamburg.

Diagnosis: A thin tubular shell with round diameter and growth lines as ornament is connected to a conical protoconch with rounded whorls. The ornament of the larval shell consists of a subsutural row of tubercles and irregular, sometimes branching and interrupted axial ribs on the lower half of the larval whorl (pl. 12/1–3). The corner to the base in the fully grown larval shell has a spiral rib and on the base fine inclined ribs are present as well as on the wide apertural lobe.

Derivatio nominis: After occurrence at Aqaba at the coast of Jordan.

Locality: Aqaba Red Sea, shallow near-shore lagoon at the Marine Station. The adult was found among algae in the lower intertidal zone at the Marine Station at Aqaba, and the larva can be regularly encountered in the plankton of the Gulf of Aqaba. Possibly this represents what has been determined as *Vermetus periscopium* BARNARD, 1863 from the Israel side of the Gulf of Aqaba (unpublished species list).

Description: The thin tubular teleoconch is connected to a rounded protoconch with 3.5 whorls. The embryonic whorl is rounded, ornamented by a groove and ridge pattern and about 0.15 mm in diameter. The ornament of the larval whorls resembles that found among the larval shell of some Cerithiopsidae (pl. 12/1–3), but the protoconch of the later is more elongate. The protoconch of *Cerithiovermetus aqabensis* is about 0.45 mm high and its larval shell has a wide apertural median lobe connected to a deep sinus below the suture.

Cerithiovermetus vinxi n. sp.

Holotype: pl. 11/10, 11 in coll. of the Geol. -Pal. Inst. Mus., Hamburg.

Diagnosis: As in genus the tubular and attached irregular teleoconch is connected to a conical and regularly shaped protoconch that consists of a little more than five whorls. The embryonic whorl measures about 0.1 mm in diameter. Its larval shell consists of evenly rounded whorls with ornament of a row of larger tubercles below the suture, a row of small tubercles in the suture, and a zone with inclined ribs as well as two spiral ribs at the edge to the base (pl. 11/10–12).

Derivatio nominis: The individuals were collected by EVA VINX and called in her honor.

Description: The characteristic protoconch is almost 0.5 mm high and consists of a little more than 5 whorls. It is slender conical in shape with the last larval whorl a little less wide than the whorl before it. The embryonic whorl is well rounded and ornamented by a ridge and groove pattern. The larval whorls have ornament of a row of tubercles below the suture which remains visible while the ornament on the lower portion of the larval shell is covered by succeeding whorls, with exception of the last larval whorl. The teleoconch is attached to substrate from its begin onwards and is coiled around the protoconch enwrapping it partly.

The embryonic whorl of *Cerithiovermetus vinxi* is quite small (about 0.1 mm) and smaller than that of *Cerithiovermetus aqabensis* (0.15 mm). Their size resembles that of the oldest known *Vermetus* from the Campanian with 0.1 mm wide embryonic shell. These are very small compared with the larval shell of *Vermetus* sp. from the Indonesian Sea in pl. 12/9 where the first whorl measures 0.4 mm in diameter. Differences in the size of the embryonic shell can be related to embryonic development, which in case of *Petalconchus erectus* from the Caribbean Sea includes the consumption of nurse eggs (BANDEL, 1975).

Locality: This vermetid species was found in the shallow sea near Satonda Island, Indonesia.

Subfamily Laxispirinae n. subfam.

Diagnosis: The subfamily is based on the Late Cretaceous *Laxispira* GABB, 1877. The teleoconch may be loosely but regularly coiled or straight forming reef-like structures with individuals supporting each other in forming a colony with each other. The whorls are of round cross section and ornament consists of spiral and beaded ribs. The protoconch consists of about three rounded whorls and is about 0.5 mm in height and width. Its embryonic whorl of about 0.1 mm in diameter has a pitted surface and larval whorls are ornamented by rows of dots. Their apertural margin is drawn out to form a strong median lobe of the outer lip. The characteristic species is *Laxispira lumbricalis* GABB, 1877 from the Late Cretaceous Ripley Formation as characterized by SOHL (1960), DOCKERY (1993).

Laxispira lumbricalis GABB, 1877 has a protoconch with three convex whorls, the second of which has rows of

very fine dots (BANDEL, 1993, pl. 7, figs. 5–6; BANDEL & KOWALKE, 1997, pl. 1, fig. 4). It resembles the protoconch of modern *Tenagodus* GUETTARD, 1770 as documented by SCHIAPARELLI (2002, fig.1) from the Mediterranean Sea and LEAL (1990, pl. 6, fig. I) from the tropical West Atlantic. Here the basal rows of tubercles in the ornament of the larval shell are fused to form lines. The teleoconch of *Tenagodus* has a slit in contrast to that of *Laxispira*.

BANDEL & KIEL (2000) discovered that *Vermetus* co-existed with *Laxispira* in the Campanian of northern Spain. Different species of *Laxispira* were distributed along the shores of the Tethys Ocean during the Late Cretaceous (Campanian to Maastrichtian) and are known from North Africa, southern and central Europe and southern USA (BANDEL & KOWALKE, 1997). The similarity of the protoconch of Cretaceous *Laxispira* with that of modern *Tenagodus* may indicate that a relation exists between these rather than between *Laxispira* and *Vermetus*. If that were the case, the *Tenagodus* relation would range back in time to the Campanian (about 80 Million years).

Subfamily Dendropomatinae BANDEL & KOWALKE, 1997

The protoconch of the Vermetidae such as in the genus *Vermetus* is barrel shaped and smooth or covered by fine tubercles or spiral lines of tubercles. The protoconch of *Dendropoma* MÖRCH, 1861, in contrast, has axial to cancellate sculpture and more conical shape (BANDEL & KOWALKE, 1997). The larval shell is ornamented by axial and spiral ribs forming a regular network (pl. 12, figs. 7, 8). *Dendropoma maxima* (SOWERBY, 1825) has only one whorl of its larval shell and it hatches from the egg case that is held in the shelter of the parental shell tube with almost 0.4 mm wide embryonic whorl. To it one larval whorl is added to form a 0.55 mm high shell. The base of larval shell has a rounded edge until in the last part of the final whorl a corner develops. At that stage the base is flattened and has spiral lines (pl. 12/7). The larva is quite common in the Plankton of the Gulf of Aqaba at all times of the year.

Another larva of similar ornament but more whorls of its shell is found less regularly in the plankton of the Gulf of Aqaba (pl. 12/8). It probably belongs to a species that is closely associated with the corals of the reef. The ornament of the embryonic shell is a groove and ridge pattern, and the whorl is about 0.16 mm in diameter. The 2.5 larval whorls are ornamented with sinuous axial ribs which end at a spiral rib near the base. This and three more such spiral ribs are on the flattened base and the upper three of them end on the extended projection of the apertural outer lip. The sinus above the apertural lobe has a thickened margin and is deep. The areas between the ribs on the base have a pattern of fine inclined lines. The protoconch is about 0.5 mm high and 0.4 mm wide.

The Dendropomatinae can be traced to the Eocene and thus had an independent evolution from the other Vermetidae for at least 50 Million years (BANDEL, 1993, pl. 7, fig. 2). They may be related to the non-vermetiform Provannidae as was suggested by BANDEL & KIEL (2000). The protoconch of *Desbruyeresia* and *Laeviphitus* is quite similar and also the radula of *Dendropoma lamellosa* as figured by BEESLEY et al. (1998, fig. 15.129 I) does not differ fundamentally from that of the two latter genera.

Family Sakarahellidae n. fam. with possible relation to *Pseudoschwartziella* n. gen.

Diagnosis: The protoconch is conical and consists of several whorls. Its larval shell has a projection of its outer lip of the aperture and ornament of a ribbon below the suture and short ribs or tubercles below that (pl. 11/3–5). The family is based on *Sakarahella* from the Jurassic of Sakaraha in SW-Madagascar.

Remarks: The protoconch resembles that of *Cerithiovermetus vinxi* in shape and ornament, also that of *Pseudoschwartziella jordanica*. While the first has a vermetiform teleoconch, the later closely resembles a *Rissoina*. It may be that protoconch shape reveals a relation between these widely different modern species that connects them to the Jurassic *Sakarahella angulata*.

Genus *Sakarahella* n. gen.

Diagnosis: The protoconch with almost 5 whorls is provided with a prominent apertural projection in the larval whorls. The smooth embryonic whorl is of about 0,1 mm in diameter. Larval whorls have a subsutural spiral ribbon and ornament of tubercles or short inclined axial lines above the suture. The teleoconch is ornamented by axial ribs and a few spiral ribs at the corner to the base. Fully grown shells are not known. The genus is based on *Sakarahella angulata* from the mid Jurassic of Sakaraha, SW Madagascar (pl. 11/3–5).

Sakarahella angulata n. sp.

Holotype: pl. 11/5 in coll. of the Geol. -Pal. Inst. Mus., Hamburg, Mid-Jurassic of Sakaraha, SW Madagascar.

Diagnosis: As family.

Derivatio nominis: After basal corner on teleoconch.

Description: The protoconch is conical with the first whorl smooth, well rounded, about 0,1 mm wide, and distinguished from the begin of the larval shell by simple straight growth lines at its end. The larval shell is of elongate conical shape with apical angle of about 45°. A row of tubercles is situated below the suture. The larval whorls are provided with a hooked outer lip of the aperture. The wide lobe of the apertural projection is ornamented with incline lines and rows of tubercles in somewhat irregular arrangement. The protoconch is 0.7 mm high and more than 0.4 mm wide and has more than 4.5 whorls. The teleoconch is ornamented with strong axial ribs of which there are about 10 on each of the first whorls. They are crossed by low spiral ribs well spaced from each other and those on the corner to the base are more strongly developed. While axial ribs are not continuous onto the base, spiral ribs cover it. The aperture is rounded and weakly notched at its anterior end. Among the many species documented from the European Jurassic by SCHRÖDER (1995), GRÜNDEL (1999a–b, 2003a–b), and KAIM (2004) a larval whorls of the protoconch as is found in *Sakarahella* has not been noted. A possible relation may exist to *Pseudoschwartziella* n. gen.

Genus *Pseudoschwartziella* n. gen.

Diagnosis: The teleoconch has the shape of that of a *Rissoina* with about 4 whorls ornamented by strong collabral axial ribs. The apertural margin of the body whorl is thickened and whorl width increases continuously less. The protoconch is elongate slender conical with more than four whorls which regular increase in width. The ornament of the larval shell consists of a row of granules below the suture which fuse to a spiral rib in later whorls. Fine rows of tubercles form an indistinct spiral ornament and growth lines reflect a large rounded apertural lobe on the outer lip. The base is ornamented by spiral lines and the outer lip flares in a wide shield like median lobe of the aperture connected to a deep sinus on either side.

Derivatio nominis: The adult shell of the genus closely resembles that of *Schwartziella* but has a protoconch with different ornament of the embryonic and larval shell. This indicates that it is not closely related to it (Pseudo-). The species is found in the shallow lagoonal waters near Aqaba, Jordan and named accordingly (*jordanica*).

Remarks: The teleoconch is much like that of *Schwartziella* NEVILLE, 1884 based on the Caribbean *Schwartziella bryerea* (MONTAGU, 1803), but the protoconch differs. While that of *Schwartziella* is smooth, the larval shell of *Pseudoschwartziella* has an ornament of granules below the suture and a spiral rib above the suture. The apertural projection of its outer lip is very extended. While *Schwartziella* lives in the tropical Atlantic, *Pseudoschwartziella* has tropical Indo-Pacific distribution.

Pseudoschwartziella jordanica n. sp.

Holotype: pl. 11/9 in coll. of the Geol. -Pal. Inst. Mus., Hamburg.

Diagnosis: The protoconch with high spire has the embryonic shell with very fine hammered ornament and composed of one whorl with about 0.12 mm in diameter. Its end is indicated by growth lines and the change in growth line pattern from simple to sinuous. The ornament of the larval shell consists of fine rows of tubercles in the first whorls which change into a spiral rib on the last larval whorl. The final whorl of the larva expands to form a large wing-like projection with ornament of spiral lines and short little inclined lines arranged spirally. The base of the larval shell has spiral ornament, which is covered by the succeeding whorl (pl. 9/10–11). The larval shell is 0.5 mm high when fully grown.

The teleoconch is like that of *Rissoina* in shape with the special features of ribs and aperture as in *Schwartziella* as described by PONDER (1985). The radula was described by PONDER (1985, fig. 139G–H).

Description: The shell is as in the diagnosis. The protoconch is about 0.5 mm high and consists of more than 4 whorls. Characteristic ornament is the spiral row and rib just below the suture, and fine growth lines of the large posterior sinus. The area of the apertural projection is ornamented by fine tubercles and these may form small

inclined ridges (pl. 11/6, 7). The teleoconch consists of about four whorls which are a little shouldered and ornamented by strong rounded and inclined collabral ribs. About 10 to 12 are present on each whorl and they are crossed by fine spiral lines. The aperture of the body whorl is thickened and has a narrow posterior notch and a wide rounded anterior margin (pl. 11/9). Shell shape and size is very close to that of *Schwartziella*, but whorls are more angular.

Derivatio nominis: After occurrence in Jordan.

Locality: Aqaba Red Sea, shallow near-shore lagoon or Marine Station. Very similar species occur at other localities of the tropical Indo-Pacific but the one studied from near Satonda in the Indonesian Sea has half a whorl more of its larval shell, and therefore appears to represent a different species (pl. 11/8).

Family Siliquariidae ANTON, 1838 (= Tenagodidae MALATESTA, 1974)

Species of this family usually live within sponges and many of them have a slit shell. The two subfamilies Stephomatinae and Tenagodinae differ strongly in regard to the shape of their protoconch. This may indicate that their relation to each other is not so close. The protoconch found in the Tenagodinae resembles closely that of *Laxispira* in shape and ornament, which may point to a connection of modern *Tenagodus* to Cretaceous *Laxispira*. The protoconch of *Stephopoma* is very different and quite unusual among Caenogastropoda in general (BANDEL, 1993, pl. 7, fig. 4). Such protoconchs with large plane whorl ornamented by strong tubercles and not differentiated into embryonic and larval shell portion is present since Oligocene time (about 30 Million years) (BANDEL & KOWALKE, 1997, pl. 3, fig. 1).

Subfamily Stephomatinae BANDEL & KOWALKE, 1997

These vermetiform species have the protoconch with characteristic planispiral shape with ornament of strong tubercles or axial ribs. In *Caporbis* BARTSCH, 1915 the protoconch has axial ribs (BANDEL & KOWALKE, 1997, pl. 3, fig. 5) while that of *Stephopoma* MÖRCH, 1860 is covered by rounded tubercles (BANDEL, 1993, pl. 7, fig. 4). BIELER (1997) revised *Stephopoma* confirming the data presented by BANDEL & KOWALKE (1997). GIBSON SMITH & GIBSON SMITH (1982, fig. 1) documented the protoconch of *Stephopoma pennatum* MÖRCH, 1860 from the Early Miocene of Venezuela, which closely resembles that of *Stephopoma* from the Late Oligocene of SW France (BANDEL & KOWALKE 1997, pl. 3, fig. 1).

The protoconch of *Stephopoma* consists of 1.5 whorls which have a planispiral coil with only a very slight dextral twist. It measures more than 1 mm in diameter in the Oligocene protoconch as well as in a modern species from the tropical Pacific. The initial shell portion is wrinkled but not well differentiated from the later whorl that is covered by large tubercles. The apertural margin is formed by an upturned rim. The young hatching from the egg capsules either crawl away or may swim off as pediveligers ready to settle after a short stay in the plankton and probably without feeding on planktic organisms. Even though the species of this genus appear to be present in many places of the tropical Indo-Pacific they did not reach the Gulf of Aqaba.

Caporbis from the tropical East African Indian Ocean has a rather similar protoconch but with ornament of strong axial ribs (BANDEL & KOWALKE, 1997, pl. 3, fig. 5).

Subfamily Siliquariinae ANTON, 1838 (= Tenagodinae MALATESTA, 1974)

Tenagodus MONTFORT, 1810 (= GUETTARD, 1770, = *Siliquaria*) is a commensal animal living within the shelter of the body of a sponge (BIELER, 1992). Its teleoconch has a slit at its aperture and further from it a selenizone. Water enters through the shell aperture which lies on the sponge surface, is filtered by the gill and discharged through the slit. The eggs are brooded in the shelter of the shell tube (MORTON, 1951)

The protoconch of *Tenagodus obtusus* (SCHUMACHER, 1817) from the Mediterranean Sea consists of two whorls with 0.3 mm in height and 0.2 mm in width. The second, larval whorl is ornamented by four spiral ridges consisting of small pustules SCHIAPARELLI (2002, fig. 1). The teleoconch grows within a sponge and has a slit developed right after metamorphosis. The larval shell of *Tenagodus squamatus* (BLAINVILLE, 1827) from the Atlantic near Barzil has ornament of tubercles on the upper part of rounded whorls while the lower part is covered by spiral ribs, which extend into the median apertural projection of the outer lip (LEAL, 1990, pl. 6, figs. I, J). SCHIAPARELLI (2002) found almost the same ornament in *Tenagodus senegalensis* RECLUZ from the Atlantic Ocean at the Senegal.

The protoconch of *Petalopoma elisabetae* SCHIAPARELLI, 2002 from the Mediterranean Sea is simplified due to yolk rich development and consists of 1.25 whorls with 0.35 mm in height and 0.26 mm in width. It is

ornamented with 4–5 spiral ridges on the side and the base, and has a sinuous apertural margin (SCHIAPARELLI, 2002, fig. 4, C, F).

The larval shells of *Tenagodus* resembles those of *Laxispira* in shape and ornament, and they differ strongly from the planispiral ones of the Stephomatinae.

Family Provannidae WARÉN & PONDER, 1991

In the family the genera *Provanna* DALL, 1918, *Alviniconcha* OKUTANI & OHTA, 1988, *Desbruyeresia* WARÉN & BOUCHET, 1993 and *Ifremeria* WARÉN & PONDER, 1991 and have been united according to the shape and ornament of their protoconch, while the teleoconch has quite differently shape. WARÉN & BOUCHET (1993) documented a slender protoconch with cancellate sculpture in case of *Desbruyeresia* and *Alviniconcha* and in case of *Provanna* with reliefs of that ornament. The species of the Provannidae have adopted to the deep sea hydrothermal vent environment and grow chemotrophic symbiotic bacteria in their gills (OKUTANI & OHTA, 1988; WARÉN & PONDER, 1991; BECK, 1991; WARÉN & BOUCHET, 1993). A Cretaceous origin of the Provannidae was assumed by KIEL & BANDEL (2000).

The radula of *Desbruyeresia* from the deep sea as illustrated by WARÉN & BOUCHET (1993, figs. 55A–B; 56C) closely resembles that of *Planaxis (Angiola) lineata* (DA COSTA, 1778) from the pebble beach of the Caribbean Sea (BANDEL, 1984: pl. 2, fig. 5), (pl. 2/1). The radula of *Provanna buccinoides* WARÉN & BOUCHET, 1993 as illustrated by WARÉN & BOUCHET (1993, fig. 56A) closely resembles that of the potamidid *Cerithidea costata* (DA COSTA, 1778) that lives on mud flats in the intertidal zone (BANDEL, 1984, pl. 3, fig. 6). The radula of *Olgakoncha* BECK, 1991 (syn. of *Ifremeria* WARÉN & PONDER, 1991) resembles that of *Alviniconcha* (BECK, 1991, pl. 4, figs. 1–5) and of *Modulus modulus* (LINNÉ, 1758) (BANDEL, 1984, pl. 3, figs. 3–4) that lives on the lower beach of the Caribbean Sea.

Desbruyeresia is about 12 mm high with slender melanoid shape and anterior siphon notch at the aperture. The Cretaceous *Desbruyeresia antiqua* BANDEL & KIEL, 2000 from the Campanian of Torallola, northern Spain has a protoconch with 3 whorls and 0.5 mm in height and 0.3 mm in width. The embryonic whorl is smooth and about 0.3 mm wide. The larval shell is ornamented by collabral axial ribs with a fine pattern of spiral lines between them. The transition to the teleoconch is abrupt and its whorls are sculptured with few axial ribs with tubercles and some minor spiral ribs, one at the corner to the flattened base (BANDEL & KIEL, 2000, figs. 4, 5). The fossil species closely resembles *Desbruyeresia cancellata* WARÉN & BOUCHET, 1993 (WARÉN & BOUCHET, 1993, fig. 44 E).

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Plate 1

- Fig. 1: Larval shell of *Cerithium cf. nesioticum* PILSBRY & VANATTA, 1906 from the plankton of the Gulf of Aqaba. The shell is about 0.3 mm high.
- Fig. 2: The protoconch of *Cerithium atratum* (BORN, 1778) from the Caribbean Sea near Santa Marta, Columbia, consists of three whorls and has the characteristic ornamental pattern of the larval shell as found generally within the genus. The shell as illustrated is about 0.5 mm high.
- Fig. 3: Juvenile shell *Rhinoclavis* from Aqaba with protoconch of the type as in fig. 12. The documented shell is 4 mm high.
- Fig. 4: Larval shell of a common larva from the plankton of the Gulf of Aqaba, probably of *Clypeomorur*. The shell is about 0.3 mm high.
- Fig. 5: Larval shell of *Royella cf. sinon* (BAYLE, 1880) from the plankton of the Gulf of Aqaba. The shell is about 0.35 mm high and demonstrated the deep subsutural lobe of the outer lip.
- Fig. 6: Larval shell of a *Cerithium* from the plankton of the Gulf of Aqaba with the expanded outer lip of the fully grown larva (about 3.5 mm high).
- Fig. 7: Larval shell of the same species of *Cerithium* as in fig. 6 from the plankton of the Gulf of Aqaba with the two deep sinuses and the expanded median shield-like lobe on the aperture.
- Fig. 8: Juvenile shell of *Cerithium egeunum* GOULD, 1849 from the Gulf of Aqaba with protoconch resembling fig. 1. The shell is 3.5 mm high.
- Fig. 9: Juvenile shell of *Cerithium cf. nodulosum* BRUGUIÉRE, 1972 from Aqaba with protoconch of ornament as in fig. 1, but consisting only of two whorls. The shell is about 4.5 mm high.
- Fig. 10: Larval shell of *Royella cf. sinon* (BAYLE, 1880) from the plankton of the Gulf of Aqaba. (about 0.35 mm high). Characteristic are the two rows of tubercles resembling the ornament as in *Argyropeza*.
- Fig. 11: Juvenile shell of *Royella cf. sinon* (BAYLE, 1880) from the Gulf of Aqaba with 1.4 mm in height.
- Fig. 12: Larval shell of *Rhinoclavis* from the plankton of the Gulf of Aqaba, which has very similar ornament as found in *Planaxis lineolatus*, but is with 0.4 mm higher.
- Fig. 13: Juvenile shell of *Cerithium cf. nesioticum* from the Gulf of Aqaba. The shell is about 3.5 mm high.
- Fig. 14: Protoconch of *Planaxis lineatus* (DA COSTA, 1778) from Galerazamba near Cartagena, Caribbean Sea. It closely resembles that of *Planaxis lineolatus* from Aqaba seen on pl. 2/3. The protoconch is about 0.3 mm high.

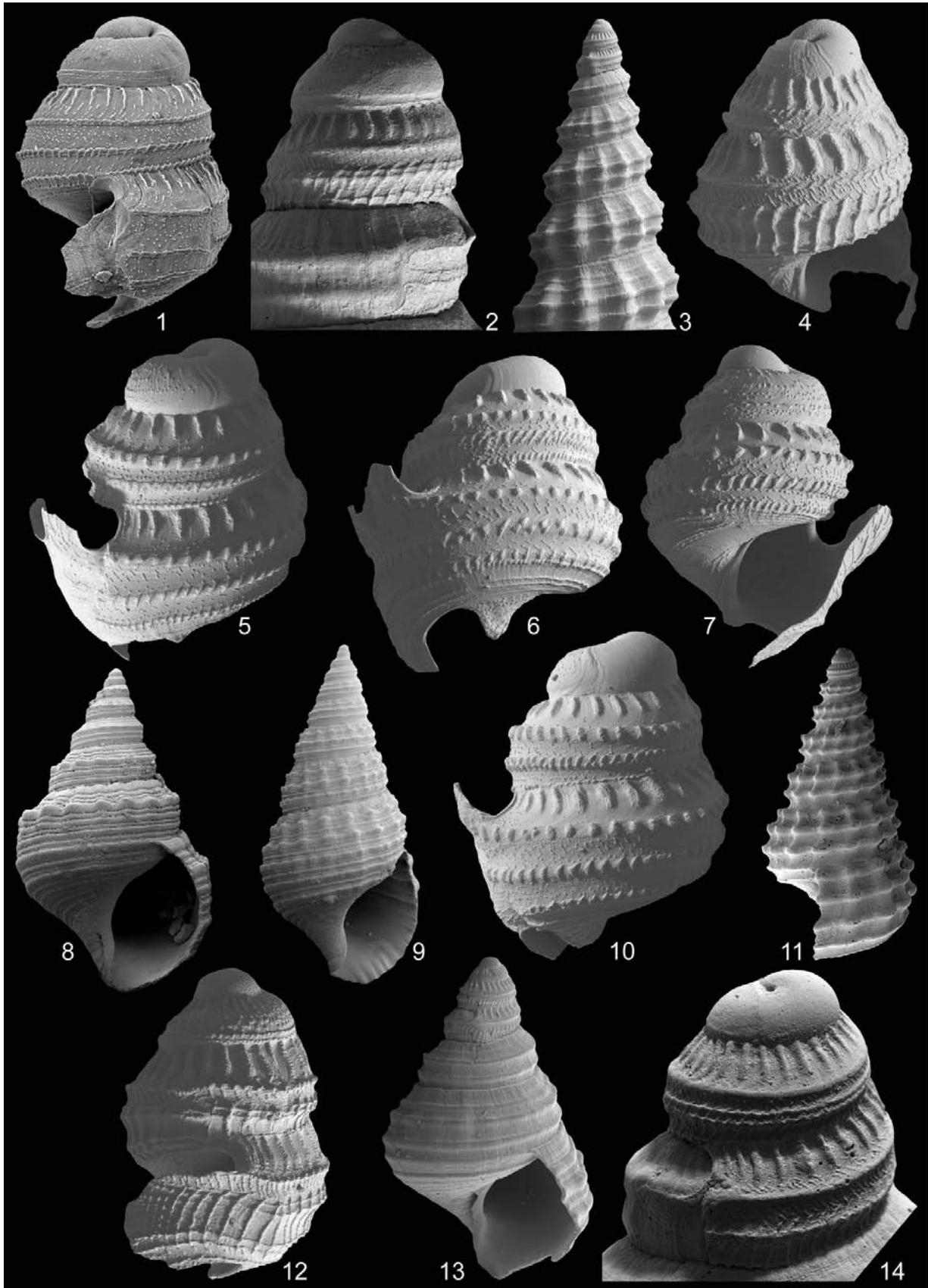


Plate 2

- Fig. 1: The protoconch of *Planaxis nucleus* (BRUGUIÈRE, 1789) from a subfossil reef at Galerazamba near Cartagena, Caribbean Sea at Colombia, differs in details from that of *Planaxis lineatus*. The visible protoconch is about 0.2 mm high.
- Fig. 2: The protoconch of *Fossarus ambiguus* (LINNÈ 1758) from the subfossil reef at Galerazamba near Cartagena Colombia, Caribbean Sea, is almost 0.3 mm high with axial ribs having a strong twist at the top of the apical median lobe of the larval shell.
- Fig. 3: Juvenile shell of *Planaxis lineolatus* GOULD, 1851 from the beach at Aqaba, Red Sea. The visible protoconch is about 0.22 mm high.
- Fig. 4: Larval shell of *Fossarus* from the plankton of the Gulf of Aqaba. The shell is about 0.28 mm high.
- Fig. 5: Larval shell of *Planaxis sulcatus* from the plankton of the Gulf of Aqaba. The rounded embryonic whorl has a groove and ridge pattern.
- Fig. 6: Larval shell of *Sansonia cebuana* BANDEL & KOWALKE, 1997 from the plankton of the Gulf of Aqaba. The shell is about 0.23 mm high, and resembles that of *Planaxis*.
- Fig. 7: Larval shell of *Planaxis sulcatus* (BORN, 1780) from the plankton of the Gulf of Aqaba. The protoconch is about 0.23 mm high with rapid change in ornament and growth-line pattern from the embryonic shell to the larval shell.
- Fig. 8: Larval shell of *Vanikoro semiplicata* (ISSEL, 1869) from the plankton of the Gulf of Aqaba. The about 3.5 mm high protoconch resembles that of *Cerithium* and *Planaxis* in size and ornament (see fig. 10), and also that of the Triassic *Coelostylina* (pl. 12/12).
- Fig. 9: Larval shell of *Planaxis sulcatus* from the plankton of the Gulf of Aqaba as in figs. 5 and 7 demonstrating the wide shield-like median lobe of the outer lip.
- Fig. 10: Larval shell of *Vanikoro semiplicata* as in fig. 8 presents the lobe in the outer lip, which is narrower than usually that of the Cerithiidae. The shell is more than 0.35 mm high and ornament of the embryonic shell is coarser than usually in Cerithiidae.
- Fig. 11: Larval shell of *Chrystella* LASERON, 1957 (Pickworthiidae) from the plankton of the Gulf of Aqaba. The larval shells of the members of this family resemble those of Cerithioidea very much. The shell is about 0.3 mm high.

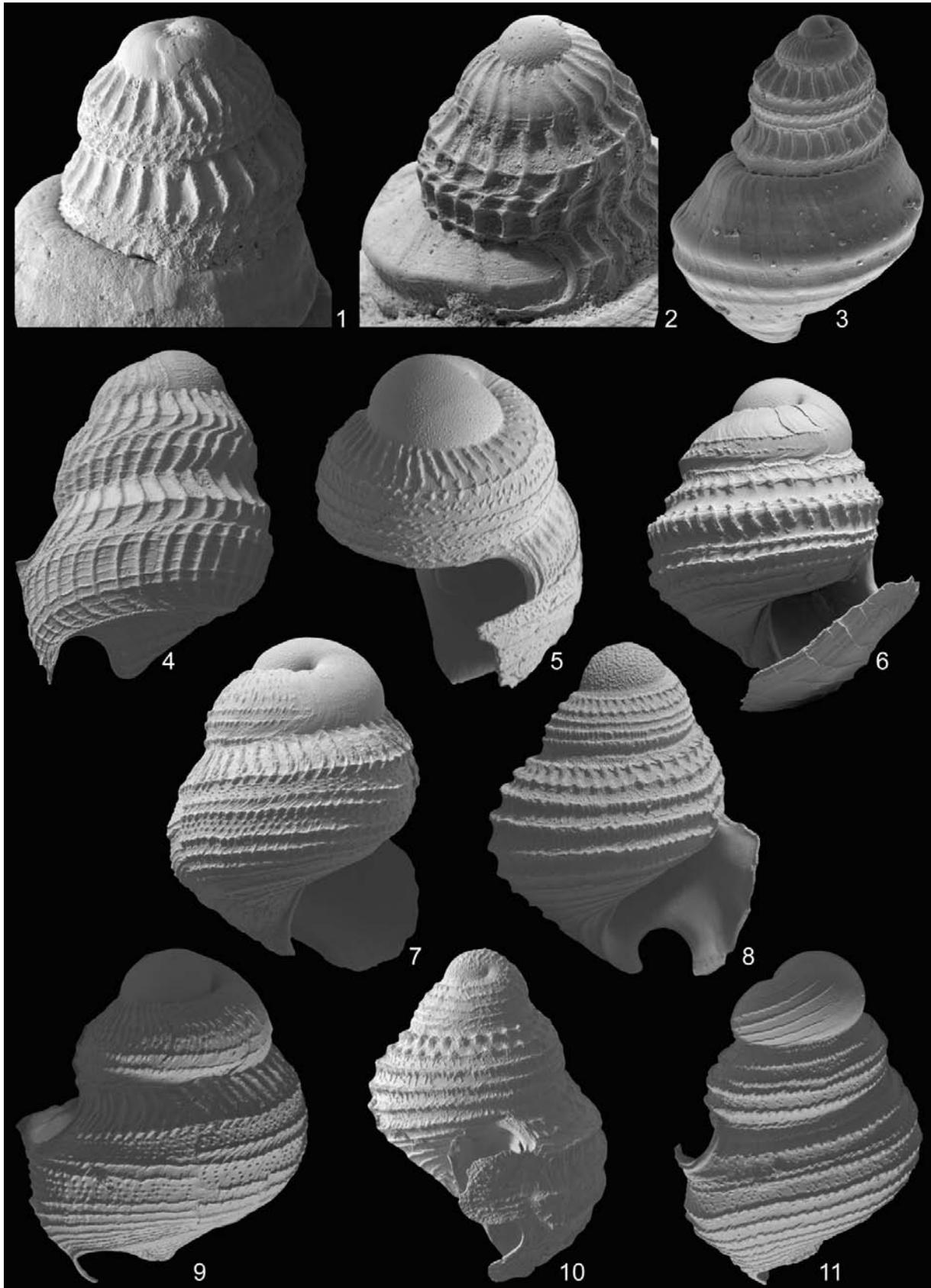


Plate 3

- Fig. 1: *Cryptaulax sakarahensis* n. sp. (holotype) with shell about 1.5 mm high, from Bajocian (Mid-Jurassic) deposits near Sakaraha, Madagascar.
- Fig. 2: A juvenile shell of *Cryptaulax sakarahensis* n. sp. that is almost 1 mm high and the transition from protoconch to teleoconch well developed, from the Mid-Jurassic of Sakaraha.
- Fig. 3: *Cryptaulax sakarahensis* n. sp. with almost 1 mm high protoconch that consists of 5 whorls and its transition into the teleoconch, from mid-Jurassic of Sakaraha.
- Fig. 4: Protoconch of *Cryptaulax sakarahensis* n. sp. with only about 0.5 mm high protoconch that consists of 4 whorls (Mid-Jurassic of Sakaraha).
- Fig. 5: About 5 mm high shell of *Cryptaulax sakarahensis* n. sp. from the Mid-Jurassic of Sakaraha with ornament of fine ribs.
- Fig. 6: About 2.2 mm long shell of *Cryptaulax sakarahensis* n. sp. from the Mid-Jurassic of Sakaraha with protoconch and straight axial ribs as ornament of the teleoconch.
- Fig. 7: The about 4 mm high shell of *Cryptaulax sakarahensis* n. sp. is ornamented by few axial ribs and almost no spiral lines, from the Mid-Jurassic of Sakaraha.
- Fig. 8: *Argyropeza* from near Satonda in Indonesia closely resembles *Cryptaulax*. The shell is about 1.8 mm high.
- Fig. 9: Protoconch of *Argyropeza* sp. from Satonda as in fig. 8 measures about 0.3 mm in height.
- Fig. 10: *Argyropeza* sp. from the Southern Chinese Sea with 2.5 mm long shell.
- Fig. 11: Protoconch of *Argyropeza* sp. from fig. 10 is about 0.3 mm high with well developed apertural lobe.
- Fig. 12: This *Argyropeza* from the Eocene of Jackson in Mississippi has some characters of *Varicopeza* in its ornament. The shell is about 2.5 mm high.
- Fig. 13: *Argyropeza* sp. as fig. 12 with the protoconch ornament as in modern *Argyropeza* from Aqaba but about one whorl less and about 0.3 mm in height.
- Fig. 14: Larval shell of *Argyropeza* from the plankton of the Gulf of Aqaba. The shell is about 0.4 mm high. The apertural lobe has the same shape as in case of *Argyropeza* from the Southern Chinese Sea (fig. 11).

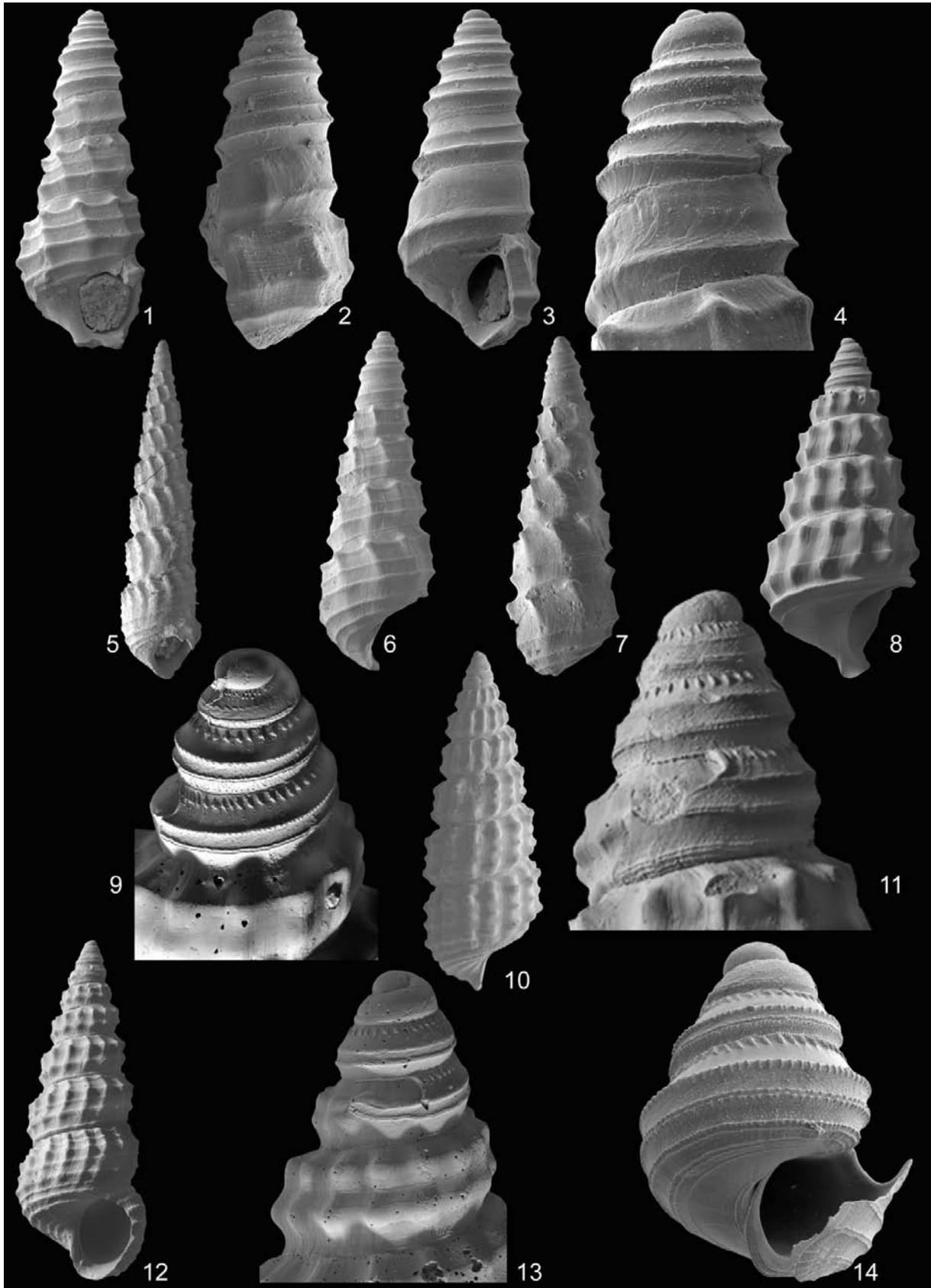


Plate 4

- Fig. 1: *Varicopeza* from the Island Satonda in the Indonesian Sea with about 3 mm high shell.
- Fig. 2: Protoconch of *Varicopeza* (fig. 1) from Satonda with about 0.25 mm in height and more complex ornament of the larval shell as in *Argyropeza*.
- Fig. 3: *Bittium* sp. from the Island Satonda, Indonesia with its shell about 2 mm high.
- Fig. 4: Protoconch of *Bittium* sp. in fig. 15 from Satonda with visible larval shell about 0.2 mm high and similar, but larger than that of *Bittium* from Aqaba and with stronger ornament of spiral lines.
- Fig. 5: *Bittium* cf. *impendens* from Aqaba with about 1.5 mm high shell.
- Fig. 6: Larval shell of *Diala* sp. from the plankton of the Gulf of Aqaba with a little less than 0.3 mm in height. The transition from embryonic to larval shell is documented by growth lines. The subsutural sinus of the larval shell has a thickened margin.
- Fig. 7: Larval shell of *Diala* sp. with less than 0.3 mm in height from the plankton of the Gulf of Aqaba. The smooth embryonic whorl is well differentiated from the ornamented larval whorl.
- Fig. 8: Larval shell of *Diala* sp from the plankton of the Gulf of Aqaba with shell almost 0.3 mm high. The apertural margin of the outer lip of the larval shell is expanded forming a shield-like process.
- Fig. 9: Larval shell of *Bittium* cf. *impendens* from the plankton of the Gulf of Aqaba seen from front with wide apertural extension of the outer lip accompanied by a wide subsutural sinus and a narrow umbilical sinus. The shell is about 0.3 mm high.
- Fig. 10: Larval shell of *Bittium* cf. *impendens* from the plankton of the Gulf of Aqaba with ornament of fine spiral lines on the base and widened aperture in the fully grown larva. The shell is almost 0.3 mm high.
- Fig. 11: *Alabina cerithioides* (DALL, 1889) from Santa Marta, Colombian Caribbean Sea. The shell is about 2.5 mm long.
- Fig. 12: Fully grown *Finella pupoides* from the Gulf of Aqaba with 2.6 mm high shell.
- Fig. 13: Protoconch of *Alabina cerithioides* as detail to fig. 11. The rounded whorls are almost smooth and the apertural lobe is angular and elongate. Protoconch height is about 0.4 mm.

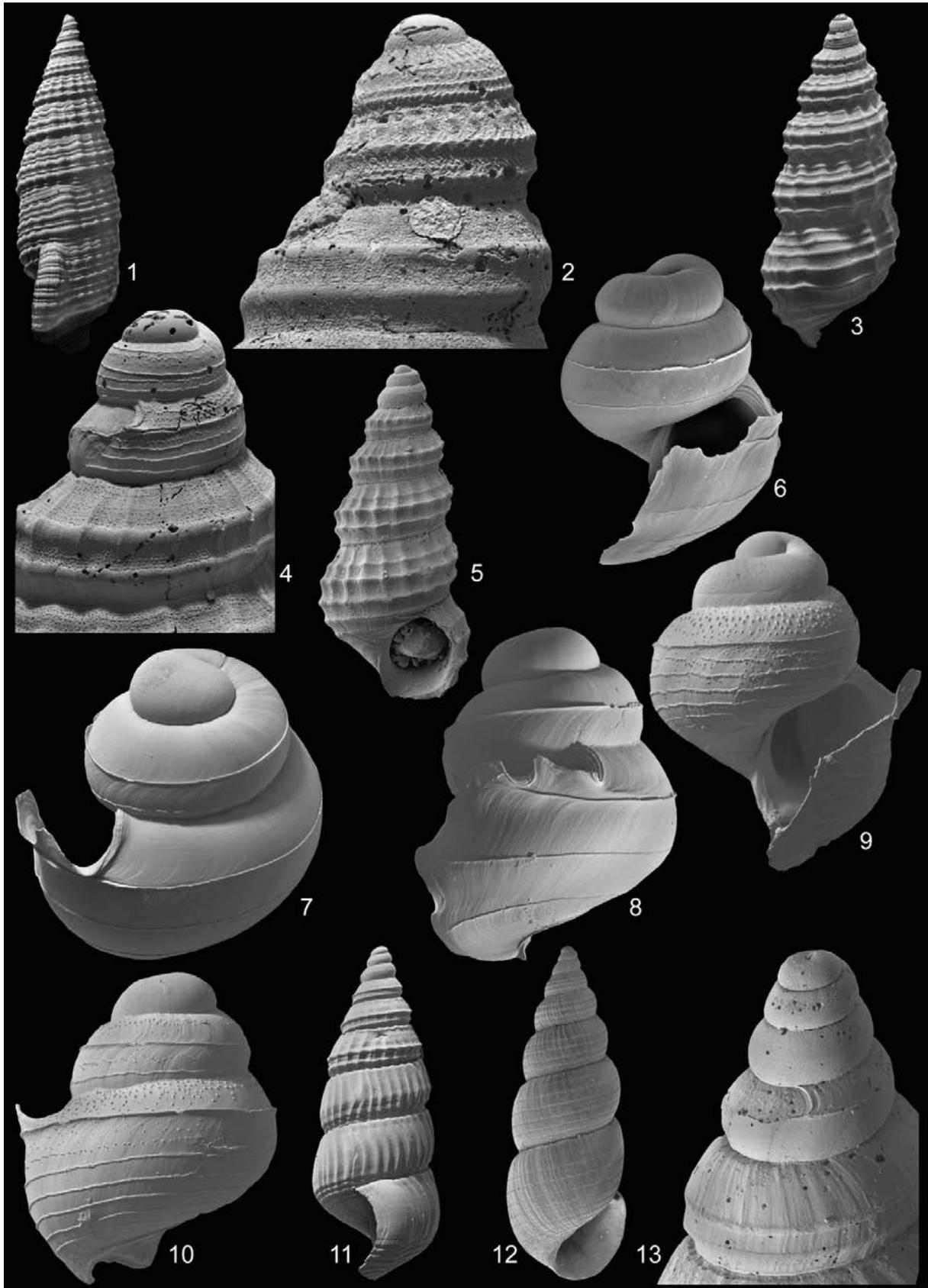


Plate 5

- Fig. 1: Not fully grown shell of *Diala* sp from the Gulf of Aqaba with about 0.8 mm in height.
- Fig. 2: Larval shell of *Finella pupoides* from the plankton of the Gulf of Aqaba with about 0.5 mm high shell. Ornament is distinct and the main spiral rib forms a corner and the upper margin of the apertural lobe.
- Fig. 3: The larval shell of *Finella* sp. from near Satonda, Indonesia, has 2.5 whorls which are rounded and smooth. Detail to fig. 4.
- Fig. 4: The shell of *Finella* sp. from Satonda is about 3 mm high and somewhat intermediate in shape between *Diala* and *Finella*.
- Fig. 5: Shell of *Finella* sp. from near Satonda in Indonesia with 3 mm high shell (detail in fig.6).
- Fig. 6: The protoconch of *Finella* sp. is about 0.4 mm high and resembles that of *Finella pupoides* in regard to spiral ribs and shell height, but not the corner on the last whorl of its larval shell.
- Fig. 7: The juvenile shell of *Bittium moesiense* JEKELIUS, 1944 from the Mid-Miocene of the Kertsch Peninsula (Ukraine) with detail in fig. 8 is about 1.5 mm high.
- Fig. 8: Protoconch of *Bittium moesiense* from Kertsch Peninsula (Crimea) with delicate ornament of fine inclined lines in the upper part and fine spiral lines in the lower part of its larval whorls, 0.3 mm high.
- Fig. 9: *Bittium varium* (PFEIFFER, 1840) from Galerazamba near Cartagena, Colombia, subfossil reef environment of the Caribbean Sea. The shell is about 2 mm high.
- Fig. 10: Protoconch of *Bittium varium* from Galerazamba near Cartagena, detail to fig. 2 with two fine spiral lines on its larval shell. The protoconch is about 0.3 mm high.
- Fig. 11: A species that could be close to *Diastoma* from the Mid-Eocene of Gant in Hungary with about 2.5 mm long shell (detail fig. 12).
- Fig. 12: The protoconch of *Diastoma* sp. from Gant consists of more than three almost smooth whorls and is more than 0.3 mm high (detail to fig. 11). The protoconch resembles that of *Potamides* of the same age, shown in pl. 8/2.
- Fig. 13: *Probittium madegascariensis* n. sp. from the Bajocian of Sakaraha with the 1.2 mm high holotype.

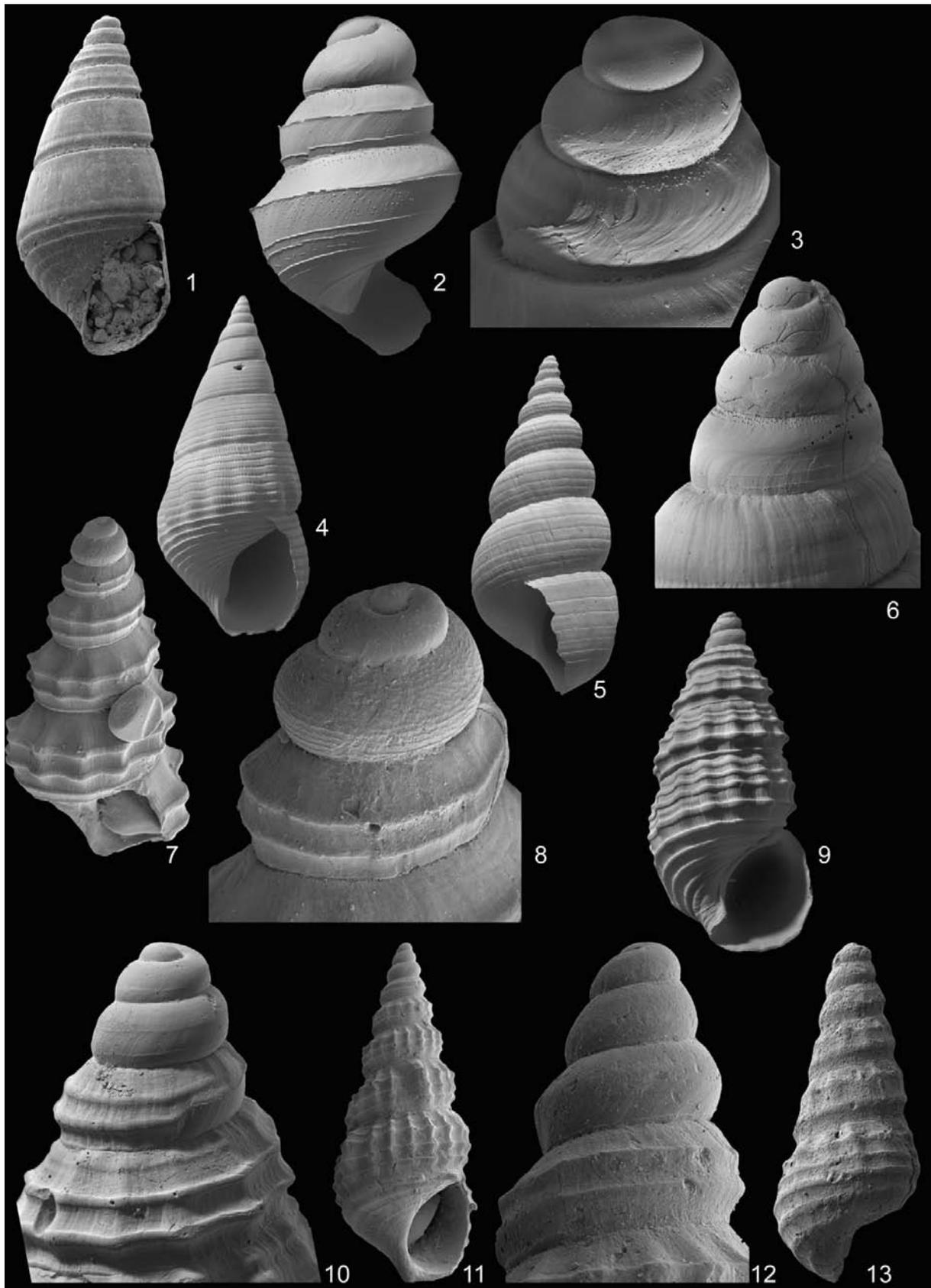


Plate 6

- Fig. 1: Apical view of the shell of *Cheilotomona acuta* (MÜNSTER, 1842) from the Late Triassic St. Cassian Formation. The first whorl represents the embryonic shell, is rounded and smooth, later with ornamented teleoconch. The illustrated shell is about 1 mm wide.
- Fig. 2: The juvenile shell of *Cheilotomona acuta* (MÜNSTER, 1842) from the St. Cassian Formation about 4 mm high and still without slit. It will appear in about the last whorl of this specimen.
- Fig. 3: The apical part of the shell of *Obtortio* from near Satonda, Indonesia, detail to fig. 6 with the characteristic collabral pattern of the larval shell (0.25 mm high protoconch).
- Fig. 4: The fully grown shell of *Obtortio* from Satonda, Indonesia, is about 2 mm high.
- Fig. 5: Ornament of the larval shell of *Obtortio* has very characteristic curving outline, reflecting the shape of the sinuous apertural margin, from Satonda, detail to fig. 6. The protoconch is about 0.25 mm wide and high.
- Fig. 6: *Scaliola bella* from the shallow water of Satonda Island in Indonesia with about 3 mm high shell and smooth protoconch and characteristic agglutination of sand grains to the teleoconch.
- Fig. 7: Larval shell of *Scaliola bella* A. ADAMS, 1860 from the plankton of the Gulf of Aqaba with about 0.3 mm in height. Ornament consists of very fine tubercles.
- Fig. 8: Larval shell of *Scaliola bella* from the plankton of the Gulf of Aqaba with the extended and somewhat twisted-off extension of its outer lip connected to a very deep subsutural sinus and a wide umbilical sinus (0.3 mm high).
- Fig. 9: Protoconch of *Scaliola* sp from Satonda, Indonesia is quite more elongate than that from *Scaliola bella* from Aqaba with almost five whorls and 0.5 mm in height and ornament by fine spiral lines on it larval shell.
- Fig. 10: The protoconch of *Terebralia subcorvina* (OPPENHEIM, 1894) from the Mid-Eocene of Gant in Hungary is about 0.25 mm high. It closely resembles that of *Pyrazus* in pl. 8/4 from the same locality.
- Fig. 11: *Alaba incerta* (ORBIGNY, 1842) from the Caribbean Sea of the fossil reef at Galerazamba near Cartagena (Columbia). The shell is about 2 mm high.
- Fig. 12: Detail of protoconch of *Alaba incerta* from the Caribbean Sea (fig. 11). The protoconch is about 0.4 mm high.
- Fig. 13: Larval shell of *Litiopa melanostoma* from the plankton of the Gulf of Aqaba with about 0.6 mm in height.

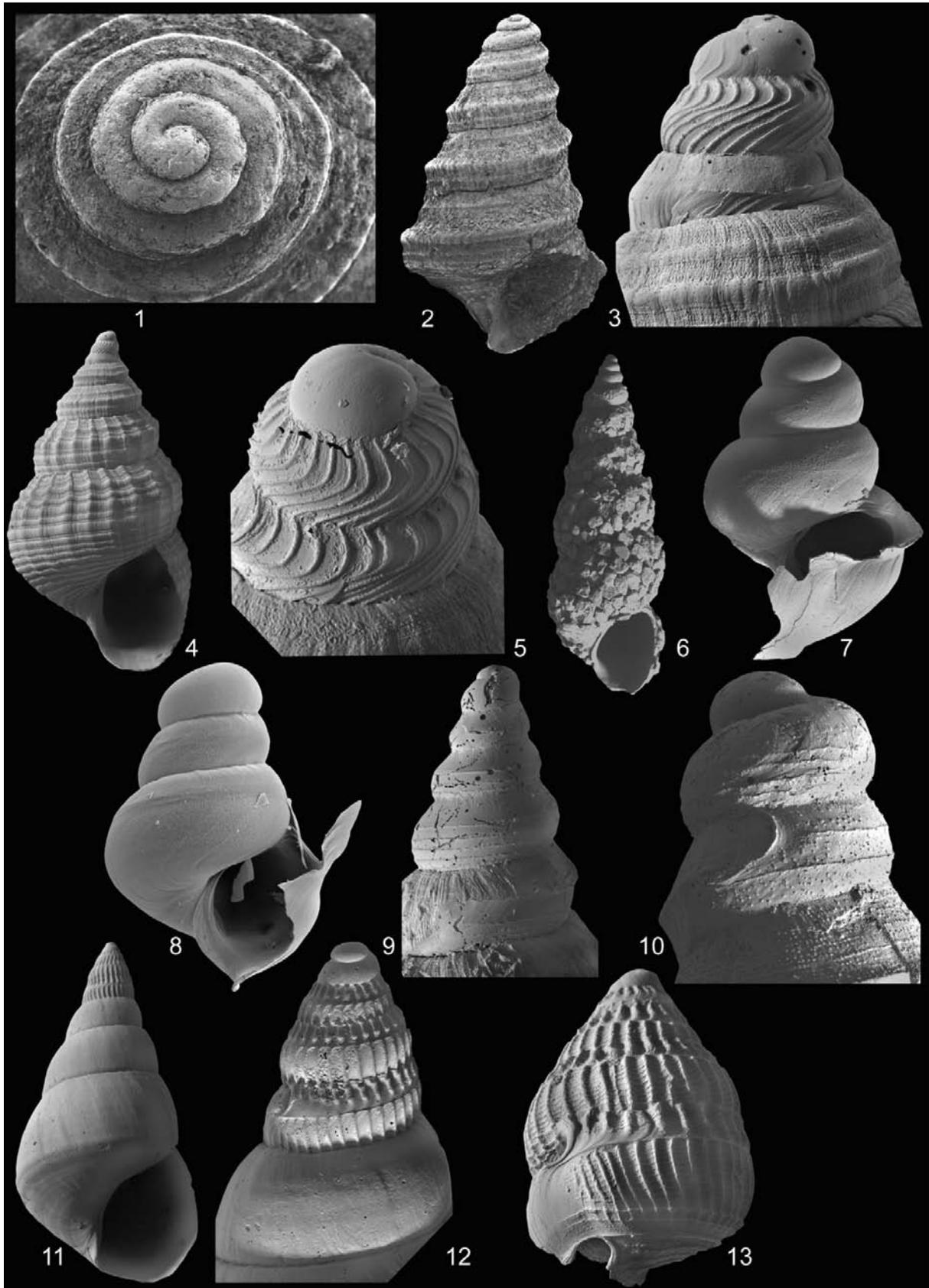


Plate 7

All from the St. Cassian Formation, Late Triassic Dolomites.

- Fig. 1: *Popenella nodosa* (ZARDINI, 1980) with juvenile shell about 2.5 mm high.
- Fig. 2: Protoconch of *Popenella nodosa* (ZARDINI, 1980) with ornament of strongly twisted axial ribs, reflecting the tongue-like apertural projection. The protoconch is about 0.3 mm high.
- Fig. 3: *Popenella nodosa* (ZARDINI, 1980) seen from the apex with about 0.7 mm wide shell.
- Fig. 4: *Popenella nodosa* (ZARDINI, 1980) seen with the ornamented protoconch as that is about 0.3 mm wide.
- Fig. 5: Protoconch of *Camposcala* has tubercle bearing spiral ridges as ornament of its larval shell and is about 0.35 mm high.
- Fig. 6: Protoconch of *Gusellella haueri* (LAUBE, 1868) with ornament of spiral ribs and tubercle rows and about 0.3 mm in height (see fig. 14).
- Fig. 7: Juvenile shell of *Camposcala biserta* (MÜNSTER, 1841) from locality Alpe di Species is about 2 mm high and has the protoconch as in fig. 5.
- Fig. 8: *Ampezzoscala* cf. *ornata* (MÜNSTER, 1841) with almost 3 mm high shell resembles *Cryptaulax* from the Jurassic.
- Fig. 9: The protoconch of *Ladinula campana* BANDEL, 1992 has its larval whorls ornamented by tubercle bearing spiral ribs and is about 0.3 mm wide.
- Fig. 10: Juvenile shell of *Ladinula campana* is about 0.8 mm high. Transition from protoconch to teleoconch is abrupt.
- Fig. 11: Juvenile shell of *Piazella subnuda* (KITTL, 1894) with about 1 mm in height.
- Fig. 12: *Piazella subnuda* (KITTL, 1894) with about 0.3 mm high protoconch with ornament of two tubercle bearing keels and a subsutural row of tubercles.
- Fig. 13: *Piazella subnuda* (KITTL, 1894) with about 0.3 mm wide protoconch.
- Fig. 14: Juvenile shell of *Gusellella haueri* (LAUBE, 1868) is 2 mm high, with protoconch in fig. 6. The protoconch has rounded whorls and is attached to the teleoconch with flattened whorls in inclined position.

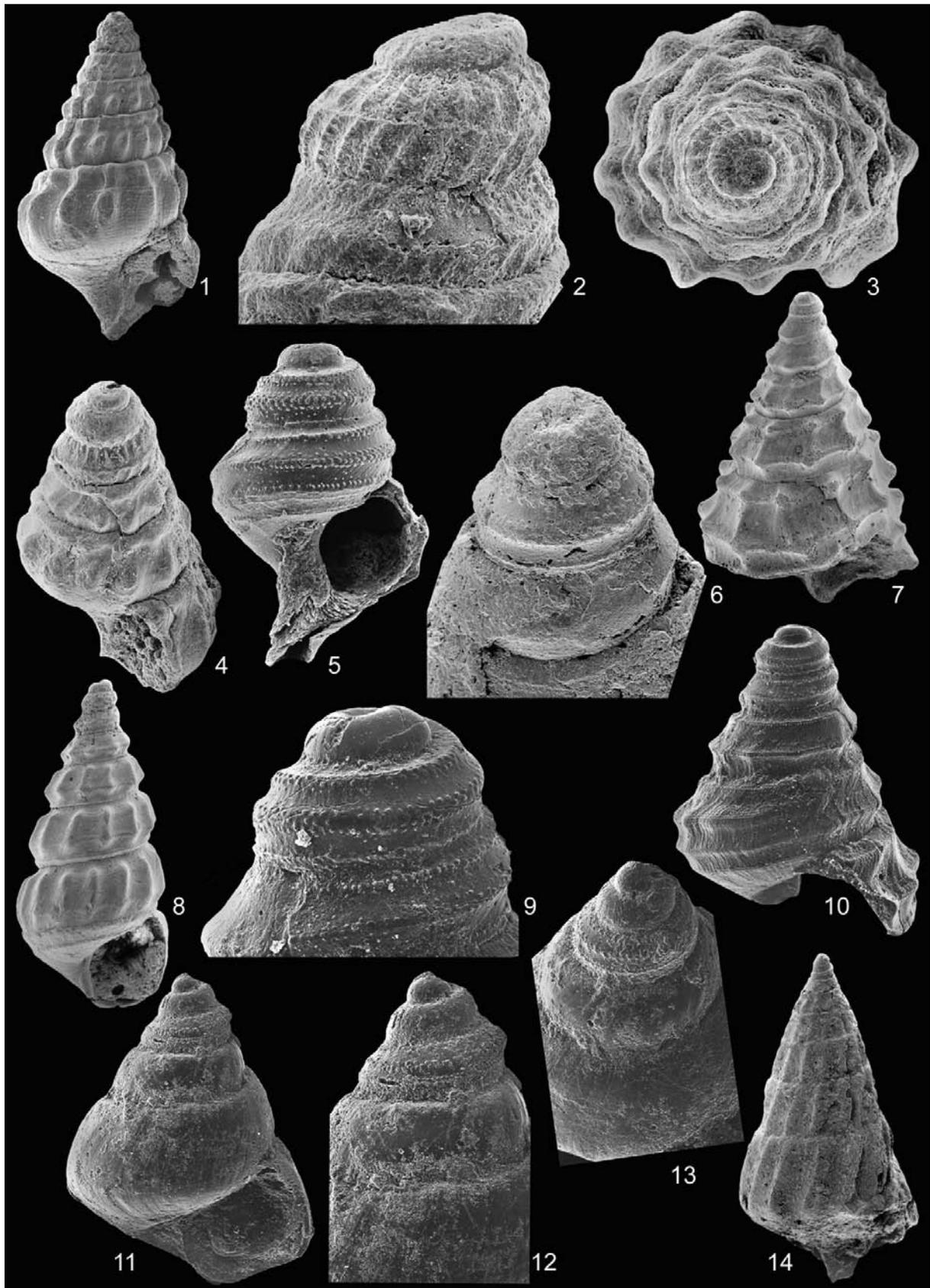


Plate 8

- Fig. 1: The juvenile shell of *Potamides* cf. *lamarcki* BRONGNIART, 1810 from the Mid Eocene of Damery, Paris Basin is about 4 mm high and has the protoconch in fig. 2.
- Fig. 2: Detail to fig. 1 of *Potamides* cf. *lamarcki* with 3.5 protoconch whorls which have smooth and rounded larval whorls. The protoconch is almost 0.4 mm high and provided with strong median lobe in the aperture and a thickened margin of the apical sinus.
- Fig. 3: *Pyrazus pentagonatus* (SCHLOTHEIM, 1820) (= *Gantmelania* KOWALKE, 2001) from the Mid-Eocene of Gant with juvenile shell of about 1 mm in height.
- Fig. 4: Protoconch of *Pyrazus pentagonatus* in fig. 3 from the Mid-Eocene of Gant is about 0.2 mm high and composed of two whorls. The larval whorl has few spiral lines and between them tubercles as ornament.
- Fig. 5: Juvenile shell of *Modulus modulus* (LINNE, 1758) from the fossil reef at Galerazamba near Cartagena of the Caribbean Sea. The protoconch is about 0.3 mm high.
- Fig. 6: Protoconch of *Modulus modulus* from Galerazamba near Cartagena (detail to fig. 1) with fine tubercles on the shoulder of the larval shell and spiral lines below which extend into the apertural projection.
- Fig. 7: *Modulostylina waageni* (KITTL, 1894) from St. Cassian, type to the genus, with larval shell about 0.4 mm in height, ornament of spiral ribs, and a lobed apertural margin and upturned apical sinus similar to that of *Modulus*.
- Fig. 8: *Zardinellopsis giauensis* (ZARDINI, 1980) from St. Cassian Formation with the larval shell characterized by a median ridge and net like ornament below it. The illustrated part of the shell is about 0.7 mm high.
- Fig. 9: *Zardinellopsis misurina* (BANDEL, 1992) from the St. Cassian Formation, locality Campo at Cortina d'Ampezzo with about 2 mm high shell and the characteristic shape of the aperture with a narrowed posterior end.
- Fig. 10: *Cortinellopsis aialensis* (ZARDINI, 1980) from St. Cassian Formation. The illustrated shell is about 0.6 mm high. The protoconch has a net-like ornament below the keel on the larval whorls.
- Fig. 11: Juvenile shell of *Cortinellopsis aialensis* (ZARDINI, 1980) from St. Cassian Formation with about 1 mm in height.
- Fig. 12: Larval shell of *Turritella* cf. *terebra* from the Plankton of the Gulf of Aqaba is 0.6 mm high. Ornament consists of spiral lines and different tubercle cover below and above them and there is an angular narrow apertural projection (apex in fig. 14).
- Fig. 13: Juvenile shell of *Turritella* cf. *terebra* from Aqaba with larval shell and strong change in whorl diameter in the transition to the teleoconch. About 1.3 mm high shell.
- Fig. 14: Detail to the larval shell of *Turritella* in fig. 12 from the Plankton of the Gulf of Aqaba with weak ornament of fine grains on the embryonic shell and a spiral lines and tubercles on the larval shell.

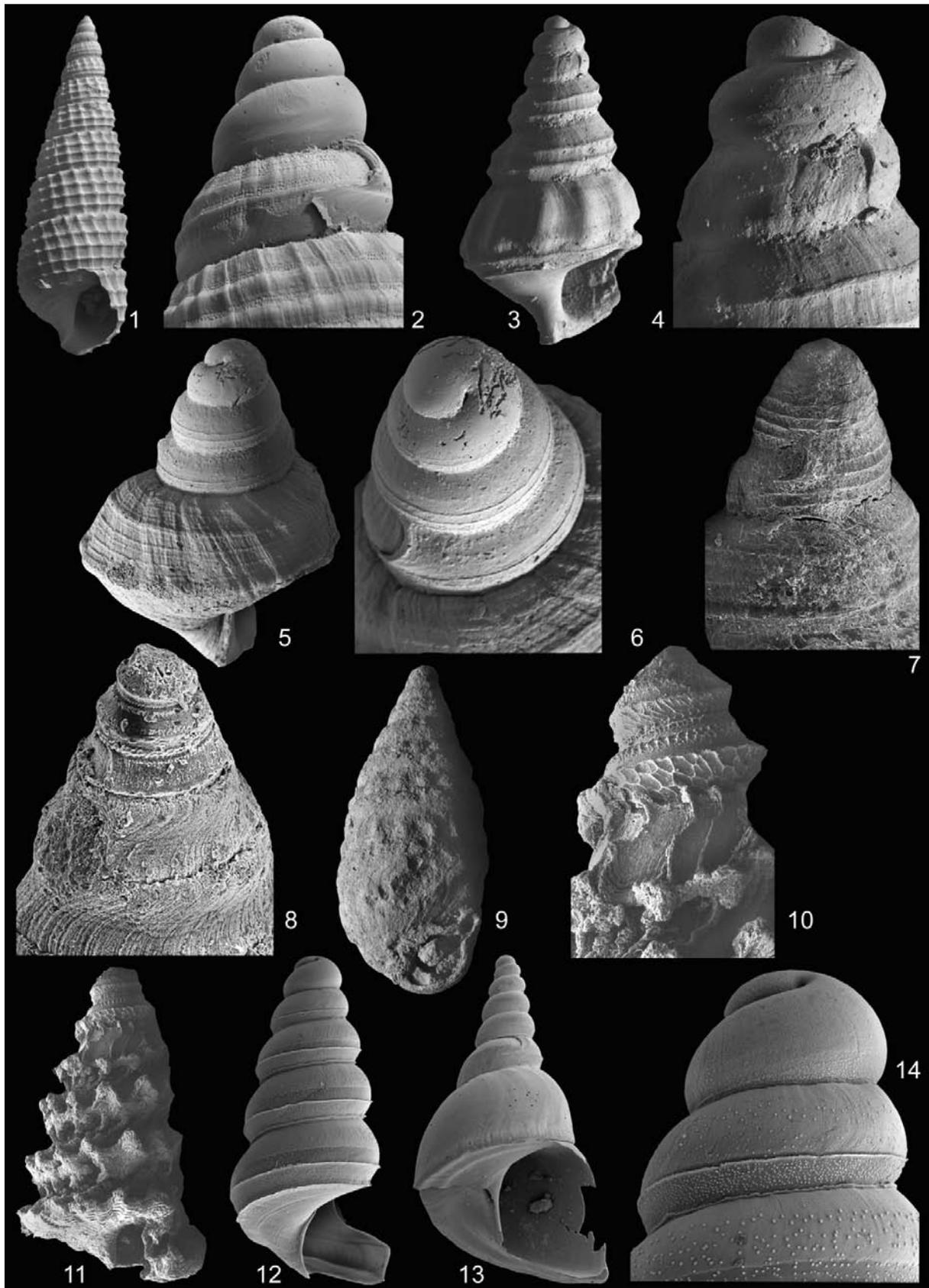


Plate 9

- Fig. 1: Juvenile shell of a second species of *Turritella* from Aqaba that has a similar larval shell to *Turritella* cf. *terebra* but a more slender teleoconch. The shell is 1.3 mm high.
- Fig. 2: *Turritella* from the Southern Chinese Sea with a protoconch with about 5 whorls and about 0.6 mm in height as that from Aqaba (pl. 8/12).
- Fig. 3: The juvenile shell of *Turritella* from Satonda of Indonesia has a protoconch closely resembling that of the Gulf of Aqaba (fig. 1). The shell is about 1 mm long.
- Fig. 4: The juveniles shell of a *Turritella* resembling modern species from the Pacific but from the Eocene of the SE of France at Gan. The shell is about 1 mm high and after five whorls of the protoconch only the last whorl belongs to the teleoconch.
- Fig. 5: The juvenile shell of *Turritella tokodensis* STRAUSS, 1966 from the Eocene of Dudar in Hungary is about 2 mm long. Its protoconch is in fig. 6.
- Fig. 6: The protoconch of *Turritella tokodensis* from Dudar consists of two whorls of which the larval has a fine spiral ornament and ends with a elongate lobe in the anterior part of its outer lip. Protoconch height about 0.35 mm.
- Fig. 7: *Turritella* sp. from the Paleocene of Matthews Landing, Alabama, with juvenile shell of about 2.5 mm in length
- Fig. 8: Protoconch of the *Turritella* sp. from Matthews Landing (fig. 7) is characteristic to the group of *Turritella* living in the Atlantic, with short stubby larval shell that consists of about 3 whorls. The protoconch is about 0.3 mm high.
- Fig. 9: The fully grown shell of *Styliferina guttulina* (SZÖTS, 1953) from the Eocene of Gant in Hungary is more slender than that of modern *Styliferina* from Aqaba and its protoconch is shorter (fig. 10). The shell is almost 2 mm long.
- Fig. 10: Protoconch of *Styliferina guttulina* from Gant has four smooth whorls and a very long extension and is a little more than 0.2 mm high.
- Fig. 11: The protoconch of *Styliferina* sp. from Satonda of the Indonesian Islands consists of almost six whorls which have strongly sinuous growth lines on the larval shell. The protoconch is about 0.6 mm high.
- Fig. 12: *Styliferina* sp. from Satonda with protoconch in fig. 11 is about 2 mm high and has an ornament of dense collabral lines crossed by indistinct spiral lines (in contrast to the smooth shell of *Styliferina* from Aqaba).
- Fig. 13: Fully grown shell of *Spirostyliferina lizardensis* n. sp. representing the holotype, from the sea grass lagoon at Lizard Island, Australian Great Barrier reef. The shell is about 0.9 mm high.
- Fig. 14: The protoconch of *Spirostyliferina lizardensis* n. sp. of the same individual as is fig. 13 has a wrinkled protoconch and a smooth larval shell with straight simple aperture. The protoconch is 0.4 mm wide.

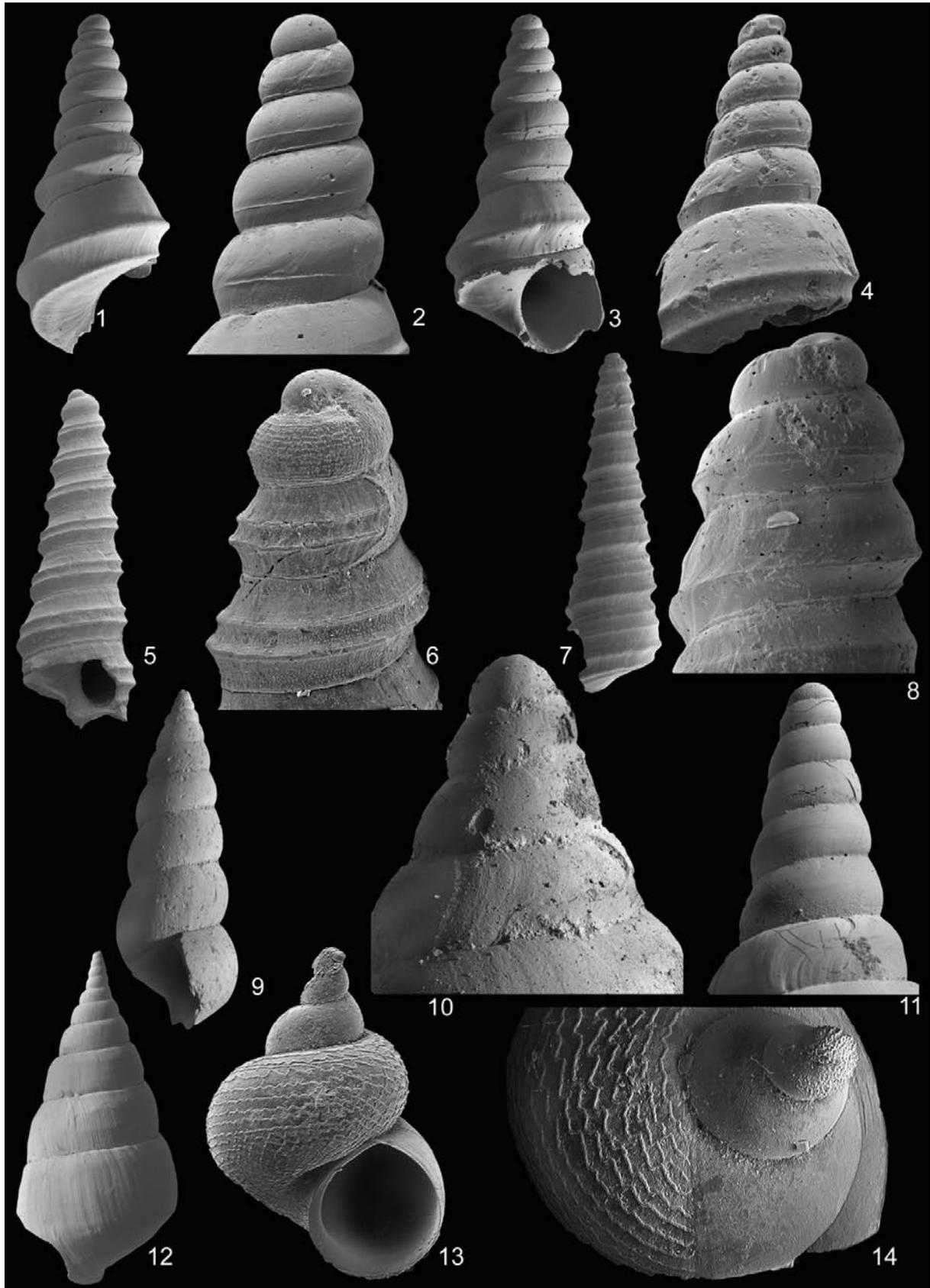


Plate 10

- Fig. 1: Not fully grown shell of *Styliferina goniochila* (A. ADAMS, 1860) from the lagoon in front of the Marine Station at Aqaba, Jordan. The shell is about 1.5 mm high.
- Fig. 2: Fully grown larval shell of *Styliferina goniochila* (A. ADAMS, 1860) from the plankton at Aqaba. The protoconch is 0.6 mm high.
- Fig. 3: Larval shell of *Plesiotrochus* from the plankton of the Gulf of Aqaba. Shell height about 0.3 mm. The larval shell has a fine pattern of tubercles and an expanded wing-like outer lip of the aperture.
- Fig. 4: Juvenile shell of *Sakarahina lugeri* n. sp. from the Mid-Jurassic of Sakaraha in SW Madagascar with the larval shell with ornament of rows of pits and with 0.7 mm high shell. The protoconch ends in a varix and a strong median lobe.
- Fig. 5: *Sakarahina lugeri* n. sp from the Mid-Jurassic of Sakaraha with the protoconch covered by fine tubercles on its larval whorls and visible shell are about 0.3 mm high.
- Fig. 6: Juvenile shell of *Sakarahina lugeri* n. sp. with ornament of rows of pits in the teleoconch, from the Mid-Jurassic Sakaraha, Madagascar, with 0.8 mm high shell (holotype).
- Fig. 7: Juvenile shell of *Amaurellina* FISCHER, 1885 from the mid Eocene of Damery in the Paris Basin with the protoconch of 0.3 mm in diameter, and larval shell with pattern of collabral lines on smooth background.
- Fig. 8: The apex of *Ampullaria* cf. *depressa* LAMARCK, 1804 from the Eocene of Saint Gobain in the Paris Basin with the protoconch about 0.3 mm wide and ending in a thickened outer rim of its larval shell.
- Fig. 9: *Amaurellina* with protoconch of about 2 whorls and 0.2 mm in diameter with ornament of sinuous collabral lines, from the Hungarian Gant (Mid-Eocene).
- Fig. 10: Protoconch of *Campanile* sp. from the Mid-Eocene of Gan in SW France with upturned sinuous margin of the apertural edge of the larval shell. The protoconch is about 0.3 mm high.
- Fig. 11: Juvenile shell of *Campanile* sp. from the Mid-Eocene of Gan in SW France that will change in ornament later on (protoconch figs. 10, 12).
- Fig. 12: *Campanile* sp. from the Mid-Eocene of Gan with characteristic protoconch and shell about 0.6 mm high.

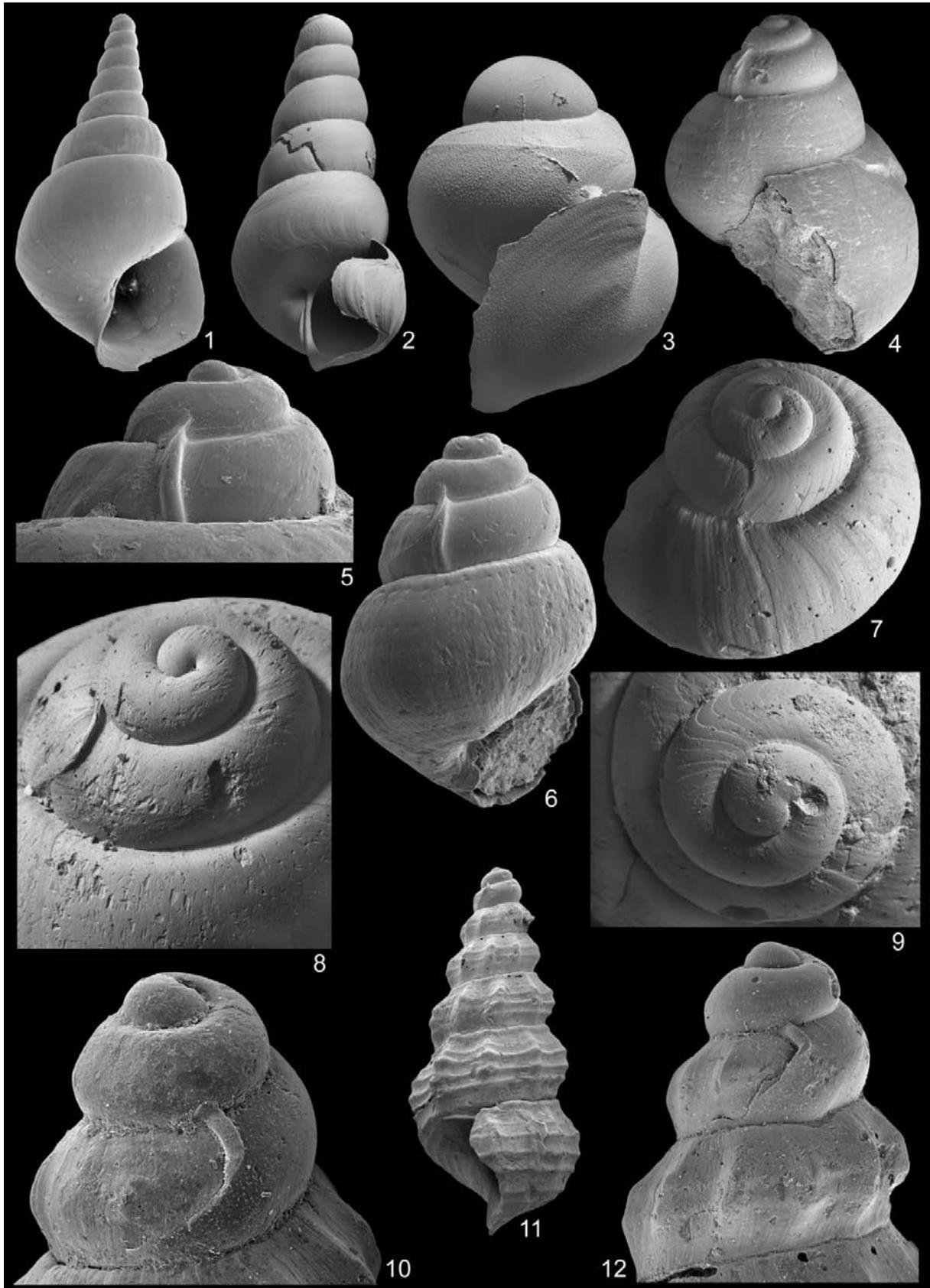


Plate 11

- Fig. 1: Protoconch of *Falorina tropediniformis* (ZARDINI, 1978) from the Late Triassic St. Cassian Formation with the larval shell ornamented by fine tubercles. The protoconch measures about 0.3 mm in width.
- Fig. 2: Juvenile shells of *Falorina tropediniformis* (ZARDINI, 1978) from St. Cassian is 0.6 mm high. The protoconch as in fig. 1 and the teleoconch has a fine pattern of spiral grooves and ridges.
- Fig. 3: The protoconch of *Sakarahella angulata* n. sp. from the Mid-Jurassic of Sakaraha, Madagascar, measures about 0.2 mm in its central part. The larval shell is ornamented by a subsutural tubercle ridge and inclined short ribs on the side.
- Fig. 4: Apical view of *Sakarahella angulata* n. sp. from the Mid-Jurassic of Sakaraha with the shell 0.6 mm in diameter and its larval part ornamented by fine tubercles.
- Fig. 5: Juvenile shell of *Sakarahella angulata* n. sp. from the Mid-Jurassic of Sakaraha with 1.3 mm high shell and the teleoconch ornamented by pit bearing fine spiral grooves.
- Fig. 6: Juvenile shell of *Pseudoschwartziella jordanica* n. sp. from the Gulf of Aqaba with protoconch consisting of 4 whorls.
- Fig. 7: Larval shell of *Pseudoschwartziella jordanica* from the plankton of the Gulf of Aqaba with 0.5 mm in height. Ornament of the larval shell is by a subsutural row of tubercles and line, fine punctae, basal spiral ribs.
- Fig. 8: *Pseudoschwartziella* sp. from Satonda, Indonesia, has 4.5 whorls of its protoconch.
- Fig. 9: Fully grown *Pseudoschwartziella jordanica* from the Gulf of Aqaba at the reef of the Marine Station, shell about 2 mm high (holotype).
- Fig. 10: Juvenile shell of *Cerithiovermetus vinxi* n. sp. from Satonda, Indonesia (holotype). The protoconch is almost 0.5 mm high.
- Fig. 11: The protoconch of *Cerithiovermetus vinxi* n. sp. from Satonda in fig. 10 is almost 0.5 mm high and has regular ornament of a subsutural row of tubercles, and short axial ribs on the bysial corner, similar as in *Sakarahella* (fig. 3).
- Fig. 12: *Cerithiovermetus vinxi* n. sp. just metamorphosed and attached side up. It is from the same location (near Satonda Island) as fig. 10 and 11.

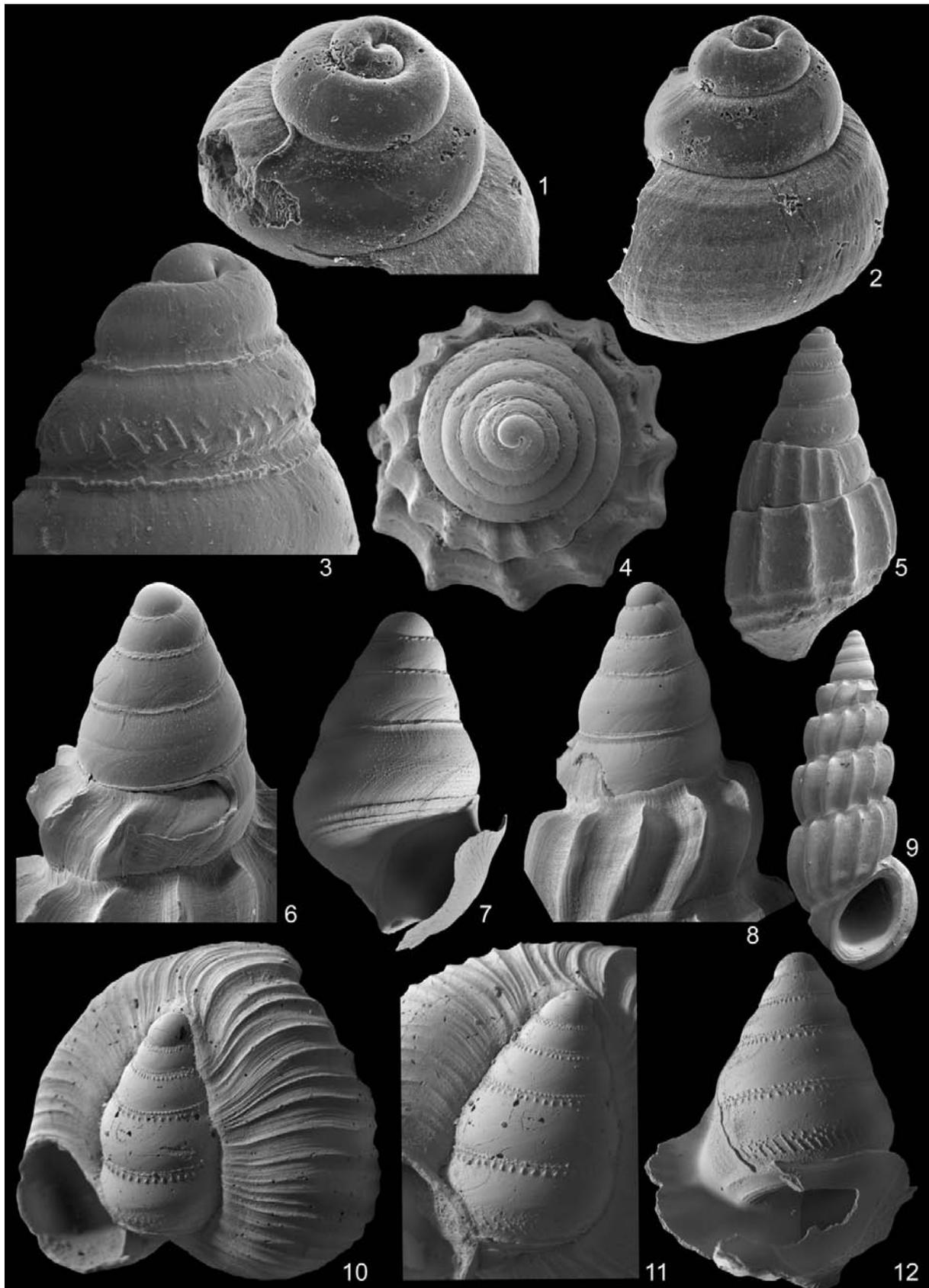
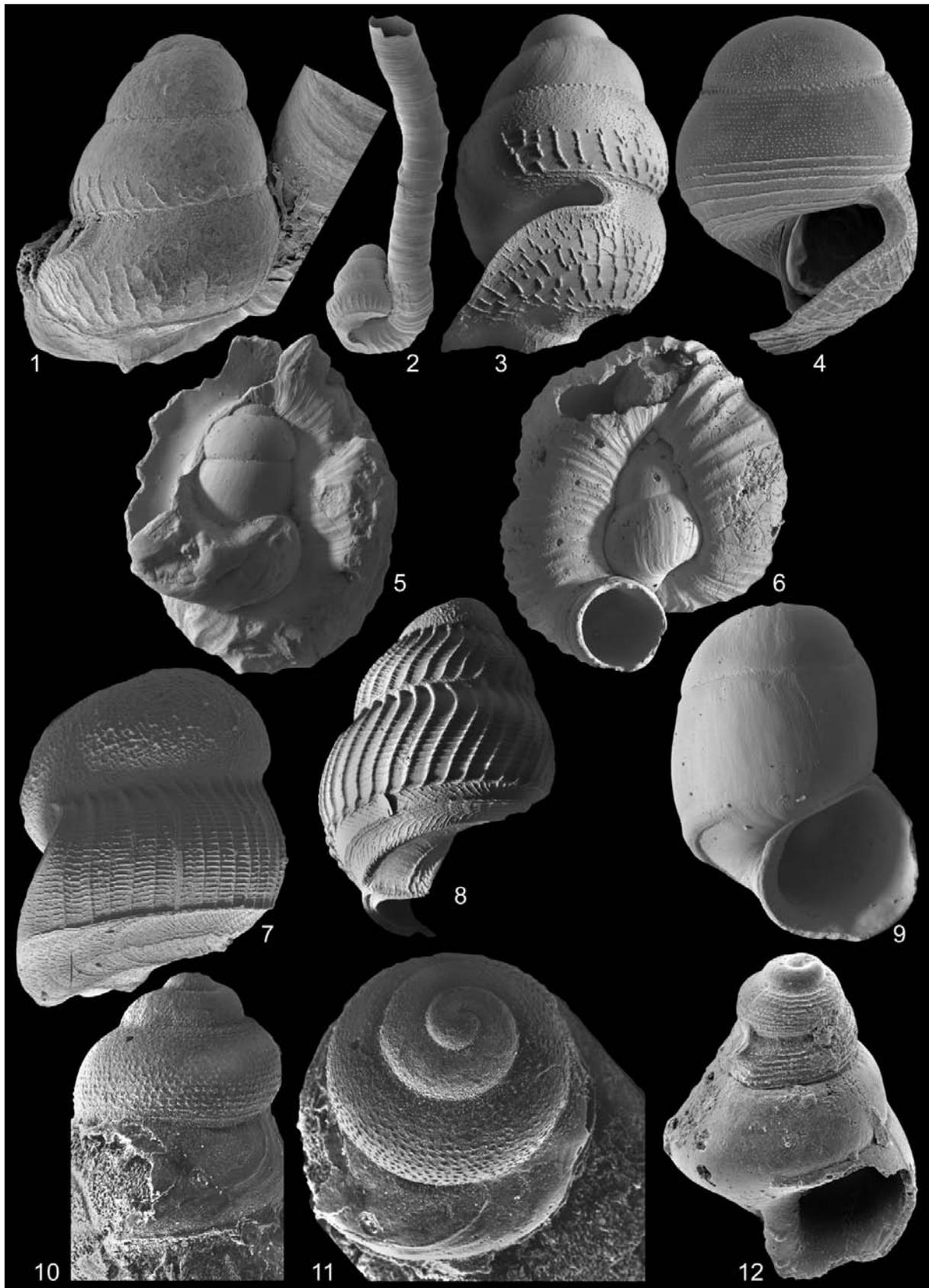


Plate 12

- Fig. 1: The protoconch of *Cerithiovermetus aqabensis* n. sp. from Aqaba is about 0.42 mm high.
- Fig. 2: Juvenile shell of *Cerithiovermetus aqabensis* of fig. 1 from Aqaba is about 1.5 mm long.
- Fig. 3: Larva of *Cerithiovermetus aqabensis* from the plankton of the Gulf of Aqaba is almost 0.45 mm high. Ornament is of a subsutural row of tubercles and short irregular axial ribs on the base connected to a spiral line on the edge.
- Fig. 4: Cf. *Vermetus* from the plankton of the Gulf of Aqaba with about 0.33 mm high shell. Ornament of the larval shell is by fine spiral rows of grains and spiral lines, and the margin of the outer lip is strongly thickened in the posterior sinus.
- Fig. 5: *Petalocochnus* cf. *erectus* with barrel-shaped protoconch surrounded by the juvenile teleoconch from the subfossil reef at Galerazamba near Cartagena, Caribbean Sea, with the shell maximally 1.2 mm in diameter.
- Fig. 6: The vermetid resembling *Petalocochnus mcgintyi* (OLSSON & HARBISON, 1953) from the Caribbean Sea near Santa Marta, Colombia, has the conical protoconch of about 0.5 mm surrounded by the attached teleoconch.
- Fig. 7: Fully grown larval shell of *Dendropoma maxima* from the plankton of the Gulf of Aqaba with 0.45 mm high shell. Embryonic whorl with groove and ridge pattern and larval shell with coarse axial and fine spiral lines.
- Fig. 8: Larva of an undetermined *Dendropoma* from the Gulf of Aqaba has a 0.5 mm high shell.
- Fig. 9: The barrel shaped larval shell of a vermetid from near Satonda Island, Indonesia, is almost 0.7 mm high and has a very large first whorl.
- Fig. 10: *Coelostylyna conica* (MÜNSTER, 1841) from St. Cassian Formation with wide pointed median lobe of the larval shell and ornament of rows of tubercles. The protoconch is almost 0.5 mm high and consists of more than 3 whorls.
- Fig. 11: The same protoconch of *Coelostylyna conica* as in fig. 10 seen with the apex from St Cassian Formation. The shell is 0.4 mm wide, and the embryonic whorl smooth and about 0.1 mm in diameter.
- Fig. 12: The juvenile shell of *Coelostylyna conica* from St. Cassian Formation with the protoconch 0.5 mm high, ornamented by regular rows of tubercles, and thickened margin of the subsutural sinus on the outer lip of the aperture.



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