

**Protoconch characters of Late Cretaceous Latrogastropoda
(Neogastropoda and Neomesogastropoda) as an aid in the reconstruction of the
phylogeny of the Neogastropoda**

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with 5 plates

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Abstract

Late Cretaceous Naticidae, Cypraeidae and Calyptraeidae can be recognized by the shape of their teleoconch, as well as by their characteristic protoconch morphology. The stem group from which the Latrogastropoda originated lived during or shortly before Aptian/Albian time (100–125 Ma).

Several groups of Latrogastropoda that lived at the time of deposition of the Campanian to Maastrichtian (65–83 Ma) Ripley Formation have no recognized living counterparts. These Late Cretaceous species include the Sarganoidea, with the families Sarganidae, Weeksiidae and Moreidae, which have a rounded and low protoconch with a large embryonic whorl. Sarganidae contains the subfamilies Sarganinae, Schizobasinae, Pseudecphorinae, and the newly defined Hippocampoidinae. The Weeksiidae resemble the modern Capulidae, except for their early ontogenetic shell. Moreidae, with subfamilies Moreinae and Pyropsinae, have a low, coiled protoconch with rounded whorls and a margin of the aperture that is not lobed. Similar protoconch shapes are found among modern Ficidae and Eratoidae of the Neomesogastropoda. Protoconchs of Eratoidae have developed as echinospira with additional scaphoconcha. Tonnoidea appear to be represented only by species resembling modern *Sassia*, but without the characteristic additional organic shell cover of their larval shell. Thus Eosassiidae, new family, is introduced based on *Eosassia*, new genus. Colombelloidea resemble *Neocolombellina*, new genus, and have a teleoconch similar to *Eosassia*, but with embryonic whorls that have tubercles. Mataxidae, new family, hold species connected to *Mataxa* and *Caveola*, with a similar larval shell, but with an embryonic shell with granules. The larval shell of Paladmetidae, with its shape and ornament of rectangles, resembles that of the Eosassiidae, new family, and Mataxidae, new family. Gyrotropidae, new family, are based on *Gyrotropis* and *Lirpsa*, have a protoconch that may have carried a scaphoconch, and resemble *Astandes* of the Trichotropidae.

The Late Cretaceous Pyrifusidae is divided into several subfamilies according to the shape of their teleoconch. Their larval shell resembles that of modern Neogastropoda with little ornament and a median lobe on the outer

lip of the aperture, as found among some Muricidae, Buccinidae and Conidae. However, they differ from them in having an indistinct and not thickened margin of their aperture as well as a gradational transition of larval shell into the teleoconch. Protoconch morphology of the Jurassic to Cretaceous Maturifusidae differs from that of the Cretaceous Latrogastropoda. Purpurinidae of the Triassic to Jurassic have a smooth protoconch and their relationships are unknown. The Jurassic Colombellinidae, in contrast, may represent the stem group to the Latrogastropoda. The Pyrifusidae may have derived from the same stem as Paladmetidae with regard to teleoconch shape, and may have given rise to modern groups of the Neogastropoda. Of these, some, such as the Volutidae, developed during the Late Cretaceous, while many families appeared during the Paleogene. Their fossil species regarding the shape of their teleoconch may be convergent to several taxa of modern Neogastropoda but they can be recognized by the characters of their protoconch.

Zusammenfassung

Spät-kretazische Naticidae, Cypraeidae und Calyptraeidae lassen sich mit Hilfe ihrer ausgewachsenen Schale erkennen, besitzen aber zudem auch eine charakteristische Gestalt ihres Protoconches. Die ursprünglichen Vorläufer der Latrogastropoda lebten kurz vor oder während des Apt/Alb vor 100–125 Millionen Jahren.

Mehrere Gruppen der Latrogastropoda, die während der Ablagerungszeit der Ripley Formation vom Campan bis ins Maastricht vor 65–83 Millionen Jahren lebten, haben heute keine lebenden Vertreter mehr. Zu diesen gehören die Sarganoidea mit den Familien der Sarganidae, Weeksiidae und Moreidae. Ihnen gemeinsam ist ein runder und niedriger Protoconch mit großer Embryonalwindung. In den Sarganidae sind die Unterfamilien der Sarganinae, Schizobasinae, Pseudecphorinae, und die neu begründeten Hippocampoidinae enthalten. Die Weeksiidae ähneln den heute lebenden Capulidae hinsichtlich der erwachsenen Schale aber nicht in Bezug auf die Gestalt der Schale des jungen Tieres. Moreidae mit den Unterfamilien Moreinae und Pyropsinae haben einen niedrig-gewundenen Protoconch mit gerundeten Windungen und einfachem nicht geschwungenem Rand der Mündung. Die heute lebenden Ficidae und Eratoidae der Neomesogastropoda besitzen eine ähnliche Gestalt ihres Protoconches. Die Eratoidae haben eine besondere Echinospira-Larve entwickelt, die eine zusätzliche äußere Schalenschicht, die Scaphoconcha, ausbildet. Unter den Tonnoidea der Kreide scheint nur eine Form der Larvenschale vertreten gewesen zu sein und diese ähnelt jener der heutigen *Sassia*. Auch fehlt noch die bei den heutigen Arten meist vorhandene zusätzliche von außen angefügte organische Schale der Larven. Daher wird hier die neue Familie Eosassiidae eingeführt, die auf der ebenfalls neuen Gattung *Eosassia* basiert. Colombellinidae einschließlich der neuen Gattung *Neocolombellina* besitzen ähnliche Gestalt der Adultschale wie *Eosassia*, haben aber eine Tuberkel-Skulptur der Embryonalschale. In der neu aufgestellten Familie Mataxidae sind Arten enthalten die mit *Mataxa* und *Caveola* in Verbindung stehen und ähnliche Larvenschale besitzen, aber eine mit körnigem Muster versehene Embryonalschale haben. Die Larvenschale der Paladmetidae hat die Gestalt und Musterung mit Rechtecken ähnlich jenem der neuen Familien Eosassiidae und Mataxidae. Die neue Familie Gyrotropidae gründet auf den Gattungen *Gyrotropis* und *Lirpsa*. Hier mag der Protoconch mit einer Scaphoconcha versehen gewesen sein und ähnelt jenem der jüngeren *Astandes* der Trichotropidae.

Die spät-kretazischen Pyrifusidae sind in mehrere Unterfamilien unterteilt, die sich hinsichtlich der Gestalt ihrer Erwachsenenachale voneinander unterscheiden. Ihre Larven-Schale ähnelt jener der heute lebenden Neogastropoda mit wenig Ornament und einem kräftigen Vorsprung der Außenlippe der Mündung, wie sie bei Vertretern der Muricidae, Buccinidae und Conidae anzutreffen ist. Allerdings unterscheiden sie sich von den heute lebenden Arten darin, dass der Rand ihrer ausgewachsenen Larvenschale nicht verdickt ist und sich nicht deutlich von jenem der ersten Jugendschale absetzt, sondern allmählich in die Schale der frühen Wuchsstadien der kriechenden Schnecke übergeht. The Gestalt der Protoconche der jurassischen und kretazischen Maturifusidae unterscheidet sich von jenem der kretazischen Latrogastropoda und eine Verwandtschaft beider Gruppen ist unwahrscheinlich trotz Ähnlichkeiten bei der Schale bei ausgewachsenen Individuen. Purpurinidae aus Trias und Jura besitzen einen glatten Protoconch und ihre Verwandtschafts-Verhältnisse bleiben unbekannt. Die jurassischen Colombellinidae könnten, im Gegensatz hierzu, die Stammgruppe der Latrogastropoda darstellen. Pyrifusidae lassen sich von der gleichen Stammgruppe herleiten aus der auch die Paladmetidae kommen. Die Gestalt ihrer ausgewachsenen Schale legt nahe, dass sich von ihnen heute lebende Gruppen der Neogastropoda herleiten. Unter letzteren entstanden etwa die Volutidae bereits während der späten Kreide, während die Vertreter der meisten Familien erst während des Alttertiärs in Erscheinung treten. Hinsichtlich der Gestalt ihres Teleoconches lassen sich Konvergenzen mehrerer Taxa moderner Neogastropoda mit solchen von Gruppen der Kreideschnecken feststellen, die sich aber oft dann auflösen lassen, wenn die Merkmale des Protoconches bekannt sind.

1 Introduction

Many families of the Neogastropoda have traditionally been recognized among Late Cretaceous species based on the morphology of their adult shell. The excellent preservation of shells from the Campanian and Maastrichtian Ripley Formation of Mississippi and Tennessee allowed us to examine the protoconch morphology of many of these taxa. For species with a planktotrophic veliger, comparisons with larvae of families of modern Latrogastropoda provide evidence for a relationship between fossil and recent taxa.

Based on comparisons of the morphology of their larval shells, we conclude that resemblances of the adult shells of many of these Cretaceous species to the adult shells of modern Neogastropoda and Neomesogastropoda are due to convergence. No species are recognized among Triassic and Jurassic Caenogastropoda that closely resemble species of Recent or Tertiary Latrogastropoda. Early Cretaceous gastropods represent a continuation of Jurassic forms. During the mid-Cretaceous Aptian-Albian, their character changes, as is noted and well documented in the morphology of their protoconch (BANDEL, 1993; SCHRÖDER, 1995).

WENZ (1938) suggested that the Neogastropoda did not appear prior to the Late Cretaceous, relying on data presented by HOLZAPFEL (1888) from the Aachen Greensand, STOLICZKA (1868) from the Indian Trichinopoly Formation, ZITTEL (1885), and WADE (1926) from the Ripley Formation in the USA. STEPHENSON (1952) recognized Fascioliidae (= Fusinidae), Volutidae, Cancellariidae from the Cenomanian Woodbine Formation of Texas. He also noted the presence of members of the Trichotropidae (*Lirpsa*), Naticidae (*Gyrodes*), Pyrifusidae (*Paleopsephaea*), Moreinae/Sarganinae (*Hillites*), and Volutoderminae (*Carota*). SOHL (1964) recognized most families of the Neogastropoda among the species of the Late Campanian to Early Maastrichtian Ripley Formation. The illustrations in the studies of SOHL (1960, 1964a, b) document very well the morphological transitions in teleoconch shape, for example, from *Sargana* to *Schizobasis* and to *Morea* and *Buccinulum*, and also from *Lupira* to *Colombellina*. TAYLOR et al. (1980) pointed out that similarities are closer among Cretaceous neogastropods than when Cretaceous and Recent taxa are compared. They concluded that the assignment of Late Cretaceous genera to Recent families was rather subjective.

RIEDEL (2000) elaborated on the suggestion of BANDEL (1993) that the Neogastropoda and Neomesogastropoda are derived from the same stock, and united them in the superorder Latrogastropoda. He assembled data on the living groups of the Latrogastropoda, discussed other classification schemes based on modern species, and proposed nine suborders on the basis of anatomical features, protoconch characters, as well as on paleontological evidence. A review of these nine groups, with special emphasis of the early ontogeny of their shells (protoconch morphology), reveals that some of these groups are well recognized among the fossil species from the Late Cretaceous, others less so, and still other groups not at all. Some Cretaceous species that appear to represent Latrogastropoda cannot be placed in any of the nine suborders. Others could be assigned to more than one, which is not unexpected, as all nine suborders of Latrogastropoda belonged to the same stem group during the Early Cretaceous. Some groups that have evolved since the Aptian–Albian have become extinct. Several of these extinctions occurred near the K/T boundary, where many groups of animals suffered a serious decline.

2 Palaeontology

Subclass Caenogastropoda COX, 1959

The shell has unidirectional coiling (mostly dextral) and an early ontogeny that includes the potential of producing a larval shell during a planktotrophic stage. Here the embryonic whorl is spirally coiled in the same direction as the larval shell and the teleoconch. The embryonic shell represents the shell that has been secreted before hatching from the egg-capsule (protoconch 1). In cases with planktotrophic development, most of the embryonic shell lacks growth lines. In contrast, the larval shell (protoconch 2) has growth lines which are usually distinguished from those of the teleoconch and differ from them in orientation. The larval shell often has a thickened aperture, and usually there is a change in growth line pattern, a change in general shape, as well as a change in surface sculpture in transition to the teleoconch. The larval shell may be missing in instances of secondary lecithotrophic development, when young are brooded in an egg capsule until hatching as crawling young. The existence of the Caenogastropoda can be traced with confidence to the Devonian (FRYDA, 1999; FRYDA et al., 2008; BANDEL, 2002).

Superorder Latrogastropoda RIEDEL, 2000

Latrogastropoda include the Neomesogastropoda and Neogastropoda. The protoconch of species with a planktotrophic larval stage has an embryonic shell of about 0.15 mm or larger (BANDEL, 1975), with the larval

shell exceeding in size that of the most other Caenogastropoda. Fossils species with such a protoconch have not been recognized before Aptian-Albian time.

Order Neomesogastropoda BANDEL, 1993

The larval shell is commonly ornamented by regular axial and spiral ribs crossing each other to form a net-like pattern. This ornament may not be present on the entire larval shell, but is often present, at least in traces, on the early larval whorls. Commonly, the larval shell has a smooth simple, rounded margin of the aperture, as in Calyptraeoida, Capuloidea, Tonnoidea, Naticoidea, but a median projection in the outer lip may also be present, as in the protoconch of Cypraeidae and Ovulidae.

The Neomesogastropoda were subdivided by RIEDEL (2000) into the suborders Naticina RIEDEL, 2000 (Naticoidea), Simrothina BANDEL & RIEDEL, 1994 (Cypraeoidea and Lamellarioidea), Troscelina BANDEL & RIEDEL, 1994 (Laubierinoidea and Calyptraeoida), Cassina RIEDEL, 2000 (Tonnoidea) and Ficina RIEDEL, 2000 (Ficoidea). RIEDEL (2000) based his classification on fossil evidence as well as on anatomical and molecular data from living species. Most species of these groups are carnivorous, but some have a filter feeding mode of life.

Suborder Naticina RIEDEL, 2000 Superfamily Naticoidea GUILDING, 1834 (Pl. 1, figs 3–7)

The shell is usually wider than high, has a flattened spire, and a sculpture of delicate spiral lines crossed by inclined growth lines, or is smooth. The body whorl is large. The protoconch is rounded in shape, of large size, has an umbilicus, and a characteristic sculptural pattern on the larval whorls. The embryonic shell usually has tubercles that may be arranged in spiral rows. The larval shell may be 1 mm in diameter, with delicate, but distinct spiral ridges and axial ribs, but may be smooth on the last half whorl. The aperture is rounded and simple. The operculum grows in a spiral with the nucleus in a central position in the young larva, and is shifted slightly to the left in the late larva. The species are usually sand burrowing, carnivorous, and drill the shells of their prey.

Family Naticidae GUILDING, 1834 Subfamily Gyrodinae WENZ, 1938 (Pl. 1, figs 1–2)

The rounded shell has a flattened spire and smooth or delicate spiral ornament of lines crossed by inclined growth lines. The body whorl with more or less wide umbilicus is without umbilical ridge (free of callus) (WENZ, 1938). It may have a tongue-like callus (POPENOE et al., 1987). The protoconch of *Gyrodex* (*Dockeryella*) *major* has 2.25 whorls and an indistinct transition into the teleoconch (DOCKERY, 1993). Drilling mode of food collection was documented from Late Santonian Umzamba Formation of South Africa (KIEL & BANDEL, 2003), where *Gyrodex* (*Dockeryella*) *rennei* KIEL & BANDEL, 2003, hunted Turritellidae.

Remarks: The living Naticoidea represent a quite uniform group in regard to their mode of life and their shell morphology/architecture. A special development occurs only in the Sininae WOODRING, 1928, which have a flattened shell with a broad aperture that is too small to enclose the animal. The protoconch of all species with planktotrophic larvae are similar in shape and sculptural patterns (BANDEL, 1999; RIEDEL, 2000).

Superfamily Cypraeoidea RAFINESQUE, 1815 (Pl. 1, figs 8–13)

The shell is convolute, with last whorl completely surrounding and enclosing all other whorls, resulting in a characteristic cowry shell shape. The larval shell (protoconch 2) has a reticulate pattern of ribs intersecting to form rectangles in the case of Cypraeidae and rhomboids in the case of Ovulidae. The embryonic whorl (protoconch 1) has ornament of a groove- ridge pattern. Only the Cypraeidae were traced into the Cretaceous.

Remarks: Suborder Simrothina BANDEL & RIEDEL, 1994, in RIEDEL (2000) included Cypraeoidea and Lamellarioidea. Only Cypraeoidea have a fossil record that extends back into the Mesozoic. No fossil species of

the other superfamilies are known from the Cretaceous or older strata. Cowry shells have been present since the beginning of the Late Cretaceous (WENZ, 1938), and also in the South African Umzamba Formation (KIEL & BANDEL, 2003, figs 4, 7–8). The characteristic shell of the Cypraeidae has changed little since their first appearance in the Cenomanian (ANDERSON, 1958). *Cypraea* and *Ovula* have their first occurrence in the fossil record during the Late Cretaceous (GROVES, 1990). *Bernaya* (*Protocypraea*) *mississippiensis* GROVES, 1990, from the Campanian Coffee Sand of Mississippi has a larval shell ornamented by rectangles that are still visible on its spire through the enveloping outer whorl (DOCKERY, 1993: pl. 21, figs 1–3). The rhomboidal larval sculpture of the Ovulidae is known only from the Paleocene onwards.

Superfamily Calyptraeioidea LAMARCK, 1809
(Pl. 1, figs 14–18)

The shell of the suspension feeding limpets is cap-shaped with the outer lip continuous and circling around the entire base. The shell rests on hard substrate, with the inner lip above the basal rim, which is reduced in size and may be totally absent. The operculum is usually lost during ontogeny. The protoconch is large, about as wide as high, with rounded whorls, a straight outer lip of its aperture, sculpture of axial and spiral lines (Hipponicidae, TROSCHER, 1861), and is simplified, with a very delicate pattern of spiral lines or spiral rows of tubercles in the Calyptraeioidea. TROSCHER (1861) and CERNOHORSKY (1968) placed both families in the same superfamily Calyptraeioidea, which was discussed and accepted by BANDEL & RIEDEL (1994) and RIEDEL (2000). Most species are filter feeders and have become functional limpets.

Thylacus CONRAD, 1860, based on *Thylacus cretaceus* CONRAD, 1860, from Ripley Formation has a large protoconch that lies in the posterior part of the limpet shell. The protoconch consists of three whorls, spanning 1.1 mm in diameter, after which the shell expands to assume a limpet shape (DOCKERY, 1993: pl. 18, figs 1–4). The embryonic shell measures about 0.13 mm across and shows a groove ridge pattern. The larval whorls are set with numerous, very fine, spiral lines and axial folds. The juvenile teleoconch has its outer lip of the aperture closing and its inner lip transformed into a crescent ridge. When fully developed the muscle support is horse-shoe shaped and the shell elongate, low, and cap-like. The species lived as some modern *Crepidula*, attached to shells carried by hermit crabs.

Members of the Calyptraeidae are recognized by their characteristic teleoconch as well. *Calyptraea primogenita* KIEL & BANDEL, 2003, from the Late Santonian Umzamba Formation of South Africa (KIEL & BANDEL, 2003: figs 4, 14–16) is very similar to *Calyptraea laevis* (PHILIPPI, 1887) from the Maastrichtian from Quiriquina Formation of Chile (BANDEL & STINNESBECK, 2000: pl. 1, C) and *Calyptraea lybicus* QUAAS, 1902, from the Maastrichtian of the Ammonite Hills of Egypt (BANDEL & RIEDEL, 1994: pl. 7, figs 2–3).

Superfamily Capuloidea FLEMING, 1822

The larval shell is a gelatinous echinospira with a soft organic cover around the calcareous protoconch. Included are the families Capulidae and Trichotropidae as well as the newly defined Gyrotropidae n. fam.

Family Gyrotropidae n. fam.
(Pl. 2, figs 1–4)

Diagnostic characters: The shell has a short spire, rapidly expanding whorls, and sculpture consisting of a sharp spiral keel, a nearly quadrate aperture with a smooth inner lip, and a sinuous umbilicus. The body whorl has two additional keels that are covered by succeeding whorls (WENZ, 1938: fig. 2624). The family is based on the genus *Gyrotropis* with the type species *Gyrotropis squamosa* GABB, 1876, from the Ripley Formation. This species has nearly two rounded protoconch whorls, with uniform, fine tubercles on a smooth surface, and a ridge above the suture. The first whorl measures about 0.3 mm in diameter. The second whorl has a median, spine-like projection of the outer lip. The ornament, size and construction of the protoconch present evidence for a larval stage in the ontogeny of the type species of the family.

The protoconch is about 0.6 mm high. *Gyrotropis* occurs in the Coffee Sand member, Ripley Formation (DOCKERY, 1993: pl. 17, figs 11–12) and had been named *Trichotropis squamosa*. The presence of tubercles on the protoconch indicates that it had not been enclosed in a gelatinous echinospira as is the case in modern Trichotropidae, in which the larval shell surface is smooth and lacks a median projection of the outer lip.

Remarks: *Lirpsa* STEPHENSON, 1952, from the Cenomanian of Texas (STEPHENSON, 1952: pl. 36, figs 4–7) was placed in the Trichotropidae GRAY, 1850, and resembles *Trichotropis mississippiensis* SOHL, 1960, which is

similar to *Gyrotropis squamosa*, but differs by having numerous fine spiral lines between its keels (SOHL, 1960: pl. 10, fig. 22). *Lirpsa* is based on *Lirpsa cornuata* STEPHENSON, 1952, from the Cenomanian Woodbine Formation of Texas. Its protoconch is unknown. It differs slightly from *Lirpsa garudamangalami* BANDEL, 2000, from the Santonian to Campanian Trichinopoly group, Kulakkalnattam Formation of southern India in having a narrower umbilicus (BANDEL, 2000).

Pl. 2, figs 5–6

Trichotropidae GRAY, 1850, are recognized with *Astandes nodosus* (DOCKERY, 1993) from Coffee Sand of Mississippi. *Astandes* is based on its type species, *Astandes densatus* WADE, 1917, from Ripley Formation (WENZ, 1938: fig. 2622). DOCKERY (1993) reported a species (as *Cerithioderma nodosa*) from the Coffee Sand that was similar in shape to *Astandes*, but which also resembled *Cerithioderma* CONRAD, 1860, a genus from Alabama with a Middle Eocene type species.

Astandes nodosus has the oval aperture extended to form a short, anterior canal that is deflected to the left. The shell of the teleoconch has a sculpture of axial ribs and spiral lines. The protoconch consists of almost three whorls that measure about 1 mm in height and width. The rounded embryonic whorl is about 0.15 mm wide and lies in the nearly planispiral first smooth whorl of the larval shell. The second larval whorl is sculptured by rectangles formed of spiral cords crossed by collabral ribs. The beginning of the teleoconch is indistinct as the spiral ribs of the protoconch continue into the ribs of the teleoconch (DOCKERY, 1993: pl. 17, figs 13–15, pl. 19, fig. 4).

KAIM (2004) interpreted *Astandes* WADE, 1917, to be related or even synonymous to *Maturifusus* SZABO, 1983, which has a similar teleoconch shape, but quite a different protoconch (SCHRÖDER, 1995; GRÜNDEL, 2001; KAIM, 2004; BANDEL, 2006). The Jurassic to Early Cretaceous Maturifusidae GRÜNDEL, 2001, have been interpreted to represent members of the stem group of the Neogastropoda (RIEDEL, 2000; KAIM, 2004), while the Late Jurassic to Early Cretaceous Colombellinidae FISCHER, 1884, were thought to give rise to the Cypraeidae and Tonnidae (SCHILDER, 1927; WENZ, 1938). Maturifusidae are based on the Jurassic genus *Maturifusus*, while *Astandes* is based on a type species from the Late Cretaceous Ripley Formation.

Superfamily Sarganoidea STEPHENSON, 1923

The shell is usually wider than high in the posterior portion of the shell, has a flattened spire and sculpture of spiral cords that may be crossed by inclined axial ribs that are increments of growth. The body whorl is large and the aperture has an anterior siphon that may be long, short, straight, inclined, reduced or even absent. The shell has an umbilicus that is often surrounded by prior canals of the siphon and is not covered by the callus of the inner lip. The protoconch is large, rounded in shape, usually with low whorls, and may be smooth or ornamented by granules on a smooth background. The embryonic shell is of more than 0.15 mm in width. The aperture of the larval shell is rounded and simple without a median lobe. Included in the superfamily are the Sarganidae, with a rounded shell and a short siphonal canal; the Weeksiidae, with angular whorls and lacking a siphonal canal; and the Moreidae, with a higher shell and a straight siphonal canal.

Family Sarganidae STEPHENSON, 1923

The shell shape is that of a low-spire, with low, conical, anterior whorls and a constricted, prominent umbilicus. The aperture is drawn out to form a short, narrow, curved siphonal canal. A posterior notch of the aperture is connected to a narrow canal, which leaves behind a scale bearing collar below the suture during shell growth. Sculpture consists of axial and spiral elements, commonly of equal width, that often produce a granular to tubercular pattern. The protoconch is low, spiral in shape, and consists of two or more whorls (BANDEL & DOCKERY, 2002). The subfamilies Sarganinae, Pseudecphorinae, Schizobasinae and Hippocampoidinae, new subfamily, compose the family. No representatives are known from younger strata beyond the Cretaceous-Tertiary boundary.

Pl. 2, figs 8–10

Sarganinae STEPHENSON, 1923, have a shell with whorls constricted in anterior position and an aperture that is notched at its posterior end and drawn out in the anterior to form a narrow, curved siphon. The collar below the suture appears on the first whorls of the teleoconch. *Sargana* STEPHENSON, 1923, has protoconch whorls that are well rounded, with little overlap at their margins (SOHL, 1964a; BANDEL & DOCKERY, 2001). *Praesargana* SAUL & POPENO, 1993, with the type species *Trophon condoni* WHITE, 1889, comes from the Californian Chico

Group, Turonian (SAUL & POPENOE, 1993: figs 27–37) and *Praesargana tupeloensis* BANDEL & DOCKERY, 2001, from Ripley Formation. They are ornamented by spiral cords crossed by collabral ribs, and have a raised and rounded ribbon below the suture.

Schizobasinae BANDEL & DOCKERY, 2002, have a low shell with a rounded to depressed, *Nerita*-like shape, a strong basal constriction, and an open umbilicus that is surrounded by a ridge formed by the termini of previous siphons. The protoconch has a low, spiral shape with rounded and smooth whorls. The aperture of the teleoconch is notched at its posterior end and has rounded outer and inner lips, the latter with an anterior ridge. A deep, narrow siphonal canal is twisted toward the umbilicus (BANDEL & DOCKERY, 2002: figs 51–53). The subfamily is based on the genus *Schizobasis* WADE, 1916, from Ripley Formation, which has strong sculpture of spiral rows of nodes (SOHL, 1964a: pl. 20, figs 27–30, 33–34; BANDEL & DOCKERY, 2002: fig. 52), and also includes *Hillites* STEPHENSON, 1952, from the Cenomanian Woodbine Formation in Texas, with spiral ribs, as well as *Natalites* BANDEL, 1999, from the Umzamba Formation of South Africa, with sculpture limited to growth increments.

Pl. 2, figs 11–12.

Pseudecphorinae BANDEL & DOCKERY, 2002, have a shell nearly shaped like a pile with anterior whorls constricted and with a hollow spindle. The aperture is indistinctly notched at its posterior end, and has a concave inner lip with a strong siphon fold at the base forming a weakly curved siphonal canal. The umbilicus is surrounded by a keel formed by the termini of previous siphons. Sculpture consists of few, strong, spiral ribs and weak growth lines. The protoconch is low, with rounded, smooth whorls and measures almost 1 mm in diameter. The type genus is *Pseudecphora* BANDEL & DOCKERY, 2002, based on *Pseudecphora proquadricostata* (WADE, 1917) from Ripley Formation. The type species has a shell of about five whorls, with a low, acute spire and a large protoconch (about 1 mm) with low spire and smooth rounded whorls (SOHL 1964a: pl. 19, figs 1, 5). The protoconch of *Pseudecphora* sp. from Coffee Sand in Mississippi consists of only two whorls, rather than three as in the species from Coon Creek (BANDEL & DOCKERY, 2002: pl. 2, figs 39–41).

Trigonostoma riplejana SOHL, 1964 (SOHL 1964a: pl. 44, figs 25, 27) was originally interpreted to represent a member of the Cancellariidae GRAY, 1853, based on similarity to the living *Trigonostoma* BLAINVILLE, 1827, from the Pacific. It is almost identical with *Blackdownia acuticarinata* (RENNIE, 1930) from Santonian-Campanian Umzamba Formation of South Africa, which has a low, rounded protoconch consisting of one nearly planispiral whorl (0.7 mm wide) (KIEL & BANDEL, 2003: figs 4, 9–13). This protoconch resembles that of *Pseudecphora*, while its teleoconch is more elongate. *Blackdownia* Kollmann, 1976, was based on *Murex quadratus* SOWERBY, 1823, from the Albian of southern England. The aperture of a fully grown individual of the very similar *Blackdownia kollmanni* KIEL & BANDEL, 2003, from the lower Campanian Umzamba Formation, has tubercles on the inner side of its outer lip.

Subfamily Hippocampoidinae n. subfam.

Diagnostic characters: The shell of Hippocampoidinae consists of tightly coiled whorls, has a short spire with a peripheral keel, and a large body whorl with a narrow siphonal canal. The aperture is higher than wide, with short anterior canal and a notch at its apical end. The protoconch is low, almost planispiral, and consists of rounded, smooth whorls. The type genus is *Hippocampoides* WADE, 1916, (type species *Hippocampoides serratus* WADE, 1916) from Ripley Formation, which has whorls with a spine bearing peripheral keel and an umbilicus surrounded by a keel that consists of growth increments.

Remarks: *Hippocampoides* resembles the modern *Thalassocyon* BARNARD, 1960, (type species *Thalassocyon bonus* Barnard, 1960) from deep water off South Africa, which has sculpture consisting of strong spiral ribs (BEU, 1969). All known species of *Thalassocyon* live in the deeper waters of the southern Hemisphere (BEU, 1969; WARÉN & BOUCHET, 1990; RIEDEL, 1994, 2000). The family Thalassocynidae was introduced by RIEDEL (1994) to characterize a primitive branch of the Ficoidea MEEK, 1864.

Family Weeksidae SOHL, 1960 (Pl. 2, figs 13–15)

The flatly coiled teleoconch with marginal corner of angular shape is connected to a simple, low, coiled protoconch with smooth, rounded whorls. The aperture is angular and wide, with the outer lip forming a sinus between the angulations. The family is based on *Weeksia* STEPHENSON, 1941, of Ripley Formation in Tennessee and Mississippi. *Lowenstamia* SOHL, 1964, can be included as well, even though the aperture extends into an

open, v-shaped anterior siphon. The protoconch of *Weeksia amplificata* (WADE, 1926) consists of 2.5 whorls, is 0.7 mm in width and height, with the embryonic whorl 0.19 mm wide and barrel-like. The two rounded and smooth larval whorls have a slightly inclined position with respect to the planispiral coil of the teleoconch (BANDEL, 1988: pl. 2, fig. 7, pl. 5, fig. 8). *Lowenstamia funiculus* SOHL, 1964, from Coffee Sand of Mississippi has an erect protoconch with several smooth and rounded whorls, and a teleoconch aperture that is wide and has a short, open, v-shaped siphon (SOHL, 1964a: pl. 21, figs 10, 14–15, 18–20, 22, 25).

Family Moreidae SOHL, 1964

The shell is pyriform to broadly fusiform with a short to long siphon. The protoconch is low, consists of few rounded and smooth whorls that are 1.8 mm in height and have a smooth, simple margin. The subfamilies Moreinae SOHL, 1964, and Pyropsinae STEPHENSON, 1941, are included.

Moreinae have a shell with a low spire that is ovate to almost round in shape, with a short canal of the siphon and an adjacent groove as a pseudo-umbilicus. Sculpture consists of intersecting strong spiral ribbons and slightly weaker radial ribs. The aperture bears a posterior canal or notch between the body whorl and the rounded outer lip. The inner lip has one or more strong oblique folds immediately above the siphon. The protoconch consists of several whorls and is globular or ovate, with a smooth surface and a straight outer lip. *Morea* CONRAD, 1860, with its type species from Ripley Formation, *Paramorea* WADE, 1917, and *Buccinopsis* CONRAD, 1857, are included in Moreinae.

The egg-shaped protoconch of *Morea marylandica* GARDNER, 1916, has a flattened apex and 3.8 smoothly rounded whorls. Its embryonic whorl measures about 0.2 mm in diameter and has scattered tubercles on a smooth background. The larval aperture has a simple, straight outer lip and a short projection into the anterior notch of the siphon. The onset of the teleoconch is rather abrupt, marked by the formation of a siphon. Spiral ridges present the main sculpture of which only traces are still present on the last larval whorl (BANDEL & DOCKERY, 2002: figs 42–44). A similar ornament may be noted on the larval shell among some Stromboidea (BANDEL, 2007: pl. 1, figs 12, 14, pl. 4, fig. 10).

Paramorea lirata WADE, 1917, from the Ripley Formation has a sculpture of raised spiral ribbons (SOHL, 1964a: pl. 19, figs 2–4, 6, 8, 10). Its protoconch has three whorls, which are smooth and well rounded, 0.8 mm wide and about 1 mm high. The embryonic whorl measures about 0.18 mm in width. The larval whorls are rounded and bear delicate growth lines that reflect a slightly sinuous outer lip with a low lobe near the anterior edge. *Buccinopsis* (= *Seminola* WADE, 1918), has the type species *Buccinopsis perryi* CONRAD, 1857, from Texas that has strong axial ribs, while *Buccinopsis solida* (WADE, 1917) from the Ripley Formation (SOHL, 1964: pl. 22, figs 4–7), is very similar to *Morea*, differing from it by a less developed pseudo-umbilicus.

Pyropsinae STEPHENSON, 1941 (Pl. 2, figs 16–18)

Pyropsinae have their fusiform to pyriform teleoconch with peripherally-swollen whorls and low spire with a broad subsutural collar or inclined ramp. The protoconch is low and consists of few rounded smooth whorls. Some genera have a shell with almost flat spire. Below the spine-bearing angular shoulder, the body is more or less roundly constricted to the elongate siphonal canal. The aperture is notched in its posterior and as a straight siphon or it is inclined to the left. The inner lip of aperture carries a swelling and is smooth or with oblique folds. The protoconch has low-coiled rounded smooth whorls. The taxon is based on *Pyropsis* CONRAD, 1860, with protoconch of two smooth, rounded whorls slightly inclined to the axis of the teleoconch in the type *Pyropsis perlata* (CONRAD, 1860) from the Ripley Formation. In case of *Pyropsis* the pyriform shell has fine ornament, in *Napulus* STEPHENSON, 1941, the ornament is coarse, axial ornament and more spindle shaped shell is present in *Hercorhyncus* CONRAD, 1868, with the type species *Fusus tippiana* CONRAD, 1860, from the Ripley Formation Mississippi (SOHL 1964a: pl. 30, figs 8–10, 13–16).

Schizofusus KIEL & BANDEL, 2003, has shell shape of *Napulus*, but its inner lip has folds. Also *Lupira* STEPHENSON, 1941, has folds on its inner lip and shell shape as *Napulus*. Ornament of *Hydrotribulus* WADE, 1916, is close to that of *Napulus*, but the siphon is more inclined. *Hydrotribulus* has a more pointed apex of its teleoconch and ornament of strong, widely spaced, spiral cords, which override the transverse ribs of the periphery and basal slope has a protoconch of two smooth rounded whorls in *Hydrotribulus elegans* SOHL, 1964 (SOHL, 1964a: pl. 36, figs 13–16,18).

Pyropsis nodifera (STOLICZKA, 1868) from Trichinopoly Formation closely resembles juvenile shells of *Trochifusus perornatus* (SOHL, 1964a: pl. 34, figs 2–4, 11, 13) with protoconch having rounded whorls. *Napulus* with similar shell shape and rounded body whorl with long, slightly curved siphonal canal has ornament of strong spiral cords and transverse ribs. The protoconch is elevated in *Napulus reesidei* SOHL, 1964, from the

Ripley Formation consisting of about 1.5 smooth, well-rounded whorls, which grade gradually into the teleoconch (SOHL, 1964a: pl. 35, figs 16–20, 24). The Indian *Napulus excavatus* STOLICZKA, 1868, from the Trichinopoly Formation is intermediate in shape between *Morea* and American Gulf Coast species of *Napulus* (BANDEL, 2000: figs 55–56). It resembles *Napulus fragilis* from Mississippi (SOHL, 1964a: pl. 35, figs 12, 21–23) and *Napulus tuberculatus* STEPHENSON, 1941, from Texas.

Schizofusus, type species *Schizofusus transkeiensis* KIEL & BANDEL, 2003, from the Umzamba Formation of NE South Africa, has shell shape that resembles that of *Napulus*. It has the inner lip of the aperture with several small folds and a larger one at the beginning of the narrow siphon. The features of the aperture connect to *Lupira* with type species *Xancus variabilis* WADE, 1926, from Coon Creek, Tennessee (SOHL, 1964a: pl. 32, figs 14–16, 24–25). It has a protoconch in shape very close to that of Colombellinidae (*Neocolomellina* n. gen), which rests on the rather slender whorls of the juvenile teleoconch with 6 axial ribs as ornament.

Suborder Cassina RIEDEL, 2000
Superfamily Cassoidea LATREILLE, 1825 (= Tonnoidea SUTER, 1913)
(Pl. 3, figs 1–6)

The planktotrophic larva of the Cassoidea has a characteristic larval organ used for shell deposition. It is formed by the margin of the periostracal gland zone of the mantle that extends beyond the shell edge. Here it consists of a mobile trunk-like extension of the mantle edge. This organ is able to deposit periostracum to the shell surface apical of the apertural margin, as long as the larval shell grows. The trunk grows after the larva has hatched from its egg capsule and it disappears at metamorphosis to benthic life. The initial larval shell has often an ornamental pattern of rectangles, but the organic cover added to the outer shell surface by the mantle trunk usually has a different ornament and covers and hides the original pattern (BANDEL et al., 1994). The fully grown larval shell is among the largest found among gastropod larvae with diameters up to 5.4 mm (RIEDEL, 1995). The teleoconch in Bursidae THIELE, 1925, Ranellidae GRAY, 1854, and Personidae GRAY, 1854, is fusiform, often showing varices, and, among the Tonnidae SUTER, 1913, is egg shaped with short spire. RIEDEL (2000) recognized members of modern families in species from the Paleogene, but it was remarked that Cassidae have such a different adult shell from the Ranellidae that they should have arisen before and already during the Cretaceous even though fossil evidence is missing.

Family Eosassinidae n. fam.

Diagnostic characters: The teleoconch of *Sassia* resembles that of *Bursa* and the protoconch has ornament of cancellation to the end of the larval shell, and there is no external organic cover added to it during larval life. The type genus is *Eosassia* n. gen. from the Campanian Coffee Sand, Mississippi.

Genus *Sassia* BELLARDI, 1837.

Fusiform to turbinate shell has angular whorls ornamented by spiral ribs crossed by axial folds which form tubercles with each other and fine crenulated spiral threads. The inner lip of the aperture is concave with nodules on its end, and smaller ones may be present on its callus. It continues in a short anterior canal. The outer lip is thickened and has about seven nodules on its inner side. The shell has about five to six whorls with thickened growth intermissions (varices) after more than half a whorl. The axial ribs disappear below the third or fourth spiral cord on the body whorl. The embryonic whorls measures about 0.2 mm across with ornament of ridges and grooves. The protoconch is dome shaped consists of 3.5 whorls, is about 2 mm high and wide. The first larval whorl is almost smooth, further whorls are ornamented with a rectangular network pattern. The genus is based on *Sassia apenninica* (SASSI, 1827) (LANDAU et al., 2004: pl. 5, fig. 1, pl. 10, fig. 3) from the Pliocene of the Mediterranean Sea (WENZ, 1938: fig. 3044). Its protoconch was noted to be almost identical to that of a *Sassia* from the Eocene, but not to any of the living species (RIEDEL, 1995).

The first species known from the geological record with a protoconch close to that of *Sassia* was documented by SCHRÖDER (1995: pl. 7, figs 3–4; Bandel, 1993: pl. 13, fig. 6) from Aptian-Albian boundary deposits in Germany. It is about 1 mm high and covered by a net of rectangles on larval whorls with only half a teleoconch-whorl preserved. The embryonic whorl was not preserved.

Genus *Eosassia* n. gen.
(Pl. 3, figs 7–10)

Diagnostic character: The genus has the type species *Gyrineum gwinae* DOCKERY, 1993, from the Campanian Coffee Sand, Mississippi. The coarsely sculptured shell has an ornament of rectangles, an aperture with a denticulate outer lip, an inner lip with three folds, and a short anterior canal. It has a dome shaped protoconch that consists of 3.5 whorls with about 1.5 mm in height and almost the same in width. Its embryonic whorl measures about 0.2 mm in diameter and has ornament of ridges and grooves. The first larval whorls is ornamented by tubercles which become arranged into axial rows which in the second larval whorl form spiral and axial lines that make a reticulate pattern. On the last larval whorl a pattern of rectangles is formed by about 18 spiral lines crossed by about 50 axial ribs. The larval shell ends without lobe or thickened margin of on its outer lip. On the first teleoconch whorl spiral ribs are dominant over axial ribs (DOCKERY, 1993: pl. 16, fig. 10, pl. 21, figs 6–9, pl. 22, figs 1–5; SCHRÖDER, 1995: pl. 7, figs 5–8; RIEDEL, 1992: pl. 16, figs 172–175, 1995, as *Sassia*).

Remarks: KIEL (2002) documented an adult shell from the Campanian of Torallola in northern Spain that is about four times larger than the largest of those figured by DOCKERY (1993) from Ripley Formation. RIEDEL (1992, 1995) suggested that during the evolution of the Tonnoidea with their characteristic larval shell the ornament of the shell was simplified, without discussing the appearance of an additional larval shell added on top of the shell that had been secreted earlier, as is characteristic to most living Ranellidae with planktotrophic development. BEU (1998) considered the Ripley species as the earliest members of the group around *Distorsio*, later preferred and earlier appearance of the genus *Sassia* instead. DOCKERY (1993) suggested similarity of the species with *Plesiotriton cretaceous* SOHL, 1960, from Ripley Formation (SOHL, 1960: pl. 18, figs 35, 41–42). *Gyrineum* LINK, 1807, that is based on *Gyrineum gyrinum* (LINNÉ, 1758) from the Indo-Pacific (WENZ, 1938: fig. 3062), in contrast to *Eosassia*, has its protoconch as wide as high with 2.5 to 3 smooth whorls that are coated by additional periostracum (RIEDEL, 2000: pl. 9, figs 7–9).

Family Colombellinidae P. FISCHER, 1884

The shell has a low spire and a thickened outer lip with tubercles on its inner side, folds on the inner lip and a siphon-like notch on both sides of the narrow aperture. Ornament of the teleoconch consists of spiral ribs crossed by axial ribs forming rectangular pattern. The genus *Colombellina* ORBIGNY, 1843, has Early Cretaceous type (*Rostellaria monodactylus* DESHAYES, 1842) with protoconch unknown. ZITTEL (1885) placed into the family next to *Columbellaria* ROLLE, 1861, also *Zittelia* GEMMELARO, 1870, and *Colombellina* ORBIGNY, 1843. He interpreted it as a predominantly Jurassic taxon that intermediates between Strombidae and Cassididae. SCHILDER (1927) suggested that *Colombellina* evolved via *Zittelia* to the Cypraeidae, and connected the Strombidae with the Cypraeidae and Tonnidae. The type species of *Colombellina* from France differs from *Neocolombellina* n. gen. from Ripley Formation by having a posterior siphon-like notch on its aperture in addition to the anterior siphon (SOHL, 1960).

Genus *Neocolombellina* n. gen.

Diagnostic characters: The genus is based on *Neocolombellina cancellata* (DOCKERY, 1993) that has a coarsely sculptured shell with ornament of rectangles and its aperture with the outer lip denticulate, the inner lip with three folds and with short anterior canal. The protoconch of this species is dome shaped and about 1 mm high and wide. The embryonic whorl is about 0.18 mm wide and ornamented by tubercles. The first larval whorl is ornamented by fine spiral ribs with dots between them. Transition from the larval shell is not abrupt even though its aperture has a basal projection. *Neocolombellina americana* (WADE, 1926) as in SOHL (1960: pl. 14, figs 1–3, 6–7) (as *Colombellina*) closely resembles *Neocolombellina cancellata* as in DOCKERY (1993: pl. 16, fig. 10). *Neocolombellina cancellata* may perhaps be conspecific with *Neocolombellina americana* and represent an immature shell with less expanded outer lip.

Neocolombellina carlea (DOCKERY, 1993) (as *Gyrineum*) has ornament as in the genus with three spiral ribs above the suture and six on the body whorl (DOCKERY, 1993: pl. 21, figs 4–5). The inner lip of the aperture is concave with teeth on its inner callus, and the outer lip is thickened and has about six nodules on its inner side. The teleoconch consists of about five whorls with varices which appear after more than half a whorl. The protoconch in shape and size closely resembles that of *Eosassia gwinae* and quite smooth embryonic whorl. 1.5 larval whorls are smooth with sinuous growth lines, further whorls are ornamented by rectangles. On the final

whorl of the larval shell four spiral ribs are crossed by about 20 axial ribs. The spiral, as well as the axial, ribs continue onto the teleoconch and transition is quite indistinct. The base of the larval shell is angular.

Family Mataxidae n. fam.

Diagnostic characters: The family is based on *Mataxa* WADE, 1916, with the type *Mataxa elegans* WADE, 1916, from Ripley Formation. The teleoconch is of pointed oval shape with thickened margin of the aperture with teeth on the inner side of the outer lip, folds on the inner lip and short siphon canal. The protoconch has a rounded apex, beehive-like shape. The embryonic shell measures about 0.2 mm and is ornamented by grooves surrounded by ridges. The first larval whorl is smooth or bears tubercles, and subsequent larval whorls may be ornamented by a rectangular pattern all over or only on the later larval shell. The aperture of the protoconch has a straight outer lip and transition from larval ornament to teleoconch ornament is not sharp. *Mataxa* and *Caveola* are contained. The mataxid teleoconch resembles that of a small *Cymatium*, but the protoconch differs by an ornament of the embryonic whorl with tubercles and the larval whorls by a rectangular pattern that covers the late larval shell.

Mataxa WADE, 1916, with the type *Mataxa elegans* WADE, 1916, from Ripley Formation (SOHL, 1964a: pl. 45, figs 20–27) has an about 10 mm high shell that consist of four to five whorls of the teleoconch. The fusiform shell with rounded body whorl has an ornament of fine spiral lines. The siphon canal is twisted, short, and inclined to the left (SOHL, 1964a: pl. 45, figs 20–27). Sutures are low and the spire comprises less than half of the body whorl in height. The protoconch is more than 2 mm high and wide and has a smooth margin of its outer lip. Transition into the teleoconch is indistinct and marked by change in ornament. The protoconch has an embryonic whorl with about 0.12 mm in width that is ornamented by tubercles on a smooth background. The fine spiral ribs composing the ornament of the first whorls of the teleoconch extend as traces onto the last part of the larval shell. Half a whorl from the end of the larval shell the early teleoconch has a varix. The teleoconch has the subsutural groove and the fine spiral ornament of lines crossed by fine, step-like growth increments. The outer lip has 9 rounded and elongate tubercles on its inner side and the inner lip bears four folds.

Caveola STEPHENSON, 1941, has the type species *Caveola acuta* (WADE, 1926) (SOHL, 1964a: pl. 44, figs 5–8) from Ripley Formation. The shell of *Caveola* is about 10 mm high, with the spire higher than the aperture. Sculpture consists of axial and spiral ribs forming a pattern of cancellation and varices. The aperture is elongate with a short siphon. The outer lip has tubercles on its inner side, and the inner lip has two folds. The protoconch is about 1.5 mm wide with about 3.5 whorls. The embryonic whorl is about 0.2 mm wide and evenly rounded. The first 2.5 larval whorls are totally smooth. The last portion of the larval whorls has the onset of adult sculpture, with spiral ribs appearing at first followed by axial ribs. The transition to the teleoconch is quite indistinct, with a varix formed within the first half teleoconch whorl. The varix has teeth on the inner side of the thickened outer lip and two folds on the apical side of the inner lip.

Family Paladmetidae SOHL, 1964

The paladmetid shell is elongate, with reticulate sculpture consisting of spiral cords and axial ribs. Varices may be present. The outer lip of the aperture lacks a notch below the suture, the inner lip is simple, and the siphon canal may be short or long. The protoconch measures more than 1 mm in height and width, has a rounded embryonic shell with ornament of tubercles. The conical larval shell consists of more than three whorls of which the last half whorl has ornament of collabral and spiral lines. A spiral rib on the apical side of the projection on the aperture comes to lie just above the suture. Besides *Paladmete* GARDNER, 1916, also *Anomalofusus* WADE, 1926, *Cantharulus* MEEK, 1876, *Lomirosa* STEPHENSON, 1941, and *Profusinus* BANDEL, 2000, can be placed here.

The type species of *Paladmete* is *Trichotropis cancellaria* CONRAD, 1858, from the Ripley Formation. The shell of this species has a *Littorina*-like shape, with a rounded aperture, teeth on the inner side of the outer lip, and short anterior notch at the end of a straight inner (columellar) lip (SOHL, 1964a: pl. 45, figs 28–34). Sculpture consists of a network of axial ribs and spiral cords, and commonly varices, indicating growth increments of about each half whorl. STEPHENSON (1952) described a flat-topped protoconch for a *Paladmete* from the Cenomanian. The protoconch of the type species from the Ripley Formation has a conical shape, with rounded top, and rounded, larval whorls that are smooth to the last whorl, which has rectangular sculpture in the indistinct transition to the teleoconch. The protoconch of *Paladmete cancellaria* resembles that of the Eosassiidae, but is more conical, its embryonic shell has tubercles instead of a groove and ridge pattern, and there is a projection of the lower part of the outer lip in the larval shell.

Anomalofusus, type species *Anomalofusus substriatus* WADE, 1926, from the Ripley Formation, has a slender, fusiform teleoconch sculptured by sinuous axial ribs that are crossed by fine spiral lines. The inner lip of the aperture is smooth and the outer lip is dentate within. The protoconch consists of about 3 smooth, regularly coiled whorls, the first of which is submerged in the level of the second (SOHL, 1964a: pl. 31, figs 1–4).

The related species *Anomalofusus subnodosus* SOHL, 1964, has a protoconch of 3.5 rounded whorls. The four spiral cords of the late larval shell develop into the primary spiral ribbons of the early teleoconch (SOHL, 1964a: pl. 31, figs 5–8, 11–13). KIEL & BANDEL (2003: fig. 6, 3–4) noted a similar ornament in *Anomalofusus umzambiensis* (RENNIE, 1930) from Umzamba Formation, South Africa. *Lomirosa* closely resembles *Anomalofusus*, which has a bit longer shell and has the same outline of its aperture.

Cantharulus has a fusiform shell with angular whorls formed by a ramp below the suture and a rounded base. The aperture is elongated, egg-shaped, with an inner lip that lacks folds. *Lomirosa* resembles *Cantharulus* in general shell shape, but differs by having a smooth shoulder.

Species of *Cantharulus* from the Coffee Sand of Mississippi, closely resemble congeners from the Trichinopolis Formation of India (BANDEL, 2000: figs 24–25), the Aachen greensands, the African Umzamba Formation, and from Cameroon. Species of both genera have a rounded protoconch with reticulate sculpture. *Hercohyncus tippanus* (CONRAD, 1860) from the Ripley Formation (SOHL, 1964a: pl. 30, figs 8–10, 13–16) is almost identical to *Galeodea (Taeria) klingerii* KIEL & BANDEL, 2003, from the Campanian Umzamba Formation (KIEL & BANDEL, 2003: figs 6–8), with rounded protoconch with flat top and spiral lines as ornament of its larval shell.

Remarks: The teleoconch of Paladmetidae can be distinguished from that of Pyrifusidae by its lack of a selenizone below the suture. The protoconch of Pyrifusidae is also more slender, elongated and conical. *Paladmete? rasoarinorae* KIEL, 2006, from the Albian of Madagascar, has a similar protoconch, with about 2 whorls, about 0.5 mm in size, with the embryonic whorl 0.2 mm wide, and sculpture of fine tubercles. *Paladmete? rasoarinorae* differs from *Paladmete cancellaria* in having a protoconch that ends in a simple, straight, margin of its aperture, a teleoconch aperture without teeth on the inner surface of its outer lip, and in lacking a siphon canal (KIEL, 2006: figs 6, 12–15).

Order Neogastropoda THIELE, 1929 (Pl. 5, figs 1–18)

The shell of a neogastropod usually has an anterior canal of the siphon. In taxa with planktotrophic development, the protoconch has an embryonic shell larger than 0.15 mm, a larval shell with sinuous growth lines, commonly with sculpture and usually with a strong median projection of the outer lip, which is usually thickened. Change in sculpture from the larval shell to the teleoconch is generally pronounced, with growth line patterns changing as well.

Remarks: Cretaceous representatives that clearly belong to one of the modern families of the Neogastropoda can only rarely be documented, with the exception of the Volutidae, which arose during the Maastrichtian (BANDEL, 2003). Several families appear at different times of the Paleogene (RIEDEL, 2000). In his characterization of the Neogastropoda, PONDER (1998) included no data on the features of the shell, but related them to the definition of THIELE (1931) of his Stenoglossa. Accordingly the more or less elongate siphon tube of the teleoconch is characteristic. The definition of the Neogastropoda is based primarily on anatomical features, especially the morphology and arrangement of the teeth of the radula, which are used to differentiate the suborder Rachiglossa GRAY, 1853, from the suborder Toxoglossa TROSCHER, 1848 (TROSCHER, 1861; THIELE, 1931; BANDEL, 1984).

Anatomical data reviewed by RIEDEL (2000) led to a different arrangement which also disagrees with that presented by BOUCHET & ROCROI (2005). SOHL (1964a, b) suggested, that except for 8 genera the remaining 46 genera of the gastropods of the Late Cretaceous of the Mississippi embayment that were described by him as Neogastropoda are known only from the Cretaceous world and had disappeared from that area after the Maastrichtian Paleocene transition.

Superfamily Pyrifusoidea BANDEL & DOCKERY, 2001

Shells are solid, medium-sized to large (1–10 cm high), usually with spiral and collabral sculpture. The aperture usually has a canal like siphon and a posterior notch or canal next to the suture on the posterior part of the outer lip. This notch gives rise to a ribbon below the suture. In species with planktotrophic development, the protoconch has an embryonic shell that is larger than 0.15 mm, and usually with tubercles on smooth ground. The larval shell is conical, with sinuous growth lines and commonly with tubercles below the suture and a spiral

rib on the posterior margin of the strong median projection of the outer lip. The families Pyrifusidae and Pseudolividae are included.

Family Pyrifusidae BANDEL & STINNESBECK, 2000

(Pl. 5, fig. 1–16)

The shell is fusiform, and may range from slender to broad, with a spire that may be high to low. Sculpture consists of axial ribs and spiral cords. The inner lip of the aperture may be smooth or have one to several anterior folds. The larval shell is smooth, conical, consists of several whorls, and measures between 0.6 and 1.0 mm in diameter. The type genus of the family is *Pyrifusus*. The family Pyrifusidae is divided into the subfamilies Pseudorapinae BANDEL & DOCKERY, 2001, Pyrifusinae BANDEL & STINNESBECK, 2000, Pholidotominae WENZ, 1938, and Volutoderminae PILSBRY & OLSON, 1954. Transitional species occur between all subfamilies, making the distinctions between them somewhat arbitrary.

Pseudorapinae have a pointed spire that is usually shorter than the last whorl. The turreted spire has a node-bearing collar below the suture. The aperture has a narrower anterior part to form an elongated siphon canal. The genus *Pseudorapa* HOLZAPFEL, 1888, occurs in the Campanian Vaals Greensands near Aachen, Germany. The subgenus *Pseudorapa* (*Stantonella*) (WADE, 1926), type species *Stantonella subnodosa* WADE, 1926, from Coon Creek, Tennessee (SOHL, 1964a: pl. 22, figs 14–15) has a wider and shorter shell than the more common *Pseudorapa* (*Stantonella*) *ripleyana* (CONRAD, 1860) (SOHL, 1964a: figs 8–9, 18–21). The protoconch of the later species, from Coffee Sand in Mississippi, consists of 4 whorls and is of a rounded conical shape, about 1 mm high and 0.8 mm wide. The embryonic shell, with a diameter of 0.15 mm, has tubercles, while the smooth larval whorls have fine growth lines that reflect a projection of the outer lip of the aperture. The subgenus *Pseudorapa* (*Aliofusus*) (STEPHENSON, 1941) with *Pseudorapa* (*Aliofusus*) *stamineus* SOHL, 1964, has the general shell shape of the genus, but is less spirally ornamented, and its ribbon below the suture appears to be rather indistinct (SOHL, 1964a: pl. 22, figs 10–11).

Pyrifusinae are fusiform in shape, and have a shorter spire, an inclined and often concave shoulder, and a large rounded body whorl, with a long siphon. The collar below the suture arises from the posterior notch of the aperture and whorls have pronounced shoulders. The body whorl is constricted in its anterior, producing an elongated canal of the siphon that is often inclined to the left. The aperture has a smooth inner lip often with an angle at the juncture with the siphon canal. The type genus of the subfamily is *Pyrifusus* CONRAD, 1858, with the type species *Pyrifusus subdensatus* CONRAD, 1858, from the Owl Creek Formation of Mississippi (SOHL, 1964: pl. 24, figs 1–4). The spire of the shell is less than half of the shell height. Sculpture consists of strong spiral cords and transverse ribs. Several species of *Pyrifusus* occur in the Ripley Formation (SOHL, 1964a: pl. 24), and *Pyrifusus oldhamianus* (STOLICZKA, 1868) from Trichinopoly Formation of southern India is very similar (BANDEL, 2001: figs 32–33). A subgenus *Pyrifusus* (*Koenenia*) HOLZAPFEL, 1888, closely resembles *Deussenia* STEPHENSON, 1941. Its spire comprises about half of the total shell height. *Koenenia speciosa* HOLZAPFEL, 1888, comes from the greensands of Vaals in Holland (WENZ, 1938: fig. 3746). *Bellifusus* STEPHENSON, 1941, is also close to *Pyrifusus*, but has a strong fold on the siphon anterior to a weaker fold on the inner lip (SOHL, 1964a: pl. 25, figs 23–24; KIEL & CARMEN PERRILLIAT, 2004). The protoconch of *Bellifusus* consist of about 4 whorls, about 0.85 mm wide and about 1 mm high, with an embryonic whorl of 0.16 mm with rounded granules. The larval shell has collabral growth lines that trace a median projection of the outer lip of the aperture. This projection continues to form the collabral rib pattern of the teleoconch but is less strongly developed in the larval shell.

Ornopsis WADE, 1916, is another similar genus that has a strong fold above the twisted siphon canal (SOHL, 1964a: pl. 29, figs 8–10, 15–16). According to SOHL (1964), the protoconch of *Ornopsis digressa* consists of about 3.5 rounded whorls that form an abrupt junction with the teleoconch. It is similar to the trochiform protoconch of *Ornopsis* (*Pornopsis*) *modica* SOHL, 1964, from Mississippi (SOHL, 1964a: pl. 29, figs 4–7). *Cryptorhytis* MEEK, 1876, closely resembles *Aliofusus*, but clearly differs in having three folds on its inner lip, while *Aliofusus* tends to have a more sharply developed periphery. *Cryptorhytis nobilis* WADE, 1926, has well-developed collar below the suture, a slightly flexed siphon and a short posterior channel. Its embryonic shell is large, about 0.3 mm, and the larval shell consists of more than three whorls. *Cryptorhytis gravida* (STOLICZKA, 1868) from the Trichinopoly Group (BANDEL, 2001: figs 40–41) is slightly larger than *Cryptorhytis nobilis* WADE, 1926, from Coon Creek in Tennessee, but otherwise could represent the same species (SOHL, 1964a: pl. 32, figs 2–3). *Odontobasis sulcata* SOHL, 1964 (SOHL, 1964a: pl. 23, figs 1–4) has a similar shell shape but with two folds on the beginning of the siphon canal.

Pholidotominae have a slender shell with a spire that is as long, or is longer than the last whorl. The aperture is notched at its posterior end and has one to three folds near the anterior of its inner lip. The siphon canal is of moderate length and is slightly inclined to the left. Slender shells occur in *Pholidotoma* COSSMANN, 1896, *Drilluta* WADE, 1916, and *Paleopsephaea* WADE, 1926.

The type is *Drilluta communis* WADE, 1916, from Ripley Formation (SOHL, 1964a: pl. 27, figs 12–13, 20–22) and similar species differ in ornament (SOHL, 1964a: pls. 26–27). *Drilluta* has a distinct collar below its suture and the canal of its siphon is slightly inclined to the left. The inner lip of the aperture has one to three folds. The protoconch of *Drilluta distans* (CONRAD, 1860) is of pointed trochispiral shape with 4.2 round-sided whorls, 0.8 mm wide and about 1 mm high. Its embryonic whorl measures 0.15 mm in width and is ornamented by tubercles on a smooth background. Larval whorls are ornamented by fine collabral lines tracing an anterior projection of the outer lip. The onset of the teleoconch is indistinct and indicated by the appearance spiral lines. A collar below the suture begins only in the second whorl of the teleoconch. The collar below the suture of the teleoconch of *Paleopsephaea* is less distinct and narrow as is the case in *Dilluta*. The protoconch of the type species *Paleopsephaea mutabilis* WADE, 1926, from Coon Creek (SOHL, 1964a: pl. 28, figs 1–6), is smooth, egg-shaped with a blunt apex and 3 whorls. The embryonic whorl is 0.22 mm wide. The entire larval shell is about 0.9 mm in height, with rounded larval whorls that have growth lines reflecting a rounded projection on the anterior outer lip of the aperture. Transition into the teleoconch is gradual. One or two axial collabral ribs appear in the last portion of the larval shell. The teleoconch begins with faint spiral lines and axial ribs have a less-curving course. A very similar species occurs in the Trichinopoly Formation in southern India (BANDEL, 2001). KIEL (2002) noted transition of species that have been placed with *Bellifusus*, *Drilluta*, *Graphidula*, and *Paleopsephaea* among representatives of this group from the north Spanish Campanian Torallola and the Maastrichtian of Temalac, Mexico (KIEL & CARMEN PERRILLIAT, 2004). SOHL (1964a: pl. 25, figs 23–24, pl. 26, figs 18–19, 23–24) found that *Bellifusus curvicostata* may be up to 5 cm long and 2.1 cm wide with 6–7 whorls. Its trochiform protoconch consists of 2.5 rounded whorls. The Indian *Bellifusus indicus* BANDEL, 2001, which has a prominent collar below the suture, is very similar to *Bellifusus angulicostata* SOHL, 1964, (SOHL, 1964a: pl. 25, figs 21–22; BANDEL, 2001: figs 34–35) from Ripley Formation of Mississippi and Tennessee.

The shells of Volutoderminae are usually large and have an ovoid shape. Their teleoconch is *Voluta*-shaped with a relatively high spire. Whorls are constricted in their posterior and may be shouldered. Sculpture consists of spiral cords and strong transverse ribs. The aperture is elongate and narrow with a posterior notch and a long broad canal of the siphon. The inner lip of the aperture commonly has three folds, but the number may be larger, or the folds absent entirely. The protoconch consists of several whorls. The genus *Gosavia* STOLICZKA, 1865, *Volutoderma* GABB, 1877, *Volutomorpha* GABB, 1877, *Longoconcha* STEPHENSON, 1941, *Liopeplum* DALL, 1890, and *Myobarum* SOHL, 1963, are included in Volutoderminae, and *Ficulopsis* STOLICZKA, 1868, may also belong here.

Gosavia with type species from the Austrian Gosau Formation resembles *Conus* with slender shape of its shell, with sculpture of spiral lines and short axial ribs on the angular shoulder and many small folds on its inner lip (WENZ, 1938: fig. 3742).

Volutoderma has a more elongate shell with spiral cords, strong transverse ribs and three folds on the anterior inner lip. It is based on a species from the Upper Cretaceous of California (STEWART, 1927; WENZ, 1938: fig. 3736; SOHL, 1964a). *Volutoderma zitteliana* (HOLZAPFEL, 1888) from Vaals greensands of Western Germany is a characteristic representative (WENZ, 1938: fig. 3739). *Volutoderma kulakunnattamia* BANDEL, 2001, from the Indian Trichinopoly Group of Santonian–Early Campanian age is an intermediate form between *Gosavia* with a shorter shell and *Longoconcha* as is found in the American Gulf Coast fauna of the Late Campanian and Maastrichtian.

Volutomorpha with short spire and *Longoconcha* with slimmer shell shape both occur in the Ripley Formation and have a glazed surface, an expansion of the callus of the inner lip of the aperture onto much of the shell surface. *Volutomorpha* is represented by several species in Ripley Formation that have a smooth protoconch (SOHL, 1964a: pl. 38–42) as found in the Pyrifusidae. Its juvenile stages resemble those of *Pyrifusus*, but, in later more fully-grown stages, the last whorl is comparatively larger. *Longoconcha* is elongate, slim, and almost cylindrical, with strong collabral lines and widely spaced spiral cords, and with three or more strong folds on the inner lip. The conical protoconch consists of at least 3 smooth whorls (SOHL, 1964a: pl. 36–37). The shell of *Liopeplum* is more slender and much more coated with callus on the exterior surface than is the case on *Volutomorpha* and *Longoconcha*. Its type species is from the Ripley Formation (SOHL, 1964a: pl. 43, figs 1–2, 6–7). A similar form from the Cretaceous of California has been assigned to the genus *Varens* SAUL & POPENOE, 1993. *Liopeplum capensis* (WOODS, 1906) from Umzamba Formation of South Africa had lecithotrophic development. Its protoconch consists of a simple rounded smooth whorl 0.7 mm in size (KIEL & BANDEL, 2003: figs 6, 9–10; BANDEL, 2003). A stout type of *Liopeplum* is represented by *Myobarum*, which has a smooth glaze over the surface and two folds on its inner lip. The blunt protoconch consists of about two round-sided whorls and is obscured by callus coating. The type species is *Myobarum laevigatum* SOHL, 1963 (SOHL, 1964a: pl. 44, figs 15–17), which resembles the species of *Parafusus*. SOHL (1964a) differentiated *Myobarum* from *Parafusus* of the same locality by its smaller size, its less developed groove of the siphon, and the presence of a strong fold bordering the siphon at the anterior end of the inner lip. *Ficulopsis* has a shell resembling that of *Ficula*, with reticulate sculpture, a posterior notch in the outer lip, and a number of folds on the inner lip. The type species of *Ficulopsis* is *Pyrula pondicherriensis* FORBES, 1845, from Late Cretaceous Trichinopoly Formation of southern

India. It resembles *Ficulomorpha* HOLZAPFEL, 1888, type species *Mitra pyruliformis* MÜLLER, 1851, from the Campanian near Aachen (HOLZAPFEL, 1888: pl. 9, figs 17–18).

A number of species assigned to Neogastropoda from the Cretaceous still need to be better known. The Pseudolividae DE GREGORIO, 1880, based on *Pseudoliva* SWAINSON, 1840, with Recent type species, have an ovate to spindle-like shell that may be smooth, or have spiral sculpture and a conspicuous groove on the basal half of the last whorl. The last whorl comprises more than 60 % of the total shell height. VERMEIJ (1998) included the Cretaceous genus *Sulcobuccinum* ORBIGNY, 1850, in Pseudolividae. It is similar or the same as *Ptychosyca* GABB, 1877, type species *Ptychosyca inornata* GABB, 1876, from the Ripley Formation, which has a smooth surface and a double groove on the basal part of the body that is divided by a raised median band (SOHL, 1964a: pl. 35, figs 1–6). *Ptychoscapa inornata* has the spire about one third of the shell height covered by a callus glaze hiding the sutures. *Eoancilla acutula* STEPHENSON, 1941, from the Owl Creek Formation (SOHL, 1964a: pl. 36, figs 1–7, 10, as *Ancilla*) may belong here. Its protoconch consists of a few rounded whorls.

Fulgerca STEPHENSON, 1941, type species *Fulgerca venusta* STEPHENSON, 1941, has a similar spindle-like shape, a blunt spire, deeper sutures, sculpture of intersecting fine spiral and axial cords, and anterior basal band, and an elongate aperture with a broad, open, siphonal canal. The trochiform protoconch consists of 3.5 rapidly increasing smooth whorls (SOHL, 1964a: pl. 36, figs 8–9, 12). *Ptychoris* GABB, 1877, type species *Voluta purpuriformis* FORBES, 1846, from Trichinopoly Group in India, has an elongate, oval shell with a pointed spire, and folds on the inner lip of the aperture. While the juvenile shell is spirally grooved, the mature shell is coated with enamel. The siphon canal has three outer and two inner folds (BANDEL, 2003). *Parafusus* WADE, 1918, type species *Hyllus callilateris* WADE, 1917, (= *Wadia* COSSMANN, 1920) from Coon Creek, has a weak indication of a low groove around the siphon (SOHL, 1964a: pl. 44, figs 22–23, 26).

Austrosphaera CAMACHO, 1949, from the Maastrichtian Quiriquina Formation, type species *Austrosphaera difficilis* (ORBIGNY, 1842), has a sculpture of minute spiral lines but appears smooth. It lived on a rocky shore in the intertidal regime, and obviously also continued to live in the region also after the Cretaceous (BANDEL & STINNESBECK, 2000). OLEINIK & ZINSMEISTER (1996) provided an evolutionary interpretation on the variability of a nearly identical species they named *Seymourosphaera*, suggesting diversification after the K/T crisis. But *Seymourosphaera* (= *Austrosphaera*) and the almost identical species from the Maastrichtian had the same variations of its shell shape.

Cryptoconinae WENZ, 1938, type genus *Cryptoconus* KOENEN, 1867, with type species *Pleurotoma filosa* LAMARCK, 1804, lived during the Eocene in Europe. *Cryptoconus mcnairyensis* (WADE, 1917) from the Ripley Formation (SOHL, 1964a: pl. 47, figs 6–9) also has a biconical shell primarily sculptured by spiral ribs. KIEL (2002: pl. 30, figs 15–17) noted a similar species from the Maastrichtian of Temalac, Mexico, but it differed in lacking sinuous growth lines, which are characteristic of *Cryptoconus*. In the Mexican species, the embryonic portion of the protoconch measured about 0.1 mm across; the larval shell comprised 2.5 to 3 smooth whorls, measuring 0.6 mm in width and 0.5 mm in height. The teleoconch had a pattern of its sculpture consisting of equally strong axial and spiral ribs. In *Cryptoconus mcnairyensis*, the spiral ribs dominate. *Tectaplica* WADE, 1916, type species *Tectaplica simplicia* WADE, 1916, has a short siphon canal and an inner lip with three low folds that resembles a little *Cryptoconus* in shell shape (SOHL, 1964a: pl. 44, figs 19–21).

A subfamily could be seen in the genus *Beretra* and related *Amuletum*. Here the slender fusiform teleoconch has an elongate siphon. The spire is about half the shell height. A deep notch at posterior corner of aperture is the origin of an indistinct (*Amuletum*) or distinct (*Beretra*) subsutural ribbon. Sculpture consists of collabral ribs crossed by finer spiral threads. The inner lip of aperture is smooth. The protoconch is conical with several smooth whorls and a projection of the aperture in its larval whorls (Pl. 5, figs 7–10). The type genus is *Beretra* Stephenson, 1941, with the type species *Beretra firma* STEPHENSON, 1941, from the Maastrichtian Navarro Group of Texas. *Beretra ripleyana* (SOHL, 1964a: pl. 46, figs 19–21), *Beretra gracilis* (WADE, 1926) (SOHL, 1964a: pl. 46, figs 15–18) and *Beretra speciosa* SOHL, 1964 (SOHL, 1964a: pl. 46, figs 22–23) are all from the Ripley Formation.

Amuletum STEPHENSON, 1941, with type species *Turricula mcnairyensis* WADE, 1962, from Ripley Formation (SOHL, 1964a: pl. 45, figs 1–9) has a slender shell with protoconch of three or four whorls and a teleoconch with an elongate siphon canal and posterior sinus in the outer lip of the aperture (Pl. 5, figs 7–10). As noted by SOHL (1964a: pl. 46, figs 7–11), *Remnita* STEPHENSON, 1941, is closely related to *Amuletum*, but has spiral elements dominating the sculpture. The type species *Remnita biacuminata* (WADE, 1926) (SOHL, 1964a: pl. 46, figs 7–8), and *Remnita anomalocostata* (WADE, 1926) are known from Ripley Formation.

SOHL (1964a: pl. 46, figs 12–14) also included *Gemmula* WEINKAUF, 1875, with *Gemmula cretacea* SOHL, 1964, that is very similar to *Amuletum* with the sinus of the outer lip lower on the shoulder and not right below the suture, but with type of the genus *Gemmula gemmata* HINDS, 1843, a Recent species of the Turridae (WENZ, 1938: fig. 3970), which probably is not related at all.

Fusimilis STEPHENSON, 1941, with the type species *Fusimilis robustus* STEPHENSON, 1941, from Texas is a little shorter and has a very long siphon canal and a strong ribbon below the suture. *Fusimilis proxima* (WADE, 1926) is more slender (SOHL, 1964a: pl. 46, figs 26–27, 34–35) than *Fusimilis kummeli* SOHL, 1964, and has with finer

ornament (SOHL, 1964a: pl. 46, figs 29–30, 32–33, 39–40) from Ripley Formation as is the individual illustrated here (Pl. 5, fig. 16).

Remera STEPHENSON, 1941, type species is *Remera microstriata* STEPHENSON, 1941, (SOHL, 1964a: pl. 31, fig. 16) is ornamented by strong axial ribs and fine spiral ribs and has a moderately long siphon. The very similar *Remera stephensoni* HARBISON, 1926, is also known from Ripley Formation (SOHL, 1964a: pl. 31, figs 17–19, 22–23). Their protoconch was described as consisting of three smooth rounded whorls, forming a cone. *Graphidula* STEPHENSON, 1941, type species *Graphidula terebriformis* STEPHENSON, 1941, (SOHL, 1964a: pl. 28, figs 24–26), has a very similar in shell shape but, in contrast to *Remera*, has folds on its inner lip. Several similar species of *Graphidula* occur in Ripley Formation. *Graphidula* closely resembles *Paleofusimitra* SOHL, 1963, type species *Paleofusimitra elongata* SOHL, 1963, (SOHL, 1964a: pl. 37, figs 1–3, 6–7), that has a protoconch of 2.5 rounded smooth whorls and gradational transition with the teleoconch. *Paleofusimitra* resembles *Mitridomus* SOHL, 1963, type species *Mitridomus ripleyana* (WADE, 1926) (SOHL, 1964a: pl. 37, figs 5, 13), with sculpture of axial ribs and fine spiral lines and four low folds on the anterior inner lip of its aperture.

Remarks: *Amuletum* was suggested to belong to the *Toxoglossa* TROSCHEL, 1866, Turridae SWAINSON, 1840, by SOHL (1964a). The protoconch of modern Turridae is often highly ornamented, while that of the Beretinae from the Coon Creek fauna is smooth and resembles the protoconch as is present in species of *Dilluta*. While the teleoconch of the *Amuletum* resembles that of a Recent *Crassispira* SWAINSON, 1940, its protoconch is like that found in the Pyrifusidae. *Amuletum* can, thus, be interpreted as a genus with convergent shell shape to the Turridae such as *Crassispira*.

Also *Perissoptera* has a similar protoconch as found among the Pyrifusidae (BANDEL, 2007: pl. 2, figs 12, 15–16, and here Pl. 5, figs 9–10), thus Cretaceous Aporrhaidae as well as modern Strombidae have quite similar larval shells (BANDEL, 2007: pl. 6 for modern Strombidae).

Genus *Concepcionella* BANDEL & STINNESBECK, 2000, early Muricidae?

The large (almost 8 cm high), thick shell of *Concepcionella*, type species *Concepcionella bonillana* BANDEL & STINNESBECK, 2000, from the Maastrichtian Quiriquina Formation, Quiriquina Island, Chile, has a fusiform shape, with the spire about as high as the body whorl. Whorls are keeled with a flattened ramp above and concave side below, up to the indistinct suture. The aperture is ovoid, with a rounded and angular posterior end, notched at the keel. It extends into a short anterior siphon canal that has a slight twist to the left. The inner side of the thickened outer lip is crenulated and the inner lip forms a shell thickening (callus) with an edge raised over the inner lip (columella).

Concepcionella has a notch in the keeled flank of the outer lip of the aperture (BANDEL & STINNESBECK, 2000) as is also noted in case of *Trophon? umzambiensis* KIEL & BANDEL, 2003, from Umzamba Formation (KIEL & BANDEL, 2003: figs 6, 11–12). Minor onsets of such a notch are also present in *Protobusycon cretaceum* (WADE, 1917) with large shell from the Ripley Formation of the USA (SOHL, 1964a: pl. 23, figs 23–24). Among modern Neogastropoda a notched keel on the outer lip is often present (e.g. in *Rapana* SCHUMACHER, 1817, *Latiaxis* SWAINSON, 1840, *Melongena* SCHUMACHER, 1817, *Busycon* RÖDING, 1798, and *Tudicla* RÖDING, 1798).

Family Volutidae RAFINESQUE, 1815

Shape of the shell may resemble that of *Buccinum*, *Strombus* and *Bulla* and is usually of relatively large size with an average of 5–20 cm in height. The inner lip of the aperture commonly bears folds (RIEDEL, 2000: fig. 110). All known species including the fossil representative described by BANDEL (2003) have or had lecithotrophic development with young hatching with one up to four whorls completed. The transition from protoconch to teleoconch may be quite indistinctly marked and the protoconch consists only of the embryonic shell and no larval shell.

Caricellinae DALL, 1907, has the teleoconch fusiform and the protoconch consists of about one large rounded whorl forming a rounded or pointed apex of the shell. Ornament of the teleoconch is smooth or has ornament of ribs crossing each other. The aperture is ovate and elongate, ending in a posterior canal and anterior siphon canal. The inner lip exhibits three or four oblique plaits. The subfamily is based on *Caricella* CONRAD, 1835, with the type is *Caricella pyruloides* CONRAD, 1834, from the Eocene of Alabama as illustrated by DOCKERY (1980: pl. 17, figs 7–8, pl. 77, fig. 3). The Maastrichtian *Caricella (Misrimelo)* BANDEL, 2003, based on *Caricella (Misrimelo) klitzschi* BANDEL, 2003, from the Late Cretaceous of Egypt is an up to 85 mm high pear-shaped shell that consists of few whorls, has a short broadly conical spire, and protoconch that is about 6 mm wide and high. The inner lip of the aperture exhibits three or four oblique plaits. It differs from *Caricella*

(*Misrimelo*) *pyriformis* (FORBES, 1846) from Trichinopoly Formation in south India that has four folds on its inner lip and no callus pad (STOLICZKA, 1868).

Misricymbiola BANDEL, 2003, is based on *Misricymbiola chalmasi* (QUAAS, 1902) from the Late Cretaceous of Egypt. It has an up to 155 mm high and 90 mm wide shell with low conical stair-like spire that carries a large rounded protoconch. It consists of about one whorl and is about 10 mm high and wide. With more than 3 whorls of the teleoconch the shell is fully grown. The angular periphery is ornamented by short axial ribs which do not continue onto the flattened sides of the whorl and onto the apical plane. The whorl flanks have two lower rounded corners and a constricted base which is extended into a supporting pillar of the long siphon canal. The inner lip bears three oblique folds. In the body whorl the folds form a swelling on the inner lip that is oriented at right angle to the axis of the spire. *Misricymbiola conocoi* BANDEL, 2003, is smaller in regard to the protoconch that is only about 5 mm high and wide and the teleoconch that reaches a size of 60 mm in height and 50 mm in width, consisting of three more rounded whorls, also from the Maastrichtian of the Sand Sea of western Egypt.

Difference: *Misricymbiola* is distinguished from *Caricella* (*Misrimelo*) by the shape of the teleoconch that resembles *Protobusyon* WADE, 1917, or *Hercorhyncus* CONRAD, 1868, among the late Cretaceous gastropods of Ripley Formation (SOHL, 1964a). Both of the latter have a much smaller protoconch with more whorls and may be similar in size.

Plicolivinae BOUCHET, 1990, is based on *Plicoliva* PETUCH, 1979, with type species *Oliva zelindae* PETUCH, 1979, from off-shore Brazil, others on the West African shelf on the opposite side of the Atlantic Ocean (POPPE & GOTO, 1992). Modern *Plicoliva* lives in 5 to 40 m deep water in sand and on rock (BOUCHET, 1990). Its shell is *Oliva*-like in shape, solid and glossy and has an inner lip with five strong folds. Subgenus *Plicoliva* (*Misriplivalva*) BANDEL, 2003, from the Maastrichtian of Egypt is evenly olive-shaped shell of about 30 mm height and 15 mm in width has a smooth surface with rounded protoconch with about 1 mm in width. *Plicoliva* (*Misriplivalva*) *bartheli* BANDEL, 2003, has four strong oblique folds on its inner lip, the lower of which surrounds the siphon notch.

3 Discussion

3.1 Characters of protoconch morphology among Muricoidea

The embryonic and larval shell of Recent Rachiglossa such as Muricidae and Coralliophilidae is quite characteristic (RIEDEL, 2000; own observations). In case of the Muricidae the larval shell is usually provided with large and strong projection of the middle of the outer lip and a varix with margin turned up and thickened features the end of larval shell growth. Thus a thickened margin is usually also seen in cases where the marginal lobe is covered by the first whorl of the teleoconch. The embryonic whorl measures about 0.18 to 0.25 mm in diameter and is covered by tubercles which may be simple or composed of granules. Its end is clearly marked by straight or weakly curving increments of growth and a rapid change in ornament. The sculpture of the larval whorl usually consists of a row of tubercles below the suture and a strong spiral rib that accompanies the margin to the base and ends in the median lobe of the outer lip (BANDEL et al., 1997: figs 18, H–J, and personal data; KAY, 1979; LAURSEN, 1981; LEAL, 1990; KOOL, 1993). From the Gulf of Aqaba the protoconch for example of *Morula anaxeres* (KIENER, 1835), *Thais savignyi* (DESHAYES, 1844), *Drupa ricina* (LINNÉ, 1758), *Nassa francolina* (BRUGUIÉRE, 1789), *Maculotrion serriale* (DESHAYES, 1830), *Pteryarchia tripterus* (BORN, 1778) and *Drupella cornus* (RÖDING, 1798) are available to characterize its general shape. All have similar protoconch shape and ornament and differ predominantly in regard to the number of whorls produced during the larval stage between two and four and protoconch height that ranges between 0.7 and 1.2 mm. The larval whorls are evenly rounded and their surface aside from the row below the suture and the rib along the margin is smooth or partly or totally covered by fine tubercles. The base with the gutter like siphon becomes covered by later whorls. A similar shape is also developed in case of *Thais haemastoma* (LINNÉ, 1758) and *Thais deltoidea* from the Caribbean Sea (KOOL, 1993; own observations).

The protoconch of Coralliophilidae has a quite different ornament on a shell with similar shape and characters of the outer lip of the fully grown larval shell. Larvae hatch with ornament of the embryonic shell that consists of rather typical pattern of hemispherical tubercles overlain and connected to each other by a wrinkled net of lamellae (BANDEL, 1975; MASSIN, 1987, 1990; BANDEL et al., 1997: figs 20, A–I; RIEDEL, 2000). The larval shell in case of *Coralliophila caribaea* and *C. aberrans* from the Caribbean Sea has sculpture axial ribs and a peripheral corner is formed by a row of nodules. The outer lip of the aperture is thickened and turned up with an angular median lobe accompanied by a deep rounded anterior sinus and a wider posterior sinus. The fully grown protoconch consists of 4.5 whorls, is about 0.8 mm high and about 0.6 mm wide with its shell quite thick and well calcified. A very similar protoconch is developed in case of *Coralliophila erosa* (RÖDING, 1798) and *C. violacea* (KIENER, 1836) from the Gulf of Aqaba, while in that of *Quoyula madreporarum* (SOWERBY, 1832) the

first larval whorl is almost smooth. *Coralliobia fimbriata* (A. ADAMS, 1852) and *Leptoconchus peronii* (LAMARCK, 1818) live in the inside of the skeleton of corals and *Magilus antiquus* MONTFORT, 1810, even grows within and along the coral leaving the regular shape of a coiled shell and acquiring worm like shape. Their protoconch is similar with 3.5 rounded whorls to 2.5 whorls and embryonic shell 0.2 to 0.3 mm wide, ornamented by granules connected to network of fine lines and the larval whorls with collabral axial ribs. Teleoconch shape of *Coralliobia* is dome like with wide oval aperture with wide inner lip and strong ornament of spiral ribs and lamella-like collabral ribs and it is covered by coral and included in it from juvenile just post-metamorphic stage onward. In case of *Leptoconchus* the adult lives in a *Fungia* coral with a shell of olive-like shape and *Magilus* deviates from normal coiled shape after establishment in the coral. A transition from Muricidae to the coral parasites of the Coralliophilidae probably occurred during the Eocene. *Coralliophila aldrichi* (COSSMANN, 1903) is from the mid Eocene of SE USA (WENZ, 1938; DOCKERY, 1980: pl. 36, fig. 5–6). Molecular phylogeny carried out by OLIVERIO & MARIOTTINI (2001) and BARCO et al. (2010) document their relation to the Muricidae with closest relation to the *Thais* (*Stramotina*) branch of the Rapaninae (Thaisinae). The earliest undoubted muricids are of Paleocene age (VOKES, 1971, 1992; BANDEL, 1993) with species closely resembling the Recent *Typhis* as documented by RIEDEL (2000: pl. 18, figs 3, 5), while those noted from the Cretaceous differ in shape and ornament.

The palaeontological record of the Coralliophilidae indicates their presences since the Eocene and thus for about 50 million years, their diversity established about 35 million years ago and a further diversification of the members of the family predominantly within the Neogene. During the Oligocene and the early Miocene of France diversity increased (LOZOUET & RENARD, 1998). *Coralliophila burdigalensis* TOURNOUER, 1874, from the Late Oligocene of SW France that protoconch as well as the teleoconch that resembles that of living species (LOZOUET & RENARD, 1996: fig. 2–3). *Coralliophila* and *Quoyula* live on corals externally while *Magilus* Montfort, 1810, and *Leptoconchus* live internally in hard or soft corals. From the Mid Miocene of the Paratethys species of both *Coralliophila* as well as *Magilus* have been described (ZILCH, 1934: pl. 15, fig. 82–86, confirmed by BALUK, 1995). Muricidae resembling modern *Typhis* are present in the Paleogene (RIEDEL, 2000; own data from the Paleocene of Alabama), but according to BARCO et al. (2010) represent the most advanced group of the Muricidae. Thus the evolution of the most derived Typhinae may have occurred earlier from muricid stock than that of the specialized Coralliophilinae also from muricid stock. The later are derives from the Rapaninae-Thaidinae branch of the Muricidae, according to the phylogenetic reconstruction shown in BARCO et al. (2010: fig. 4) base on molecular data. Apparently the groups which have been recognized among the living Muricidae have evolved since begin of the Tertiary as did, most probably, also their characteristic protoconch.

3.2 Characteristics of the protoconch of Buccinidae, Nassariidae, Columbelloididae and Mitridae

Among the Buccinidae many species have lecithotrophic development and thus the characteristic shape and ornament of the larval shell is lost in these cases. A protoconch with 2.5 whorls and the larval shell ornamented by axial lines of grains forming ribs was noted in case of *Pisania tinctoria* (CONRAD, 1846) from off the Brazilian coast (LEAL, 1990: pl. 19, fig. F). The protoconch of *Trachypollia* WOODRING, 1928, *Cantharus* RÖDING, 1798, *Pisania* BIVONA, 1832, and *Latirus* MONTFORT, 1819, from the tropical West Atlantic as documented by LEAL (1990) all have quite characteristic ornament of their larval shell. *Pisania* (*Pollia*) *tinctoria* (CONRAD, 1846) from the Caribbean Sea near Santa Marta has the larval shell of 2.5 whorls with rounded embryonic shell. The later was described as *Cantharus tinctorius* and resembles that of *Pisania pusio*, with 0.4 mm in diameter (BANDEL, 1975: pl. 16, figs 9, 12, pl. 17, fig. 4). It is ornamented by fine granules and growth lines indicate the time of hatching from the egg capsule as veliger larva. The larva continues shell growth by changing the outline of the outer lip to a wide lobe accompanied by a sinus on either side and by enlarging the siphon canal. The larval whorls have an ornament of somewhat irregular axial ribs developed on the lower half while the upper half is smooth. When the shell of the larva is fully grown the last portion of the whorl forms axial folds up to the thickened outer lip. The strong hook of the outer lip is covered when the first teleoconch is added. The protoconch is about 1 mm high. The relatives of this genus live worldwide and a similar larval shell occurs in the plankton of the Gulf of Aqaba.

The protoconch of *Nassarius* is distinguished from that of most other species of the Neogastropoda by low rounded shape almost as wide as high and sculpture of one to several spiral keels. Nassariidae have thus quite characteristic shape of the shell in case of species with planktotrophic larva (BANDEL, et al. 1997: figs 18, A–D). Five species of *Nassarius* live in the Gulf of Aqaba, two of these, *N. arcularius* and *N. conoidalis* prefer the shallow sands, and three live on deeper sandy and muddy bottom. The protoconch of *Nassarius arcularius*, *N. conoidalis* and *N. sinusigerus* has similar shape and measures approximately 0.9 mm in height and width. Its ornament consists of three spiral ribs. The embryonic whorl of *N. arcularius* has folds which distinguish from that of *N. conoidalis* with one more larval whorl, and *N. sinusigerus* with similar shape but brown tinge and the median lobe of the aperture with more ribs. In case of *Nassarius pauperus* the embryo remained in the egg

capsule feeding on liquid yolk, as is also the case in *Nassarius vibex* and *N. albus* from the Caribbean Sea (BANDEL, 1975: pl. 17, figs 7–10).

Shape and ornament of the protoconch within the Columbellidae SWAINSON, 1840, differs more among the species as is the case among the Muricidae or the Coralliophilidae and also that of the Nassariidae. Commonly a ribbon bordered by two spiral lines with specific ornament between them occurs near the corner to the base. The dimensions of the embryonic whorl among species lies between 0.15 mm and 0.30 mm and the young may hatch as veliger with their shell already provided with a short siphon. Ornament of the embryonic shell consists of zigzag lines and spiral rows of tubercles or may be absent (BANDEL, 1975: pl. 14, fig. 12, pl. 15, figs 5–6). Small veliger larvae are propelled by a two lobed velum and more grown larvae swim with a velum consisting of four long lobes. Species with large larval shell of four whorls have a complex ornament with dense pattern of fine axial ribs in addition to the characteristic spiral ribbon. The pillar of their siphon is ornamented by axial ribs often crossed by spiral ribs. The outer lip of the aperture has a large median lobe that is accompanied by a sinus below and above and ornament of the teleoconch inserts without transitions to the larval shell in shape and ornament. Larval shells from the Gulf of Aqaba in case of *Euplica varians* (SOWERBY, 1832), *E. festiva* (DESHAYES, 1834), *E. ionida* (DUCLOS, 1840) *Mitrella albina* (KIENER, 1841), *M. nympha* (KIENER, 1841), *Zafra selasphora* (MELVILLE & STANDEN, 1901), *Zafra isomella* (DUCLOS, 1840) consist of 3–4 whorls and all resemble each other, but have minor differences which are specific to the species. Several species from the western Atlantic are similar (THIRIOT-QUIEVREUX, 1980: figs 49–52; LEAL, 1990: pl. 20, figs H–J; own observations), and TAYLOR (1975) in KAY (1979) from Hawaii. Data assembled by SLEURS (1982, 1985, 1987) and RIEDEL (2000) of some Pacific species also fit.

In regard to their early ontogenetic shell members of Mitridae and Costellariidae with planktotrophic larva are close to each other, and it appears as if most species from the tropical seas have a free larval stage in their ontogeny. The embryonic shell is about 0.15–0.30 mm wide with rounded shape and smooth surface. First growth-lines appear with begin of the larval shell that consists of 2–3 rounded whorls and grows to about 1 mm in height, bears a short siphon and has a lobe on the outer lip. Ornament often consists of minute tubercles which may be arranged in fine spirals, a more or less distinct spiral rib to the base and a few short ribs on the siphon pillar. After metamorphosis to benthic life, individuals change to a carnivorous mode of feeding. The larval shell of species from the Gulf of Aqaba belonging to *Mitra* LAMARCK, 1798, *Vexillum* RÖDING, 1798, *Cancilla* SWAINSON, 1840 and *Scabricola* SWAINSON, 1840, is similar to each other and to that noted by KAY (1979: figs 100, 106) on 10 species of mitriform veligers from the plankton of Hawaii. All had four lobes and all were strong swimmers. BANDEL et al. (1997: fig. 14) recognized one larva in the plankton of the Red Sea belonging in the relation to *Mitra* with 1.1 mm high and 0.6 mm wide shell. Embryonic and larval shells are sculptured by minute granules and larval whorls in addition an inconspicuous ridge next to the suture. The outer lip of the larva has a rounded projection and the inner lip carries three ridges (RIEDEL, 2000: pl. 16, figs 15–16, 19). Morphological change to the teleoconch is very distinct regarding shape and ornament, while the folds on the inner lip characteristic to the teleoconch are also present on the shell of the veliger larva.

3.3 Characteristics of the protoconch morphology among Toxoglossa

The planktotrophic larva belonging to the Conidae FLEMING, 1822, and Terebridae MÖRCH, 1852, form a shell of similar shape. The protoconch of the Turridae ADAMS & ADAMS, 1853, in contrast, is quite variable in shape and ornament and can be a useful guide to their place in one of several subfamilies. PUILANDRE et al. (2008) confirmed by molecular analysis that the Toxoglossa may represent a monophyletic group within the Neogastropoda as had been suggested by TROSCHER & THIELE (1856–1896) and (THIELE 1931) based on the morphology of the teeth of the radula. MARCUS & MARCUS (1960) analyzed the anatomy of *Hastula cinerea* (BORN, 1780) of the Terebridae and came to the conclusion that Terebridae and Conidae were both derived independently from a stem group of the Turridae. Their separated evolution has since been confirmed by PUILANDRE et al. (2008) based on molecular data. The independence of Terebridae and Conidae within the Toxoglossa had also been suggested by RIEDEL (2000). New classification of the Toxoglossa into 15 families has been presented by BOUCHET et al. (2011). They regarded Conidae and Terebridae as families on equal level to the families into which the “Turridae” have been differentiated. WENZ (1938) assumed that the whole group with its many species has evolved only during the Tertiary, which is confirmed by RIEDEL (2000).

Conus veliger-larvae hatch with an embryonic shell usually ornamented by rows of fine tubercles (Pl. 4, figs 11–13; BANDEL, 1975: pl. 19, figs 10–11, pl. 20, figs 1–12; for references and discussion see RIEDEL, 2000) and these are have approximately 0.3 mm in width. The larval shell may consist of up to 4.5 whorls (RIEDEL, 2000: pl. 9, fig. 14, pl. 10, figs 1–4). It has a wide projection of its outer lip and there may be an ornament of fine tubercles as well as a spiral rib below the suture. Near the margin of the outer lip of the fully grown veliger shell a rounded ridge accompanies the end of the whorl that is quite characteristic to *Conus* (Pl. 4, fig. 12) and differs from other species with similar elongate conical larval shell. In case of *Terebra* the veliger may add a larval shell

during planktotrophic life that closely resembles that of *Conus* (RIEDEL, 2000: pl. 10, figs 8–17). PULLANDRE et al. (2008) suggested that Terebridae MÖRCH, 1852, are a monophyletic unit but their relationship with other groups of Toxoglossa is not resolved. *Conus* has diversified since its appearance during the Eocene to develop about 500 living species (KOHN, 1990; DUDA & KOHN, 2005) which form a monophyletic unit among the Toxoglossa.

Turrioidea ADAMS & ADAMS, 1853, without *Conus* and *Terebra* relation have been split into several quite different groups according to the morphology of the teeth of their radula (THIELE, 1931; TAYLOR et al., 1993) or based on their molecular composition (PULLANDRE et al., 2008). Most of the families recognized by BOUCHET et al. (2011) can be differentiated by their shape and ornament of the protoconch including characters of the embryonic and larval shells. Thus among the Turridae SWAINSON, 1840, with *Gemmula monilifera* (PEASE, 1861) and *Lophiotoma cingulifera* (LAMARCK, 1822) from the Red Sea a large conical protoconch with ornament of axial ribs is developed (pl. 4, figs 15–16), quite like those as known from the Indian Ocean at Natal (KILBURN, 1983: figs 6–11). The ribs are twisted towards the lobe in the aperture near the base. In case of *Lophiotoma* this protoconch has a height of approximately 2 mm with embryonic whorl that is 0.2 mm across and covered by tubercles. The five larval whorls are smooth at first and with the second have ornament of axial ribs (BANDEL et al., 1997: textfig. 22; RIEDEL, 2000: pl. 13, fig. 13). Very similar shells, including the protoconch are from Turridae of the Paleocene of Alabama (RIEDEL, 2000: pl. 17, fig. 16; own data).

Horaiclavidae (BOUCHET et al., 2011) include *Ceritoturris* DALL, 1924, with characteristic larvae from the plankton of the Gulf of Aqaba (Pl. 4, fig 14). Here the protoconch is approximately 0.9 mm high with 0.17 mm wide embryonic shell covered by tubercles and almost three larval whorls sculptured by two keels and a complex pattern of tubercles. The position of one keel is next to the suture and the other next to the base and both end in a sharp, almost triangular beak on the outer lip (BANDEL et al., 1997: figs 24, A, B, C). KAY (1979: fig. 114A) documented the protoconch of *Ceritoturris bittium* DALL, 1924, from Hawaii and KILBURN (1988) illustrated the protoconch of *Ceritoturris nataliae* KILBURN, 1988, and both resembles that of the two species from Aqaba.

A distinct character is found in *Carinapex minutissima* (GARRETT, 1873) from Hawaii (KAY, 1979: fig. 114C, 115O) which is the same or a closely related species in Aqaba and is here very common in the plankton. Its characteristic protoconch is 0.65 mm wide and 0.85 mm high with the 0.17 mm wide embryonic whorl covered with tubercles and is clearly demarcated from the larval shell. The larval whorl carries two spiral ridges with inclined axial ribs between them and end on the outer lip in a triangular lobe. The larva of *Carinapex* appears to be able to cross the Pacific Ocean and to live with minute adults of no more than 3 mm long shell from Hawaii, Australia (KOHN, 1998: fig 15.174G) to the Red Sea. It was placed with the Clavatulidae GRAY, 1853, which is interpreted to hold species usually with larger teleoconch size (BOUCHET et al., 2011).

A group around the genus *Lienardia* JOUSSEAUME, 1884, *Clathurella* CARPENTER, 1857, and *Etrema* HEDLEY, 1918, is interpreted to be represented by the family Clathurellidae ADMS & ADAMS, 1858. Their protoconch is provided with a larval shell ornamented by one spiral keel and otherwise smooth surface. *Lienardia globulosa* HERVIER, 1896, and *Lienardia mighelsi* IRELAND & TOMLIN, 1917, from Aqaba have that same character, the larval shell of *Lienardia* from Hawaii as studied by TURNER (1975) and illustrated by KAY (1979: fig. 114D) as that from Taiwan by CHANG (2007) has that same character.

Family Mitromorphidae CASEY, 1904, with *Mitromorpha metula* (HINDS, 1843) includes species with small shell and axial and spiral ornament of about equal strength somewhat convergent to *Columbella* and its relatives among the Columbelloidea. The protoconch is characterized as with up to 4.5 smooth whorls with scattered tubercles and with basal spiral rib and sudden change of ornament at the onset of the teleoconch. *Mitromorpha metula* has no operculum, the radula is as characterized by THIELE (1931) characteristically toxoglossate, and *M. metula* in Hawaii look just like that in Aqaba. Thus this species appears to be able to migrate during its larval part of ontogeny through most of the tropical Pacific. The larval shell of *Mitromorpha* differs from that of all other Turrioidea by conical shape and ornament only by fine tubercles and weak basal spirals, similar to the protoconch of many muricids which usually have the margin of the final aperture more thickened by a varix, while it is low in *Mitromorpha*. In case of lecithotrophic development obviously locally many species have evolved, as was noted from the Indian Ocean at the African coast (KILBURN, 1986).

Mangelidae FISCHER, 1883, with *Eucithara* FISCHER, 1883, and *Pseudorhaphitoma* BOETTGER, 1895, are common in the plankton of the Gulf of Aqaba with about three whorls and 0.6 mm high shell. The embryonic whorl has only fine tubercles and the larval shell is sculptured by collabral ribs ending on or near a basal spiral rib that ends in the lobe of the outer lip. The protoconch of *Eucithara* as documented by RIEDEL (2000: pl. 11, fig. 7) documents these characteristics.

The species of the second large unit of the Turrioidea are connected to each other by the ornament of their embryonic shell with spiral ribs of prickly wire shape. *Vepracula* MELVILL, 1917, from Aqaba has its small, not more than 3 mm high shell of fusiform shape with the relatively high spire with spines. The 3.5 whorls of the protoconch have the embryonic shell of 0.17 mm in width sculptured by spiral ribs which are interconnected by axial lines which often end before meeting with the next spiral rib, and are thus prickly wire like in shape. The larval whorls differ by having the outer lip with a hook-like projection and spiral rib at the corner to the base

ending in it. Sculpture consists of 15–20 narrow axial ribs with median tubercles and irregular wrinkles. The veliger larvae have a remarkable behavior in that they do not retract into their shell but wrap the four velar lobes around their shell. The protoconch of *Microdaphne* MCLEAN, 1971, is similar but of more conical and shorter shape (RIEDEL, 2000: pl. 12, figs 7–11).

Raphitomidae such as *Kermia* (Pl. 4, figs 17–18) has the embryonic shell with sculpture spiral ribs which at regular intervals have straight side branches which may connect to a net of rectangles or end before meeting the neighbor rib thus with prickly wire like ornament. The diameter of the embryonic whorl measures about 0.22 mm and it ends with growth lines. The larval shell has axial ribs on the shoulder which turn into curving ribs in the lower half of the whorl. These are connected to each other by ribs vertical to them thus forming a net of rhombs (BANDEL et al., 1997: figs 24 D–E). The juvenile shell of the teleoconch has very different ornament. The margin of the outer lip of the larval shell is raised and the evenly rounded median lobe is accompanied by a wide regular apical sinus. *Philbertia linearis* MONTAGU from the North Sea has a similar larval shell as was described by THORSON (1946). This is very similar in *Pleurotomella* and *Taranis* (RIEDEL, 2000: pl. 12, figs 12–16, pl. 13, figs 1–5). Similar net sculpture as in living Raphitomidae is found only since the Eocene (RIEDEL, 2000).

Regarding the protoconch in species with a planktotrophic larva Conidae and Terebridae have a similar shape while a large number of shell types is presented in the Turridae (including all other families of the Toxoglossa outside of Conidae and Terebridae as in PUILANDRE et al., 2008; BOUCHET et al., 2011), indicating that they represent a diverse lot. This confirms RIEDEL (2000) who grouped the Toxoglossa as Turrina in three independent families, Conidae, Terebridae and Turridae. He also noted that the larval shell as well as the teleoconch of the Turridae has a wide range of shapes and ornaments, while it is of the same type within the Conidae and Terebridae. In case the reconstruction of the tree of evolution within the Toxoglossa as presented by PUILANDRE et al. (2008), and BOUCHET et al. (2011) reflects reality, the complex ornament of many larval shells found among the Toxoglossa evolved from the relatively simple ones possibly of the type as has been conserved in the Conidae.

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Plate 1

- Fig. 1: The protoconch of *Gyrodes (Dockeryella) major* has 2.25 whorls and an indistinct transition into the teleoconch.
- Fig. 2: The juvenile shell of *Gyrodes* in fig. 1 seen from the side is about 1.8 mm high, from Ripley Formation, Mississippi.
- Fig. 3: The protoconch of *Polinices (Polinices) mammilla* (LINNÉ 1758) consists of more than three whorls with indistinct transition into the teleoconch. It measures about 0.8 mm in width and 0.7 mm height. Plankton Aqaba, Red Sea.
- Fig. 4: The embryonic shell as in fig. 3 is ornamented with fine granules and distinct from the larval shell. It measures about 0.11 mm across.
- Fig. 5: The embryonic shell of the protoconch of *Eunatica papilla* (GMELIN, 1791) has ornament of granules arranged in spiral lines and is 0.16 mm wide. Plankton Aqaba, Red Sea.
- Fig. 6: The fully grown larval shell that may belong to *Natica gaultieriana* (RECLUZ, 1844) is almost 0.7 mm wide and 0.6 mm high. The operculum is spiral with the nucleus in central position in the young larva and shifted somewhat to the left in the late larva. Plankton Aqaba, Red Sea.
- Fig. 7: The embryonic whorl of the shell in fig. 6 measures about 0.12 mm across and is densely ornamented with large tubercles. Adults are common just below the beach at Aqaba.
- Fig. 8: Embryonic shell and begin of larval whorl of *Cypraea* sp. from the plankton off Aqaba. Shell is 0.3 mm wide.
- Fig. 9: Fully grown larval shell of *Cypraea* sp. from the plankton off Aqaba with apertural projection and thickened margin. The shell with about three whorls is about 1.2 mm high.
- Fig. 10: The embryonic shell in the grown larval shell is coated by external shell deposits from the larval mantle. Detail to fig. 9, embryonic whorl 0.15 mm wide.
- Fig. 11: Protoconch of *Cypraea* sp. from Aqaba with transition of larval shell to the first whorl of the teleoconch well differentiated. Change from larval to adult ornament is abrupt. The shell is 2 mm high.
- Fig. 12: Fully grown larval shell of a member of the Ovulidae such as in *Prosimnia* with ornament of oblique rectangles and about 1.2 mm high shell. The aperture has a wide rounded lobe and its margin is thickened. Gulf of Aqaba.
- Fig. 13: Embryonic whorl of the shell of the larva of Ovulidae from the species in fig. 12 with pit and ridge ornament and about 0.15 mm in width. Caught in the plankton of the Gulf of Aqaba
- Fig. 14: Fully grown larval shell of *Sabia conica* from the plankton of the Gulf of Aqaba consists of 2.3 whorls, has a straight aperture and measures about 0.5 mm in diameter.
- Fig. 15: Embryonic whorl of the shell in fig. 14 measures 0.15 mm across and is sculptured by a fine groove and ridge pattern that ends abruptly with first onset of growth lines.
- Fig. 16: Juvenile shell of *Sabia conica* about 2 mm across from the Gulf of Aqaba with change in shape and ornament in the transition from the larval shell to the teleoconch.
- Fig. 17: The protoconch of *Thylacus cretaceus* from the Campanian Coffee Sand, Ripley Formation, is rounded consists of three whorls with about 1 mm in size. The larval shell has delicate ornament of fine spiral lines crossed by collabral lines and its aperture has a low lobe on its outer lip. Shape of the larval shell is similar to that of modern *Sabia*.
- Fig. 18: The embryonic whorl of the protoconch of *Thylacus* in the detail to fig. 17 measures 0.15 mm across and has fine groove and ridge pattern.

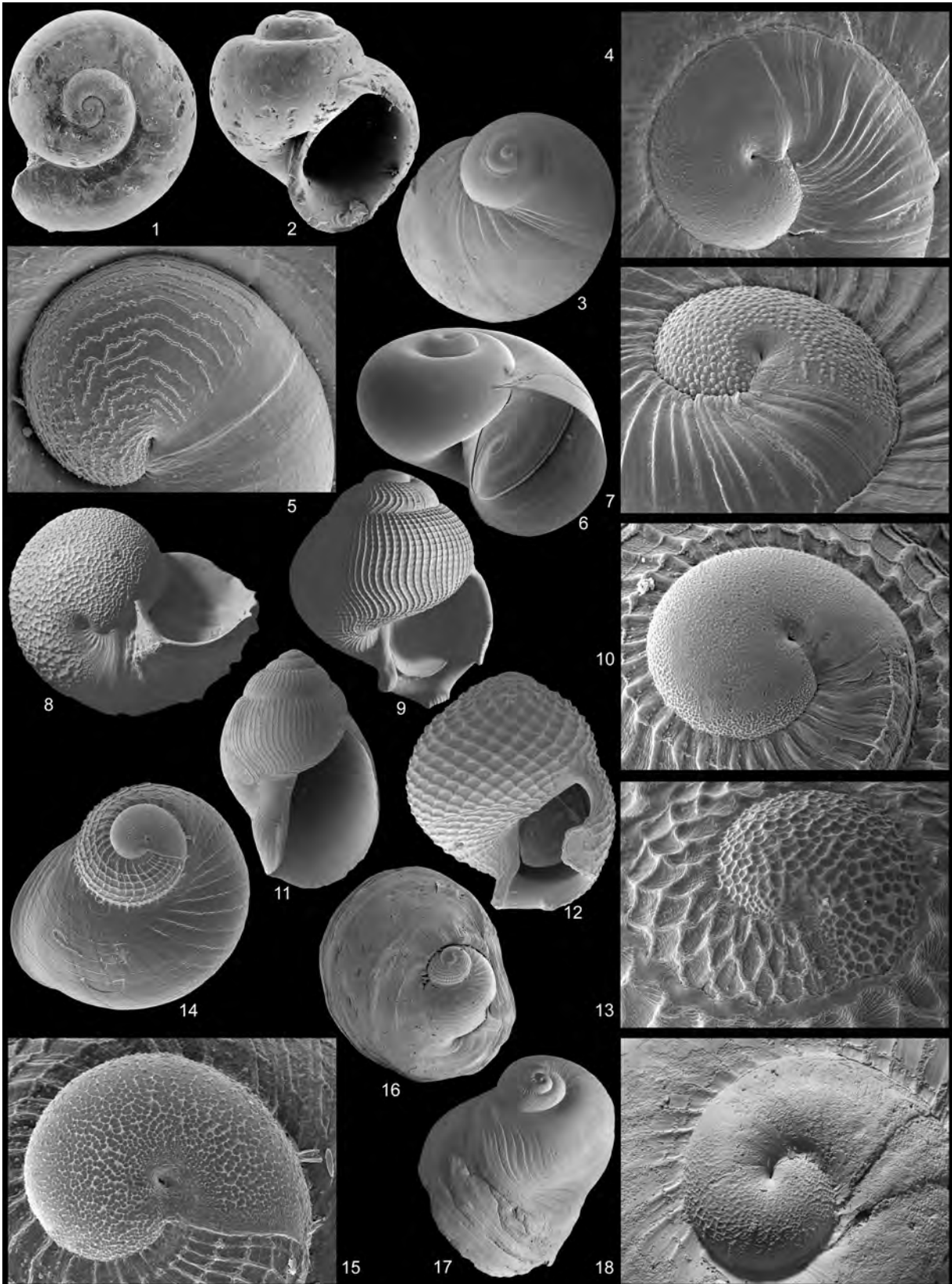


Plate 2

All figures represent species from Ripley Formation, Mississippi and Tennessee.

- Fig. 1: Apical view of *Gyrotropis squamosa* shows the larval shell of almost two rounded whorls with smooth surface (detail in fig. 4) and 0.3 mm in width.
- Fig. 2: Apertural view of fig.1 has the shell of about 2.8 mm in height and its conical protoconch with flat top.
- Fig. 3: The larval shell of *Gyrotropis squamosa* has a median spine-like projection of the outer lip, axial ribs as in the teleoconch in the last part of its larval shell. The protoconch is about 0.6 mm high.
- Fig. 4: Apical view of fig. 3 with embryonic whorls in the flat top, smooth early larval shell and transition to the axially ornamented larval shell near the end of the larval shell.
- Fig. 5: Protoconch and early teleoconch of *Astandes nodosus* from Coffee Sand Mississippi has details in fig. 6. The protoconch consists of almost three whorls of about 1 mm in height and width.
- Fig. 6: Protoconch of *Astandes nodosus* with its spiral ribs continuing across the transition from larval shell to the teleoconch. The embryonic whorl is about 0.15 mm wide and lies in the flat and smooth top of larval whorl, which later is ornamented by rectangles.
- Fig. 7: The protoconch of *Neocolombellina carlea*, detail to pl. 3, fig. 18, has a smooth embryonic whorl and also smooth early larval shell that is 0.6 mm wide. It resembles *Astandes*, but has a rounded and not concave top.
- Fig. 8: The embryonic whorl of *Sargana stantoni* (WELLER) measures almost 1 mm in diameter and has transition into the teleoconch visible in growth line pattern.
- Fig. 9: Juvenile shell of *Sargana* with 3.3 mm diameter and change from rounded protoconch to teleoconch with corner.
- Fig. 10: The embryonic whorl of *Sargana* is lowly trochospiral as seen in umbilical view. Transition from almost 1 mm wide protoconch to teleoconch is indicated by and apertural margin and growth lines.
- Fig. 11: The protoconch of *Pseudecphora proquadricostata* is a low coil with rounded smooth whorls and is almost 1 mm in diameter, the juvenile shell measures about 2.8 mm in diameter.
- Fig. 12: The detail to fig. 11 of *Pseudecphora* documents the change from the protoconch with rounded whorls to the teleoconch with a spiral keel.
- Fig. 13: The larval shell of *Weeksia amplificata* is trochospiral in the flat teleoconch.
- Fig. 14: The protoconch of *Weeksia amplificata* has 2.5 whorls and 0.7 mm in width and height.
- Fig. 15: Embryonic whorl of *Weeksia amplificata* as detail to fig. 13 with ornament of tubercles present on smooth shell, diameter of first whorl 0.23 mm.
- Fig. 16: Juvenile shell of *Pyropsis* sp. with folds on the inner lip and barrel shaped larval shell. The shell is 2.7 mm high.
- Fig. 17: *Pyropsis* sp. as in fig. 16 with larval shell 1.8 mm high and without apertural projection and adult ornament printed into its last portion.
- Fig. 18: Same shell as figs 16–17 of *Pyropsis* sp. shows the embryonic whorl about 0.2 mm wide and larval shell about 1 mm wide.

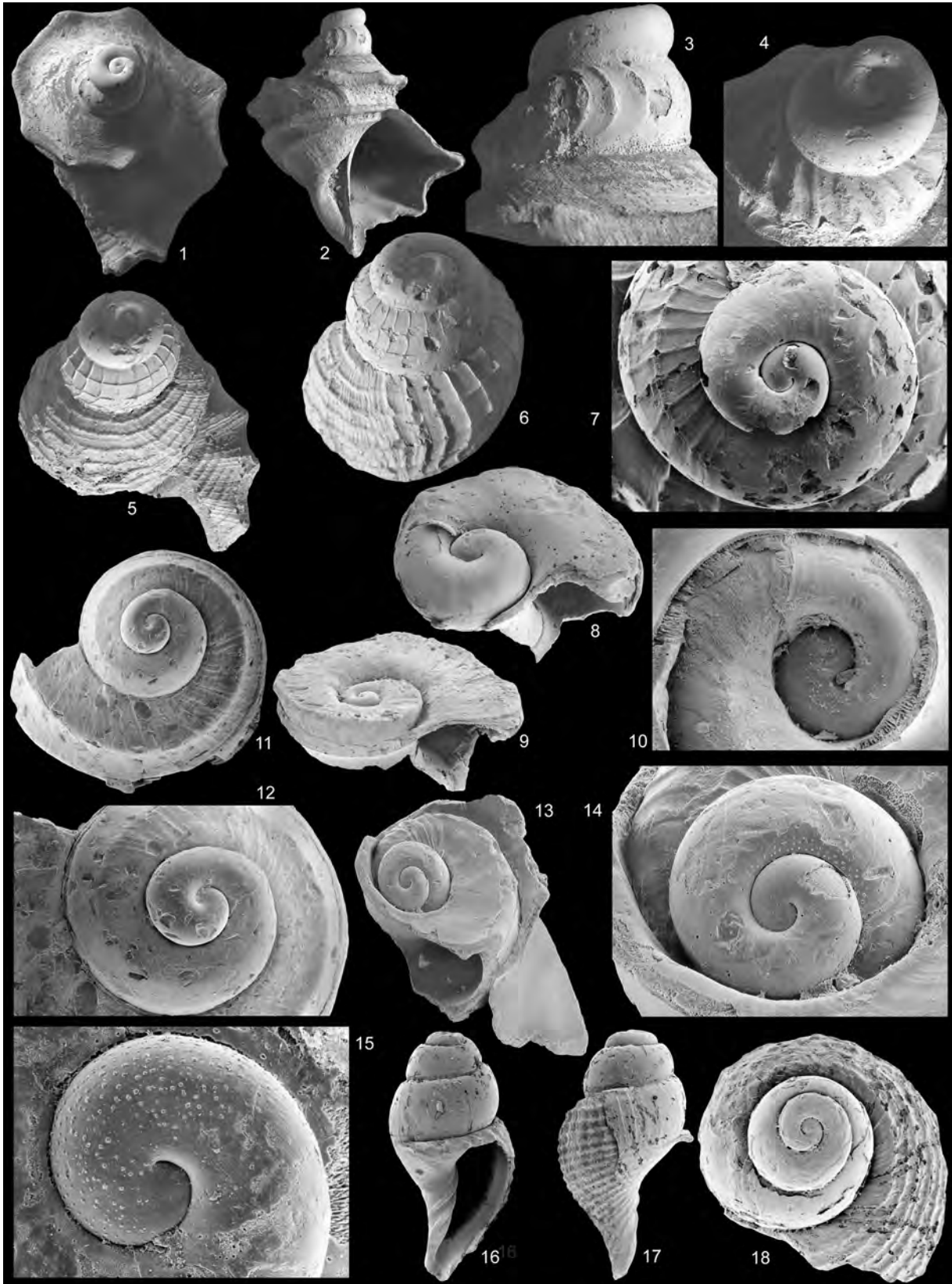


Plate 3

- Fig. 1: The embryonic shell of *Cymatium* from the Red Sea has a pit a ridge ornament, is about 0.18 mm wide and partly coated by spines that have been produced together with the larval shell.
- Fig. 2: The early larval shell of *Cymatium* is from the Red Sea with 0.6 mm wide shell. The embryonic shell is partly covered by spines of organic periostracum.
- Fig. 3: The larval shell of *Phalium* with the operculum in place, shell about 3 mm wide. The ornamented whorl is coated with smooth periostracum. Shell from plankton, Gulf of Aqaba.
- Fig. 4: The larval shell of *Cymatium* in the larval stage with shell about 2 mm high and early shell portion covered by deposits of periostracum as produced by the larval trunk. The larva is from the plankton of the Gulf of Aqaba.
- Fig. 5: The protoconch of *Cymatium* on the juvenile shell from Aqaba is 2.8 mm high and distinct from the teleoconch by ornament and thickened aperture.
- Fig. 6: The protoconch of *Tutufa* is about 2.8 mm high and distinct from the early teleoconch in sharp change of ornament at its aperture, from the reef at Aqaba.
- Fig. 7: The embryonic whorl of *Eosassia gwinae* from Coffee Sand, Mississippi, measures about 0.2 mm in diameter and has ornament of ridges and grooves while the early larval shell has tubercles as ornament.
- Fig. 8: Transition from the dome shaped protoconch of *Eosassia gwinae* consisting of 3.5 whorls with about 1.5 mm in height and almost the same in width is with continuation of general pattern, and simple. Coffee Sand, Mississippi.
- Fig. 9: View on first varix of thickened outer lip of *Eosassia gwinae* and teeth on the inner side of the aperture seen in the shell that is about 2.2 mm high. Coffee Sand, Mississippi.
- Fig. 10: The embryonic whorls of *Neocolombellina cancellata* is ornamented with tubercles and 0.18 mm wide. Coffee Sand, Late Campanian, Mississippi.
- Fig. 11: Juvenile shell of *Eosassia gwinae* with the first larval whorls ornamented by dots which become arranged into axial rows which in the second larval whorl form spiral and axial lines that make a reticulate pattern. 2.2 mm high shell. Coffee Sand, Mississippi.
- Fig. 12: The protoconch of *Neocolombellina cancellata* consists of 3.5 whorls with about 1 mm in width and height. It is succeeded by the first larval whorl with ornament of spiral lines and dots between them. Fig. 10 is a detail.
- Fig. 13: Juvenile shell of *Neocolombellina cancellata* is about 2 mm in height. The last part of the larval shell has axial ribs forming a pattern of cancellation. The teleoconch begins with strong ornament of axial folds, and margin of the protoconch is simple. Coffee Sand, Mississippi.
- Fig. 14: The protoconch of *Caveola acuta* is about 1.5 mm wide with 3.5 whorls. The embryonic whorl is about 0.2 mm wide and first 2.5 larval whorls are, later adult ornament enters with spiral ribs, later also axial ribs. The transition to the teleoconch is quite indistinct. Ripley Formation, Mississippi.
- Fig. 15: Juvenile teleoconch of *Caveola acuta* with first varix shows teeth on the inner side of the outer lip, 2.2 mm high. Ripley Formation, Mississippi.
- Fig. 16: The protoconch of *Mataxa elegans* is more than 2 mm high and wide and has a smooth margin of its outer lip. The first varix on the teleoconch has teeth on its inner side. The shell is 3.5 mm high. Ripley Formation, Mississippi.
- Fig. 17: The embryonic whorl of *Mataxa elegans* is 0.12 mm in width that is ornamented by tubercles on a smooth background. Detail to fig. 16.
- Fig. 18: Apical view of *Neocolombellina carlea* has the transition from embryonic shell to smooth larval shell and ornament of larval shell indistinctly into the ornament of the early teleoconch. Detail in pl. 2, fig. 7. Shell is 1.8 mm wide. Coffee Sand, Late Campanian, Mississippi.
- Fig. 19: Juvenile shell of *Neocolombellina carlea* with shell added after the first varix of the juvenile teleoconch. Shell height 3 mm.
- Fig. 20: In the transition from the larval shell of *Neocolombellina carlea* to the teleoconch the spiral ribs continue while axial ribs change in shape. The larval shell is 1.5 mm wide.



Plate 4

- Fig. 1: Fully grown larva of a muricid (*Morulaanaxeres*) from Aqaba with about 1 mm high shell with thickened margin of the outer lip.
- Fig. 2: Fully grown larva of the coralliophilid [Muricoidea, *Quoyula madreporarum* (SOWERBY; 1832)] from Aqaba with ornamented embryonic and larval shell and thickened aperture, 0.9 mm high shell.
- Fig. 3: Highly ornamented larval stage of *Coralliophila erosa* (RÖDING, 1798) is distinct from the ornament in the embryonic shell, from the plankton of the Gulf of Aqaba. Shell height 0.4 mm and apertural margin of growing larval shell not thickened.
- Fig. 4: Juvenile shell of *Coralliophila erosa* from Aqaba with strong change in ornament and shape from protoconch to teleoconch, larval shell margin thickened, about 1 mm high.
- Fig. 5: Juvenile shell of a columbellid [*Zafrona isomella* (DUCLOS, 1840)] from Aqaba has strong change in ornament from protoconch to teleoconch. Shell height 1.2 mm.
- Fig. 6: Fully grown larval shell of a columbellid from the plankton of the Gulf of Aqaba with apertural margin thickened, detail in fig. 7, shell 1 mm high.
- Fig. 7: Embryonic ornament of columbellid in fig. 5 consists of spiral lines, width of embryonic whorls about 0.25 mm.
- Fig. 8: Juvenile shell of *Nassarius delicatus* from Aqaba has the protoconch distinct from the teleoconch by ornament, shape and thickened margin of the fully grown larval shell, height about 1.2 mm.
- Fig. 9: Juvenile shell of a mitrid (*Mitra Swainsonia fissurata*) from Aqaba has larval shell distinct in ornament and shape from teleoconch, shell 1.6 mm high.
- Fig. 10: Early teleoconch of the mitrid *Neocancilla filaris* from Aqaba with aperture of larval shell thickened even though apertural projection was broken off before metamorphosis, shell 1.8 mm high.
- Fig. 11: Juvenile shell of *Conus* sp. from Aqaba had the projection of the outer lip broken, but still thickened, shell 1.3 mm high.
- Fig. 12: Fully grown larval shell of *Conus* sp. from the plankton of the Gulf of Aqaba has rounded projection of the outer lip, shell 1.2 mm high.
- Fig. 13: Embryonic shell of *Conus* as in figs 11 and 13 has ornament of rows of tubercles, first whorl 0.2 mm in diameter.
- Fig. 14: The larval shell of the turrid Horaiclavidae *Ceritoturris* sp. from the plankton of the Gulf of Aqaba has strongly ornamented embryonic a larval shell and outer lip extended in a hook. Shell height 0.9 mm.
- Fig. 15: Juvenile turrid (*Gemmula* sp.) from the Red Sea at Aqaba has indistinct transition from the larval shell to the teleoconch, but strong ornament on embryonic and larval whorls. Shell is 2.5 mm high.
- Fig. 16: Earliest benthic stage of member of the Turridae (*Tritonoturris* sp.) has ornament of larval shell totally different from that of teleoconch. Shell height 0.8 mm.
- Fig. 17: Juvenile shell of a member of the Raphitomidae (*Kermia* sp.) from Aqaba with strongly ornamented larval shell well distinct from the teleoconch. The embryonic ornament is spiral, the larval ornament consists of rhombs and the adult is of axial and spiral ribs, shell 1 mm high.
- Fig. 18: Larval shell of a member of the Raphitomidae from the plankton of the Gulf of Aqaba has 0.6 mm high shell. Ornament of the embryonic whorl is by strong spiral ribs and axial elements, very different from larval whorl and aperture is sinuous and thickened.

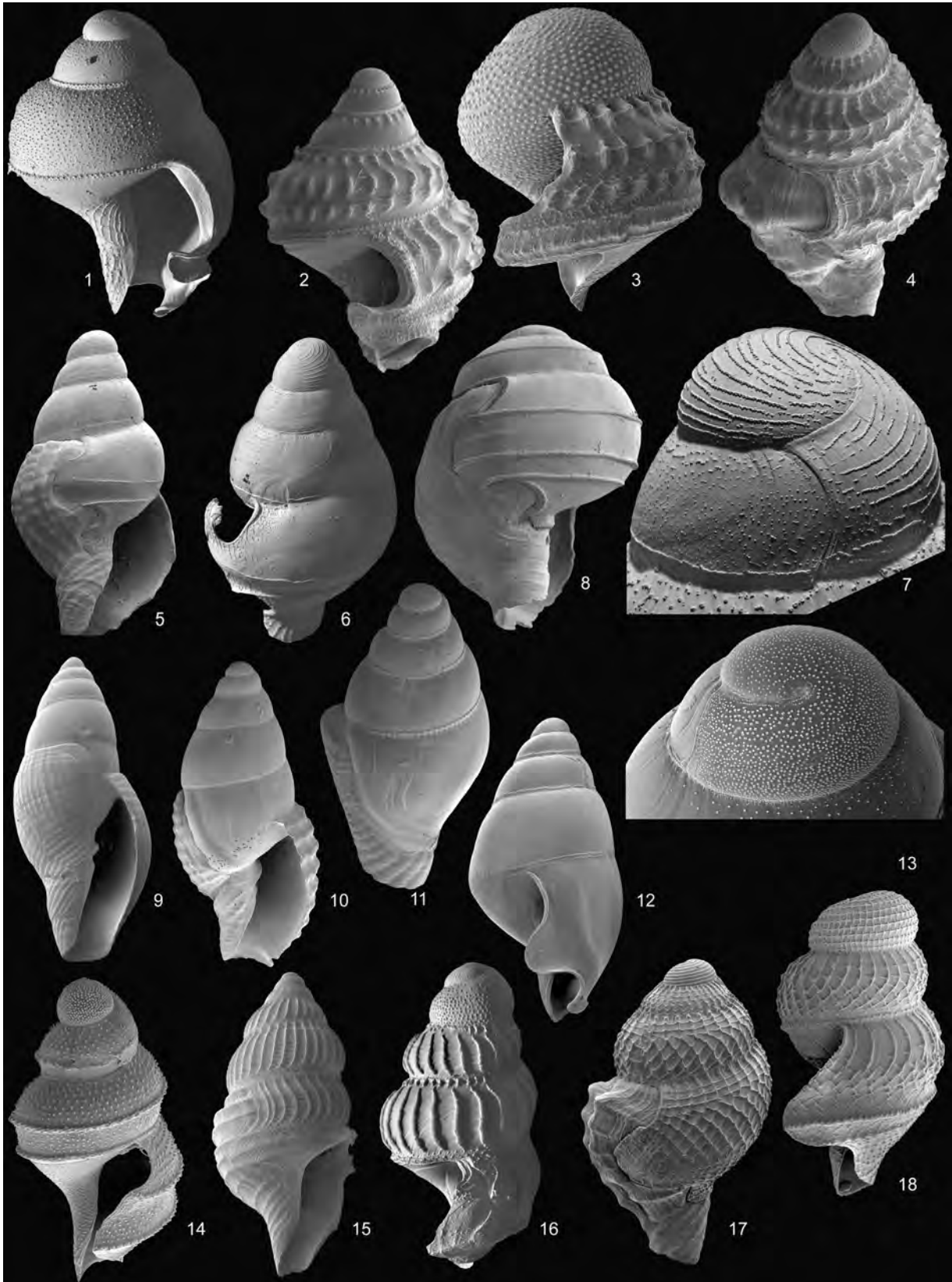


Plate 5

- Fig. 1: Protoconch of *Bellifusus* sp. with large, smooth embryonic whorl from above. Detail to fig. 15.
- Fig. 2: The protoconch of *Bellifusus* cf. *curvicostatus* WADE has an angle of about 50°, is almost 2 mm high, and consists of about three whorls and the embryonic shell is about 0.18 mm wide.
- Fig. 3: Embryonic shell of *Deussenia* cf. *ripleyana* HARBISON from Ripley Formation, with well rounded whorl that is about 0.15 mm wide and ornamented by somewhat irregular tubercles. Detail to fig. 5.
- Fig. 4: Protoconch of *Stantonella* sp. has more than four whorls and transitional ornament from larval shell to teleoconch. Ornament of larval whorls consists of sinuous growth lines and a row of tubercles below suture. The last larval whorl was repaired. Shell about 1 mm wide. Detail in fig. 6.
- Fig. 5: The conical protoconch of *Deussenia* cf. *ripleyana* consists of almost 4.5 whorls with about 55 ° apical angle and is about 0.9 mm wide and 1.5 mm high. Shell height about 2 mm.
- Fig. 6: Embryonic whorl of *Stantonella* sp. with about 0.18 mm in diameter, detail to fig. 5, with fine ornament of granules and a subsutural row of tubercles on the larval whorl.
- Fig. 7: The embryonic whorl of *Amuletum* is about 0.15 mm wide and ornamented by tubercles in dense pattern. Detail to fig. 8.
- Fig. 8: The protoconch of *Amuletum* cf. *wadei* from Ripley Formation consists of a little more than 4 whorls with about 50° apical angle and is about 0.7 mm wide and almost 1 mm high.
- Fig. 9: The embryonic shell of *Perissoptera* sp. (Aporrhaidae) from Ripley Formation is only about 0.12 mm wide (fig. 10), with granules as ornament. The protoconch of about four whorls with conical shape has the apical angle about 70°. The larval shell has a large, rounded median hook of the outer lip, and first teleoconch is dominated by a dense pattern of curving axial ribs.
- Fig. 10: Embryonic whorl, detail to fig. 9, also with tubercles on smooth background.
- Fig. 11: Embryonic whorl of *Drilluta* cf. *major* is 0.15 mm wide and ornamented by tubercles on a smooth background. Detail to fig. 12.
- Fig. 12: The protoconch of *Drilluta* cf. *major* WADE from Ripley Formation consist of 4.2 round-sided whorls, 0.8 mm wide and about 1 mm high. A line follows the anterior projection of the outer lip, and granules are present below the suture. Transition from the larval shell to the teleoconch is gradational.
- Fig. 13: Detail to fig. 14 of *Graphidula* with the embryonic whorl of 0.18 mm in diameter and distinct from larval shell by simple straight growth increment.
- Fig. 14: Protoconch of *Graphidula* sp. from Ripley Formation with more than 4 whorls and 1 mm in width, with ornament of granules on smooth larval whorls and tubercles on the embryonic whorl (fig. 13).
- Fig. 15: Juvenile shell of *Bellifusus* sp. from Ripley Formation with fig. 1 documenting the embryonic whorl. About 2 mm high.
- Fig. 16: Juvenile shell of *Fusimilis* sp. from Ripley Formation with 2 mm in height and about 3.5 whorls of larval shell with strong median projection and granular ornament of the embryonic whorl.
- Fig. 17: *Paladmete* sp. from Ripley Formation with about 0.2 mm wide embryonic shell ornamented with tubercles. Detail to fig. 18.
- Fig. 18: The protoconch of *Paladmete* sp. has a strong basal lobe on the margin of the outer lip of the larval shell. Shell height 1.8 mm.



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