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About the larval shell of some Stromboidea, connected to a review of the classification and phylogeny of the Strombimorpha (Caenogastropoda).

by Klaus Bandel, Hamburg
with 23 figures & 11 plates

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Extended abstract

Shell growth in Stromboidea is terminate as indicated by an expanded, often thickened, usually lobed or spine-bearing outer lip. Final shell size and shape is acquired before sexual maturity. During adult life the only addition to shell is by calcareous deposits mostly to the inside of the shell, in the area of the inner lip, sometimes also on top of the periostracum, and even as cover of much or all shell surface. Ontogeny mostly includes a planktotrophic veliger larva. The young hatches with the embryonic shell with a rounded aperture. The larval shell has a sinuous outer lip and its shape may change before metamorphosis. The protoconch is barrel shaped to conical, consisting of several whorls and growing to a size of around 1 mm and more. The transition to the teleoconch is often indistinct without marginal thickened aperture. After metamorphosis not only the shell shape

and ornament change but ornament of the early teleoconch may be imprinted onto the thin last part of the larval shell from below it. The function of the operculum may change from forming a protective closure of the aperture to an aid in defense and locomotion.

Strombidae exist since the Oligocene. Its many species have a similar ecology being herbivorous inhabitants of the tropical sea on well illuminated bottom. Based on differences in shell morphology and size 29 subgenera of *Strombus* can be distinguished, and they may also be interpreted as genera. This system is here extended to include formerly unrecognized taxa such as *Afristrombus* n. subgen., *Thersistrombus* n. subgen., *Decostrombus* n. subgen., *Hawaiistrombus* n. subgen., *Fusistrombus*, n. subgen., *Margistrombus* n. subgen., *Ministrombus* n. subgen., *Sinustrombus* n. subgen., and *Latissistrombus* n. subgen. with some of the known fossil species included.

Dilatilabridae n. fam. with *Dilatilabrum* resemble *Strombus* in shell shape with expanded outer lip but has no stromboid notch next to the siphon. They lived during the Paleogene and may represent the stem group to the Strombidae. Thersiteidae is redefined and interpreted as sister group to the Dilatilabridae, and it includes *Oostrombus* and *Orthaulax*. Both families appear to have evolved from the *Hippochrenes* relation. Hippochrenidae n. fam. existed from the Late Cretaceous to the Mid Tertiary. Here Hippochreninae with relatively smooth shell and evenly curving and flaring outer lip can be distinguished from the Wateletinae n. subfam. with ornamented spire and sinuous outer lip, both with posterior slit below the outer lip. Within the family *Terebellopsis* comes close to the spindle shaped cylindrical shell as in *Terebellum* of the Seraphsidae. The flat and relatively large protoconch of *Paraseraphs* from the Eocene resembles that of living *Terebellum.*

Rostellariidae have among living species the relation of *Tibia* with their larval shell fusing quite indistinctly with the teleoconch. *Varicospira* and its similar fossil relatives *Rimella* and *Ectinochilus* have similar smooth and conical protoconchs. These Rimellinae appear during the Late Cretaceous contemporaneously with the Calyptraphorinae n. subfam. with *Calyptraphorus* from the Paleogene and the Cretaceous *Eocalyptraphorus* n. gen. They covered much or most of their shell with callus originating from the expanded mantle on the inner lip and mantle tissue extending from the apical end of the outer lip. The dorsal callus in Calyptraphoridae connects them with the Rimellinae, and distinguishes from the Pugnellidae.

Late Cretaceous Pugnellidae have their adult shell coated by callus that alters shape and ornament of the juvenile. The protoconch of *Pugnellus* and *Gymnarus* is broader and larger as is the usual case among Stromboidea and resembles that of *Pterocerella*. Two groups the Pugnellinae and the Tundorinae n. subfam. evolved parallel to each other, both ranging from the Cenomanian to the Maastrichtian. They differ by the shape of the outer lip and by the mode in which the adult shell is coated by callus.

Some of the Jurassic and Early Cretaceous Alariidae resemble the Aporrhaidae which appear during Mid Cretaceous time, but in contrast to the first the later often have varices on their spire. Genera of the Alariidae differ from each other, by the shape of their expanded outer lip. *Cuphotifer* has here one spine, two spines are present in case of *Dicroloma*, three spines with connecting shell between them represent *Cuphosolenus*. Sheets between the spines of the outer lip form a shield with four ribs represent *Quadrinervus.* In case of *Phyllocheilus* the outer lip is attached to the spire and has several ribs ending in spines on its margin, and in *Harpagodes* the outer lip has many spines and connect closely to a short spire. Similar species to *Harpagodes* with reduced spines and large rounded body whorl may connect with the problematic Cretaceous Tylostomatidae based on *Tylostoma*. The spines of the outer lip are reduced to lobes or short spikes in *Diarthema* and *Monocuphus*, and a varix about half a whorl before the final aperture may broad the body whorl. Jurassic Spinigeridae differ from the Alariidae by having spine bearing varices.

Cretaceous Pterocerellidae n. fam. are distinguished from contemporaneous Aporrhaidae by a large and rounded protoconch and a teleoconch without varices. The protoconch of the Xenophoridae is also wider than high and has remained basically unchanged since the Late Cretaceous. The Maastrichtian *Misritropis* n. gen. and its type *Misritropis bartheli* n.sp. from Egypt may connect with Xenophoridae and with Haloceratidae, the later of which have no known fossil representatives. Their protoconch resembles that of *Xenophora* and has species specific shape and ornament. A new species, based on protoconch morphology from the Gulf of Aqaba, is described as *Zygoceras aqabaensis* n. sp.

Aporrhais lives in deeper and colder water than *Strombus.* The change from the smooth larval shell to the teleoconch is indistinct due to ornamented shell being added to the flexible larval shell from below it, and after metamorphosis to bottom live. The morphology of the living species of Aporrhaidae overlaps and definition of distinct species is difficult. The shell as in *Arrhoges* with one lobe and a long or short spine next to the spire on the outer lip is common among species from the Cretaceous with many varieties placed into different genera, while the *Aporrhais*-like shell with several spines appears in the Tertiary. It was present with distinct species also in the Southern Hemisphere and in this region during the early Tertiary the Struthiolariidae evolved from them having a simple aperture with thickened margin. The Aporrhaidae of the Cretaceous have a protoconch morphology that in case of *Anchura*, *Latiala*, and *Perissoptera* is very similar to that of the Rostellariidae as well as some Strombidae.

The teeth of the radula throughout the genus *Strombus* are similar to each other, and they resemble those of *Xenophora* and *Aporrhais*. The resemblance also extends to Cerithimorpha on one side and some Neomesogastropoda on the other, indicating the possible origin of the Stromboidea in Triassic Cerithimorpha and that of the Neomesogastropoda near them as sister group or even from them during the Early Cretaceous.
Pereiraea has a no terminate morphology that marks the adult stage as in the Strombidae and thus represent the Pereiraeidae n. fam.. Colombellinidae have a resemblance to some Alariidae and may connect to Latrogastropoda that appear at Mid-Cretaceous time. The stem group of the later could also represent a sister group of the Stromboidea as well as the Heteropoda. The Latrogastropoda branch may have evolved during the late Triassic or early Jurassic. Living larvae of Atlantidae resemble those of Strombidae and the shells of several species of *Atlanta* are documented for comparison.

Erweiterte Zusammenfassung

Bei den Stromboidea endet das Schalenwachstum mit oder kurz vor dem Erreichen der Geschlechtsreife. Dabei erweitert sich der Mündungsrand, wird verdickt, und die Schale vergrößert sich nicht weiter. Oft sind Stachel, Loben und Einbuchtungen entwickelt. Während des weiteren Lebens, welches noch mehrere Jahre fortdauern kann, verdicken Kalkablagerungen meist nur noch die Innenseite der Schale und verstärken sie. Manchmal treten auch glatte Kalkschichten im weiteren Bereich der Innenlippe auf und artspezifisch werden Teile des äußeren Periostracums, bestimmte Teile der Schalenoberfläche oder auch die ganze Schalenaußenseite von aragonitischen Ablagerungen überdeckt. In der Ontogenese der meisten Arten tritt eine Plankton-fressende Larve auf. Sie verläßt ihr Gelege mit einer Embryonalschale versehen, die eine einfach gerundete Außenlippe aufweist und aus etwa einer Schalenwindung besteht. Die im Meere schwimmende Veliger-Larve hat meist eine geschwungene Außenlippe, deren Mittelsattel aber vor der Metamorphose zum Bodenleben wieder verschwinden kann. Der Protoconch ist etwa 1 mm hoch oder höher, besteht aus mehreren gerundeten Windungen und hat rundlich- oder spitz-konische Gestalt. Der Übergang in den Teleoconch ist meist undeutlich, da der Mündungsrand der ausgewachsenen Larvenschale nicht verdickt ist. Nach der Metamorphose verändert sich sowohl das Ornament der Schale als auch ihre Gestalt, wobei Rippen der juvenilen Schale sich von innen her der letzten Windung der Larve aufprägen. Ihre Skulptur wird so auf die vormals glatte Oberfläche durchgepaust. Das Operculum schließt die Mündung der Larvenschale, kann seine Funktion und Form nach dem Übergang zum Bodenleben verändern und zur Abwehr von Feinden wie bei der Fortbewegung benutzt werden.
Die Strombidae gibt es erst seit dem Oligozän. Ihre vielen Arten leben herbivor im tropischen Meer im Bereich der vom Sonnenlicht belichteten Böden. Basierend auf Unterschieden in der Gestalt der Schale kann man *Strombus* in 29 Untergattungen untergliedern, die auch als Gattungen angesehen werden können. Das bestehende System ist hier dergestalt erweitert, daß neben den bisher beschriebenen Taxa zudem die neu definierten Taxa *Afristrombus* n. subgen., *Thersistrombus* n. subgen., *Decostrombus* n. subgen., *Hawaiistrombus* n. subgen., *Fusistrombus*, n. subgen., *Margistrombus* n. subgen., *Ministrombus* n. subgen., *Sinustrombus* n. subgen. und *Latissistrombus* n. subgen. hinzugefügt werden. Einige bekannte fossile Arten werden diesen Taxa zugeordnet.
Die Dilatilabridae n. fam. mit *Dilatilabrum* ähneln den Strombiden in der Gestalt ihrer Schale, insbesondere bezüglich der erweiterten und verdickten Endlippe. Sie haben aber keine Bucht an der vorderen Außenmündung ihrer Schale neben dem Sipho, wie sie für *Strombus* typisch ist. Dilatilabridae n. fam. lebten im Alttertiär and können die Stammgruppe der Strombidae darstellen. Die verwandten Thersiteidae werden hier neu gefaßt, in dem ihnen *Oostrombus* und *Orthaulax* mit zugeordnet werden. Beide Familien haben sich wahrscheinlich aus der Verwandtschaft von *Hippochrenes* entwickelt. Die Hippochrenidae n. fam. lebten von der späten Kreide bis zum mittleren Tertiär. Ihre Vertreter werden in zwei Unterfamilien aufgegliedert, von welchen die Hippochreninae n. fam. eine im Wesentlichen glatte Schale mit nach außen gebogener einfach kurviger Außenlippe haben, deren Rand bis an den Apex reicht. Die Watelininae n. subfam. haben hingegen sowohl ein ornamentiertes Gewinde, als auch eine komplexere Gestalt ihrer Außenlippe. Beiden gemeinsam ist ein schlitzartiger Kanal, der unter der hinteren Außenlippe gelegen ist und von einer verdickten Wulst der Innenlippe begleitet wird. Innerhalb der Hippochrenidae besitzt *Terebellopsis* eine ähnlich zylindrische Schalengestalt wie die noch lebende *Terebellum* und die Seraphsidae im Allgemeinen. Der flache und verhältnismäßig große Protoconch von *Paraseraphs* aus dem Eozän ähnelt der frühontogenetischen Schale von *Terebellum*.
Bei lebendend Arten von *Tibia* unter den Rostellariidae treten Larvenschalen auf, die ganz allmählich und undeutlich in den frühen Teleoconch übergehen. Die noch heute lebende *Varicospira* besitzt sehr ähnliche fossile Vertreter unter den Gattungen *Rimella* und *Ectinochilus*, beide auch mit ähnlich glattem, konischem Protoconch. Diese Rimellinae treten zuerst in der späten Kreide zusammen mit den Calyptraphorinae n, subfam. auf, die allerdings bereits nach dem Eozän wieder verschwinden. Ihre frühesten Arten gehören zu *Eocalyptraphorus* n. gen der späten Kreide. Calyptraphorinae n. subfam. sind an ihrem auf der ausgewachsenen Schale gebildeten Kallus erkennbar. Seine Bildung geht von der Innenlippe und vom hinteren Fortsatz der Außenlippe aus. Beide Ablagerungen können die Schale weitgehend bedecken und in ihrer Gestalt verändern,

Die dabei gebildete, nach hinten verlaufende Kallusrinne, ist auch bei den Rimellinae anzutreffen. Die Bildung der sekundären Außenschicht erfolgte bei den Rostellariidae von zwei getrennten Bereichen aus, bei den Pugnellidae hingegen nur von der Innenlippe her.
Pugnellidae lebten in der jüngeren Kreide und bedeckten nach Abschluß des Größenwachstums ihrer Schale von außen mit glattem Kallus. Dabei wurde die Schalengestalt teils stark verändert wobei Merkmale des Mündungsrandes gerundet wie auch die Skulptur der Schale geglättet und überdeckt wurden. Der Protoconch ist bei *Pugnellus* und *Gymnarus* breiter und größer als üblicherweise bei Vertretern der Stromboidea der Fall ist. Die Form der Larvenschale ähnelt jener der Pterocerellidae n. fam.. Es lassen sich zwei Unterfamilien der Pugnellidae voneinander unterscheiden, die sich nebeneinander seit dem Cenoman entwickelten und mit Ende der Kreide ausstarben. Unter ihnen die Außenlippe der Tundorinae n. subfam. dornig, und die Bedeckung mit Kallus erfolge auf eine etwas andere Weise als bei den Pugnellinae, deren Schalenform im erwachsenen Tier besonders stark vom Kallus verändert wurde.
Einige Arten der jurassischen und früh-kretazischen Alariidae ähneln den Aporrhaidae, die mit der mittleren Kreide deutlich in Erscheinung treten. Im Unterschied zu den älteren Alariidae haben Jugendschalen der jüngeren Aporrhaidae meist Varizen als Ornament. Die Gattungen der Alariidae sind durch die Ausbildung der Stachel ihrer Mündungsaußenlippe voneinander zu unterscheiden. *Cuphotifer* besitzt neben dem langen Sipho einen Stachel, bei *Dicroloma* sind es zwei Stachel, und bei *Cuphosolenus* liegen drei Stachel vor. Zwischen den vier Stacheln bei *Quadrinervus* erscheinen Verbindungswände, und im Falle von *Phyllocheilus* sind die so miteinander verbundene Stachel zu einem bis zum Apex reichenden Schild vereinigt. Bei *Harpagodes* sind die Jugendwindungen breit und die Außenlippe hat mehrere Stachel. Von der generellen Schalenform ahnliche und großwüchsige Arten aus der Kreide leiten zu den noch problematischen Tylostomatidae mit *Tylostoma* über, bei der in der verdickten Außenlippe ein welliger Rand das Ende von Spiralrippen nachzeichnet. Auch bei *Diarthema* und *Monocuphus* ist die Außenlippe vereinfacht, und hier tritt zudem oft eine Verdickung vor der Außenlippe des ausgewachsenen Tieres auf. Das Auftreten stacheltragender Varizen im jugendlichen Teleoconch trennt die jurassischen Spinigeridae von den gleichzeitig lebenden Arten der Alariidae.
Die Pterocerellidae n. fam. der Kreide unterscheiden sich von den Aporrhaidae der gleichen Zeit durch den großen Protoconch mit gerundeten Windungen, sowie eine Jungendschale ohne Varizen. Zur gleichen Zeit treten die ersten Xenophoridae mit konischen Protoconch und runden Windungen auf und verändern sich seit dem ersten Auftreten in der mittleren Kreide bis heute kaum noch. *Misritropis* n. gen. aus der späten Kreide mit dem Typus *Misritropis bartheli* n. sp. aus dem Maastricht von Ägypten könnte hinsichtlich seiner Schalengestalt die Xenophoridae mit den Haloceratidae verknüpfen, allerdings kennt man von letzteren noch keine fossilen Vertreter. Mit Hilfe der charakteristischen Larvenschale wird aus dem Golf von Aqaba *Zygoceras aqabaensis* n. sp. definiert. Die Larven der Strombidae ähneln denen der Xenophoridae, die ihrerseits denen der Haloceratidae noch ähnlicher sind, die verwandtschaftlichen Beziehungen bleiben ungeklärt.
Aporrhais lebt auf Meeresböden in oft tieferem und kälteren Wasser als *Strombus*. Der Übergang von der glatten Larvenschale zur Jugendschale ist meist undeutlich und zudem oft fließend ausgebildet, weil die Skulptur des ersten Teleoconches von innen her der Endwindung des Protoconches aufgeprägt wird. Innerhalb der Aporrhaidae ist die Abgrenzung der Gattungen voneinander problematisch, da zahlreiche Übergänge existieren, etwa von *Anchura* nach *Latiala* und *Perissoptera*. Die Schalengestalt der einzigen lebenden Art von *Arrhoges* verknüpft diese mit Arten aus dem Tertiär aber auch aus der Kreide, während die typische Form von *Aporrhais* mit mehreren Mündungsstacheln erst während des Tertiärs in Erscheinung tritt. Im Bereich der Südhalbkugel und seither beschränkt auf ihn, entstanden schon im Alttertiär die Struthiolariidae.
Im Vergleich der Zähne der Radula zueinander ähneln diejenigen von *Strombus* denen von *Xenophora* und *Aporrhais*. Eine Verwandtschaft in der Gestalt der Radula ist auch zu manchen der Cerithimorpha auf der einen Seite und einigen Vertretern der Neomesogastropoda auf den anderen Seite festzustellen. Das kann eine Herkunft der Stromboidea von triassischen Vorfahren unter den Cerithimorpha plausibel machen, wie auch die Entwicklung der Neomesogastropoda als Schwestergruppe der Strombimorpha oder sogar aus ihrer Mitte heraus als Möglichkeit erscheinen lassen.
Pereiraea hat kein abgeschlossenes Wachstum der Schale, wie für die Stromboidea bestimmend ist, sollte demnach ein eigenes Taxon *Pereiraeidae* n. fam. darstellen, dessen Bezug zu den Strombiden unklar bleibt. Die spätjurassischen bis kretazischen Colombellinidae ähneln einigen Alariiden und verbinden diese möglicherweise mit den Latrogastropoda, die in der mittleren Kreide plötzlich vielgestaltig in Erscheinung treten. Die Stammgruppe der Stromboidea könnte mit ihnen in Verbindung stehen wie auch mit den Atlantidae der Heteropoda, deren den Larven von *Strombus* sehr ähnlichen Larven am Beispiel der rezenten Arten von *Atlanta* zum Vergleich belegt werden.

1 Introduction

The planktotrophic larva of members of the Strombidae have characteristic shape and the transition of their shell to the shell of the benthic young is often quite indistinct (LEBOUR, 1933, 1945; THIRIOT-QUIEVREUX, 1969; BANDEL et al., 1997). These larvae resembles those of the Atlantidae of the Heteropoda by swimming with a velum consisting of six lobes, while larvae of the other Caenogastropoda usually have a velum with two or four lobes only. Modern stromboid larvae have been described for example by LEBOUR (1945), THORSON (1940), FRETTER & PILKINGTON (1970), THIRIOT-QUIEVREUX (1976, 1983), EISAWY & SORIAL (1968, 1976), BANDEL (1975, 1982, 1993), BANDEL et al. (1997), and DAVIS (1998, 2000, 2005). It can be noted that all known larval conchs of Stromboidea resemble each other in size and shape, compared to those found in other groups of the Caenogastropoda.

Extant Stromboidea fall into five groups, namely Strombidae, Aporrhaidae, Rostellariidae, Struthiolariidae and Seraphsidae (= Terebellidae), (BOUCHET & ROCROI, 2005). Most species of the Strombidae live in well lightened shallow water collecting algae for food, raking them into their mouth with the teeth of the radula. They move on the surface of the bottom while feeding and bury in the sediment when resting. Seraphsidae live in shallow tropical environment mostly buried in sand. Aporrhaidae and Struthiolariidae are deposit and suspension feeding in cold or temperate water. They usually remain in the same area buried shallowly in soft substrate and can also be found in deeper water as most Strombidae. The mode of life of the Rostellariidae resembles that of the Strombidae with life in the tropical sea, as deposit feeders, as is also the case in Xenophoridae.

COSSMANN (1904) had defined most genera of the Stromboidea quite precisely and determined their type species. He arranged the fossil species on seven plates according to his interpretation of their phylogeny, distinguishing two larger units, the Strombidae and the Aporrhaidae and two smaller ones, the Struthiolariidae and Colombellinidae (spelled Columbellinidae by him). WENZ (1938) accepted this scheme with only minor changes. In the following discussion based on fossil and modern Stromboidea and gastropod taxa, which may be related to them, it is intended to suggest a classification that integrates data derived from the early ontogenetic shell with data based on the time of occurrence in the fossil record as well as general morphology of the shell. When the fossil species belonging to the Stromboidea are compared with the species of the extant families, they differ in regard to some diagnostic characters of their shell. Therefore, several new taxa on family and subfamily level need to be established.

The shape of the protoconch has changed little within the Stromboidea in general since their appearance in the Jurassic. Protoconch morphology of the Alariidae from the Jurassic resembles that found in the Aporrhaidae (SCHRÖDER, 1995; GRÜNDEL, 2001, 2003, 2005; KAIM, 2004). Species which resemble modern *Aporrhais* in its *Arroghes* shape (THIELE, 1939; ABBOTT, 1974) such as *Drepanocheilus*, *Perissoptera* and *Helicaulax* appear during the Mid-Cretaceous. A dividing line of these members of the Aporrhaidae to the more ancient Mesozoic Alariidae is difficult to draw. On the other hand protoconch shape allows to distinguish some of the fossil groups more clearly, such as the Pugnellidae and the species around *Pterocerella*. Features of the teleoconch, on the other hand, distinguish *Hippochrenes* and *Dilatilabrum* from *Strombus*.

A relation of the Xenophoridae with the Strombidae has been postulated by THIELE (1929) and accepted by WENZ (1938) even though the lowly trochospiral shell of the Xenophoridae contrast to the higher than wide shell of the Strombidae. The foot of *Xenophora* functions in a similar way to that of *Strombus* as was shown by MORTON (1958) and PONDER (1983) and that of *Aporrhais* studied by WEBER (1925). According to BOUCHET & ROCROI (2005) the Xenophoroidea are considered an independent superfamily as had been suggested by PONDER (1998). The protoconch of *Xenophora* differs considerably from that of *Strombus* by having low shape and often a carina. It resembles that of the Haloceratidae, as will be documented below.

2 Taxonomy

Phylum Mollusca LINNAEUS, 1758
Class Gastropoda CUVIER, 1797
Subclass Caenogastropoda COX, 1959
Order Meta-Mesogastropoda BANDEL, 1993

The order includes the Stromboidea and Xenophoroidea, perhaps also the Haloceratidae and may well represent the sister group to the pelagic planktic Heteropoda. The group originated during the transition from the Triassic to the Jurassic around 200 Million Years ago. A possible stem group may be represented in the Purpurinoidea ZITTEL, 1895 with Triassic and Jurassic species (BANDEL, 1993).

Superfamily Stromboidea RAFINESQUE, 1815

Diagnostic characters: The low-conical to turreted shell is more or less of fusiform shape with the columella sometimes drawn out and aperture with a channel at is anterior end. All members of the Stromboidea exhibit determinate shell growth. The outer lip of the fully grown shell is and thickened often expanded wing-like or may extent into finger-like processes. The protoconch is conical with rounded whorls and in species with planktotrophic development consists of about four whorls of a size of about 1 mm.

The families Aporrhaidae, Strombidae, Struthiolariidae, Rostellariidae, and Seraphsidae are included which have living species, the Alariidae, Spinigeridae n. fam., Pugnellidae, Pterocerellidae n. fam., Hippochrenidae n. fam. and Dilatrilabridae n. fam. have only fossil representatives. The Thersiteidae are newly arranged to include also *Oostrombus* and *Orthaulax*. Other terms to describe the Stromboidea have been Alata LAMARCK, 1809 (STOLICZKA, 1868), stirps Strombacea (THIELE, 1929).

2.1 Family Alariidae KOKEN, 1889

Diagnostic characters: The spire of the shell is conical and ornamented by axial and spiral elements, have no varices with the exception of *Diarthema* with varices on the body whorl. The fully grown shell has the outer lip expanded. It margin extends into one to several spines with groove on their inner side. The siphon (rostrum) is also a spine-like canal that may be straight or curved to the left or right. The protoconch is conical with rounded whorls of the morphology as found in modern *Aporrhais*. The embryonic whorl is rounded and smooth, the larval shell is ovoid with smooth rounded whorls, with a posterior sinus and a basal lobe on its outer lip and size of about 1–1.5 mm in height. The transition to the teleoconch is not thickened and indistinct. The ornament of the teleoconch develops gradationally, usually spiral ornament first, and if present axial ornament later.

Remarks: With begin of the Early Jurassic species that resembles modern Aporrhaidae developed explosively. The most obvious character by which genera have been differentiated is the shape of their outer lip in the fully grown shell. The original concept of the genus *Alaria* MORRIS & LYCETT, 1854 can be defined and restricted to Jurassic species, so that the family name based on it by KOKEN (1889) can be used. MORRIS & LYCETT (1854) described with *Alaria armata* and *Alaria hamus* two species which have later been suggested to represent members of two distinct genera by COSSMANN (1904). *Alaria* was found to be synonym to a worm and a butterfly (BOUCHET & ROCROI, 2005). It was therefore substituted by *Dicroloma* GABB, 1866 (with shell shape as in *Alaria armata* with two spines in its outer lip) and *Pietteia* COSSMANN, 1904 (with shell shape as *Alaria hamus* with one spine, that has received the name *Cuphotifer* PIETTE, 1876 before). The other genera belonging here are discussed in the following.

Genus *Cuphotifer* PIETTE, 1876

The type is based on *Rostellaria hamulus* ETUDES-DESLONGCHAMPS, 1843 from the Mid-Jurassic of France and England (MORRIS & LYCETT, 1856: pl. 3, fig. 4; PIETTE 1876, 1891: pl. 18, fig.1–3, pl. 19, figs. 2–6). It very closely resembles *Rostellaria hamus* ETUDES-DESLONGCHAMPS, 1843 from the same stratigraphic horizon that is the type species to *Pietteia* COSSMANN, 1904 (MORRIS & LYCETT, 1856: pl. 3, fig. 2; PIETTE, 1876: pl. 3, fig. 7–10, pl. 5, figs. 1–11, HUDLESTON, 1889: pl. 7, fig. 9; WENZ, 1938: fig. 2704). *Cuphotifer* has priority and *Piettaia* is a synonym, as well as *Bicorempterus* GRÜNDEL, 2001, as was suggested by KAIM (2004).

Diagnostic characters: The shell has the slender spire ornamented by spiral lines crossed by more or less inclined and discontinuous axial ribs strongest on the median corner. The keel that forms a corner on the whorls ends in the median narrow wing. A second rib on the body whorl may be present (*Alaria hamus*) or absent (*Alaria hamulus*). The wing is pointed, grooved on its lower side and curved in apical direction. The siphon is spine-like and curved (WENZ, 1938: fig. 2700, GRÜNDEL, 2003b: pl. 17, fig. 4). The shell is about 20–30 mm high.
The slender teleoconch consisting of about 11 whorls in which ornament changes from axial ribs on early whorls to spiral keels on the body whorl (HUDLESTON, 1888: pl. 4, figs. 8–9, pl. 7, fig. 9; WENZ, 1938: fig. 2704; GRÜNDEL, 2003a: pl. 11a, figs. 1–8, 12–15). The protoconch has a low dome-shaped embryonic whorl and a conical larval shell with rounded whorls, and is more than 1 mm high with 3.5 to 4 whorls (GRÜNDEL, 2003a: pl. 12, figs. 1–4; KAIM, 2004: fig. 56C). The larval shell has a wide upper sinus and a lobe that is covered by the succeeding whorl. Ornament begins on the teleoconch with axial ribs, and one spiral which may also appear within the first whorl of the teleoconch (KAIM, 2004: figs. 56, 57).

Remarks: *Cuphotifer* closely resembles *Pietteia* and is said to differ by having a hamiform median spine on it outer lip (COSSMANN, 1904). But this difference is here regarded as minor and *Pietteia* is interpreted a synonym. The possible identity of *Alaria hamus* with *Alaria hamulus* had been noted by LAUBE (1866) in his discussion of the species from the Mid Jurassic of Balin (western Ukrainia). GRÜNDEL (2003b: pl. 17, figs. 3–4) illustrated a species determined as *Pietteia* and another one as *Cuphotifer*, both from erratic material transported by the glacier of northern Germany that could be considered to represent the same species. COSSMANN (1904) distinguished *Pietteia* by the presence of two larger spiral ribs on the body whorl, and *Cuphotifer* based on a fragmented shell with only one larger spiral rib at the corner. But this difference in ornament is minute since there are many fine spiral ribs present as well and variability of shell ornament has been documented (PIETTE, 1976: pl. 5, figs. 1–11) as was supported by GRÜNDEL (2003a). *Bicorempterus* GRÜNDEL, 2001 is based on *Alaria bispinosa* (PHILLIPS, 1829) var. *elegans* HUDLESTON, 1884 from the Callovium of England (HUDLESTON, 1884: pl. 6, fig. 8; GRÜNDEL, 2001). This *Bicorempterus elegans* (HUDLESTON, 1884) of GRÜNDEL (2003b: pl. 16, figs. 9–10, pl.17, figs.1–2) was interpreted by KAIM (2004) to represent a synonym of *Pietteia*. Protoconch shape is also the same (GRÜNDEL, 2005: pl. 4, fig. 6). The transition to the teleoconch of *Bicorempterus pseudopellatus* (GERASIMOV, 1992) from the Callovian of Russia is gradational with axial ribs and spiral ribs entering the final portion of the larval shell, as is the case in modern *Aporrhais pespelicani*. The upper keel on the body whorl is continuous onto the upper spine of the outer lip, while the lower keel curves into a keel that lies on the siphon which is an elongate spine (rostrum) (GERASIMOV, 1992).
The genus *Alaria* as utilized by LAUBE (1866), STOLICZKA (1868) and HUDLESTON (1884) was interpreted by WENZ (1938: fig. 2702) to represent a synonym to *Dicroloma* GABB, 1868. But the original genus into which most of these species of *Alaria* has been placed was *Pterocera* LAMARCK, 1801 and the genus *Alaria* had not been defined with a type species by MORRIS & LYCETT (1854). WENZ (1938) regarded *Pietteia* as well as *Dicroloma* as subgenera of *Anchura* CONRAD, 1860 which is based on a species that lived during the Late Cretaceous Maastrichtian time almost 100 Million Years after the appearance of *Alaria* and about 80 Million years later than the type species of *Dicroloma* and *Cuphotifer* (= *Pietteia*). COSSMANN (1904), in contrast, had interpreted *Pietteia* to represent a subgenus of *Dicroloma*, which makes more sense since both resemble each other and lived at about the same time.

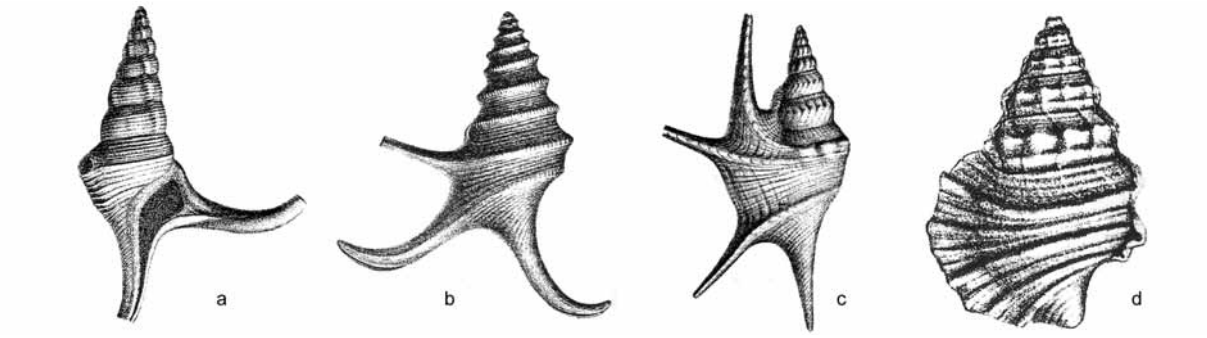

Fig. 1: a – *Cuphotifer rarispina* taken from PIETTE, 1891; b – *Dicroloma cochleata* taken from PIETTE, 1891; c – *Cuphosolenus tetracer* taken from PIETTE, 1891; d – *Diarthema paradoxa* taken from PIETTE, 1891.

Genus *Dicroloma* GABB, 1868

The type species is *Pterocera lorierei* ORBIGNY, 1860 from the Mid Jurassic of France and England designated by COSSMANN (1904), (MORRIS & LYCETT, 1854: pl. 3, fig. 11; PIETTE, 1876: pl. 2, figs. 12–14, pl. 4, figs.1–3).

Diagnostic characters: The turreted shell has rounded smooth whorls of the protoconch, later angular whorls of the juvenile teleoconch, and the final whorl bears two keels (KAIM, 2004: fig. 54). The aperture has a narrow, pointed and back-twisted rostrum (curved siphon) and the outer lip extends into two finger-like projections of which the anterior one is wider than the posterior one. The spines are gutter-like with the canal open to the aperture (GRÜNDEL, 2003b: pl. 16, figs. 5, 7). The protoconch of *Dicroloma nudispira* KAIM, 2004 has a low dome-shaped embryonic part that is about 0.18 mm wide and consists of 3.5 whorls. The larval shell is about 0.6–0.7 mm high and wide has a rounded projection near its base, but no sharp border to the teleoconch (GRÜNDEL, 2003a). The end of the larval shell is distinctive due to change in growth lines from sinuous larval pattern to more simple adult pattern (KAIM, 2004: fig. 55). The juvenile teleoconch whorls have a corner that has short axial ribs or a keel with pustules, later only ornament of fine spiral ribs in addition to the keels.

Remarks: Among the species of *Alaria* described by MORRIS & LYCETT (1854) *Alaria laevigata*, and *Alaria trifida* have two narrow spines on their aperture and belong to *Dicroloma*, even though the spire in case of *Alaria laevigata* has more rounded whorls as are characteristic to the type *Alaria lorierei* (PIETTE, 1876: pl. 2, fig. 12–14; HUDLESTON, 1988: pl. 6, figs. 5–6). *Alaria myurus* (ETUDES-DESLONGCHAMPS, 1843) is very similar but has more pronounced spiral ornament (PIETTE, 1876: pl. 2, figs. 8–11; LAUBE, 1866; HUDLESTON, 1884: pl. 7, figs. 4–6, 1988: pl. 6, fig. 4) and *Alaria armata* MORRIS & LYCETT, 1854 has also axial ribs (MORRIS & LYCETT, 1854: pl. 3, fig. 1). COSSMANN (1904) mentioned a number of species of *Dicroloma* with the earliest having lived in the Liassic and species present throughout the Jurassic of Western and Middle Europe. *Dicroloma subpunctata* (MÜNSTER, 1844) from the Upper Toarcium to Aalenium (BRÖSAMLEN, 1909) has the larval shell that had been suggested by SCHRÖDER (1995) to belong here (KAIM, 2004). *Dicroloma cochleata* (QUENSTEDT, 1857) from the Bajocian of Germany consists of 8 whorls and is about 20 mm high (GRÜNDEL, 2003a: pl. 10, figs. 11, 12, 14). Its protoconch is smooth and rounded with remnants of ornament on the larval shell. Whorls of the teleoconch have a spiral keel that is continuous into the upper upturned wing in the outer lip with thin and long posterior spine (GRÜNDEL, 2005: pl. 3, fig. 14, pl. 4, figs.1–4). A lower keel on the body whorl continues into the middle wing of the outer lip. The Cretaceous *Anchura* differs from *Pietteia* and *Dicroloma* by the split posterior spine on the outer lip of its aperture, by a rounded shape of its whorls, and by the presence of varices on the spire.

Genus *Cuphosolenus* PIETTE, 1876

The type is *Pterocera tetracer* ORBIGNY, 1847 from the Late Jurassic of France (PIETTE, 1876: pl. 43, fig. 7, pl. 60, figs. 1–5, the latter of which were copied by WENZ, 1938: fig. 2691).

Diagnostic characters: *Cuphosolenus* PIETTE, 1876 was introduced for species of *Alaria* with three spines. The spire is like that of *Dicroloma*, but the outer lip has four elongate slender spines, one parallel to the spire but not attached to it, two on the median outer lip and the fourth representing the siphon, all like the rostrum with a canal on their inner side.

Remarks: *Cuphosolenus tetracer* as in the reconstruction presented by (COSSMANN, 1904: pl. 5, fig. 4, spelled *Cyphosolenus*) may have an exaggerated length of the spines and the long siphon. In case of *Cuphosolenus dyoniseus* (BUVIGNIER, 1852) from the Late Jurassic the shell also resembles that of the living *Aporrhais pesgallinae*. *Cuphosolenus* may have the outer lip expanded and reaching the spire with its margin, so that it grades into *Quadrinervus* with more than three spiral keels ending in spines on one side and to *Diarthema* and *Monocuphus* with short outer lip. KELLUM & APPELT (1964) described a *Cuphosolenus mexicanus* from the Albian of Mexico which has a spire more resembling that of *Pterocerella* than *Cuphosolenus*.

Genera *Diarthema* PIETTE, 1864 and *Monocuphus* PIETTE, 1876

The type is *Pterocera paradoxa* ETUDES-DESLONGCHAMPS, 1843 (PIETTE, 1876: pl. 9, figs. 1–12; COSSMANN, 1904: pl. 5, figs. 17 & 19) and *Pterocera camelus* PIETTE, 1855 for *Monocuphus* (PIETTE, 1876: pl. 10, figs. 1–3; COSSMANN, 1904: pl. 4, figs. 6–7, spelled *Monocyphus*), both from the Mid-Jurassic.

Diagnostic characters: The whorls of the relatively wide spire have a smooth protoconch and later ornament of strong spiral ribs and median corner or keel that may bear short axial ribs. The spiral ribs continue into the outer lip forming a spike with it an posterior outer short gutter-like extension. The body whorl is somewhat deformed by one or two varices in front of the outer lip, the first one about half a whorl back. A large posterior outer thorn, a smaller basal thorn and a narrow channel-like siphon characterizes *Monocuphus* (COSSMANN, 1904: pl. 4, figs. 6 & 7). Shell shape and shell ornament is similar in *Diarthema* which has the outer lip more expanded with several short spikes the largest of which lies on the posterior margin (PIETTE, 1876: pl. 9, figs. 1 & 2; BRÖSAMLEN, 1909: in South Germany). *Diarthema* (spelled *Diartema* by COSSMANN, 1904) bears a strong varix on the body whorl about half a whorl in front of the final aperture. The body whorl is thus broadened in *Diarthema paradoxa* as well as in *Monocuphus tumidus* (LAUBE, 1866) from the Ukrainian Jurassic.

Remarks: Shell shape and shell ornament of *Monocuphus* appears to be transitional to *Diarthema*, and both have the characteristic varices in front of their final outer lip. *Monocuphus vespa* (ETUDES-DESLONGCHAMPS, 1843) and *Monocuphus atractoides* (ETUDES-DESLONGCHAMPS, 1843) from the Bathonian of the Normandy in France have the wing-like outer lip, but not expanded to the spire (PIETTE, 1876: pl. 11, fig. 6, pl. 15, fig. 8; MORRIS & LYCETT, 1854: pl. 3, fig. 7). Both could also resemble *Cuphosolenus* since their body whorl appears to have no

additional varix. *Diarthema spinigera* (ETALLON) from the Kimmeridge (PIETTE, 1876: pl. 43, figs. 1–5) has a weakly expanded lip without spines and a well developed varix half a whorl before the outer lip. *Quadrinervus piettei* (BUVIGNIER, 1852) from the Late Jurassic (PIETTE, 1978: pl. 52, figs. 2–5) has short spines on it outer lip. It was placed with *Quadrinervus* by COSSMANN (1904) but more resembles *Monocuphus*. The shell of *Monocuphus camelus* from the Mid-Jurassic of France, and of *Diarthema tumida* (LAUBE, 1866) from strata of similar age from the western Ukrainia closely resemble each other.

Genus *Quadrinervus* COSSMANN, 1904

The type species is *Pterocera ornata* BUVIGNIER, 1852 from the Late Jurassic of France (COSSMANN, 1904: pl. 5, fig. 11).

Diagnostic characters: The spire is pointed elongate with ornament of axial and spiral ribs, and a median angulation may be present. The body whorl has three main keels along with many smaller spiral ribs and the outer lip has four finger-like processes. The anterior siphonal canal is straight and pointed or curved. The posterior spine of the outer lip is attached to the spire and continues to its apex or even beyond it (WENZ, 1938: fig. 2693).

KAIM (2004: fig. 58) illustrated the transition from the short conical protoconch with smooth rounded whorls to the ornamented teleoconch. The later ornament is of equally strong axial and spiral ribs forming a regular pattern of squares. The analyzed species is from the Valanginian of Poland, and may be considered gradational between Late Jurassic *Quadrinervus* and Late Cretaceous *Pterocerella*. *Quadrinervus muscus* (ETUDES-DESLONGCHAMPS, 1843) as illustrated by PIETTE (1876: pl. 44, figs. 7, 8) resembles *Phyllocheilus* by having part of its wing-like aperture attached to the spire and *Cuphosolenus* with similar outer lip but the apical margin of it not next to the spire (PIETTE, 1876: pl. 43, fig. 6, 7).

Genus *Phyllocheilus* GABB, 1868

The type is *Pterocera ponti* BRONGNIART, 1821 from the Late Jurassic (Kimmeridge) of France (PIETTE, 1876: pl. 66, fig. 4, pl. 70, figs. 4–6, pl. 72, figs. 8 & 9). PIETTE (1876: pl. 24, figs. 1 & 2) suggested *Malaptera* as name for the genus, but with the type *Pterocera polypoda* BUVIGNIER, 1852 from the Oxfordium (COSSMANN, 1904: pl. 4, fig. 4). *Malaptera* is a synonym of *Phyllocheilus*.

Diagnostic characters: The spire is conical with whorls spirally ornamented as in *Diarthema* but the outer lip is wing-like with up to ten keels ending in spines. The spire is relatively broad and short (WENZ, 1938: fig. 2696). *Phyllocheilus bentleyi* (MORRIS & LYCETT, 1851) from the Mid-Jurassic has a web like outer lip and the tube like siphon turned to the left (MORRIS & LYCETT, 1851: pl. 3, fig. 15; HUDLESTON, 1888: pl. 3, fig. 1) very similar to *Phyllocheilus hirsutus* (DOLLFUSS) from the Kimmeridge (PIETTE, 1876: pl. 62, figs. 1–4). Ornament of the spire is spiral and the spiral ribs on the body whorl continue into the six spines of the outer lip. The spines in the web represent gutters with a groove in their base.

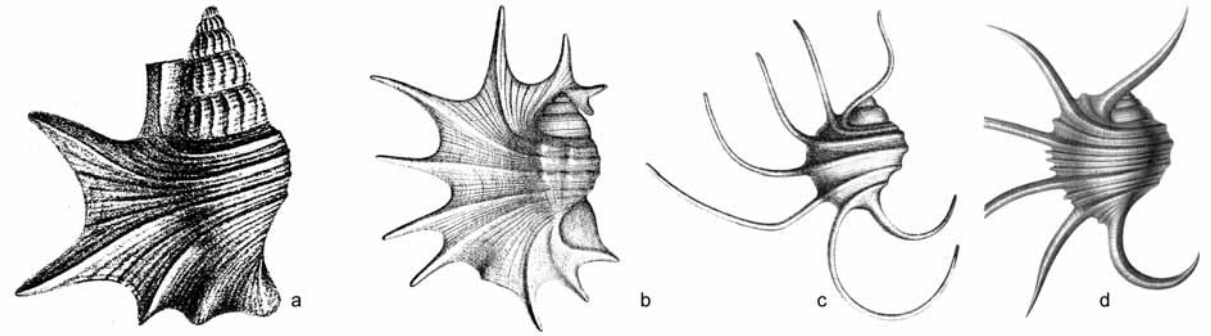

Fig. 2: a – *Quadrinervus intermedius* taken from PIETTE, 1891; b – *Phyllocheilus polypoda* taken from PIETTE, 1891; c – *Harpagodes pelagi* taken from ORBIGNY, 1843; d – *Harpagodes aranea* taken from PIETTE, 1891.

Remarks: *Phyllocheilus* with less expanded outer lip resembles *Quadrinervus* which has similar web-like but less expanded outer lip. With longer spines it comes close to *Harpagodes* and also has a short spire, and similar wing-like outer lip with spines. *Phyllocheilus polypoda* has the outer lip attached to the shell and extending over the spire (PIETTE (1876: pl. 24, fig. 91), so it is very close in shape to *Harpagodes*. COSSMANN (1904) traced species of *Phyllocheilus* (spelled *Phyllochilus*) from the Bathonian to the end of the Cretaceous suggesting a connection with *Aporrhais*.

Genus *Harpagodes* GILL, 1870

The type is *Pterocera pelagi* BRONGNIART, 1821 from the Early Cretaceous (Barreme) of France.

Diagnostic characters: The shell resembles modern *Lambis* with the outer lip of the fully grown individual with 6 spines. The spire is relatively short and ornament of the short stout body consists of spiral ribs (COSSMANN, 1904: pl. 8, fig. 1; WENZ, 1938: fig. 2701). The protoconch is unknown and the teleoconch may be quite large (about 150–180 mm).

Remarks: It is difficult to understand why COSSMANN (1904) considered *Phyllocheilus* to represent a subgenus of *Chenopus*, while *Harpagodes* represents as genus by itself. The study of PIETTE (1876) very clearly documents that the Jurassic of France holds all the species needed to connect these two taxa with each other by intermediates. *Phyllocheilus* on the other hand grades into *Quadrinervus*, which was accepted by COSSMANN (1904) who included both as subgenera in the same genus, and also connected them with *Cuphosolenus*. *Harpagodes aranea* (ORBIGNY, 1847) from the Oxfordian of France (PIETTE, 1876: pl. 39, fig. 1, pl. 40, fig. 1, pl. 54, figs. 6 & 8) and *Harpagodes pelagi* resemble *Harpagodes thirriae* (CONTEJEAN) from the Late Jurassic (Kimmeridge) of France (PIETTE, 1976: pl. 71, figs. 1 & 2) and of Langenberg (Oker) in northern Germany with six spines arranged at regular distance from each other on the margin of the wing of the outer lip and the siphon is curved to the left.
A subfamily Harpagodinae PCHELINTSEV, 1963 based on *Harpagodes* would have the outer lip of the fully grown shell has a wing-like extension and six long spines extending from its margin. The spire is low and covered by the most posterior spine of the outer lip. Species from the Mid-Jurassic to the Cretaceous could be united (COSSMANN, 1904). It can be speculated that the group connects to the large and rounded shells of the Tylostomatidae STOLICZKA, 1868 based on *Tylostoma* SHARPE, 1868 (WENZ, 1938: fig. 2941) that lived in the Late Cretaceous from the Iberian Peninsula to that of India (STOLICZKA, 1868). In the Cenomanian of Jordan and Egypt shells of up to 180 mm in size are found which have the body as in *Harpagodes* with low spire and apparently without spines on the outer lip. They are preserved only by internal molds which indicate a thickened aperture and thus a final growth stage (own observations). Tylostomatidae were considered to represent Strombidae by KOLLMANN et al. (2003) after they had been placed with the Globulariinae of the Naticoidea by WENZ (1938: fig. 2941). Tylostomatidae is still problematic and can only be evaluated when better preserved shells become known. It can be speculated that large sized *Harpagodes* have represented the stem group, but there is no prove for that assumption available up to date.
By way of *Quadrinervus* the Harpagodinae connect to the stem group of the Alariidae and here the Dicrolomatinae KOROTKOV, 1992. Alariidae were considered synonymous with the Arrhoginae POPENOE, 1983 (BOUCHET & ROCROI, 2005), as well as with the Dicrolomatidae. While *Dicroloma* has been created to substitute part of the Jurassic *Alaria*, the genus *Arrhoges* GABB, 1868 is based on a living species. It thus represents an end-member of an evolution that proceeded for more than 150 Million Years. To make taxonomy even more complex, *Arrhoges* has been included in the genus *Aporrhais* based on comparison among its living species (see below). Since the Alariidae of the Jurassic appear to represent the stem group to all other families of the Stromboidea, including the living Aporrhaidae, the later are here interpreted as distinct family, even though some of their species have similar characteristics.

2.2 Family Spinigeridae KOROTKOV, 1992

Diagnostic characters: In contrast to the usual case among the Alariidae and Aporrhaidae the species of *Spinigera* have a regular pattern of varices with hollow thorns. *Spinigera* appeared in the Early Jurassic (Toarcian) and resembles *Dicroloma* regarding shell shape (COSSMANN, 1904: pl. 7, fig. 2; WENZ, 1938: figs. 2708 & 2709). But shell growth, in contrast to that of the Alariidae, was with intermissions that had spines on their outer lip. Only the first two whorls of the teleoconch have no such interruptions of growth in case of *Spinigera* (KAIM, 2004: fig. 59). Even later spine bearing varices appear in *Diempterus*. The spire is slender with a median corner and the protoconch is smooth with about 3.5 whorls and indistinct transition into the teleoconch.

The family is based on the genus *Spinigera* ORBIGNY, 1850 which has the type species *Ranella longispina* ETUDES-DESLONGCHAMPS, 1842 from the Mid-Jurassic (GRÜNDEL, 2003: pl. 12, figs. 5–7). Species existed from begin to the end of the Jurassic (COSSMANN, 1904).

Differences: Alariidae have no varices, Spinigeridae have them. Also most species of the Aporrhaidae have varices in the juvenile stage of shell growth, but only the terminal adult stage has a thickened apertural margin that may have had spines. Growth of the shell in Spinigeridae was periodic. After a species specific stage of growth it stopped after every half whorl of faster growth (PIETTE, 1876: pls. 88–92; COSSMANN, 1904; KAIM, 2004: fig. 59; GRÜNDEL, 2005: pl. 4, figs. 8 & 9). In the other genera placed in the Aporrhaidae the varices are low ridges or a varix is present only in the fully grown individuals as in living *Aporrhais*.

Genus *Spinigera* ORBIGNY, 1850

The type species is *Ranella longispina* ETUDES-DESLONGCHAMPS, 1842 from the Bajocian of the Normandy, France (HUDLESTON, 1888: pl. 3, fig. 4).

Diagnostic characters: The shell consists of 11 whorls with slender spire and about 3 cm in size. The smooth conical protoconch with more than three rounded whorls and about 1 mm in height and width is succeeded by the early teleoconch with a spiral median row of short axial ribs. In the next teleoconch whorls only a median corner of the whorl remains and spiral ribs are added. Varices appear which are present after each half whorl, which are aligned with the margin of the body whorl. These early stops in growth had spines which differs from the other Alariidae. The aperture continues in a long siphon (rostrum), a long spine on the outer lip is to the side with a groove on its inner side.

Genus *Diempterus* PIETTE, 1876

The type species is *Diempterus lonqueueanus* PIETTE, 1876 from the Kimmeridge of northern France (PIETTE, 1876: pl. 58, figs. 1–4; COSSMANN, 1904; WENZ, 1938: fig. 2708).

Diagnostic characters: The shell is about 28 mm high with pointed spire ornamented by as spiral keel and fine spiral ribs. The aperture of the body whorl has one abandoned margin with traces of two spines, and one final margin with the two spines in the same orientation but half a whorl later. The siphon is narrow and elongate resembling the spines.

Remarks: PIETTE (1876) had also species from the Mid Jurassic such as *Diempterus bialatus* PIETTE, 1876 and COSSMANN (1904) selected as type a species from the Kimmeridge. *Diempterus* differs from *Spinigera* by having spines duplicated only on the body whorl and with half a whorl between them. Former varices, if present at all, are not reported to have traces of former spines, which contrasts to *Spinigera*. A similar duplication of the varix on the body whorl is present also in case of *Diarthema*, but the later has no spines on the varix as well as on the final outer lip.

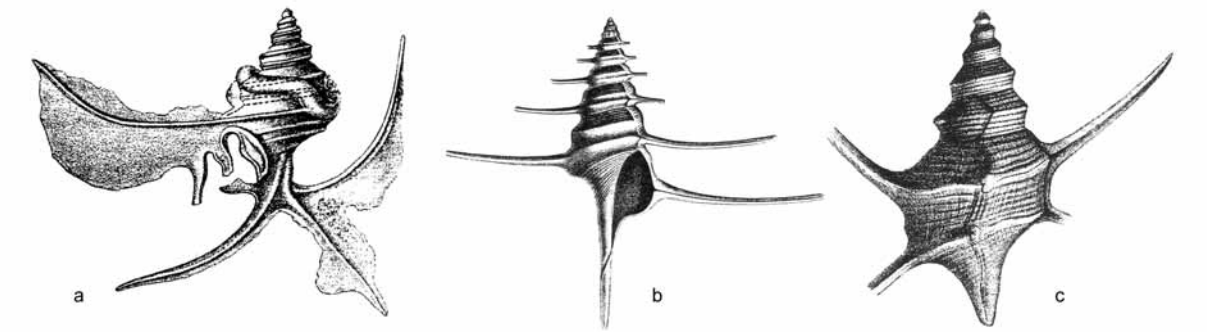

Fig. 3: a – *Pterocerella arachnoides* taken from HOLZAPFEL, 1888; b – *Spinigera longispina* taken from PIETTE, 1891; c – *Diempterus lonqueueanus* taken from PIETTE, 1891.

2.3 Family Aporrhaidae GRAY, 1850

The family is based on *Aporrhais* DA COSTA, 1778 with the type *Strombus pespelicani* LINNÉ, 1758 from the eastern Atlantic and the Mediterranean Sea.

Diagnostic characters: The shell has a tall conical spire with apical angle about 35° to 40°. Its ornament consists of a median keel accompanied by a flattened upper and lower side, and spiral lines as well as collabral ribs. Often the keel bears short thickened axial ribs. On the body whorl stronger spiral ribs may be present the upper of which end in the flaring outer lip. In the fully grown shell the outer lip expands and continues into more or less flattened spines or lobes with a central groove on their inner side. The siphon may be short or long and has a similar inner groove as the spines. The protoconch is dome-shaped and in most species belonged to a planktotrophic veliger. It has about 3.5 whorls with rounded embryonic shell and the larval shell may have a fine pattern of tubercles or is smooth with fine sinuous growth lines. Transition into the teleoconch is often quite indistinct (Pl. 1/13–16).

Remarks: COSSMANN (1904) regarded the Aporrhaidae as the taxon in which *Chenopus* PHILIPPI, 1836 (based on *Aporrhais pespelicani*) includes several Jurassic and Cretaceous subgenera and *Arrhoges* GABB, 1868 (based on *Aporrhais occidentalis*) has Jurassic and Cretaceous subgenera (*Drepanocheilus* and *Monocuphus*). WENZ (1938) also included several Jurassic and Cretaceous taxa in the genus *Aporrhais* and interpreted the living *Arroghes* (= *Aporrhais occidentalis*) to represent a subgenus to the Cretaceous *Depanocheilus* (= *Drepanochilus*). Both classifications are based on the similarities of the shell but the arrangement of subgenera in the genera differs. They have in common that living species were connected closely to such that have existed during the Early Jurassic more than 190 Million years ago. Here it is preferred to place the Jurassic genera in the separate family Alariidae even though some of their species are morphologically close to some modern Aporrhaidae, especially *Aporrhais occidentalis*. A dividing line is difficult to draw but appears to lie among Mid Cretaceous species. Major groups within the superfamily Stromboidea such as Pugnellidae, Strombidae, Rostellariidae, Thersiteidae and Hippochrenidae n. fam. came to existence only during the Mid to Late Cretaceous and even later. The stem group to all these can be assumed to lie within the Alariidae.
THIELE (1931) dealing only with the living species regarded the Aporrhaidae as one of the four families of the Stromboidea, and these were accepted by WENZ (1938), who included into them several fossil genera. BOUCHET & ROCROI (2005) suggested that Aporrhaidae can be divided in the subfamilies Aporrhainae GRAY, 1850 and Arrhoginae POPENOE, 1983, among the groups with living representatives. They included also the fossil subfamilies Harpagodinae PCHELINTSEV, 1963, Perissopterinae KOROTKOV, 1992, and Spinigerinae KOROTKOV, 1992 and thus adopted a part of the classification of the Aporrhaidae as had been suggested by KOROTKOV (1992), but basically that of WENZ (1938). This extends the existence of the family Aporrhaidae to the base of the Jurassic, which differs from the classification presented in the present paper.
Perissopterinae KOROTKOV, 1992 have the spire elongate pointed with ornament of fine, or indistinct spiral ribs that may be crossed by larger, rounded axial ribs. The expanded outer lip of the aperture consists of a broad central lobe, and a narrow posterior spine or branch attached to it. The siphon is a long anterior canal. Genera consist predominantly of Cretaceous species, mostly occurring between Mid-Cretaceous to Maastrichtian. The juvenile shell may have rounded varices representing interruptions during growth, and the protoconch is of the type as found in *Aporrhais*.
Characters that distinguish the genera predominantly regard the outer lip of the fully grown shell. *Perissoptera* has a large median lobe connected to a narrow posterior spine, which in *Helicaulax* is partly attached to the spire. *Anchura* has the median extension of its outer lips split at its end into a larger posterior and a smaller anterior spine, and in *Pseudanchura* that median spine is very elongated. *Latialia* has a wide median lobe and short posterior spine attached to the spire. In *Gracilialia* the median lobe is pointed and elongate and the posterior spine is also attached, as it is in *Drepanocheilus* with its median pointed lobe with two keels, one of which forms a median keel on the spire in *Tulochilus*. *Kaunhowenia* is similar to *Drepanocheilus* with the posterior spine attached to the spire but continuous over the apex.

Genus *Perissoptera* Tate, 1865

The type is *Rostellaria reussi* TATE, 1865 from the Mid-Cretaceous of England according to WENZ (1938: fig. 2706). COSSMANN (1904) had chosen *Rostellaria parkinsoni* MANTELL, 1822 from the Albian of England as type species. The question of the type species was discussed by SAUL (1998).

Diagnostic characters: The high spire consists of about nine whorls with ornament of coarse axial and fine spiral ribs. The outer lip of the aperture has a broad central lobe separated by a sinus from a posterior spine that lies free from the spire. The anterior siphon is a narrow, straight and long canal.

Remarks: *Perissoptera marginata* (SOWERBY, 1829) from the Santonian-Campanian of Aachen in western Germany has spiral ornament crossed by short inclined axial ribs and a large wing on its outer lip with quadrate shape and long curved spine on the posterior corner with canal on its lower side (COSSMANN, 1904: pl. 6, fig. 3). *Perissoptera prolabiata mississippiensis* DOCKERY, 1993 from the Campanian of Mississippi (DOCKERY, 1993: pl. 14, fig. 1) closely resembles *Perissoptera schlotheimi* ROEMER by HOLZAPFEL (as *Lispodesthes*) from Vaals Greensand (compare HOLZAPFEL, 1888: pl. 12, fig. 11–13 with DOCKERY, 1993: pl. 14, fig. 1). The protoconch is large and conical consisting of five smooth and rounded whorls which end in a thickening (DOCKERY, 1993). *Perissoptera prolobiata* (WHITE, 1876) has a short posterior spine in contrast to that of *Perissoptera reussi* (GEINITZ, 1874) from the Cenomanian/Turonian of Saxony and the Czech Republic which has a large spine (KOLLMANN, 1978).

Genus *Anchura* CONRAD, 1860

The type is *Anchura abrupta* CONRAD, 1860 from Ripley Formation of the south-eastern USA (DOCKERY, 1993: pl. 15, figs. 1–3). COSSMANN (1904) had as type *Rostellaria carinata* MANTELL, 1822 from the Albian of Folkstone in England, which could be placed in *Pseudanchura*.

Diagnostic characters: The spire consists of many whorls. The teleoconch is ornamented by spiral and axial ribs forming a relatively coarse ornament of rectangles and nodes where crossing each other. Varices occur rarely (SOHL, 1960: pl. 12, figs. 2, 3, 13; ELDER & SAUL, 1996). The outer lip of the aperture has a broad central lobe and a narrow short posterior canal. The aperture of the fully grown shell is elongate with the wing of the outer lip split into a larger posterior branch with median keel and the narrow shorter one (DOCKERY, 1993: pl. 16, figs. 1–3, pl. 15, figs. 7–8, pl. 14, figs. 4–7; ELDER & SAUL, 1996: fig. 2). The inner and outer lip may be thickened by callus deposits (KIEL & BANDEL, 2002: fig. 4). The siphon is long and straight or curves to the left. The protoconch is conical with pointed apex (KIEL & PERRILLAT, 2001: figs. 3 & 1). In case of *Anchura chapelvillensis* DOCKERY, 1993 from the Campanian of Mississippi it is more than 1 mm high and 1 mm wide with rounded whorls and rounded apex (see below).

Remarks: ELDER & SAUL (1996) found *Anchura* to be very common in the Late Cretaceous of the North American Pacific slope. Here they represent a succession of species, several of these had been described by ALLISON (1955). *Anchura* was known from the Mid-Cretaceous to the Turonian (COSSMANN, 1904) but occur from the Albian to the Paleocene (ELDER & SAUL, 1996). KIEL & PERRILLIAT (2001) described *Anchura denticulata* KIEL & PERRILLIAT, 2001 from the Maastrichtian of Mexico. BANDEL (2000: pl. 3, fig. 1) and KIEL & BANDEL (2002: fig. 4) documented that *Anchura* also had species with very similar shell shape living in India and Cameroon during the Late Cretaceous.
HOLZAPFEL (1888: pl. 12, figs. 1–4, 10) placed *Anchura* from the Vaals Greensand (Aachen- and neighboring Belgium-Netherlands) with *Aporrhais* (*Aporrhais beisseli* and *Aporrhais granulata*). STEPHENSON (1952) described some species from the Cenomanian of Texas which could be placed in the genus *Anchura* as well as *Latialia*, such as *Anchura turricula* with wide apertural lobe and *Anchura horreana* with shorter lobe and *Anchura whitneyensis* with wide lobe, all quite similar to each other. In case of *Anchura chapelvillensis* the protoconch teleoconch transition is abrupt with smooth larval whorls and a keel on the first whorl of the teleoconch. This species resembles the Jurassic *Pietteia* COSSMANN, 1904 (compare DOCKERY, 1993: pl. 14, figs. 4–7, pl. 15, figs. 7 & 8 with KAIM, 2004: figs. 56 & 57).

Genus *Pseudanchura* KOLLMANN, 2005

The type is *Rostellaria* (*Fusus) carinella* ORBIGNY, 1843 from the Albian of France (KOLLMANN, 1978), which had been placed with *Anchura* by COSSMANN (1904).

Diagnostic characters: The spire is elongate slender and the outer lip has a long spine that bifurcates at its end. The ornament of the narrow elongate spire of the type consists of a spiral keel. The difference to *Anchura* lies in the large size of the apertural spine and its branching end. In case of *Pseudanchura carinata* (MANTELL, 1822) from the Albian of the Normandy, France the ornament of the spire consists of a keel with short ribs, and the median spine of the outer lip is split into two long spikes (COSSMANN, 1904: pl. 6, figs. 8 & 9).

Genus *Helicaulax* GABB, 1868

The type species is *Rostellaria ornata* ORBIGNY, 1843 from the Turonian of France (COSSMANN, 1904: pl. 5, fig. 12).

Diagnostic characters: The whorls of the slender spire have ornament as in *Anchura*. The posterior digit of the outer lip is long and attached to several whorls of the spire. The middle spike and its connection to the siphon (rostrum) resembles *Gracilialia*. The median extension of the outer lip is pointed and flattened before its end and there is a sinus on its anterior margin and a groove on its lower side. The large siphon is an open tube with its right side a little longer. In case of *Helicaulax buchi* (MÜNSTER, 1839) from the Campanian of Germany the posterior apertural spine extends beyond the apex and the median spine has a keel and is of paddle-like shape in its middle and extends into a backward twisted point. Ornament is by fine spiral ribs and a keel on the body whorl (as *Rostellaria buchii* in GOLDFUSS, 1844).

Differences: The species of *Anchura* described in detail by DOCKERY (1993: pl. 14, figs. 2–7) are very similar and also have a posterior spine of unequal length. His species *Anchura chapelvillensis* and *Anchura corniculata* could also be placed with *Helicaulax*.

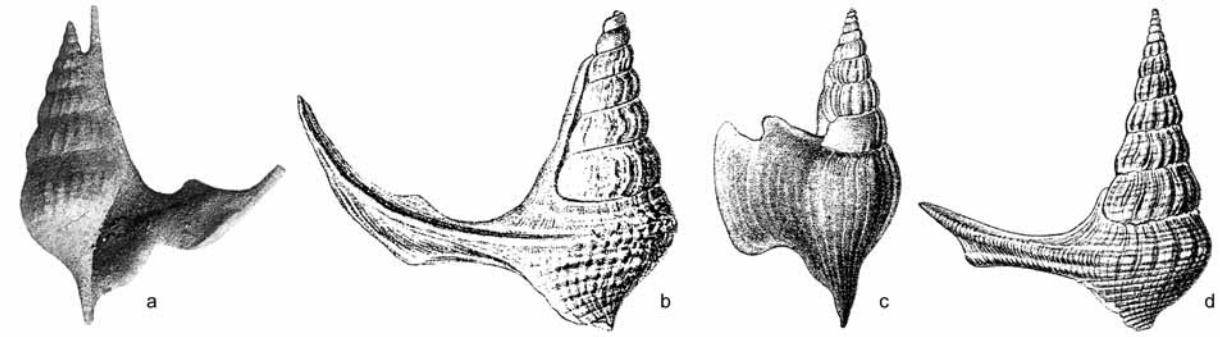

Fig. 4: a – *Helicaulax ornata* taken from COSSMANN, 1904; b – *Helicaulax granulata* taken from HOLZAPFEL, 1888; c – *Latiala schlotheimi* taken from HOLZAPFEL, 1888; d – *Anchura stegoptera* taken from HOLZAPFEL, 1888.

Genus *Kaunhowenia* ABDEL-GAWAD, 1986

The type is *Aporrhais* (*Helicaulax*) *carinifera* KAUNHOWEN, 1897 from the Maastrichtian of Maastricht in the Netherlands with strong spiral ornament.

Diagnostic characters: The margin of the outer lip of the body whorl continues onto the spire to its apex, and from there on down on the other side of the spire. The outer lip has a posterior groove and anterior sinus. The spire has a median angulation and ornament by spiral lines and, sometimes, short tubercle-like axial ribs.

Kaunhowenia punctata KIEL & BANDEL, 2002 from the Campanian of northern Spain has spiral ornament connected to tubercles on the ribs and the callus ridge on the side of the spire has a median groove (KIEL & BANDEL, 2002: fig. 2A, B), while *Kaunhowenia catalanica* KIEL & BANDEL, 2002 from the same locality and age has less granular spiral ornament and the canal from the outer lip continuous across the apex of the spire (KIEL & BANDEL, 2002: fig. 2C).

Difference: *Kaunhowenia* differs from *Latiala* by the attachment of its outer lip to the spire for its whole length and even reaching across and over the apex. In *Latiala* the posterior spine ends before reaching the apex.

Genus *Latiala* SOHL, 1960

The type is *Anchura lobata* WADE, 1926 from the Late Cretaceous Ripley Formation, Maastrichtian (SOHL, 1960: pl. 11, figs. 13–15).

Diagnostic characters: The spire has simple axial ribs and intercalated varices. The medium sized shell (about 2–3 cm high) has a broad, thick outer lip that is thickened and bears two lobes at its outer lip. One lobe is directed upward or to the side and a second blunter lobe is directed downward. The interior of the outer lip is smooth and the inner lip has a thin callus. The protoconch resembles that of *Strombus pugilis*.

Remarks: *Latiala* is close to *Anchura* in shell shape but the outer lip of the aperture is characteristic in forming one wing-like extension (SOHL, 1960: pl. 11, figs. 9–15). In case of *Latiala*? *ponsi* KIEL & BANDEL, 2002 from the Campanian in northern Spain the protoconch is smooth and conical and consist of 4.5 whorls, is 1.5 mm wide and 1.35 mm high. Its embryonic whorl measures 0.15 mm across (KIEL & BANDEL, 2002: fig. 2K & L). The adult shell has up to ten convex whorls, is about 24 high and 13 mm wide with ornament of axial ribs and fine spiral lines. The outer lip has a posterior spine that is attached to the spire. This distinguishes this species from *Latiala papilionacea* (GOLDFUSS, 1844) from India and *Latiala lobata* where the posterior spine of the outer lip is attached only to the last whorl (SOHL, 1960; BANDEL, 2000: pl. 2, fig. 10; KIEL & BANDEL, 2002). The Albian *Latiala besairiei* (COLLIGNON, 1949) from Madagascar has a dome shaped protoconch of 2.3 mm in height and 2 mm in width with flat embryonic whorl of 0.13 mm in diameter and 2.5 larval whorls. Transition to the teleoconch is marked by change in ornament. The eight whorls of the spire have irregular varices and ornament of rounded axial ribs and fine spiral ribs. The fully grown shell measures about 30 mm in height, with the outer lip expanded to a triangular wing (KIEL, 2006: fig. 5.12–5.16).

Genus *Gracilialia* SOHL, 1960

The type is *Anchura calcaris* WADE, 1926 from Ripley Formation (SOHL, 1960: pl. 11, figs. 1–4).

Distinctive characters: The shell consists of about 8 whorls which are ornamented by rounded axial ribs crossed by fine spiral lines. Varices are present in irregular distance to each other (SOHL, 1960: pl. 11, figs. 1–4, 6, 13–16). The fully grown shell has a narrow short anterior siphonal-canal. The outer lip is expanded to form a long narrow wing ending in a point and with a groove on its internal side. The point curves a little backwards, and the posterior margin of the outer lip ends on the whorls of the spire. The anterior internal margin of the outer lip can have short spikes. The protoconch has conical shape with rounded whorls.

Difference: *Gracilialia* differs from *Latiala* by having a narrower and more elongate and pointed median lobe of its outer lip. *Perissoptera* has a more rounded central wing and a narrow pointed spine next to the spire on its outer lip. In *Helicaulax* that posterior spine is even longer and the median lobe as pointed as in *Gracilialia*. The body whorl of *Drepanocheilus* has spiral keels which continue onto the curved and pointed lobe of the outer lip. *Anchura* has the outer lip with a wing that forks at its end, as is the case in *Pseudanchura* that has a more slender spire.
Gracilialia quaasii KIEL & BANDEL, 2002 from the Maastrichtian of the Western Desert in Egypt has the outer lip with the posterior spine attached to the spire for three whorls (KIEL & BANDEL, 2002: fig. 2D), while *Gracilialia latealata* (RIEDEL, 1932) from the Late Cretaceous of Mungo River, Cameroon has the posterior margin of the outer extending even further onto the spire (KIEL & BANDEL, 2002: fig. 3A, B, E, F). KIEL (2006) noted that species of *Gracilialia* may come very close in shape to that of *Latiala* when the outer lip lobe is more pointed or more rounded. He suggested that they should be regarded as sister taxa, which at Albian time appear to merge with each other.

Genus *Mexopus* KIEL & PERRILLIAT, 2001

The type is *Mexopus mexicanus* KIEL & PERRILLIAT, 2001 from the Maastrichtian of southern Mexico.

Diagnostic characters: The spire is slender and almost smooth with irregular axial ribs and fine spiral lines on the upper whorl. The callus of the inner lip of the body whorl extends in a ribbon in apical direction onto the spire up to the apex (KIEL & PERRILLIAT, 2001: fig. 4.1). The protoconch has a rounded apex and consists of several smooth rounded whorls. The outer lip extends onto the whorls of the spire, but its exact shape remains unknown, supposedly is similar to that of *Latiala*.

Remarks: *Mexopus robustus* from the same locality as the type has flatter sides of the spire and the outer lip of the aperture attached to the spire in a similar way as in *Rimella* (KIEL & PERRILLIAT, 2001: figs. 4.4–5). *Mexopus* resembles *Latiala* regarding general shell shape but has a continuation of the margin of the outer lip onto the spire as in *Rimella*, or *Kaunhowenia*.

Genus *Drepanocheilus* MEEK, 1864

The type is *Rostellaria evansi* COSSMANN, 1904 from the Maastrichtian Fox Hills Sandstone, South Dakota, USA.

Diagnostic characters: The small to medium sized shell (10 to 20 mm high) has a smooth protoconch. The early teleoconch is ornament of sloping axial ribs and fine spiral lines with varices at about each half whorl (SOHL, 1960: pl. 11, fig. 22). The body whorl is ornamented by two or more keels (in difference to *Arrhoges* with one or no keel). The upper of these keels continues onto the single, upward turned wing that forms a posterior lamella that may connect partly to the shell. The aperture is narrow and ends with a short siphonal canal in front. The inner lip of the aperture is thickened with callus forming a distinct ribbon with sharp border.

Difference: COSSMANN (1904, pl. 5, fig. 14) described *Drepanocheilus calcaratus* (SOWERBY) from the Cenomanian that resembles *Anchura* from the Cenomanian of Texas (WOODRING, 1952). WENZ (1938: fig. 2683) based *Drepanocheilus* on *Drepanocheilus americana* (EVANS & SHUMARD, 1857) from the Campanian of Fox Hill Formation. He included into this genus as subgenus among other subgenera from the Cretaceous also the living *Arrhoges*. *Anchura* resembles *Drepanocheilus* and differs in having only one keel on the body whorl, the wing of the outer lip may be longer and the ornament of the spire coarser. *Anchura whitneyensis* STEPHENSON, 1952 has a very similar aperture, *Anchura turricula* STEPHENSON, 1952 has a very similar ornament of the spire as found in *Drepanocheilus*. Both species from the Cenomanian of Texas (STEPHENSON, 1952: pl. 40, figs. 16, 17, 23) resemble *Drepanocheilus* sp. from the Paleocene of Greenland (KOLLMANN & PEEL, 1983: fig. 107 & 108). SOHL (1960, pl. 11, figs. 12 & 22) documented two species of *Drepanocheilus* from the Ripley Formation.

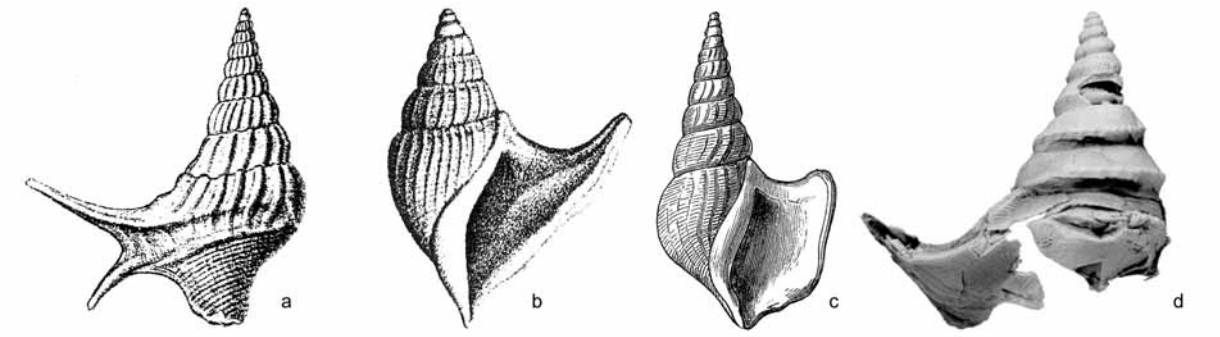

Fig. 5: a – *Anchura beisseli* taken from HOLZAPFEL, 1888; b – *Drepanocheilus analogus* taken from DESHAYES, 1866; c – *Arrhoges occidentalis* taken from CHENU, 1858; d – *Struthiochenopus bandeli* from NIELSEN, 2005.

Genus *Tulochilus* FINLAY & MARWICK, 1864

The type is *Drepanocheilus* (*Tulochilus*) *bensoni* FINLAY & MARWICK, 1937 from the Danian (Paleocene) of the Wangaloan Formation, New Zealand (BEU & MAXWELL, 1990: pl. 2, fig. e).

Diagnostic characters: The shell has an angled spire that bears oblique, blunt tubercles. The type species is about 11 mm high. The body whorl has a spiral rib as well as axial ribs. The outer lip is a narrow pointed wing as in *Drepanocheilus*. The Santonian *Tulochilus jouberti* KIEL & BANDEL, 2002 from the lower portion of the Umzamba Formation in South Africa has a protoconch with four smooth whorls. The embryonic whorl is small, the following increasing rapidly in size.

Difference: *Tulochilus* differs from *Drepanocheilus* MEEK, 1864 as well as *Arrhoges* by details of the ornament, especially of the body whorl. The axial ribs of its spire continues onto the body whorl, which also has two spiral keels which continue into the outer lip. Regarding the shape of the outer lip *Tulochilus* resembles *Anchura* but has the posterior continuation of its outer lip fully attached and short. The outer lip of *Arrhoges* is more angular, but that is probably a species specific character and variable in individuals.

Genus *Arrhoges* GABB, 1868

The type is *Chenopus occidentalis* BECK, 1836 that lives off the East coast of North America.

Diagnostic characters: The spire is high and ornamented by collabral ribs crossed by fine spiral ribs. The body whorl has three stronger spiral ribs present of which the posterior stronger ones end in the corners of the angular expanded outer lip.

Remarks: According to ABBOTT (1974) several varieties have been named which differ in regard to ornament or spiral angle. The variety *Aporrhais pespelicani bilobatus* from the North Sea is quite similar to the American species by having the median lobes fused to a wing.
PERRON (1978) studied *Arrhoges occidentalis* off-shore the North American east coast regarding its behavior on the sea floor. He found that young as well as fully grown individuals are buried in the sediment for many months of the year. Its larval shell consists of 1.5 whorls, is wider than high (0.7 mm) and has a wide umbilicus (THIRIOT-QUIEVREUX, 1980: figs. 42 & 43).
Aporrhais analoga DESHAYES, 1865 from the Eocene of the Paris Basin (Thanetian) has ornament of inclines axial ribs and a triangular wing of its outer lip with one median keel that discontinues on the whorls of the spire, resembling the American *Arrhoges occidentalis*. *Peruchilus* OLSSON, 1931 from the Oligocene of Peru as well as *Tulochilus* from the Paleogene of New Zealand resembles *Arrhoges*. From the Paleocene of Greenland three species have been described (KOLLMANN & PEEL, 1983: figs. 107–111) which resemble *Arrhoges* in regard to the shape of the spires as well as the outer lip in the body whorl.

Genus *Struthiochenopus* ZINSMEISTER & GRIFFIN, 1995

The type species is *Struthiochenopus magellanicus* ZINSMEISTER & GRIFFIN, 1995 from the Oligocene and early Miocene of Tierra del Fuego, Argentina, as defined by NIELSEN (2005).

Diagnostic character: The shell is about 35 mm high with about 9 whorls ornamented by a keel that is crossed by short axial ribs, very similar as in *Aporrhais*. The apical angle of the spire is about 45°. The aperture has one prominent posterior digitations with the spiral keel ending in its upper margin. The protoconch of *Struthiochenopus bandeli* NIELSEN, 2005 from the Miocene of Chile consists of 2.5 whorls with almost flat embryonic whorl and the larval whorl as high as wide and smooth and rounded. Transition into the teleoconch is like that in *Aporrhais pespelicani* with indistinct end of the larval shell and the begin of regular spiral ribs crossed by collabral ribs forming a regular pattern. Later on a keel develops and the body whorl has two of them. *Struthiochenopus philippi* ZINSMEISTER & GRIFFIN, 1995 from the Navidad Formation (Miocene) of central Chile is of similar size, has similar protoconch shape (NIELSEN, 2005: figs. 3.13–3.14) but has a more narrow spire (30°) and a shorter digit on its outer lip.

Difference: *Aporrhais* has three apertural digits, while *Struthiochenopus* has here a single wing- like triangular spine (*Struthiochenopus philippi*) or an angular projection as in *Struthiochenopus bandeli*. In difference to *Arrhoges* the spiral ornament of the whorls predominates with axial characters minor. *Arrhoges* in contrast has axial ribs predominating and spiral ornament is fine. The history of *Struthiochenopus* can be followed to the Late Cretaceous within the Weddelian Province (ZINSMEISTER & GRIFFIN, 1995). *Austroaporrhais* ZINSMEISTER & GRIFFIN, 1995 from the Maastrichtian to Paleocene of the Weddelian Province differs only little from *Hemichenopus* (NIELSEN, 2005). *Hemichenopus araucanum* from the Neogene of southern South America and *Peruchilus culberti* OLSSON, 1931 from the Oligocene of Chile (WENZ, 1938: fig. 2686). *Peruchilus* has a keel on the body whorl as is found in *Drepanocheilus* from the Late Cretaceous of North America, which resembles ornament of *Struthiochenopus*, and all of them resemble the living *Aporrhais occidentalis*.

Genus *Goniocheila* GABB, 1868

The type species is *Goniocheila lirata* (CONRAD, 1865) (as *Alipes*) from the Oligocene of Vicksburg, Mississippi (WENZ, 1938: fig. 2681, from CONRAD, 1865).

Diagnostic characters: The spire has nine whorls which are ornamented by rounded curved axial ribs and fine spiral lines. On the body whorl the axial ribs are swollen in the middle. The outer lip has triangular shape with a median point turned in posterior direction and the posterior canal attached to the spire (MACNEIL & DOCKERY, 1984: pl. 28, figs. 11 & 12). The shell is about 8–25 mm high.

Difference: *Aporrhais* has the outer lip with spines, *Arrhoges* has the outer lip with the same shape, but its posterior canal not attached to the spire as far up as in the case in *Goniocheila*. *Aporrhais speciosa* var. *megapolitana* BEYRICH from the Oligocene of Germany is very similar (MACNEIL & DOCKERY, 1984). *Goniocheila menthafontis* MACNEIL, 1984 also from the early Oligocene of Mississippi, resembles *Goniocheila lirata* but has the spire higher and axial ornament less strong MACNEIL & DOCKERY, 1984: pl. 15, figs. 28–31, 33), but is also larger (about up to 25 mm in comparison to about 9 mm). Regarding the shape of the outer lip it is like the type, and both differ from living *Aporrhais occidentalis* very little, but are smaller (*Aporrhais occidentalis* measures up to 50 mm, as is the case in *Aporrhais pespelicani*, but fully grown individuals of both species can also be much smaller).

Remarks: COSSMANN (1904) placed *Goniocheila* in the synonomy of *Arroghes*, while actually it has page priority over the latter (MACNEIL & DOCKERY, 1984). *Arroghes* was regarded a subgenus of *Drepanocheilus* by WENZ (1938), while SAUL & PETIT (2001) regarded it as distinct genus, and described a new species *Goniocheila wilsoni* from the Oligocene of North Carolina. According SAUL & PETIT (2001) the species of *Goniocheila* from the American Oligocene have a keel or stronger spiral ribs on their body whorl, which is supposedly not found on *Arrhoges*, otherwise differences are minute.

Genus *Hemichenopus* STEINMANN & WILCKENS, 1908

The type is *Chenopus araucanus* PHILIPPI, 1887 from the Tertiary of central Chile (NIELSEN, 2005: figs. 2.4, 2.5, 2.9)

Diagnostic character: The spire is conical with ornament of spiral keels. The shell closely resembles that of *Aporrhais* with the whorls of the spire ornamented by a keel, and two keels on the body whorl. The outer lip has two prominent digitations with gutter-like base. The posterior spine points to the side. The anterior digit lies between it and the gutter-like siphon, that forms the third spine (NIELSEN, 2005). The shell is about 20 mm high.

Remarks: *Hemichenopus zelandica* (MARSHALL, 1919) from the Eocene of New Zealand was suggested to belong to *Dicroloma* by BEU & MARSHALL (1990: pl. 6g). It has a short spire and two apertural spines NIELSEN (2005: figs. 2.6–2.8). *Hemichenopus zelandicus* has the shell up to 30 mm high with about 6 whorls and wide apical angle. The aperture has three spine-like extensions of which the anterior one represents the straight siphon. The species from the Eocene of New Zealand closely resembles *Hemichenopus araucanus* from the Miocene of Chile.

Difference: The outer lip consisting of two digits distinguishes *Hemichenopus* from *Aporrhais* with three digits, rarely even four. The similarity of the Northern Hemisphere *Aporrhais* with the Southern Hemisphere *Hemichenopus* can be interpreted as evidence for an occurrence of Aporrhaidae with several spines on their outer lip in a much wider range as today and at least since the Eocene.

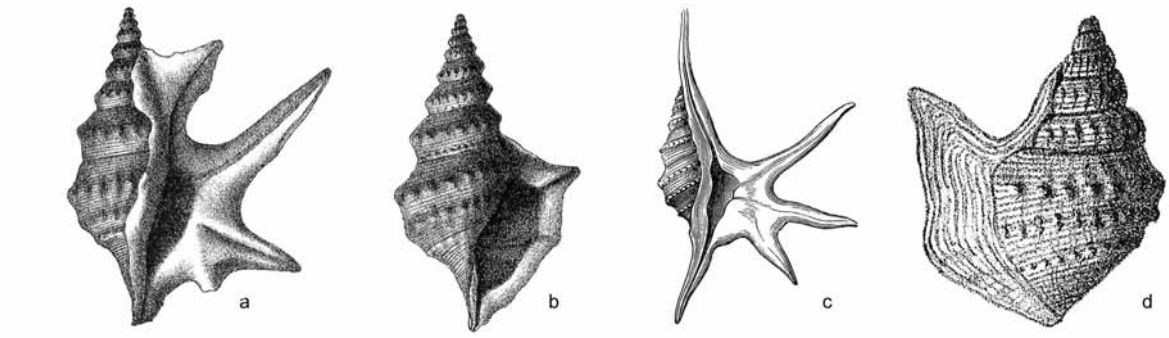

Fig. 6: a – *Aporrhais pespelicani* taken from QUENSTEDT, 1884; b – *Aporrhais pespelicani* taken from QUENSTEDT, 1884; c – *Aporrhais serresianus* taken from CHENU, 1858; d – *Aporrhais tridayctylus* taken from QUENSTEDT, 1884.

Genus *Aporrhais* DA COSTA, 1778

The type species is *Strombus pespelicani* LINNÉ, 1758 from the eastern Atlantic (Island to Mediterranean Sea) (THIELE, 1931: fig. 261; WENZ, 1938: fig. 2689).

Diagnostic characters: The solid shell has a tall spire consisting of about 10 whorls with ornament of knobs and finer spiral ridges. The last whorl occupies about half of the shell height. Its outer lip is greatly expanded into a plate shaped like the webbed foot of a bird with four or five extensions. The shell can be 50 mm high and 30 mm wide but may also be much smaller when fully grown. One of the spine-like extensions is in posterior direction and is either free or attached to the spire for some way even all the way, may be short or even extend beyond the spire. The second and third spine terminate laterally and on their outer surface lies the continuation of the keels of the body whorl. The anterior of these spines is of the same length or is shorter than the posterior one. It may consist of more or less fused two independent lobes. Spines are gutter-like on the inner side. The siphonal canal is the anterior spine. It may be short, long, straight and often inclined towards the left.
The protoconch of *Aporrhais pespelicani* is smooth with rounded whorls and consists of about three whorls which are about 1 mm high and 0.8 mm wide (Pl.1/13–16). The embryonic whorl is 0.2 mm wide and smooth ending with begin of growth lines. The early larval shell has a basal projection of the outer lip which disappears after 1.5 to 2 whorls. Spiral ornament of the early teleoconch inserts in the last half whorl still carried by the veliger larva and metamorphosis is usually documented by increase in the density of growth lines.

Remarks: Five extant species of *Aporrhais* can be recognized if *Arrhoges* is included, which lives along the North American East Coast. *Aporrhais pespelicani* lives from Norway to the African coast (Mauretania according to KRONENBERG, 1991) in the Eastern North Atlantic and in the Mediterranean Sea and the Black Sea (GRAHAM, 1988: fig. 120). *Aporrhais pesgallinae* BARNARD, 1963 lives next to the West African coast in water deeper than 100 m. *Aporrhais serresianus* (MICHAUD, 1828) lives from off Scotland to the Mediterranean Sea. *Aporrhais senegalensis* (GRAY, 1838) lives along the African coast of Senegal to Angola.
Aporrhais pespelicani lives as detritus feeder that is partly buried in muddy-sandy bottoms. In adult life the grooves on the lower side of the apertural spines and the siphonal canal serve as channels for tentacles. Water is filtered with the ingoing stream at the anterior umbilical side next to the siphonal canal and flows through the mantle cavity with the outgoing stream leaving it along the posterior canal. The outer lip with its spines or digits forms the roof of a filtering chamber and provides separation for the inhalant and exhalant currents. Water is pumped from near the anterior rostrum and leaves from a sinus at the posterior region of the aperture. Tentacles on the head are of equal length with the eyes near their bases. Locomotion of *Aporrhais* was studied by WEBER (1925), FRETTER & GRAHAM (1962), and HAEFELFINGER (1968). In case the *Aporrhais* twist around it pushes its operculum in the sediment lifts the shell and twists into right position. On hard substrate the foot takes hold with its sole and the animal is pulled around (COSEL, 1977). *Aporrhais* rights itself by quickly extending the foot toward the substrate inserting the operculum into the substrate and flipping the foot laterally.

Differences: *Aporrhais pesgallinae* with its posterior spine not attached to the spire resembles *Cuphoselenus tetracer* that lived 150 Million years before on the northern shelf region of the Tethys Ocean. *Aporrhais pespelicani* differs from *Aporrhais pesgallinae* by having less slender spines and by the spine next to the siphon split into two independent ones. The aperture usually has three spines and a spine-like siphon. Sometimes an additional short spine is present between the two spines next to siphon. The latter is straight or inclined, which creates as transitions to *Aporrhais serresianus* with four, sometimes even five elongate and slender spines and the siphon. Its shells can be up to 50 mm high, but may also grow to only about half that size. The spine next to the siphon sometimes may have a short additional spine at its base. The posterior spine of *Aporrhais serresianus* may be free of the spire as the case in *Aporrhais pesgallinae* or it may partly attach to the spire as in *Aporrhais pespelicani*. The outer lip of *Aporrhais senegalensis* from the African coast is more compact with four spines of which the posterior is attached to the spire almost to its top. The shell is only about 25 mm high (COSEL, 1977).
Aporrhais meridionalis (BASTEROT, 1825) from the Miocene with two prominent spiral ribs on the body whorl ending in the median spines of the outer lip resemble *Aporrhais pesgallinae* and *Aporrhais senegalensis* with similar ornament. In *Aporrhais uttingeriana* (RISSO, 1826) from the Pliocene of Italy has the median spines are united by lamella and also the posterior spine is attached to the spire and may be even longer than the spire is high. SOLSONA et al. (1999) regarded it the same species as *Aporrhais meridionalis*.
Aporrhais pespelicani did not change much for more than 15 Million years. It or very similar species lived in Europe at Mid Miocene time in the warm Paratethys sea (STRAUSZ, 1966; BALUK, 1995; SOLSONA et al., 1999). *Aporrhais speciosa* (SCHLOTHEIM, 1820) from the English Oligocene has the two median spines fused to each other. The most posterior spine its attached to the spire (illustration in WIENEKE, 2007). This species and *Aporrhais megapolitana* BEYRICH, 1854 from the Oligocene (Chattian) of NE-Germany have similar protoconchs (WIENEKE 2007, and Pl. 4/9–10), which also resembles those of living *Aporrhais* (Pl. 1/14). The posterior spine of *Aporrhais margerini* (DE KONINCK, 1838) from the Oligocene of Belgium reaches the apex. Another species from the Oligocene of the northern Alps that resembles *Aporrhais senegalensis* and has been called *Aporrhais haeringensis* (GÜMBEL, 1861), (LÖFFLER, 1999). *Aporrhais claredonensis* (WRIGLEY, 1938) from London Clay is only 15 mm high and closely resembles the small variety of the *Aporrhais pespelicani* documented by BALUK (1995: pl. 7, figs. 4–6). A similar small form from the Middle Miocene of western

Germany was called *Aporrhais dingdenensis* MARQUET, GRIGIS & LANDAU, 2002. Quite like the latter is *Aporrhais scaldensis* VAN REGTEREN ALTENA, 1954 from the Pliocene of Holland that also has a small shell (VAN REGTEREN ALTENA, 1954). It does not differ much from *Aporrhais alata* EICHWALD, 1830 from the Miocene of western Germany (JANSSEN, 1984: pl. 7, fig. 18, pl. 52, fig. 3a–b). *Aporrhais callosa* (ROTH VON TELEGD, 1915) is covered by callus deposits and *Strombopugnellus digitolabrum* KOCH, 1911, from the Late Oligocene of Hungary represents a species with even thicker callus coating (BALDI, 1963; WENZ, 1938). Among the unusual individuals of living *Aporrhais pespelicani* such callus covered varieties are also rarely noted.

Genus *Digitolabrum* COSSMANN, 1904

The type is *Rostellaria princeps* VASSEUR, 1880 from the Eocene Lutetian of the Paris Basin (COSSMANN, 1904: pl. 3, figs. 13 & 14; WENZ, 1938: fig. 2725).

Diagnostic characters: The spire is pointed and its about 12 whorls are cornered with a fine regular pattern of axial and spiral ribs. The siphon is straight and resembles a narrow spine. The margin of the outer lip of the body whorl carries long and slender grooved spines on its posterior part and short spines on the anterior part in case of *Digitolabrum zigni* (GREGORIO, 1880) that has three to five slender spines, while *Digitolabrum princeps* has only two elongate posterior spines. The anterior spines are reduced to short spikes. *Digitolabrum zigni* from the Early Eocene of Italy has long spines, the lower of which forms around 90° with the siphon (SAVAZZI, 1991: fig. 6K). All spines have a central channel and the posterior spine is free of the spire (see *Rostellaria gracilidigitata* of DESHAYES (1830–1832, pl. 92, fig. 10). Species of *Digitolabrum* may carry only short spines on their outer lip.

Remarks: COSSMANN (1904) included *Digitolabrum* as subgenus of *Dientomochilus*, but the type of the latter is *Dientomochilus ornatus* from the Eocene of the Paris Basin with *Rimella*-like shape. It has a relatively short spire and comparatively wide outer lip (see Rimellinae below).

Genus *Araeodactylus* HARRIS & BURROWS, 1891

The type is *Ischnodactylus plateaui* COSSMANN, 1889 from the Paleocene from France (COSSMANN, 1904: pl. 5, figs. 16 & 20).

Diagnostic characters: The slender shell with narrow spire has its body whorl with a long straight spine-like siphon. With about 90° to it and the axis of coiling, a spine is attached to the outer lip with gutter like shape. A second spine points backwards and is fully attached to the spire continuing to the apex. The spire consists of more than ten whorls with ornament of spiral ribs of which a median one forms a corner.

Difference: The spines on the outer lip, one arranged in vertical orientation to the axis of shell coiling and the other attached to the spire characterizes *Araedactylus*, while the spire resembles that of *Digitolabrum*. Both genera are well differentiated from each other and also from *Aporrhais*, but appear to be more related to the Aporrhaidae than with any other group.

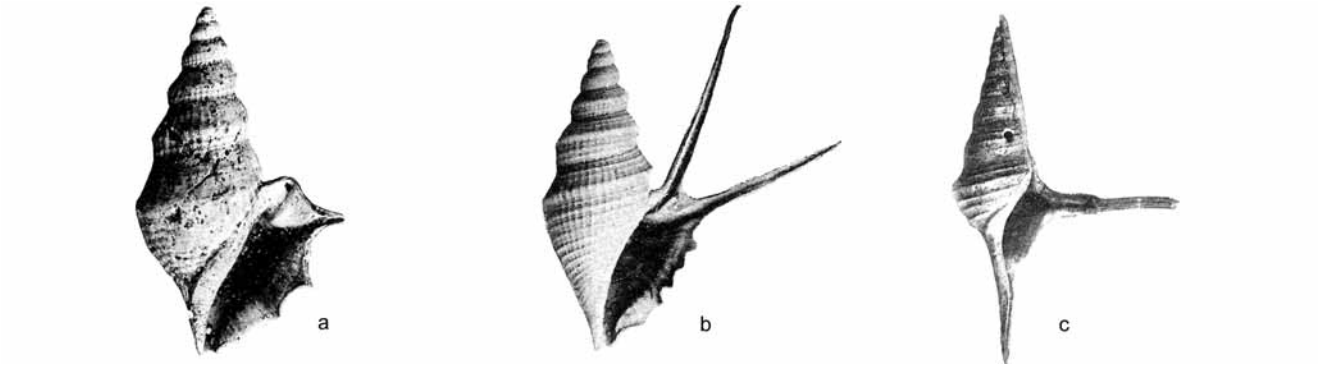

Fig. 7: a – *Digitolabrum boutillieri* taken from COSSMANN, 1904; b – *Digitolabrum princeps* taken from COSSMANN, 1904; c – *Araeodactylus plateaui* taken from COSSMANN, 1904.

2.4 Family Struthiolariidae GABB, 1868 (= FISCHER, 1884)

Diagnostic characters: Thick ovate shells with large aperture and stout whorls. It has the aperture heavily surrounded with polished callus and the apertural margin is detached from the shell as a continuous ring. The siphon is a short notch. The operculum is clawed and used in righting when the overturned shell is heaved back upright. The protoconch is simple and smooth without larval shell that is not sharply distinct from the ornamented teleoconch (Pl. 7/14–15).

Remarks: Members of the family Struthiolariidae from the southern Hemisphere are represented by *Struthiolaria*, and *Pelicaria* from New Zealand, *Tylospira* from southern Australia, and *Perissodonta* with circum-Antarctic range (MORTON, 1956; WELLS, 1998). Species feed from filtering suspended material from the water with their gill (MORTON, 1951). Movement is usually by creeping on the broad sole of the foot, but the claw of the operculum is also used for raising the shell of the ground and leaping forward, not only for defense (MORTON, 1956). Fossil species are traced to the Miocene in Australia (DARRAGH, 1991), and the Paleogene of New Zealand and Chile (ZINSMEISTER & CAMACHO, 1980; NIELSEN, 2005).

Genus *Struthiolaria* LAMARCK, 1816

The type is *Struthiolaria papulosa* (MARTYN, 1784) with benthic large and clumsy protoconch and relative high teleoconch. The tall spires shell has markedly stepped whorls. The callus of the inner lip expands onto the last whorl, and the shell is u to 8 cm high. *Struthiolaria papulosa* has benthic young hatching. The spawn is retained in a brood pouch in the mantle, where eggs incubate.
Struthiolaria is found in the latest Oligocene of New Zealand and has since lived there (BEU & MAXWELL, 1990). *Struthiolaria calcar* HUTTON, 1886 from the Miocene is very similar to the living species and other species were also present at that time and many species have lived in the region since that time.

Genus *Pelicaria* GRAY, 1857

The type is *Pelicaria vermis* (MARTYN, 1784) from South Australia and New Zealand (WELLS, 1998: fig. 15.122). The small and solid shell has a high spire with impressed sutures. It has a simple multi-coiled protoconch and relative short teleoconch that resembles the earliest species of the genus known from the Paleocene of New Zealand (BEU & MAXWELL, 1990). Females in both species have a brood pouch in the mantle cavity where eggs are incubated (MORTON, 1950). The protoconch of *Pelicaria vermis* has a little more than one whorl (Pl. 7/14–15). *Pelicaria* has been living in New Zealand since the Miocene (MORTON & MILLER, 1968). Fossil species are traced to the Miocene in Australia (DARRAGH, 1991).
Pelicaria canaliculata (ZITTEL, 1864) from the Pliocene of New Zealand has quadrate whorls and a thickened apertural margin and conspicuous ornament is by spiral ribs, and there have been quite a few more species since that time (BEU & MAXWELL, 1990: pl. 42a–c, e). The difference of *Pelicaria* from species placed with *Struthiolaria* is, sometimes, quite minute, and today species of both genera in New Zealand live near the shore and in the low tidal region (MORTON & MILLER, 1968). In natural position the animal lies at rest a few centimeters below the surface with open inhalant and exhalent canals produced by the proboscis and stabilized by mucus lining the burrow. A long slender tentacle of the mantle edge reaches through the exhalent channel probing the surrounding. The head has two long thin tentacles with the eyes at their base. Food particles are filtered by a mucus sheet that is expanded over the surface of the gill. Particles are trapped by the mucus and are transported by cilia to the base of the gill filaments. Here they form a continuous food string that passes into a food groove running forward along the floor of the mantle cavity. It ends behind the right tentacle of the head. The collected organisms of the phytoplankton and other particles are plucked by the mouth of the elongate proboscis and gripped by the teeth of the radula.

Genus *Tylospira* HARRIS, 1897

The type is *Buccinum scutulatum* MARTYN, 1786, representing a littoriniform shell with oval aperture and spire almost as high as last whorl. The siphon is short and wide the outer lip sinuous with lobe in its lower part and thickened and the inner lip expanded as callus. Ornament on the body whorl consists of curving growth lines and on the spire there is a spiral keel and spiral finer ribs, usually corroded in the fully grown shell. Size about 50 mm and higher than wide. *Tylospira* from the Pliocene of South Australia is shorter and has more angular whorls (DARRAGH, 1991).

Genus *Monalaria* MARWICK, 1924

The type is *Struthiolaria concinna* SUTER, 1917 from the Eocene of New Zealand. Here the shell is about 30 to 40 m high and not quite as wide with up to 6 whorls of the teleoconch. The spire is short and ornamented by axial ribs crossed by finer spiral ribs. The aperture is rounded and thickened with broad anterior canal and thick callus of the inner lip. *Monalaria monalaria* MARWICK, 1924 from the Eocene of New Zealand is very similar (BEU & MAXWELL, 1990: pl. 6a & b). Here the early whorls of the teleoconch have spiral ornament and later curved axial ribs are added. The aperture is marginally thickened and the siphon wide and short.

Genus *Conchothyra* Hutton, 1877

The type is *Pugnellus australis* MARSHALL, 1916 from the Paleocene of New Zealand (BEU & MAXWELL, 1990: pl. 2, fig. 2g & h). *Conchothyra* is quite similar to *Struthiolaria*, while *Pelicaria* is more slender and appears in the Late Miocene of New Zealand (BEU & MAXWELL, 1990). Also *Monalaria concinna* resembles *Conchothyra australis* (BEU & MAXWELL, 1990: pl. 6a & b) with small differences in the height of the spire. *Struthiolaria* appears later and is found since the late Oligocene of New Zealand (BEU & MAXWELL, 1990: pl. 15a).

Genus *Perissodonta* Martens, 1878

The type is *Struthiolaria mirabilis* SMITH, 1875 living at Kerguelen Islands. NIELSEN (2005: fig. 4) described the Miocene species *Perissodonta ameghinoi* (IHERING, 1897) anew and also *Perissodonta chilensis* (PHILIPPI, 1887) which both are in all essential features as the modern living species. It had a high diversity during the Eocene of the Weddelian Province (ZINSMEISTER & CAMACHO, 1980). The two living species connect to the Miocene ones from deep water environment of Chile and the Eocene species that lived in the high southern seas (NIELSEN, 2005).

Genus *Antarctodarwinella* ZINSMEISTER, 1976

The semi-globular shell is heavy with low conical spire and about 5 whorls. Ornament consists by strong growth increments on the body whorls which reflect the posterior sinus of the outer lip. The callus of the inner lip is thick and the siphon is a wide short canal. The type species is *Antarctodarwinella ellioti* ZINSMEISTER, 1976 from the Eocene-Oligocene of Seymour Island, Antarctica that is very similar to *Antarcodarwinella nordenskjoldi* (WILCKENS, 1911) and perhaps a little more rounded (ZINSMEISTER, 1976: figs. 1–8). Both resemble *Conchothyra* that has a less rounded inner lip and a spiral rib with nodes on its spire.

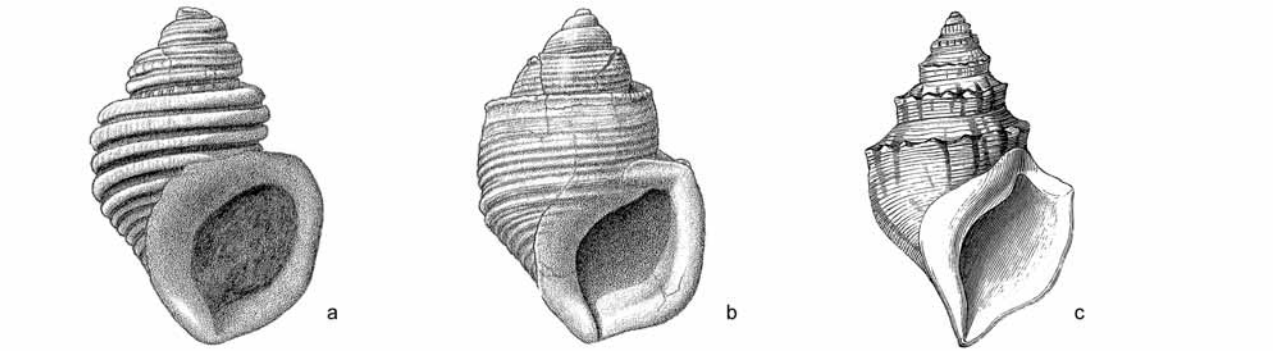

Fig. 8: a – *Pelicaria canaliculata* copied from BEU & MAXWELL, 1990; b – *Pelicaria zelandiae* copied from BEU & MAXWELL, 1990; c – *Struthiolaria papulosa* copied from CHENU, 1859.

2.5 Family Pterocerellidae n. fam.

Diagnostic characters: The spire consists of angular whorls with two or three spiral keels and relatively wide apical angle. The outer lip has three spikes with keels on the upper side and a groove on the lower side and the siphon is twisted upwards and to the side. In case of *Pterocerella* the marginal spines of the aperture may branch and be interconnected to each other by a web, in case of *Tessarolax* the spines have no lamellae on their sides.

The protoconch is relatively wide with relatively large and lowly coiled embryonic whorl, smooth rounded larval shell of more than 1.5 mm in width and height and abrupt transition from larval shell to the teleoconch. Species existed from Mid Cretaceous to the end of the Cretaceous.

Here *Pterocerella,* and *Tessarolax* are included, while *Tridactylus* is probably a synonym of *Pterocerella*, and *Ceratosiphon* can considered synonymous with *Tessalolax*.

Derivatio nominis: The family is named after *Pterocerella* which represents the genus of the group that is best known.

Genus *Pterocerella* MEEK, 1864

The type species is *Harpago tippana* CONRAD, 1858 from the Maastrichtian of the Ripley Formation in Mississippi, USA (SOHL, 1960).

Diagnostic characters: The shell has a spire of moderate height (about 20 mm) and angular smooth whorls smooth with keels. The outer lip extends into six flat and thin digitations. They are marginally fused in the two posterior and two anterior digits and the median one is single. The protoconch is large, dome-shaped with three to four smooth whorls and straight outer lip. Change from protoconch to teleoconch is seen in the begin of the spiral keels in the ornament of the later (Pl. 2/1–3).

Pterocerella maryea DOCKERY, 1993 has a rounded protoconch with about 3.5 whorls (DOCKERY, 1993: pl. 16, figs. 8 & 9). The slightly younger *Pterocerella poinsettiformis* STEPHENSON, 1941 has a wider spire with smooth whorls and three spiral keels (DOCKERY, 1993: pl. 16, figs. 6 & 7) and a protoconch also with 3.5 whorls which are evenly rounded and smooth. Transition to the teleoconch is abrupt with straight margin and keels on the teleoconch initiating at it. *Pterocerella tippana* as described by SOHL (1960: pl. 13, figs. 3, 5, 19) resembles the other two species, but also *Tridactylus*.

Remarks: *Pterocerella* has been observed on both sides of the northern Atlantic Ocean in Campanian to Maastrichtian sediments (HOLZAPFEL, 1888; DOCKERY, 1993: pl. 16, figs. 4–9; KIEL & BANDEL, 2002), (Fig. 3c). The large and rounded protoconch of *Pterocerella maryea* resembles that of *Pugnellus*, but teleoconch shape is quite different.
COSSMANN (1904) included *Aporrhais macrostoma* SOWERBY from the Cenomanian of England with *Pterocerella*. *Tridactylus* GARDNER, 1875 has the type species *Aporrhais cingulata* PICTET & ROUX, 1885 from the Albian. *Rostellaria arachnoides* MÜLLER, 1847 from the Campanian of Vaals was also placed in that genus (COSSMANN, 1904: pl. 6, fig. 5), while it belongs to *Pterocerella*. The latter noted that *Tridactylus* is quite similar to *Pterocerella*, but still placed *Pterocerella* as subgenus to *Chenopus* (= *Aporrhais*) and *Tridactylus* as subgenus with *Dicroloma*. HOLZAPFEL (1888: pl. 13, figs. 1–8) placed species of *Pterocerella* from the Vaals Greensand with *Cultrigera* BÖHM, 1885, which according to WENZ (1938) is a synonym of *Tridactylus*. *Pterocerella arachnoides* resembles *Pterocerella poinsettiformis* from Mississippi, and *Pterocerella nilssoni* (MÜLLER, 1847) from Aachen has the narrow spire of *Pterocerella maryea*.

Genus *Tessarolax* GABB, 1864

The type is *Aporrhais* (*Tessarolax*) *distorta* GABB, 1864 from the Late Cretaceous (Campanian) of USA (WENZ, 1938: fig. 2690). According to COSSMANN (1904) *Ceratosiphon* GILL, 1870 is a synonym with type from the late early Cretaceous, as supported by KIEL (2006).

Distinctive characters: The conical spire has ornament of two spiral keels and the outer lip has spines of which the posterior one is attached to the spire and the anterior one forms the siphon and is bent to the outside. Two more spines are in the middle part of the lip. The protoconch is conical, smooth and change to the teleoconch is indicated by change in ornament. COSSMANN (1904) suggested as very close to the type *Rostellaria retusa* SOWERBY, 1836 from the Mid-Cretaceous (Albian) of Folkstone in England which was found to be practically identical with *Tessarolax retusa* (SOWERBY, 1836) from the Albian of Madagascar (KIEL, 2006: figs. 6.1–6.3). Its conical protoconch consists of about 3.5 rounded smooth whorls, which have collabral ornament on the larval whorls. The outer lip is convex with a strong lobe in its anterior part. The teleoconch is conical with about five whorls and ornament of two keel-like spiral ribs and smaller ones between them. The outer lip of the body whorl

has three spines, of which the posterior one is attached to the spire, the median one is almost straight, and the anterior one forms the rostrum that is bent to the outward side.

Remarks: KIEL (2006) considered *Tessarolax retusa* from Madagascar to represent the same species as that described by GARDNER (1875) from England (Isle of White). *Tessarolax* contains some species which had been placed in *Ceratosiphon* GILL, 1870 by KASE & MAEDA (1980) and again by KOLLMANN (2005). It would be based on the type species *Pterocera moreausiana* ORBIGNY, 1843 from Mid-Cretaceous of Germany and France. Its description of the spire with conical shape and corner and fine spiral finer ribs as ornament, the siphon long and curved towards the left, and the outer lip with three spines of which the apical one lies on the spire forming a canal agrees with that of *Tessarolax*. KOLLMANN (2005) joined *Tessarolax retusa* and *Pterocera bicarinata* (DESHAYES, 1866) in *Ceratosiphon*. Here, in contrast, the interpretation of KIEL (2006) is accepted.

2.6 Family Pugnellidae KIEL & BANDEL, 1999

The family is based on *Pugnellus* CONRAD, 1860 with the type species *Pugnellus densatus* CONRAD, 1860 from the Maastrichtian Ripley Formation of Mississippi.

Diagnostic characters: The shell has a low spire, is bulbous with an enlarged and thickened outer lip, often with horn-like extensions, and a callus-coated inner lip. The callus is commonly spread out to cover large parts of the shell (SOHL, 1960: pl. 14, figs. 4, 5, 9, 13–16, 19, 20; KIEL & BANDEL, 1999). The protoconch of *Pugnellus* is conical and composed of four smooth convex whorls (DOCKERY, 1993: pl. 12, figs. 3 & 4). It is wider than high, has curving growth lines on its larval shell and a corner to the base.

Remarks: The Pugnellidae have started their evolutionary history with *Gymnarus* and *Lispodesthes* in the Cenomanian (STEPHENSON, 1952; KASE, 1984), and occurred to the end of the Cretaceous (SOHL, 1960; DOCKERY, 1983; KIEL & BANDEL, 1999).

Subfamily Pugnellinae KIEL & BANDEL, 1999

Here callus may cover the fully grown shell all over. In the Pugnellinae, the siphonal canal is short and open, often accompanied by a lobe, well seen in *Gymnarus*, *Pyctes*, *Bizarrus* less well in *Pugnellus*, *Perustrombus* and *Tephlon*. The genera of the Pugnellinae can be distinguished from each other by the lobes and projections of their outer lip. *Gymnarus* has one long lobe with a twist to the inside of its end, as in *Bizarrus*, but here altered by callus deposits. *Pugnellus* has a wide wing, *Pyctes* has two lobes, as in case of *Bizarrus*, but in the latter the posterior lobe is strongly altered by callus additions. In *Perustrombus* the outer lip is thickened and continues evenly covering also the spire all the way to the siphon.
One could argue, that all the genera can also be included in one genus *Pugnellus* with short spire and thick callus cover on the shell of the adult as was suggested by WENZ (1938). Differences of species or subgenera would regard the size of the projections of the outer lip, the more or less prominent presence of the stromboid notch and the thickness of the callus cover. But as was shown by KIEL & BANDEL (1999) the systematic categories of the Pugnellidae can be recognized over a long period of time ranging from the Cenomanian to the end of the Cretaceous, perhaps even into the Paleogene, and they occur at various far distant places on the globe.

Genus *Pugnellus* CONRAD, 1860

The type species is *Strombus densatus* CONRAD, 1858 from the Maastrichtian Ripley Formation of Mississippi, USA (COSSMANN, 1904: pl. 7, figs. 4 & 5; SOHL, 1960: pl. 14; DOCKERY, 1993: pl. 12, figs. 3 & 4).

Diagnostic characters: The spire is low and the body whorl has a thick and expanded outer lip. Callus coats the body in adult shells which is about 30 mm in height and obscures its original shape and ornament as well as the shape of the spire. The siphonal canal is thickened wide and short. The outer lip has a larger posterior lobe and an almost straight anterior part ending in the anterior sinus resembling a stromboid notch. The protoconch is conical and large, composed of four smooth whorls. The teleoconch has five whorls. The first juveniles which are not covered by callus deposits have ornament of fine closely spaced spiral lines, later collabral coarse fold like ribs are developed. These can also still be recognized under the cover of the callus.

Remarks: *Pugnellus* has no horn on the outer lip, which distinguishes it from *Gymnarus* GABB, 1864. The first *Pugnellus* appeared in the Turonian of SE North America with *Pugnellus densatus* and existed to the Maastrichtian. *Pugnellus klitzschi* KIEL & BANDEL, 1999 from the Maastrichtian of Egypt differs by the shape of its siphonal canal, which is upwards bent (KIEL & BANDEL, 1999).

Genus *Gymnarus* GABB, 1868

The type is *Pugnellus manubriatus* GABB, 1864 from the Cenomanian of California.

Distinctive characters: The body whorl occupied about two thirds of total shell height. Ornament consists of coarse axial ribs and fine spiral lines in the juvenile shell (POPENOE, 1983). The outer lip is expanded thickened and with posterior lobe and anterior sinus often with a low lobe in its center. The outer lobe is twisted inwards to form a hook. The callus of the inner lip is expanded to cover part of the spire. The siphonal groove is short.

Remarks: *Gymnarus* existed to the Maastrichtian and differs from *Pugnellus* by the lobe on its outer lip. *Gymnarus abnormalis* (WADE, 1926) from the Ripley Formation is described by SOHL (1960) and DOCKERY (1993: pl. 12, figs. 5–9) and represents the largest species of the genus (65 mm). Species such as *Gymnarus auriculatus* (WOODS, 1906) and *Gymnarus congolensis* (BEBION, 1956) from the Campanian of South Africa, and *Gymnarus fraasi* (RIEDEL, 1932) from Cameroon have been described by KIEL & BANDEL (1999: fig. 2).The species are all quite similar to each other.

Genus *Pyktes* POPENOE, 1983

The type species is *Pyctes aspris* POPENOE, 1983 from the Coniacian of California, USA.

Diagnostic characters: The shell resembles that of *Gymnarus* but has two lobes on its outer lip. The posterior projection is the larger one and the anterior projection is smaller. The adult shell is covered by callus. The juvenile shell has ornament of fine spiral lines and a carina at the suture (POPENOE, 1983).

Pyktes appeared in the Turonian of California, is found in the Santonian of South Africa with *Pyctes popenoi* KIEL & BANDEL, 1999. It differs only little from *Gymnarus* by its two projections on the outer lip. According to POPENOE (1983) the ornament of the spire is spiral, which was not confirmed by KIEL & BANDEL (1999: fig. 2J–L).

Genus *Torgnellus* OLSSON, 1944

The type species is *Torgnellus peruvianus* OLSSON, 1944 from the Maastrichtian of northern Peru.

Diagnostic characters: The pugnellid shell has a heavy cover of callus deposits on its shell and no ornament. *Torgnellus* is endemic in northern Peru and appears to be a descendant of the West African *Gymnarus* that reduced all ornament on spire and body whorl (KIEL & BANDEL, 1999: figs. 2D & 2E).

Genus *Perustrombus* OLLSON, 1944

The type species is *Perustrombus wheeleri* OLLSON, 1944 from the Maastrichtian of northern Peru and species also lived in Africa and India.

Diagnostic characters: The spire is short and the fully grown shell completely covered by callus. The shell resembles that of *Erato* but the inner side of the aperture is smooth. The spire is totally concealed and the siphon is a short open straight canal. *Perustrombus africanus* KIEL & BANDEL, 1999 from the Maastrichtian of the Eastern Desert of Egypt and *Perustrombus indicus* KIEL & BANDEL, 1999 from the Kallankurichchi Formation of Southern India both had an about up to 25 mm high shell (KIEL & BANDEL, 1999: fig. 3G, H, J, K).

Difference: *Perustrombus* OLLSON, 1944 differs from *Pugnellus* in the spire/body whorl relation which is one to three for *Pugnellus* and one to five for *Perustrombus*. *Pyktes* has a second extension on the outer lip.

Genus *Bizarrus* KIEL & BANDEL, 1999

The type is *Pugnellus dietrichi* RIEDEL, 1932 from the Coniacian of Cameroon (KIEL & BANDEL, 1999: fig. 3F).

Diagnostic characters: The shell is totally covered by thick layer of callus and the outer lip provided with an internal wide groove. The anterior lobe of the outer lip has a small projection next to the stromboid notch. Distinctive is the smooth shell surface which consist of the callus cover forming grooves on the outer lip. *Bizarrus dietrichi* and *Bizarrus incertus* (RIEDEL, 1932) are from the Late Cretaceous of Mungo River, of Cameroon (KIEL & BANDEL, 1999: fig. 3A, B, F).

Remarks: *Bizarrus* first appeared in the Coniacian of Cameroon and it and is known from the Maastrichtian of Morocco and USA. It probably descended from *Gymnarus* by reduction of the ribs and by enlarging the posterior horn.

Genus *Tephlon* POPENOE, 1983

The type is *Tephlon tumidus* (GABB, 1860) from the Maastrichtian of Quiriquina Formation, Chile.

Diagnostic characters: The fully grown shell has the whorls of its spire with a median corner bearing tubercles and strong growth lines. The extended outer lip has a single spur-shaped posterior and lateral spine that is bent backwards in the central part of the outer lip. Adult shells are covered with callus.

Differences: *Tephlon tumidus* has a fairly high spire and differs markedly from all others pugnellids especially by the ridge on its spire (KIEL & BANDEL, 1999: fig. 4A–E; BANDEL & STINNESBECK, 2000: pl. 1D & E). *Tephlon* occurs only in the Maastrichtian of Chile and may represent a long isolated descendant of an early Indo-Pacific *Gymnarus.*

Remarks: *Pugnellus hauthali* WILCKENS, 1905 from the Senonian of Southern Patagonia can be interpreted to represent an intermediate species between *Gymnarus* and the Weddellian *Conchothyra*, which in turn could quite possibly represent the ancestor to *Antarctodarwinella*. If so the range of the Pugnellidae would be extended to the Eocene (KIEL & BANDEL, 1999). The Struthiolariidae could thus be interpreted to have descended from them and not the Aporrhaidae. *Antarctodarwinella* shares a number of features with representatives of the Struthiolariidae, such as a massive callus, blunt slightly produced wing, and obsolete spiral sculpture (ZINSMEISTER & CAMACHO, 1980). They suggested that it may have diverged at an early date from the main evolutionary line of *Struthiolarella*.

Subfamily Tundorinae n. subfam.

Diagnostic characters: Terminate growth with spines on the outer lip places the Tundorinae with the Stromboidea. Distinct are the short spire with rounded whorls granulated spiral ribs and low sutures. The aperture has three free spines and a long siphon that looks very similar to these, and one posterior spine that is totally attached to the spire. This attached spine is the continues into a callus ridge that forms the border of a smooth callus of the inner lip that covers only the posterior inner side of the shell.

Derivatio nomins: The subfamily is named after *Tundora* which is the best known.

Differences: The smooth callus that covers only the apical part on the lower side of the shell and the continuation of its outer margin across the apex into the ridge formed by the attached posterior spine of the outer lip is not known from any other member of the Stromboidea. Callus covering the shell in the Pugnellidae

Lispodesthes may be covered by such a thick external layer of callus that every part of the former shell surface is well rounded and smooth, but the two distinct projections of the outer lip can still be recognized. In case the shell is not so strongly coated over by callus the ornament exposed consists of spiral ribs. This connects *Lispodesthes* with *Tundora* that has only a relatively small and local callus cover of its shell. Both together are here united in the Tundorinae n. subfam.

Genus *Lispodesthes* WHITE, 1876

The type species is *Anchura nuptialis* WHITE, 1876 from the mid Late Cretaceous of New Mexico (WENZ, 1938: fig. 2692).

Diagnostic characters: The shell has a conical spire and shorter conical base with rounded corners and a long narrow curving siphon in front and two projecting spurs on the middle outer lip. When not fully grown whorls increase rapidly in diameter have rounded sides and shallow sutures. Ornament consists of spiral ribs and the apical angle is about 40°. When after little more than four whorls of the teleoconch the shell has reached its final size the aperture has two spines, one larger one curves towards the apex, and a smaller one towards the siphon. All shell surface may than become covered by a layer of callus. Callus growth begins along the continuation of the posterior end of the outer lip onto the spire on one side and the spreading callus of the inner lip on the other side. The last parts of the shell surface to be covered by callus lie on the side above the aperture. The callus of the inner lip spreads over the shell surface until it meets with the margin of the posterior continuation of the outer lip onto the spire. When coming close to each other there may still be a groove, which later also disappears and the shell surface is polished and smooth all over.

Lispodesthes panda STEPHENSON, 1952 and *Lispodesthes patula* STEPHENSON, 1952 from the Cenomanian of Texas have preserved intermediate growth stages with parts of the ornament of the shell still visible (STEPHENSON, 1952: pl. 39, figs. 1–6, 12–16). Here the growth stage in which the backside of the shell is still largely free of callus, and the callus ridge of the outer lip onto the spire is seen in his fig. 4 and fig. 6. Remnants of spiral ornament are seen in fig. 13 and fig. 15, and the groove formed when both callus layer touch is seen in fig. 16. Callus covering the shell completely is illustrated in fig. 14. The difference between both species may actually lie only in more or less expanded callus cover. *Lispodesthes lilipus* KIEL & PERRILLIAT, 2001 from the Maastrichtian of Mexico is about 2 cm high and consists of six whorls with the last whorl twice as high as the spire (KIEL & PERRILLIAT, 2001: figs. 3–5). The species is close to *Lispodesthes amplus* DOCKERY, 1993 from Coffee Sand of Mississippi (DOCKERY, 1993: pl. 13, figs.1–2) that is more than 60 mm high, in contrast to the three times smaller species from Mexico. Both these species represent fully adult shells with callus coating them with a smooth polish all over.

Genus *Tundora* STEPHENSON, 1941

The type species is *Tundora tuberculata* STEPHENSON, 1941 as illustrated by DOCKERY (1993: pl. 27, figs. 1–2, pl. 40, figs. 1–2) from Ripley Formation (Campanian-Maastrichtian).

Diagnostic characters: The ovoid shell with low spire has ornament of its whorls with numerous spiral ribs. The body whorls has three spine-like grooved projections of the outer lip, the two spines with spiral keels ending on them, and the third representing the siphon. A callus ridge in the continuation of the posterior edge of the outer lip. The inner lip is expanded to form a callus with a marginal ridge that covers the inner side of the shell including its apex.

Difference: The short and wide spire resembles that of *Tessarolax* and *Pterocerella*, but spiral ornament on rounded whorls and callus of the inner lip forming a marginally thickened pad that covers the shell to the spire is quite distinctive to *Tundora*.

2.7 Family Rostellariidae GABB, 1868

Diagnostic characters: The shell is slender fusiform with high spire and the body whorl ovoid. Its growth is terminate. On the final whorl the species specific characters are developed. The siphonal canal is an open groove that is short with the outer side longer than the inner side in Rimellinae and is a long mostly straight canal in Rostellariinae and Calyptraphorinae. The posterior end of the aperture usually continues in a narrow canal that continues onto the spire, with the only exception of *Strombolaria*. The apical canal may be straight or curving, short or long, with its sides spread out onto the shell in case of the Calyptraphorinae. The outer lip is thickened and may or may not have a basal sinus (stromboid notch) and may or may not bear wrinkles, ridges or spines.

The family is based on *Tibia fusa* (LINNÉ, 1758), the type to *Rostellaria* LAMARCK, 1799 that had been described a year before as *Tibia* RÖDING, 1798.

Rostellariidae is recognized from the Late Cretaceous (Maastrichtian) to the Recent and three subfamilies are distinguished. The Rimellinae STEWART, 1927 are known since the Cretaceous, Calyptraphorinae n. subfam. appeared at about the same time and disappeared with the end of the Eocene, and the Rostellariinae GABB, 1868 are known from the Oligocene, perhaps from the Eocene onward. *Calyptraphorus* and related genera are interpreted to belong to the Rostellariidae, Calyptraphorinae n. subfam. connected to members of the subfamilies Rostellariinae and Rimellinae.

Remarks: GABB (1868) suggested the Rostellariinae based on *Rostellaria*. COSSMANN (1904) are distinguished in the genus *Rostellaria* several subgenera (of two levels) such as *Sulcogladius* SACCO, 1893, *Amplogladius* COSSMANN, 1889 (based on a juvenile), *Hippochrenes* MONTFORT, 1810, *Wateletia* COSSMANN, 1899, *Calyptraphorus* CONRAD, 1857, and *Semiterebellum* COSSMANN, 1894. Of these only *Rostellaria, Sulcogladius* and *Calyptraphorus* are here considered to belong with the Rostellariidae. WENZ (1938) included in *Tibia* (= *Rostellaria*) several additional subgenera such as *Rostellariella* THIELE, 1929 and several fossil taxa such as *Chedevillia* COSSMANN, 1906, *Aulacodiscus* DOUVILLÉ, 1923, and *Terebellopsis* LEYMERIE, 1846, and also *Calyptraphorus* and *Hippochrenes*. Of these the later genus is considered to represent the characteristic genus of the Hippochrenidae n. fam.. *Chedevillia* and *Terebellopsis* are here placed with the Hippochrenidae. KRONENBERG & BURGER (2002) suggested to accommodate in the Rostellariidae the taxa with *Tibia*-like shell and some fossil genera as well as *Rimella*-like species. Since species of *Rimella* and *Calyptraphorus* lived in the Late Cretaceous (KIEL & PERRILLIAT, 2001) they have a long independent history which places them in distinct taxonomic groups, the Rimellinae and Calyptraphorinae n. subfam.. A separate evolution can be stated as well for the Rostellariidae on one side and the Hippochrenidae n. fam. on the other, the later of which were also recognized since about 70 Million years ago (KIEL & BANDEL, 2002). While the *Rimella* relation may have evolved into the more elongate and larger *Tibia*, the *Hippochrenes* relation appears to have given rise to the Strombidae (see below).

Subfamily Rimellinae STEWART, 1927

Diagnostic characters: Shell shape is spindle-like with whorls of the teleoconch ornamented by axial ribs and variable varices. The body whorl is of about the same height as the spire. The aperture is elongate with open short siphonal canal. Its outer margin is commonly elongate and pointed. The apical end of the outer lip forms together with the continuation of the callus of the inner lip a narrow canal that continues onto the spire. The outer lip may or may not have a distinct stromboid notch, that is a sinus next to the siphon.

The subfamily was based on the genus *Rimella* AGASSIZ, 1841 by STEWART (1927) that according to COSSMANN (1904) has the type *Rostellaria fissurella* from the Eocene. WENZ (1938) still included here also living species which since have changed the name to *Varicospira* EAMES, 1952, with type species *Strombus cancellatus* LAMARCK, 1816 from the tropical Indo-Pacific.

Genus *Rimella* AGASSIZ, 1841

The type is *Rostellaria fissurella* LINNÉ, 1758 (= LAMARCK, 1804) from the Eocene (Lutetian) of France.

Diagnostic characters: The medium sized to small (10–40 mm) elongate shell with high spire consists of about 10 whorls of which those of the teleoconch are ornamented by fine spiral lines and stronger rounded axial ribs. The body whorl is about as high or a little higher than the spire. The aperture is relatively wide and continues in a narrow posterior canal formed by the margin of the outer lip and the continuation of the callus. It is of species specific length and species specific orientation towards the apex. The outer lip is simple or crenulated on its inner side. The inner lip consist of thick narrow callus ribbon that continues to the outer end of the siphon on one side and into the apical groove on the spire on the other side. There is no sinus near the siphon (no stromboid notch). The siphon is wide and short with its outer side pointed, hook-like.

Rimella fissurella has the posterior continuation of the outer lip and the rim of the inner lip forming a groove that continues straight to the apex (COSSMANN, 1904; WENZ, 1938: fig. 2717). *Rimella multiplicata* (BELLARDI) from the Eocene of Italy has similar shape and ornament but the apical callus canal twists to the side before it reaches the apex of the spire (SAVAZZI, 1991: fig. 6G). The protoconch of *Rimella fissurella* is smooth, about 1 mm in high and less wide with more than three rounded whorls (Pl. 3/6 & 9). The embryonic whorls is rounded and the larval whorls have sinuous growth lines. The juvenile shell has ornament of larger axial ribs crossed by fine spiral ribs and varices (Pl. 3/7).

Rimella mexcala KIEL & PERRILLIAT, 2001 is the most ancient representative of this genus known from the Maastrichtian of Mexico. Its conical protoconch consists of four whorls and 1.5 mm in height. The teleoconch of about 17 mm in height and consists of seven whorls. Their ornament is by broad axial ribs and fine spiral lines and two varices on most whorls. The posterior end of the aperture forms a groove that continues towards the apex of the spire bending down before reaching it (KIEL & PERRILLIAT, 2001: fig. 1.1–3), quite similar as is found in *Rimella multiplicata* that lived 25 Million years later.

Difference: The continuation of the apical end of the aperture as elongate groove distinguishes *Rimella* more clearly from *Varicospira* than does the presence or absence of a stromboid notch. While the latter character is variable the callus groove is short in *Varicospira*. In *Strombolaria* the shell has the shape and ornament of *Rimella* but no apical posterior canal at all. Shell ornament is less strongly developed in *Ectinochilus* and *Cyclomops*. *Dientomochilus* has a similar teleoconch shape but more stout shell shape and stronger developed apertural margin.

Remarks: COSSMANN (1904) chose *Rostellaria fissurella* as the type to the genus *Rimella* AGASSIZ, 1840 (= RÖDING, 1798). *Rimella* and *Cyclomolops* were interpreted as subgenera of *Rimella* by WENZ (1938), and COSSMANN (1904) had included in addition also *Orthaulax* and *Strombolaria.* The latter two were considered to represent independent genera of the Strombidae by WENZ (1938). *Orthaulax* is here placed with the Thersiteidae (see below).

Genus *Varicospira* EAMES, 1952

The type species is *Strombus cancellatus* LAMARCK, 1816 living the shallow warm sea of the Pacific Ocean near the Philippines.

Diagnostic characters: The shell resembles that of *Rimella* but has a distinct sinus on the outer lip in position next to the siphon. The posterior continuation of the outer lip in a callus groove is short and curved.

Varicospira cancellata and *Varicospira tyleri* (H. & A. ADAMS, 1863) closely resemble *Varicospira crispata* (SOWERBY, 1842). The latter lives in shallow water near the coast of tropical Australia (WILSON, 1993; WELLS, 1998) and around the Philippines. *Rimella spinifera* (MARTIN, 1899) from the Pliocene of Java closely resembles *Varicospira tyleri*. The shell of *Varicospira crispata* is about 20 mm long and consist of more than 8 whorls with a regular ornament of axial folds which are crossed by spiral ribs. The outer lip is thickened with smooth spiral ridges on its inner side. Its posterior end extends a little onto the last whorl of the spire as channel with hook-like twist back toward the suture. It consists of a broad rounded groove with its inner margin formed by the continuation of the callus of the inner lip. The siphon is short and straight and forms an open wide canal. The whorls of the spire may have varices or not the spire. *Varicospira* has stalked eyes as those of *Strombus*, but with the tentacles on them longer than the eye stalks (THIELE, 1929). He also noted that their radula resembles that of *Aporrhais*.
Rimella decussata (GRATELOUP, 1847) from the Mid Miocene of the Paratethys is up to 30 mm high with the inner side of the aperture weakly crenulated, and ridged. The posterior end of the outer lip and the callus of the inner lip form a curved groove-like canal that turns around similar to *Varicospira cancellata*. Ornament is of rounded axial ribs crossed by fine spiral lines. The anterior siphon is short and straight. The outer lip is thickened and has an low anterior sinus next to the siphon (SAVAZZI, 1991: fig. 7J). The species is common in the Mid-Miocene of Varpalota, Hungary (STRAUSZ, 1966: pl. 23, figs. 10–12, pl. 24, figs. 1–7). *Rimella rimosa* (SOLANDER, 1766) is 17 mm high with stromboid notch and lived about 40 Million years ago in the shallow warm sea that covered southern England (LOWRY, 1866).

Remarks: EAMES (1952) introduced the taxon *Varicospira* to describe species from the Eocene of Pakistan. It was originally interpreted as subgenus of *Dientomochilus* COSSMANN, 1904 and in spite of that based on the living *Strombus cancellatus* LAMARCK, 1816. COSSMANN (1904: pl. 3, fig. 21) had selected as type to *Dientomochilus* the species *Strombus ornatus* DESHAYES, 1866 from the Eocene of the Paris Basin (WENZ, 1938: fig. 2724). *Dientomochilus ornatus* differs from *Varicospira cancellata* by a much wider outer lip with thorns on its margin, and the relatively broad shell has a rather indistinct “stromboid notch”. *Dientomochilus* (*Varicospira*) *rakhiensis* EAMES, 1952 and *Dientomochilus* (*Varicospira*) *pakistanicus* EAMES, 1952 from the Eocene of Pakistan are not even similar to *Varicospira cancellata* regarding ornament and shell shape, and their posterior canals are so badly preserved that they can not be characterized. Even tough both species named by EAMES (1952) are not close to the type of *Varicospira* as proposed by EAMES, the proposed type species can be recognized. It should, therefore, be used (KRONENBERG, pers. comm.). A taxon *Dientomochilus* (*Varicospira*)

EAMES, 1952, in contrast, is not useful since it combines two distinct taxa representing different genera of the Rimellinae.

Genus *Dientomochilus* COSSMANN, 1904

The type species is *Strombus ornatus* DESHAYES, 1866, from the Eocene (Lutetian) of the Paris Basin (COSSMANN, 1904: pl. 3, fig. 21).

Diagnostic characters: The general shell shape resembles that of *Rimella*, but the shell is broader and the body whorls occupied more than half of shell height. Ornament consists of strong narrow spiral ribs and rounded axial ribs that cross each other forming right angles. The outer lip of the aperture of the body whorl is expanded, has short spines in continuation of the spiral ribs on its margin which is thickened and covered by smooth ridges on the inner side. The inner lip is formed by thickened narrow callus that may bear callus ridges. The continuation of the inner lip and the margin of the outer lip form a callus groove that continues across the last whorl of the spire and twists to the side.

In case of *Dientomochilus bartonensis* (SOWERBY, 1813) from the Eocene of England the outer lip is even more thickened and flaring than in *Dientomochilus ornatus* while the posterior canal is similar (COSSMANN, 1904: pl. 3, fig. 21). Here inner and outer lip of the adult shell are covered by transverse callus ridges.

Remarks: *Dientomochilus* was considered to represent a genus and a member of the Strombidae (WENZ, 1938: fig. 2724). The shell does in fact resemble that of the living *Strombus helli* KIENER, 1843 (*Hawaiistrombus)* from Hawaii with 11–27 mm high shell and similar ornament. It differs by having large tubercles on the shoulder of the body whorl and no callus groove in the continuation of the posterior outer lip (see below). The species determined as *Dientomochilus decussatus* from the Miocene of France has wide spaced blunt axial ribs and indistinct spiral ribs (COSSMANN, 1904: pl. 3, figs. 22 & 23) and resembles *Rimella*. It is quite similar to *Cowlitzia washingtonensis* CLARK & PALMER, 1923, in WENZ (1938: fig. 2729), that is found in the Eocene of the US West Coast. COSSMANN (1904) suggested as subgenus to *Dientomochilus* also *Digitolabrum* COSSMANN, 1804. This was not accepted by WENZ (1938: fig. 2725), who considered *Digitolabrum* to represent and independent genus, based on *Rostellaria princeps* from the Eocene of the Paris Basin (COSSMANN, 1904: pl. 3, figs. 13 & 14). *Digitolabrum* is here considered to represent a genus of the Aporrhaidae (see above).

Genus *Strombolaria* GREGORIO, 1880

The type species is *Rostellaria crucis* BAYAN, 1870 from the Eocene of Italy (COSSMANN, 1904: pl. 5, fig. 8).

Diagnostic characters: The *Rimella*-like shell has no callus canal as continuation of the posterior margin of its aperture. Ornament consists of axial ribs and fine spiral ribs with varices on the juvenile shell at irregular intervals. The aperture of the fully grown shell is simple and thickened with a low lobe at is anterior end and short wide siphonal canal. The protoconch is quite similar to that of Rimella Fissurella from the Eocene of the Paris Basin (Pl. 3/6).

Difference: *Strombolaria crucis* has a shell that is quite similar to that *Rimella* and *Varicospira* but without posterior canal on its aperture (WENZ, 1938: fig. 2723). *Strombolaria* from the Eocene (Lutentian) of Vicenza, Italy also has no posterior canal (SAVAZZI, 1991). Of the two individuals determined as *Rimella* (*Strombolaria*) *crucis* by COSSMANN (1904: pl. 5, figs. 8 & 9) only the specimen in fig.8 can be considered here and is comparable to the individual described by SAVAZZI (1991: fig. 7i).

Genus *Ectinochilus* COSSMANN, 1889

The type is *Strombus canalis* LAMARCK, 1804, from the Eocene (Lutetian) of the Paris Basin (COSSMANN, 1904: pl. 3, figs. 17 & 18).

Diagnostic characters: The ovoid elongate shell of 10-30 mm in height has indistinct sutures and fine ornament, contrasting to the coarser rib ornament of *Rimella* and *Varicospira*. The margins of the outer lip and the callus of the inner lip continue as groove (gutter) several whorls onto the spire. Ornament consists of fine spiral lines and low axial ribs. The body whorl is about as high as half of the total shell and its outer lip is simple or may have

low angular projections on is thickened outer margin. The inner lip consist of narrow ribbon of thick callus that extends onto the outer margin of the wide and short siphon that is hook-like. A sinus on the outer lip near the siphon may or may not be present.

Ectinochilus texanus (HARRIS, 1895) from the Eocene of Texas (Brazos River) is quite close to the type of the genus (HARRIS, 1895: pl. 9, fig. 1). Its shell has a high spire and measures about 30 mm in height and 10 mm in width. The first six whorls of the protoconch are smooth, and the first whorl of the teleoconch is ornamented by many low rounded spiral ribs separated from each other by narrow grooves (pl. 4, figs. 17 & 18). Later axial ribs increase in number and acquire more regular pattern, and spiral ribs increase in strength. The fully grown teleoconch consists of up to 7 whorls with 35 axial ribs in early whorls decreasing in number on later whorls. The last whorl has 2–3 spiral cords adjacent to the suture and its base bears 15–25 spiral ribs. The callus on the inner lip is raised and reflected and continues onto the outer margin of the siphon. The outer lip is thickened and broadly flaring. The aperture is wide with an anterior notch (stromboid notch) and bears an anterior siphon (rostrum). The posterior end of the aperture continues in a callus canal formed by the inner lip and the outer lip and extends in posterior direction across about three whorls than curves away from the apex.
Ectinochilus texanum closely resembles *Ectinochilus laqueatus* (CONRAD, 1833) from the Gosport Sand Formation Alabama (PALMER, 1937: pl. 33, fig. 1; HARRIS & PALMER, 1946). This latter species has irregular varices and rounded straight larger axial ribs crossed by fine spiral lines. *Ectinochilus planum* (BEYRICH) from England with about 9 mm high shell with the posterior canal up to the top of the shell and down a little on the other side. Also the siphon has a hook on its point. Ornament is by fine spiral lines and axial ribs. *Ectinochilus antipodarum* (BURGER & KRONENBERG, 2006) from the Eocene of New Zealand (BURGER & KRONENBERG, 2006: fig. 3).

Difference: *Ectinochilus* existed from Eocene to the Oligocene. BURGER & KRONENBERG (2006) noted that *Ectinochilus* is almost identical to *Rimella* in general shell form. They noted that COSSMANN (1889) distinguished *Ectinochilus* from *Rimella* by having a stromboid notch and a thickened outer lip, but that both characters are variable among species with otherwise similar shell shape. *Rimella* and *Varicospira* differ by having a stronger ornament, and the latter also by having a shorter apical gutter at the posterior end of its aperture.

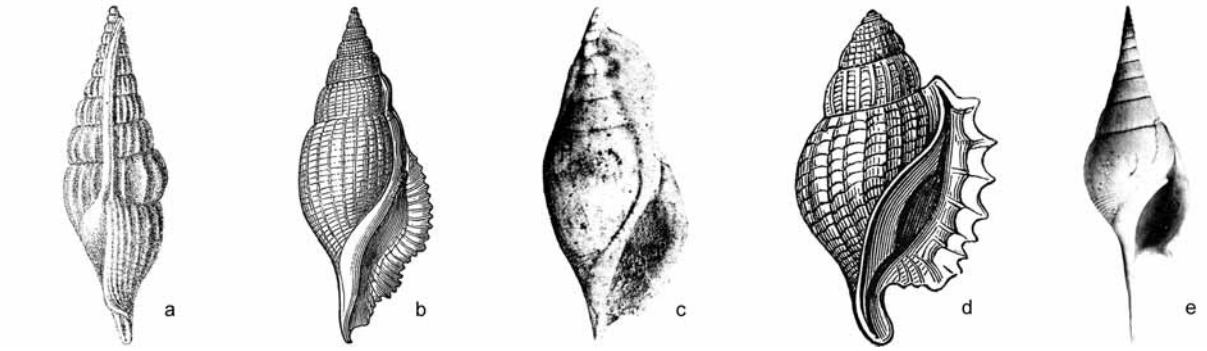

Fig. 9: a – *Rimella fissurella*; b – *Varicospira cancellata* taken from CHENU, 1859; c – *Cyclomops sublaevigata* taken from COSSMANN, 1904; d – *Dientomochilus bartonensis* taken from CHENU, 1859; e – *Tibia dentata* taken from COSSMANN, 1904.

Remarks: *Ectinochilus* had quite a number of species during the Eocene, and WENZ (1938) considered it to include the subgenera *Cowlitzia* CLARKE & PALMER, 1923, *Macilentos* CLARKE & PALMER, 1923, *Vaderos* CLARKE & PALMER, 1923 and *Dasystoma* STEWART, 1927, which all are similar to each other and have been described from North America, from the Eocene of NW USA (TURNER, 1938: pl. 18, figs. 1–4) and from Mississippi (WENZ, 1938: figs. 2727–2730). RUTSCH (1930) noted that ornament and shape of the apical canal on the spire varied within the species and are not of value to discriminate subgenera. TURNER (1938) noted that the posterior canal in case of *Macilentos* on certain individuals may go over the summit of the spire and on others it may be deflected a number of whorls before the summit. by from the Eocene of New Zealand. *Ectinochilus antipodarum* from New Zealand closely resembles *Macilentos macilenta* WHITE, 1889 from Oregon but has more axial ribs (25 on each whorl, while the American species has here 10 ribs). Similar species from the Eocene of Nigeria such as *Africoterebellum* EAMES, 1957 and *Amekichilus* EAMES, 1957 have a short curved posterior canal (NEWTON, 1922: pl. 4, figs. 3–7, pl. 2, figs. 14–17; SAVAZZI 1991: fig. 8F–G).

Cyrtulotibia EAMES, 1957 has a wider shell than *Amekichilus* EAMES, 1957 with the ridge formed by the inner lip next to the curved posterior canal quite thick (SAVAZZI, 1991: fig. 8A).

Subfamily Rostellariinae GABB, 1868

The type genus is *Tibia* RÖDING, 1798, with related subgenera, which have been raised to genus status by KRONENBURG & BURGER (2002) such as *Tibia*, *Rostellariella* THIELE, 1929 and *Rimellopsis* LAMBIOTTE, 1979 (= *Sulcogladius*).

Diagnostic characters: The spire consists of many whorls and sometimes is higher than the body whorl. The fully grown shell has a very high spire, a well developed long rostrum, tooth-like or digit-like projections of the outer lip, and an operculum that seals the aperture. The apical canal that arises from the continuation of the upper end of the outer lip and the callus of the inner lip is short and curved backwards. Unconfirmed species of *Tibia* occurs since the Eocene and of *Sulcogladius* since the Oligocene.

Genus *Tibia* RÖDING, 1798

Rostellaria LAMARCK, 1799 represents a synonym of *Tibia* (THIELE, 1929; WENZ, 1938) and the type species is *Murex fusus* LINNÉ, 1758, from the western Pacific.

Diagnostic characters: The shell has a long slender and high spire, a long siphon (rostrum), a tooth like continuation of the posterior outer lip, and an operculum that seals the aperture completely. The outer lip of the elliptical aperture has finger-like projections. The early whorls of the teleoconch have a reticulate ornament. The protoconch consists of smooth, convex whorls with rounded blunt apex (KRONENBURG & BURGER, 2002). No sharp change into the teleoconch was noted in case of *Tibia fusa* and *Tibia insulaechorab*.

Tibia fusa has the posterior groove of the outer lip short and narrow, and strongly curved back. The slender shell with more than 15 whorls of the teleoconch is about 250–300 mm high. Six spines extend from the thickened apertural margin of the outer lip. A thin long straight siphon may occupy halve the length of the spire. The protoconch consists of only two whorls (Pl. 4/11–12) and indicates a lecithotrophic development.
Tibia curta (SOWERBY, 1842) has the outer posterior margin of the outer lip extended to a slightly curved relatively broad callus groove. The 120–170 mm long smooth shell with many whorls has five stubby little fingers on the outer lip and a short straight siphonal canal. A low and relatively wide sinus lies between the last spine on the outer lip and the straight siphon, so one could interpret it as stromboid notch. Individuals from southern India have stalked eyes with the tentacles on them thin and long (PINN, 1990). *Tibia insulaechorab* RÖDING, 1798 has the posterior extension of the outer lip as straight canal covering one and a half whorls. The siphon is relatively short. The shell resembles that of *Tibia curta*, but with its posterior can almost straight. Here the spawn has been observed to be deposited in circles on the sand and agglutinated with it (SCHMID, 1990). The large and complex eyes are on long stalks which are stretched out from below the shell on both sides of the siphon or next to it the spines of the outer lip. The position of the tentacles on the stalks below the eyes is similar to those of *Strombus* but tentacles are longer. The shelly tube of the anterior siphonal canal can be used as a snorkel when buried in the sand.
Tibia dentata (GRATELOUP, 1840) has smooth shell that is also about 15 cm high. With exception of the early whorls of the teleoconch further whorls are smooth. Juvenile whorls have ornament of fine spiral lines and rounded larger axial ribs. The later whorls are smooth. The canal on the apical part of the outer lip is attached to the last whorl of the spire and curves to the side (COSSMANN, 1904: pl. 2, figs. 12 & 13; STRAUSZ, 1966: pl. 23, figs. 5–9; SAVAZZI, 1991; fig. 8C), as in *Tibia curta*. *Tibia dentata* from the Mid-Miocene of southern France and Spain is a little stouter and has a slightly shorter body whorl than is present in the living *Rostellariella martini*. The outer lip has fewer spines at its margin. The protoconch of the fossil *Tibia dentata* (Pl. 4/7–8) resembles that of the living *Tibia fusa* but has one more whorl. It documents that there was probably a planktotrophic larva. COSSMANN (1904) suggested this species to represent the type of the genus among the fossil species of *Rostellaria* = *Tibia*, an opinion that is here supported. Some more fossil species were discussed by KRONENBERG & BURGER (2002).

Genus *Rostellariella* THIELE, 1929

The type species is *Rostellaria delicatula* NEVILL, 1881 from the Indo-Pacific in the SE Asian region.

Diagnostic characters: The early whorls of the teleoconch have ornament of spiral ribs, the later ones only a four which end in the spines of the outer lip in *Rostellariella delicatula*. The posterior canal of the outer lip is a short notch. The outer lip five short spines and the siphon in pointed and short. KRONENBERG & BURGER (2002) characterized the protoconch as consisting of 5 smooth whorls with the last two whorls of the larval shell ornamented by a carina next to and just above the suture.

Rostellariella lorenzi (MORRISON, 2005) from Indonesia has the rostrum in line with the outer side of the body whorl thus incline to the right. *Rostellariella martini* (MARRAT, 1877) has a shell with about 12 whorls, is up to 150 mm high with elongate straight siphon. The margin of the outer lip is a little thickened with 9 short spines, of which the most anterior has no notch between it and the siphon. The number spines and their distance from each other on the margin of the outer lip is variable. Fine spiral lines may be present on early whorls as well as next to the siphon on the base. The protoconch of *Rostellariella delicatula* from the Philippines and the south Chinese Sea is conical, consists of about 5 whorls with rather indistinct change over into the teleoconch (Pl. 4/13–15). The larval shell that is more than 1.6 mm high has a strong projection on its outer lip that is accompanied by a spiral rib on its apical side.

Genus *Sulcogladius* SACCO, 1893

The type species is *Rostellaria collegnoi* BELLARDI & MICHELOTTI, 1840, from the Miocene of Italy (COSSMANN, 1904: pl. 6, figs. 4 & 6).

Diagnostic characters: Shell shape is like that of *Tibia* but with strong spiral ornament on all whorls of the teleoconch. The spiral ribs may form ornament of a reticulate pattern on the early whorls due to the presence of collabral lines. On the body whorl one stronger spiral forms a corner with shoulder and one or several somewhat stronger spirals end in the strongest thorns of the margin of the outer lip. The rostrum is straight and elongate. The posterior margin of the outer lip is turned back forming a short gutter that may extends onto the anterior third of the last whorl of the spire.

The shell of *Sulcogladius powisii* (PETIT, 1840) is about 50–70 mm long consist of more than 11 whorls with pointed elongate rostrum. Early teleoconch whorls may have varices or not. It has ornament of spiral ribs, with the thickened apertural margin of the body whorls with 5 short spines. The posterior end of the outer lip extends in a short canal onto the whorl before forming narrow groove. On the body whorl one or two of the spiral ribs are larger than the others and not all of the spiral ribs end in marginal spines. The shape of the protoconch that indicates the presence of a planktotrophic larva in its ontogeny. According to the sketch presented by KRONENBERG & BURGER (2002) the early ontogenetic shell resembles that of *Rostellariella delicatula*. *Tibia powesii modesta* (MARTIN, 1899) from the Pliocene of Fiji (LADD 1972: pl. 15, figs. 2 & 3) has ornament and aperture as in *Sulcogladius powisii* with short extension of the margin of the outer lip onto the last whorl.

Remarks: *Rimellopsis* LAMBIOTTE, 1979 is based on the living *Sulcogladius powisii* which has basically the same shell characters as *Sulcogladius collegnoi* and can be considered a synonym to *Sulcogladius* as characterized by WENZ (1938: fig. 2732). KRONENBERG & BURGER (2002: fig. 3) recognized that the concept of *Sulcogladius* presented by COSSMANN (1904) fits with the living *Sulcogladius powisii*.
Sulcogladius haueri that lived during the Oligocene of the northern Alps according to LÖFFLER (1999) may be the same species as *Rostellaria excelsa* GIEBEL, 1864, (KOENEN, 1889) or a similar species. *Sulcogladius powisii* can be placed in this genus or subgenus as well (SAVAZZI, 1991: fig. 8E), as was discussed by KRONENBERG & BURGER (2002) who included some fossil species from the Eocene of the Paris Basin here, such as *Rostellaria hupei* ROUAULT, 1849, as well as *Rostellaria excelsa*.
COSSMANN (1904) described a *Rostellaria goniophora* from the Eocene which deviates strongly in shell shape and may actually represent the spire of a member of the Aporrhaidae. *Amplogladius* COSSMANN, 1889, was based on *Rostellaria athleta* ORBIGNY from the Eocene and apparently represents a *Hippochrenes* with its outer lip broken off (COSSMANN, 1904: pl. 11, fig. 11). The reconstructed shell illustrated by WENZ (1938: fig. 2733) is originated from a illustration of DESHAYES (1866) where it was even more fragmentary.
Tibia (*Eotibia*) GREGORIO, 1880, with the type *Eotibia pellegrini* GREGORIO, 1880, from the Eocene of Italy represents an elongate shell is provided with a long spine-like siphon and whorls of which there are about 11 have ornament of strong somewhat nodular axial ribs crossed by fine spiral ribs (SAVAZZI, 1991: fig. 6J). The outer lip is slightly expanded and of angular shape. Its place among the Rostellariidae needs to be confirmed. Also *Alarimella* ELDER, 1990, that was found to have the juvenile ornament of the shell similar to that of *Calyptraphorus* by SAUL (1998) was not confirmed by KIEL & PERRILLIAT (2001). *Tibiaporrhais* ELDER, 1990, is based on poorly preserved specimens and was interpreted to connect *Tibia* with Aporrhaidae.

Subfamily Calyptraphorinae n. subfam.

Diagnostic characters: The juvenile shell resembles that of *Rimella* or *Ectinochilus* in shape and ornament. When fully grown a callus is added to the slender conical shell and its shape changes due to a broadening of the sides. The callus of the inner lip joins the callus of the margin of the outer lip and extends onto the spire forming a groove and pad. Callus may also cover the surface of the apertural side of the shell. Callus covers part of the shell in *Eocalyptraphorus* n. gen., and it completely transforms shell shape by additions of callus in *Calyptraphorus*. The shell of *Aulacodiscus* is extremely coated over with callus. *Cyclomops* has the shell similar to *Ectinochilus* with callus sheets attached to the margins of the apical callus groove and thus broadening the body whorl.

Derivatio nominis: The subfamily is named according to the characteristic genus *Calyptraphorus* belonging here.

The species of the Calyptraphorinae document a change from the juvenile stage to the adult stage that represents a similar drastic reconstruction of the shell during ontogeny as noted in Aporrhaidae and Strombidae among the living Stromboidea. While the adult stage is characterized by a much widened apertural region that aids in having a stable position when moving openly on soft substrate (SAVAZZI, 1991), the juvenile shell is slender and thin that helps in rapid growth and moving through entangled vegetation and within the sediment, as is the case with juvenile *Strombus* (BANDEL & WEDLER, 1987). Calyptraphorinae have made that change by shell additions to the sides and by adding smooth callus to the upper and lower side of the shell. Shell was secreted by mantle tissue that was extended over the shell, and spread out to add shell material over its surface.
The genus *Calyptraphorus* is characteristic to the Calyptraphorinae n. subfam. with type species *Calyptraphorus velatus* from the Eocene of Mississippi. *Eocalyptraphorus* n. gen. lived in the Tethys Ocean during the Late Cretaceous of Mexico (PERRILAT & VEGA, 1997) and India (STOLICZKA, 1868). No species are known from later than the Eocene (COSSMANN, 1904), and the subfamily existed for more than 35 Million years.

Genus *Calyptraphorus* CONRAD, 1857

The type species is *Rostellaria velata* CONRAD, 1857, from the Late Eocene of Jackson, Mississippi (WENZ, 1938: fig. 2737, followed in spelling *Calyptrophorus* the example of COSSMANN, 1904*).*

Diagnostic characters: The shell is slender elongate with pointed outer margin of the siphonal canal and a deep sinus on its side to the outer lip. The adult shell is covered by callus. The juvenile shell is weakly ornamented by axial ribs, and later the spire is totally enveloped in a callous mass. The outer lip is narrow and simple, the anterior siphon canal is straight and of moderate length (COSSMANN, 1904: pl. 3, figs. 1 & 2).

Calyptraphorus velatus has a posterior canal that may have functioned as exhalant sinus (ALDRICH, 1921; SAVAZZI, 1991: fig. 7H). The characteristic shape of the callus of the inner lip is connected to the rim of the outer lip by a groove that lies next to large callus pad. This groove contained mantle tissue as the snail lived in the soft sediment on the sea floor. With mantle tissue the other parts of the shell, at least periodically, were coated with a smooth polished layer.
Calyptraphorus jacksoni CLARK, 1896, was described from the Paleocene of Maryland (CLARK & MARTIN, 1901). The same or a very similar species from Matthews Landing on the Alabama River lived on soft bottom in the large bay of the Proto-Gulf of Mexico that at the time was part of the Tethys Sea as well as the Atlantic Ocean. Its protoconch is about 2 mm high and consists of 6 smooth whorls while the first whorl of the teleoconch has axial ribs with collabral curving outline Pl. 3/10–12, 14). Many spiral and lowly rounded ribs separated from each other by narrow grooves crossed by the axial ribs are present on the first three whorls (Pl. 3/12, 14). About 12 axial ribs are present on each these whorls and one or two stronger varices. In the fourth whorl of the teleoconch axial ribs decrease in strength. In the following three whorls they have disappeared and ornament is by fine spiral lines with growth lines crossing which reflect the presence of a low lobe at the rounded corner to the base.
The final growth stage was acquired with the formation of the thirteenth whorl. The fully grown shell is between 30 and 40 mm high and of regular conical shape with simple spindle shaped aperture (Pl. 4/1). The thin outer lip had a low basal lobe when transformation to a fully callus covered shell began. This change also included a transformation from rounded diameter of bilaterally compressed shape. Callus began forming independently on the ventral and the dorsal side. On the ventral side the inner lip expanded and on the upper side a curved margin of a wide channel with rounded outer side and a grooved inner side began to be deposited and expanded into a callus plate (Pl. 4/5–6). The change of the shell form to bilateral shape is due to expansion of the inner lip that forms a callus coat on the basal side (Pl. 4/4). Here the corner to the base became evenly rounded on the ventral

side and the spire became coated over until its surface was totally concealed by the smooth callus on that side of the shell. The dorsal side of the spire at that stage was still uncovered while the curving channel margin had been deposited on the surface of the body whorl and the pene-ultimate whorls. The layers were spread out from the sides coming from the inner lip as well as the channel of the outer lip until its margins met. During this process the callus cover of the sides increased in thickness more strongly. The apical angle was thus increased from about 35° to 45°. On the upper shell side the callus covers the apex of the spire and continues in a smooth wide ridge on the margin of the groove (Pl. 4/2–3). This latter is the continuation of the at first wide, latter continuously narrower posterior end of the aperture. The original sinus on the back of the shell thus became a narrow groove in the dorsal callus pad (Pl. 4/3–4). It ends on the other side at about the same height as the aperture of the shell. Thus a central shield was deposited with a rim next to the groove and a thick callus continuation on top of the last whorl above the aperture. The central part of the shield is a depression of a thinner callus covering the whorls of the spire (Pl. 4/3). When the shell was totally covered it acquired bilateral shape with sides wider due to the callus added there in greater thickness.
Summarizing shell growth of *Calyptrophorus jacksoni* it can be recognized that it is totally without callus deposits until grown to full height (Pl. 4/1). The callus formed afterwards expands from two sources, one representing the mantle that covered the inner lip and deposited callus on the side of the shell that was always in contact with the sediment, the other representing a lobe of the mantle that extended from the apical end of the aperture in a similar manner as was the case in the *Rimella* and *Ectinochilus* relation. In contrast to the later the dorsal canal was wider when callus deposition began (Pl. 4/5–6), and expanded with callus deposition. In fully outgrown shells both callus fields met and fused with each other.

Remarks: *Calyptraphorus jacksoni*, *Calyptraphorus septentrionalis* STANTON, 1920, *Calyptraphorus trinodiferus* CONRAD, 1857, are known from the Paleogene of the USA (COSSMANN, 1904; GARDNER, 1945; PALMER & BRANN, 1966; DOCKERY, 1977; MCNEIL & DOCKERY, 1984). *Calyptraphorus velatus stamineus* (CONRAD, 1854) from the Eocene of Jackson (Mississippi) (SAVAZZI 1991: fig. 7H) and *Calyptraphorus trinodiferus* from the Eocene of Alabama (SAVAZZI, 1991: fig. 7E–G) resemble the species from Matthews Landing. In case of *Calyptraphorus trinodiferus*, SAVAZZI (1991) noted the continuation of the anterior canal of the outer edge of the aperture, but he placed no weight on that feature.

Genus *Eocalyptraphorus* n. gen.

The type species is *Calyptraphorus binodiferus* PERRILLAT & VEGA, 1997 from the Maastrichtian of Mexico (PERRILLAT & VEGA, 1997: figs. 1–8).

Diagnostic characters: The shell resembles that of *Rimella* in shape and ornament and the callus deposits on the adult shell are similar to those of *Calyptraphorus.* In difference to the latter the callus deposits do not cover the spire and the body whorl in total. They cover only the sides of the spire and the widened inner lip of the body whorl.

Derivation nominis: An early (eo) group of the Calyptraphorinae with shell resembling that of Calyptraphorus.

Calyptraphorus binodiferus PERRILLIAT & VEGA, 1997 from the Maastrichtian of Mexico has a 2 mm high protoconch with rounded apex and embryonic whorl 0.13 mm wide. The teleoconch consists of six whorls which are ornamented by rounded axial ribs and some fine spiral lines and the shell is about 30 mm high. A large callus extends from the aperture and covers much of the shell with exception of the apex. It is bordered by a slit that is covered by the lobe on the side formed by the continuation of the outer lip (KIEL & PERRILLIAT, 2001: fig. 1.4–5, 2.1–3). This slit-like canal forms a curved channel through the callus up to the fourth whorl of the spire then cures downward (PERRILLIAT & VEGA, 1997).
In difference to *Calyptraphorus velatus* the callus with the groove does not cover the whole spire but only the sides and the surface of the apertural side of the shell. The slit and its callus rims extends from the posterior part of the outer lip to the other side of the shell crossing the apex, and ends before reaching again the callus cover of the body whorl. The Indian *Eocalyptraphorus palliatus* (FORBES, 1846) resembles *Eocalyptraphorus binodiferus*, both are of Maastrichtian age (STOLICZKA, 1868: pl. 2, fig. 20). The Indian species has more rounded whorls but also a callus that does not cover the total shell. The groove in the callus ridge is open to the dorsal side of the shell, as in the Mexican species. *Eocalyptraphorus palliatus* from the Maastrichtian of Tamil Nadu, India and *Eocalyptraphorus binodiferus* have characters as found in *Rimella*, but the callus with the slit-like groove in it is quite similar to that of *Calyptraphorus velatus*.

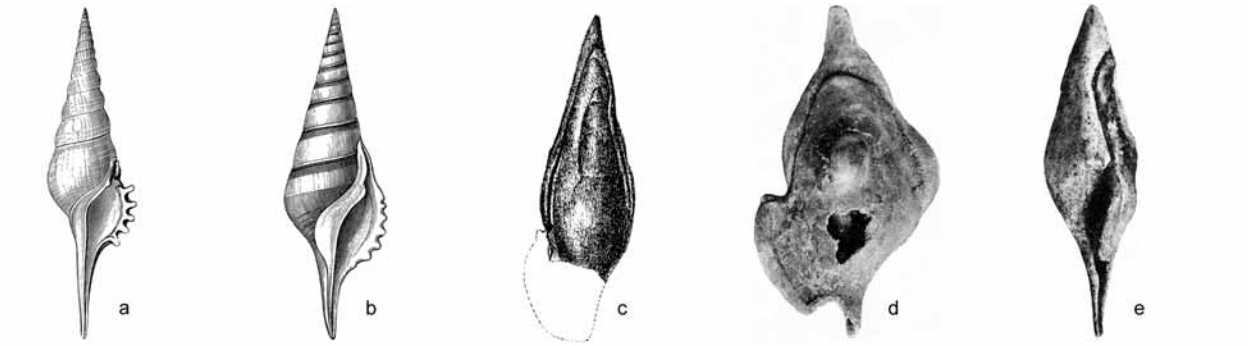

Fig. 10: a – *Tibia fusa* taken from CHENU, 1859; b – *Tibia insulaechorab* taken from CHENU, 1859; c – *Eocalyptraphorus binodiferus* taken from STOLICZKA, 1868; d – *Calyptraphorus trinodifera* taken from COSSMANN, 1904; e – *Calyptraphorus velatus* taken from COSSMANN, 1904.

Genus *Aulacodiscus* DOUVILLE, 1923

The type species is *Tibia* (*Aulacodiscus*) *lissoni* DOUVILLÉ, 1923, from the Eocene of Peru. The callus production on the adult shell in *Aulacodiscus* is extreme (OLSSON, 1928; WENZ, 1938: fig. 2738) and the shell was reconstructed by SAVAZZI (1991: fig. 6M–O).

Genus *Cyclomolops* GABB, 1868

The type species is *Rostellaria sublaevigata* DESHAYES, 1866, from the Eocene (Cuisian) of the Paris Basin (DESHAYES, 1866: pl. 90, figs. 5 & 6; COSSMANN, 1904: pl. 3, fig. 5; WENZ, 1938: fig. 2718) with outer lip continuous from the apex to the siphon.

Diagnostic characters: The fusiform shell of the shape as in *Ectinochilus* is connected to a callus continuation of the inner and outer lip that runs to the top of the spire and covers it. The margins of the slit are formed by the upturned lamellar outer lip and a lamella-like continuation of the callus of the inner lip. The slit ends near the apex. The body whorl has fine spiral lines only on its anterior part. The outer lip with smooth and thickened margin continues without interruption from the short siphon to almost the apex. He callus of the inner lip forms a sheet that also covers the apex of the shell.

Differences: *Eocalyptraphorus* has the canal formed by the callus sheets not continuous onto the backside of the spire, while the callus curves across the whorl to the side ending there. The shell is smooth and resembles that of *Rimella multiplicata* (BELLARDI) from the Eocene of Italy (SAVAZZI, 1991: fig. 6G), but has less ornament. *Cyclomolops subhumerosa* (OPPENHEIM) from the Eocene of Togo has a similar smooth shell, but a callus extension of the inner lip added to the continuation of the outer lip (SAVAZZI, 1991: fig. 6E–F). COSSMANN (1904: pl. 3, fig. 5) and WENZ (1938) regarded *Cyclomolops* a subgenus of *Rimella*.

2.8 Family Hippochrenidae n. fam.

Diagnostic characters: The outer lip is wing-like with evenly rounded or lobed margin that extends to the apex of the spire. It forms is attached to the top of the spire, merging here with the callus of the inner lip forming a fissure. This groove extends from the apical end of the aperture to the apex of the shell. The outer lip is usually thin and smooth on its outer and inner side. The callus of the inner lip expands to form a smooth ridge or sheet posterior of the aperture. A posterior canal in the continuation of the aperture and bordered by the smooth outer lip and the expanded sheet- like inner lip extends to the apex. The whorls of the spire may be smooth or ribbed. The family is known from the Late Cretaceous (Maastrichtian) to the Oligocene, existing about 50 Million years. The taxa here contained are *Hippochrenes* with predominantly smooth shell and wide outer lip, *Semiterebellum* with similar shape of the spire and outer lipless expanded next to the spire, forming the Hippochreninae, and *Wateletia, Maussenetia* and *Chedevillia* with ornamented spire and wide outer lip are united in the Wateletinae n. subfam..

Derivatio nominis: *Hippochrenes* is the characteristic genus of the new family, which is named accordingly.

Differences: The outer lip has no anterior sinus like a "stromboid notch" before it merges with the margin of the siphon, and it is thin, both characters differ from the Strombidae. The inner side of lobes or wings of the outer lip have no grooves as are present in the Aporrhaidae. Rostellariidae have the outer lip not expanded to be shield-like. Calyptraphorinae n. subfam. also have a groove bordering the expanded callus of the inner lip, but no wing-like outer lip. In addition the groove may be expanded to cover the dorsal side of the shell and the callus of the inner lip may be spread out. Seraphsidae have an ovoid shape with similar anterior end of the aperture as in Hippochrenidae, but their outer lip is not expanded and the body whorl covers much of the former shell. Thersiteidae including *Orthaulax* have the thin outer lip but it may not continue to the apex and their inner lip forms a callus pad on which the outer lip rests. The outer lip of the Dilatilabridae n. fam. has also no stromboid notch, but it is thick and there is no apical canal.

Subfamily Hippochreninae n. subfam.

Based on *Hippochrenes* with almost smooth shell and expanded wing like outer lip and fissure formed by continuation of the inner lip to the apex and inner side of outer lip or its extension to the apex.

Genus *Hippochrenes* MONTFORT, 1810

The type is *Rostellaria macroptera* LAMARCK, 1799 from the Eocene of the Paris Basin (COSSMANN, 1904: pl. 2, fig. 9; WENZ, 1938: fig. 2734; SAVAZZI, 1991: fig. 6a).

Diagnostic character: The medium to large shell has a high spire has almost smooth whorls with weak sutures. Early whorls of the teleoconch are ornamented by spiral lines which are stronger imprinted on the anterior. The expanded wing-shaped outer lip in the body whorls is evenly curved with thin outer margin and extends onto the posterior whorls to the apex (in the type species) and even beyond it [*Hippochrenes baylei* (DESHAYES, 1865)]. The aperture is elongate with its posterior part forming a narrow canal that continues up to the apex. This canal is bordered on the inner side by a sheet-like or ridge-like continuation of the callus of the inner lip (low and rounded in the type species, sheet-like in *Hippochrenes baylei*). The siphonal canal (rostrum) is straight or bent to the right (as in the type species) and can be long and pointed (*Hippochrenes dewalquei*). The siphonal canal forms a sinus or indentation with the outer lip. There may be a posterior sinus (not in the type species, well developed in *Hippochrenes fissura* and the whorls of the spire are smooth or have weak rounded axial ribs. The protoconch of *Hippochrenes macroptera* is conical (Pl. 3/1, 2, 5), about 1 mm high with about four whorls, and closely resembles that of *Rostellariella delicatula* of the Indian Ocean.

Remarks: *Hippochrenes* can be traced from the Late Cretaceous to the Oligocene (COSSMANN, 1904; KIEL & BANDEL, 2002). WENZ (1938) interpreted it as subgenus of *Tibia*. This placement can not be supported based on several arguments. First *Tibia* s. s. is based on living species with short thickened outer lip with spines. Second the continuation of the aperture in only a short apical canal, contrasts to the long narrow posterior canal present in *Hippochrenes* and relation. ZITTEL (1885) noted a similarity with *Orthaulax* regarding the rounded outer lip. But *Hippochrenes* has no thickened callus-pad on the posterior inner lip that occurs in *Orthaulax* even on the whorls formed before the body whorl. The spire is ornamented by axial ribs in case of *Wateletia* or by strong spiral ribs in case of *Chedevillia*.
Hippochrenes macroptera has the spine of the siphon curved to the left, the early whorls of the spire are smooth, and the wing-like outer lip extends to the apex (COSSMANN, 1904: pl. 2, fig. 9; WENZ, 1938: fig. 2734), as is the case in *Hippochrenes subtilis* PETHÖ, 1906, which differs by having a larger apical angle (PETHÖ, 1906: figs. 4 & 5). *Hippochrenes nuda* (BINKHORST, 1861) (in: KAUNHOVEN, 1897: 74, pl. 8, figs. 13–15) from the Maastrichtian of the Netherlands possesses an angular notch between wing and rostrum. The similar *Hippochrenes kussi* KIEL & BANDEL, 2002, from the Maastrichtian Dakhla Formation of the Western Desert of Egypt (Ammonite Hills, Sand Sea) has a high spire with apical angle of 25° and straight sided whorls and body whorl a little higher. The outer lip is wing-like and attached to the entire spire. Ornament consists of axial ribs that fade away on the high, 20 mm wide (KIEL & BANDEL, 2002: fig. 3C, G).
Hippochrenes ampla SOLANDER, 1766, from the Middle Eocene of England and France has the posterior margin of its outer lip extending beyond the apex and covering it. It has a straight siphon, and evenly rounded flaring outer lip. The inner lip covers the spire to the apex while the outer side of the shell is smooth with only growth lines as ornament. *Hippochrenes baylei* from the Mid Eocene (Lutetian) of the Paris Basin is close to *Hippochrenes macroptera* in general shell shape but has a straight siphon, the outer lip evenly rounded and flaring. The inner lip covers the whole of the lower side of the spire. At the posterior margin of the aperture the callus plate of the inner lip expands into a lamella that extends from the posterior end of the aperture to the apex.

A groove-like fissure lies between this callus ridge and the inner side of the outer lip (COSSMANN, 1904: pl. 2, fig. 8). The inner lip callus obviously may be thin or rather thick, and the lamella to the apex is more or less strongly developed depending on callus thickness. *Hippochrenes incrassata* (DESHAYES, 1865) from the Mid-Eocene of the Paris Basin as described by SAVAZZI (1991: fig. 2B, C) may represent the same species with the lower side of the spire totally covered by the callus of the inner lip.
Hippochrenes dewalquei (DESHAYES, 1865) has the whole inner side of the spire covered by callus, while the outer side is free of it. The outer lip forms a thin shield that ranges from the base of the spine-like straight siphon to beyond the apex, coating it and extending a little over its top. This resembles *Chedevillia* as documented by SAVAZZI (1991: fig. 2H, I) with the inner lip expanded on the margin of the posterior canal. It also resembles *Hippochrenes baylei.*
Hippochrenes fissura (COQUEBERT & BRONGNIART, 1793) has the shield-like outer lip only in front and extended onto the spire in an apical spine. An anterior sinus is present and the siphon is elongate, spine-like (SAVAZZI, 1991: fig. 2D, E). The outer lip, thus, forms a thin shield that extends to the posterior end of the body whorl only. From its posterior its margin continues to the apex and is accompanied by the extension of the inner lip forming a narrow straight groove with it (CHENU, 1859: fig. 1640 as *Rostellaria columbaria*). *Hippochrenes fissura* in general outline resembles *Wateletia geoffroyi* (WATELET, 1853) while *Tibia marceauxi* (= *Semiterebellum* COSSMANN, 1889) has an even smaller outer lip (SAVAZZI, 1991: fig. 5A). *Hippochrenes murchisoni* DESHAYES, 1865 by ZITTEL (1895: fig. 961) as documented by LOWRY (1866) is also known as *Tibia murchisoni* and *Rostellaria murchisoni*. It has the evenly rounded outer lip expanded as shield only to about the middle of the spire and from there on it continues as thin attached ridge to the apex. It forms an open groove to the apex together with the enlarged and expanded callus sheet of the inner lip. *Hippochrenes macroptera* has similar shape regarding the curved siphon and the groove to the apex, but with its outer lip short.

Genus *Semiterebellum* COSSMANN, 1889

The type species is *Rostellaria marceauxi* DESHAYES, 1865 from the Eocene (Thanetian) of the Paris Basin (COSSMANN, 1904: pl. 2, fig. 4).

Diagnostic characters: The slender shell with conical spire and rounded pointed body whorl has a relatively narrow wing-like outer lip with thin margin. The posterior end of the outer lip may or may not continue to the apex. The anterior shell forms a wide sinus of the open short siphon next to the pointed outer margin of the siphon. The inner lip continues in a margin to a groove that extends from the posterior margin of the aperture to the apex.

The outer lip forms a narrow shield in *Semiterebellum marceauxi* from the Paleocene of the Paris Basin France (COSSMANN & PISARRO, 1911: pl. 31, fig. 157–13; JUNG, 1974: pl. 15, figs. 13–15) and it extends in an even line into a ridge to the apex (SAVAZZI, 1991: fig. 6A).

Remarks: The apertural end of the shell resembles that of *Terebellum*, and there is also no stromboid notch. COSSMANN (1904) suggested that *Semiterebellum* represents a subgenus of *Calyptraphorus,* which can not be supported, since characteristic features of *Calyptraphorus* such as the callus added to the body whorl and a low callus canal on the spire are not found in *Semiterebellum*. But the later closely resembles *Hippochrenes murchisoni* which differs only by having a wider outer lip. *Semiterebellum marceauxi* also resembles *Mauryna* GREGORIO, 1880 which has a narrower aperture as was noted by SAVAZZI (1988, 1991: fig. 6A, B) in case of *Mauryna bellardi* GREGORIO, 1880. The latter species was placed in the genus *Terebellopsis* by PACAUD & LEROY (2006). They state that the type of the genus, *Mauryna plicatum* (ARCHIAC, 1854), differs from the Italian *Mauryna bellardi*, and suggested that the genus was not correctly chosen by SAVAZZI (1988, 1991: fig. 6C–D). Obviously *Semiterebellum*, *Mauryna* and *Terebellopsis*, which lived during the Paleogene along the tropical margins of the Tethys Ocean are quite similar to each other. *Semiterebellum marceauxi* was placed as subgenus to *Tibia* by WENZ (1938: fig. 2739). But aside from having a narrow apertural lip it resembles *Hippochrenes*. While *Hippochrenes murchisoni* could be placed with *Semiterebellum* since it differs predominantly by having a less slender spire, *Semiterebellum* could also be regarded related to the Seraphsidae, especially to *Mauyna*.

Subfamily Wateletinae n. subfam.

Diagnostic characters: As the characteristic genus is *Wateletia* COSSMANN, 1889 illustrated by COSSMANN (1904: pl. 3, fig. 7) with *Rostellaria* (*Wateletia*) *geoffroyi* (WATELET, 1853) from the Eocene of the Paris Basin (DESHAYES, 1865: pl. 89, fig. 1, pl. 90, fig. 1).

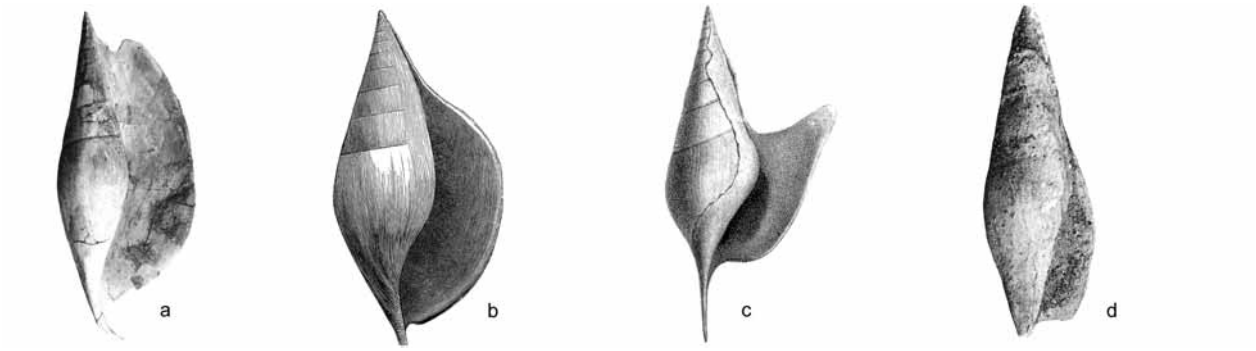

Fig. 11: a – *Hippochrenes macroptera* taken from COSSMANN, 1904; b – *Hippochrenes murchisoni* taken from ZITTEL, 1895; c – *Hippochrenes fissura* taken from DESHAYES, 1866; d – *Semiterebellum marceauxi* from COSSMANN, 1904.

The three genera *Wateletia*, *Chedevillia* and *Maussentia* from the Paleogene of France and Italy are similar to each other in general features especially regarding the fissure formed by the inner side of the outer lip and the calls ridge in continuation of the inner lip as is the case in *Hippochrenes.* In difference to it they have an ornamented and fusiform conical spire with rounded whorls and distinct sutures, and the thin outer lip forms a wide expanded and thin shield to the apex that may have spines and spikes.

Derivatio nominis: The subfamily is called according to the genus *Wateletia*.

Genus *Wateletia* COSSMANN, 1889

The type is *Rostellaria geoffroyi* WATELET, 1853, from the Eocene (Cuisien) of the Paris Basin (COSSMANN, 1904: pl. 3, fig. 7; WENZ, 1938: fig. 2736 from DESHAYES, 1865).

Diagnostic characters: The whorls of the spire are ornamented by axial ribs, which decrease in number and increase in height toward the body whorl. The outer lip flares as in *Hippochrenes* but it has two large sinuses, one next to the elongate siphon, and the other next to the extension that expands beyond the apex of the spire. On the inner side of the outer lip a groove formed by the continuation of the callus of the inner lip extends to the apex. The outer lip resembles that of *Hippochrenes fissura* which also has a median lobe and two projections, one to the tip of the spire and the other bordering the siphonal rostrum (COSSMANN, 1904: pl. 3, fig. 7; WENZ, 1938: fig. 2736; SAVAZZI, 1991: fig. 2D–E). *Wateletia* existed from the Paleocene to Eocene (SAVAZZI, 1991: fig. 2F–G).

Remarks: *Wateletia geoffroyi* from the Paris Basin resembles *Aporrhais* in general shell shape but has in contrast a shield- like thin outer lip with no grooves on the lower side. It also has a narrow fissure extending to the apex present on the inner side of the outer lip.

Genus *Chedevillia* COSSMANN, 1906

The type is *Rimella munieri* CHÉDEVILLE, 1904 from the Middle Eocene (Lutetien) of the Paris Basin (WENZ, 1938: fig. 2735, from COSSMANN, 1906).

Description: The 30 to 60 mm high biconical shell consists of 6–10 convex whorls with shallow sutures. It is ornamented by fine rounded spiral ribs and strong rounded axial folds. The outer lip of the body whorl is wing-like, rounded in outline with short anterior canal that twists to the right. The posterior outer lip continues to the apex and its margin may even descend several whorls on the opposite side. Thus a well rounded shield is expanded reaching from the apex to the siphon. The inner lip continues in a sheet that extends to the apex and forms a fissure with the inner side of the outer lip. The protoconch consists of about four whorls which are quite smooth and rounded with indistinct transition to the ornamented teleoconch.

Chedevillia begiati (GREGORIO, 1880) from the Eocene of Italy has the shell consisting of about 8 whorls with pointed apex and rounded body whorl of egg-shape with pointed short siphon. The callus of the inner lip is

detached and forms the thin lamellar side of a posterior canal that is deep and extends to the end of the outer lip which lies beyond the apex, and may even continue on its opposite side (SAVAZZI, 1988: 12–17), very similar to *Rostellaria mirabilis* DESHAYES, 1865 (pl. 89, figs. 7, 8) and as *Rimella mirabilis* by COSSMANN (1904: pl. 3, fig. 20).

Genus *Maussenetia* COSSMANN, 1904

The type species is *Maussenetia staadti* (COSSMANN, 1904) from the Paleocene of northern France (COSSMANN 1904: pl. 4, figs. 8 & 9).

Diagnostic characters: The conical spire is ornamented by spiral ribs of which the median forms a weak keel on the rounded whorls with distinct sutures. The outer lip is wing-like and expanded to connect to the spire almost to its top. Its general shape resembles that in *Wateletia* with rounded median lobe and a posterior spine, which in contrast is free of the spire. Also the margin of the large lobe has short spikes. The lobe continues to the tube-like siphon forming a sinus at its inner margin. The callus of the inner lip forms a narrow ribbon that continues as ridge onto the spire and forms a cleft between it and the inner side of the outer lip, as is characteristic to the Hippochrenidae.

Differences: *Wateletia* grew to large size (more than 150 mm high), *Chedevilla* to about half that size and *Maussenetia* a little larger (about 90 mm). COSSMANN (1904) suggested that *Wateletia* represents a section to *Hippochrenes* which he considered as subgenus to *Rostellaria* (= *Tibia*). He also suggested a similarity of *Maussenetia* with some species of *Hippochrenes*, but regarded it as subgenus to *Aporrhais* (*Chenopus*) and here as one of the three sections of *Phyllocheilus*. It is thus suggested to stand together with the Jurassic *Phyllocheilus*, the Cretaceous *Pterocerella* and the Paleogene *Maussenetia*. *Hippochrenes abichi* ALEKSEEV, 1963 (seen on the WIENEKE 2007 Wikipedia homepage) has a similar outer lip and the fusiform spire with fine spiral ornament. But it lacks the apical spine on the posterior outer lip, that is characteristic in *Maussenetia staadti*.

The spire in *Chedevillia* is shorter and broader than in *Hippochrenes* and is distinctly ornamented by axial and spiral ribs (WENZ, 1938: fig. 2753). SAVAZZI (1988) described *Chedevillia* and noted that *Chedevillia begiati* resembles *Hippochrenes* (SAVAZZI, 1991: fig. 2H–J). The similar *Chedevillia saltonensis* SQUIRES & ADVOCATE, 1986 lived during the Eocene in the Pacific Ocean at California. The outer lip of the type to the genus has spines, while its margin is uninterrupted shield-like in *Chedevillia begiati*. *Chedevillia insuturata* (GREGORIO, 1880) from the Paleogene of Italy has spiral ornament on its spire connected to short axial ribs on the body whorl, and the margin of its outer lip with spines, quite close in shape to *Maussenetia*, to which it could be placed just as well as to *Chedevillia*.
Dientomochilus has a similar rounded egg-shape spire but the outer lip is not as expanded and resembles that as present in *Tibia*. *Dientomochilus bartonenis* is somewhat intermediate with its outer lip more expanded than in the type to the genus. This latter species and genus is here placed with the Rimellinae (see there).

2.9 Family Seraphsidae GRAY, 1853 (= Terebellidae H.& A. ADAMS, 1854)

Diagnostic characters: The shell is torpedo-like in shape with the last whorl covering much or all of the former whorls. The outer lip of the aperture may be slightly flaring or thin. The anterior shell has no stromboid notch and forms a wide siphonal groove of which the outer margin may be spine-like. With the exception of *Terebellum terebellum* all Seraphsidae represent fossil species.

Remarks: According to JUNG (1974) the Seraphsidae with fossil *Seraphs* MONTFORT, 1810, *Paraseraphs* JUNG, 1974 and modern *Terebellum* RÖDING, 1798, developed as burrowing branch of the Stromboidea during the Upper Cretaceous and flourished in the Tertiary. There is no evidence that Strombidae are more ancient than the Seraphsidae (KIEL & BANDEL, 2002), but rather in the contrary the former appeared only with the Oligocene. Hippochrenidae as interpreted here contain the genera *Semiterebellum*, which is rather close to the Seraphsidae. *Semiterebellum* has its outer lip flaring, and it is therefore placed with the Hippochrenidae, the outer lip of the similar *Terebellopsis* is not expanded and, therefore, it is placed with the Seraphsidae. *Paraseraphs* on the other hand has also features of the shell seen in Rostellariidae such as *Ectinochilus* or *Eocalyptraphorus* (a callus groove to the apex) which also have their roots in the Late Cretaceous as is the case in *Hippochrenes*.
THIELE (1929) and WENZ (1938) placed the genus *Terebellum* in the family Strombidae. WENZ (1938) followed COSSMANN (1904) by including in *Terebellum* the subgenera *Seraphs*, *Mauryna*, and *Diameza*. An independent

evolution of the group was postulated by JUNG (1974). JUNG & ABBOTT (1967) noted a canal from the aperture to the apex in *Terebellum* and connected it to it mode of life as burrower in the sand, as did SAVAZZI (1991). But it has to be noted as well, that *Terebellum* resembles *Strombus terebellatus* and *Strombus fragilis*, both of which have similar shell shape and a narrow margin of their outer lip that is not expanded. In difference to *Terebellum* the two species of *Strombus* have a stromboid notch as independent sinus next to the siphonal canal on the outer lip, as is characteristic to the genus.

Genus *Terebellum* RÖDING, 1798

The type species is *Terebellum terebellum* (LINNAEUS, 1756) from the tropical Indo-Pacific.

Diagnostic characters: The shell is slender, cylindrical, tightly coiled, and smooth with shallow sutures. The margin of the outer lip is straight and its has no stromboid notch.

The only living species is *Terebellum terebellum* that lives in the tropical Indo-Pacific including the Red Sea. It has a characteristic cigar-like and stream-lined shell that is almost 40 mm long.
Terebellum burrows in sand and is thought to extract from it small algae and other food particles. Its eyes lie on long stalks without tentacles on their base (THIELE, 1929). When burrowed in sand one of its stalked eyes reaches above the sand surface, each eye taking turns to survey the water above the sand surface. The hollow siphon is used to hold the periscope eyestalks. Eye stalks are more slender than in the similar *Strombus terebellatus* that also may look out from under its shell extending its eyes by way of the wide sinus of the anterior end of its aperture.

Remarks: Seraphsidae such as *Terebellum* as well as *Seraphs* and *Paraseraphs* have no sculpture on their spire while Strombidae generally have here some kind of spiral sculpture, axial ribs or knobs. Affinities with the Strombidae have been demonstrated by the operculum and the radula (TROSCHEL, 1856). *Terebellum* has a different type of protoconch (JUNG, 1974) which was described by WENZ (1938) as flattened at the top and with few whorls. It resembles that found in *Paraseraphs* as documented below. *Terebellum* can leap during locomotion as is the case in *Strombus*. SAVAZZI (1991) noted that *Terebellum terebellum* crawling on the sand may react to direct contact with a moving object by quickly swimming backwards. Fossil species have been reported from the Eocene of the Paris Basin as well as Italy (COSSMANN, 1904: pl. 2, fig. 10).

Genus *Seraphs* MONTFORT, 1810

The type species is *Seraphs convolutum* (LAMARCK) from the Mid-Eocene of the Paris Basin.

Diagnostic characters: The short cylindrical, egg-shaped shell has the last whorl surrounding and covering all former ones. As in *Paraseraphs* the posterior aperture continues in a curved callus groove to the apex and the anterior is occupied by a wide siphon groove with the outer margin extended (COSSMANN, 1904: pl. 1, fig. 1; JUNG, 1974; SAVAZZI, 1991: fig. 13F, I, J). There are slender species such as *Seraphs convolutum* (WENZ, 1938: fig. 2742) and shorter ones such as *Seraphs isabella* (DESHAYES, 1865) and *Seraphs medium* (DESHAYES, 1835) (WENZ, 1938: fig. 2744). They differ only by the size of their outer lip and several species have been reported from the Eocene of the Paris Basin and also from England (LOWRY, 1866).

Genus *Paraseraphs* JUNG, 1974

The type species is *Paraseraphs tetanus* JUNG, 1974 from the Lutetian of the Paris Basin.

Diagnostic characters: The shell in shape resembles that of *Terebellum* with a spire of few whorls covered to a large extend by the last whorl and with narrow aperture. The shell has the early shell totally covered by the late whorl. The aperture extends in a posterior canal beyond the apex which is curved and a channel- like similar siphon on its front. The callus of the inner lip is prominent and extends as a band just above and along the suture to the apex. Growth lines are curving, and the largest diameter of shell lies near the base. The siphonal canal is wide and short. The protoconch lies as flat whorls on the apex (Pl. 3/3, 4, 8). The genus existed from the latest Paleocene to the end of the Eocene.

Difference: In contrast to *Terebellum* the posterior end of the aperture of *Paraseraphs* extends in a curving canal that continues to the apex. The general shell shape of *Paraseraphs tetanus* is as in *Terebellum* with similar wide anterior canal has the last whorl extending to the apex and covers the whole spire (JUNG, 1974: pl. 10). The outer lip of the aperture in *Terebellum* is not thickened as in *Paraseraphs* where it continues in a ribbon to the apex and may descends a short distance along the opposite side of the spire (SAVAZZI, 1991: fig. 13G). He interpreted it as having had a sensory function.

Genus *Diameza* DESHAYES, 1865

The type species is based on *Ovula media* DESHAYES (COSSMANN, 1904: pl. 3, figs. 9–12) that was determined as *Seraphs intermedius* (DESHAYES, 1865) by (SAVAZZI, 1991: fig. 13L). The shell resembles that of the ovulid *Volva* with the last whorl surrounding all others and both apical and posterior ends drawn out to a narrow point (WENZ, 1938: fig. 2744). Species lived exclusively in the Eocene and are known from Northern Italy as well as the Paris Basin (COSSMANN, 1904).

Fig. 12: a – *Wateletia geoffroyi* from DESHAYES, 1866; b – *Terebellum terebellum* taken from CHENU, 1859; c – *Chedevillia mirabilis* from DESHAYES, 1866; d – *Paraseraphs sophitum* taken from ZITTEL, 1895; e – *Diameza media* taken from COSSMANN, 1904.

Genus *Mauryna* DE GREGORIO, 1880

The type species is *Terebellum plicatum* ARCHIAC, 1854 from the Eocene of Sind (Pakistan).

Diagnostic characters: The shell is terebelliform and composed of about 8 whorls. The spire is spindle shaped with ornament of axial ribs on the early whorls of the teleoconch. The adult lip is expanded and thickened and continues in a narrow posterior canal that continues above the apex forming a curved continuation over and above it. The anterior siphon is short and straight.

Remarks: The shell of *Mauryna* resembles that of *Seraphs* with the last whorl covering the spire. It has growth increments (COSSMANN, 1904: pl. 5, fig. 10; WENZ, 1938: fig. 2743). *Mauryna* differs from *Terebellum* by having axial ribs on the early whorls of the teleoconch. Also its outer lip has a thickened margin that forms with a ridge of the callus of the inner lip a groove on the spire. PACAUD & LEROY (2006) suggested that *Mauryna* resembles *Rimella* and *Ectinochilus*.

Genus *Terebellopsis* LEYMERIE, 1846

The type species is *Terebellopsis brauni* LEYMERIE, 1846, from the Eocene of France.

Diagnostic characters: The shell is fusiform with about nine whorls and the last whorl covers the former whorls. The margin of the outer lip is thickened and continues to the apex or even beyond it. With the callus of the inner lip that extends to the apex is forms a groove. Among different species the shell is more or less elongate, consists of five to nine whorls which are ornamented by fine collabral ribs. The last whorl covers the whole shell. The siphon is short and its outer margin forms an anterior spine. The callus of the inner lip continues beyond the posterior end of the aperture in the margin of a callus groove that ends at about the apex

Differences: *Terebellopsis brauni* was considered a subgenus of *Tibia* by WENZ (1938: fig. 2740) who remarked on its similarity with *Semiterebellum*, which is a little less slender. He also compared the not so well preserved type representing a steinkern of *Terebellopsis* with a much better preserved *Semiterebellum*. The shell resembles that of *Rimella* in regard to general shape and ornament of the juvenile whorls and has the shape of *Terebellum* with the last whorl covering the other. It differs from *Paraseraphs* by having a thickened margin of the outer lip, which also distinguishes from *Terebellum* and also from *Hippochrenes* that has the outer lip strongly expanded, but not thickened. PACAUD & LEROY (2006) described two species of which *Terebellopsis chantalae* has a relatively short fusiform shell that resemble the type, and *Terebellopsis merlei* has a very slender elongate shell. The authors noted that there are five species of the genus known all from the Paleogene. One of these, *Terebellopsis bellardi*, had been placed with *Mauryna* by SAVAZZI (1988: figs. 1–11) and described as *Mauryna bellardi* (GREGORIO, 1880) in detail, which could be interpreted as a very elongated relative of *Hippochrenes kussi*.

2.10 Family Dilatilabridae n. fam.

Diagnostic characters: Shell shape resembles that of *Strombus* with thick, flaring outer lip, which has a sinus on its posterior end, a wide siphonal canal, but lacks the characteristic stromboid notch of the Strombidae. The type is *Dilatilabrum fortisi* BRONGNIART, 1823 with shell about 130 mm high from the Eocene of Italy (COSSMANN, 1904: pl. 1, fig. 7), and Hungary (STRAUSZ, 1966: pl. 10, fig. 4, pl. 11, figs. 2 & 7).

Derivatio nominis: The family is named according to the genus *Dilatilabrum*.

Dilatilabrum fortisi has a massive shell with wide outer lip and short conical spire. It resembles a *Strombus* with its outer lip greatly thickened, but without sinus next to the siphon (COSSMANN, 1904: pl. 1, fig. 7; WENZ, 1938: fig. 2757; STRAUSZ, 1966: pl. 10, fig. 4). It has a flattened shoulder with angular corner and a wide outer lip (SAVAZZI, 1991: fig. 8I, J). Dilatilabridae represent Stromboidea of the Eocene with the general shape as in *Strombus* with flaring outer lip in the grown shell but without a stromboid notch. They can probably be considered close to the stem group of the Strombidae. First species of the later appear during the Oligocene.

Difference: The shell is thick and the outer lip expanded and thickened in Dilatilabridae, while the shell is delicate and outer lip thin in case of the Hippochrenidae. The callus of the inner lip is not thickened to form an apical pad of the aperture as is the case in the Thersiteidae. The outer lip has no sinus next to the siphon as is the case in Strombidae. Dilatilabridae has an angular body whorl and keel bearing spire, *Oostrombus* in contrast has a rounded apical body whorl and rounded whorls of the spire, and a posterior callus ridge on its inner lip that is characteristic to the Thersiteidae.

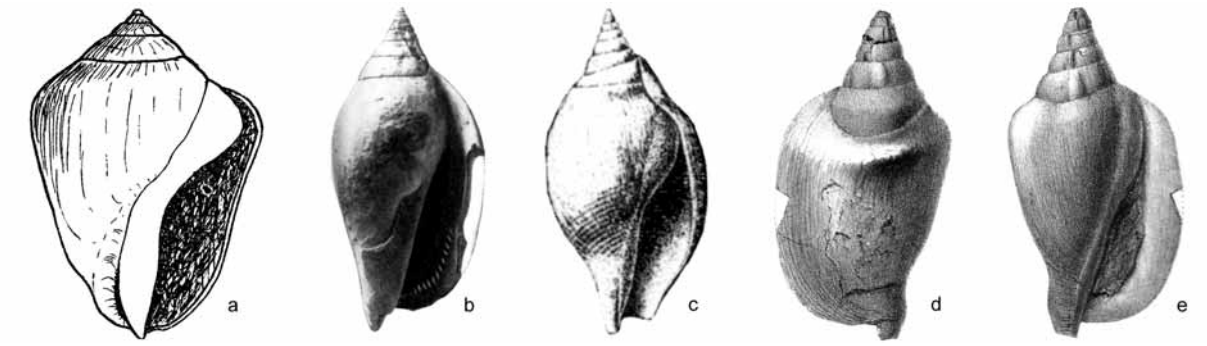

Fig. 13: a – *Thersitea* from SAVORNIN, 1914; b – *Oostrombus leurus* taken from WOODRING, 1928; c – *Orthaulax gabbi* taken from COOKE, 1921; d – *Oostrombus pulcinella* taken from OPPENHEIM, 1897; e – *Oostrombus pulcinella* taken from OPPENHEIM, 1897.

Remarks: Dilatilabridae may have evolved from the Hippochrenidae as well as the Thersiteidae. COSSMANN (1904) regarded the genera *Dilatilabrum* COSSMANN, 1904 and *Oostrombus* SACCO, 1893 to be closely related to each other and to *Strombus*. Both have a wide, wing-like outer lip with no stromboid notch, which represents a central character of the shell in *Strombus*. *Dilatilabrum sublatissimum* as mentioned by HARZHAUSER et al., (2007), in contrast, is a member of the Strombidae since it has a stromboid notch.

2.11 Family Thersiteidae SAVORNIN, 1915

Diagnostic characters: The ovoid to short conical shell has the callus of the inner lip greatly thickened on the posterior inner side of the aperture. This callus pad forms a fissure with the margin of the outer lip. The evenly curving outer lip has no stromboid notch and ends in a wide and short siphonal canal. The aperture is elongate with wide anterior siphon and narrow posterior fissure. The apertural callus pad appears during growth of the juvenile teleoconch and is present well before formation of the body whorl. The family is based on the genus *Thersitea*, which resembles *Oostrombus*, and *Orthaulax.*

Difference: Like the Dilatilabridae the outer lip of Thersiteidae has no sinus on the outer lip next to the siphon. In contrast to *Dilatilabrum* the inner lip forms a thick callus pad in posterior position of the aperture. This thickening of the callus appears during growth of the juvenile shell which differs to a thickened callus of the inner lip as is found in *Strombus* (*Gibberulus*) *gibberulus. Thersitea* resembles *Orthaulax* in regard to the thick callus but its whorls have a shoulder and juvenile whorls are keeled.

Remarks: The classification of BOUCHET & ROCROI (2005) includes among established families of the Stromboidea also the Thersiteidae based on *Thersitea* COQUAND, 1862, while WENZ (1938: fig. 3576) interpreted *Thersitea* it to be a doubtful member of the Fasciolariidae (Neogastropoda), and *Orthaulax* as a member of the Strombidae.

Genus *Oostrombus* SACCO, 1893

The type is *Strombus problematicus* MICHELOTTI, 1861 from the Oligocene of France (COSSMANN, 1904), which represents a synonym for *Oostrombus auricularius* (GRATELOUP, 1834), according to HARZHAUSER (2004).

Diagnostic characters: The cone-shaped shell consists of about 9 whorls and is up to 19 mm high. It has a smooth body whorl and a wide outer lip without stromboid notch. The spire is pointed with shallow sutures and with ornament of coarse axial ribs crossed by fine spiral lines. Succeeding whorls conceal much of the former ones. At the shoulder the shell wall is thicker than at other parts of the shell (HARZHAUSER, 2004: pl. 11, figs. 1 & 2). The reason for that lies in the construction of the inner lip that consists of callus that is thickest in the posterior part of the aperture (COSSMANN, 1904: pl. 2, fig. 1; WENZ, 1938: fig. 2750).

Oostrombus auricularius from the Oligocene of France has rounded shell shape (SAVAZZI, 1991: fig. 9A), and its inner lip appears to be less thickened than that as of *Oostrombus naticiformis* (OPPENHEIM, 1901) from the Oligocene of Italy. The later resembles *Orthaulax*. *Oostrombus auricularius* was noted to have lived in the Western Tethys during the Oligocene, from France to Iran (HARZHAUSER, 2004: pl. 10, figs. 1–6).
Oostrombus cedroensis CLARKE & DURHAM, 1946 is known from the Eocene of Colombia (CLARK & DURHAM, 1946), and WOODRING (1959: pl. 24, figs. 1, 8, 9, 11) determined a species from the Miocene of Panama as close to it. The later has a high spire with varices and axial ribs and the characteristic wide rounded body whorl with posterior callus pad on the inner lip that had been present before final growth stage as is reflected in rounded swellings. *Oostrombus tournoueri* (BAYAN, 1870) was described from the Eocene of Italy as *Strombus pulcinella* BAYAN, 1870 by OPPENHEIM (1896: pl. 13, fig. 1). It is also known from the Eocene of Hungary (STRAUSZ, 1966: pl. 10, fig. 1, 2), where it lived together with a larger species of *Oostrombus* that has a more rounded apex, a thicker inner lip and the shell is 100 mm high (STRAUSZ, 1966: pl. 9, fig. 11, pl. 10, figs. 3, 5). COSSMANN (1904) suggested that *Strombus scurrus* OPPENHEIM, 1896 represents a species of *Oostrombus.* It may represent a variety of *Oostrombus pulcinella* that has a the shell consisting of 9 whorls which are smooth and have irregular varices distributed on the spire, a swelling on the body whorl, and is about 80 mm high.

Remarks: In case of *Orthaulax* the outer lip may extend to the apex and cover the whole shell. COSSMANN (1904) discussed the possible relation of *Thersitea* with *Oostrombus* and criticized its comparison with modern *Strombus gibberulus*. He correctly stated that the stromboid notch on the outer lip, as is characteristic to *Strombus,* is not present in *Oostrombus.* The thickened callus in the posterior part of the inner lip of *Thersitea* and *Oostrombus* is neither developed in *Strombus gibberulus,* nor any other species of *Strombus,* Strombidae. *Strombus problematicus* MICHELOTTI, 1861 (= *Strombus auricularius* GRATELOUP, 1893), was mentioned by THIELE (1931) as section to *Canarium* (*Strombus*), and accepted as such by WENZ (1938: fig. 2750) as subgenus *Oostrombus* of the genus *Canarium* SCHUMACHER, 1817. This taxonomic place is not accepted and *Oostrombus* is neither a member of the genus *Strombus* nor to either its subgenera *Canarium* of *Gibberulus*.

Genus *Orthaulax* GABB, 1873

The type species is *Orthaulax inornatus* GABB, 1873 from the Miocene of Santo Domingo (WENZ, 1938: fig. 2719).

Diagnostic characters: Growth of the shell is allometric with increasing relative length of the outer lip in comparison to the height of the spire. During juvenile growth the outer lip expands in posterior direction and reaches the apex before the shell is fully grown. During further growth whorls may cover the whole shell and increase the apical angle. Whorls of the spire are rounded and have a fine ornament of low axial ribs and fine spiral lines besides occasional varices. The inner lip is narrow in front and has a callus pad next to the posterior part of the outer lip. Growth is terminated with the outer lip of the body whorls expanded outward and posterior callus pad thickened forming the margin of a narrow fissure to the end of the outer lip on the spire. The whorls of *Orthaulax inornatus* remain visible and a fine spiral ornament covers the base of the body whorl.

The juvenile teleoconch of *Orthaulax gabbi* DALL, 1890 (= *Orthaulax pugnax* (HEILPRIN, 1887)) is smooth with occasional varices (Pl. 7/12–13). The outer lip covered the shell half way up when five whorls were formed, while the sixth whorls is expanded to cover the spire and, in addition, a thick callus developed on its posterior inner lip. With further addition of whorls the spire were totally covered and each added whorls increases the apical angle. With the ninth and final whorl the apical angle is the largest. The callus pad of the inner lip was largest before the formation of the final part of the body whorl and forms a rounded bump on the upper shell side (Pl. 7/13). The short siphon is upturned (COOKE, 1922; WOODRING, 1959; VOKES & VOKES, 1968; SAVAZZI, 1989, 1991). The callus of the inner lip extends to the apex, forming in its posterior portion a ridge, so that the groove is similar to such a groove present on the spire of *Hippochrenes*, but without a thickened callus pad in the later.
Orthaulax leurus (WOODRING, 1928) from the Miocene of the Dominican Republic (as *Strombus*) is about 6 cm high and the adult shell resembles juveniles of *Orthaulax pugnax*. The outer lip is evenly curving without stromboid notch, ends on the spire and is only little thickened. The convex whorls of the spire exhibit an ornament of narrow axial ribs crossed by very fine spiral lines and some varices. The callus of the inner lip continues into a swelling that borders the apical fissure of the aperture. In contrast to *Orthaulax pugnax* the outer lip ends before reaching the apex, and the species can just as well be placed with *Oostrombus*, which extends the stratigraphic range of that genus to the Miocene.

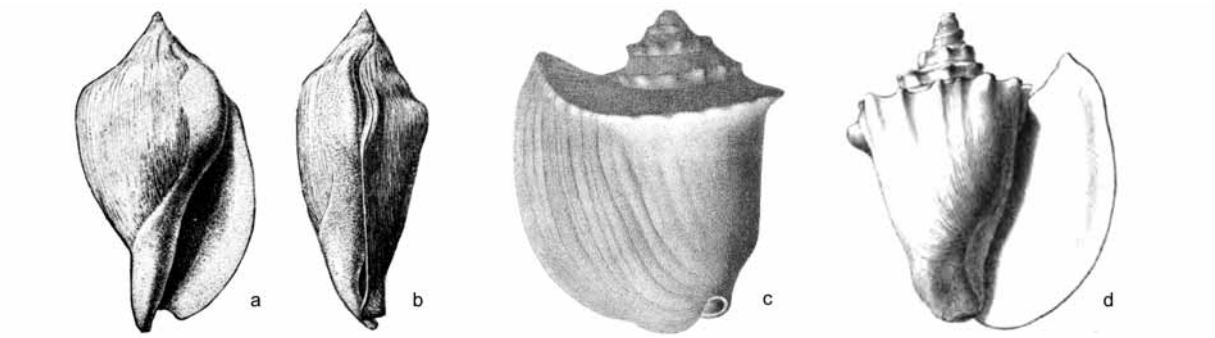

Fig. 14: a – *Orthaulax gabbi* taken from COOKE, 1921; b – same as Fig. a; c – *Dilatilabrum fortisis* taken from QUENSTEDT, 1884; d – *Dilatilabrum fortisi* taken from BRONN, 1837.

Remarks: *Orthaulax* existed from the Eocene of the Tethys Ocean through the Oligocene into the Miocene of the Caribbean Region. SAVAZZI (1989) suggested that the extension of the mantle in a posterior canal may have been expanded and formed a sheet that enveloped the former whorls and coated them with a polished callus. Actually only the lower side of the shell is coated with callus of the inner lip, in case of *Orthaulax pugnax*. While *Thersitea* was described only from the Eocene of the Maghreb (SAVORNIN, 1915) and Italy (SAVAZZI, 1991), *Orthaulax* lived during the Miocene in the Caribbean area (COOKE, 1922; WOODRING, 1928).

Genus *Thersitea* COQUAND, 1862

The type species is *Thersitea gracilis* COQUAND, 1862 from the Eocene of Tunesia.

Diagnostic characters: The callus on the inner lip forms a thickened posterior pad. The shell is more angular than that of *Orthaulax* but has a similar aperture. Between callus pad of the posterior inner lip and the outer lip a narrow slit is developed (SAVAZZI, 1991: fig. 9C–F) and the thick callus pad of the posterior inner lip had been present also in some juvenile whorls of the teleoconch.

Remarks: ABBOTT (1960) agreed with COSSMANN (1904) and WENZ (1938) that *Thersitea* from the Eocene is not a member of the Strombidae. SAVORNIN (1915) noted two species from the Eocene NW Africa, of which *Thersitea gracilis* has a pointed spire and *Thersitea ponderosa* COQUANDE, 1862 has a short spire. *Thersitea* is the least well known of the three genera of the Thersiteidae and has been named earliest. It may be that difference of the species representing the family are so small, that one genus is sufficient, which should be *Thersitea*.

2.12 Family Strombidae RAFINESQUE, 1815

Diagnostic characters: The spire may be low or high and of conical shape. Its whorls often have a median angle and axial ribs crossing it, often tubercles or spines may expand from them. Thickened rounded varices are often present especially on the whorls of the early teleoconch. Shell growth stops when the animals reach maturity. The fully grown shell has a expanded and thickened outer lip, often strongly flaring and greatly thickened. The aperture is narrow with short siphon (rostrum) that is straight or curves to the side of upwards. Next to the this anterior channel a U-shaped indentation is characteristically present ("stromboid notch"), (ABBOTT, 1960). It serves to expose one (right) eye of the two eyes which are placed on stalks. The left eye utilizes the siphonal canal. The posterior margin of the outer lip differs among subgenera (genera) and there may be a notch, a groove, a sinus, spines and thorns, or it may have straight or curved shape covered by more or less callus. The fully grown shell of different species varies from about 12 mm to 400 mm in height, and shell size within a species may vary from individuals of about one third to one half the size of others.
The protoconch of the planktotrophic larva is conical and pointed with rounded whorls and a median lobe on the outer lip of the aperture in at least part of the shell. The embryonic shell may be ornamented by tubercles (Pl. 5/5) or may be smooth. It ends with first growth lines (Pl. 5/4). The larval shell has sinuous growth lines (Pl. 1/4) and may be smooth or ornamented (Pl. 1/1, 2), and protoconch size is usually more than 1 mm.

The operculum closes the protoconch of the larva (Pl. 5/8). In the benthic stage it changes shape to being solid, long and pointed narrow (Pl. 5/13–14) and is used during locomotion. Species of the family are present since about the Mid-Tertiary for about 30 Million years.
The shell of living species of the Strombidae have been documented well in several well illustrated books, such as ISSEL & TAPPARONE CANEFRI (1876), KEEN (1971), KAY (1979), DANCE (1974), ABBOTT & DANCE (1990), KREIPL & POPPE (1999), SHARABATI (1984), WILSON (1993), and illustration of all species can also viewed in the internet with WIENEKE (2007) as guide.

Genus *Strombus* LINNÉ, 1758

Diagnostic characters: As in the family, with changes of the morphology of the shell several times during its ontogeny. The final change occurs when the individual reaches the adult stage and sexual maturity. The shell stops growing in size thereafter.

The different subgenera of the genus *Strombus*

The genus *Strombus* has been differentiated into a number of subgenera which have been regarded to represent genera by different authors. The subgenera are listed below with their type species, and their diagnostic characters are given. Species that may be regarded to belong to the same taxon are included. For those species that were not found to be fitting in the diagnostic characters of the shell of an existing taxon a new subgenus is proposed below and its type species is characterized. Subgenera are arranged into nine groups and are based primarily on their morphology, but also on their geographic occurrence.

a) Atlantic and West Pacific species of four subgenera often with large size:

Strombella SCHLÜTER, 1838

The type species is *Strombus pugilis* LINNÉ, 1758 with conical spire (75°) and median keel, in the last whorls with spines, has the outer lip with rounded posterior margin, inserting on the body whorl in the row of spines. The siphon is short, open and turned upwards, with callus of the inner lip near the aperture or expanded. The size ranges between 65–85 mm (CLENCH & ABBOTT, 1941: pl. 4). Included is *Strombus costatus* GMELIN, 1791 with relatively shorter shell, which is similar to *Strombus* (*Afristrombus*) *latus*, differing from it by the evenly rounded outer lip and shorter spire.
Strombus pugilis has the ornament of the teleoconch in the first whorls with fine spiral ribs and rounded varices, later a median keel is added that in the last whorls of the spire develops spines. The body whorl is about the 10th whorls of the teleoconch. The outer lip has a rounded apical sinus and inserts u-shaped indentation and inserts below the row of spines. It margin is thickened and there is a deep stromboid notch with a rounded lobe to the short and wide siphon that is slightly curved upwards. The inner lip is a broad smooth callus that covers the basal shell side (CLENCH & ABBOTT, 1941).
The protoconch measures about 1 mm in height and consists of 3.5 whorls (Pl. 1/11). Ornament in the begin of the teleoconch is with axial ribs, and larger rounded varices on the juvenile teleoconch (Pl. 1/9, 11).
The spire of *Strombus costatus* is pointed. Before maturity the shell is cone-like in shape with the corner formed by the spiral rib and on the sides regular low spiral ribs separated by narrower grooves. The juvenile shell has no stromboid notch and its siphon is wide. On the body whorl ornament continues as large rounded spikes in line with the rounded posterior projection of the outer lip. The latter is smooth thickened and evenly rounded to the shallow stromboid notch separated from the deeper open siphon by a rounded lobe. The outer lip is attached to the upper edge of the last whorl, and the inner lower side of the shell is evenly callus covered by the expanded inner lip. The shell consists of about 10 whorls, its height is about 120 mm (80 to 180 mm, CLENCH & ABBOTT, 1941).
Strombus pugiloides GUPPY, 1873 from the Miocene of Jamaica has a shell that is about 55–65 mm long. Ornament of the spire is by axial ribs and weak spiral line in the inter-space. Later a keel develops as edge of the shoulder and the axial ribs become swollen into nodes. On the next to the last whorl the nodes become spines which on the body whorl are absent. The base of the shell has spiral ribs and the siphon is short and wide. The outer lip is thickened and attached to the whorl below or at the corner. The inner lip is spread out on the lower side as callus covered. Whorls are shouldered and the interior of the outer lip has elongate callus ridges. Variability of ornament is present, so that also the body whorl may be node bearing. WOODRING (1928: pl. 23, figs. 1 & 2) noted that *Strombus pugiloides* resembles *Strombus pugilis* and is also known from the Pliocene of Costa Rica.

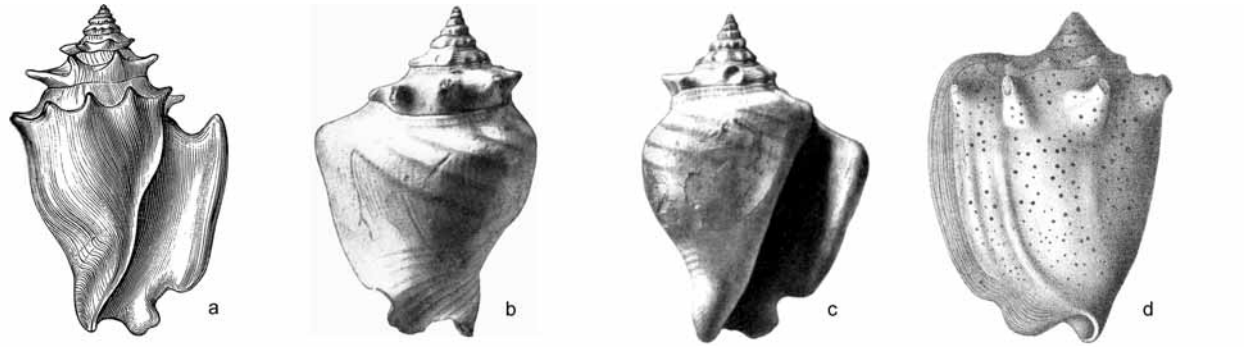

Fig. 15: a – *Strombus* (*Strombella*) *pugilis* taken from CHENU, 1859; b – *Strombus* (*Strombella*) *pugiloides* taken from WOODRING, 1928; c – *Strombus* (*Strombella*) *pugiloides* taken from WOODRING, 1928; d – *Strombus* (*Afristrombus*) *coronatus* taken from QUENSTEDT, 1884.

Strombus bifrons SOWERBY, 1850 from the Miocene of the Dominican Republic has a shell that is about 50–60 mm high with high spire ornamented by many axial ribs with fine spiral lines between them. The axial ribs are transformed into nodes and these into spines with further whorls and their distance to each other is farther. The body whorl has strong spiral ribs. The outer lip has a deep stromboid notch (WOODRING, 1928: pl. 23, figs. 2, 3). This species resembles *Strombus diegelae* PETUCH, 1991 and *Strombus chipolanus* DALL, 1890 from the Chipola Formation of Florida. *Strombus bifrons* has similar shape to *Strombus pugiloides* but is smaller and heavier. WOODRING (1928) compared *Strombus bifrons* with *Strombus proximus* GUPPY, 1876 that has a lower row of

spines but the early whorls as in *Strombus bifrons.* Similar is also *Strombus gatunensis* TOULA, 1909 from the Miocene Gatun formation of Panama (WOODRING, 1959: pl. 38, figs. 15, 19, 10, 23) that is more than 40 mm high. Shell shape here closely resembles that of *Strombus pugilis* with the spines on the spire lower and the outer lip of the body whorl not as much expanded. It documents that *Strombus pugilis*-like species have been living in the area of the Caribbean Sea during the last 15 Million years and well in advance of the closure of the Isthmus of Panama.

Afristrombus n. subgen.

The type species is *Strombus latus* GMELIN, 1791 with conical stair like spire (60–70°) with axial ribs, tubercles on corner, outer lip rounded attached to corner of body whorl, siphon short wide and twisted to the right, thin wide callus of inner lips, size range 60–130 mm. It resembles *Strombus* (*Strombella*) *pugilis* but differs by a strong posterior sinus on the outer lip. *Strombus* (*Lentigo*) *lentigo* and *Strombus* (*Lentigo*) *lentiginosus* have their outer lip attached higher up.
Strombus latus has a short spire with blunt tubercles that form two or three spiral rows on the body whorl. It has conical shape with thick evenly rounded outer lip and strong stromboid notch. There are at least eight whorls. The body whorls has spiral ribs with strong tubercles and smooth callus of the inner lip. The posterior end of the outer lip ends on the nodes of the upper spiral of the body whorl without notch. *Strombus latus* lives along the African East Coast from Senegal and Cape Verde and resembles *Strombus* (*Eustrombus*) *goliath* from Brazil. Its outer lip is rounded but not as wide and does not reach as far onto the last whorl of the spire. It closely resembles and is probably related to *Strombus bubonius* from Mediterranean Pleistocene.
Strombus coronatus DEFRANCE, 1827 from the Miocene of the Paratethys and the Pliocene of the Mediterranean has a massive short shell. It has dull conical shape with low conical spire. Ornament consists of solid triangular thorns which are largest on the body whorl. The outer lip is thickened and ends with a narrow rounded sinus that is attached to the last whorl. The margin is straight ending in a deep stromboid notch next to the wide short siphon. The outer lip is thick with rounded posterior margin and stromboid notch next to the short and wide siphonal canal. *Strombus coronatus* was noted from the Pliocene of Tuscany in Italy and is found in the Mid-Miocene from the Paratethys of Hungary with up to 20 mm high shell (STRAUSZ, 1966) and also in France, and Italy. It has a shorter spire than *Strombus bonelli*, which occurred at the same time in the Paratethys Sea. It may have evolved into *Strombus bubonius* and the African *Strombus latus*, its modern counterpart. The *Strombus* sp. from early Messinian (late Miocene) deposits from Libya (Pl. 7/8–9) resembles *Strombus coronatus* but is larger, about 40 mm high, and had its shell totally transformed into gypsum (BANDEL et al., 1986).
Strombus bubonius LAMARCK, 1822 has its shell smaller than that of the living *Strombus latus* from the Guinea and Senegal and the tubercles of the spiral ribs appear relatively larger. Usually the shell is very thick. This species lived during warm intermissions of the ice age in the Mediterranean region. *Strombus bubonius* lived for example in the shallow water near Almeria, now found on the raised marine deposits Cerro Largo of middle Pleistocene age in Spain (HILLAIRE-MARCEL et al., 1986). It is also found in other deposits of coastal sediments in the Western Mediterranean.
Strombus leidyi HEILPRIN, 1886 from the Miocene and Pliocene of Florida has its large shell with a conical spire with a node bearing spiral rib above the suture and flattened whorls with spiral ribs. The outer lip resembles that of the living *Strombus latus* from the African coast of the varieties with more acute spire. The shell is large and thick and about 80–140 mm long. It was placed in the subgenus *Gallinula* by COSSMANN (1904). *Strombus leidyi* from Caloosahatchee Formation of the Pliocene is large and thick and resembles *Strombus haitensis* with 85 mm length from the Pliocene of the Dominican Republic.

Eustrombus WENZ, 1939

The type species is *Strombus gigas* LINNÉ, 1758 with acute spire (45°) with spines, outer lip flaring without sinus, attached to last spine on body whorls, siphon short, wide and turned to the left, callus of the inner lip expanded near aperture, size range 100–350 mm (CLENCH & ABBOTT, 1941: pl. 9). Included is the very large *Strombus goliath* SCHRÖTER, 1805 (*Titanostrombus* of PETUCH, 1994) and *Strombus galeatus* SWAINSON, 1823. They resemble *Strombus* (*Latissistrombus*) *latissimus* that differs by its outer lip being attached higher up on the spire.
Strombus gigas has a planktotrophic larval stage with larval shell of 1.2 mm in height (Pl. 1/7–8). Its adult shell is heavy when old, and very old individuals with thickened shell and the outside corroded due to wear were named *Strombus samba* CLENCH, 1937. A wide low sinus lies at the apical margin of the outer lip. Often a bump on the outside is present where the outer lip connects to the last rounded node on the body whorl. The seven whorls of the spire before the last have a corner with a row of low pointed spines and smaller spiral ribs. This

ornament and the number of whorls resemble that of *Strombus pugilis* but the shell of *Strombus gigas* is much larger. Also its outer lip is more expanded and attached to the last spine on the body whorl without apical sinus. The stromboid notch is wide and low and separated by a rounded lobe from the short and wide siphonal notch. *Strombus gigas* lives in the tropical Western Atlantic. CHENU (1859) regarded the species as type to the subgenus *Strombus* as did COSSMANN (1904).
Strombus goliath has a body as in *Strombus gigas* but with shorter spire and outer lip forming an even, wide and rounded wing that has a low stromboid sinus near the short wide siphon. Its posterior end is attached to the last whorl of the spire. The lower side of the shell is covered by a smooth callus of the inner lip that connects smoothly with the inner side of the outer lip. The margin of the outer lip is wide expanded and flat. Shell size is about 270 to extreme 400 mm in height. *Strombus goliath* occurs in the southern Atlantic near Brazil. The outer lip is wider than in *Strombus* (*Strombella*) *costatus* and callus covers part of the inner side of the spire up to the whorl before the last. The spire resembles the South American *Strombus (Monodactylus) peruvianus),* and in general shell shape the African *Strombus* (*Afristrombus*) *latus* appears related.
Strombus galeatus SWAINSON, 1823 has an ovoid shape when the shell is fully grown with about 180 mm in height (150–220 mm), with low conical spire and spiral ornament. This species from the tropical American Pacific coast has a rather rounded shape and the outer lip rounded as well and attaches to the body whorl. It resembles the fossil *Strombus pugiloides*. The large species *Strombus goliath* from the Brazilian coast has a similar shell with a much more expanded and thickened outer lip.

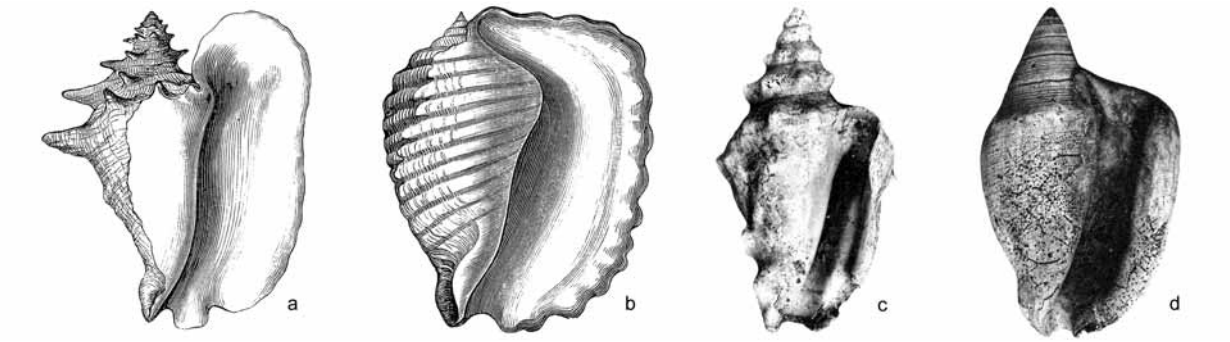

Fig. 16: a – *Strombus* (*Eustrombus*) *gigas* taken from CHENU, 1859; b – *Strombus* (*Eustrombus*) *galeatus* taken from CHENU, 1859; c – *Strombus* (*Persististrombus*) *aldrichi* taken from COSSMANN, 1904; d – *Strombus* (? *Persististrombus*) *leydii* taken from COSSMANN, 1904.

Monodactylus KLEIN, 1753

The type species is *Strombus gallus* LINNE, 1758 with spire with keel and spines (45°), outer lip with posterior outer gutter-like twisted spine, attached to upper body whorl with narrow groove, siphon twisted to the right with left thorn. The callus of the inner lip extends onto the spire, size ranges between 120–160 mm (CLENCH & ABBOTT, 1941: pl. 3). Included are *Strombus peruvianus* SWAINSON, 1823 with triangular grooved apical outer lip and *Strombus raninus* GMELIN, 1791 that has a shorter posterior lobe on outer lip and also a spread out callus. It resembles *Strombus* (*Euprotomus) aurisdianae* and related species which live in the Indo-West Pacific.
Strombus gallus lives in the Caribbean Sea and differs from *Strombus raninus* by the outer lip with lobed shape and a gutter-like spine at the outer margin of the apical sinus as a prong-like posterior expansion. A protoconch is known from off the coast of Brazil (LEAL, 1990: pl. 14, figs. A & B) and consists of about 4.5 whorls with no ornament preserved on the smooth rounded whorls.
Juveniles of *Strombus raninus* resemble with their conical shape *Strombus costatus* but are less slender when fully grown. The whorls of the spire have a median corner with short spines, which on the last whorl decrease in number and increase in size. Several spiral ribs (up to 12) are present of which three have knobs or gutter-like short spines. Shell size is quite variable from 40 to 120 mm, and the shell consists of about 10 whorls. The spire is conical and relatively high (55°). The outer lip has a posterior, thickened. rounded spike with margin to the shoulder of the last whorls that forms a rounded sinus. The callus of the inner lip is extensive. A deep stromboid notch lies next to the short siphonal canal that is somewhat twisted to the right. *Strombus raninus* was suggested to belong to the subgenus *Lobatus* IREDALE, 1921 by PETUCH (1994), which was criticized by JUNG & HEITZ (2001) and KRONENBERG & LEE (2006).
Strombus peruvianus with wide conical spire (almost 90°) has a shell size of up 180 mm. The triangular outer posterior margin of the outer lip has a straight elongate posterior side ending in the triangular posterior wing, an almost straight thickened and rounded margin to the deep stromboid notch. The short and wide siphon is twisted

to the left side. The callus of the inner lip covers the base of the body whorl and may be grooved. The inner side of the outer lip has callus ridges. *Strombus peruvianus* from the American Pacific coast resembles *Strombus raninus* and *Strombus gallus* from the Caribbean Sea.
Strombus trigonodus GRATELOUP, 1833 from the Miocene of France (COSSMANN, 1904) has the outer lip of the body whorl with a posterior thickened and rounded spike connected to a rounded and thickened margin across to the shoulder of the last whorl. The callus of the inner lip forms a ribbon from the posterior end of the outer lip to the wide and short anterior siphon. The outer lip is thickened smooth wing to the shallow stromboid notch. The whorls of the spire have a median corner that bears a row of nodes and on the body whorl this becomes the corner with stronger nodes, the last one forming the final spike. The fossil species resembles the living *Strombus raninus* of the Caribbean Sea. At the time of its existence the Atlantic Ocean was less wide and the Caribbean Sea open to the Pacific Ocean.

b) Pacific species of five subgenera which may be interrelated and have their inner lip expanded and smooth:

Persististrombus KRONENBERG & LEE, 2007

The type species is *Strombus granulatus* SWAINSON, 1822, with acute spire (45°) with nodules on keel, outer lip with deep posterior sinus ending on the last whorl, short straight siphon, callus of the inner lip coating lower side and continuous in a furrow with the outer lip, size range 30–110 mm (KEEN, 1971).
Similar is *Strombus* (*Thersistrombus*) *thersites* SWAINSON, 1823 with similar outer lip that is attached to the spire higher up and has a larger shell size. A similar pointed spire with strong median corner and extended inner lip is present in *Strombus* (*Sinustrombus*) *taurus* with spines on the outer lip and *Strombus* (*Euprotomus*) *aurisdianae* and relation with posterior horn.
Strombus granulatus occurs in the tropical Pacific at the Central American coast and the Galapagos Islands (KRONENBERG & LEE, 2007). Its spire is pointed which resembles that of *Strombus* (*Eustrombus*) *gigas* in shape and ornament. The shell has more than 8 whorls and is 30 to 70 mm high. Three or four axial swellings per whorls are on early whorls of the teleoconch, with a varying number of axial ribs in the interspaces. Only the posterior of these remains uncovered by succeeding whorls The body whorl has two or more spiral row of knobs. The outer lip is attached to the last whorl of the spire at about the median keel has a simple apical margin forming a low sinus with thickened margin that turns to the vertical margin that ends in the wide and low stromboid notch. The siphon is rounded short and lightly twisted upwards separated from the notch by a rounded lobe.
Strombus radix (BRONGNIART, 1823) from the Oligocene of Europe has a shell with the spire relatively high and pointed. The body whorl composes about half shell height. Ornament of the spire is by strong and short axial ribs forming spikes crossed by fine spiral ribs. This ornament continues onto the body whorls. The outer lip it attached to the body whorl has simple outline with wide stromboid notch and wide short siphon that is twisted upwards. The fossil *Strombus radix* from the Oligocene of France (KRONENBERG & LEE, 2007: fig. 4) resembles living *Strombus granulatus* from the American Pacific. COSSMANN (1904: pl. 1, fig. 8) documented *Strombus aldrichi* DALL, 1890 from the Oligocene and Early Miocene of the Caribbean region that is very similar in shape. From Chipola Formation of Florida *Strombus aldrichi* is about 45–50 mm long (KRONENBERG & LEE, 2007: fig. 1).
Strombus bonelli BRONGNIART, 1823 from the Miocene of Europe has its spire high and conical with ornament of axial ribs crossed by fine spiral ribs. The shell has at least 9 whorls. The outer lip is simple with begin on the shoulder of the body whorls. A wide pointed posterior canal distinguishes from the smooth inner lip and the siphonal notch is well developed next to the wide and short siphonal channel (KRONENBERG & LEE, 2007: fig. 2). This species from the Oligocene and Miocene of France and Hungary (Paratethys) resembles the Central American *Strombus granulatus*. It occurred in the late Oligocene of France and with a lower spire have been living in the Paratethys during Mid Miocene time. Apparently the species connected to each other in the subgenus *Persististrombus* by KRONENBERG & LEE (2007) connect species of the European Paratethys with such of the Caribbean region of the Miocene and Pliocene persisting in the Pacific along Central America after closure of the Isthmus of Panama.

Thersistrombus n. subgen.

The type species is *Strombus thersites* SWAINSON, 1823 (ABBOTT, 1960: pl. 17, fig. 1–2) with apical angle about 45°, shell of about 9 whorls, size of 130 to 170 mm, with the spire ornamented with a median corner and short ribs on it which continue onto the body whorls forming here 4 to 5 large rounded nodes. The siphonal canal is upturned and accompanied by deep stromboid notch. The outer lip has a thickened straight side, a posterior lobe

and a wide low sinus from it to the attachment to about the corner of the last whorl of the spire. The body whorl has with weak spiral ribs below the nodes and the upper corner ends in the posterior edge. It occurs in the western Pacific from the Philippines and Japan to New Caledonia and Tonga.

Derivatio nominis: The subgenus is called according to the type *Strombus thersites*, connected to form *Thersistrombus*.

Strombus thersites resembles *Strombus* (*Persististrombus*) *granulatus* in shape of the spire and has similar outer lip that is attached further up on the shell and it also has larger shell size. A similar pointed spire with strong median corner and extended inner lip is present in *Strombus* (*Sinustrombus*) *taurus* with spines on the outer lip and *Strombus* (*Euprotomus*) *aurisdianae* and relation with posterior horn. The biogeographic position also distinguishes *Strombus* (*Persististrombus*) *granulatus* that lives at the American coast of the Pacific, from *Strombus* (*Thersistrombus) thersites* that lives between Japan and New Caledonia in the western Pacific.

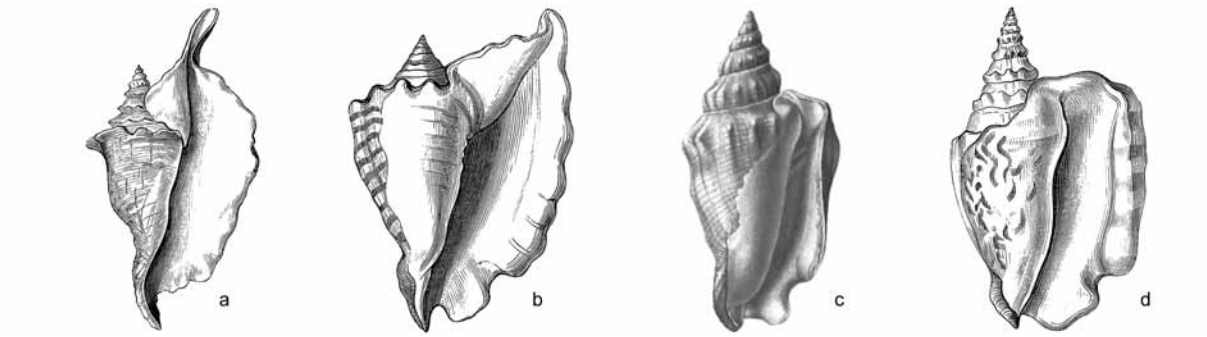

Fig. 17: a – *Strombus* (*Monodactylus*) *gallus* taken from CHENU, 1859; b – *Strombus* (*Monodactylus*) *peruvianus* taken from CHENU, 1859; c – *Strombus* (*Persististrombus*) *granulatus* taken from REEVE, 1878; d – *Strombus* (*Thersistrombus*) *thersites* taken from CHENU, 1859.

Tricornis JOUSSEAUME, 1886

The type species is *Strombus tricornis* LAMARCK with spire (45°) ending in strong knobs, outer lip heavy with posterior lobe, posterior sinus attached to spire, wide and short siphon, callus of inner lip expanded onto spire, size range 140 mm (ABBOTT 1960: pl. 17, figs. 6 & 7). I resembles *Strombus* (*Sinustrombus*) *oldi* that has additional lobes on the outer lip, and is transitional to *Strombus* (*Sinustrombus*) *taurus*. Similar is also *Strombus* (*Monodactylus*) *gallus* that has narrow groove on apical outer lip and more pointed spire, *Strombus* (*Eustrombus*) *gigas* with more pointed spire and outer lip attached to body whorl, *Strombus goliath* and *Strombus* (*Eustrombus*) *galeatus* by shape of the outer lip, *Strombus thersites* (*Thersistrombus*) differs by more angular outer lip and more pointed spire.
Strombus tricornis from the Red Sea to the Indian Ocean has a large shell with a heavy outer lip, a smooth inner lip and ornament of strong knobs. The latter are not present on the earlier teleoconch whorls. The outer lip has a posterior outer lobe and shallow wide posterior sinus. The margin is simple rounded and smooth until the strong stromboid sinus and the anterior wide and short siphon. The shell measures between 65 and 170 mm in height. The development is lecithotrophic with veliger hatching from the spawn that has 1.5 whorls and no change from embryonic to larval shell and drastic change to teleoconch (Pl. 7/3, 4, 6, 7).
The shape of the outer lip of *Strombus tricornis* comes close to that of *Strombus* (*Monodactylus*) *costatus* from the Caribbean Sea, but has no posterior lobe on it smooth thickened outer lip. A similar shape of the outer lip is found in the fossil *Strombus* (*Monodactylus*) *trigonodus*. *Strombus* (*Monodactylus*) *gallus* from the Caribbean Sea and *Strombus* (*Monodactylus*) *peruvianus* from the eastern Pacific along the coast from Mexico to Peru also have a triangular gutter-like extension of their posterior outer lip.

Euprotomus GILL, 1870

The type species is *Strombus aurisdianae* LINNÉ, 1758 with spiral ribs, a median corner and a pointed spire (40–45°). Ornament is present on the body whorl, the outer lip is flaring, rounded and ending in posterior outer projection. It is attached to the spire with wide sinus. The siphon is open and twisted to the side and up with a thorn-like outer side. The callus of the inner lip is wide and expanded onto the spire (ABBOTT, 1960: pl. 14, fig. 1–4). Included with a more extensive callus is *Strombus bulla* RÖDING, 1798, and very similar shell shape is

present in *Strombus aurora* KRONENBERG, 2002, *Strombus vomer* RÖDING, 1798, 1798, *Strombus hawaiiensis* PILSBRY, 1917, *Strombus chrysostomus* KURODA, 1942, *Strombus iredalei* ABBOTT, 1960 and *Strombus atratum* RÖDING, 1798. *Euprotomus* was revised by KRONENBERG (2002) and the species *Strombus aurora* described.
Strombus aurisdianae has strong spiral sculpture on the body whorl and measures between 45 mm to 70 mm in height and consist of about 10 whorls. The early whorls of the teleoconch have fine spiral ribs. Axial ribs come in later and form nodes on a corner that is the periphery and lies close to the suture. There is a short finger-like projection from the posterior end of the lip and a deep stromboid notch at the other. The callus of the inner lip is extensive to almost the apex. The outer lip has a deep stromboid notch that is separated from the siphonal canal by a high narrow rounded lobe and is attached to spire on the middle of the fore last whorl. The callus of the inner lip is especially extensive in *Strombus bulla* with about 60 mm high shell that lives in the Pacific near the Philippines. The tip of its outer lip is coated with smooth callus of the inner-lip. VERMEIJ (2005) considered that callus to represent a sign for envelopment of the shell by the body. But this callus is deposited only during short and intermediate periods of the snails life.

Lentigo JOUSSEAUME, 1886

The type species is *Strombus lentiginosus* LINNE, 1758 with conical spire and wide angle (70–80°). The outer lip is wing-like with undulating margin, attached to the spire above the body whorl. The siphon is short and wide. Callus of the inner lip is expanded and covers the basal surface of body whorls and extends onto the spire. Shell size varies between 60–85 mm (ABBOTT, 1960: pl. 17, figs. 11 & 12). Included is *Strombus pipus* RÖDING, 1798 with more pointed spire, which is similar to *Strombus* (*Decostrombus*) *fasciatus* with conical shape, higher spire, narrow callus. *Strombus* (*Persististrombus*) *granulatus* is more slender with narrow callus, outer lip attached to body whorl. *Strombus* (*Afristrombus*) *latus* has a rounded outer lip and callus of the inner lip only near the aperture.
Strombus lentiginosus has a conical spire with relatively wide angle that is ornamented with spiral ribs one of which forms a corner covered with short pointed ribs. Its inner lip is smooth and expanded to cover the whole lower side of the shell reaching up onto the spire. The shell is about 9–10 cm high and consist of about 9 whorls. The outer lip is wing-like and has a narrow sinus on its posterior end and a deep stromboid notch near the short siphon canal. The outer lip is wavy and polished smooth on the inner side. The lobe between stromboid notch and siphon is high and dented. The margin of this outer lip extends onto the whorl before the body whorl ending near its suture. The siphon is a little twisted to the left. The species lives in the Indo-West Pacific to Japan.
Strombus pipus has an oval shell shape and is about 40–82 mm high with conical spire and simple rounded outer lip which distinguishes from the more elongate *Strombus fasciatus* (*Decostrombus*) and is close to *Strombus lentiginosus*. As in the latter the lobe between stromboid and siphonal notch is dented.
Strombus schroeckingeri HÖRNES, 1880 from the Miocene of Austria and Hungary has its outer lip attached to part of the spire extending two whorls above the body whorl which is ornamented by five or more spiral ribs of which four bear irregular nodes. The outer lip has a wide posterior sinus a straight margin to a wide stromboid notch and a wide siphonal channel. The ribs on the body whorl extend onto the outer side of the outer lip. *Strombus schroeckingeri* resembles *Strombus* (*Persististrombus*) *radix* but has stronger ornament and a more expanded outer lip that is attached higher up on the spire. The species could quite well be ancestral to the Indo-Pacific *Strombus lentinginosus*, but also resembles the Caribbean *Strombus* (*Monodactylus*) *raninus*. COSSMANN (1904) knew of no fossil species belonging to *Euprotomus*, while STRAUSZ (1966) placed *Strombus schroeckingeri* from the Miocene of Vienna Basin with *Euprotomus*. Somewhat similar species to the latter are *Strombus gijskronenbergi* and *Strombus bernilandaui* from Oman (HARZHAUSER et al., 2007), which apparently aside from size have their greatest difference from each other regarding their stratigraphic position, the first of Miocene and the latter of Late Oligocene age.

c) Pacific Strombus with simple outer lip, divided into two subgenera with living species and one based on a fossil species:

Decostrombus n. subgen.

The type species is *Strombus fasciatus* BORN, 1778, spire 70° with median corner, with characters of *Conomurex* with exception of the ornament of the body whorl that has short ribs or nodes on the corner of the body whorl. The size ranges between 30–60 mm (ABBOTT, 1960: pl. 14, figs. 16 & 17). The inner lip is narrow and smooth and the outer lip is attached to the row of nodules on the body whorl with a short posterior sinus. The siphon is wide and twisted upwards. Included is *Strombus decorus* RÖDING, 1798, with shorter spire. *Strombus granulatus* (*Granostrombus*) differs by higher and more pointed spire, more flaring outer lip, and stronger nodular

ornament. General shell shape connects with *Strombus* (*Lentigo*) *lentiginosus* that has an expanded outer lip and *Strombus* (*Canarium*) *erythrinus* with shorter an more triangular body whorl.

Derivatio nominis: The subgenus is called according to the combination of *Strombus decorus* to form *Decostrombus*.

Strombus fasciatus from the Red Sea and Indo-Pacific has the outer lip ending on the body whorl and the body whorl is conical in shape, more so than in *Strombus decorus* from the Red Sea and the Indian Ocean. The latter is 30–80 mm high with short but pointed spire and rounded triangular body whorl with short open siphon twisted up. The nodes on the corner of the body whorl are here more rounded as is commonly the case in *Strombus fasciatus*.
Strombus fasciatus resembles *Strombus* (*Conomurex*) *luhuanus* but has the corner of its body whorl ornamented by short ribs or spikes.

Conomurex FISCHER, 1884

The type species is *Strombus luhuanus* LINNÉ, 1758 with conical spire (about 90°) and rounded peripheral corner, outer lip thickened and weakly expanded, attached to the body near apical corner. The siphonal notch is wide and short, twisted to right. The callus of the inner lip is narrow and smooth. Shell size ranges from 20–70 mm (ABBOTT, 1960: pl. 14, fig. 15). Included is *Strombus persicus* SWAINSON, 1821 with more pointed spire.
Strombus (*Decostrombus*) *fasciatus* differs by its ornamented periphery of the body whorl and the fossil *Strombus* (*Austrostrombus) medinae* has a sharp apical corner.
Strombus luhuanus from the Indo-Pacific has a conical shell with narrow anterior and wide posterior end of the body whorls and conical low spire. Its outer lip is simple and attached to the body whorl. It has a deep stromboid notch next to the wide short wide siphon. The apical margin of the outer lip forms a short but distinct flank with a sinus.
Strombus persicus has its conical shell widest at the posterior end of the body and a conical spire and rounded corner. The outer lip ends at the corner and has a rounded narrow posterior sinus. The stromboid notch is an even sinus separated from the straight short and wide siphon by a low rounded lobe. The shell is about 50 mm high. This species from the Arabian Sea and Persian Gulf lives in shallow water of 2–3 m in depth. The spire is higher than in *Strombus luhuanus*.

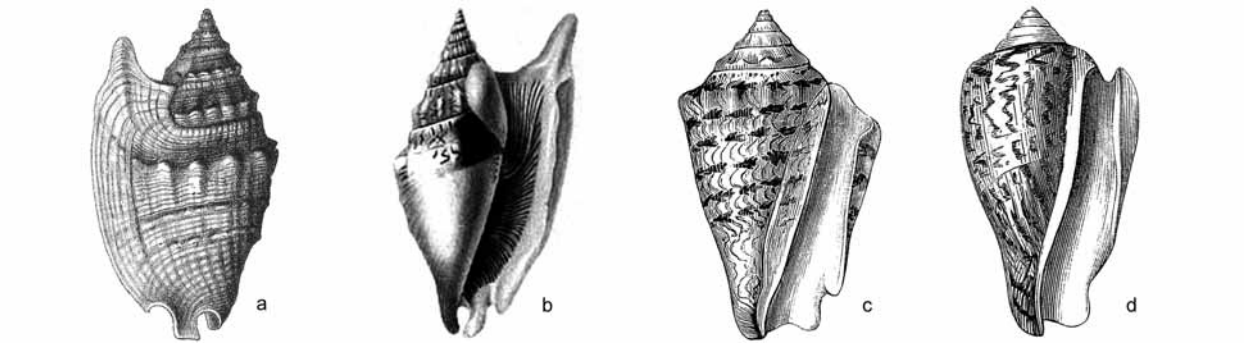

Fig. 18: a – *Strombus* (*Euprotomus*) *aurisdianae* taken from QUENSTEDT, 1884; b – *Strombus* (*Euprotomus*) *auridianae* taken from CHENU, 1859; c – *Strombus* (*Decostrombus*) *fasciatus* taken from CHENU, 1859; d – *Strombus* (*Conomurex*) *luhuanus* taken from CHENU, 1859.

Austrostrombus NIELSEN, 2005

The type species is *Strombus medinae* (PHILIPPI, 1887) from the Late Miocene of Central Chile (NIELSEN, 2005: fig. 2.1–3), (Pl. 7/1–2). It has a conical spire (80°), its outer lip ends on the corner, and the periphery is angular (NIELSEN, 2005: fig. 2.1–3). The shell is about 90 mm high, smooth and has a distinct keel around the periphery. It differs from the similar *Conomurx* by that sharp corner. Body whorls with sharp corner are similar to *Strombus* (*Margistrombus*) *marginatus*, but the outer lip is thin (not well known) and not extended. The apical angle is wider. A specimen of that species has been photographed by Sven Nielsen in the collection of the Natural History Museum at Santiago and it s illustrated in plate 7, figures 1 and 2.

d) Small Pacific Strombus with narrow inner lip and callus ridges in the apertural margin representing three subgenera:

Gibberulus JOUSSEAUME, 1888

The type species is *Strombus gibberulus* LINNÉ, 1758 with the shell asymmetrically coiled, spire with broad varices (70° angle), outer lip ending on the body whorl with a deep posterior sinus. The siphon is short, wide and slightly turned to left and up. The inner lip forms a narrow ribbon with a rounded posterior callus pad, and callus ridges may or may not be present on inside of outer lip. Shell size ranges from 30–70 mm (ABBOTT, 1960: pl. 14, figs. 26–28). The body whorl and the whorl before it deviate from regular spiral coiling and the final suture is inclined with a final twist up. *Strombus* (*Canarium*) *maculates* has similar shape but differs by a symmetrical body whorl.
Strombus gibberulus is most irregular coiled on the last two whorls of its shell. Varices are broad and there may be about 10 of them present on the spire. The outer lip ends before reaching the corner of the body whorl. The stromboid notch is deep. The shell consists of about 10 whorls with three whorls of the protoconch. The early teleoconch is ornamented by spiral incised lines on the upper parts of the whorls (Pl. 6/5–7). The body whorl has spiral ribs on the base. The outer lip has callus ridges on its inside. The species lives in the Indo-Pacific, and at Aqaba it commonly occurs on sand and sea grass bottom below the reef, determined as *Strombus gibberulus albus* in ABBOTT (1960: pl. 14, fig. 27).

Canarium SCHUMACHER, 1817

The type species is *Strombus urceus* LINNÉ, 1758, with conical spire (60–70°) ornamented by a median keel and short axial ribs. The simple outer lip is attached to the body whorl. The siphon is wide and open. Callus of the inner lip is narrow and has transversal ridges. Shell size range from 15–35 mm (ABBOTT, 1960: pl. 20, figs. 26–29). Included are *Strombus mutabilis* SWAINSON, 1821, with rounded whorls and fine ornament, *Strombus rugosus* SOWERBY, 1825, with angular whorls and strong ornament, *Strombus haemastoma* SOWERBY, 1842, with high spire, varices and axial ribs, *Strombus ochroglottis* ABBOTT, 1960, with smooth shell and short spire, the similar *Strombus maculates* SOWERBY, 1842, with more pointed spire, and *Strombus labiatus* RÖDING, 1798, with pointed spire and corner with axial ribs, which resembles the more slender *Strombus erythrinus* DILLWYN, 1817. *Strombus* (*Hawaiistrombus*) *helli* has the inner and outer lip thickened, with ridges and shorter shell shape, *Strombus* (*Fusistrombus*) *fusiformis* has the outer lip extended forming a groove onto the spire.
Strombus mutabilis has an elongate, ovate shell is elongate, about 15 to 45 mm high, with maximum size 60 mm, and conical spire (70°). It has a barrel-shape body whorl with outer lip of evenly smooth shape and the aperture narrow at its posterior end. The margin of the inner and outer lip merge with each other on the upper part of the body whorls before reaching its corner. The inner lip is covered by callus with elongate smooth ridges. The stromboid notch is deep and relatively far from the wide siphon. Sexual dimorphism exists with males a little smaller than females. Growth sages are documented in plate 5, figures 1–14.
Strombus rugosus has distinctive ornament of two spiral keels and axial ribs as well as spiral ones more strongly developed than in the other species. The shell consists of about 9 whorls with high spire (60°) and a size of 30 to 50 mm. On the last part of the body whorl the axial ribs as well as the spiral keel are weak or may disappear, while the fine spiral ribs continue to the margin. The outer lip ends well below the posterior of the body whorl and aperture is narrow and surrounded by a callus with ridges which are also on the inner side of the outer lip. The stromboid notch is wide and separated from the short siphonal notch by a rounded lobe. *Strombus haemastoma* and *Strombus labiatus* may be very close in shape and ornament. *Strombus haemastoma* from the Pacific Islands appears to represent only a color variety of *Strombus labiatus*. Its shell is about 18 mm high and ornament and shape of the spire as well as the body whorl and general features of the outer lip are quite similar.
Strombus erythrinus has a slender shell that is 20 to 50 mm high. The conical spire is more elongate than that of *Strombus mutabilis* (ABBOTT, 1960: pl. 20, figs. 1–5), (45–50°). The shell consists of more than 8 whorls with a median corner crossed by axial ribs with not fixed number decreasing towards the body whorls which end before they reach the sutures. The outer lip is simple and thickened to the stromboid notch with ridges on its inner side and they may or may not be present on the narrow callus of the inner lip. The aperture extends only to the upper third of the body whorl ending well below the corner to the apical ramp.
The fossil *Strombus albirupians* DALL, 1890, with a shell that resembles that of *Strombus mutabilis* in general outline, differing from it in regard to the posterior aperture that is more angular. Also the ornament of the spire consists of larger and fewer tubercles while the general basal ornament also consists of spiral ribs. The inner lip callus is narrow and has callus ridges. In case the reconstructed fossil was correctly drawn *Strombus albirupians* can be included in the subgenus *Canarium*.

Remarks: *Strombus albirupians* was originally described by DALL (1890) with the locality Claiborne Bluff of Upper Eocene age (Jackson, Moodys Branch Formation) from Alabama (HARRIS & PALMER, 1947: pl. 40, figs. 1 & 2), but it may have been derived from overlying beds of Oligocene age (David Dockery pers. communication).

Hawaiistrombus n. subgen.

The type species is *Strombus helli* KIENER, 1843, with its spire forming an 55° angle and ornament of axial ribs and almost as large spiral ribs, and a median keel. The body whorl is short and rounded with ornament of axial ribs and spiral lines continuous onto its surface. The outer lip is attached to body whorl, the siphon is short and twisted to right, and the characteristic callus of the inner lip forms a thickened narrow ribbon and with transversal ridges, as are also present on inner side of outer lip (ABBOTT, 1960: pl. 20, figs. 7 & 8; KAY, 1979). Shell size ranges between 11 an 27 mm, and the species occurs in shallow water of Hawaii.
The small shell consist of about 9 whorls and has concave flanks on the spire and rounded whorls with increase in width in the body. The diameter of the last two whorls of the shell increases more rapidly and sides in overall view appear a little concave. The body whorl composes about two thirds of shell height and has the same ornament as the spire up to the margin of the outer lip. Ornament of even rounded axial ribs crossed by fine spiral lines is substituted by one to three rounded varices on each whorl. Posterior of the stromboid notch the margin of the outer lip is featured by three lobes in decreasing size. The callus of the inner lip forms a thickened ribbon-like pad with many elongate callus ridges, similar but larger as those on the inner side of the outer lip. The outer lip ends before reaching the corner of the body whorl and has a large lobe between shallow stromboid notch and wide short siphon.

Derivatio nominis: *Strombus helli* occurs around Hawaii, and the subgenus is called accordingly, combining Hawaii with *Strombus*.

Strombus helli differs from the species of *Canarium* by its relatively shorter shell, the continuation of the ornament of the juvenile shell onto the body whorl, and the especially strong callus of the inner lip as well the thickened outer lip, both with their transversal callus ridges. *Strombus* (*Canarium*) *urceus* may have a similar ridged inner lip but a more elongate shell.

e) Terebellimorph Pacific Strombus placed in three subgenera:

Tridentarius KRONENBERG & VERMEIJ, 2002

The type species is *Strombus dentatus* LINNÉ, 1758, with spire (45°) with median corner, short axial ribs, outer lip inserted on the body whorls, aperture with narrow posterior canal, narrow callus with ridges on the inner lip and on the inside of the outer lip, siphonal notch next to two of more notches and pointed lobes. Shell size ranges to about 50 mm (ABBOTT, 1960: pl. 14, fig. 23). It resembles *Strombus* (*Fusistrombus*) *fusiformis* which has the outer lip attached higher up on the spire. *Strombus* (*Terestrombus*) *terebellatus* and *Strombus fragilis* have the outer lip smooth, but attached in a similar way as *Strombus dentatus* to the body whorl.
Strombus dentatus has a shape with axial ribs and spines on the outer lip resembling those of *Tibia*, but in contrast to the latter a short open siphon. The shell has more than 8 whorls. The outer lip ends below the upper third of the body whorls and the callus of the inner lip forms a narrow smooth band. Ornament of the spire consists of rounded axial folds which continue onto the body whorls. Characteristically the siphonal notch is accompanied by two notches which have pointed lobes separating them from each other and there is a fourth lobe further upwards on the margin of the outer lip.
Strombus dentatus differs from *Strombus* (*Terestrombus*) *fragilis* by a thicker callus of the inner lip, ornament of sigmoid axial ribs, and a weak median corner on the whorls of its spire. The outer lip as well as the ornament distinguishes from *Strombus* (*Fusistrombus*) *fusiformis.*

Fusistrombus n. subgen.

The type species is *Strombus fusiformis* SOWERBY, 1842, with spire ornamented by spiral lines (45°), rounded whorls, outer lip thickened with ridges on the inner side and attached to the base spire with narrow canal, into it thee callus of inner lip extends that has ridges, siphon is short and wide open, size range from 22 to 50 mm

(ABBOTT, 1960: pl. 20, fig. 30). Similar to *Strombus* (*Margistrombus*) *marginatus* and *Strombus* (*Margistrombus*) *dilatatus* but with more slender shell.
Strombus fusiformis lives in the tropical Indian Ocean and the Red Sea. Its elongate fusiform shell has evenly rounded whorls, consists of about 9 whorls, is ornamented by fine spiral lines. The outer lip of the aperture extends to the base of the former whorl forming with the callus of the inner lip a narrow canal. The whorls of the spire are ornamented by fine spiral lines and rounded smooth varices at irregular distance. The anterior margin of the outer lip forms low lobes next to the stromboid notch and the siphon is wide and short.

Derivatio nominis: The subgenus is formed by a free combination of *Strombus fusiformis* to *Fusistrombus*.

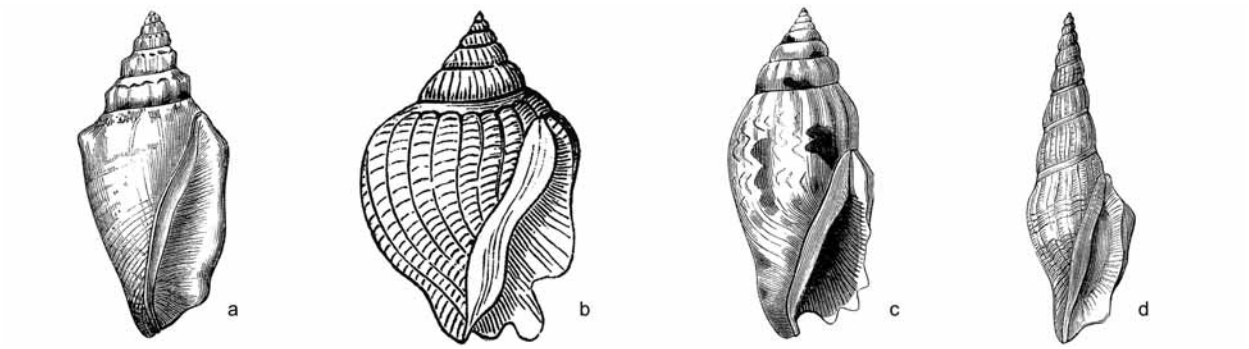

Fig. 19: a – *Strombus* (*Canarium*) *urceus* taken from CHENU, 1859; b – *Strombus* (*Hawaiistrombus*) *helli* taken from CHENU, 1859; c – *Strombus* (*Tridentarius*) *dentatus* taken from CHENU, 1859; d – *Strombus vittatus* taken from CHENU, 1859.

Terestrombus KRONENBERG & VERMEIJ, 2002

The type species is *Strombus fragilis* RÖDING, 1798, with olive shape, spire 40° but increasing shell diameter resulting with concave sides of the spire. Later the shell is narrow in last two whorls. The outer lip is thin not flaring, attached low on body whorl, with wide short siphon. The callus of the inner lip is indistinct and thin. Shell size ranges from 30–35 mm (ABBOTT, 1960: pl. 14, fig. 30). Included is *Strombus terebellatus* SOWERBY, 1842, of similar size and shape. It resembles *Strombus* (*Tridentarius*) *dentatus* but has a wide siphon bordered by a not dented outer lip.
Strombus fragilis has about nine whorls. Its body whorl has the suture slightly turned upwards in its latest part, otherwise whorls are smooth and evenly rounded with shallow suture. The outer lip forms crenulations at its anterior end with a lobe posterior of the wide stromboid notch and that with a lobe separating it from the wide short siphon. It lives in the tropical Pacific, for example close to Guam.
Strombus terebellatus has the shell of about 25–40 mm high and consists of about 9 whorls. It has polished slender olive-like shape. The outer lip is attached deep down on the body whorls and the aperture has a narrow posterior end and a wider angular anterior end. The outer lip is relatively thin and smooth to the margin of the wide shallow stromboid notch that has a short rounded spike on its posterior and anterior side. The latter borders the wide, rounded, short siphonal canal. *Strombus terebellatus* has the siphonal front so wide that the eyes may look out from under the shell as is the case in *Terebellum*, but the small stromboid notch is also used. These eyes are on stalks and have tentacles at their side, which contrast to the case in *Terebellum terebellum*. The species live around the Philippines.

f) Strombus marginatus-plicatus group with species from the Pacific, all with relatively large body whorl, differentiated into five subgenera:

Dolomena IREDALE, 1931

The type species is *Strombus pulchellus* REEVE, 1851, that is the same or very similar to *Strombus plicatus* RÖDING, 1798, with pointed spire (45°) ornamented with axial ribs, corner and spiral lines. The outer lip has a narrow to wide posterior sinus, and is attached to top of the body whorl or the whorl before it. The callus of inner lip is narrow with ridges, which are also present on the inner side of the outer lip. The siphon is wide, short, and twisted up. Shell size ranges from 25–60 mm (ABBOTT, 1960: pl. 18, fig. 1–3). Included are *Strombus labiosus* WOOD, 1828, with its outer lip more flaring, and the inner lip not ridged. Also *Strombus variabilis* SWAINSON,

1820, with the outer lip resembling that of *Strombus labiosus* and the inner lip with no ridges belongs here. *Strombus hickeyi* WILLAN, 2000 (= *Strombus troglydates* of CHENU), has the outer lip attached to the spire slightly higher than is the case in *Strombus pulchellus.*
Strombus pulchellus from the Philippines according to ABBOTT (1960) represents as subspecies *Strombus plicatus*, and *Strombus hickeyi* has the same shape of the shell with slightly more expanded outer lip but differs in respect to the color in its aperture. The spire is pointed and relatively high and the outer lip of the body whorls extends in a narrow apical part that reaches onto the last two whorls of the spire. *Strombus plicatus* has an about 40 mm long shell that has a sculptured spire and the body whorl composing about two thirds of the shell in height. About four to six knobs are on the shoulder, and the outer lip is thick and has a wide margin. The inner lip may be finely grooved and bear ridges which may however also be absent. *Strombus hickeyi* has its outer lip attached in a similar way but has a posterior sinus on its margin and the body whorl bears many spiral ribs.
Strombus labiosus has a high spire with strong ornament while the body whorl is weakly ornamented to smooth with a callus coat on the ventral side of the shell. The outer lip is smooth and forms a thickened wing. It forms a rounded lobe with a wide margin that extends to its attachment on the last whorl of the spire without canal.

Margistrombus n. subgen.

The type species is *Strombus marginatus* LINNÉ, 1758, with pointed spire (45°) and ornament of axial ribs. The outer lip has a narrower posterior end that is attached to the spire. Callus of the inner lip is narrow and smooth. Shell size ranges from 40–50 mm (ABBOTT, 1960: pl. 18, figs. 6–11). Included is *Strombus succinctus* LINNE, 1758 with similar shape but less allometric growth and posterior canal long and expanded to the left, and the *Strombus dilatatus* SWAINSON, 1821 with smoother body whorl, a little wider outer lip that is attached to the spire in inclined position forming a canal pointed to the left.

Derivatio nominis: The subgenus *Margistrombus* is a free combination of *Strombus* and *marginatus*.

Strombus marginatus has its shell with pointed spire and evenly ovoid body whorl. There are about 8 whorls of the spire and these increase regularly in size to about the sixth and beyond that they widen more rapidly. The spire thus appears concave. The outer lip is moderately expanded and smoothly rounded. Its posterior margin is attached above the body whorl and forms a canal with the callus of the inner lip. The protoconch consists of about four smooth whorls and the transition to the teleoconch is indistinct with spiral ribs of the first whorl imprinted onto the last part of the larval whorl from the inside (Pl. 1/10–11). Occurrence in the Indo-Pacific.
Strombus succinctus has similar shell shape but is less allometric in growth and its posterior canal is longer. The eight whorls of the spire increase in size more regularly and the sides of the shell have only a weak concavity. *Strombus dilatatus* from Australia resembles *Strombus* (*Dolomena*) *variabilis*, has a relatively narrow spire with corner and ornament of axial ribs and larger smooth body whorl. But it differs by having the posterior end of the outer lip attached to the spire further to the left and higher up on the last whorl.

Gallinula KLEIN, 1753 (= *Labiostrombus* OOSTINGH, 1925)

The type species is *Strombus epidromis* LINNÉ, 1758, with pointed spire (50°) with corner and axial ribs. It body whorl is smooth, with outer lip evenly flaring and rounded, attached on the last whorl with a shallow posterior margin. The callus of the inner lip is narrow and smooth. The siphon s wide and short, twisted upwards. Shell size ranges from 40–93 mm (ABBOTT, 1960: pl. 17, fig. 17). *Strombus epidromus* lives around Australia and the SE Asian Pacific with the type-species from the Philippines.
According to COSSMANN (1904) *Strombus epidromis* is the type to the subgenus *Gallinula* KLEIN, 1753, and not to *Labiostrombus* as was stated by WENZ (1938). Its spire is high and has ribbed ornament with spiral lines. The body whorl is smooth with indistinct spiral lines. The outer lip is expanded to cover the whorl before the last. It forms a narrow pointed posterior end of the aperture (WENZ, 1938: fig. 2752). The thick lip with wing-like margin is accompanied by a wide stromboid notch, and wide, short siphonal canal (WILSON, 1993).

Laevistrombus KIRA, 1955

The type species is *Strombus canarium* LINNÉ, 1758 with conical spire (45° and more), that increases in width ornament by equal spiral and axial ribs, smooth rounded shell, outer lip with upper sinus, attached to body whorl, callus of the inner lip narrow and smooth, siphon wide short and twisted left upward, size range 30–75 mm (ABBOTT, 1960: pl. 17, figs. 15 & 16). The shell is thick with rounded margin of its flaring outer lip (DANCE,

1974). Also here included is *Strombus turturella* RÖDING, 1798, with the body whorl even more rounded and contrasting to the conical spire with ornamented whorls. Shell growth is quite allometric with body whorl more expanded and smooth, and shell size is between 50 and 115 mm.

Ministrombus n. subgen.

The type species is *Strombus minimus* LINNÉ, 1771, with pointed spire (40°) with a median corner that bears nodes. The outer lip forms a lobe on a ridged end and is attached above the body whorl. A thickened callus ridge of inner lip continuous to the posterior canal. The siphonal canal is wide and upturned. Shell size ranges from 20-50 mm (ABBOTT, 1960: pl. 18, figs. 4 & 5).
Strombus minimus consists of about 9 whorls of which those of the long, stepped spire have a distinct median corner with nodes on it. These continue in a ridge onto the body whorl and end in a rounded lobe on the outer lip, which has a smooth rounded thickening and is attached to the last whorl of the spire. Here it forms a ridge which joins with the callus of the inner lip. Between this posterior callus and the rounded lobe on the lip lies a distinct sinus. The stromboid notch is well developed and the siphonal canal wide and straight. The species lives in SE Asia.

Derivatio nominis: The subgenus received its name by a free combination of *Strombus minimus* to *Ministrombus*.

Differences: *Dolomena* resembles *Strombus* (*Margistrombus*) *marginatus* which has the outer lip narrower at its posterior end and the inner lip narrow and smooth. *Strombus* (*Dolomena*) *labiosus* has the most flaring outer lip and no posterior canal, while *Strombus* (*Dolomena*) *variabilis* has the outer lip resembling that of *Strombus* (*Dolomena*) *pulchellus* and *Strombus* (*Dolomena*) *hickeyi*. *Strombus* (*Ministrombus*) *minimus* has the callus of the inner lip forming a ridge with the attachment of outer lip, which is characteristic to the subgenus and distinguishes from *Strombus* (*Gallinula*) *epidromis* with outer lip ending on body without canal. *Laevistrombus* has a similar outer lip as in *Strombus* (*Dolomena*) *labiosus* and *Strombus* (*Labiostrombus*) *epidromis* with ribbed shell. But *Strombus* (*Laevistrombus*) *canarium* has a smooth shell. *Strombus* (*Margistrombus*) *dilatatus* resembles *Strombus* (*Ministrombus*) *minimus* with exception of the callus of the inner lip forming ridge with attachment of outer lip in the latter. *Strombus* (*Gallinula*) *epidromis* in contrast has its outer lip ending on body without canal. The posterior end of the outer lip of *Strombus* (*Ministrombus*) *minimus* differs from the similar *Strombus* (*Margistrombus*) *succinctus* and *Strombus* (*Margistrombus*) *dilatatus* both with narrow canal formed by posterior outer lip.

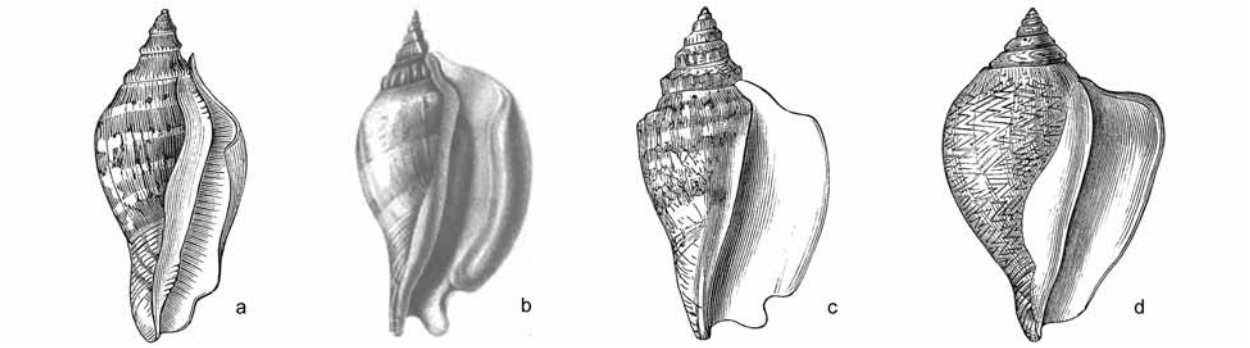

Fig. 20: a – *Strombus* (*Margistrombus*) *succinctus* taken from CHENU, 1859; b – *Strombus* (*Margistrombus*) *dilatatus* taken from REEVE, 1878; c – *Strombus* (*Dolomena*) *hickeyi* taken from CHENU, 1859; d – *Strombus* (*Canarium*) *canarium* taken from CHENU, 1859.

g) Group of Pacific Strombus with high spire and two subgenera:

Doxander IREDALE, 1931

The type species is *Strombus vittatus* LINNÉ, 1758, with very high, pointed spire (30°) with corner and axial ribs. The outer lip is wing-like and forms a long apical canal. The callus of the inner lip is narrow and smooth. The siphon is wide with its outer side higher. Shell size ranges from 40–90 mm (ABBOTT, 1960: pl. 17, figs. 13–14,

18). Included are *Strombus campbelli* GRIFFITH & PIDGEON, 1834, with flattened whorls, and *Strombus japonicus* REEVE, 1851, both with shorter spire than in type.
Strombus campbelli has its shell consisting of about 10 whorls with flattened sides and ornament of strong axial ribs. It is from Australia and 40 to 50 mm high. It is smaller than the similar *Strombus vittatus* that may be the same species as *Strombus japonicus*. The spire is here strongly ornamented by axial ribs crossed by finer spiral ribs, and whorls are evenly rounded with deep sutures that have a band. The siphonal notch has ridges on its inner side. The thin outer lip is attached next to the suture and the shell is up to 90 mm long. with but is smaller. The species resembles the shorter *Strombus* (*Dolomena) hickeyi* which could be the same as *Strombus* (*Dolomena) plicatus.*

Mirabilistrombus KRONENBERG, 1999

The type species is *Strombus listeri* GRAY, 1852, with high pointed spire (30°), long narrow body whorl, outer lip flaring with posterior sinus and attached to the body whorl. The callus of the inner lip is narrow and thin. Siphon is long and slightly turned to the left and up. Shell size ranges between 120–140 mm. It resembles *Strombus* (*Doxander) vittatus* but has its outer lip with wing-like extension and with posterior sinus.

h) Group of transitional species to the spider conchs with two subgenera:

Sinustrombus n. subgen.

The type species is *Strombus taurus* REEVE, 1857, with pointed spire (45°) with ornament of short median ribs. The outer lip has lobes at end of ribs and spines on the posterior corner. It is attached to the spire. The callus of the inner lip expands onto the base of spire but remains close to the aperture and narrow. The siphon is short, open and twisted up. Shell size ranges between 85–130 mm (ABBOTT, 1960: pl. 17, figs. 3–4). *Strombus oldi* EMERSON, 1965, is included that has a more rounded projections on the outer lip. *Strombus taurus* resembles *Strombus* (*Lambis*) *lambis* regarding the outer lip, but has shorter spines. Similar is *Strombus* (*Tricornis*) *tricornis* that connects to *Strombus* (*Latissistrombus*) *latissimus* with comparable shell size but its outer lip wider and more thickened.

Derivatio nominis: The subgenus has received its name from the sinus bearing outer lip in free combination to *Sinustrombus*.

Strombus taurus from the tropical Pacific Islands such as Marshall Island lives on sand in the illuminated zone and has a shell of about 100 mm in height. The spire is high and pointed and there are at least nine whorls of the shell. Ornament is by a subsutural spiral rib that bears tubercles which on the body whorl are fewer and larger. The body whorls has two more irregular spiral ribs which end in the undulations of the outer lip and the stromboid notch is narrow and deep. The posterior margin of the lip with the outermost two of these is undulations have been extended to form spines, of which the posterior one in the longest. The attachment of the lip is also with a low rounded spine to the last three whorls of the spire.
Strombus oldi from the Arabian Sea has an angular posterior lobe and some more small lobes on the margin of the outer lip which represent the ends of about 7 spiral ribs of the body whorl. The posterior of these ribs splits into three at the begin of the wing like outer lip. The outer margin of the outer lip is attached at the posterior margin of the last spire and it is thickened with undulation on the outer side reflecting the spiral ribs. The stromboid notch is deep with the lobe forming a lappet to the equally wide siphonal notch. The spire is high and the shell consists of about 10 whorls and is about 110 mm high.

Latissistrombus n. subgen.

The type species is *Strombus latissimus* LINNÉ, 1758, with conical acute spire (40°–70°) median ridge or shoulder. The outer lip expands beyond the apex and is attached to the spire. The body whorl has spiral keels and a shoulder. The short straight siphonal canal is open. The callus of the inner lip is wide covering part of spire, and is spread out next to aperture. Shell size ranges between 120–180 mm (ABBOTT, 1960: pl. 17, fig. 5).

Derivatio nominis: The subgenus is named from *Strombus latissimus* combined to form *Latissistrombus*.

Strombus latissimus resembles *Strombus* (*Eustrombus*) *galeatus* with rounded but less expanded outer lip, larger apical angle, *Strombus (Eustrombus*) *goliath* with outer lip even more expanded and rounded and *Strombus (Eustrombus*) *gigas* differing by the outer lip attached on the last whorl. It resembles *Strombus* (*Sinustrombus*) *taurus* which has a less expanded outer lip that is also crenulated but also has a large shell.
Strombus latissimus LINNÉ, 1758, lives in the tropical Pacific of SE Asia, between Japan and Fiji. The outer lip expanding beyond the apex and forming a wide even sinus with the straight side ending in a deep narrow stromboid notch. The body whorl has six spiral keels that continue into the margin of the outer lip that may form low sinuses between them. The shell consists of more than 8 whorls.
Strombus sublatissimus ORBIGNY, 1852, lived during the Oligocene in the Western Tethys (HARZHAUSER, 2004) and may connect the SE-Central Pacific *Strombus latissimus* with *Strombus goliath* from the Atlantic near Brazil with *Strombus galeatus* from the tropical Central American Pacific with the outer lip rounded as well. It may have been able to cross into the Atlantic Ocean before the closure of the Panama sea way and connect to African species. But similarities can just as well be convergence in shell shape, as a molecular check of Strombus latissimus with the Caribbean and Easter Pacific species can elucidate.

i) Group of the spider conchs consisting of three subgenera:

Lambis RÖDING, 1798

The type species is *Strombus lambis* LINNÉ, 1758, with thick shell with conical spire (60°) with coarse spiral ridge. The outer lip has seven finger-like projections. The larger female has the spines near the stromboid notch bent upwards, while the spines of the male are shorter and are directed backwards. The siphon is elongate and with slight twist to right. Shell size ranges between 100–150 mm (ABBOTT, 1961: pl. 121, fig. 4). Included are *Strombus truncata* HUMPHREY, 1786 and *Strombus crocata* LINK, 1807. Species of *Lambis* have apparently appeared relatively late in the geological history, only by the late Miocene of the Western Pacific Fiji (LADD, 1972: pl. 10, figs. 5–6), and the relation to Pacific species of Strombus is close (STONE, 2003a, b).
Sexual differences of *Lambis lambis* were noted by (ABBOTT, 1961; SAVAZZI, 1991; WILSON, 1993). The shell has ornament of coarse transverse ridges and large tubercles. *Lambis truncata* has a large reversed elongated-egg-shaped shell with a moderately high spire ornamented by spiral lines and nodes. The narrow aperture continues into an anterior curved canal and extends into a flaring outer lip with several gutter-like spines, the most posterior one contacting the spire and extending beyond it. In the Red Sea it lives in the lagoon in 1 to 1.5 m deep water but also enters the reef platform. The large adults prefer to roam the reef platform while juveniles live in deeper zones in the lagoon next to the reef. The egg masses are half-moon shaped and consist of sticky tubes to which sand is agglutinated as soon as they have been produced by the female. This egg mass is partly glued to hard substrate. This contrasts to *Strombus tricornis* where the spawn lies on the sand and is not attached.

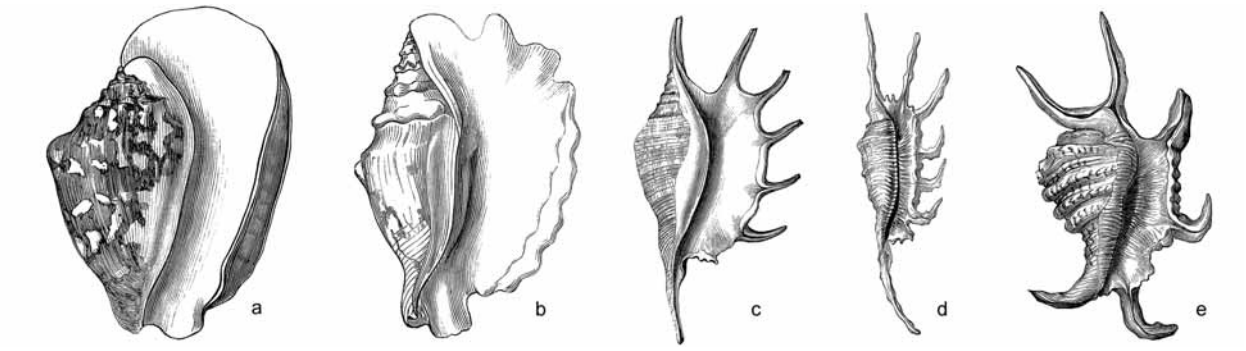

Fig. 21: a – *Strombus* (*Latissistrombus*) *latissimus* taken from CHENU, 1859; b – *Strombus* (*Sinustrombus*) *sinuatus* taken from CHENU, 1959; c – *Strombus* (*Lambis*) *lambis* taken from CHENU, 1859; d – *Strombus* (*Millepes*) *scorpio* taken from CHENU, 1859; e – *Strombus* (*Harpago*) *chiraga* taken from CHENY, 1859.

Harpago MÖRCH, 1852

The type species is *Strombus chiraga* LINNÉ, 1758, with wide, pointed spire (80°). The outer lip has six curved finger-like projections. Shell size ranges between 150-300 mm (ABBOTT, 1961: pl. 121, figs. 10–12). The siphon (rostrum) is curved toward the left. *Strombus chiraga* lives on coral reef areas among see weed in shallow water

in sandy areas on south Indian shores, but also in Polynesia and Australia. The larva remains in the plankton for only as short time after it hatched from its egg provided with much maternal yolk and its embryonic whorl measures more than 0.3 mm in diameter (see below).

Millepes MÖRCH, 1852

The type species is *Strombus millepeda* LINNÉ, 1758, with conical spire ornamented by rounded short ribs (60°). The outer lip has about 10 curved projections, and the siphon is elongate and almost straight. Shell size range between 100–130 mm (ABBOTT, 1961: pl. 121, fig. 6). Included is also *Strombus scorpius* LINNÉ, 1758, with seven stout curved projections on its outer lip. *Strombus millepeda* has the heavy shell with stout projections and lives in the South-West Pacific.

3 Taxa with relation to the Stromboidea

3.1 Family Colombellinidae FISCHER, 1884 (= Columbellinidae ZITTEL, 1895)

Diagnostic characters: The shell has a low spire and a thickened outer lip with tubercles on it inner side, folds on the inner lip, and a siphon on both sides of the narrow aperture. Ornament of the teleoconch consists of spiral ribs crossed by axial ribs forming a rectangular pattern. The type species for the genus *Colombellina* is *Rostellaria monodactylus* DESHAYES, 1842, from the Early Cretaceous. Its protoconch is unknown.

ZITTEL (1885) placed *Colombellaria*, *Zittelia* GEMMELARO, 1870, and *Colombellina* ORBIGNY, 1843, in the Colombellinidae, and interpreted the family as predominantly a Jurassic taxon intermediate between the Strombidae and Cassidae. SCHILDER (1927) suggested that a *Colombellina-Zittelia* lineage developed into the Cypraeidea, thus connecting the Strombidae with the Cypraeidae and Tonnidae (WENZ, 1938). According to BOUCHET & ROCROI (2005) the spelling Columbellinidae is based on *Columbellina* GEINITZ, 1846, and unjustified emendation of *Colombellina*.
Colombellina has similar shell shape and ornament as *Columbellaria*, but its outer lip has an anterior canal a little distant from the body whorl (COSSMANN, 1904: pl. 7, figs. 6–11).

Genus *Columbellaria* ROLLE, 1861

The type species is *Cassis corallina* QUENSTEDT, 1857, from the Late Jurassic of Nattheim, Germany (QUENSTEDT, 1857; BRÖSAMLEN, 1909: pl. 22, figs. 37 & 38; WENZ, 1938: fig. 2712).

Diagnostic characters: The egg-shaped shell is ornamented by strong axial ribs and fine spiral ribs and has a large body whorl. The inner lip is formed by a callus plate with sharp margin and bears small teeth, the outer lip has a posterior channel near its margin and teeth on its inner side. The anterior short siphon is open. *Columbellaria* cf. *tuberculosa* (BINKHORST, 1861) from the Cenomanian of Germany resembles the Maastrichtian *Columbellaria tuberculosa* from the Netherlands, which has a more slender spire (KIEL & BANDEL, 2004: fig. 7O, P). The Japanese *Columbellaria brevisiphonata* has a more slender body whorl (KASE, 1984: pl. 23, fig. 13).

A connection to the Strombidae was also suggested by TAYLOR & MORRIS (1988) who interpreted the Colombellinidae as stem group to the Cypraeoidea and Tonnoidea. TAYLOR et al. (1980) included the Colombellinidae in the Tonnoidea (= Cassoidea) as earliest family, also derived from the Stromboidea during Jurassic time, as had been suggested ZITTEL (1885) almost 100 years before. Among the Alariidae species placed with *Monocuphus* and *Diarthema* resemble somewhat species of the Colombellinidae from the Late Jurassic (COSSMANN, 1904: pl. 7, figs. 6, 7, 10, 11) and to *Colombellina* of the Cretaceous, as documented by SOHL (1960: pl. 14, figs. 1–3, 6, 7).

3.2 Family Pereiraeidae n. fam.

Diagnosis: The family is based on *Pereiraea* CROSSE, 1868, with only one known species. The large shell has a high spire with ornament of a spine bearing keel. The body whorl has ornament of growth lines and four spiral

ribs which end in spines of the outer lip. Shell continued with narrow and coarse growth increments even in the adult, and was thus not terminate. The outer lip forms a posterior narrow and deep recess where attached to the spire and has spines with lobes between them, the anterior ones smaller but of about equal size, without distinct stromboid notch. The callus of the inner lip covers the lower side of the body whorls up to the spire.

Derivatio nominis: The family is called according to the genus *Pereiraea*.

Remarks: All characters were noted by COSSMANN (1904) and had also been documented by WENZ (1938: fig. 2761, based on an original illustration of VIDAL).

Difference: The non-terminate outer lip distinguishes from Strombidae and Dilatilabridae, the simple inner lip without posterior callus pad from the Thersiteidae, non terminate growth distinguishes from the Rostellariidae in general, the shape of the spire from Rimellinae and the short wide siphonal notch from the Rostellariinae.

Genus *Pereiraea* CROSSE, 1868

The type species is *Pleurotoma gervaisi* VÉZIAN, 1856, from the Miocene of Spain (Catalonia) (COSSMANN, 1904: pl. 2, fig. 2 & 3) that also lived in the sea of the Paratethys Basin (FUCHS, 1870; HOERNES & AUINGER, 1891; STRAUSZ, 1966: pl. 24, figs. 8–10; WENZ, 1938: fig. 2761).

Diagnostic characters: The about 9 whorls of the shell with about 100 mm in height has a conical spire with a keel that has large hollow spines as ornament. The keel lies just above the suture. The body whorl has no spines and the keel continues to the outer lip ending in a spine. Also a strong posterior and two smaller anterior spiral ribs of the body whorl end in spines on the margin of the outer lip. The outer lip is attached to the body whorl with a deep slit with its anterior margin evenly curving to the upper spine. The outer lip below that spine has a sinus to the next spine and below that one to three smaller indentations posterior of the open canal of the siphon. Strong growth lines crossed by the three spirals form the final ornament.

Difference: SAVAZZI (1991: fig. 9B) suggested a relation of *Pereiraea* with *Thersitea* since both have a sinus at the posterior end of the outer lip and a groove along the suture. *Pereiraea* was considered a member of the Strombidae by CROSSE (1868) and COSSMANN (1904) because they interpreted one of the sinuses of the outer lip as representing a stromboid notch. But *Pereiraea* differs from *Strombus* quite distinctly. The aperture is not flaring or thickened, and the sinuses on its margin are not a stromboid notch, but rather depressions between apertural spines. The spire has a row of hollow spines in the three whorls before the body whorl, the outer lip attached below the keel with spines forming a deep narrow pointed slit that connects to the deep suture, the outer lip is not thickened as in *Strombus*. Most important, strong growth lines on the last quarter whorl of the body whorl indicate continued growth of the outer lip when the animal had reached adulthood. The shell is one with not terminate growth. The outer lip has thorns and recesses between these but no single stromboid notch. *Pereiraea* does not belong to the Strombidae and belongs into its own family, separate form the Strombidae and perhaps even the Stromboidea. This family Pereiraeidae is represented by a single genus and species.

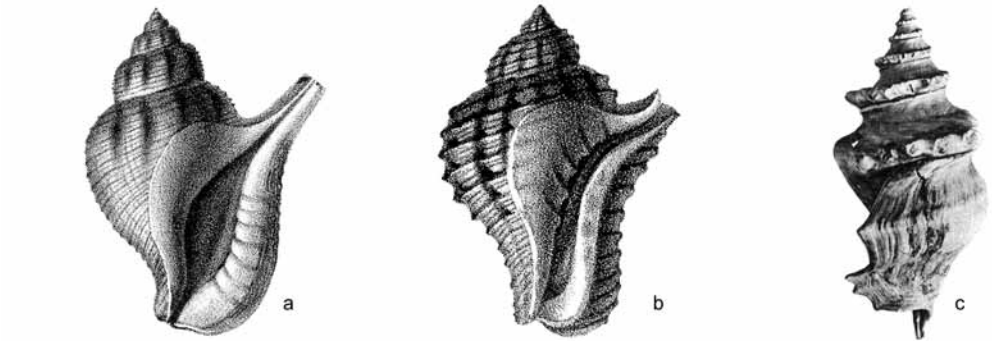

Fig. 22: a – *Columbellina monodactylus* taken from ORBIGNY, 1843; b – *Columbellina ornata* taken from ORBIGNY, 1843; c – *Pereiraea gervaisi* taken from COSSMANN, 1904.

3.3 Family Xenophoridae TROSCHEL, 1852

Diagnostic characters of the superfamily Xenophoroidea TROSCHEL, 1852: The shell has conical low trochospiral shape. Whorls of the protoconch are rounded and smooth or with spiral rib and median corner (Pl. 8/10–11). The teleoconch a peripheral keel on the corner to the base. The aperture is strongly oblique with thin margins, and shell is added to them throughout life (Pl. 8/1, 2, 7, 8). Modern species are all contained in the Xenophoridae.

Remarks: PONDER (1998) suggested that Xenophoroidea represents the sister group of the Stromboidea as well as the Calyptraeoidea. The morphology of the larval shell indicates a relation to the Haloceratidae, but not to the Calyptraeoidea (BANDEL & RIEDEL, 1994). Regarding characters of the teeth of their radula Xenophoridae resemble those of the Haloceratidae as well as Calyptraeoidea and the Strombidae (WARÉN & BOUCHET, 1991: figs. 35–43; BANDEL, 1984: pl. 6).

Diagnostic characters of the family (= Onustidae H. ADAMS & A. ADAMS, 1854): The shell is low and broadly conical. The teleoconch is tent-shaped with sharp basal edge. Its base is flattened and the aperture is strongly inclined. Growth increments are added throughout life and shell growth, therefore, is not terminate. The margin of outer lip commonly has skeletal particles or stones cemented to its dorsal surface and they are agglutinated by the periostracum (Pl. 8/1, 2, 7, 8). The protoconch of species with planktotrophic larval stage consists of several whorls with rounded base and about 1 mm or more in size. A sinus and lobe are present on the outer lip of the aperture of the larval shell (Pl. 8/1–15). In case of lecithotrophic development the embryonic whorls is larger and the protoconch consist of less than 1.5 whorls. Attachment of particles to the shell begins with metamorphosis to benthic life and with deposition of the teleoconch (Pl. 8/1, 2, 7, 8). The operculum is organic and with smooth margin or has a serrated edge.

Remarks: PONDER (1983) suggested that one genus represents all living species, while WENZ (1938) distinguished two genera *Xenophora* and *Tugurium*, and DANCE (1974) three genera, as third *Stellaria*. Cretaceous representatives of the Xenophoridae can be recognized (HOLZAPFEL, 1888: pl. 14, fig. 28; SOHL, 1960; KIEL & BANDEL, 1999; 2001; KIEL et al., 2002) with the oldest from about Mid Cretaceous. The family existed for about 100 Million years.

Genus *Xenophora* FISCHER VON WALDHEIM, 1807

The type species is *Xenophora conchyliophora* BORN, 1780, from the tropical Atlantic.

Diagnostic characters: The low conical shell has a broad flattened concave base and a periphery with a lamellar keel. The aperture is oblique low and wide without siphonal canal. The operculum is organic stout and ovate with lateral nucleus. The protoconch consists of conical whorls, usually several of them in case of planktotrophic larval development (PONDER, 1983; BANDEL, 1993: pl. 12, fig. 1; DOCKERY, 1993: pl. 20, fig. 4). A species from Ripley Formation (SOHL, 1960: pl. 10, figs. 19, 23–27), *Xenophora leprosa* (MORTON, 1834) has a protoconch that consists of 3.5 smooth and rounded whorls and resembles the modern ones (Pl. 9/14–16). The teleoconch consist of about five whorls and measures 20 mm in height and 25 mm in width.

Remarks: PONDER (1983, 1998) recognized within the genus *Xenophora* 22 species, all resembling one another. He noted for the subgenus *Stellaria* 5 species with spines on the peripheral flange. In case of *Onustus (= Tugurium)* with 4 species the ventral side of the periphery has a mineralized flange. In *Xenophora* with 13 species the peripheral flange is narrow and many species include objects in their shell which they collect from the sea bed.

Genus *Acanthoxenophora* PERRILLIAT & VEGA, 2000

The type species is *Acanthoxenophora sinuosa* PERRILLIAT & VEGA, 2000, from the Maastrichtian Mexcala Formation in southern Mexico (KIEL & PERRILLIAT, 2001: fig. 5, 3–5). It has its teleoconch as well as the protoconch in shape quite close to those of *Xenophora leprosa* (MORTON, 1834) from the Campanian Coffee Sand of Mississippi (DOCKERY, 1993: pl. 20, figs. 1–4; KIEL, 2002: pl. 22, figs. 3–5). The ornament of the teleoconch is distinctive by bearing large spines in somewhat irregular orientation. They may point into different directions and are distributed in one growth zone and only a few in one whorls (KIEL & PERILLIAT, 2001). This

differs from *Stellaria*, where these spines are on the basal keel, while they are on the sides of the whorls, also the shell is relatively broader.
Acanthoxenophora existed during the Late Cretaceous not only in Mexico at the Maastrichtian, but also in northern Germany during the Middle Santonian (KIEL & KRÜGER, 2006).

Genus *Tugurium* P. FISCHER, 1876 (= *Onustus* GRAY, 1847)

The type species is *Xenophora exuta* REEVE, 1842, from the Indo-Pacific.
It has a larval shell with 3.5 smooth and shallow trochospiral whorls resembling that of *Xenophora.* During construction of its teleoconch it gathers only few shells and foreign objects. *Tugurium exutum* with surface of the shell of crossing small ridges and margin extending into a thin lamella with rounded and short flattened tubes. It consists of more than four whorls of the teleoconch and up to 10 cm wide, conical with sutures indistinct and umbilicus wide open. *Tugurium longleyi* (BARTSCH, 1931) from the Caribbean has the whorls of the teleoconch forming a stair with the edges not in the plane of the next whorl, similar to the fossil subspecies *Acanthoxenophora* from Maastrichtian. It attaches some objects or not and its shell is quite solid. In case it does it is on the rim, which has irregular outline and overhangs on the periphery. The similar *Tugurium caribaeum* (PETIT DE LA SAUSSAYE, 1857) has a lower shell and resembles *Tugurium indicum* (GMELIN, 1791) with the some size has the margin without such extensions, irregular and thin, from the central Indo-West-Pacific.

Genus *Stellaria* SCHMIDT, 1832

The type species is *Trochus solaris* LINNÉ, 1864, from the Philippines and the Chinese Sea.
The larval shell with 4.5 whorls is a little higher than is the case with *Xenophora*, otherwise it is similar. The shell consists of about four whorls of the teleoconch and is up to 10 cm wide, and less than half as high. The margin of its teleoconch extends into long hollow and flattened spines. In succeeding whorls the marginal spines are integrated into the following shell surface. No objects are attached to the shell, sometime only to the juvenile teleoconch. The aperture is wide and spread out on the flat base.
Stellaria chinensis (PHILIPPI, 1841) attaches some particle next and below the suture to the lamellar keel. These are connected to shell deposits so that rays are on the rim. The shell otherwise closely resembles that of *Xenophora* and is also similar in shape and size with almost 10 cm in diameter. *Stellaria gigantea* (SHEPMAN, 1909) from South Africa is similar to the latter and *Stellaria testigera* (MARTENS, 1878) is higher with few rather irregular spines. It may include attached particles or not. *Stellaria kriegerbartholdi* NIELSEN & DEVRIES, 2002, from the Miocene of Chile has its margin with blunt digitations and some agglutinated shells (NIELSEN & DEVRIES, 2002: figs. 17–20).

Remarks: *Xenophora* moves by leaping, with the shell lifted and then thrust forwards to fall down after the leap (MORTON, 1958; LINSLEY & YOCHELSON, 1973). The locomotion of *Xenophora* resembles that of members of the Strombidae (BERG, 1974). *Xenophora* moves forwards in jerks produced by anchoring the operculum in the ground and jumping with sudden contraction of the shell muscle and twist of the foot is similar to that of *Strombus,* as *Xenophora conchyliophora* BORN, 1780, from the Caribbean Sea (BANDEL & WEDLER, 1987). Here the operculum large enough to be able to seal the aperture when the animal withdraws in its shell. The foot may be extended to reach around the shell when the animal is turned around in a position with its apex toward the ground, and twist the shell back into normal position with one stroke. The head bears two long cylindrical tentacles with the eyes near their outer base (PONDER, 1983).

Genus *Misritropis* n. gen.

Diagnostic characters: The shell is about 35 mm high and consists of about 6 triangular whorls of the teleoconch with a sharp corner shape and a helicospiral, rounded protoconch. The aperture is strongly inclined of almost round outline with the inner lip straight and forming a ridge at the inner edge of the open umbilicus. The outer lip is thin. The base and the side of whorls are flat and the margin to the base is formed by a lamellar frill. Ornament may consists of spiral ribs and inclined increments of growth and the spirals may also be absent. The apical angle is about 55°.

Derivatio nominis: The shell resembles in shape a *Trichotropis* and is from the Egyptian Western Desert (Egypt is Misr in Arabic). The name is a free combination of Misr and the last part of *Trichotropis*.

Misritropis bartheli n. sp.

Derivatio nominis: Collected by K. WERNER BARTHEL on the Ammonite Hills in the Sand Sea, and called in his honor and memory.

Diagnostic characters: As genus. The protoconch is not well preserved but appears to have consisted of about two rounded whorls. The frill at the corner to the base forms flat triangles of which about 30 are on one whorl. Growth lines are inclined and quite irregular, and the spiral ribs on the flattened sides are in differing number from 10 to 5 or none. Below the frill a groove is present and the flattened base also has three to four spiral ribs. The center of the base is a slit or in younger individuals a narrow umbilicus. Five specimen have been studied (Pl. 7/10, 11).

The holotype is the illustrated specimen in Pl. 7/11 from the Ammonite Hill in the Sand Sea, west of Dahkla Oasis from Upper Maastrichtian deposits, Dakhla Formation, deposited in the collection of the Geology Department of the Technische Univerität Berlin (BARTHEL & HERMANN-DEGENS, 1981), coll nr.G 94 from SFB 69. Four additional individuals are present.

Remarks: The species was called *Alaria* sp. by QUAAS (1902) but there is no evidence of the presence of a final aperture. It resembles *Trichotropis* in general shape but the large marginal frill does not fit. That frill resembles the margin to the base as is present in *Tugurium*, but the shell of *Misritropis* is higher than wide. It is higher than the shell of *Acanthoxenophora* and has a frill instead of single spines.

3.4 Family Haloceratidae WARÉN & BOUCHET, 1991

The type is *Haloceras* based on *Haloceras cingulata* (VERRILL, 1884) from the northern Atlantic (WARÉN & BOUCHET, 1991: 53–55 adult shell, 113–115 protoconch).

Diagnostic characters: The teleoconch consists of few whorls, are disc shaped to trochiform with simple rounded aperture without siphonal canal, with spiral ornament and open umbilicus. The larval whorls form a trochospiral shell with up to 2.5 mm in size. The embryonic whorls is ornamented and rounded with growth lines at its end. The larval shell is trochospiral and has angular larval whorls ornamented by two or three spiral keels and other minor elements. The fully grown shell is 2 to 9 mm in size. The aperture is wide with a siphonal notch (BOUCHET & WARÉN, 1993; WARÉN & BOUCHET, 1991).

Genus *Haloceras* DALL, 1889

Diagnostic characters: The protoconch with rounded whorls is lowly trochiform and about 2 mm n diameter. Its embryonic whorl is ornamented by spiral lines and measures about 0.2 to 0.35 mm in diameter. The larval shell has three spiral keels of which one becomes covered by succeeding whorls. The teleoconch has conical shape with angular outline of the whorls with rapid increase in diameter (WARÉN & BOUCHET, 1991; BOUCHET & WARÉN, 1993).

Remarks: The radula of *Haloceras* and *Zygoceras* resembles that of other Caenogastropods such as among Calyptraeidae or some Cassoidae (WARÉN & BOUCHET, 1991; BOUCHET & WARÉN, 1993), but also of *Strombus* and *Trivia* (BANDEL, 1984). RIEDEL (2000) placed the Haloceratidae with the suborder Troschelina BANDEL & RIEDEL, 1994, and here the superfamily Calyptraeoidea LAMARCK, 1809. The protoconch of Haloceratidae has the outer lip of the larval shell extended to form a median lobe as is not found in the larval shell of members of the Capulidae, Calyptraeidae and Hipponicidae. These differences indicate that the groups united within the Troschelina may have to be reevaluated in regard to their phylogenetic position. BOUCHET & ROCROI (2005) placed the Haloceratidae with the Vanikoroidea, together with Vanikoridae and Hipponicidae. The protoconch of Haloceratidae differs strongly from that of both later families. Haloceratidae as members of the Vanikoroidea is, thus, unlikely to be correct (see BANDEL, 2006).

Genus *Haloceras* sp. Santa Marta

Haloceras carinata (JEFFREYS, 1883) as described by WARÉN & BOUCHET (1991: figs. 59–61, 105–108) and which occurs in deep water off Florida closely resembles the protoconch attached to the juvenile shell found in

shallow water of Santa Marta, Caribbean Sea at Colombia (Pl. 9/7, 8). Here the embryonic whorl measures about 0.2 mm in diameter and is ornamented by spiral ribs composed of irregular granules. The larval shell is quite different in ornament with two spiral keels in position above the suture and one on the base. The ornament of the larval shell in the second larval whorl changes by the addition of collabral ribs which reflect the presence of an apertural projection that is bordered by the spiral keels (Pl. 9/8). The ribs begin weakly and increase in size and density towards the aperture of the larval shell, which was broken in the juvenile not long after metamorphosis to bottom life.
The protoconch measures about 0.75 mm in diameter coinciding with the data presented by WARÉN & BOUCHET (1991). The difference to their description lies in the relatively strong ornament of collabral ribs on the last half of the larval shell found in the individual from Santa Marta. Also metamorphosis and early benthic life of the individual from Santa Marta occurred in shallow water of less than 3 m depth. This contrasts to the observation that all species of *Haloceras* live on the outer part of the continental shelf and the slope to the deep sea. This is obviously different in the warm tropical waters of the Colombian coast.

Genus *Zygoceras* WARÉN & BOUCHET, 1991

The type species is *Zygoceras tropidophora* WARÉN & BOUCHET, 1991 from near New Caledonia (WARÉN & BOUCHET, 1991: figs. 84, 85, 121, 122).

Diagnostic characters: The shell is lowly coiled with angular whorls and almost planispiral protoconch bearing spiny keels. The embryonic whorl has about 0.3 mm in diameter and a larval shell that consists of 1.6 whorls and measures 1.4 mm in diameter. The teleoconch is depressed with angular whorls that have a rapid increase in diameter.

Zygoceras aqabaensis n. sp. from Aqaba

Diagnostic characters: The teleoconch is unknown. The larval shell consists of 2.5 whorls coiled in low trochospiral shape and 1 mm wide. The embryonic whorl is ornamented by coarse spiral ribs that grade into rows of tubercles at transition into the larval shell. Growth lines are sinuous with two spiral keels that accompany the median projection of the outer lip. Shell ornament of the early teleoconch is smooth with flattened top, two keels on the side and short base.

Derivatio nominis: The larva occurs in the Plankton of the Gulf of Aqaba at Aqaba and the species to which it belongs was called accordingly.

The holotype is the specimen in Pl. 9/6 that has the begin of the teleoconch, and is deposited in the Collection of the Geologisch-Paläontologisches Institut of the University of Hamburg.

Description: The first whorl measures about 0.25 mm in diameter (Pl. 9/3–5). Growth increments indicate that the larva hatched from its spawn with an about 0.3 mm wide shell bearing a little more than one whorl. The whole protoconch consists of 2.5 almost planispiral, lowly trochospiral whorls and measures about 1 mm in width (Pl. 9/1, 6). The median apertural projection is accompanied by deep lobes, one next to the suture and the other at the corner to the base. Two spiral keels bear a serration and border the median projection of the outer lip on both sides (Pl. 9/2). The area between these keels is flattened. Ornament on the apical whorl flanks consists of rows of tubercles, which insert already on the embryonic shell and are continuous across its margin.

Difference: The larval shells of *Zygoceras* species documented by WARÉN & BOUCHET (1991: figs. 121–16) differ from *Zygoceras aqabaensis* by the stronger ornament of the embryonic whorl. In the new species it is much stronger while it consists of single spiral ribs in the formerly described species.

4 Protoconch and larval shell within the Stromboidea, comparison with Xenophoridae, Haloceratidae and Atlantidae

The fully grown planktotrophic larva of members of the Strombidae swims with a large, six lobed velum (BANDEL et al., 1997), as is the case in larvae of *Aporrhais* (LEBOUR, 1933; THIRIOT-QUIEVREUX, 1969). These larvae resembles those of the Atlantidae of the Heteropoda, and the Xenophoridae and Haloceratidae, and, to some degree, that of the Lamellariidae. The six velum lobes distinguishes Stromboidea and their potential sister

groups among the Meta-Mesogastropoda during the planktotrophic larval stage from many other larvae of the Caenogastropoda. They usually have a velum with two or four lobes only. Especially the relatively large larvae having a similar size as found among the Stromboidea, the Tonnoidea, Cypraeoidea, Naticoidea, and Calyptraeoidea, in contrast, swim with a velum that consists of four large lobes.

The spawn of *Aporrhais* consists of single egg capsules, each with one egg, attached singly or in small groups to the substratum. After about 14 days the veliger hatches (FRETTER & GRAHAM, 1961). The fully grown larva has six short and rounded wings of the velum (LEBOUR, 1933, 1937; THIRIOT QUIEVREUX, 1969: pl. 2, fig. 1; FRETTER & PILKINGTON, 1970: fig. 4b, c, d; RICHTER & THORSON, 1975: pl. 7, figs. 50 & 51). Own observations of *Aporrhais pespelicani* from the Mediterranean Sea near Banyuls-Sur-Mer confirmed that fully grown larvae swim with a velum of six lobes. The protoconch has a 0.2 mm wide embryonic whorl (Pl. 1/16) and is up to 1 mm high and 0.8 mm wide when fully grown (Pl. 1/14). A basal lobe occurs on the outer lip and the inner lip is straight and has a depression next to it in the umbilicus. The shell is very thin at metamorphosis and still elastic, but it was observed to subsequently mineralize the protoconch rapidly. Within three days the young benthic animal secretes up to 1.5 new whorls (Pl. 1/15). These are ornamented by about 14 low and broad spiral ribs. The ribs of the early teleoconch are also present on the part of the shell that forms below the last whorl of the larval shell. Due to the flexible and predominantly organic composition of this thin shell the ribs are printed through shell surface here. A larval ornament consist only of fine and indistinct tubercles on a smooth background (Pl. 1/13). It is changed subsequently from smooth to ribbed in that last shell portion, but only after establishment as benthic young. Spiral ornament is thus not a larval feature, but imprinted into and onto the larval shell by the crawling young after establishment of benthic life.

The protoconch of a fossil *Aporrhais* from the Oligocene of the Baltic Sea (WIENEKE, 2007) closely resembles that of living *Aporrhais* from the Mediterranean Sea. The protoconch consists of almost three whorls, with the embryonic whorl on the flat top (Pl. 4/9, 10). The rounded smooth larval whorls have sinuous growth lines reflecting a lobe on the outer lip. Transition to the ornamented teleoconch is indistinct since spiral ribs have been imprinted onto the last part of the larval shell from below (Pl. 4/10). Within the first teleoconch whorl axial ribs appear and later form a regular pattern of rectangles with the spiral ribs (Pl. 4/9). The early ontogenetic shell appears to be very similar among the two species, *Aporrhais speciosa*, and *Aporrhais megapolitana*, both from the Chattian (Oligocene) of the Baltic Sea (WIENEKE, 2007).

Arrhoges occidentalis breeds periodical at spring time (PERRON, 1978) and larva occur during early summer having metamorphosed by the end of it. The larval shell caught in the Atlantic Ocean near North Carolina consists of 1.5 whorls, is wider than high (0.7 mm) and has a wide umbilicus (THIRIOT-QUIEVREUX, 1980: figs. 42 & 43). A lobe is present on the anterior margin as the larva undergoes metamorphosis to bottom life.

Struthiolariidae such as *Pelicaria vermis* from New Zealand hatch as crawling young with large simple protoconch (Pl. 7/14, 15).

The protoconch of *Anchura chapelvillensis* DOCKERY, 1993 from the Campanian of Mississippi from the Ripley Formation resembles that of modern Stromboidea. It measures about 1 mm in height and width, but was higher when fully grown larva, since that is the part exposed in the apex of the teleoconch (Pl. 2/7, 8). It consists of 3.5 whorls with the embryonic whorl rounded and about 0.18 mm wide. The larval whorls have sinuous growth lines which are present up to the fully grown protoconch. A large basal lobe was present on the outer lip throughout larval life. In case of *Anchura* sp. from Ripley Formation the protoconch is of more conical pointed shape and higher than wide with teleoconch transition not seen (Pl. 2/9, 10). Larval whorls are smooth with sinuous growth lines while the first whorl of the teleoconch has ornament of spiral lines. Sometimes spiral lines as found on the first whorl of the teleoconch are imprinted onto the surface of the last half whorl of the larval shell from the shell added to it from below.

Perissoptera sp. resembling *Perissoptera prolabiata* WHITE, 1876, as described by DOCKERY (1993) from the Campanian of Mississippi has a conical protoconch with about 0.15 mm wide embryonic shell with rounded shape and ornament of tubercles. The larval shell is about 1.2 mm high and has a subsutural zone with short ribs arranged spirally on the three rounded whorls with sinuous growth lines (Pl. 2/15, 16). The transition to the teleoconch in gradational with sinuous axial ribs of the teleoconch merging with the hook of the outer lip of the larval shell (Pl. 2/13, 15).

Latiala sp. from Coffee-Sand of the Campanian of Mississippi have a conical protoconch with the whorls of the larval shell covered by distant tubercles, the embryonic shell with denser pattern of tubercles (Pl. 2/11, 12, 14). The apertural margin of the larval shell is provided with a strong basal lobe, and transition into the teleoconch is quite indistinct (Pl. 2/11, 12).

Graciliala sp. from Ripley Formation of Mississippi has a conical protoconch with about 4.5 whorls and about 1 mm in height (Pl. 2/9, 10). Here tubercles are present on the embryonic shell that is rounded and about 0.15 mm wide and also on the larval shell, here concentrated on the rounded whorls below the suture. The larval shell end with a wide basal hook on the outer lip, and transition into the teleoconch with predominant axial ornament in gradational.

Characteristics of the protoconch of *Strombus*

The protoconch differs in shape reflecting the mode of development. In case of yolk-rich eggs and crawl away or not planktotrophic hatchlings the protoconch has only one relatively large embryonic whorl, as documented in *Strombus tricornis* (Pl. 7/3, 4, 6, 7) In case of planktotrophic development the embryonic shell is distinguished from the larval shell by shape and ornament, as documented in *Strombus mutabilis* (Pl. 5). The two species, *Strombus mutabilis* and *Strombus gibberulus* (Pl. 6) are common in Aqaba, and also two different larvae could be distinguishes from the Plankton here. One has almost four whorls and the other 4.5 whorls. In the Red Sea several more species of *Strombus* occur. The two types of larval shells from Aqaba were traced on juveniles, the one with more whorls on the smaller *Strombus mutabilis*, and the other with less than four whorls on *Strombus gibberulus*.

When fully grown *Strombus mutabilis* may be quite small, only little more than 15 mm in size, but is may also measure about 45 mm in height. Its spire is conical and the body whorl of ovoid shape. It was encountered in the lagoon with sea grass near Lizard Island in the Great Barrier Reef of Australia as well as just below the gravel beach on the margin of the narrow shallow lagoon in the Gulf of Aqaba near Aqaba, Arabia. Juveniles at both places are present in the very shallow water on rocks covered by algae or within entangled algal thickets. Shortly after metamorphosis the juvenile can still close its aperture with the operculum that has an anterior thorn that fits into the siphonal canal (Pl. 5/7). At that stage of growth the head carries two long tentacles with the eyes at their base. Only during further benthic life the operculum changes its function to be used during locomotion and defense and the stalks of the eyes increase in length, as is characteristic for *Strombus* throughout. When about five post-larval whorls are present the eyes have become characteristic in their position on long solid stalks and thin tentacles rise on their side which are still of about the same length. A long tentacle is attached to the margin of the mantle near the anus and next to the suture in the posterior part of the aperture. Mantle margin is rimmed by additional fine papillae which are also present on the mantle next to the anterior canal.

With begin of teleoconch growth of *Strombus mutabilis* ornament changes and fine spiral ribs cover the first whorl (Pl. 5/9). The juvenile shell grows more or less continuously and is almost isometric. But grooved margins represented in varices document intermediate halts in growth. In some individuals varices are arranged quite regularly, in others they occur irregularly and in some they are not present at all, as is commonly the case in this species (Pl. 5/10, 11). The shell remains thin throughout the juvenile and immature stage. After some time the final growth stage results in a widening of the outer lip and the specific shape of the species is acquired. While the early ontogenetic shell of most species is quite similar and juveniles are difficult to distinguish from each other, the final shell shape is usually species specific. After the final shell size is acquired the shell is only thickened by addition of mineral layers to the inner surface and on top of the former shell in the region of the inner lip. Sexual dimorphism exists in that males often are moderately smaller than females.

The protoconch has 4.5 whorls when the larva is fully grown (Pl. 5/1, 2, 7). The embryonic shell is about 0.14 mm wide, well rounded and covered by a dense pattern of tubercles (Pl. 5/4, 5). The larval shell begins after formation of first growth lines and may be ornamented by tubercles with different pattern as present on the embryonic whorl (Pl. 5/4, 6). The aperture of the first larval whorls has a strong median projection of its outer lip accompanied by a wide posterior sinus and a narrow and deep anterior sinus. The anterior shell extends into a conical siphon. In the late stage of the larval shell the outer lip changes to more straight outline and the inner lip is straight and accompanied by an umbilicus. The margin of the fully grown larval shell is not thickened. The operculum can seal the aperture with pointed anterior end that fits into the siphon (Pl. 5/2, 7), while it is rounded and grows with crescent increments right after hatching (Pl. 5/12). While in the plankton the shell may be damaged frequently and repaired, sometimes with selenizone-like patterns on the larval whorl (Pl. 5/8).

Strombus gibberulus is common in the Red Sea at Port Sudan as well as at Aqaba. It prefers sandy ground with or without sea grass. When buried in sand the eyes may project above the surface of the sand. On lagoonal bottoms it is found from 20 cm to 5 m depth. The spawn consists of a cushion of 4–5 cm length and 1–2 cm width composed of a single egg tube forming a regular curving mass of about 5 mm height and coated by sand. After only 3–4 days of development whitish veligers hatch, one from each egg. The development of the protoconch with almost four rounded whorls goes through three distinct stages. Whorl diameter increases and apical angle changes from 65° in the first three whorls to 80° in the fully grown larval shell and in the early teleoconch to 55°.

The embryonic shell measures 0.15 mm in diameter, is strongly ornamented by spiral ribs of elongated tubercles in fish-bone pattern and has a simple apertural margin (Pl. 6/3, 8). The second early larval stage consists of two rounded whorls with a strong lobe on the outer lip (Pl. 6/10, 12), and fine spiral ornament composed of tubercles (Pl. 6/3, 9). On the last whorl of the larval stage the shell width increases and its shape is more globular (Pl. 6/1, 2, 5). The lobe in the outer lip almost disappears and an umbilical pore and a pointed siphon form (Pl. 6/13, 14). Total height of the protoconch is about 1 mm and width 0.8 mm. The aperture has an evenly rounded outer lip and a narrow siphonal notch with slight inclination to the left (Pl. 5/1, 14). The inner lip (columella) has a raised

margin. The operculum fits perfectly into the apertural opening (Pl. 6/14). Its pointed posterior end and one straight side fit well on the inner lip and the siphon, and the well rounded right side fits with the outer lip.
Larvae swim with a velum consisting of six lobes of which each is almost twice as long as the conch. The shell is carried with head with tentacles and eyes pointing in swimming direction and long narrow foot with operculum is held in behind. The mantle cavity holds a large ciliated gill and osphradium. During growth of the larva attacks of animals of prey are common and the shell often shows repair (Pl. 6/13).
Strombus fasciatus from the Red Sea with shell 25 to 50 mm high near Port Sudan preferred sandy bottom with sea grass and buries in the sand. Near Suakin it utilized a brown alga with funnel like shape as substrate to attach its spawn which consists of irregularly curving tubes which are glued to the fronds of the *Padina*. Of the larva considered to belong to *Strombus fasciatus* by BANDEL et al. (1997) the embryonic shell has a diameter of 0.13 mm and is ornamented by tubercles in dense pattern. The larval shell is ornamented by coarse granules in the first whorl and in the third whorl overlaps onto the second whorl with a thin sheet that covers the suture. The succeeding ornament is by spiral lines until the protoconch is fully grown with 4.5 whorls.
One of the two larvae differentiated by BANDEL et al. (1997) had yellow striped tentacles, the other was here evenly gray or olive in coloration. One belongs to *Strombus gibberulus* and the other to *Strombus fasciatus*, both of which are very common in the Red Sea (EISAWY & SORIAL, 1976; BANDEL et al., 1997: fig. 2, fig. 18A–D). In Aqaba *Strombus mutabilis* is the more common species and its larva apparently resembles closely that regarded to belong to *Strombus fasciatus* in the Red Sea.
Strombus pugilis from the coast of Colombia lives on the sea grass flats (BANDEL & WEDLER, 1987). Large population may be encountered in about 1.5 m of depth. When reproducing adults form packages of an about 5 m long tube holding the eggs and bury them in the sand. From one spawn about 25000 veliger hatch after about 6 days of development (BANDEL, 1976: fig. 2) and swim off with a velum with two lobes. After only a few hours in the Plankton the veligers has four lobes, and as the veliger grows the velum increases to have six lobes. The fully grown protoconch is about 1 mm high and 0.8 mm wide, consists of about four whorls, with apical angle about 55°, similar to that of *Strombus gigas*. The embryonic whorl is rounded, lowly trochospiral and measures 0.23 mm in diameter. Larval whorls are smooth and their outer lip has two lateral lobes next to an acute basal projection on its outer lip (Pl. 1/3, 4, 9, 11). When the fully grown veliger is ready for metamorphosis the outer lip is almost without a lobe and has a straight columellar lip forming the inner side of a siphonal canal. In transition to the teleoconch sculpture as well as growth line pattern change, but characters of the first whorl of the teleoconch may be imprinted onto the larval shell from below (Pl. 4/16). The teleoconch is ornamented by spiral ribs and the apertural margin simple. Larval life lasts for about 3-4 weeks, and shell growth within the period of half a year in a hatchery will be up to 6 cm (BROWNELL, 1977; BRITO-MANZANO & ALDANA ARANDA, 2002; ALDANA ARANDA & PATINO-SUAREZ, 1998). *Strombus pugilis* reaches sexual maturity with about one year of age. The early teleoconch has three rounded whorls with straight axial ribs and numerous fine spiral ribs, and in the fourth whorl profile becomes angular and apical angle begins to increase (Pl. 1/9). In case of *Strombus raninus* the first angular whorl appear earlier, and the apical angle is wider (Pl. 1/5–6), and in case of *Strombus gigas* the ornament has more delicate spirals and angle width increases in later whorls (Pl. 1/3).
The life history of *Strombus gigas* has been assembled in quite some detail (APPELDOORN, 1985a, b; APPELDOORN & RODRIGUEZ, 1994; DAVIS, 1998, 2000, 2005), since embryonic and larval development have been observed in the field and also completely in culture. The egg masses are deposited on or just below the surface of the sediment, and a whole population may be encountered in the process at the same time of the year (BANDEL, 1976), usually when water is warmest (DAVIS, 2005). The egg capsules are interconnected to a gelatinous string of about 1 mm in thickness, which is several meters long and tangled to a heap (D'ASARO, 1965; BANDEL, 1976). Each capsule contains one embryo. About 300000 to 400000 veligers hatch after about 6 days of development (BANDEL, 1976; DAVIS, 2005; CRESWELL & DAVIS, 1991) with a velum of two lobes. After four days in the Plankton the larva swims with four lobes, and after about 8 days it has six lobes (DAVIS, 2005: fig. 7). Metamorphosis occurs when the fully grown protoconch is about 1.2 mm high (Pl. 1/8) and the larva has been in the Plankton for at least 21 days. But larval existence may last up to eight weeks. After begin of bottom life and within two weeks they grow to about 3.5 mm in shell size (BERG, 1974, 1976; ALDANA ARANDA & PATINO-SUAREZ, 1998). The protoconch closely resembles that of *Strombus pugilis*, and the juvenile teleoconch has more or less well developed varices (Pl. 1/7). Here ornament changes from first two whorls similar to those of *Strombus pugilis* but with finer spiral ornament, but later whorls more angular with fewer nodules on the median corner (Pl. 1/7–8), and a more regular increase in shell diameter within the next 8 whorls, that is straight and not concave shape of the sides of the spire. In the juvenile shell the protoconch appears to be totally smooth.
The conical protoconch of *Strombus raninus* from the Caribbean Sea at Santa Marta consists of four whorls, of which the last one is well rounded. It apical angle is almost 70° and thus larger than that of *Strombus pugilis* with about 55°. Its embryonic whorl is rounded, the succeeding larval shell smooth with a basal lobe at first, but smooth in the indistinct transition to the teleoconch (Pl. 1/5–6, Pl. 4/16). Whorl diameter increases in such way that protoconch margins are slightly concave, in contrast to the protoconchs of *Strombus pugilis* and *Strombus gigas*, which have a regular increase in whorl diameter. The early teleoconch has distinct varices and ornament

of distinct fine spiral ribs crossing the straight axial ribs (Pl. 1/5). Later axial ribs change into large blunt spines in the last two whorls (JUNG & HEITZ, 2001: fig. 18). The first two whorls of the teleoconch are rounded, later a corner as well as a ribbon above the suture appear with shape becoming more angular and sutures deeper. The larval shell resembles that of *Strombus gallus* from off the coast of Brazil (LEAL, 1990: pl. 14, figs. A, B). It consists of about 4.5 whorls with no ornament seen on the rounded whorls.
Incase of *Strombus tricornis* with large shell with a heavy outer lip and size between 65 and 170 mm the development is lecithotrophic with veliger hatching from the spawn that has 1.5 whorls and no change from embryonic to larval shell and drastic change to teleoconch (Pl. 7/3–4). The species occurs in the Red Sea to the Gulf of Eden and was found near Port Sudan commonly together with *Lambis truncata* in the lagoons behind reefs. Here they graze algae on the sediment and can be of variable size. Smaller individuals were noted on sea grass flats near the shore at Suakin (near Port Sudan), while large ones live in the Senganab lagoon of the off-shore atoll near Port Sudan. The spawn produced by the larger individuals is also larger and has a higher number of eggs than that secreted by the smaller individuals. The egg mass consists single round tubes which are irregularly knitted up into bundles. They may be of several meters in length, have a rubbery consistence and are never attached but covered by sand that is glued to its sticky surface. In the tube rounded capsules form a row and each holds one whitish-yellow egg. The large young that leaves the egg is a veliger larva with a four lobed velum, tentacles and eyes, and the foot well developed carrying a large, almost round operculum (Pl. 7/6). Even though it is far developed it can not yet crawl, but swims off into the plankton. The embryonic shell is totally organic and consists of about 1.3 whorls of which the first three-quarters have no growth lines (Pl. 7/6–7). The shell becomes very thinly mineralized when the veliger is swimming in the plankton for only short time and without feeding. During this time about one-fourth whorl is added and a low rounded projection of the outer lip at the basal edge forms before metamorphosis occurs. Benthic life begins with a size of 0.86 mm and 1.5 whorls. The whole shell becomes well mineralized by a continuous layer of crossed lamellar structure (Pl. 7/5). Young individuals are found in very shallow and warm water near the shore.
Strombus chiraga spawn was observed in Lizard Marine Station in the Great Barrier Reef Australia where it had been secreted below a stone in the lagoon. The pink eggs are about 0.3 mm wide and contained within a round transparent capsule. The latter lies in a gelatinous layered sphere of about 1 mm diameter which is surrounded by a membrane that extends into two handles. These extensions of the outer egg membrane interconnect the egg-capsule balls with each other forming one row of capsules. This row is arranged in a tight spiral within a tube-like ribbon in such a way that three capsules beside each other form its diameter. The interconnection of capsules with each other. After about five days of development the embryos are ready to hatch. They swim with a velum with four short lobes, with short knob-like tentacles with eyes and large pulsating larval heart within a pallial cavity. The adult heart has also developed and is almost ready for function. The foot holds the operculum and has a rim of red glandular spots on its margins below it. The veliger most probably remains only a short time in the plankton after it hatched from its egg. Its embryonic whorl measures more than 0.3 mm in diameter.

Protoconch of Alariidae and Spinigeridae

The protoconch of Alariidae in case of *Cuphotifer* has a rounded embryonic whorl and a conical larval shell with rounded whorls, and is more than 1 mm high with 3.5 to 4 whorls (SCHRÖDER, 1995: pl. 6, figs. 18–20; GRÜNDEL, 2003a: pl. 12, figs. 1–4; KAIM, 2004: fig. 56C). The larval shell has a wide upper sinus and a lobe that is covered by the succeeding whorl. Ornament begins on the teleoconch with axial ribs, and one spiral which may also appear within the first whorl of the teleoconch (KAIM, 2004: figs. 56 & 57). The protoconch of *Dicroloma* closely resembles that of *Cuphotifer* (= *Pietteia*) with about 0.18 mm wide embryonic whorl and 3.5 whorls. The larval shell is about 0.8 mm high and wide has a rounded projection near its base, no sharp border to the teleoconch but with distinctive change in growth line pattern (KAIM, 2004: figs. 54 & 55). In case of *Spinigera* from the Mid-Jurassic of Poland the smooth conical protoconch with more than three rounded whorls and about 1 mm in height and width is succeeded by the early teleoconch with a spiral median row of short axial ribs (KAIM, 2004: fig. 59).

The protoconch of different genera of the Rostellariidae

The protoconch of *Rimella fissurella* is smooth and barrel shaped with more than three rounded whorls (Pl. 3/6, 7, 9). The embryonic whorl is rounded and almost 0.2 mm wide. The specimen from the Eocene of Damery in the Paris Basin has the protoconch of about 1 mm in height and 0.75 mm in width. It consists of more than three smooth rounded whorls. Fine growth lines on the larval shell reflect the presence of a short rounded projection of the anterior outer lip and a shallow sinus posterior and a deeper one anterior of it. Even thought the margin of the end of the larval shell not thickened the transition to the teleoconch is distinct due to a change in growth line

pattern (Pl. 3/8). The juvenile shell has broad rounded varices at irregular intervals and is ornamented by rounded axial ribs crossed by fine spiral ribs which are best developed at the base (Pl. 3/10). The protoconch is quite similar to that of Anchura from the Ripley Formation.

Ectinochilus texanus from the Eocene of Texas has the protoconch with six smooth whorls of rounded conical shape and is 1.8 mm high (Pl. 4/17–18). The embryonic shell is 0.13 mm wide, with smooth rounded whorl of dextral coiling mode. It ends with the appearance of growth lines. Transition to the larval shell is indicated by a change a more sinuous growth line pattern. The larval shell has basal lobe on the outer lip. A narrow keel marks the upper edge of the apertural lobe. Transition from the larval shell to the teleoconch is indistinct, and the keel continues in a basal spiral line that disappears on the seventh whorl. Growth lines on the teleoconch are less sinuous.

The protoconch of *Tibia dentata* from the Miocene of France has similar shape as that of the living *Rostellariella delicatula,* but also with *Strombus* and *Aporrhais.* The protoconch of *Tibia dentata* has 3.5 rounded smooth whorls with about 1 mm in height (Pl. 4/7–8; WIENEKE, 2007). The transition to the ornament of the early teleoconch is gradational and the rectangular pattern of the first whorl of the teleoconch enters the last larval whorl. Later on the ornament of the teleoconch is dominated by axial ribs, and on the last whorls the shell appears smooth. The protoconch of *Tibia fusa* from an individual from Cebu (Philippines) differs considerably from the fossil species (Pl. 4/11–12). Here the rounded smooth embryonic whorl changes indistinctly into to the larval shell that has fine sinuous growth lines. The growth lines present evidence for the young hatching from the egg as veligers which swim off with lot of yolk reserves. The first whorl measures almost 0.5 mm indicating that the eggs had been at least as large. Yolk, therefore, is sufficient to provide that larva with food until metamorphosis without the need of planktotrophic feeding. In the tropical environment larval life should be short, a maximum of a few days only. This takes into account that the size of the embryonic shell reflects the original size of the egg (BANDEL, 1975, 1982).

Rostellariella delicatula from the Philippines resembles *Ectinochilus* from the Eocene of Texas in regard to the shape of its protoconch, but is with over two mm in height larger (Pl. 4/13–15). While the protoconch of the fossil species is pointed conical that of *Rostellariella delicatula* is a little fusiform with slender first whorls, a little wider fifth whorl and less increase in width in the first whorl of the teleoconch. A spiral line is present just above the suture that marks the upper corner of the larval projection that was present on the outer lip of the larval shell. Transition into the teleoconch is quite indistinct and documented best by the change in growth line pattern. On the larval shell it reflects the presence of a hook on the outer lip near the basal corner connected to a wide sinus posterior of it. This sinus as well as the projection of the outer lip become shallower in approach to the teleoconch. On the first whorl of the teleoconch the growth lines is shallowly curving and there is no basal lobe. Also broad low rounded varices are developed, about one one each whorl, and distributed at irregular intervals.

Calyptraphorus jacksoni from the Paleocene of Alabama also has a protoconch that resembles that of *Rostellariella* and *Ectinochilus*. It consists of more than 6 whorls and is about 2 mm high (Pl. 3/10–12, 14). The embryonic whorl is 0.13 mm wide and rounded with smooth and clearly dextral appearance (Pl. 3/13). It is well differentiated from the larval shell by the begin of simple growth lines. On the early larval shell increments of growth are transformed to curving shape reflecting the presence of basal lobe on the outer lip (Pl. 3/15). In the transitional zone from the larval shell to the teleoconch the basal lobe of the outer lip disappears and change into the teleoconch is gradual (Pl. 3/10, 12). The first whorl of the teleoconch has ornament on many fine spiral ribs crossed by curving axial ribs and also rounded varices may or may not be present (Pl. 3/11, 14).

Protoconch of Pterocerellidae

Pterocerella maryea has a rounded protoconch with about 3.5 whorls (DOCKERY, 1993: pl. 16, figs. 8 & 9), as well as *Pterocerella poinsettiformis* STEPHENSON, 1941. Transition to the teleoconch is abrupt with straight margin and keels on the teleoconch initiating at it (Pl. 2/1–3). The relatively wide protoconch has a smooth larval shell and abrupt transition from larval shell to the teleoconch (Pl. 2/1). The embryonic shell is almost planispiral in coiling and almost 0.2 mm wide. The larval shell has a little more than three rounded smooth whorls and measures about 1.8 mm in height and about 1.5 mm in width. Its margin is straight and simple with the begin of the teleoconch indicated by change in shape from rounded to angular and the begin of two spiral ribs.

Pterocerella protoconch is thus quite different in shape from that of *Anchura* and *Strombus*, regarding its large size and its rounded outline. It resembles that of *Pugnellus* which is also large (Pl. 2/4–5) and its is more rounded and higher than that of *Xenophora*, in addition to having a smooth outer lip contrasting to the lobed outer lip of the larva of *Xenophora*.

The protoconch of Pugnellidae

The protoconch of *Pugnellus densatus* is of conical shape with wide angle and 4.5 smooth whorls (Pl. 2/4–5). The embryonic whorl lies in the flat apex and measures about 0.12 mm in diameter (Pl. 2/6). The following larval whorls are rounded and smooth and compose a 1.5 mm wide and 1.2 mm high protoconch with rounded sides and a corner to the base. Growth lines are fine and indistinct, but indicate that the larval aperture has a rounded lobe on the middle outer lip. The large protoconch thus differs from that of *Pterocerella* by having a corner to the base, and by being wider than high (Pl. 2/5). When the shell of *Pugnellus* is adult and fully grown with eight whorls, the spire including the protoconch become coated over by callus.

Protoconch of Xenophoridae and Haloceratidae

The protoconch morphology indicates the existence of a planktotrophic larva in most species of *Xenophora* (PONDER, 1983) while PONDER & DE KEYZER (1998: figs. 15, 128, K) stated that larvae had not been observed, but BANDEL et al. (1997) had described the veliger larva of *Xenophora* from the Red Sea. It carried a shell with 4.25 whorls and swims with a velum consisting of six lobes. The embryonic shell measures 0.08–0.11 mm across (BANDEL, 1993). In the swimming larva the apertural projection of the outer lip separated right from left tentacle and hold velum bases in place. The anus ends within the pallial cavity that is crossed by a ribbon of cilia. A large gill that consists of 9 filaments which are quite distant from each other also produces a flow of water. The apical whorls are filled by the digestive gland.

Larvae of *Xenophora* from the Gulf of Aqaba were observed from the Plankton caught in front of the Marine Station. They can be connected to *Xenophora calculifera* (REEVE, 1842) of which juveniles were found in the shallow sea at Aqaba (Pl. 8/1, 2, 7, 8). The larva swims with the six slender elongate lobes of the large velum, of which three are extended on either side of the large median apertural hook of the aperture. Slender tentacles with eyes at their base extend from the head below the apertural projection to each side. The elongate foot is placed next to the shell, which is transparent with its keel tinged with brown. The slowly pulsating larval heart and the more rapidly pumping adult heart are both active at the larval stage that is ready for metamorphosis.

The embryonic whorl has fine tubercles distributed on a smooth surface, measures about 0.2 mm in diameter and ends with the first growth lines (Pl. 8/6). To it 2.5 larval whorls are added during planktic life (Pl. 8/3–5, 10). They form a low, trochospiral shell with whorls exposed on the apical side while the basal side exhibits wide umbilicus. The outer lip of the larval shell has a large median projection that is accompanied by deep lobes, one next to the suture and the other next to the edge to the rounded base. A short wide funnel next to the umbilicus forms a siphon (Pl. 8/4). Fine spiral ribs accompany the median projection of the outer lip on its apical and umbilical side especially in the first two larval whorl (Pl. 9/9–11). In addition very fine tubercles are arranged in spiral lines, which on the median projection are a little inclined (Pl. 9/9). The umbilical lobe on the outer lip gives rise to a smooth selenizone with margins of rows of tubercles (Pl. 8/4). The fully grown larval shell measures almost 1 mm in diameter.

In the Plankton of the Gulf of Aqaba larvae (Pl. 9/14–15) of another species have a more smooth and lower shell with angular sides consisting of 3.5 whorls with a diameter of 1.5 mm and almost 1 mm in height with flat apical side and rounded base. The embryonic whorl has ornament of tubercles arranged in spiral lines and measures about 0.15 mm ending in growth lines. The ornament continues onto the first half larval whorl and ends here later only sinuous growth lines are present. The corner is formed by a keel and below it there is a second spiral keel, both keels present on the strong median projection of the outer lip.

Zygoceras differs from *Haloceras* by the general shape and sculpture of the protoconch. In case of *Zygoceras aqabaensis* it has a low spire (wider than high), while in *Haloceras* it is almost as high as wide. A uniting factor lies in the presence of spiral and granular ornament on the embryonic shell and the presence of two or three keels on the larval shell. These protoconchs differ from that of *Xenophora* by having more distinct spiral ornament on the embryonic whorl (Pl. 9/3–5), by having less than three whorls of the protoconch instead of more than three (Pl. 9/1, 6). Otherwise the rounded shape of whorls and the general type of ornament is close among all species including those of *Xenophora*. The later documents the presence of a large median projection of the apertural lip of the larval shell. This apertural feature appears to have become broken during metamorphosis among most species that have been illustrated by WARÉN & BOUCHET (1991).

Comparison with the larval shell of Heteropoda

The fully grown veliger larva of the Atlantidae swims with six velar lobes as is the case among the larvae of the Strombidae. The Heteropoda as well as the Stromboidea appeared in the fossil record quite suddenly at the base of the Jurassic (Meta-Mesogastropoda in BANDEL, 1993). The morphology of the modern veliger as well as the

time of origin of both groups about 180 Million Years ago suggest a common stem group from which both have been derived. Since at least that time Heteropoda and Stromboidea evolved in quite different ways.

Family Atlantidae RANG, 1829

The holoplanktic species of the Atlantidae have an embryonic shell of about 0.1 mm in diameter. In all species its ornament consists of tubercles but the patterns formed by them are characteristic to the species. After hatching from the egg all species live some time as planktotrophic larvae. The larval shell of *Atlanta* develops a prominent median lobe in the outer lip of their aperture. A thin calcareous keel surrounds the compressed and planispiral teleoconch. It represents the continuation of a median slit in the outer lip of the aperture of the protoconch of *Atlanta*.
Metamorphosis occurs after an extended period of larval life. Transformation from the larval shell to the juvenile teleoconch with a carina occurs while the larva is ready for metamorphosis. It changes from swimming with the ciliated velum to swimming with the fin-like foot (THIRIOT-QUIEVREUX, 1969; PILKINGTON, 1970; BANDEL & HEMLEBEN, 1987; NEWMAN, 1990), or to drifting (LALLI & GILMOR, 1989). During metamorphosis the mantle becomes attached to the keel (BANDEL & HEMLEBEN, 1987). This keel forms at the edges of the slit, which in most cases develops from the transformed basal apertural sinus of the larval shell. From the Red Sea JANSSEN (2007) recently described the species of *Atlanta*.
Atlanta fusca SOULEYET, 1852, and *Atlanta turriculata* ORBIGNY, 1836, have a similar transition of the basal sinus of the aperture of the larval shell into the slit of the teleoconch (Pl. 11/2–3). The high conical protoconch of *Atlanta fusca* consists of almost 4 whorls (Pl. 11/1–2). The embryonic shell ornament ends with first growth lines. Spiral lines ornament the first larval whorl, while on the second larval whorl most spiral ribs take a zigzag course. The apertural margin in the first two larval whorls has a shallow wide apical sinus, a rounded wide shallow median lobe, and a concave umbilical portion. Later the apical sinus acquires rounded shape, the middle lobe is wide and rounded. The slit with upraised margins (keel) appears abruptly in the lower part of the larval whorl a quarter whorl before the protoconch is ended. It has changed its position into the middle of the whorl only within the first teleoconch. Metamorphosis of the body is not totally in phase with the reconstruction of the shell from protoconch to teleoconch. Animals were observed with shell having a carina and slit and still swimming with the velum. Reorganization to the adult type of swimming with aid of the fin occurs after construction of the larval shell with ornament into the adult shell that is smooth and has the slit with keels. The fully grown shell is up to 2 mm wide with its protoconch of 0.55 mm in size (Pl. 11/7).
Atlanta turriculata has the embryonic whorl covered by a dense pattern of fine, rounded tubercles (Pl. 11/13). The begin of larval ornament is by about five spiral rows of tubercles of which the third changes into a low keel on a corner after about half a whorl. The first two larval whorls form a high spire including the round embryonic whorl, while the last larval whorls changes into planispiral coiling mode. Here shell width expands (Pl. 11/3–4). The aperture has a wide apical sinus and a deep narrow basal sinus. The base is ornamented by zigzag ribs and has a round umbilicus. The basal sinus transforms into the slit of the teleoconch while the apical sinus is closed. The teleoconch has a high keel that is well mineralized and begins and ends low and is highest in its middle part. It consists of a little more than one whorl with rounded aperture.
In case of *Atlanta helicinoides* SOULEYET, 1852, the slit inserts on the base of the median lobe in a similar way to that of *Atlanta inflata* SOULEYET, 1852. The veliger holds its brownish shell with the apex to one side and the foot on the other, the umbilical side. The middle lobe of the outer lip lies in the middle of the velum with three of its wings on either side and with the shell hanging down below them. The protoconch is lowly conical of depressed shape and consists of 4.7 whorls (Pl. 11/5–6). Its embryonic whorl is ornamented by a fine and dense pattern of tubercles. The larval whorls are ornamented by many spiral ribs, at first are tightly coiled, and later less tightly exposing the ornament on the spire. The rounded marginal sinuses of the outer lip are low, and only in the fourth whorl a wide basal lobe appears. This median zone is ornamented by about 10 spiral lines and the area above and below is more weakly ornamented. Fully grown larvae are common in the plankton and may swim in this growth stage for an elongate period of time. At metamorphosis the slit and its keels forms only in the region of the apical margin of the basal sinus. Here a narrow sinus forms that continues in the slit of the teleoconch.
Atlanta inflata has a lowly conical protoconch with 3.5 whorls, with the last half whorl almost totally consisting of the large tongue like projection of the outer lip. The embryonic shell is ornamented by fine and dense granules as in (Pl. 11/16). The teleoconch of specimen from the Red Sea measures only 1.2 to 1.5 mm in width and is quite flat. The protoconch is colored with pink and the following shell either transparent without color or also a little pink.
Atlanta plana RICHTER, 1972, has its larval shell with angular shape and 3.5 whorls (Pl. 11/11). The embryonic shell is smooth with indistinct increments of growth. The first whorl of the larval shell is ornamented by one or two spiral lines and a lamellar spiral rib on the corner. The lamella of the corner continues into the elongate

tongue like apertural projection of the fully grown larval shell with smooth base and 0.6 mm in diameter and 0.5 mm in height. At metamorphosis the slit forms at the base of the angular median apertural tongue from the basal angular furrow, as is also the case in *Atlanta frontieri* RICHTER, 1993, that differs by having one more whorl of its larval shell (JANSSEN, 2007: pl. 11, figs. 1–3). The teleoconch of *Atlanta plana* coils tightly, consists of one and a quarter whorls, and may be up to 4 mm in diameter.
Atlanta oligogyra TESCH, 1906, forms its slit in a smooth simple rounded aperture, very different from the other species of *Atlanta* (Pl. 11/10, 12). The end of the larval shell has no apical or basal lobes and the slit initiates as if on a teleoconch with symmetric plane coiling mode, while the protoconch is trochospiral. The protoconch consists of only about 2.5 whorls with the small embryonic whorl of about 0.06 mm in diameter. This first whorl with small rounded tubercles can have a wrinkled surface. It ends with well visible growth lines. The larval shell is smooth with ornament of indistinct tubercles and measures less than 0.4 mm in diameter. Its margin is curving so that there is a lobe in the middle of the outer lip. Transition from larval shell to teleoconch is quite gradational and the sinus on the basal side is closed before the slit forms. The whorl of the teleoconch expands rapidly in width while it remains low. The very last part of the teleoconch detaches and the slit an keel are well developed. The fully grown shell with a little more than one whorl of the teleoconch measures about 2 mm in maximum diameter.
Atlanta inclinata LESUEUR, 1817, larvae are commonly present in the plankton in front of the marine station at Aqaba. The veliger carries its colorless transparent shell with 0.8 mm in height below the six lobes of the velum with the conical apex to one side and the large umbilicus to the other and the tongue like projection of the outer lip over the head. The black eyes are conspicuous and the foot with the large operculum is held in inclined position opposite of the apertural projection. The protoconch consists of about five whorls and has rounded beehive like conical shape. It lies with its axis of coiling in inclined position in relation to the teleoconch (Pl. 11/14–15). The embryonic shell ornamented by fine granules. The first larval whorl is smooth with very fine growth lines reflecting a lobed outer lip. Later ornament consists of fine rows of tubercles, and the base has a wide umbilicus. The broad median tongue-like projection of the outer lip has a fine line on its upper and lower margin, with the lower line covered by the succeeding whorl. In the last whorl of the larval shell mode of coiling changes to planispiral and the basal sinus comes into a more median position. The keel appears by the basal sinus becoming upturned and narrowed. While it is transformed into the slit, and the apical sinus is closed.

5 Remarks on the radula of the Strombimorpha

The radula of *Aporrhais* was illustrated by TROSCHEL (1856), its use characterized by ANKEL (1938), described in more detail by MORTON (1956) and by scanning electronic microscope by BANDEL (1984). As had originally been noted by TROSCHEL the radula of *Aporrhais* resembles that of *Xenophora*. THIELE (1931) connected the Xenophoridae, Struthiolariidae, Aporrhaidae and Strombidae with each other based on shape of their radula, that has a central tooth with a denticulate cutting edge, relatively wide lateral teeth and long and narrow marginal teeth. ABBOTT (1960) noted that the radula throughout the genus *Strombus* shows little diversity. But he also stated that characteristics found on some teeth are correlated with the marine province rather than the assumed phylogenetic relationships.
The radula of *Aporrhais pespelicani* resembles that of *Xenophora conchyliophora* (BANDEL, 1984: pl. 7, figs. 1, 98, 99). The radula of different species of *Xenophora* is quite similar (PONDER, 1983: figs.7–12). As had been noted by TROSCHEL (1856), THIELE (1931), MORTON (1958) the radula of *Xenophora* is not only closely related to that of *Aporrhais* but also resembles that of the Struthiolariidae as well as the Strombidae.
Within *Strombus* some differences can be noted (BANDEL, 1984: fig. 104), not so much regarding the general shape of the teeth, but in regard to the number and shape of cusps on their cutting edges. Marginal teeth in *Aporrhais*, *Xenophora* and *Strombus* are very long and slender. Their denticulation lies only on the inner margin. *Strombus pugilis*, *Strombus gigas* and *Strombus raninus* can be distinguished from each other by small differences of the cusps number on the teeth. The radula of *Strombus raninus* is practically identical to that of *Strombus gallus*. *Strombus gibberulus*, *Strombus fasciatus*, *Strombus mutabilis*, *Strombus erythrinus*, *Strombus tricornis* and *Lambis truncata* were found to be quite similar to each other (BANDEL, 1984: figs. 104–109), and they also resemble that of *Terebellum terebellum* (JUNG & ABBOTT, 1967). The teeth of the radulae in all these species are so similar to each other that they can not be used to distinguish subgenera of *Strombus* from each other.
The radula represents evidence to the close interrelation of species of *Strombus* with each other, and also to the similarity of their feeding mode. This also includes the Struthiolariidae of which the radula has been described by POWELL (1951). He noted their similarity to each other and to those of *Aporrhais* as well as *Xenophora*. The radula of *Perissodonta* resembles that of *Aporrhais*, but has shorter lateral teeth and as very exceptional feature more than two marginal teeth on each side (up to four pairs of marginal teeth) (MORTON, 1956: fig. 1). *Tylospira* also has a small radula that resembles in shape that of *Aporrhais*, but has a characteristic triangular central tooth

and short marginal teeth. MORTON (1956) suggested that Struthiolariidae represent southern derivatives of the Aporrhaidae, which was supported based on evidence of shell features by BEU & MAXWELL (1990).

6 Phylogenetic model of Stromboidea evolution and results

Model to the phylogeny and diversification of the Stromboidea

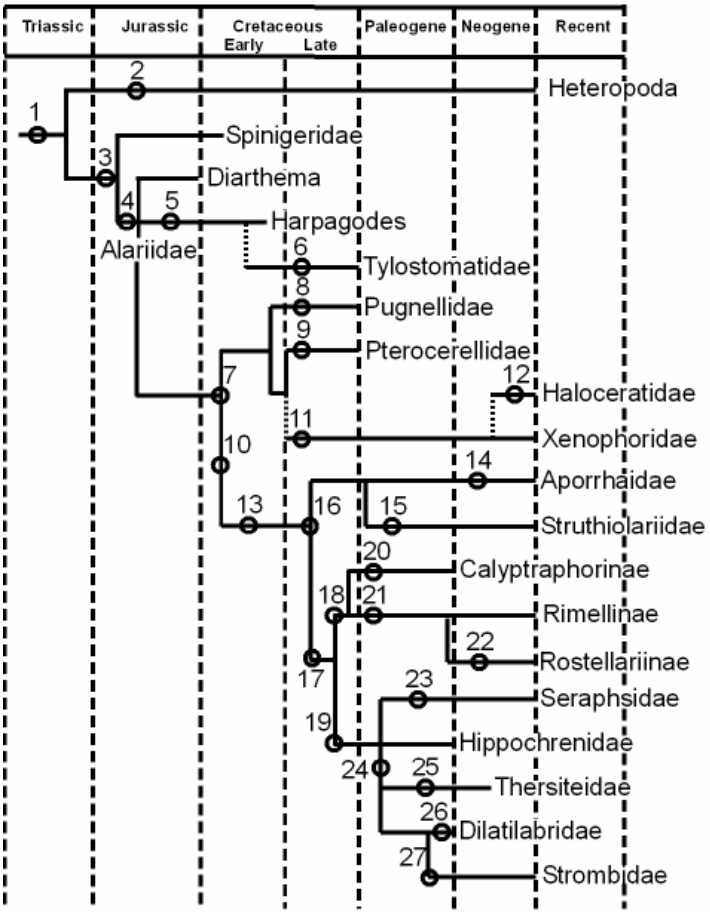

Fig. 23: Cladogram – for explanation, see text.

The Late Triassic–Early Jurassic diversification of the Caenogastropoda from Cerithimorpha stock (node 1) may have given rise to the holoplanktic Heteropoda on one side (node 2) and the Stromboidea on the other (node 3). Early Jurassic stromboidean differentiated into Spinigeridae with spine bearing varices and the Alariidae such as *Cuphotifer* and *Dicroloma* resembling *Aporrhais* but without varices. During Mid-Jurassic diversification within the Alariidae (node 4) species with one or few apertural spines evolves such with a web like outer lip (node 5) and here *Harpagodes* and from these the Tylostomatidae with expanded rounded and large body whorls in the Cretaceous (node 6) can have originated. From the Alariidae an explosive radiation during the Early Cretaceous (node 7) resulted in the Pugnellidae (node 8), the stem of the Pterocerellidae (node 9) and to that of modern Stromboidea (node 10). The similarity of the protoconch of some *Pterocerella* with that of the Xenophoridae may indicate a relation (node 11), and by the same evidence the relation to the Haloceratidae (node 12). From the Aporrhaidae with *Arrhoges* like species (node 13), the *Aporrhais* group with several spines on the outer lip (node 14), and the Struthiolariidae arose in the Southern Hemisphere (node 15) after the transition from the Cretaceous to the Tertiary. The relation of Cretaceous Aporrhaidae to those living today is still unresolved (node 16). A radiation in the Late Cretaceous (node 17) gave rise to the Rostellariidae (node 18) as well as the Hippochrenidae (node 19). Rostellariidae further diversified into the Calyptraphorinae (node 20) and the *Rimella* group (node 21). From the later the Rostellariinae evolved during the Paleogene (node 22). The Hippochrenidae can have given rise to the Seraphsidae on one side (node 23) by developing a cylindrical shell, and the Dilatilabridae and Thersiteidae on the other side (node 24) with *Strombus*- like morphology. Here Thersiteidae

(node 25) with callus pad and the Dilatilabridae (node 26) both without stromboid notch evolved. From one of these the Strombidae (node 27) arose with strong diversification since the Oligocene.

Conclusions

Fossil Stromboidea represented by the Alariidae are known to have existed from the early Jurassic onward. This group of Caenogastropoda has come into being about 200 Million years ago and developed into several families since. Of these only the members belonging to the five families Aporrhaidae, Struthiolariidae, Rostellariidae, Seraphsidae and Strombidae range to the Present, when their questionable relatives such as Xenophoridae and Haloceratidae are excluded. The similarity of the veliger larvae of the Heteropoda with those of Stromboidea indicate a relation that connects them. Heteropoda and Stromboidea arose at about the same time during the Early Jurassic (BANDEL & HEMLEBEN, 1987; BANDEL, 1993). While Heteropoda specialized to a pelagic life and became carnivorous, the early Stromboidea adopted to live on and in soft sediment on the sea bottom, as is still the case in living *Aporrhais,* feeding on algae filtered from suspension, or collected from deposits or picked from growths on the substrate.

The juvenile teleoconch of the Alariidae has no periodical shell thickenings (varices) while these are usually present in members of the Aporrhaidae. During transition from the Alariidae to the Aporrhaidae the general characters of the shape of the shell has changed little and this transition occurred during the Early Cretaceous less than 140 Million years ago. Spinigeridae with the juvenile shell provided with varices that bear spines evolved parallel to the Alariidae and appear to discontinue beyond the Jurassic–Cretaceous transition. Some genera of the Alariidae such as *Diarthema* produced a final whorl with a varix on the body whorl half or a quarter of a whorl before the final outer lip. From such species, it could be hypothesized, during the end of the Jurassic, the Colombellinidae may have evolved. The later have been interpreted to represent a transitional group to some Neomesogastropoda (ZITTEL, 1885; COSSMANN, 1904; SCHILDER, 1927; WENZ, 1938; TAYLOR et al., 1983). In case they represent the stem group of the Cypraeoidea, as was suggested by SCHILDER (1927), not only the shape of the adult shell must have changed drastically but that of the protoconch. Cypraeidae not only have a strong ornament of their larval shell and a drastic change of ornament to the teleoconch, but also the mantle of the larva can be extended to cover the larval shell and deposit shell material to its outer side (BANDEL et al., 1997). In case of the Tonnoidea, in addition, a special tentacle formed by the larval mantle began to deposit periostracum layers on top of the larval shell during its growth (BANDEL et al., 1994). Other members of the Neomesogastropoda also have characteristics of their own distinguishing them from Stromboidea, and all show a very well developed end of larval growth documented by a marginal thickening of the fully grown larval shell and usually drastic change in ornament between protoconch and teleoconch.

As STOLICZKA (1868) had noted *Diarthema paradoxa* (ETUDES-DESLONGCHAMPS, 1843) appears somewhat related to *Ranella* LAMARCK, 1854, that is to the Bursidae relationship within the Tonnoidea. These have been interpreted to be related to the Colombellinidae by WENZ (1938) which may be close to the stem groups of the Neomesogastropoda that diversified during the Mid Cretaceous. At that time distinct families arose (RIEDEL, 2000) of which Calyptraeoidea, Cypraeoidea, Naticoidea, and Tonnoidea are still diverse. Members of the Colombellinidae are recognized to the end of the Cretaceous but their relation to the Alariidae (Stromboidea) remains in doubt. The Neogastropoda arose from a still unrecognized stem which probably was close in relation to that of the Neomesogastropoda. The former diversified into several groups of which some became extinct at the end of the Cretaceous, while others became visible during the late Cretaceous and many at the Paleogene, and since that time have diversified into several families.

The shape of *Perissoptera* resembles that of the other Cretaceous species of the genera *Anchura*, *Latiala* and *Drepanocheilus.* These genera are connected with each other by species that have intermediate shapes of their outer lip (KIEL & BANDEL, 2002). *Drepanocheilus,* in addition, is so close to *Arrhoges* that a distinction from the Arrhoginae POPENOE, 1983, based on the living *Arrhoges occidentalis* appears artificial. The apertural characters of the body whorl of *Arrhoges*, *Drepanocheilus*, *Tulochilus* and *Anchura* are similar to each other, and the early ontogenetic shell usually confirms this similarity. A historical and paleogeographical discussion of the Late Cretaceous Aporrhaidae was presented by KIEL & BANDEL (2002), but it was recognized that their evolution may prove to be more complex when additional data from fossil faunas become known.

The living *Arrhoges occidentalis* may be closely related to *Aporrhais*, as was suggested by ABBOTT (1974: fig. 1576) who determined it as *Aporrhais occidentalis*. But it may also have a longer independent history, and THIELE (1931) interpreted it as distinct genus. WENZ (1938) even placed *Arrhoges* in the genus *Drepanocheilus*. It appears that the transition with Cretaceous genera of the Aporrhaidae is gradational with most species having

apertural features which resemble those of *Arrhoges* while several spines on the apertural margin as is the case in *Aporrhais* appear later. Regarding the ornament of their spire *Latiala* and *Drepanocheilus* had species living at about the same time during the Cretaceous connected to each other by intermediate genera. They appear related to the species of *Struthiochenopus* from the mid Tertiary of the southern Hemisphere. *Tulochilus* from the Paleocene of New Zealand has a spire with ornament of coarse axial ribs, the living *Arrhoges occidentalis* has curved ribs on the spire and body whorl, and *Anchura* from the Cenomanian of Texas (STEPHENSON, 1952) as well as *Goniocheila* from the Oligocene of Mississippi has ornament of axial ribs all over.

The transition from Aporrhaidae to the Struthiolariidae has probably occurred with begin of the Tertiary (ZINSMEISTER & GRIFFIN, 1995; NIELSEN, 2005). MORTON (1956) suggested that Struthiolariidae represent southern derivatives of the Aporrhaidae, which was supported by BEU & MAXWELL (1990). Living and fossils species of the family are known only in the Southern Hemisphere. Possibly their origin ay also lie in the Pugnellidae, as was discussed by KIEL & BANDEL (1999). KRONENBERG & BURGER (2002) suggested that the definition of the Pugnellidae could also include some living Strombidae such as *Tricornis*, and *Euprotomus*, and the fossil *Calyptraphorus* of the Rostellariidae. And they though it necessary to more clearly define the Pugnellidae. Aside from the spread out callus on large parts of the surface of their shell and their appearance in the fossil record more than 60 Million years earlier than the Strombidae, an additional distinctive character of the Pugnellidae is now recognized in the large and broad protoconch of *Pugnellus.* It has quite a different shape and size compared to that of *Strombus*. The fully grown shell of *Pugnellus* is coated from the outside with callus with deposition beginning on the spire which distinguishes from *Strombus*. Aporrhaidae and Alariidae differ from Pugnellidae by usually having a high spire. Also they possess spines or lobe-like extensions on the outer lip which are free of callus deposits. The outer lip of the Struthiolariidae is of more simple outline, not extended and thickened as in the Pugnellidae. Callus deposits here remains near the inner lip. The Rostellariidae have a more slender shell as that of the Pugnellidae. In case the shell is covered by callus as in the Calyptraphorinae n. subfam. its formation is connected to a canal as continuation of the apical part of the aperture, which is not present in Pugnellidae. The mode in which callus was deposited on the surface of the shell as well as the features of the outer lip with two spines or no spines distinguish the subfamilies of the Pugnellidae, Pugnellinae and Tundorinae n. subfam..

The Colombellinidae have a shell with low spire as present in the Pugnellidae and commonly show a denticulate inner and outer lip with additional posterior canal. The shell of *Colombellina* and *Columbellaria* is not covered by callus outside of their inner lip, and the protoconch differs in shape and ornament (BANDEL & DOCKERY, in prep.).

A distinct group is here recognized in the *Pterocerella* relation on hand of a characteristic protoconch as well as by features of the teleoconch. The Pterocerellidae n. fam. have a large protoconch of relatively low shape, but not low as is the case among the Late Cetaceous to modern species of *Xenophora*. *Pterocerella* resembles somewhat the Jurassic relation of *Dicroloma* (*Alaria*) with sometimes similar ornament their spire, which usually is wider. The aperture may also have a long anterior curved canal but it remains within the plane formed by the spines on the outer lip, for example in *Dicroloma* (KAIM, 2004: fig. 54), while it is twisted to the back and the side in *Pterocerella* and also *Tessarolax*, also with the posterior spine of the outer leaving the plane. *Misritropis bartheli* n. sp. from the Late Cretaceous has the characters of the teleoconch resembling those of *Xenophora*, including a basal frill, but the shell is relatively higher than any known member of the Xenophoridae. It may represent a species of a side branch of the stem group of the Xenophoridae connecting to the Stromboidea.

The Rostellariidae appear in the fossil record with Rimellinae and Calyptraphorinae n. subfam., while Rostellariinae evolved later, probably derived from Rimellinae. While Rimellinae survived to the Present, the Calyptraphorinae n. subfam. became extinct by the end of the Eocene. *Calyptraphorus* represents one of the two different groups of Stromboidea in which the shell is covered with aragonitic deposits from the outer side. Callus deposition of the early Calyptraphorinae n. subfam. such as *Eocalyptraphorus* n. gen. is less than in later genera and connects with the Rimellinae. *Tibia dentata* from the Mid-Tertiary resembles modern *Tibia* and *Rostellariella* as well as *Rimella* regarding ornament of the early teleoconch as shape and size of the protoconch. The subfamily Rostellariinae is the latest group within the Rostellariidae to appear in the fossil record. BOUCHET & ROCROI (2005) suggested to include the subfamily Rostellariinae GABB, 1868 (Rimellinae STEWART, 1927 = Tibiinae GOLIKOV & STAROBOGATOV, 1975) in the Strombidae. Based on to the antiquity of some these taxa and also to the relative late origin of the family Strombidae (based on *Strombus*) a different classification is here suggested.

The Hippochrenidae n. fam. are a distinct group which appear in the geological record at about the same time as the Rostellariidae, both having derived from still unrecognized Stromboidea, probably close to Cretaceous members of the Aporrhaidae. Modern species that had their origin in one of the two families Hippochrenidae n. fam. and Rostellariidae, such as *Terebellum* of the Seraphsidae and living representatives of the Rostellariidae and the Strombidae, have similar characters of their head and foot, as had been recognized by STOLICZKA (1868). He connected them with each other and distinguished them from the Aporrhaidae and Struthiolariidae. Hippochrenidae n. fam. are distinct by the characters of their expanded and thin outer lip and the groove and ridge formed by the inner lip on it inner side and extended to the tip of the spire. Ornament of the spire and shape of the margin of the outer lip allow to distinguish the Hippochreninae n. subfam. from the ornamented Wateletinae n. subfam.. Thersiteidae and Dilatilabridae n. fam. may have evolved from members of the Hippochrenidae n. fam.. The genus *Hippochrenes* ranges from the Cretaceous to the end of the Eocene. *Strombus* and relation ranges from the Oligocene (Dilatilabridae n. fam. since Eocene) to the Recent. WENZ (1938) included *Hippochrenes* as subgenus of *Tibia* within the Strombidae. COSSMANN (1904: pl. 3, fig. 7) connected the genus *Hippochrenes* (spelled *Hippochrene*) with *Wateletia* COSSMANN, 1904, and later also *Chedevillia* COSSMANN, 1906 (both as subgenera of *Hippochenes*). KRONENBERG & BURGER (2002) suggested to place *Hippochrenes*, *Semiterebellum* and *Terebellopsis* with the Rostellariidae, following here WENZ (1938), who had interpreted all these taxa as subgenera of *Tibia*. Hippochrenidae n. fam. have evolved parallel to the Rostellariidae for more than 70 Million years and both derived from a common ancestor that probably lives during the Late Cretaceous.

The stem group of the Strombidae as well as the Seraphsidae is interpreted to be represented by the Hippochrenidae n. fam.. The Seraphsidae with the only species of *Terebellum* has its own history (JUNG, 1974) ranging back to the Paleogene. The first tropical Strombidae occur in the late Oligocene and intermediate species such as *Dilatilabrum*, that resembles in general shape modern *Strombus* but lacks the characteristic stromboid notch of the shell, occurred in the Eocene. That genus is taken to define the Dilatilabridae n. fam.. Among the fossil species of Strombidae fitting into the definition of the family as provided ABBOTT (1960), only such species can be included which lived from the Oligocene onward. The sinus of the stromboid notch in its position next to the siphonal sinus is used by all extant species of *Strombus* to look out under their thick shell (ABBOTT 1960, 1961). The genus *Strombus* has traditionally been subdivided into subgenera which by some authors have been interpreted to represent genera. This system was reviewed above and substituted by additional taxa in cases where the proposed subgenus is not fitting to the species in question. Fossil species are includes in the system, that is based predominantly on shell morphology. Older species with general character of the shell as in *Strombus* but without some characters such as the stromboid notch on the outer lip and an even callus of the inner lip may represent stem Strombidae are recognized in the Dilatilabridae n. fam. and perhaps the Thersiteidae, both discussed above. Both later families may connect to the Hippochrenidae n. fam..

In case connections that have been reconstructed in the presented tree and the discussion of it can be verified, for example by molecular methods, Stromboidea may either represent the stem group of the Latrogastropoda RIEDEL, 2000, or they have evolved parallel to them as sister group. In the first case Neogastropoda and Neomesogastropoda could have derived from a group that arose from the Alariidae at during the Early Cretaceous. In the second case Latrogastropoda came from a relative of the stem of the Stromboidea that lived during the Triassic. An early bursts of evolutionary novelties out of the stem group leading to the Stromboidea during the latest Triassic could also unite them (Strombidae, Rostellariidae and Aporrhaidae together) with the Heteropoda, which have similar larvae in their family Atlantidae. Radula morphology can be interpreted as evidence for a relation of the Strombimorpha to the Cerithimorpha among the Caenogastropoda (BANDEL, 1984, 2006), but ancestral species common to both have lived during the Triassic, and both groups Cerithimorpha and Strombimorpha have evolved parallel to each other for at least 200 Million years.

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Plate 1

Fig. 1: The fully grown larval shell of the *Strombus* in Fig. 2 with almost six whorls in allometric growth and rounded last whorl with simple aperture. The shell is about 1.2 mm high.

Fig. 2: Early whorls of the larval shell of a *Strombus* from the southern Chinese Sea, detail to Fig. 2 with ornamented first larval whorls similar to *Strombus gibberulus*.

Fig. 3: Juvenile shell of *Strombus pugilis* from the Caribbean Sea at Santa Marta (Colombia) with details of the larval shell in Fig. 4. The shell is about 5 mm high.

Fig. 4: The larval shell of *Strombus pugilis* is smooth and has curving growth lines on smooth background.

Fig. 5: The juvenile shell of *Strombus raninus* from the Caribbean Sea at Santa Marta (Colombia) is about 6 mm high with strong varices and the protoconch as detail in Fig. 6.

Fig. 6: The protoconch of *Strombus raninus* is smooth and consists of more than 4.5 whorls (detail to Fig. 5)

Fig. 7: Juvenile shell of *Strombus gigas* from the Caribbean Sea at Santa Marta (Colombia) with detail in Fig. 8. the shell is about 4 mm high and ornament includes rounded varices.

Fig. 8: The detail to Fig. 7 with the protoconch with gradational transition into the teleoconch and a height of about 1.2 mm.

Fig. 9: *Strombus pugilis* from the Caribbean Sea at Colombia with the detail in Fig. 11. The juvenile shell changes shape and ornament during growth. The shell is about 6 mm high.

Fig. 10: The juvenile shell of *Strombus marginatus* from the Indian Ocean near Pondicherry (SE India) with axial and spiral ornament, detail of protoconch in Fig. 12, shell height about 6 mm.

Fig. 11: The protoconch of *Strombus pugilis* with the detail of the larval ornament in Fig. 4 has weak change into the teleoconch.

Fig. 12: *Strombus marginatus,* as in Fig. 10, with the ornament of the early teleoconch imprinted onto the larval shell from the inside. Protoconch height about 0.8 mm.

Fig. 13: Ornament of the larval whorl of *Aporrhais pespelicani* is smooth with very fine granules.

Fig. 14: The transition of larval shell to teleoconch in *Aporrhais pespelicani* is not distinct and teleoconch ornament enters below the final larval whorl, with 1 mm high and 0.8 mm wide shell.

Fig. 15: *Aporrhais pespelicani* shortly after metamorphosis with first teleoconch added and almost 2 mm high shell.

Fig. 16: Embryonic shell of *Aporrhais pespelicani* is rounded and about 0.2 mm wide, set off from the larval shell by growth lines.

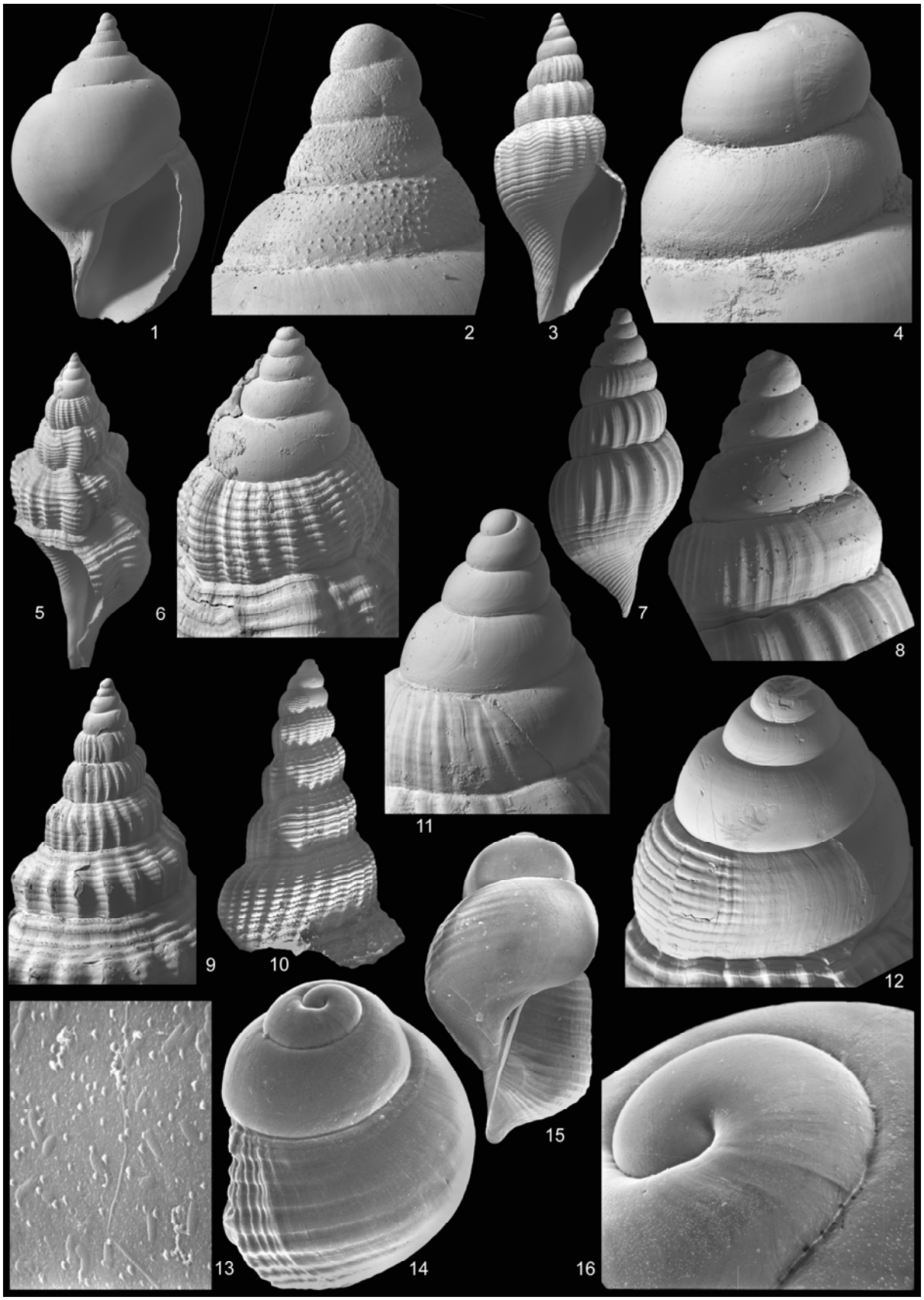
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Plate 2

Fig. 1: The protoconch of *Pterocerella* from the Late Campanian Coffee Sand of Mississippi with evenly rounded whorls and smooth margin. Height of the shell is about 2 mm.

Fig. 2: Change from the protoconch of *Pterocerella* (same locality as Fig. 1) to teleoconch is distinct and not gradational. Shell about 2 mm high.

Fig. 3: The juvenile shell of *Pterocerella maryea* from Coffee Sand in Mississippi with the shell about 6 mm high.

Fig. 4: The protoconch of *Pugnellus densatus* from Coffee Sand in Mississippi (Campanian) has a small embryonic whorl (detail in Fig. 6) and large larval shell of 1.5 mm in diameter.

Fig. 5: The protoconch of *Pugnellus* from the Campanian Coffee Sand, Mississippi seen from the side. The shell is about 1.2 mm high.

Fig. 6: The embryonic whorl of the shell of *Pugnellus* measures only 0.12 mm wide. Detail to Fig. 4.

Fig. 7: The juvenile shell of *Anchura chappelvillensis* from Coffee Sand in Mississippi has curving axial ribs and varices, and its protoconch is in Fig. 8. The shell is 8 mm high.

Fig. 8: The protoconch of *Anchura chappelvillensis* in Fig. 7 consists of 3.5 whorls and grades in ornament into the early teleoconch.

Fig. 9: *Anchura* sp. from Ripley Formation of Union County Lake in Mississippi (Early Maastrichtian) has a conical protoconch that is about 1 mm high with the spiral ribs of the teleoconch entering onto the last part of the larval shell.

Fig. 10: *Anchura* sp. from Ripley Formation with about 2 mm high shell and transition from the protoconch to the teleoconch that is quite indistinct.

Fig. 11: The juvenile shell of *Latiala* from the Campanian Coffee Sand, Mississippi is about 3 mm high with the transition from protoconch to the teleoconch quite indistinct, detail in Fig. 12.

Fig. 12: The juvenile shell of *Perissoptera* sp. from Ripley Formation (Maastrichtian) has a smooth conical protoconch and densely ribbed early teleoconch. The shell is about 2.5 mm high.

Fig. 13: The embryonic whorl of *Latiala* in detail to Fig. 12 measures about 0.15 mm in diameter and has ornament of granules.

Fig. 14: The larval shell of *Latiala* has a very strong basal projection of its outer lip in the fourth whorl of its protoconch. The shell is about 1 mm high.

Fig. 15: Apical view of *Perissoptera* as in Fig. 13 with the protoconch about 0.12 mm high and provided with a basal apertural lobe in transition from larval shell to the teleoconch.

Fig. 16: The smooth protoconch in the ribbed teleoconch is about 0.8 mm wide. Ornament of the larval shell of *Perissoptera* as in Fig. 12 and 15 consists of subsutural short spiral ribs.


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Plate 3

Fig. 1: The juvenile shell of *Hippochrenes macroptera* with about 5 mm long shell has the first 1 mm composed of the protoconch.

Fig. 2: The first four whorls of *Hippochrenes macroptera* from the Eocene of the Paris Basin are the larval shell. They closely resemble those of living *Rostellariella* (Pl. 4/13–14). The shell is about 2 mm high.

Fig. 3: Apical part of the shell of *Paraseraphs tetanus* with the detail of the apex in Fig. 3, and the visible shell about 5 mm long and displays the groove that extends from posterior end of the aperture to the apex, along the outer lip that covers the spire.

Fig. 4: The two embryonic whorls of *Paraseraphs tetanus* from the Eocene of the Paris Basin are 0.35 mm in diameter and form a plane protoconch in the apex of the shell (Figs. 5 & 6).

Fig. 5: Detail to *Hippochrenes macroptera* from Fig. 2 of the larval shell with strong basal projection reflected in growth line pattern, and a spiral rib on the upper margin of the lobe.

Fig. 6: *Rimella fissurella* from the Eocene of Damery in the Paris Basin with 1 mm high shell as detail to Fig. 10 with begin of the teleoconch and smooth protoconch.

Fig. 7: The juvenile shell *Rimella fissurella* from the Eocene of Damery with 1.5 mm high shell and the basal lobe of the larval shell displayed.

Fig. 8: *Paraseraphs tetanus*, detail of Fig. 3.

Fig. 9: *Rimella fissurella* from the Eocene of Damery with about 2 mm high shell with regular ornament and wide rounded varix, detail to Fig. 7.

Fig. 10: *Calyptraphorus jacksoni* from the Paleocene of Matthews Landing on Alabama River with shell almost 2 mm high and sinuous growth lines on the larval part. Figs. 11 to 15 are from the same species and locality.

Fig. 11: *Calyptraphorus jacksoni* with 2.5 mm high shell and quite indistinct transition from the smooth larval shell to the ornamented teleoconch.

Fig. 12: Juvenile *Calyptraphorus jacksoni* with protoconch of almost five whorls.

Fig. 13: The embryonic whorl of *Calyptraphorus jacksoni* is about 0.12 mm in diameter and continues into the larval shell without break in ornament but with change to sinuous growth lines.

Fig. 14: *Calyptraphorus jacksoni* protoconch and early teleoconch with a weak varix and the larval shell of almost four whorls. The shell is about 2 mm high.

Fig. 15: Part of the larval shell of *Calyptraphorus jacksoni* with only ornament of sinuous growth lines and corner to the base.

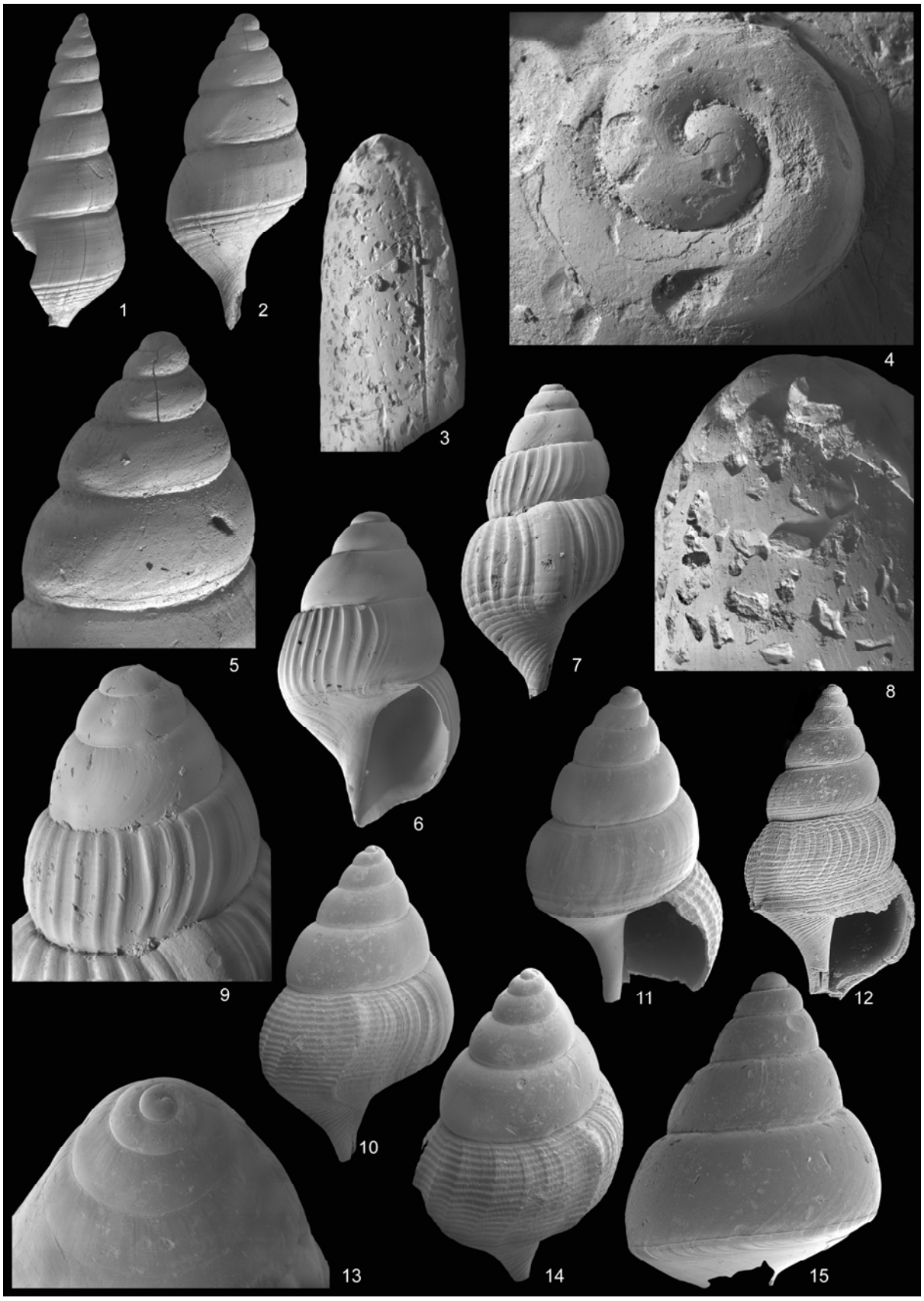
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Plate 4

Fig. 1: *Calyptraphorus jacksoni* with the shell 35 mm high is fully grown in size, but has no callus cover.

Fig. 2: *Calyptraphorus jacksoni* from the Paleocene of Matthews Landing on Alabama River seen from the side with full callus cover and the apical canal.

Fig. 3: *Calyptraphorus jacksoni* of the same as in Fig. 2 seen with the callus covered ventral side that is flattened and the sides are thickened by the deposits.

Fig. 4: *Calyptraphorus jacksoni* of same as in Fig. 2 seen with the callus groove on the dorsal side where ventral callus extended over the spire and dorsal callus meet in the margin of the curving canal.

Fig. 5: *Calyptraphorus jacksoni* with begin of callus cover and wide groove on the side (same as Fig. 6)

Fig. 6: *Calyptraphorus jacksoni* of the same as in Fig. 5 with the dorsal side and the round shape of the margin of the groove.

Fig. 7: The early teleoconch of *Tibia dentata* from the Miocene of France with ornament of axial ribs, early shell in Fig. 8. About 6 mm high shell.

Fig. 8: The protoconch of *Tibia dentata* has transitional ornament of the early teleoconch imprinted onto the final larval shell and rectangular pattern on the first whorl as in Tibia fusa. Protoconch height about 1 mm.

Fig. 9: Protoconch and first whorl of the teleoconch from *Aporrhais speciosa* from the Oligocene (Chattian) of the Sternberger erratic stones, NE-Germany. Shell 3 mm high.

Fig. 10: *Aporrhais megapolitana* with transitional ornament imprinted on the last larval whorl, detail to Fig. 9. Protoconch about 1 mm high. Sternberger erratic stomes, Chattian.

Fig. 11: The juvenile shell of *Tibia fusca* from the Pacific Ocean at Cebu (Philippines) has a regular pattern of axial and spiral ribs. The protoconch is in detail in Fig. 12. The shown shell is about 6 mm high.

Fig. 12: The embryonic shell of *Tibia fusca* is about 1 mm high and ends with a lobe on the aperture with clear distinction to the begin of the teleoconch.

Fig. 13: The juvenile shell of *Rostellariella delicatula* from the Pacific near the Philippines is about 7 mm high with rather indistinct transition from the larval shell to the teleoconch (details in Figs. 14 & 15).

Fig. 14: Juvenile shell of *Rostellariella delicatula* as in Fig. 13 seen from the other side, and in detail of the larval shell in Fig. 15.

Fig. 15: The larval shell of *Rostellariella delicatula* is smooth, consists of more than 5 whorls and has sinuous growth lines and a spiral rib at the top of its basal sinus of the outer lip. Height about 1.6 mm.

Fig. 16: The protoconch of *Strombus pugilis* from the Caribbean Sea at Santa Marta with transitional ornament between last larval whorls and first whorl of the teleoconch. Shell of about 1.5 m in height.

Fig. 17: *Ectinochilus texanus* from the Eocene of Brazos River in Texas with conical protoconch with 6 whorls and ornamented first whorl of the teleoconch, height about 3 mm.

Fig. 18: *Ectinochilus texanus* from Brazos River, detail to Fig. 17 with ornament of the larval whorls of sinuous growth lines. Protoconch about 1.8 mm high.

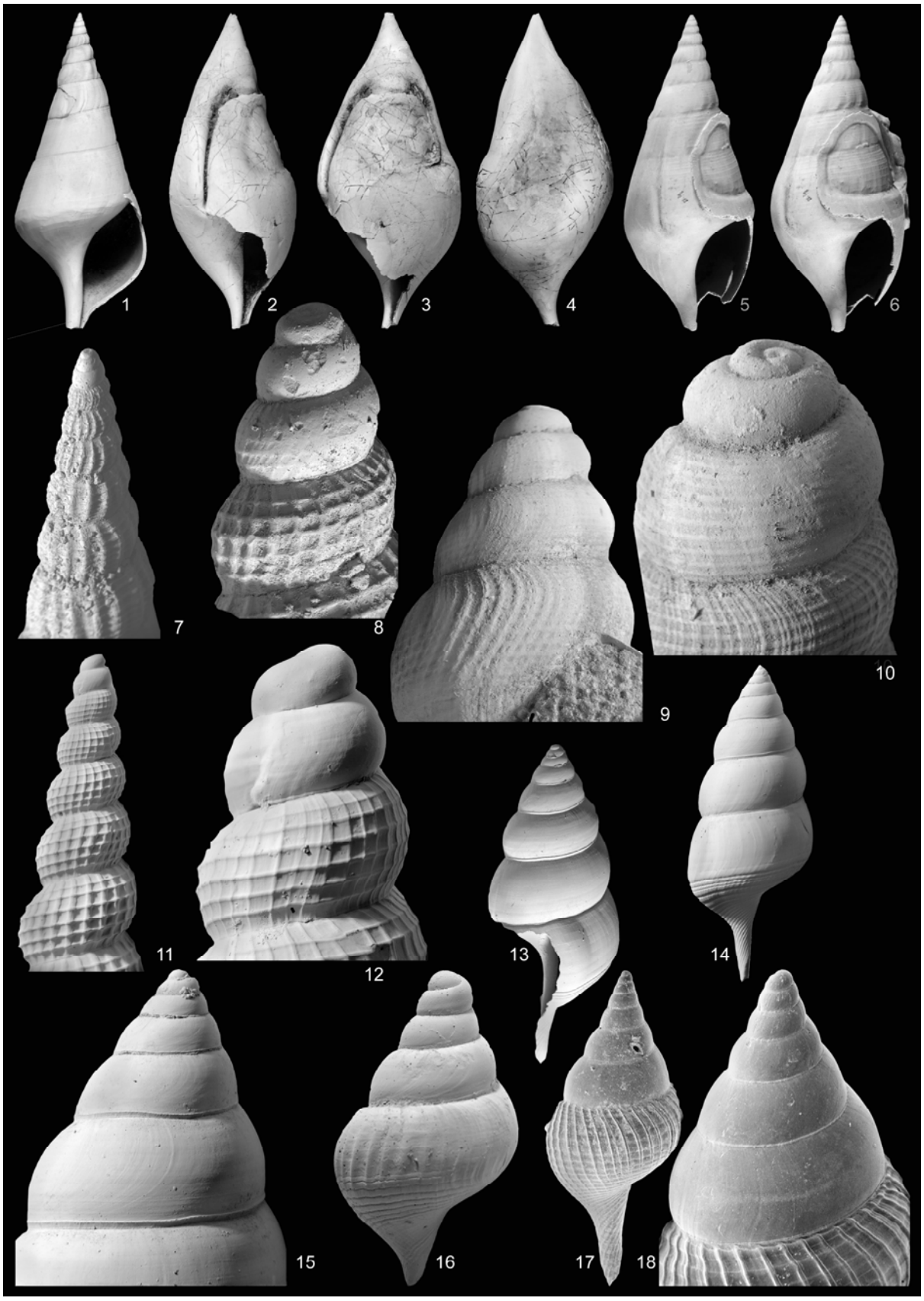
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Plate 5

All figures from *Strombus mutabilis* from the Gulf of Aqaba.

Fig. 1: Fully grown larval shell documenting several repaired shell fractures. Shell size about 1 mm.

Fig. 2: Fully grown larval shell with the operculum sealing the aperture, detail of inner lip in Fig. 3.

Fig. 3: The inner lip has a callus layer of scaly mineral pattern as may also be found on the inner lip of fully grown individuals.

Fig. 4: The embryonic shell has an ornament of fine tubercles and a similar pattern also continues onto the first larval whorls, with first growth line. Embryonic whorl about 0.15 mm wide.

Fig. 5: The embryonic whorl with about 0.15 mm in diameter is here better visible due to the growth line.

Fig. 6: On the second larval whorl ornament changes from granules to spiral lines, and the third larval whorl is attached on the whorl above. Visible height about 0.35 mm.

Fig. 7: The fully grown larva can close its shell with a large operculum (detail in Fig. 12). Shell about 1 mm high.

Fig. 8: A repair of the larval shell may have the shape of a selenizone, but that is an individual feature. This last whorl of the larval shell is about 0.4 mm high.

Fig. 9: The juvenile documents the allometric growth and also rapid decomposition of the larval ornament.

Fig. 10: The operculum of the juvenile with two whorls of the teleoconch resembles that of the adult in shape and function. Shell height 4 mm.

Fig. 11: As in Fig. 10 but with one more whorl and the apical part quite strongly corroded. Shell height 7mm.

Fig. 12: The early part of the operculum is rounded (about 0.05 mm in diameter), first larva growth is by crescent additions.

Fig. 13: Juvenile operculum of growth stage as in Fig. 10, about 2 mm long.

Fig. 14: Juvenile operculum as in Fig. 11

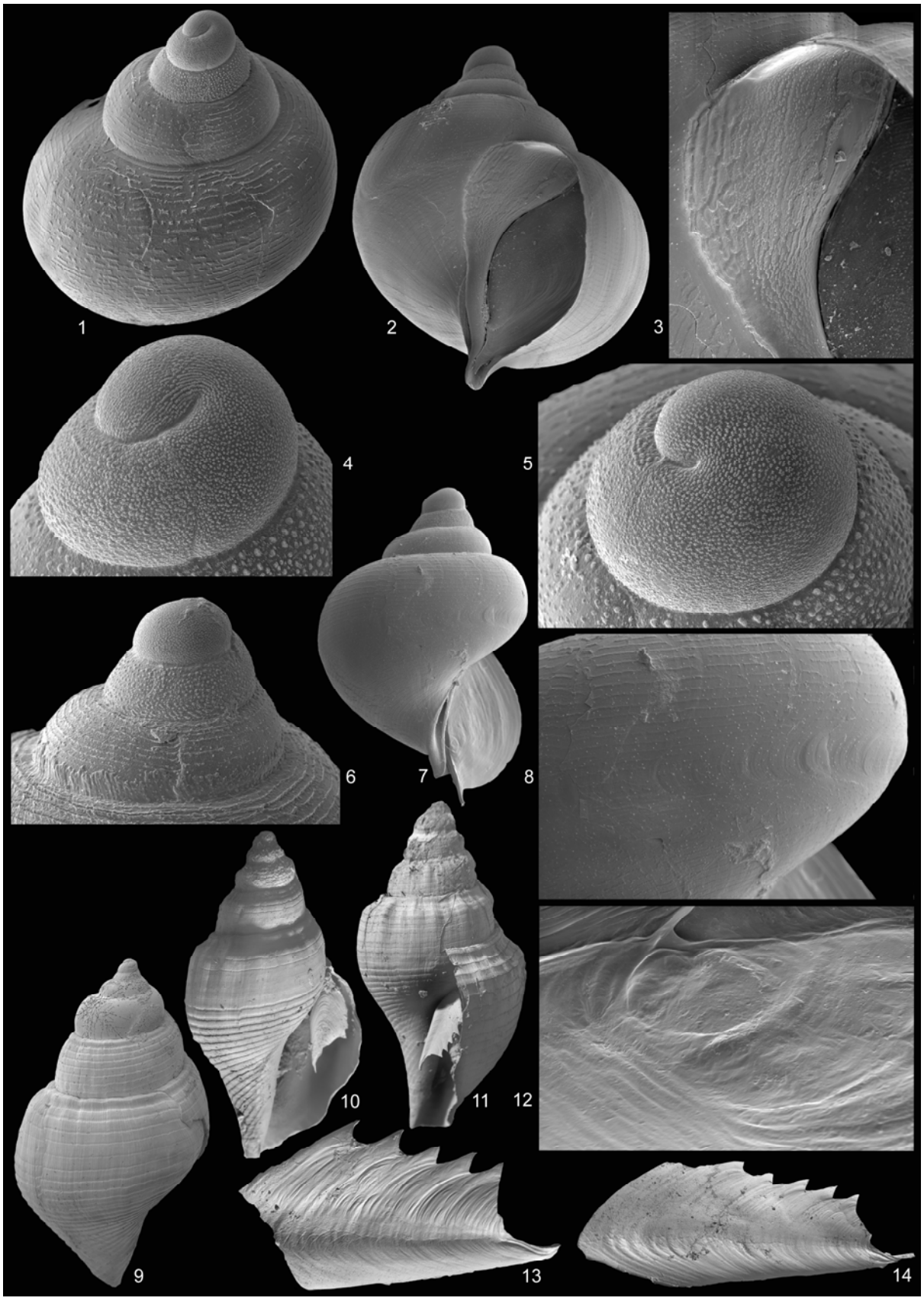
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Plate 6

All from figures represent *Strombus gibberulus* from the Gulf of Aqaba.

Fig. 1: Fully grown larval shell with about 0.9 mm in height.

Fig. 2: Larval shell, detail in Fig. 3, with about 0.9 mm in height.

Fig. 3: Embryonic whorl with 0.18 mm in diameter is distinct from larval whorl by first growth line.

Fig. 4: Transition from larval shell to teleoconch with larva about 0.7 mm in width.

Fig. 5: Early teleoconch with allometric growth and about 1.5 mm in height.

Fig. 6: Early teleoconch with first varix and 2 mm in height.

Fig. 7: Rounded varices occur in irregular pattern. Shell about 2,1 mm high.

Fig. 8: Ornament of the embryonic whorl is by short spirally arranged ribs with fishbone pattern. The shown shell portion measures about 0.07 mm.

Fig. 9: Ornament of the first larval whorls is coarse and partly consists of inclined short ribs. Shown section is about 0.3 mm high.

Fig. 10: The early veliger larva has a strong median projection of its outer lip. Shell height about 0.4 mm.

Fig. 11: Ornament changes from coarser pattern to finer granules on the third larval whorl and the operculum seals the aperture. Shell about 0.45 mm high.

Fig. 12: Ornament of the second larval whorls is tubercles and spiral ribs on the corner to the elongate base, and large angular apertural projection, about 0.4 mm high shell.

Fig. 13: The larval shell is commonly repaired and the fracture shows the irregular pattern as in the brittle shell.

Fig. 14: The inner lip of the almost fully grown larval shell is straight and the outer lip almost evenly rounded, with operculum fitting tightly.

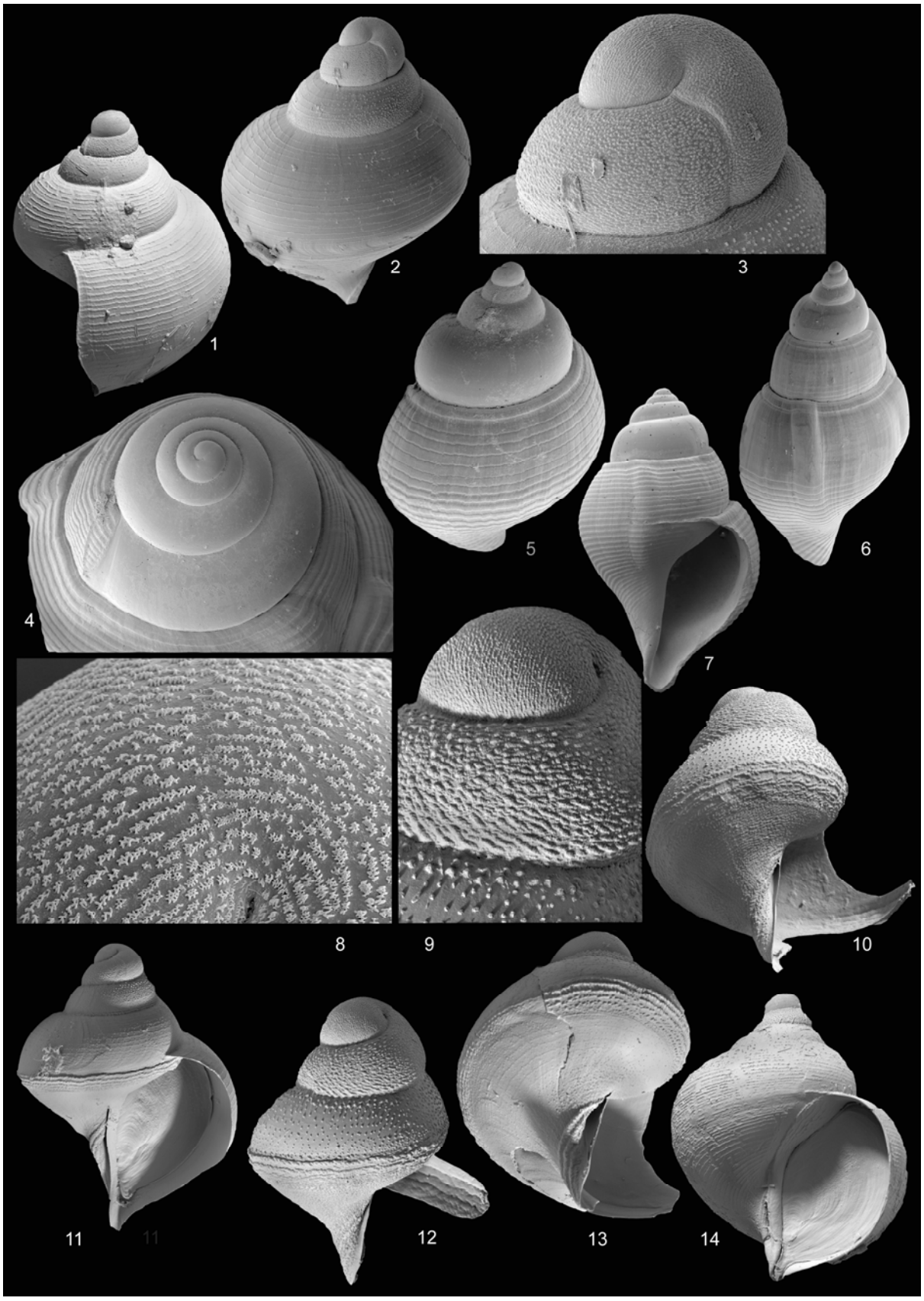
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Plate 7

Fig. 1: *Strombus* (*Austrostrombus*) *medinae* from the Miocene Navidad Formation of Chile.

Fig. 2: *Strombus* (*Austrostrombus*) *medinae* same as in Fig. 1 with about 90 mm high shell.

Fig. 3: *Strombus tricornis* from Port Sudan, Red Sea with juvenile shell shortly after begin of benthic life with wrinkled embryonic shell.

Fig. 4: *Strombus tricornis* from the Red Sea of the same type as in Fig. 3 with transition to the teleoconch. Shell almost 2 mm high.

Fig. 5: *Strombus tricornis* from the Red Sea after hatching rapidly calcifies the shell, which in fracture shows the mineral shell of well ordered crossed lamellae. About 1000x magnified.

Fig. 6: *Strombus tricornis* from the Red Sea at hatching from the spawn with still predominantly organic shell. About 1 mm high.

Fig. 7: *Strombus tricornis* from the Red Sea as in Fig. 6 with its organic shell with wrinkles. The shell is 0.9 mm high.

Fig. 8: *Strombus* cf. *coronatus* from the Messinian of Libya in apical view.

Fig. 9: *Strombus* cf. *coronatus* from the Messinian of Libya with apertural view, with its shell transformed from aragonite into gypsum. The shell is about 40 mm high.

Fig. 10: *Misritropis bartheli* from the Maastrichtian of the Western Desert in Egypt with shell height of 24 mm high and 20 mm wide.

Fig. 11: The holotype of *Misritropis bartheli* from the same locality as Fig. 10 is 35 mm high and 25 mm wide.

Fig. 12: *Orthaulax gabbi* DALL, 1890 from Chipola Formation, Blountstown, Florida with the shell 65 mm high.

Fig. 13: *Orthaulax gabbi* DALL, 1890 seen from the other side with the rounded thickening above the callus pad visible on its outer side.

Fig. 14: *Pelicaria vermis* with 0.9 mm wide protoconch and change into the striped teleoconch from New Zealand.

Fig. 15: The embryonic shell of *Pelicaria vermis* is 0.9 mm in diameter and without larval shell but gradational change into the teleoconch.

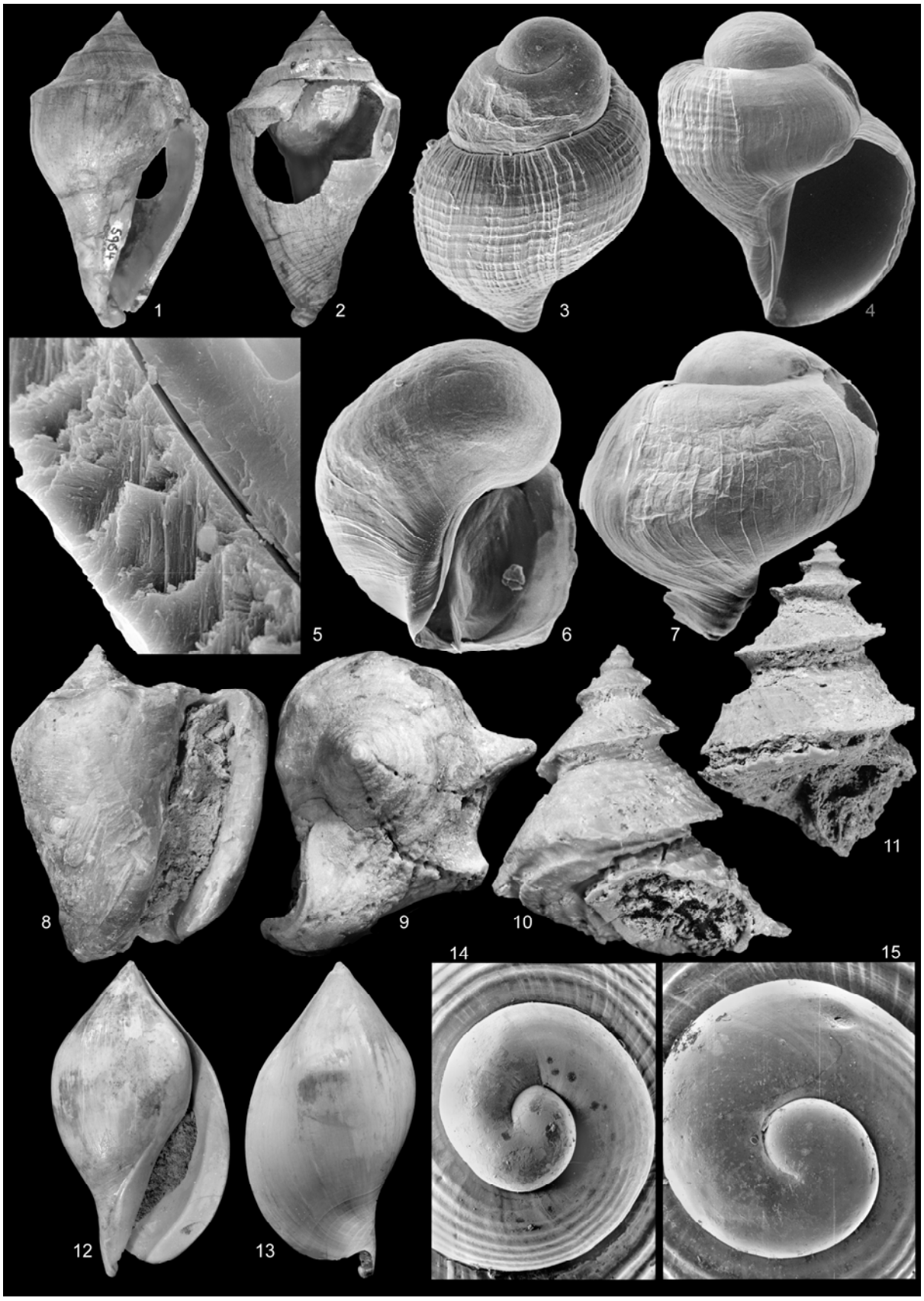
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Plate 8

All figures represent *Xenophora* from the Gulf of Aqaba.

Fig. 1: Juvenile shell of *Xenophora calculifera* from the Gulf of Aqaba at Aqaba, same as in Fig. 2. The shell is about 3 mm wide.

Fig. 2: The same as in Fig. 1 with the larval shell and the juvenile teleoconch with foraminifers attached to their periostracum.

Fig. 3: The fully grown larval shell with about 1 mm in diameter and the first part of the teleoconch that has irregular surface due to formerly attached particles.

Fig. 4: The larval shell of *Xenophora calculifera* seen from below with open umbilicus and wide siphon-like base of the aperture. Shell width 1 mm.

Fig. 5: Almost fully grown larval shell of *Xenophora calculifera* with wide apical sinus and almost 1 mm in width.

Fig. 6: The embryonic whorl of *Xenophora calculifera* is about 0.2 mm wide and ornamented by fine tubercles. Its margin is indicated by first growth lines.

Fig. 7: Juvenile shell of *Xenophora calculifera* with shell of about 6 mm in diameter.

Fig. 8: Same as in Fig. 7 with foraminifers and shell fragments agglutinated to the periostracum of the teleoconch.

Fig. 9: Embryonic and first larval shell of *Xenophora calculifera.*

Fig. 10: The aperture as a wide median lobe in the larval shell of *Xenophora calculifera* from the Gulf of Aqaba.

Fig. 11: The larval shell of *Xenophora calculifera* during growth has two deep rounded indentations at the sides of the median lobe of the outer lip. Shell diameter abut 1 mm.

Fig. 12: The embryonic whorl of *Xenophora calculifera* is about 0.2 mm wide and ornamented by fine tubercles. Its margin is here not indicated by first growth lines, as in case of Fig. 6.

Fig. 13: Fully grown larval shell of *Xenophora* from the Gulf of Aqaba with concentrated growth lines indicating long stay in the plankton. Shell size about 1 mm.

Fig. 14: Different species of a species of the Xenophoridae from the Plankton of the Gulf of Aqaba. The larval shell is 1.8 mm in diameter. Detail in Fig. 15.

Fig. 15: The detail to Fig. 14 with relatively flat apex and two keels on the flattened sides. The embryonic whorl is ornamented with rows of tubercles and 0.22 mm wide.

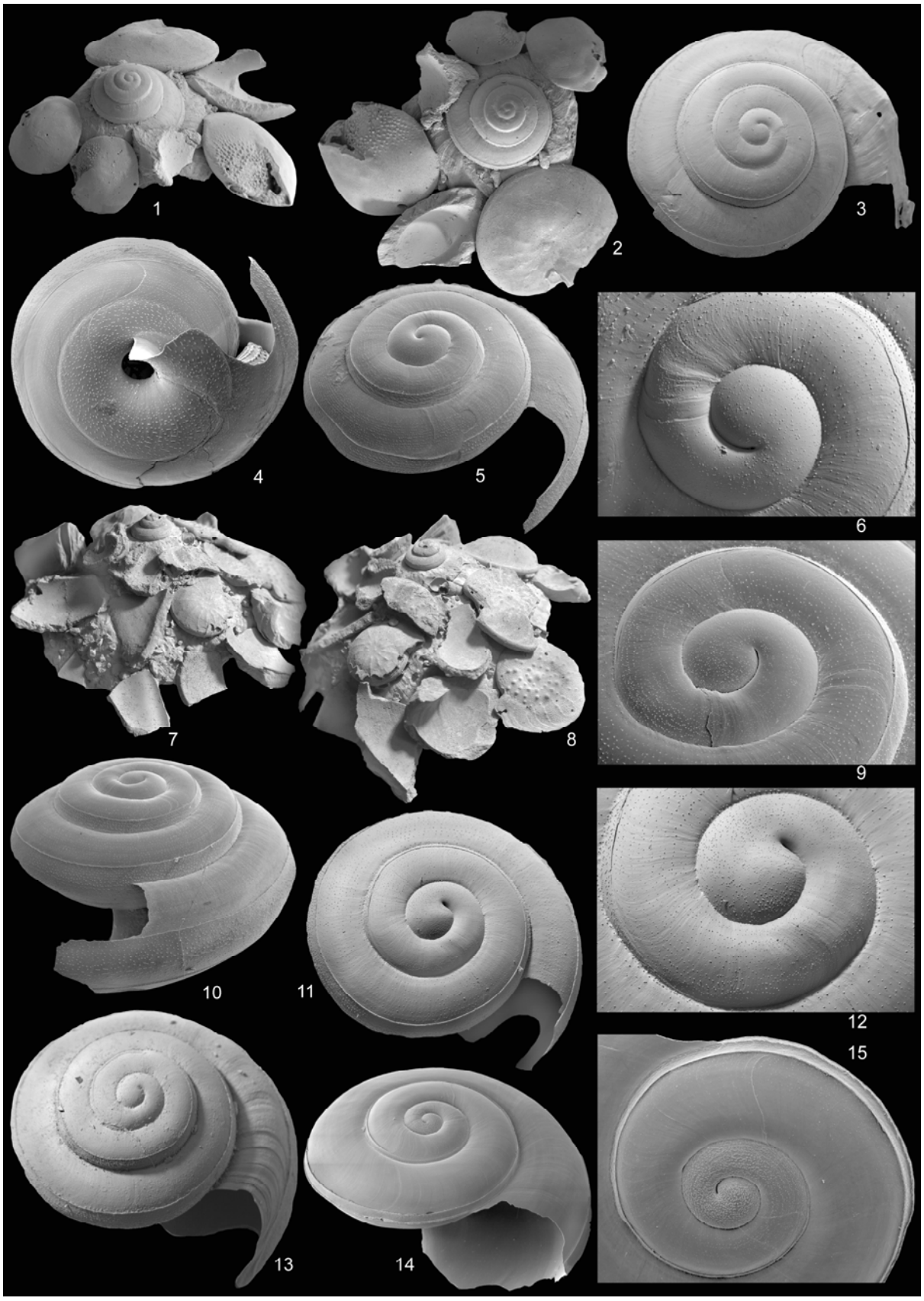
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Plate 9

Fig. 1: The larval shell of *Zygoceras aqabanensis* n. sp. with about 1 mm in diameter and details of the embryonic shell in Fig. 3 and of the margin of the last whorl of the larval shell in Fig. 2. Shell width 0.8 mm.

Fig. 2: *Zygoceras aqabaensis* from the Plankton of the Gulf of Aqaba at Aqaba with the thorn bearing keel on the corner of the last larval whorl, detail to Fig. 1.

Fig. 3: The embryonic whorl is about 0.25 mm wide and its transition into the larval shell is indistinct. Ornament changes from spiral ribs to elongate granules.

Fig. 4: *Zygoceras aqabaensis* with embryonic whorls and first larval whorl with ornament of spiral rows of granules.

Fig. 5: A different larval shell of *Zygoceras aqabaensis* with more distinct change from the embryonic into the larval shell documented by growth increments after the first whorl. Diameter of shell about 1 mm.

Fig. 6: *Zygoceras aqabaensis* with larval shell and the begin of the teleoconch. This specimen represents the holotype and measures about 1 mm in diameter.

Fig. 7: *Haloceras* sp. from the shallow Caribbean Sea at Santa Marta (Colombia) with the 0.2 mm wide embryonic whorl ornamented by granular spiral lines.

Fig. 8: *Haloceras* sp. from Santa Marta with the shell of a juvenile displaying the whole protoconch with change in ornament from two keels on the first larval whorls to sinuous axial ribs above the keels which ornament the projection of the outer lip on the larval shell. The shell is about 1 mm high.

Fig. 9: Ornamented shell of the half grown larva of *Xenophora* from the Gulf of Aqaba as in Figs. 10 and 11 that resembles that of the Haloceratidae. Width 0.75 mm.

Fig. 10: Larval shell from the Gulf of Aqaba of *Xenophora* as in Fig. 9 with one more whorl (0.75 mm wide) and more rounded final shape of the larval shell.

Fig. 11: Shell of *Xenophora* with very extended median lobe of its outer lip (0.8 mm in width of not fully grown larva.

Fig. 12: Juvenile *Xenophora* from the Eocene (Damery) of the Paris Basin with 1,2 mm wide protoconch.

Fig. 13: The same as Fig. 12 in apical view with teleoconch that had shells attached to its periostracum, with shell width 1.4 mm.

Fig. 14: *Xenophora leprosa* from the Campanian of Coffee Sand, Ripley Formation of Mississippi, shell about 4 mm wide.

Fig. 15: *Xenophora leprosa* from Ripley Formation, detail in Fig. 16

Fig. 16: *Xenophora leprosa* detail to Fig. 15 with the larval shell about 1.4 mm in width and shape a little higher than that of the living species from the Gulf of Aqaba.

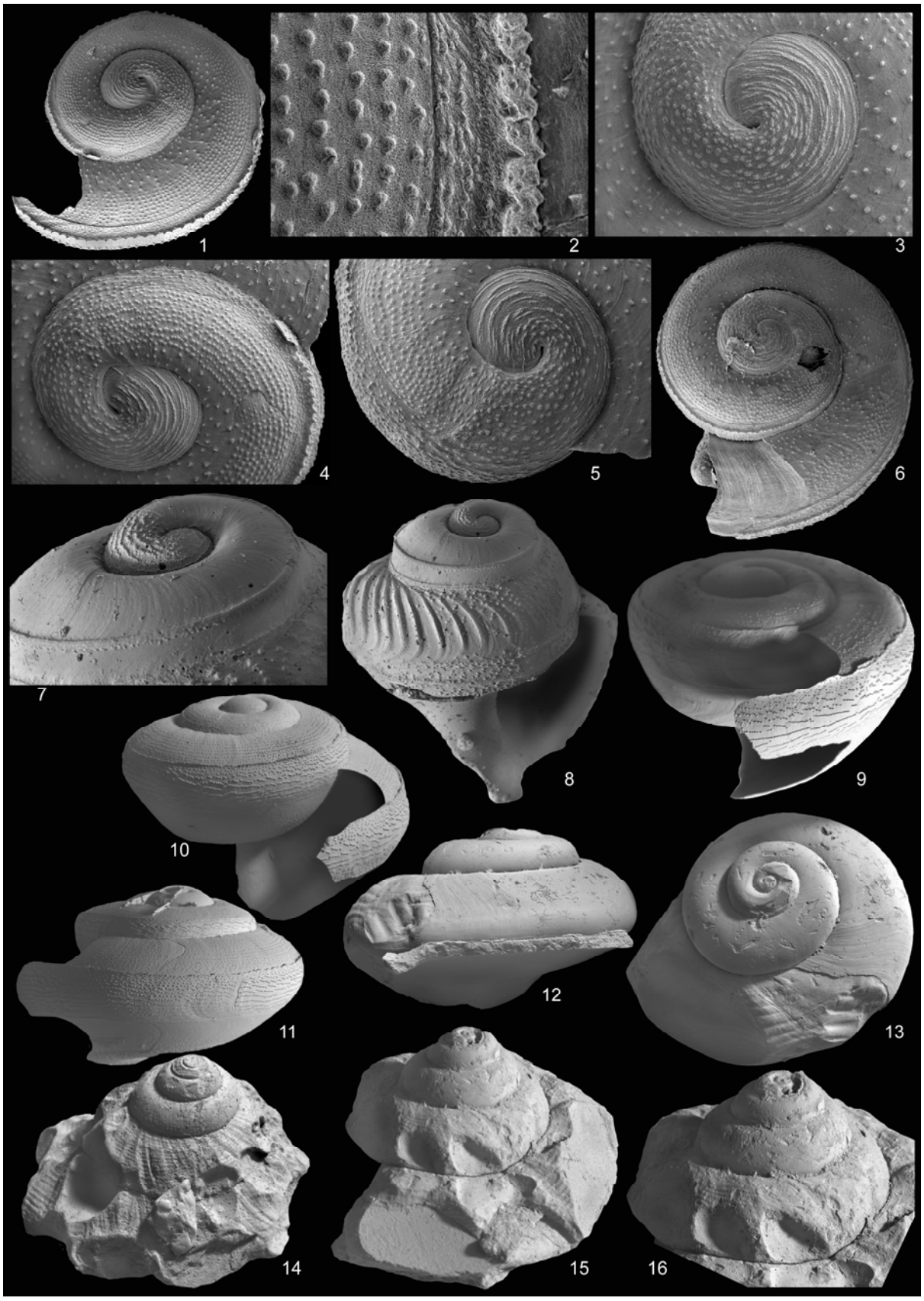
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Plate 10

Fig. 1: Radula of *Strombus gibberulus* from Aqaba with 2 mm wide ribbon.

Fig. 2: Ribbon of radula with 0.9 mm width of *Strombus mutabilis* from Aqaba.

Fig. 3: Radula of *Xenophora conchyliophora* from the Caribbean Sea at Santa Marta, Colombia with ribbon almost 1 mm wide.

Fig. 4: Ribbon of radula of *Aporrhais pespelicani* from the Mediterranean Sea near Banyuls-Sur-Mer with width of about 0.8 mm, detail of the central teeth in Fig. 9.

Fig. 5: Radula of *Strombus gigas* from Santa Marta, Caribbean Sea with the ribbon about 0.5 mm wide.

Fig. 6: Radula of *Strombus erythrinus* from the Red Sea at Port Sudan with ribbon about 1 mm wide.

Fig. 7: Half a radula ribbon of *Strombus tricornis* from the Red Sea at Port Sudan with the teeth of the radula worn by use, and about 0.4 mm wide ribbon section.

Fig. 8: Half a radula ribbon of *Strombus (Lambis) truncata* from the Red Sea at Port Sudan with the visible part of the radula rows about 0.5 mm wide.

Fig. 9: The central teeth of the radula of *Aporrhais pespelincani*, detail to Fig. 4.

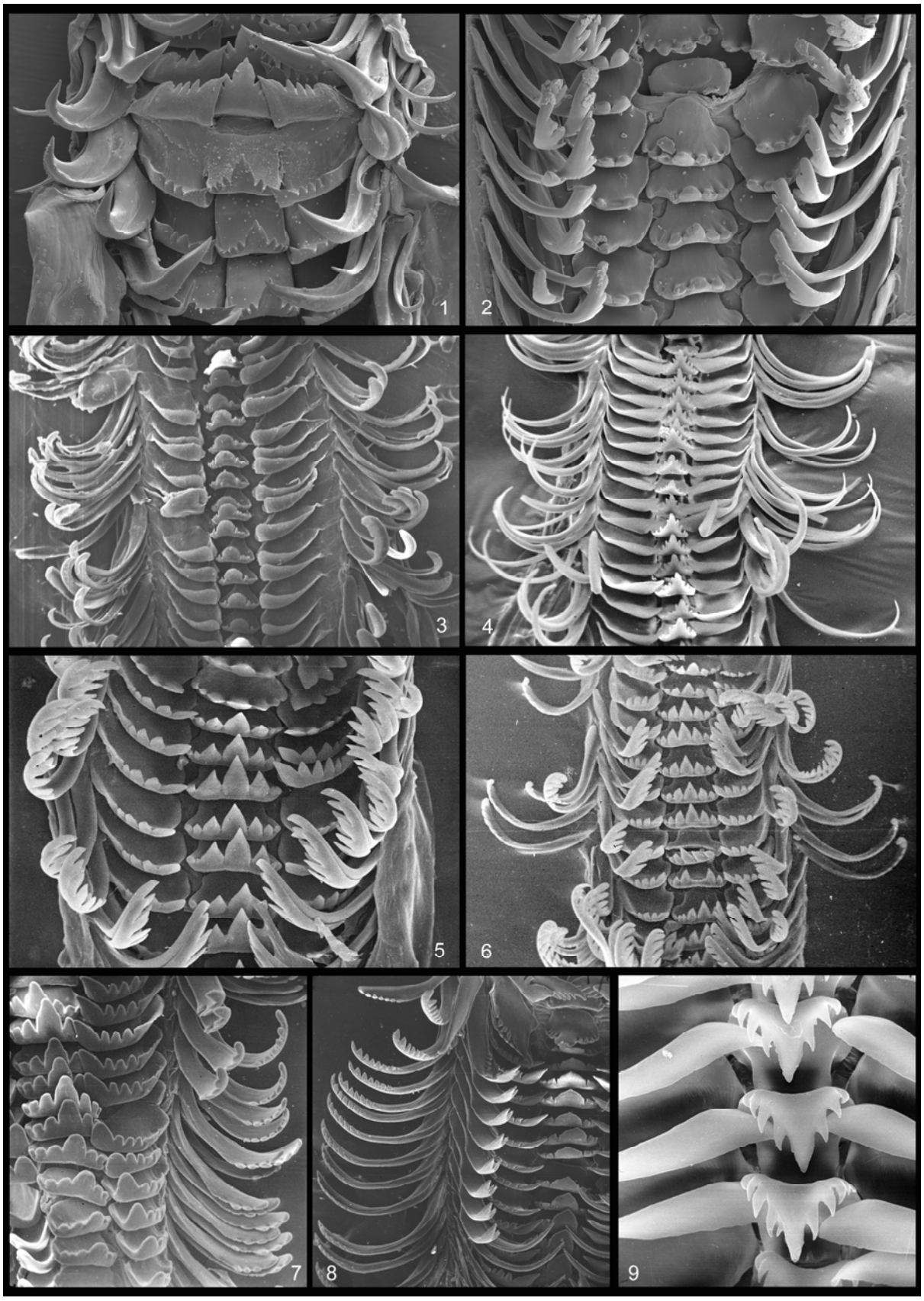
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Plate 11

Fig. 1: Adult shell of *Atlanta fusca* with about 2 mm in diameter from the Gulf of Aqaba.

Fig. 2: The fully grown larval shell of *Atlanta fusca* measures about 0.55 m in diameter and is ornamented with zigzag lines.

Fig. 3: The fully grown larval shell of *Atlanta turriculata* with the apical sinus and the large median lobe of the outer lip measures about 0.5 mm in height.

Fig. 4: Protoconch and early teleoconch of *Atlanta turriculata* with about 0.7 mm in size.

Fig. 5: Fully grown larval shell of *Atlanta helicinoides* measures about 0.6 mm in diameter.

Fig. 6: Protoconch of *Atlanta helicinoides* in its teleoconch with weakly mineralized keel and size of about 1.5 mm.

Fig. 7: Fully grown *Atlanta fusca* with about 1.5 mm in diameter.

Fig. 8: Adult shell of *Atlanta plana* measures about 2 mm in diameter.

Fig. 9: The transition of the larval shell into the teleoconch in *Atlanta plana*, with larval shell about 0.4 mm

Fig. 10: Larval shell of *Atlanta oligogyra* with indistinct transition to the teleoconch and 0.4 mm in width.

Fig. 11: Larval shell of *Atlanta plana* measures about 0.5 mm in width.

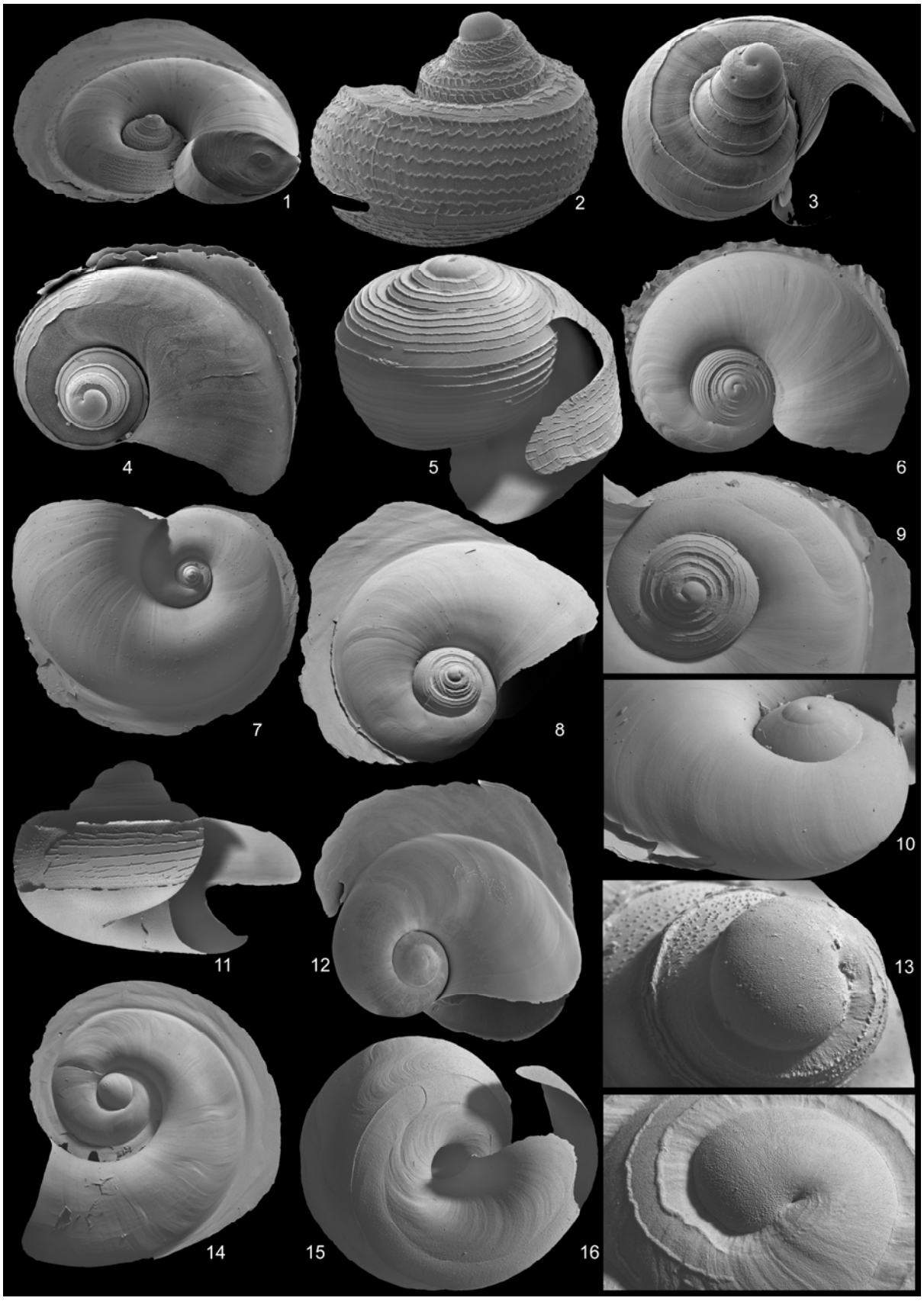
Fig. 12: Adult shell of *Atlanta oligogyra* is about 2 mm in diameter.

Fig. 13: The embryonic whorl of *Atlanta turriculata* with dense granular ornament and 0.1 mm in width.

Fig. 14: Adult shell of *Atlanta inclinata helicinoides* with 2.5 mm wide shell

Fig. 15: Larval shell of *Atlanta inclinata* with deep basal sinus and before begin of keel. The shell is about 0.7 mm wide.

Fig. 16: Embryonic whorl of *Atlanta helicinoides* is granulated and about 0.08 mm wide.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