On the origin of the carnivorous gastropod group Naticoidea (Mollusca) in the Cretaceous with description of some convergent but unrelated groups

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Professor Dr Ekkehard Herrig dedicated to his 65th birthday.

ABSTRACT: The naticids represent a natural group of Neomesogastropoda which together with the other groups of this taxon have arisen during mid-Cretaceous time. Naticids usually move through the sediment and have probably very much at the begin of their history taken up the characteristic mode of feeding by hunting prey with external skeleton and drilling a hole into its shell to reach its soft parts. They also have developed the rather large globular protoconch that connects them to Cretaceous species which might represent stem group representatives of the Naticoidea. Among these the genus *Schizobasis* WADE 1916 of which the new species *Schizobasis kilburni* is described, as well as *Hillites*, and the new genus *Natalites* with the species *Natalites herberti*. These genera still had a narrow siphon and a subsutural ribbon, the later of which is still found in the shell of the subgenus *Gyrodes (Gyrodes)* of the Gyrodinae of the Naticidae. The subsutural ribbon is a character that unites many of the late Cretaceous stem group representatives of Neomesogastropoda and Neogastropoda. It formed as the result of the presence of a posterior apertural notch. Within the Gyrodinae to which the two new subgenera *Gyrodes (Dockeryella)* and *Gyrodes (Banis)* are added, the characteristic features of Naticidae form and features of later convergencies within the group are observed here. Naticids living trough Tertiary times to now have been differentiated into many genera and higher taxa, but classification does not appear to reflect well the natural course of evolution. Until this is elucidated it appear best to distinguish only three subfamilies, the Polinicinae with horny operculum, the Naticinae with calcareous operculum, and the Sininae with reduced operculum that no longer seals the aperture, and commonly with a body that is to large to withdraw fully into the shell. The protoconch is a very good character to determine a naticoid and to differentiate convergent but unrelated groups, especially the Pseudamauridae and relation, which have been common from the Jurassic to the end of the Eocene. The protoconch of the pseudamaurids *Ampullina*, *Amaurellina*, and *Crommium* from the Eocene are described and differentiated from naticid protoconchs by their size, shape and ornament. Within the naticids protoconchs show characteristic shape in planktotrophic species while lecithotrophic development is very well distinguished by altered shape and size.

KEYWORDS: Gastropoda, Naticoidea, phylogeny, taxonomy, new taxa, Cretaceous, Tertiary

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KURZFASSUNG: Über den Ursprung der räuberischen Naticoidea (Gastropoda, Mollusca) in der Kreide verbunden mit der Beschreibung einiger konvergenter aber nicht verwandter Gruppen.

Die Naticiden sind eine natürliche Einheit der Neomesogastropoda, die während der mittleren Kreide entstand. Diese in der Regel im Boden wühlend sich fortbewegenden Schnecken haben wahrscheinlich schon zu Beginn ihrer Geschichte, ihre charakteristische Ernährungsweise, des eine beschalte Beute-Aufbohrens, entwickelt und zudem eine rundliche und vergleichsweise große Embryonal- und Larvalschale ausgebildet. Die Gyrodinae stellen die ursprünglichste Gruppe der Naticiden dar, zu deren Stammgruppenvertretern die Gattungen *Schizobasis* mit der neuen Art *Schizobasis kilburni*, *Hillites* und die neue Gattung *Natalites* mit der Art *Natalites herberti* gehören können. Vor allen Dingen letztere läßt sich ganz gut mit der Untergattung *Gyrodes (Gyrodes)* in Verbindung bringen, da diese noch das charakteristische subsuturale Band besitzt, welches der kretazischen Basisgruppe vieler der Neomesogastropoda und Neogastropoda gemein ist. Es stellt das Bildungsprodukt des hinten in der Apertur gelegenen Kanals dar. Innerhalb der Gyrodinae, deren Untergattungen um die beiden Taxa *Gyrodes (Dockeryella)* und *Gyrodes (Banis)* erweitert werden, entsteht die typische naticide Gehäusegestalt. Die während des Tertiärs und heute lebenden Naticiden sind zwar in viele Gattungen und höhere Taxa aufgeteilt, doch erscheint dieses System weitgehend künstlich. Hier wird der natürliche Gang der Evolution sicher von der Taxonomie noch nicht widergespiegelt und am Besten sind nur drei Unterfamilien aufzuführen, die Polinicinae mit organischem Operkulum, die Naticinae mit kalkigem Operkulum und die Sininae mit reduziertem Operkulum und häufig nicht mehr den Weichkörper völlig fassender Schale. Die Gestalt, Größe und das Ornament des Protoconches sind ein sehr gutes Merkmal, um Naticiden zu erkennen und von anderen Gruppen mit ähnlichem Teleoconch zu unterscheiden. Unter letzteren sind besonders die Pseudamauridae und ihre Verwandtschaft zu nennen, deren Protoconch von *Ampullina*, *Amaurellina* und *Crommium* aus dem Eocän beschrieben wird. Ihn unterscheidet Größe, Gestalt und Ornament von jenem der Naticiden. Pseudmauridae waren vom Jura bis zum Eozän divers, sind mit Naticiden nicht verwandt, wurden aber weithin mit ihnen verwechselt. Innerhalb der Naticiden ist die planktotrophe Entwicklungsweise sehr gut von jener der lecithotrophen Lebensweise an der Gestalt des Protoconch zu erkennen.

STICHWORTE: Gastropoda, Naticoidea, Phylogenie, Taxonomie, neue Taxa, Kreide, Tertiär

1. INTRODUCTION

Representatives of the caenogastropod super-family Naticoidea living in modern seas represent a natural well circumscribed group of Neo-mesogastropoda (see BANDEL & RIEDEL 1994). Their habit of drilling a hole into the shell of their prey, commonly bivalves and other gastropods, has made them well known. Naticoidea contain a group of species unified in a number of extant and fossil genera, many of which are rather similar to each other. The modern representatives of these carnivorous Neomesogastropoda are easy to recognize and determine by features of their anatomy. Fossil members, in contrast, are difficult to recognize because of the rather general heliciform to littoriniform shape of the shell and rather simple outline of the aperture. Such shell shape is found in many, quite unrelated groups of gastropods.

In a review on the taxonomy of the group KABAT (1991) suggested that about 2700 species of Naticoidea have been described. They have been attributed to 25 family level names of which, according to KABAT 6 are valid and the remainder represent synonyms. According to the same author there are 65 genus level names in current usage and 253 have been proposed in literature. KABAT (1991) expressed the opinion that there are about 200 valid recent species, so most of the described species apparently represent fossil species of the group. KABAT (1996) suggested that about 260 to 270 Recent species are actually living in the seas, with most species and genera in the tropical region. Considering the problem of convergence in the recognition of fossil naticoids (see below) the large number of fossil species does not reflect the evolutionary history of the Naticoidea, but represents an artefact.

WENZ (1938) adopted the classification of THIELE (1931) to include fossil species. He proposed the existence of six subfamilies in the Naticidae which are the only family of the superfamily Naticoidea. Only the subfamily Gyrodinae consists of

exclusively fossil representatives. The Globulariinae holds mainly fossil representatives and has only the name giving *Globularia* SWAINSON 1840 living today. Polinicinae, Globisininae, Sininae and Naticinae have fossil representatives but are basically founded on species that live today. Globisininae consist of a single genus *Globisinum* MARWICK 1924 with a number of species that lived since the beginning of the Tertiary predominantly near New Zealand. MARINCOVICH (1977) recognized four subfamilies in his review on Naticidae of the north American West Coast, the Naticinae, Polinicinae, Sininae and Ampullospirinae, including the Gyrodinae within the Polinicinae. This classification was accepted by MCLEAN (1996) as well. Naticinae, Polinicinae and Sininae had been recognized by RÖDING as early as 1798 (KABAT 1991). The subfamily Ampullospirinae COX 1930 more or less includes the Globulariinae of WENZ (1938) but besides *Globularia* also holds the genera *Amauropsis* MÖRCH 1857 and *Pseudopolinices* GOLIKOV & SIRENKO 1983 which are based on extant species.

PONDER & WARÉN (1988) distinguished in the superfamily Naticoidea the fossil family Ampullinidae COSSMANN 1918 (= Ampullospiridae) and the extant family Naticidae. The latter was split into the Naticinae, Polinicinae, Sigaretinae CUVIER 1817 (= Sininae) and Tylostominae STOLICZKA 1868. The last taxon is based on the genus *Tylostoma* SHARPE 1849 from the Cretaceous of Europe. As KABAT (1991) mentioned correctly, the type of this genus, *Tylostoma globosum* SHARPE 1849, remains uncertain in its systematic placement. It is not even certain that this genus belongs to the Caenogastropoda (compare WENZ 1938: fig. 2941). KABAT (1996) regarded the Ampullospirinae as a grade and not a clade of naticids primarily found in the Arctic and Antarctic seas. In the same way he treated the Polinicinae as a grade with only the taxa Sininae and Naticinae remaining in the extant fauna as monophyletic clades.

Among the fossil species of supposedly naticoid relation especially the Late Cretaceous to Eocene members of the Pseudamauridae represent a major problem. These have just recently been recognized to represent probable Cerithiimorpha and not members of the Naticoidea (KOWALKE & BANDEL 1996). Their ecology and early ontogeny differ from that of the Naticidae. Pseudamauridae apparently are related to the Ampullininae (= Ampullospirinae) of the Jurassic as is evidenced by the genus *Ampullospira* HARRIS 1897 from the English Mid-Jurassic that had a similar ontogeny as *Pseudamaura* from the Cretaceous and *Ampullina* BOWDICH 1822 from the Eocene, due to the shape of their protoconch (SCHRÖDER 1995). *Ampullospira* and relation have induced CARRIKER & YOCHELSON (1968) to assume that naticids arose in the early Jurassic. But also some fossil Neritimorpha like the Triassic *Hologyra* KOKEN 1892 closely resemble naticids and had been included in these by a number of authors in last century (see WENZ 1938). Due to the similarity of *Hologyra* and Triassic relation regarding the shape of the teleoconch, BOUCHET & WARÉN (1993) and KABAT (1996) suggested that Naticidae existed during the Triassic. WENZ (1938) had recognized their place in the Neritoidea which was supported by the analysis of their protoconch (BANDEL 1988). KABAT (1991) was more reluctant to place Triassic gastropods with the Naticidae, but provided no reason for his doubts. He suggested though that naticids arose in the Jurassic following WENZ (1938) who placed the genus *Pictavia* COSSMANN 1925 with Jurassic type in the Naticoidea. TAYLOR (1988) suggested that Prealbian Naticidae did not bore shells but also that they can be recognized in fossil shells as old as the base of the Jurassic.

From Middle Cretaceous onward the activity of naticids can be traced on the presence of boreholes in bivalve shells (TAYLOR et al. 1980, for references). In the Albian only few bore holes have been recognized (TAYLOR et al. 1983, TAYLOR 1988) while their frequency increased during the course of the Late Cretaceous (SOHL 1969), to reach modern intensity by Eocene (POPENOE et al. 1987). Since Eocene the intensity of production of boreholes by naticids has remained stable (DUDLEY & VERMEIJ 1978).

While modern naticids can easily be recognized by their mode of life and anatomy, fossil representatives are more difficult to recognize and include within the taxon Naticoidea. According to MARINCOVICH (1977) the significant features in distinguishing fossil and extant naticids from other gastropods and differentiating subfamilies and genera from each other by the shell are prominently its umbilical area, the ornament and shape of the shell, the presence and absence of a calcareous operculum and the sculpture of the calcareous operculum. The shape and ornament of the protoconch was not at all considered by MARINCOVICH (1977). But this later character has proven since to be extremely important in

recognizing fossil naticids and distinguishing them from unrelated gastropods with convergent shell shape. Triassic neritimorphs (Bandel 1988, 1993) and especially Jurassic, Cretaceous and Paleogene cerithiimorph caenogastropods like the Pseudamauridae (Kowalke & Bandel 1996) are commonly similar to the Naticidae and occurred in similar marine environments as modern naticids. Both these groups had numerous species up to the end of the Eocene and in many cases can be distinguished from true naticids only by the ornament, shape and dimension of their protoconch.

The history of the Naticidae is thus clouded by unrecognized convergent fossil species belonging to unrelated groups of gastropods. This has become even more evident when it was recognized that the higher Caenogastropoda including Neomesogastropoda and Neogastropoda most probably did not develop earlier than mid-Cretacous times (Bandel 1993, Bandel & Riedel 1994).

2. ECOLOGY AND MODE OF FEEDING

Members of the Naticidae are carnivorous marine gastropods which usually burrow their way through loose sediment in order to reach their shelled prey. In contrast to other burrowing gastropods like Oliva Martyn 1786 their path within the sediment may lie so deep that it can not be spotted from the surface (Bandel & Wedler 1987). Naticids have a flat and large foot that helps them to burrow through the loose sandy or muddy sediment and to take hold of their prey. During motion within the sand and during resting and feeding the foot covers much of the shell and adds a thin varnish to it, so it commonly appears well polished. As soon as the position of a potential prey is recognized by the smell/taste of it the gastropod buries its way to the prey and drills its shell (Ziegelmeier 1954, Bergh 1976). During this process a large amount of mucus may be secreted that surrounds the prey and prevents its flight (Richter 1962). If the prey lies on the sediment the gastropod enwraps it with its foot and carries it from the surface into the sediment. Prey is usually devoured while the gastropod is in the sediment (Fretter & Graham 1962, Bandel & Wedler 1987).

The proboscis reaches the surface of the shell by way of a fold in the anterior foot (Ziegelmeier 1954). The bore hole is produced by a special gland zone that lies next to the radula in the proboscis (Carriker 1981). It is formed by interaction of a boring organ with acid and encyme secretions, and the radula, both lying next to each other in the proboscis. The shell of the prey is thus dissolved chemically and the radula is utilized only to scratch out the detached particles and to produce a fresh surface to which the boring organ can newly be applied. But still the teeth of the radula become quite worn during this boring process (Bandel 1984). Shell debris is swallowed, goes through the digestive system and is extracted by way of the gut (Ziegelmeier 1954). The later author also observed that some naticids may detach from the sediment and swim off with undulating movements of the foot, mainly the propodium. This behaviour can save the snail from predating enemies like starfish and carnivorous gastropods. In the Caribbean Sea such a predating gastropod was recognized in *Fasciolaria tulipa* (Linneaus 1758) [Bandel 1976a].

3. RADULA

Troschel (1856-1863) had studied the radulae of a number of species of the Naticoidea and came to the conclusion that this group of gastropods represents a natural entity, with members closely related to each other. This general similarity found in the radulae was supported by Bandel (1984) who compared the radulae of 8 species from the Caribbean Sea, the Mediterranean Sea and the Red Sea and related them to those that have been described in literature. These radulae are all very similar to each other and they also resemble the radulae found in some other caenogastropod groups. In a general way those of the Calyptraeidae are similar in shape, but also those of representatives of the Vermetidae, the Ampullariidae and the Littorinidae. They thus have features which appear to be basic within Caenogastropoda.

4. SPAWN

The characteristic collars of agglutinated sand containing the eggs within egg capsules are quite distinctive for representatives of this group, and is characteristic of the superfamily. The egg masses usually consist of many thousand egg capsules, which are interbedded with sandy grains. Each capsule houses one or several embryos, which in

species with planktotrophic development hatch out as bilobed veligers. The spawn of *Polinices lacteus, P. hepaticus, Natica livida* and *N. canrena* was described by BANDEL (1976b, see here older lit., also in KNUDSEN 1992) and here the relation to egg masses of other naticids were discussed. Also *Amauropsis* has an egg collar that is characteristic to that of the naticids in general (THORSON 1935) and each capsule in it contains one large egg that develops into a crawling young before hatching quite similar to that of *Natica clausa* from the North Sea. The egg mass of *Sinum* also resembles that of the Naticidae in general (KNUDSEN 1994).

5. PROTOCONCH

The most important character that can be used for the recognition of fossil species is the protoconch. It is rounded in shape, of large size, and has a characteristic ornamental pattern when a planktotrophic larva is developed. The embryonic shell measures more than 0.1 mm in width and may be densely ornamented with spiral rows of tubercles (BANDEL 1975, 1976b), but may also have a pattern of small grooves. The transition to the larval shell is commonly characterized by distinct growth increments, which develop to axial ridges. The larval shell has a more or less spherical outline, a whitish, nearly transparent appearance and may reach a size of almost 1 mm (BANDEL 1993, BANDEL et al. 1997; Pl. 4: Figs. 1-6). Sculptural elements are delicate, but distinct spiral ridges, and axial ribs, which are marked on the early larval shell and can hardly be recognized on the last half whorl are common. The aperture is large and of more or less spherical outline, with angularity at the sutural portion. The operculum grows in a spiral, the nucleus lying central in the young larva and shifted only little to the left in the late larva. The umbilicus is pronounced.

The late larval shell is carried by veligers observed to swim with a quadrilobate velum, each lobus having about two times the length of the conch. A larva that is ready for metamorphosis has a large ctenidium that extends for half a whorl and next to it a filamentous osphradium and the heart. The larva is equipped for oxygen exchange by the heart pumping blood from the main vein that passes through the axis of the gill and for finding prey by tasting the water by osphradium action. When ready for metamorphosis the foot is functional while the velum remains functional as

well. This pediveligers may already enter the sediment, thus, testing the substrate before metamorphosis begins. The foot not only carries the operculum on its back but also extends in lobes onto the shell covering it totally just as is the case in the fully grown individuals, while the velum is folded back into the space of the mantle cavity. If testing is not successfull the pediveliger can unfold the velum and swim off again and repeat this process. Metamorphosis is rapid and finished within an hour or so and the newly benthic animal will start drilling a hole into a prey right away if this is at hand and available.

6. TELEOCONCH

The shell has a short spire and the body whorl is large. Sutures are not deeply impressed. The aperture is oval to semicircular and the umbilicus broad, often filled with callus. The operculum is paucispiral and organic with or without calcareous cover. The teleoconch of the typical naticoid shape, roundish with the spire usually rather low and the base rounded is found not only in naticoids but also among others. This is especially so when the umbilicus is closed or of simple shape. In the marine environment such groups as the Lacunidae among the Littoriniformia, or the Amphibolidae among the Archaeopulmonata have a very similar shell, and in fresh water Ampullariidae like *Pila* RÖDING 1798 and *Ampullaria* MONTFORT 1810 as well as Hydrobiidae like *Lithoglyphus* HARTMANN 1821 are rather similar in general teleoconch shape to that of naticids.

7. SOME NOTES ON THE CLASSIFICATION OF MODERN NATICOIDEA

The superfamily Naticoidea FORBES 1838 is characterized as having members with a globose, to egg-shaped or auriform shell with low spire and large final whorls, with semicircular oblique aperture. There is no siphonal canal but the animal has a long fleshy siphon. The mode of life of naticoids is that of sand burrowing carnivorous, shell-drilling gastropods. In those species with planktonic larvae the protoconch is globose and large with embryonic shell of pitted sculpture network or granules and fine spiral lines on the larval shell. In species with lecithotrophic development the protoconch is large and simplified.

Naticoidea differ from their closest relatives among the Caenogastropoda, with the Neomesogastropoda in regard to features of the teleoconch and the protoconch. The Calyptrae-oidea may have a similar protoconch but their teleoconch is limpet-like and they live an almost completely sessile life and usually filter their food from the water. The Cypraeoidea differ in regard to the shape of the cauri teleoconch as well as in regard to ornament of the larval shell, that has a reticulated pattern, and the mode of life as grazing carnivores to omnivores. The Lamellarioidea have an echiniospira larva and reduce the shell even more than is seen in some Sininae of the Naticoidea, and live on tunicates. Eratoidea also have an echinospira larva along with the cauri shape of their teleoconch and prefer also tunicates as their diet. The most similar protoconchs can be found among the Cassoidea while teleoconchs here differ in shape. Those cassoids with siphon resemble Neogastropoda, while those with more globular shell shape have a wide aperture and resemble some Naticoidea, but usually they have specialized to feed on echinoderms (BANDEL & RIEDEL 1994, RIEDEL 1995).

Naticoidea represent a well recognized branch of the order Neomesogastropoda BANDEL 1991 with Early Cretaceous origin (BANDEL & RIEDEL 1994). THIELE (1931) recognized the independant status which the Naticidae have among the Caenogastropoda (Mesogastropoda and Neo-gastropoda in THIELE) being not directly related to any of the other living species groups. They belong in the suborder Simrothina BANDEL & RIEDEL 1994 which is united by its naticoid teleoconch and its pedial ganglia with anterior lump. Within the Simrothina the superfamily Naticoidea differs from the other superfamilies of this suborder, the Lamellarioidea and Cypraeoidea by having an accessory boring organ. Since mid-Cretacous time the existence of naticids can be recognized with evidence of their boring actvities seen in holes found in the shells of molluscs and other shelled organisms (TAYLOR et al. 1983). The inflatable foot of Naticidae may cover the shell and add glaze to the outer shell surface. On the protoconch the cancellation originally found among the Simrothina is reduced to spiral lirae or a few axial ribs. In case of lecithotrophic ontogeny protoconch ornament as well as shape are altered so that recognition is more difficult or impossible. Due to these alterations the ornamental pattern usually disappears and the number of whorls decreases as well as transition to the teleoconch becomes unrecognizable. But this loss of information in protoconch morphology due to lecithotrophic development is a normal feature found among marine Caenogastropoda (BANDEL 1975, 1982).

The family Naticidae FORBES 1838 is the only family of the Naticoidea in most classifications (THIELE 1931, WENZ 1938, MARINCOVICH 1977, PONDER & WARÉN 1988). The living members of the subfamilies of the Naticidae are rather similar to each other and the three most important taxa can be distinguished by their operculum. According to WENZ (1938) or MARINCOVICH (1977) it is calcareous in the Naticinae, organic in the Polinicinae and can no longer seal the aperture in front in the Sininae. But according to CERNOHORSKY (1972) these features may not actually reflect the relation existing between these gastropods. He noted that RISBEC (1956) while examining the anatomy of tropical Naticidae combined *Polinices* and *Natica* in a single genus despite their different opercula. *Polinices* and *Natica* are placed in two separate subfamilies by WENZ (1938) on basis of corneous or calcareous opercula, on basis of the radula however both genus-groups would be regarded as congeneric (TROSCHEL 1856-1863, BANDEL 1984). This classification was obviously not adopted by KABAT (1996) who suggested that only Naticinae represent a monophyletic clade, while Polinicinae are only a grade, and the extant species and genera of the Polinicinae should either be placed with the Naticinae or with the Sininae.

Many writers interpret genetic affinities in the Naticidae not only on basis of opercula but also on the arrangement of the funicle within the umbilicus (MARINCOVICH 1977, BOUCHET & WARÉN 1993). But POPENOE et al. (1987) remarked in their review of the Cretaceous Gyrodinae that the development of an umbilical callus in such naticids complicates classification within the family Naticidae. Umbilical callus sheets, pads or plugs apparently have formed convergently in different groups of naticids.

Only three subfamilies remain when the Recent species of *Amauropsis*, *Globularia* and *Globisinum* are separated from their fossil counterparts which commonly are not naticids anyhow, as is shown below. These three genera can be placed with the Polinicinae, to which they are anatomically close. There is no reason to raise the subfamilies into higher taxonimic level but, in contrast, there may well be reason to see these

taxa only as groupings of a natural unit among the Simrothina sufficiently described as family Naticidae. Similarily there are interconnections within the genera of different subfamilies as is discussed below, so that classification of the Naticoidea has more than a touch of being artificial.

The subfamily Polinicinae GRAY 1847 may unite the genera *Polinices, Amauropsis, Globularia, Lunatia, Neverita, Bulbus, Calinaticina, Friginatica, Choristes, Propesinum, Falsilunatia, Kerguele-natica,* and *Uberella.* Of these *Amauropsis* MÖRCH 1857 is confusing since it has a thin walled shell with elongated, stepped profile, channelled sutures, ornament of spiral costellae and small to slit-like simple umbilicus, as is commonly found also in fossil species from Jurassic to Eocene times (like the Jurassic *Ampullospirina*) which actually do not represent naticids at all (see below). The genotype is *Amauropsis islandica* (GMELIN 1791) from the Arctic seas that enters the northernmost North Sea. According to POWELL (1951) several species of *Amauropsis* live in the Antarctic and Subantarctic region. VAUGHT (1989) therefore united *Amauropsis* with *Globularia* in the Ampullospirinae which is not acceptable (see below).

According to BOUCHET & WARÉN (1979) *Amauropsis* is somehow related to the genera *Bulbus, Falsilunatia* and *Choristes. Bulbus* BROWN 1839 with the type species *B. fragilis* (LEACH 1819) (MARINCOVICH 1977: Pl. 31, Figs. 4-7) with circumboreal occurrence in cold water has a relatively small, thin, globose to slightly elongate shell with evenly rounded whorls with ornament of weak spiral lirae and narrow umbilicus with thin callus cover. *Bulbus* lacks the deeply channeled sutures and more elongate shell shape of *Amauropsis,* the more widely open umbilicus of *Choristes,* and is rounder than *Calinaticina. Choristes* CARPENTER 1872 unlike *Bulbus* has channeled sutures and distinctly open umbilicus without callus pad. The type is *Choristes elegans* CARPENTER 1872 from the Pleistocene of Canada and several species live in the deep water of the northwestern Atlantic and the northeastern Pacific. *Calinaticina* BURCH & CAMPBELL 1963 with globose, thin shell has a flattened base but also a widely open umbilicus. Its type is *Sigaretus oldroydii* DALL 1897 from the northeastern Pacific (MARINCOVICH 1977: Pl. 31, Fig. 3). The inner lip is reflected to partly concealing the umbilicus, not unlike *Gyrodes (Sohlella)* in the Cretaceous of California (POPENOE et al. 1987). The operculum is horny and smaller

than the aperture. In this way *Calinaticina* appears to be intermediate in shell form between *Sinum* and naticids that can seal their aperture with the operculum.

Spiral ornament as in *Globisinum* POWELL 1933 is also present in species of *Sinum, Eunatica,* and *Propesinum,* as well as *Polinices propeovatus* (MARWICK 1924) (BEU & MAXWELL 1990: Pl. 29 I). Since there is similarity with *Bulbus* regarding the radula and with *Sinum* regarding the ornament of the teleoconch, the Globisininae POWELL 1933 do not deviate very much from the other naticids. They can just as well be included within the Polinicinae. With exception of the fossil *Globisinum elegans* (SUTER 1917) with wide umbilicus, species of *Globisinum* are readily distinguished from other New Zealand naticids by having a globose or ovate shell and distinct spiral sculpture, and in being narrowly umbilicate or non umbilicate. The genus *Globisinum* has only one living species *Globisinum drewi* (MURDOCH 1899) as discussed by BEU & MAXWELL (1990). Its radula differs from that of other naticids (POWELL 1933), but DELL (1956) noted similarities to *Bulbus* from the Arctic Ocean and the North Atlantic Ocean. *Globisinum* can be recognized first in the Early Paleocene of New Zealand and from than on lived from the mid-shelf to the the upper slope (BEU & MAXWELL 1990).

Polinices MONTFORT 1810 has a globose to ovate shell with inflated smooth whorls commonly ornamented with microscopic spiral lines and growth increments. The suture is impressed and the umbilicus is open with slender to massive callus. The genus is based on *Polinices albus* MONTFORT 1810 from the Indo-Pacific which is the same as *Nerita mammilla* LINNEAUS 1758 (KABAT 1991). BOUCHET & WARÉN (1993) described several species from the northern Atlantic Ocean, of which GRAHAM (1988) placed some into the genus *Lunatia. Polinices* is thus very close in shape to *Lunatia* and characteristic *Polinices* differs by having a more solid callus in the umbilicus and by having more indistinct sutures than typical *Lunatia.* SOHL (1960: Pl. 17, Figs. 1-4, 8, 9) included the late Cretaceous *Polinices kummeli* SOHL 1960 from Owl Creek (Mississippi) in this genus, and MARINCOVICH (1977) noted that species of *Polinices* have been living along the California coast during most of the Tertiary up to now. *Lunatia* GRAY 1847 is described as having well rounded whorls. The umbilicus is open and deep and only slightly covered by the callus and columellar wall of the inner lip. The type is *Lunatia*

heros (SAY 1822) that lives along the Atlantic coast of northern America. The shell of *Lunatia* or *Polinices* closely resembles that of fossil *Euspira* and it has been suggested that *Lunatia* should be placed in that genus. But *Euspira* is based on a fossil species from the Eocene of western Europe. Here members of the non-naticid pseud-amaurellids are common, and the type species to *Euspira* may be one of them, but it may also represent a naticid. This can perhaps be decided, when the protoconch of the type species of *Euspira* becomes known. Similarily KABAT's (1991) suggestion to place *Lunatia* and *Laguncula* BENSON 1842 with Chinese type species as synonyms of *Euspira* should not be followed. According to BEU & MAXWELL (1990) *Lunatia* is a long-ranging genus that occurred from the Cenomanian onward and was present in New Zealand only during the Paleocene, later no more.

Neverita RISSO 1826 based on *Neverita josephina* RISSO 1826 from the Mediterranean Sea (WENZ 1938: Fig. 2952) has a globose to ovate shell with an ornament of microscopic spiral costellae or smooth surface and sutures that are slightly impressed. The umbilicus is closed by broad and massive callus that is a pad-like continuation of the parietal callus. *Neverita* is a warm water genus with one late Eocene representative in New Zealand (BEU & MAXWELL 1990: Pl. 8 d). The later authors distinguished *Neverita* from *Polinices* by a less widely spreading callus and from *Taniella* FINLAY & MARWICK 1937 by not having a marked gap between the umbilical callus and the parietal callus. *Uberella* FINLAY 1928 from New Zealand resembles *Lunatia* very much (BEU & MAXWELL 1990). *Falsilunatia* POWELL 1951 with genotype *F. soluta* (GOULD 1848) has an ovoid shell, oblique aperture and fine spiral ornamental pattern and can only be distinguished from other naticids by the shape of the characteristic unicuspid central teeth of its radula (HAIN 1990: Pl. 21, Figs. 2-4; POWELL 1951, BARNARD 1963, BOUCHET & WARÉN 1993). *Friginatica* HEDLEY 1916 with small globose shell is distinguished by a circumumbilical sulcus running from the base of the aperture. The type species lives near south-eastern Australia. In New Zealand it occurred from late Eocene onward (BEU & MAXWELL 1990: Pl. 8 e).

Propesinum IREDALE 1924 with auriform, lowly spired shell has a concave base and is narrowly umbilicate. Ornament consists of narrow, spiral, flat topped cords with interstitial threads, interupted by growth-lines. The strongly oblique apertur is ovate and the narrow inner lip callus is reflected over the upper part of the umbilicus. The type is *Propesinum umbilicatum* (QUOY & GAIMARD 1832) living near Tasmania (Australia). *Propesinum* resembles *Sinum* but is of more rounded shape. Jointly with the higher *Globisinum* this genus represents a transition to the *Sinum* group. But this is also true with the genus *Globularia* SWAINSON 1840 that is based on *Globularia fluctuata* (SOWERBY 1825) that lives off the Philippine Islands. Its shell is rounded with pointed spire and very large last whorl without open umbilicus (WENZ 1938: Fig. 2929). Its operculum is reduced and the animal cannot withdraw totally into its shell, as is characteristic to the Sininae, but also to *Calinaticina*.

Members of the **subfamily Sininae** WOODRING 1918 have a thin, auriform to nearly globose shell with the final whorl greatly enlarged. The ornament consists of spiral costellae. The animal is too large to retract fully into its shell. Members of this group are distinguished from the Naticinae by having no calcareous operculum, from the Polinicinae by an aperture that is larger than the operculum. The subfamily Sininae WOODRING 1918 (= Sigaretinae CUVIER 1817) is thought to include the genus *Sinum* RÖDING 1799, *Eunaticina* FISCHER 1885, and *Haliotinella* SOWERBY 1985 (WENZ 1938; KILBURN 1976; MARINCOVICH 1977; PONDER & WARÉN 1988; VAUGHT 1989). In *Sinum* RÖDING 1798 (= *Sigaretus* LAMARCK 1799) the whorls of the shell are depressed and ornamented with distinct, delicate spiral costellae. The umbilicus is slit-like or closed. The type is *Helix haliotoidea* LINNAEUS 1758 from West Africa. *Eunaticina* FISCHER 1885 has a small, globose to elongate and thin shell ornamented by spiral ribs and incised interspaces. The umbilicus is broadly open with or without callus. The operculum may be calcified (!) or entirely organic. The type species is *Nerita papilla* GMELIN 1791 living in the western Pacific. *Heliconatica* DALL 1924 represents a synonym (according to WENZ 1938). *Haliotinella* SOWERBY 1885 has a small, thin shell of ear-like shape with haliotid last whorl and small spire consisting only of 2.5 whorls. It consists of limpet-like sand dwellers with a few species living in the Caribbean Sea as well as the Indo-Pacific. The type is *H. montrouzieri* SOWERBY 1885 from near New Caledonia.

In the **subfamily Naticinae** FORBES 1838 the shell is usually globose and mostly smooth. The spire is low or moderately elevated. The umbilicus has a funicle that is separated from the parietal callus (inner lip callus) by a sulcus, or the umbilical

callus may be a semicircular plug. The operculum has an external calcareous layer. Here species of the genera *Natica*, *Naticarius*, *Cryptonatica*, *Stigmaulax*, *Tectonatica* according to VAUGHT (1989) and in addition *Lunaia*, *Carinacca*, and *Glyphepithema* according to MARINCOVICH (1977) are united. KABAT (1996) included in addition to these also the genera *Cochlis*, *Tanea*, and *Notocochlis*, that had been regarded as subunits of of *Natica* by VAUGHT (1989). *Natica* SCOPOLI 1777 has a globose shell with low spire and outer surface smoot or ornamented by axial and spiral lines. The umbilicus usually bears a funicle and a callus. The type is *Natica vitella* (LINNAEUS 1758) from the Indo Pacific. The European *Natica clausa* BRODERIP & SOWERBY 1829 occurs around the globe in Arctic seas and off western Europe in deep water.

Naticarius DUMÉRIL 1806 commonly has axial sculpture of sharply incised grooves that extend from the suture part way to the periphery. The narrow umbilicus with excavated sulcus has a slender callus and a funicle. The type is *Naticarius canrenus* (LINNAEUS 1758) from the Caribbean Sea and there are a number of tropical species. In *Carinacca* MARWICK 1924 there is a broadly open, wide umbilicus that is bounded by a strongly raised cord. There is a compact umbilical callus and a narrow funicle. The type is *Carinacca waihaoensis* (SUTER 1917) from the Eocene of New Zealand. The very similar *Carinacca allani* (MARWICK 1924) was described by BEU & MAXWELL (1990: Pl. 6h). MARINCOVICH (1977: Pl. 39, Figs. 10-12) described as species *C. rosensis* HANNA 1927 from the Eocene of California that has a circumumbilicar ridge as seen in *Gyrodes* but a more globular shell similar to a *Natica*. A wide umbilicus but with a cord emerging from the base is also found in *Stigmaulax* MÖRCH 1852 with the type *Nerita sulcata* BORN 1778 from the Caribbean Sea (ABBOTT 1974: Fig. 1727).

Features of the umbilicus characterize *Lunaia* BERRY 1964 with the type *Lunaia lunaris* BERRY 1964 from the tropical eastern Pacific (MARINCOVICH 1977: Pl. 40, Figs. 2, 3) and *Glyphepithema* REHDER 1943 with the type *G. idiopoma* PILSBRY & LOWER 1932 from the tropical eastern Pacific (MARINCOVICH 1977: Pl. 40, Figs. 4,5). In *Cryptonatica* DALL 1892 the umbilicus is completely covered by a solid calcareous pad, which along its free side is demarcated by a semicircular furrow, filled by less

solid calcareous material. Here according to BOUCHET & WARÉN (1993) the genotype is *Natica clausa* BRODERIP & SOWERBY 1829 from the Arctic Sea while according to KABAT (1991) and MCLEAN (1996) it is *Natica floridana* DALL 1892 from the Tertiary of the southeastern USA. GRAHAM (1988) preferred to classify *Natica clausa* with the genus *Natica*. *Tectonatica* SACCO 1890 with the type *T. tectula* SACCO 1890 from the Pliocene of Italy differs from *Cryptonatica* in not having the umbilicus completely closed by callus. *Tectonatica rizzae* (PHILIPPI 1844) has been illustrated and its complex nomenclature been resolved by BOUCHET & WARÉN (1993: Fig. 1841-1843).

This short account on some of the genera proposed within the Naticidae (but see WENZ 1938; KABAT 1991, 1996) indicates quite clearly that it is difficult to differentiate genera and groups of genera from each other. One could just as well classify by using fewer generic names. It is quite likely that features of shell form, operculum calcification, and umbilical characters like plugs, callus covers and callus ridges have appeared in several lineages convergently. This may be different where histories of lineages in one and the same geographic setting were analysed such as by BEU & MAXWELL (1990) from New Zealand. But also here it is difficult to distinguish immigrants coming from lineages that have developed in regions far away. That this sudden appearance of new lineages is quite possible can be comprehended, when the early ontogenetic shell (protoconch) is seen, which in many species belonging to different naticid lineages consists of a large larval shell. Such larvae can be encountered far from the living place of their parents in the open ocean and many of them can swim in the sea for many weeks and even months (BANDEL et al. 1997) and reach far distances provided they travel in the correct current.

8. ABOUT THE PROTOCONCH

Protoconch features very much depend on the type of development and differ much between species that have planktotrophic larvae on one hand and non planktotrophic larvae or crawling young hatching on the other hand (BANDEL 1975, 1976b).

8. 1. The planktotrophic case

In case of *Lunatia alderi* (FORBES, 1838) the shell of the veliger larva is well known and has been described by LEBOUR (1936), THORSON (1946), THIRIOT-QUIVREUX (1969), and RICHTER AND THORSON (1975). Its spawn and the development of the embryo within it has been described by ZIEGELMEIER (1961) (called *Lunatia nitida*). Own observations on *L. alderi* were conducted in the Laboratoire Arago at Banyuls-Sur-Mer in southern France and the Adriatic Sea near Rovinje (Istria). The veliger hatches with an embryonic shell of about 0.2 mm in width and an intitial cap of 0.07 mm width. It consists of about one whorl rapidly increasing in diameter. Three fourth of it are ornamented by a ridge groove pattern in which the ridges are separated from each other by five microns. The last fourth of the shell has strong growth increments which indicate the time of hatching.

During life as plankton-feeding larva the shell grows until the colorless transparent shell of the pediveliger measures 0.65-0.8 mm in diameter and consists of 2.25 whorls (not 1.5 as suggested by RICHTER & THORSON 1975: Pl. 9, Figs. 61, 62). The larval shell is ornamented by delicate spiral rows of tubercles with 0,5 to 1 micron width that have a distance of 12 micron from each other. (Pl. 1: Figs. 5, 6) The pediveliger ready for metamorphosis swims with a large four-lobed velum as illustrated by FRETTER & PILKINGTON (1970). Directly following rapid metamorphosis the new benthic animal begins to drill the shells of small bivalves, when available.

A very similar larval shell connected to a juvenile naticoid teleoconch was observed on a fossil species from the Miocene of Dingden in northwestern Germany (Pl. 1: Fig. 4). From nearby Winterswijke-Miste JANSSEN (1984) described Naticidae with *Lunatia* (= *Euspira*), *Neverita*, *Polinices*, *Natica* and *Sinum*. The analysed protoconch is so close to that of *Lunatia* cf. *alderi*, that it probably belongs to the similar *Lunatia helicina* (BROCCHI 1814) and its varieties which probably have not differed much from modern *L. alderi*.

Planktotrophic larvae have also been described by THORSON (1950), BANDEL (1975), GOHAR & EISAWY (1967), RICHTER & THORSON (1975), FRETTER & GRAHAM (1981), and BANDEL et al. (1997). BOUCHET & WARÉN (1993: Fig. 1858-1859) illustrated the larval shell of *Polinices montagui* (FORBES 1838) from the Atlantic Ocean of which

the planktotrophic larva had been noted by (THORSON 1946). All these are rather similar to each other (Pl. 1: Fig. 3).

Ornament of the embryonic shell in case of *Polinices lacteus* GUILDING 1834, *P. hepaticus* RÖDING 1798, *Naticarius canrenus* (LINNEAUS 1758) and *Natica livida* PFEIFFER 1840 from the Caribbean Sea of Colombia were described by BANDEL (1975a). To these *Polinices mammila* (LINNEAUS 1758) (Pl. 2: Fig. 4), *Natica lurida* SOWERBY 1883, and *Polinices mammata* RÖDING 1798 (Pl. 2: Fig. 1) from the Red Sea at Port Sudan can be added. All these show that ornament consists of more or less fine tubercles that may be arranged spirally or not (Pl. 2: Figs. 1, 4, 5). These tubercles may cover the whole embryonic shell or may be arranged into spiral rows on part of that shell or may even unite to spiral lirae still on that shell. In fossil cases the same pattern is observed, the oldest coming from the Santonian of Jordan (BANDEL 1993: Pl. 12, Fig.3).

Their larval shells are quite large, in case of *P. lacteus* amounting to almost 3.5 whorls with about 1 mm in diameter (Pl. 2: Fig. 5). In the others the protoconch reaches similar dimensions. A fully grown larval shell from the Red Sea with 1.2 mm wide shell could very well represent *Polinices mammata* (Pl. 2: Fig. 2). A Paleocene polinicine species from Matthews Landing at the Alabama River in Alabama has delicate tubercules on the embryonic whorl that measures about 0.12 mm across (Pl. 3: Fig. 4). Growth lines indicate the onset of the larval shell that has smooth surface with faint spiral lirae and consists of about two whorls. The whole protoconch consist of a little more than three whorls and measures about 1.3 mm in width and 1 mm in height. The beginning of the teleoconch is very indistinct. The early teleoconch resembles that of *Lunatia fusca* (BLAINVILLE 1825) with a callus of ridge and groove pattern extending into the umbilicus (GRAHAM 1988). An Eocene species from the Yazoo Clay in Mississippi has a tuberculate embryonic shell of about 0.15 mm in diameter (Pl. 3: Fig. 5) succeeded by a larval shell with fine indistinct spiral lirae. A similar case is observed in the Eocene of Moodys Branch Formation in Jackson, Mississippi. Pl. 2: Fig. 9, here the protoconch and teleoconch merge with each other, but probably the protconch ends where regular fine axial striae begin in the ornament. It would than have a size of about 1.3 mm in width. A rather similar species from the Eocene of Texas, Brazos River near College

Station, has a smaller embryonic shell with similar ornament, again a very indistinct transition of the larval shell into the teleoconch, but obviously more whorls of the protoconch (Pl. 3: Fig. 8).

The protoconch of *Sinum perspectivum* (SAY 1831) was studied from specimen collected in the Caribbean Sea near Santa Marta (Bay of Santa Marta and Bay of Chengue) (Pl. 1: Fig. 3) and compared to individuals from the SE coastal shelf of the USA (Pl. 1: Fig. 1). It consists of a little less than 2.5 whorls and is about 1.5 mm wide. The embryonic portion of almost one whorl is 0.24 mm wide and ornamented by fine spiral rows of tubercles (Pl. 1: Fig. 2). Hatching is indicated by begin of growth lines and the larval whorls are ornamented by spiral ribbons of which about 35 are found on the last whorl and which are separated from each other by narrow furrows. The ornament is continuous onto the teleoconch but here spiral lirae are wider and separated from each other by wider interspaces. A juvenile shell of a member of the Sininae from the Eocene of the Paris Basin (Damery) has a protoconch consisting of 2.8 whorls and 1.5 mm width and about 1.3 mm in height (Pl. 3: Figs. 1, 2). The embryonic whorl measures only about 0.1 mm in diameter, is delicately tuberculated in its initial portion, and becomes smooth near the onset of the first growth lines. Within the first whorl of the larval shell an ornament of broad spiral ribbons separated by narrow furrows begins and continues to the aperture of the protococh. The juvenile teleoconch is almost smooth with only weak spiral liration present as ornament. An American species of the Sininae from the Eocene of the Moodys Branch Riverside location in Jacksonville, Mississippi has an embryonic shell with a groove ridge pattern and almost 0.14 mm in diameter (Pl. 1: Fig. 9). It is succeeded by 2.4 whorls of the larval shell with an ornament by very faint spiral striae and short axial ribs. These begin at the sutures with an angle and continue onto the whorl side endinge there. They are short and step-like resembling similar ornament that can commonly be noted on juvenile shells of naticids. The protoconch ends with a simple aperture that is very well distinguished from the onset of the teleoconch with spirally lirated ornament. The protoconch here consists of a little more than three whorls and measures 1.4 mm in diameter and is a little more than half as high.

8. 2. The intermediate case

Lunatia intricatoides from the Mediterranean Sea near Banyuls-sur-Mer was observed hatching from its spawn with metamorphosis just happening or completed (BANDEL 1975b). The protoconch measures 0.75-0.85 mm in diameter, has a 0.15 mm wide intitial cap and is smooth but with well visible growth lines and rather indistinct spiral lirae. (Pl. 1: Figs. 7, 8) Hatching from the egg mass is indicated by an increase in the density of growth lines. The aperture is of rounded shape and the umbilicus is deep when hatching.

8. 3. The lecithotrophic case

As has been observed by ZIEGELMEIER (1961) the embryonic development of *Lunatia catena* (DA COSTA 1778) from the North Sea proceeds within the egg collar until crawling young hatch from it. From egg masses collected in the intertidal and shallow sea of the Belgian coast during June the development was observed. The characteristic spawn consists of a collar forming less or about one whorl, is about 10 cm long, 3 cm wide and egg cases in it are about 1.5 mm high, which is also the height of the collar. The egg collars have relatively little agglutinated sand and may be distinguished from those of *L. alderi* by size and arrangement of the egg capsules within them (GRAHAM 1988), but also by the type of development of the young within them. Of the up to one hundred eggs contained within each capsule of the egg-collar only one to eight embryos develop, while the other lumb together to form a mass of yolk. From this source of nutrients the embryos as soon as having developed to the veliger stage collect yolk particles with the aid of their cilia that cover the margins of their velum. Veligers with two lobed velum and around 0.3 mm large shell were observed to feed in this way for a period of about 18 days. During this time their shell continues to grow in a similar way as is the case in planktotrophic veligers. The shell is calcified within the capsule when metamorphosis is near. Also opercula have a perfect fit with the aperture and embryos contract back into their shell when they are disturbed. Young hatch only after metamorphosis is completed as miniature crawling, benthic animals.

A very similar development was observed in *Lunatia* cf. *catena* from the Mediterranean Sea near Banyuls-Sur-Mer which also hatches from its egg mass as crawling young (BANDEL 1975b). Here the initial whorl without growth lines measures 0.3 mm in diameter with an initial cap wider than 0.1 mm. This primary shell formed when mantle and shell have not separated from each other in the embryo (BANDEL 1982) is succeeded by another 1.5 whorls amounting to a shell of almost 1 mm in width when the young is hatching (Pl. 3: Fig. 3). The secondary shell bears strong growth increments and is formed by the yolk feeding embryo before and after metamorphosis. This type of embryogenesis results in a total disappearance of ornament except for growth lines on the protoconch and a rather large embryonic-larval shell. Embryonic and larval phase are compressed into a simplified early protoconch (compared to that of the planktotrophic veliger) and hatching occurs when a well developed up to 1 mm large juvenile leaves the spawn.

L. intricatoides develops from large eggs, while *L. catena* that hatches long after metamorphosis develops by eating nurse eggs. The resulting protoconchs of these different types of embryonic feeding differ in shape. Thus the protoconch of an Eocene fossil species from Saffré in the Paris Basin can be interpreted. Here a smooth protoconch consisting of about two whorls and 0.6 mm in hight and width is present. The initial three quarter of protoconch whorls representing the embryonic shell measure 0.2 mm across. This case of lecithotrophic development thus has probably proceeded in a similar way as in *L. intricatoides* from large yolk-rich eggs and not by feeding on nurse eggs like *Lunatia catena*.

As was observed by THORSON (1950) and FRETTER & GRAHAM (1981) *Lunatia pallida* hatches as crawling young with a little more than one whorl. BOUCHET & WARÉN (1993: Fig. 1860) described two deep water species, but found protoconch preserved only in *A. sphaeroides* (JEFFREYS 1877). The young hatch very large, and 1.5 whorls are 2.5 mm high. Embryogenesis must be with much yolk. The protoconch puzzled BOUCHET & WARÉN (1993) since embryos carried a 1.1 mm large shell with 1.25 whorls, corresponding with the smallest free living individuals. The apex of teleoconchs of individuals living nearby show a scar with 2.2 whorls and

1.5 mm diameter. Thus they have observed the great variability that goes along with yolk rich embryonic food. The embryonic shell of *Cryptonatica affinis* (GMELIN 1791) is figured by BOUCHET & WARÉN (1993: Fig. 1818-1820). It has 1.2 whorls and measures 1.6-2.2 mm in width. The first half whorl seems to be only wrinkled, and the second half shows fine indistinct spiral lirae. BOUCHET & WARÉN (1993) figured the protoconch of *Polinices obtusa* (JEFFREYS 1885) which has a rapidly enlarging initial whorl and is smooth. The young hatch crawling with almost 2 mm large shell.

The largest embryonic shell found in a naticid species apparently is known from the cold Weddell Sea. Here the spawn of *Amauropsis* described by HAIN (1990) consists of a collar of large, about 1 cm wide capsules in which one embryo develops for more than one year before it hatches with a 5.5 mm large shell as crawling miniature adult. Here an exteme amount of albuminous yolk is provided for embryonic feeding that occurs in water of a temperature below 0°C. The embryonic shell consists of one whorl, is smooth with very fine spiral striae, and has an open umbilicus (HAIN 1990). This author recognized from the Antarktic Weddell See 4 species of Naticidae (Polinicinae) that all develop within the typical collar-like spawn with large individual capsules into crawling young.

But lecithotrophic development is also found among tropical naticids as is evidenced by two species one from the shallow water of Bali (Indonesia) (Pl. 2: Fig. 7) and the other from somewhat deeper water in the southern Chinese Sea (Pl. 2: Fig. 8). The primary shell without growth lines of the specimen from Bali measures about 0.6 mm in diameter. Growth lines indicate the following prehatching shell that grades into the teleoconch without apparent interruption. The same is noted in the species from the Chinese Sea with 0.35 mm large primary shell that grew within the egg capsule to a size of about 1 mm forming a protoconch of globular shape. From there on the teleoconch formed. Both demonstrate a simplification of shell shape and ornament, which is characteristic to lecithotrophic development in Caenogastropoda in general (BANDEL 1975a, 1982). A rather similar juvenile naticid from Bali differs by having planktotrophic development (Pl. 2: Fig. 6).

8. 4. Generalities regarding protoconch shape and ornament

There are only few features that characterize the protoconch of the Naticidae. It has a low spire with rounded whorls and open umbilicus. The embryonic whorl is normally ornamented with simple tubercules and the larval shell is covered by more or less visible spiral lirae. The apertural margin is simple and straight without sinusigera notch. The protoconch does not reflect the subfamily status of Polinicinae, Naticinae and Sininae and the operculum is always non calcified and closes the aperture near its margin. The larval shell consists of quite a lot of organic material and after metamorphosis usually aquires a more or less corroded appearance.

9. A CRETACEOUS TAXON OF THE NATICIDEA, THE GYRODINAE

Subfamily **Gyrodinae** WENZ 1938

The naticiform shell is usually wider than high, has a flattened spire and delicately lirated spiral ornament crossed by inclined growth lines, or is smooth. The body whorl is large and the shell usually wider than high with usually wide umbilicus that is not covered by callus of the inner lip (WENZ 1938), or may have a tongue-like callus (POPENOE et al. 1987). The umbilicus may be accompanied by an umbilical ridge that separates it from the rounded base. The shell surface is featured by growth lines and is not polished. Naticinae differ in having a less prosocline growth line that lacks the broadly U-shaped umbilical, antispiral sinus.

Genus **Gyrodes** CONRAD 1860

Description: The subglobose, low spired shell has a deep umbilicus with crenulate and sharp umbilical margin and is crenulated near the suture. Growth lines near the suture may be notched (POPENOE et al. 1987). The aperture is oval in outline and inclined. The genotype is *Gyrodes crenatus* CONRAD 1860 from Coon Creek (Ripley Formation; Tennessee, U.S.A.) according to WENZ (1938) which is a synonym of *Rapa supraplicatus* CONRAD 1858 according to STEPHENSON (1941). The later (Pl. 51: Figs. 13-16) and SOHL (1960: Pl. 16: Figs. 1-5, 9, 13, 19)

illustrated the type *Gyrodes supraplicata* (CONRAD 1858) from the Owl Creek of the Ripley Formation (Mississippi, U.S.A.), Maastrichtian.

SOHL (1960) distinguished three groups among the species of the Ripley Formation which was deposited near the coast of the Cretaceous Gulf of Mexico. The first is around the type *G. supraplicatus* (CONRAD 1858) with crenulate and sharp umbilical margin and crenulations also present near the suture. The second is around *G. major* WADE 1926 with similar shell shape but smooth umbilical ridge. The third is *G. spillmani* GABB 1941 with more rounded shell shape, distinctly channeled suture ending in a keel or edge on the upper whorl surface, a rounded umbilical margin, and a thin wall-like inner lip bordering the umbilicus.

POPENOE et al. (1987) placed the first of these in the subgenus *G. (Gyrodes)*, the third in the subgenus *G. (Sohlella)* and found the latter to develop a callus sheet that forms an umbilical callus in the subgenus *G. (Hypterita)*. If we are to include the well-known species of *Gyrodes* into subgenera, *G. major* and relation and the genus *Banis* need to be included as well.

Subgenus **Gyrodes** CONRAD 1860

Description: The subglobose, low spired shell has a deep umbilicus with crenulated and sharp umbilical margin and is crenulated near the suture. The umbilicus is free of callus deposits. The aperture is posteriorly notched with a subsutural ribbon formed behind the notch. The type is *Gyrodes supraplicata* (CONRAD 1858) from the Maastrichtian of Mississippi (SOHL 1960: Pl. 16, Figs. 1-5) that may be 9 cm in width and 7 cm in height (STEPHENSON 1941).

Difference: *Gyrodes (Gyrodes)* differs from the other subgenera of *Gyrodes* by having a subsutural ribbon that arises from a posterior apertural notch.

Remarks: *G. (Gyrodes)* based on *Gyrodes supraplicata* CONRAD 1858 is a large shell with distinct suture bordered by a broad shallow sulcus that is accompanied by a low crenulated ridge. A new species of *Gyrodes (Gyrodes)* has to be described (BANDEL in prep.) from the Coniacian/Santonian of the Trichinopoly Group of southern India. It has a shell that is slightly wider than high with low spire. The suture is accompanied by a narrow notch forming a

subsutural ribbon with crescentic growth increments as present in the Pyrifusidae. The last umbilicus is wide and of conical shape. Cresecentic ribs ornament the flattened shoulder and the margin of the umbilicus. With 5 whorls the shell is about 2.5 cm wide. The aperture is obliquely suboval with a narrow notch next to the suture. *Gyrodes* sp. resembles *Gyrodes dowelli* WHITE 1889 from California [POPENOE et al. 1987: Fig. 4 (1, 5, 7)] but has a sharper edge at the shoulder, and it is very similar to *G. (Gyrodes) supraplicatus* CONRAD 1859 from the Maastrichtian of Mississippi (SOHL 1960: Pl. 16, Figs. 1-5).

Subgenus *Dockeryella* n. subgen.

Description: The large sized shell has a slightly concave subsutural ramp not connected to a apertural notch, and a broad umbilicus with noncrenulate margin. The type is *Gyrodes major* WADE 1926 from Coon Creek (SOHL 1960: Pl. 16, Figs. 6, 7, 10) and from Coffee Sand of the late Campanian in Mississippi (DOCKERY 1993: Pl. 20, Figs. 13, 14). According to DOCKERY (1993) the protoconch of *Gyrodes (Dockeryella) major* has 2.25 whorls with indistinct transition into teleoconch.

Difference: *G. (Dockeryella)* differs from *G. (Gyrodes)* by having no subsutural ribbon in consequence of the absence of a notch at the posterior margin of the aperture. The wide shell shape and the ridge around the wide umbilicus distinguishes from *G. (Sohlella)* and the additional absence of any callus sheets extending into the umbilicus distinguishes from *G. (Hypterita)* and *G. (Banis)*.

Remarks: *Gyrodes robustus* WARING 1917 lived in the Paleocene of California (MARINCOVICH 1977: Pl. 21, Figs. 3-9) and represents the only Cenozoic *Gyrodes* known from the Pacific Coast of the United States, which was also supported by POPENOE et al. (1987) who placed this species with the subgenus *G. (Gyrodes)*. But this placement can not be upheld, because *G. robustus* had no subsutural ribbon that arose from a notch in the posterior outer lip. If *Gyrodes robustus* is a naticid, it should be placed with *Gyrodes (Dockeryella)*. A species described as *Gyrodes tenellus* STOLICZKA 1868 by RENNIE (1930: Pl. 25, Figs. 1-3) from the South African Umzamba Formation (Santonian) in part belongs to the subgenus *G. (Dockeryella)* (BANDEL in prep). Here

characteristically on early whorls the suture is flattened and becomes depressed on the last whorl and the umbilical margin is a sharp angulation. The shell is 26 mm wide and 24 mm high. The African species resembles *Gyrodes (Dockeryella) major* WADE 1926 from Coon Creek but has a more rounded umbilical margin.

Subgenus *Sohlella* POPENOE, SAUL & SUZUKI 1987

Description: The shell is wider than high or about as wide as high with low spire. The suture is accompanied by a shallow groove that forms the tabulate shoulder. Whorl profile is obliquely rounded and the umbilical margin is rounded biangulate with steeply sloping umbilicus. The aperture is subovate, oblique with a straight inner lip that overhangs the conical umbilicus and with an outer lip that has no posterior notch. The inner lip borders the umbilicus with a thin wall in its posterior columellar portion. The type is *Gyrodes canadensis* WHITEAVES 1903 from the Campanian of Vancouver Island.

Difference: *G. (Sohlella)* has no subsutural ribbon rising from a notch as is characteristic of *G. (Gyrodes)* and it has a narrower umbilicus as *G. (Dockeryella)* and higher shell shape. If an umbilical callus sheet is developed it is short and not extended as in *G. (Hypterita)* or *G. (Banis)*.

Remarks: The Indian *Gyrodes (Sohlella) tenellus* STOLICZKA 1868 from the Coniacian-Santonian Trichinopoly Group is very similar to *Gyrodes (Sohlella) quercus* POPENOE et al. 1987 from the Coniacian to Santonian of California (BANDEL in prep.). It perhaps, has a slightly narrower umbilicus. Very similar species are also *Gyrodes (Sohlella) spillmani* GABB 1861 (DOCKERY 1993: Pl. 20, Figs. 11-12) from the Campanian Coffee Sand in Mississippi and *Gyrodes subcarinatus* STEPHENSON 1941 (STEPHENSON 1941: Pl. 52, Figs. 20-26) from the Maastrichtian Navarro group of Texas. DOCKERY (1993) described the protoconch of *Gyrodes (Sohlella) spillmani* to consist of 2.25 whorls with indistinct transition into teleoconch, but did not illustrate it.

Subgenus *Hypterita* WOODRING 1957

Description: The smooth shell with depressed spire has a wide umbilicus into which a thin overhanging callus tongue with concave surface extends from the inner lip. The sutures are shallow

and bordered by indistinct concave band. The aperture is subovate and obliquely oriented. The type *Natica helicoides* GRAY 1825 from the Miocene to Recent in Baja California and Panama [POPENOE et al. 1987: Fig. 4 (20,24,25)].

Difference: According to POPENOE et al. (1987) who connected the living *Gyrodes* (*Hypterita*) *helicoides* with the Maastrichtian *G.* (*Hypterita*) *robsauli* POPENOE et al. 1987 the difference to *G.* (*Sohlella*) lies in the callus sheet that overhangs the umbilicus extending from the inner lip. This sheet is lamellar and not thickened as in *G.* (*Banis*).

Subgenus *Banis* (STEPHENSON 1941)

Description: The smooth shell with depressed spire has a wide umbilicus into which a thick callus pad is reflected from the inner lip. The suture is bordered in front by a narrow shoulder without forming a subsutural ribbon. The aperture is subovate, rounded in front and angular in the rear. The type *Banis siniformis* STEPHENSON 1941 from the Natacoch sands of the Campanian to Maastrichtian Navarro Group in Texas measures 14 mm in width and 8 mm in height.

Difference: *Gyrodes* (*Banis*) resembles modern *Sinum* with wide umbilicus, which in contrast to that of *Gyrodes* is partly filled by a thick reflected inner lip. *G.* (*Gyrodes*) differs by having no callus pad, umbilical and apical ribs and a subsutural ribbon. *G.* (*Dockeryella*) differs by having no umbilical callus reflection of the inner lip. *G.* (*Sohlella*) has a thin inner lip that forms the inner wall of the umbilicus and may or may not expand somewhat into the umbilicus, while *G.* (*Hypterita*) (WOODRING) always has the expanded inner lip callus that is thin in contrast to the thick callus on a short rounded inner lip of *G.* (*Banis*).

Remarks: STEPHENSON (1941: Pl. 50, Figs. 14-16) described *Banis siniformis* STEPHENSON 1941 from the Natacoch sands and compared it with *Sinum*, but not with *Gyrodes*. POPENOE et al. (1987) noticed this similarity of *Banis* with *Gyrodes*, especially since their subgenus *G.* (*Sohlella*) represents an intermediate form, with callus projection present in some and not present in others.

Remarks to the subgenera of *Gyrodes*:

The interconnection of a Cretaceous species belonging to the genus *Gyrodes* with a modern still living species of naticids that resembles *Gyrodes*, as suggested by POPENOE et al. (1987) in case of *G.* (*Hypterita*) may be wrong, but it certainly demonstrates that it is very difficult to separate some of the widely umbilicate naticids of Cretaceous times from widely umbilicate species that lived later or are still living today.

Gyrodes demonstrates the disappearance of the subsutural notch which is present in *G.* (*Gyrodes*) and has disappeared in the very similar *G.* (*Dockeryella*). When shells become as high as wide, take more globular shape as is the case in *G.* (*Sohlella*), the transition to shapes that we see in naticids of our time with simple and open umbilicus are apparent. In *G.* (*Hypterita*) and *G.* (*Banis*) the character of the original diagnosis presented by WENZ (1938) of the Gyrodinae has been violated, since they have produced a callus of the inner lip that extends into the umbilicus. But POPENOE et al. (1987) had demonstrated that species of the *G.* (*Sohlella*) group have transitional forms, so that this violation occurred in nature and thus has to be accepted by the taxonomist. Apparently it occurred independently starting from a thin inner lip bordering the umbilicus in *G.* (*Sohlella*) to *G.* (*Hypterita*) in the Pacific region and by thickening this inner lip to a plug-like structure as in *G.* (*Banis*) in the Mid-Atlantic Gulf area.

As soon as the callus plug of the inner lip is not in a marginal position but in a central position on the inner lip forming the wall to the umbilicus, POPENOE et al. (1987) consider otherwise gyrodiform shells to belong to the Naticinae. They recognize in these species like *Natica conradiana* (GABB 1864) from the late Turonian of California and Oregon a member of the genus *Natica*, even though an operculum is not known and the umbilicus is wide.

10. POTENTIAL CRETACEOUS STEM GROUP REPRESENTATIVES OF THE NATICOIDEA

Genus *Schizobasis* WADE 1916

Generic description: The depressed neritaform shell has a strong and deep basal constriction. The ornament consists of strong nodose
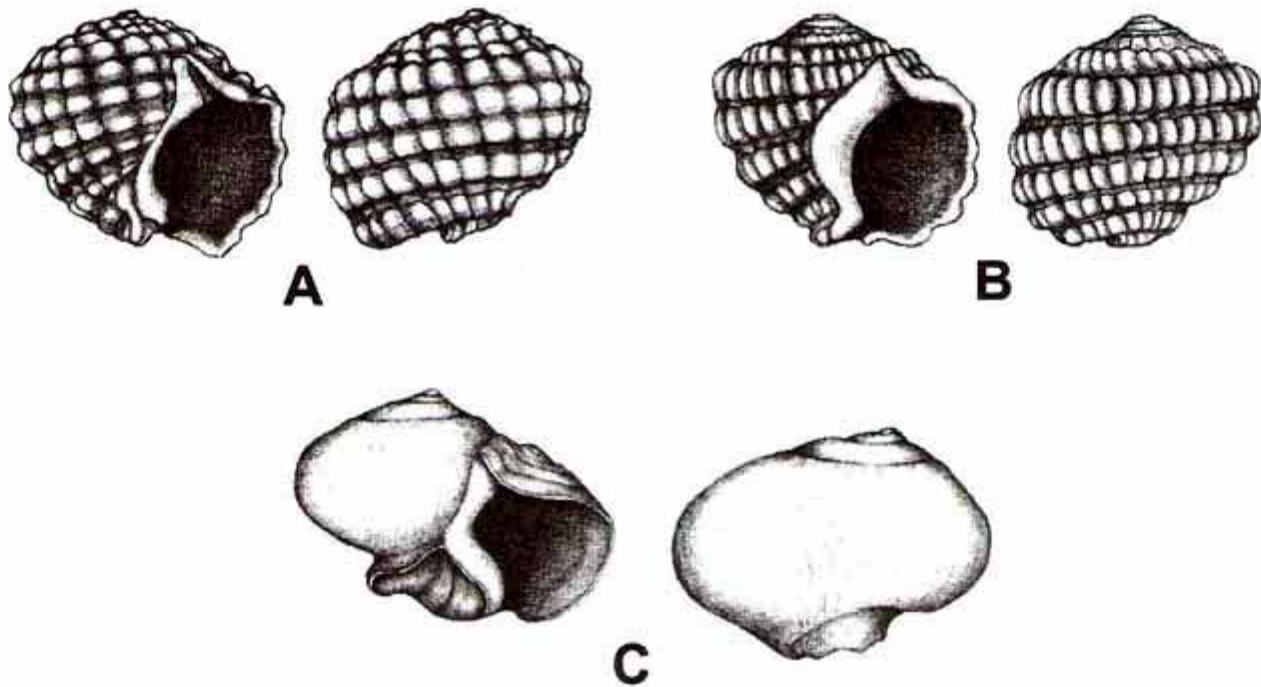
Fig. 1: (A) *Schizobasis kilburni* n. sp. with lowly rounded shell is ornamented by 5 to 6 strong nodose spiral cords and has a narrow, curving siphonal canal that is strongly bent back and pressed against the shell base. This species from the Umzamba river mouth in the northeastern-most Cape Province of South Africa is very similar to *Schizobasis depressa* (B) from the Ripley Formation of northern Mississippi and southwestern Tennessee, USA with about 2 cm high and wide neritiform shell. (C) *Natalites herberti* n. sp. with 1.5 cm wide and high, subglobose shell has rounded, smooth shell that contrast to that of Naticidae by having a siphonal canal that is narrow, deep and twisted to the left. The species comes from the Umzamba river mouth in the northeastern-most Cape Province of South Africa (Pondoland, northeastern Transkei).

spiral cords. The aperture is subovate, notched posteriorly, and anteriorly drawn out to a narrow, moderately long curving siphonal canal that is strongly bent back and pressed against the shell base. The outer lip is simple and prosocline in profile. The inner lip bears a sharp fold at the base of the columella and immediately above the siphonal canal (SOHL 1964). The genotype is *Schizobasis depressa* WADE 1916 from Coon Creek, Tennessee (SOHL 1964: Pl. 20, Figs. 27-30, 33, 34).

Differences: The distinctive siphonal canal allies *Schizobasis* with *Hillites* (SOHL 1964, STEPHENSON 1952), but the ornament differs consisting of spiral ribs in *Hillites* and coarse spiral lines of nodes on *Schizobasis*. In general shape *Schizobasis* resembles *Sargana* STEPHENSON 1929 but has a more nodular ornament and a more rounded apex. Probably the protoconch is raised, similar to that of *Weeksia* STEPHENSON 1941 (BANDEL 1993: Pl. 13, Fig. 4).

Remarks: STEPHENSON placed *Sargana*, *Schizobasis* and *Hillites* in the family Sarganidae. SOHL (1964) placed *Schizobasis* together with *Paramorea* and *Morea* into the subfamily Moreinae and *Sargana* in the Rapaninae and both together in the Muricidae. BANDEL & DOCKERY (in prep.) suggest to unite in the Sarganidae along with *Sargana* only such similar genera among the late Cretaceous gastropods, that also have a planispirally or low naticoid protoconch as is characteristic to *Sargana* (BANDEL 1993: Pl. 13, Fig. 3). Thus, *Schizobasis* is considered to represent a member of the Moreinae with rounded naticoidal protoconch as found in *Morea*, but the Moreinae as being closely related to the Sarganinae.

Schizobasis kilburni n. sp.
Fig. 1A; Pl. 4: Fig. 9

Diagnosis: The lowly rounded, wider than high shell with basal constriction and very short and

hollowed siphonal pillar is ornamented by 5 to 6 spiral cords of which 4 are on the rounded sides and the other feature the base. The subovate aperture is provided with a posterior notch and anteriorly with a curving siphonal canal. The inner lip forms callus-wall that borders the inner side of the narrow umbilicus (Pl. 4: Figs. 9, 10).

Description: The depressed shell is a little wider (23 mm) than high (21 mm) and has a strong and deep basal constriction. The ornament consists of 5 to 6 strong nodose spiral cords. Four of these cords are of about equal strength and feature the rounded whorl sides. The aperture is subovate and has a posterior notch present between callus on the inner lip and onset of the thick outer lip. Anteriorly the almost round aperture is drawn out to a narrow, curving siphonal canal that is strongly bent back and pressed against the shell base. The outer lip is solid, and the inner lip forms a posterior callus and folds up at the base of the columella and immediately above the short umbilicus that is bordered by a wide ridge on the other side.

Remarks: This species from Umzamba Formation at the northeastern corner of Transkei (South Africa) is extremely similar to *Schizobasis depressa* from the Ripley Formation. According to SOHL (1964: Pl. 20, Figs. 27-30, 33, 34; Pl. 21, Figs. 1-4) *Schizobasis depressa* (Fig. 1B) has an about 2 cm high and wide neritaform shell with ornament of 7 coarsely nodded strong spiral cords, of which 5 about equal sized ones are seen on the rounded whorl flanks, while there are 4 seen in *Schizobasis kilburni*. *Schizobasis immersa* WADE 1926 demonstrates even 7 such spiral noded ribs on the whorl sides (SOHL 1964: Pl. 20, Figs. 31, 32, 35, 36).

Derivatio nominis: Named for Dick Kilburn, a distinguished Malacologist of the Natal Museum in Pietermaritzburg.

Locus typicus: Umzamba river mouth in the northeastern-most Cape Province of South Africa.

Stratum typicum: Santonian Umzamba Formation.

Holotype: The illustrated specimen (Pl. 4: Figs. 9, 10) will be deposited in the South African Museum of Natural History in Cape Town, South Africa.

Genus *Hillites* STEPHENSON 1952

Description: The medium sized (about 3 cm), subglobose shell with low rounded, dome shaped spire of three whorls with round profile is ornamented by closely spaced and dominant spiral ribs crossed by sinuous axial ribs and growth laminae of foreward oblique inclination. The aperture is broadly lanceolate with acute angulation by a posterior notch of the outer lip. The siphonal canal is narrow, deep and twisted to the left. The umbilicus is open. The genotype is *Hillites mutilirae* STEPHENSON 1952 from the Cenomanian Woodbine Formation in Texas.

Difference: *Hillites* closely resembles *Schizobasis* regarding shell shape, but differs from it by the fine ornament dominated by spiral ribs. It is like *Natalites* in shape but in contrast to it not smooth but ornamented by spiral ribs.

Remarks: The Cenomanian of Texas holds members of the Moreinae (*Hillites*), the Volutoderminae (*Carota*), the Pyrofusinae (*Bellifusus, Aliofusus* and *Paleopsephaea*). The diversion into separate groups from a stem group should, thus, have occurred earlier, perhaps the Aptian/Albian as suggested by TAYLOR et al. (1980, 1983), BANDEL (1993) and SCHRÖDER (1995), but intermediate species lived in a worldwide scale up to Campanian and Maastrichtian time.

Genus *Natalites* n. gen.

Generic diagnosis: The subglobose shell is as wide as high and provided with lowly rounded spire. Ornament consists only of growth laminae. The elongate aperture has a narrow posterior notch and narrow, deep siphonal canal curving to the left. The narrow umbilicus is bordered by the reflexed inner lip and a carina on the base. The genotype is *Natalites herberti* from the Umzamba Cretaceous of South Africa.

Natalites herberti n. sp.
Fig. 1B; Pl. 4: Figs. 7-8

Diagnosis: As genus.

Description: The around 1.5 cm wide and high, subglobose shell has a low rounded spire of three whorls with round profile. Its ornament consists of sinuous collabral growth laminae. The aperture is broadly lanceolate with a narrow posterior canal forming a notch of the outer lip at its onset on the former whorl. The siphonal canal is narrow, deep and twisted to the left. The umbilicus is open with the columellar lip reflexed on the right side and bordered by a carina on the other side.

Difference: *Natalites herberti* resembles species of *Gyrodes* with a strong carina around the umbilicus. It differs from these by the narrow siphon which is never present in *Gyrodes* or any other naticoid species. *Schizobasis* differs because of the presence of spiral ornament, which is absent in *Natalites herberti*. The columella with the surrounding lamellar ridge resembles to similar features found in *Sargana*, and *Hippocampoides* WADE 1916 (SOHL 1964: Pl. 21, Figs. 5-7, 11-13).

Derivatio nominis: Named after David Herbert, distinguished malacologist of the Natal Museum in Pietermaritzburg.

Locus typicus: Umzamba river mouth in the northeastern-most Cape Province of South Africa (Pondoland, northeastern Transkei).

Stratum typicum: Santonian Umzamba Formation.

Holotype: The specimen will be deposited in the South African Museum of Natural History in Cape Town, South Africa (Pl. 4: Figs. 7, 8).

Remarks: Naticidae of our time are provided with a snorkel-like, fleshy siphonal tube, but have no siphonal canal on their shell. If their ancestors were similar to *Natalites*, which is here suggested, than they had a shell feature matching the siphon of todays naticids. On their way into the sediment this feature of a siphonal canal was lost as is seen already in the Cretaceous *Gyrodes*. Similarities exist to the genus *Hippocampoides* which was considered to represent a member of the Magilidae (= Coralliophilidae) by SOHL (1964). This represents only a convergence as is evident when the smooth and almost planispiral protoconch of *Hippocampoides* is compared to the complexly ornamented and high spires ones of the modern coral living species like *Coralliophila* H. & A. ADAMS, 1853 (BANDEL 1993: Pl. 15, Fig. 6). STEPHENSON (1941) considered the

genus *Hippocampoides* to belong to the Euomphalidae without stating a specific reason. This placement is definitely wrong since we know that *Euomphalus* and relation belong to a characteristic Paleozoic group of Gastropoda that is quite independant from all others and represent an own and long distinct subclass of its own (BANDEL & FRYDA 1998).

11. THE CONVERGENT FOSSIL PSEUDAMAURIDAE

The family Pseudamauridae KOWALKE & BANDEL, 1996 holds caenogastropods of naticoid shape with globular to egg-conical shell, with whorls rounded or flattened at the sides, and large final whorl of globular or egg-like shape. The name giving genus *Pseudamaura* FISCHER 1885 is based on type *Natica bulbiformis* SOWERBY 1831 from the Late Cretaceous Gosau deposits in the northern Alps. This species lived in tropical, lagoonal environment. Its thick walled egg-shaped shell consists of rounded, posteriorly tabulated whorls and narrow umbilical slit that is wider in younger individuals. The aperture is almost oval or spindle shaped and the inner lip may be provided with a columellar callus and a callus pad that covers the shell (KOWALKE & BANDEL 1996: Pl. 6, Figs. 3-6). The Late Cretaceous *Pseudamaura lyrata* (SOWERBY 1831) was considered a typical representative to the family (KOWALKE & BANDEL 1996). Here the protoconch consists of 1.7 whorls, has a diameter of 0.31 mm and the large first whorl (0.18 mm across) indicates lecithotrophic development.

Pseudamaura lepta SOHL 1964 with high spired naticoid shell with channeled sutures and delicate spiral sculpture from the Coffee Sand (Late Campanian of Mississippi; SOHL 1964: Pl. 55, Figs. 3-5, DOCKERY 1993: Pl. 20, Figs. 5, 6) and *Pseudamaura lirata* (WADE 1926) from Coon Creek (Early Maastrichtian of Tennessee) are similar species of a less tropical environment in the former Northern Hemisphere. *Pseudamaura nobilis* (STOLICZKA 1868) from the Trichinopoly group in southern India represented a related species in the former Southern Hemisphere (Bandel in prep). STEPHENSON (1952: Pl. 35, Figs. 27-38) described *Natica humilis* CRAGIN 1893, *Natica striaticostata* CRAGIN 1893, *Natica dorothiensis* STEPHENSON 1952, *Natica rivulana* STEPHENSON 1952 from the Cenomanian Woodbine Formation of Texas, which all may represent one

and the same somewhat variable species of the Pseudamauridae in occurrence predating the genus *Pseudamaura*.

KOWALKE & BANDEL (1996) interpreted *Pseudamaura* to represent a caenogastropod of questionable relation to the Cerithiimorpha. Members of the genera *Ampullina* BOWDICH 1822, *Amaurellina* FISCHER 1885, *Deshayesia* RAULIN 1844, *Crommium* COSSMANN 1888 and *Euspira* AGASSIZ 1838 with type species that have lived in the Eocene may all belong to relation of the Pseudamauridae and not to the Naticidae as was assumed by WENZ (1938) and MARINCOVICH (1977).

The genus *Ampullina* BOWDICH 1882 has a typically large sized, thick, high spired, rather globose naticoid shell with stepped whorls and spiral rows of fine punctae. Its umbilicus is small and limited by a well defined limb. The aperture is narrowly semilunar. Its inner lip has thick columellar and parietal callus. The genus is based on *Ampullina depressa* (LAMARCK 1804) from the Middle Eocene of the Paris Basin. DOCKERY (1993: Pl. 20, Fig. 15) placed the Campanian *Ampullina potens* WADE 1926 from Coffee Sand of Mississippi in this genus. *Ampullina* was also recognized from the coal swamp facies of the Hungarian Eocene, for example *Ampullina perusta* (DEFRANCE 1823). It represents a common shell in Gant (SZÖTS 1953: Pl. 5, Figs. 1-10), Dudar (STRAUSZ 1966) and Dorog (KECSKEMÉTY-KÖRMENDY 1972: Pl. 19, Figs. 1, 2, 4). The protoconch of *Ampullina* from the Eocene of the Paris Basin (Damery) and from the Eocene of Gan in the northern Pyrenees has a protoconch with sinusigera shape. Here the embryonic whorl measures about 0.1 mm in diameter and it is succeeded by more than one whorl formed by the larva ending in a strongly sinuous thickend apertural margin. The protoconch measures about 0.3 mm in width and is of rounded trochiform shape with sinuous growth lines as only ornament (Pl. 3: Fig. 7; Pl. 4: Fig. 1).

Amaurellina FISCHER 1885 is a medium sized naticoid shell has a body whorl taking about two-third of the height, with shouldered whorls of the spire (narrowly tabulate). The shoulders are excavated with narrowly channeled suture. The aperture is subovate with the inner lip anteriorly expanded and reflected. The base has a reduced umbilical sheath that extends up into the umbilicus (notched umbilicus). Thus a slender cord arising at the anterior inner lip is directed into the umbilicus. Genotype is *Amaurellina spirata*

(LAMARCK 1804) from the Middle Eocene of the Paris Basin. From the Coffee Sand DOCKERY (1991: Pl. 20, Fig. 7, 8) described *Amaurellina stephensoni* WADE 1926 which is related to *Pseudamaura lirata* (WADE 1926) from Coon Creek (SOHL 1960: Pl. 17, Figs. 20, 21, 23). MARINCOVICH (1977: Pl. 20, Figs. 11-13) described *Amaurellina caleocia* VOKES 1939 from the Eocene of California. This latter species has fine spiral sculpture and a slender cord entering the umbilicus from the anterior inner lip. An *Amaurellina* from the Eocene of the Paris Basin (Daméry) has the protoconch well preserved (Pl. 4: Figs. 2, 3, 4). The smooth embryonic whorl measures a little more than 0.1 mm in diameter and it is clearly set off from the larval shell by beginning growth lines. The larval shell consists of 1.5 whorls and is ornamented of regularely arranged sinuous collabral lines on a smooth surface. The whole protoconch is of similar height and width, consists of a little more than two whorls and measures about 0.3 mm across.

MARINCOVICH (1977) found that Cenozoic gastropods which he considered to represent members of the Ampullospirinae in western North America are known only from Paleocene and Eocene formations. He expressed the opinion that most, if not all, Tertiary ampullospirines of the American westcoast evolved from indigenous Cretaceous ancestors. But many of the Paleocene species of the genera *Ampullospira*, *Eocernina*, *Crommium*, *Lacunaria* probably do not even represent naticids. This accounts also for *Tejonia*, and *Pachycrommium* which have been living in the Eocene of the Pacific coastal area and to a large extent became extinct at the Eocene / Oligocene transition.

Deshayesia RAULIN 1844 based on an Eocene species was considered by WENZ (1938: Fig. 2932) to represent a subgenus of the naticid *Globularia* because their shells resemble each other. Thus STRAUSZ (1966: Pl. 11, Fig. 6) recognized a *Globularia incompleta* (ZITTEL 1862) in the Eocene of the Hungarian Dudar. It is about 3 cm high and 2.5 cm wide. It has a thick inner lip and the umbilicus is almost covered by a callus plug. KECSKEMÉTY-KÖRMENDY (1972: Pl. 19, Fig. 5) and SZÖTS (1953: Pl. 5, Figs. 22-25) distingushed it from *Deshayesia* s. s. present with *Deshayesia alpina* (ORBIGNY 1850) in Dorog and Gant (Hungary) with about 2 cm high and almost as wide shell in which the spire forms stairs.

The genus *Lacunaria* CONRAD 1866 has a thin and subglobose to elongate shell with moderately

elevated spire and weakly tabulate whorls. The umbilicus is slit like and sculpture consists of minute spiral lirae. The type is *Natica (Gyrodes) alabamiensis* WHITFIELD 1865 from the Paleocene of Alabama. A Paleocene species from California called *Lacunaria striata* (GABB 1869) is figured by MARINCOVICH (1977: Pl. 17, Figs. 11-14). Similarly the genus *Crommium* COSSMANN 1888 with medium sized to large globose to slightly elongate shell with the spire moderately elevated is based on the type *Ampullaria willemetii* DESHAYES 1825 from the Eocene of France of which the protoconch is unknown. *Crommium* differs from *Lacunaria* only by a generally more globular shape of the teleoconch. MARINCOVICH (1977: Pl. 18, Figs. 3-13) included here the species *Crommium andersoni* (DICKERSON 1914) and *C. pinyonensis* (DICKERSON 1914) from the Paleocene and Eocene of Oregon to California. A *Crommium* from the Eocene of the Paris Basin (Damery) has a protoconch reflecting a planktotrophic larva very much of the same type as observed in *Amaurellina* from the same locality. The ornament of the larval shell also consists of collabral lirae reflecting the sinuous outline of the outer lip. After metamorphosis the growth line pattern changed from sinuous to simple. in difference to the larval shell of *Amaurellina* that of *Crommium* is wider (0.3 mm) than high. (Pl. 4: Figs. 5, 6).

The genus *Eocernina* GARDNER & BOWLES 1934 differs from *Crommium* by the presence of an umbilical callus, otherwise it is very similar. MARINCOVICH (1977: Pl. 19, Figs. 1-4) described its type *Eocernina hannibali* (DICKERSON 1914) from the Eocene of California, Oregon and Washington and related this fairly variable species with *E. chiapasensis* (GARDNER & BOWLES 1934) from the Eocene of Mexico. Also the genus *Euspirocrommium* SACCO 1890 with elongate shell and strongly elevated spire and evenly rounded whorls with closed umbilicus is based on *Natica elongata* MICHELOTTI 1861 (= *Crommium (Euspirocrommium) degensis* SACCO 1890) from the Oligocene of Italy. According to MARINCOVICH (1977: Pl. 20, Figs. 1-3) *Euspirocrommium hewitti* (HANNA & HERTLEIN 1949) from the Eocene of California belongs here and is characterized by the elongate shell shape, rounded whorls and closed umbilicus, which differs from tabulate *Tejonia* and *Ampullospira* and spirally ornamented *Crommium* with open umbilicus.

The genus *Tejonia* HANNA & HERTLEIN 1943 includes subglobular to moderately elongate shells with elevated spire and narrowly tabulate shoulders. The suture is simple and the umbilicus slit-like. A low cord arises at the anterior inner lip and enters the umbilicus. The ornament appears smooth with fine spiral striae. The type is *Natica alveata* CONRAD 1855 = *Amaurellina moragai* STEWART 1927 from the Eocene of California and Oregon (MARINCOVICH 1977: Pl. 19, Figs. 6-12). *Tejonia* differs from *Crommium* and *Eocernia* by its strongly tabulate, stair-like whorls and by the cord entering the umbilicus from the anterior inner lip. Also the genus *Pachycrommium* WOODRING 1928 based on *Pachycrommium guppyi* GABB 1873 from the Miocene of the Dominican Republic with elongate shell that has a strongly elevated spire with more or less tabulate outline. MARINCOVICH (1977: Pl. 20, Figs. 4-10) included *Pachycrommium clarki* (STEWART 1927) from the Eocene of California, where this species is extremely common. It is considered similar to *Ampullospira* but lacks the channeled suture.

COSSMANN (1925) included *Ampullina* and *Euspira* AGASSIZ 1838 in his family Euspiridae. which later were tranformed into the Ampullospirinae by COX (1930). The genus *Globularia* SWAINSON 1840, subgenus *Ampullella* COX 1931 (= *Ampullina*) has a spire that is moderately high, has a siphonal fasciole and a callus in the umbilical region. It is present in the Ripley Formation with the species *Globularia (Ampullella) umbilica* (WADE 1926), according to SOHL (1960: Pl. 18, Figs. 39, 40).

The genus *Euspira* is based on a medium to large sized globose naticoid shell that has abutting to impressed sutures (suprasutural ramp). The umbilicus is of small to medium size and without edge or ridge surrounding it. The shell is smooth and has a semicircular aperture. Its type species *Euspira glaucinoides* (SOWERBY 1812) from the Middle Eocene of Great Britain and of the Paris Basin has been redescribed and figured by WRIGLEY (1949), but without the protoconch. There are numerous modern species which have been considered to belong to the genus *Euspira* which is the older name to *Lunatia* (KABAT 1991). But until the protoconch of the Eocene type species has not been demonstated to belong to a naticid it may also represent a pseudamaurinid species. It is not wise to replace the generic name *Lunatia* which is based on a living species with *Euspira*, as long as the protoconch of the latter is unknown.

Other more ancient potential members of the Pseudamauridae may be represented with the genus *Ampullospira* HARRIS 1897 with the type

Ampullospira canaliculata (MORRIS & LYCETT 1851) from the Middle Jurassic of England (HUDDLESTON 1892: Pl. 20, Fig. 16). *Ampullospira* has an elongate shell with elevated spire, narrowly tabulate shoulder, narrowly channeled suture, and slit-like umbilicus. The ornament consists of fine spiral lines. MORRIS & LYCETT (1851) distinguished among the Mid-Jurassic gastropods of England with naticoid appearance two subgenera of *Natica*, one supposedly representing *Natica* s. s., the other *Euspira*. In their opinion the species with rounded shoulders belong to *Natica* (*Natica*) and with square shoulders to *Natica* (*Euspira*). COSSMANN (1925) placed all these Jurassic species in the genus *Ampullina*. *Euspira* and *Ampullina* have type species that lived in the Eocene of the Paris Basin. It is thus better and safer to use the generic name *Ampullospira* with type that lived during Mid Jurassic time, to not complicate matters more.

Protoconchs belonging to Jurassic *Ampullospira* have been discovered by SCHRÖDER (1995: Pl. 4, Figs. 8-11) from the Aalenium of northern Germany. They differ from those of the Naticidae in having totally smooth and helicospirally coiled whorls which have a thickened and distinctly sinuous apertural margin (sinusigera shape). From the Pseudamaurinidae s. s. they differ by not having the collabral lirae and by having a more pronounced and stronger thickened apertural margin of the fully grown larval shell. *Ampullospira* is the type genus to the Ampullospirinae COX 1930, and therefore the latter are no members of the Naticidae or even the Naticoidea. Ampullospirinae may belong into the stem group of the Pseudamauridae or may even be a part of this taxon. In the later case the Pseudamauridae had Jurassic representatives which could perhaps be related to the Coelostylinidae COSSMANN 1909 and here genera like *Ampezzoella* BANDEL 1992 from the Late Triassic of the Dolomites (BANDEL 1992: Pl. 8, Figs. 2-5).

12. CONCLUSIONS

The Naticoidea are a natural group among the Caenogastropoda and they have been in existence since mid-Cretaceous times. Naticoidea have probably been connected right from the start with their specific mode of life as carnivorous hunters of shelled epifaunal and infaunal animals of soft marine substrates. The hallmark of their existence is also that they open the shell of their prey by drilling a hole into it. Apparently naticoids can be connected to those gastropods from which also most, if not all, of the Neogastropoda have taken their origin but also most if not all of the Neomesogastropoda (BANDEL 1993). The genera *Schizobasis*, *Hillites* and *Natalites* may represent related gastropods to the stem group representatives from which Naticidae arose. In case of *Gyrodes* s. s. a member of the Naticidae still has the characteristic subsutural ribbon of that stem group, which was already lost within the other subgenera of this genus.

Regarding teleoconch shape the transition from more fusiform members of the stem group to such as found in *Natalites* is connected with the loss of external ornament of the shell. It may well be that prior to this in a genus like *Hillites* with spiral ornament of the teleoconch this sculptural pattern had extended onto the larval shell and subsequently been preserved in the naticoid lineage. Another feature of the shell that was lost on the evolutionary pathway of the Naticoidea is the shell siphon. In *Schizobasis* and *Hillites* it has become short and narrow and in *Natalites* even more so, but it is still present. In *Gyrodes* and all other naticids there is a well developed fleshy siphon, but the shell no longer has a siphon, which may have gone along with ist streamlining in order to burry well in loose sediment. There are others that burry their way through the sediment and have retained a shell siphon, but these are of fusiform and not globular shape as in the naticids (such as Olividae, many Marginellidae etc).

Characteristic to the group and to all Neomesogastropoda and Neogastropoda is a large protoconch which in case of the Naticidae is of globular shape with almost flattened apical portion and fairly large size commonly reaching 1 mm in diameter in fully grown larvae. This is so at least since Santonian time (BANDEL 1993: Pl. 12, Fig. 3) from which the oldest naticid protoconch has been recognized in the Amman Formation of Jordan. The members of the stem group of the Naticoidea are related to species like *Sargana* and *Morea* which are known to have similarily large protoconchs, and from these connections to the group around *Pyrifusus* can be constructed, which had a conical, large, smooth larval shell and tuberculate pattern on the embryonic shell (BANDEL 1993: Pl. 15, Figs. 1, 2) [Pl. 3: Fig. 6].

Gyrodes with its wide umbilicus developed species with callus of the inner lip entering the umbilicus in different ways which is used for the differentiation of three subgenera. As soon as the

umbilical callus became similar to that seen among some modern Naticinae, the Cretaceous species involved were interpreted to represent members of such Naticinae (POPENOE et al. 1987) even though the remaining part of the shell is like a *Gyrodes* and thus like that of members of the Gyrodinae. Members of the genera *Polinices* and *Lunatia* (= *Euspira*) were recognized in Cretaceous naticoid shells with narrower umbilicus as is usually present in the Gyrodinae (SOHL 1960, DOCKERY 1993 for lit.). The characteristic feature of the naticine shell among the modern species is the calcareous operculum, which has, up to date, not been reported from any Cretaceous species. Taking all this into consideration, it become quite evident that the established classification rests strongly on only one character, the shape and position of the umbilical callus. It has become quite evident in this review of the naticoids that umbilical features have developed similar shape in several independent lineages. Classification of a Cretaceous gyrodiform naticid with Naticinae solely based on the shape of the inner lip callus can thus not present to us a lot of phylogenetic information.

Among Tertiary and modern Naticidae classification is actually also quite simplistic and based mainly on the presence and absence of a calcareous operculum between Naticinae and Polinicinae and the increase of body volume connected to the reduction of the shell and operculum in the Sininae. It may well be that the calcareous operculum was invented only once in naticid history, but the increase in body volume and related widening of the body whorl apparently has occurred several times and in several independant lineages.

The elucidation of naticoid evolutionary history is made difficult by the fact, that a large group of probably herbivorous gastropods developed alongside that may have had connections to the Coelostylinidae of Triassic times (BANDEL 1992), probably to Ampullospirinae of Jurassic times and the Pseudamauridae of Late Cretaceous and Paleogene times. MARINCOVICH (1977) noted that the ampullospirine species, which he considered to belong to the Naticidae, along the western shore of the USA became extinct before the beginning of the Oligocene. But what he actually observed was the last occurrence of the Pseudamauridae. Only much later some naticids like the cold water genus *Amauropsis* developed convergent shell shape. The same observation can be made in Europe and here it has been recognized that many of the *Natica*-like species in the Eocene actually do not belong to the Naticoidea at all (BANDEL 1993). The protoconch of the Pseudamauridae is not of naticid type but has a rather characteristic shape that distinuishes members of the group from all other known caenogastropod families (KOWALKE 1998). Many of the species of the Pseudamauridae can be differentiated from Naticidae only when their protoconch is known.

13. ACKNOWLEDGMENTS

14. REFERENCES

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Plate 1-4

Plate 1

Fig. 1:   The protoconch of *Sinum perspectivum* (SAY 1831) consists of a little less than 2.5 whorls and is about 1.5 mm wide. From the SE coastal shelf of the USA.

Fig. 2:   The close-up of the embryonic shell of *Sinum perspectivum* shows that it is ornamented by fine spiral rows of tubercles. [Same specimen as in Fig. 1.]

Fig. 3:   The protoconch of *Sinum perspectivum* (SAY 1831) is well differentiated from the juvenile shell in a specimen from the Caribbean Sea near Santa Marta (Bay of Santa Marta and Bay of Chengue). The shell is about 5 mm wide.

Fig. 4:   A very similar larval shell as is found in modern *Lunatia alderi* is connected to a juvenile naticoid teleoconch of a fossil species from the Miocene of Dingden in northwestern Germany. The embryonic shell ends with first growth lines and measures about 0.2 mm across.

Fig. 5:   The larval shell of *Lunatia alderi* (FORBES 1838) measures 0.65-0.8 mm in diameter and consists of 2.25 whorls. The larval shell is ornamented by delicate spiral rows of tubercles with 0.5 to 1 micron width that have a distance of 12 micron from each other. From the Mediterranean Sea near Banyuls-Sur-Mer.

Fig. 6:   The veliger hatches with an embryonic·shell of about 0.2 mm in width and an initial cap of 0.07 mm width. It consists of about one whorl rapidly increasing in diameter. Three fourth of it are ornamented by a ridge groove pattern in which the ridges are separated from each other by five micron. The last fourth of the shell has strong growth increments which indicate the time of hatching. [Detail to Fig. 5.]

Fig. 7:   Apertural view of the embryonic shell of *Lunatia intricatoides* from the Mediterranean Sea near Banyuls-Sur-Mer. Here young hatch from their egg mass crawling with almost 1 mm wide shell.

Fig. 8:   Apical view of the same shell as in Fig. 7 with the initial whorl without growth lines that measures 0.3 mm in diameter with an initial cap wider than 0.1 mm. It is succeeded by another 1.5 whorls amounting to a shell of almost 1 mm in width when the young is hatching.

Fig. 9:   A member of the Sininae from the Eocene of the Moodys Branch Riverside location in Jacksonville, Mississippi has an embryonic shell with a groove ridge pattern and almost 0.14 mm in diameter succeeded by 2.4 whorls of the larval shell with an ornament by very faint spiral striae and short axial ribs. The protoconch here consists of a little more than three whorls and measures 1.4 mm in diameter.
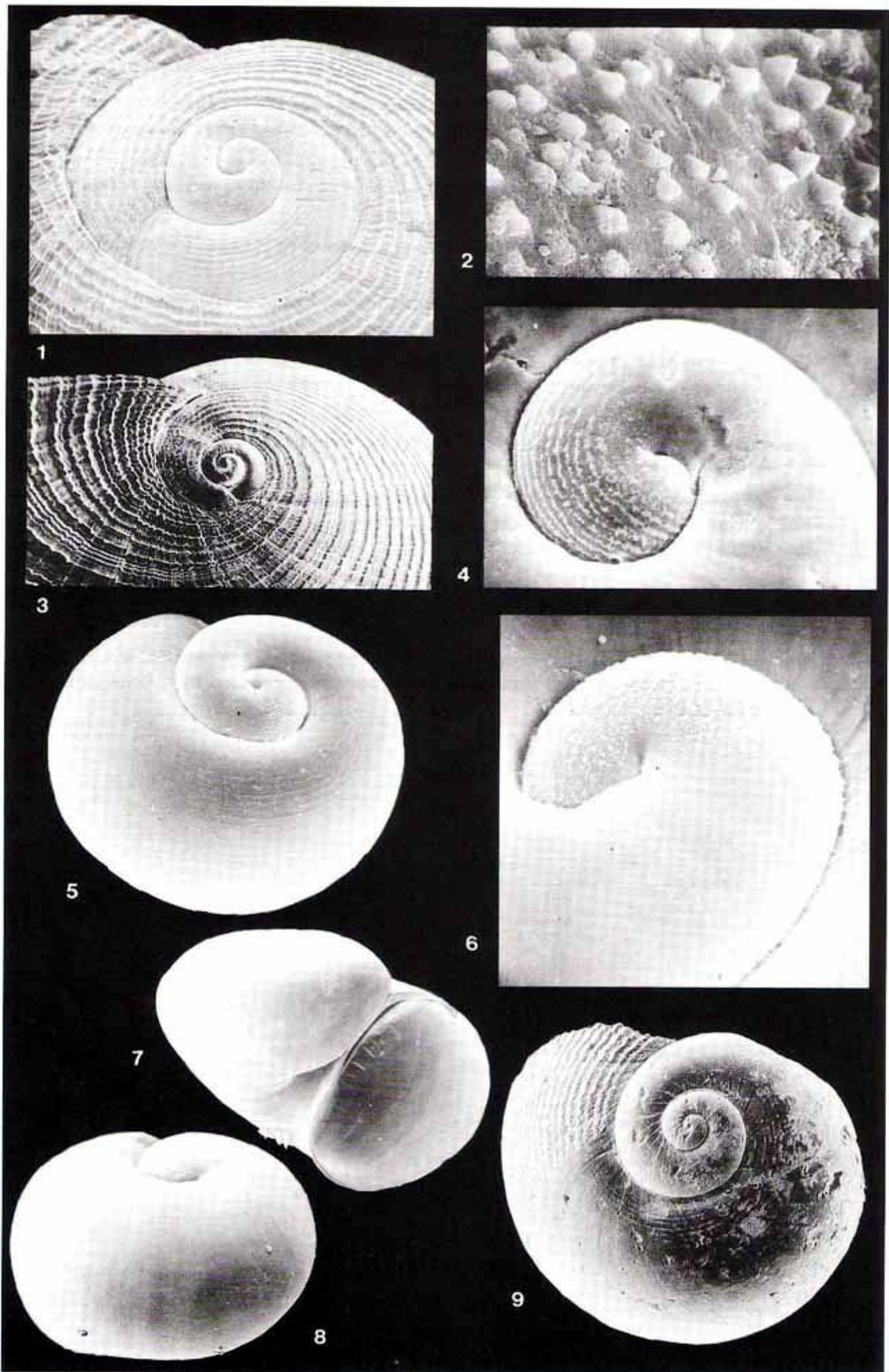
Plate 2

Fig. 1: Ornament of the embryonic shell in case of *Polinices mammata* RÖDING 1798 from the Red Sea at Port Sudan consists of rows of tubercles. The shell of the freshly hatched veliger measures about 0.2 mm across.

Fig. 2: A fully grown larval shell from the Red Sea with 1.2 mm wide shell could very well represent *Polinices mammata*.

Fig. 3: A veliger swimming in the Red Sea that is equipped with a shell as in Fig. 2. The velar lobes are rather large and long.

Fig. 4: The embryonic shell of *Polinices mammila* (LINNEAUS 1758) as it hatched from its spawn at Port Sudan, Red Sea, measures about 0.2 mm across and is ornamented by tubercles.

Fig. 5: The embryonic shell of *Polinices lacteus* GUILDING 1834 as it hatched from its spawn in Curacao, Caribbean Sea, is partly covered by tubercles arranged into spiral rows which grade into spiral lirae still on that shell. The shell measures almost 0.3 mm across.

Fig. 6: The about 3 mm large juvenile naticid shell from the Indo-Pacific Ocean at Bali has a large protoconch of the type seen in Fig. 2.

Fig. 7: Another juvenile naticid shell from Bali has direct development as is indicated by a protoconch of simple shape. The primary shell without growth lines measures about 0.6 mm in diameter. Growth lines indicate the following prehatching shell that grades into the teleoconch without apparent interruption.

Fig. 8: A juvenile naticid shell from the Southern Chinese Sea demonstrates a 0.35 mm large primary shell that grew within the egg capsule to a size of about 1 mm forming a protoconch of globular shape. From there on the teleoconch formed.

Fig. 9: The embryonic shell of a naticid from the Eocene of Moodys Branch in Jackson, Mississippi, has a tuberculated embryonic shell of about 0.15 mm in diameter succeeded by a larval shell with fine indistinct spiral lirae.
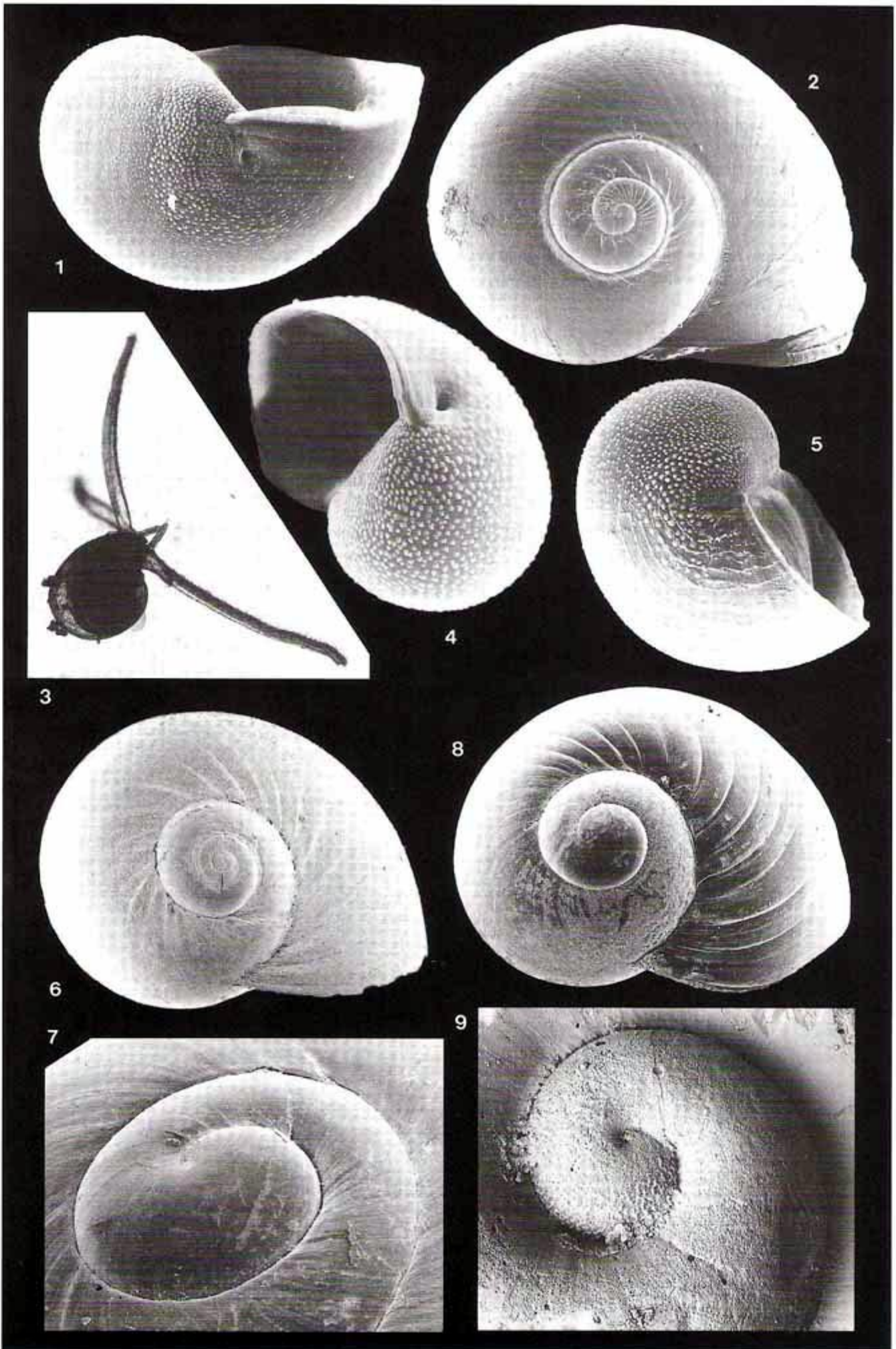
Plate 3

Fig. 1: A juvenile shell of a member of the Sininae from the Eocene of the Paris Basin (Damery) has a protoconch consisting of 2.8 whorls and 1.5 mm width. Within the first whorl of the larval shell an ornament of broad spiral ribbons separated by narrow furrows begins and continues to the aperture of the protoconch.

Fig. 2: Detail to Fig. 1 with the embryonic whorl that measures only about 0.1 mm in diameter. It is delicately tuberculated in its initial portion and becomes smooth near the onset of the first growth lines.

Fig. 3: *Luntia catena* (DA COSTA 1778) hatches long after metamorphosis, and its protoconch consists of a large about 0.3 mm wide embryonic whorl of simplified structure. The shell is from the Mediterranean Sea at Banyuls-Sur-Mer.

Fig. 4: A Paleocene polinicine species from Matthews Landing at the Alabama River in Alabama has delicate tubercules on the embryonic whorl that measures about 0.12 mm across. Growth lines indicate the onset of the larval shell that has smooth surface with faint spiral lirae and consists of about two whorls. The whole protoconch consist of a little more than three whorls and measures about 1.3 mm in width.

Fig. 5: An Eocene species from the Yazoo Clay in Mississippi has a tuberculate embryonic shell of about 0.15 mm in diameter succeeded by a larval shell with fine indistinct spiral lirae. Protoconch and teleoconch merge with each other, but probably the protconch ends where regular fine axial striae begin in the ornament. It would than have a size of about 1.3 mm in width.

Fig. 6: The embryonic shell of *Gyrodes* sp. from the Maastrichtian Ripley Formation of Coon Creek in Tennessee is a little wider than 0.2 mm and has a fine ornament of tubercles.

Fig. 7: The juvenile shell of *Ampullina* sp. from the Eocene of Gan in the northern Pyrenees. The protoconch is illustrated on Pl. 4: Fig. 1.

Fig. 8: A juvenile shell of a naticid from the Eocene of Texas, Brazos River near College Station, has a very indistinct transition of the larval shell into the teleoconch (seen in the center of the body whorl). The shell measures about 1 mm across and developed the characteristic columellar folds.
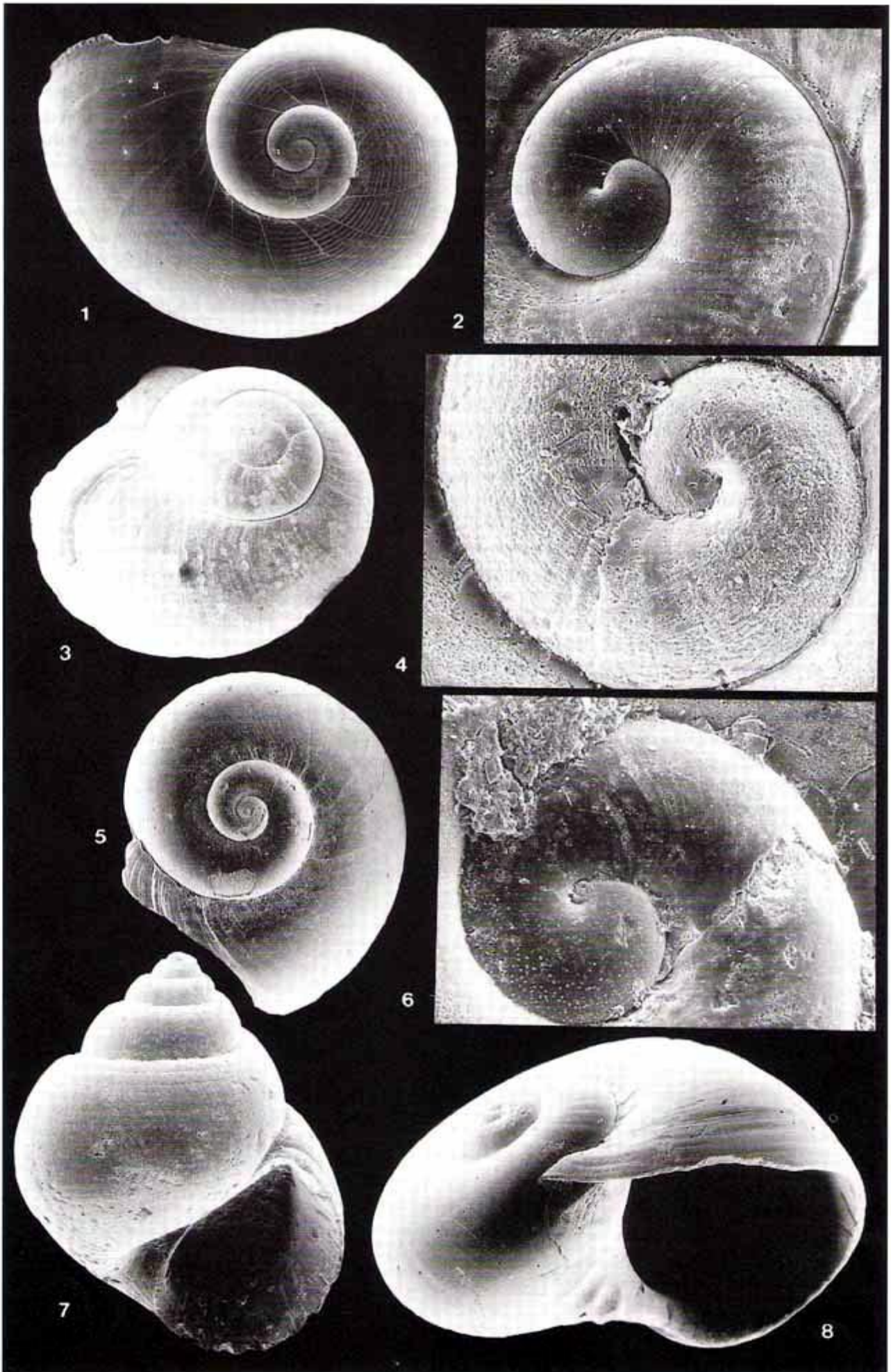
Plate 4

Fig. 1: The protoconch of *Ampullina* sp. from the Eocene of Gan in the northern Pyrenees has a protoconch with sinusigera shape (detail to Pl. 3: Fig. 7). Here the embryonic whorl measures about 0.1 mm in diameter and it is succeeded by more than one whorl formed by the larva ending in a strongly sinuous thickened apertural margin. The protoconch measures about 0.3 mm in width and is of rounded trochiform shape with sinuous growth lines as only ornament.

Fig. 2: An *Amaurellina* sp. from the Eocene of the Paris Basin (Daméry) has the protoconch with smooth embryonic whorl that measures a little more than 0.1 mm in diameter, and it is clearly set off from the larval shell by beginning growth lines. The larval shell consists of 1.5 whorls and is ornamented of regularely arranged sinuous collabral lines on a smooth surface (see Fig. 3).

Fig. 3: *Amaurellina* sp. as in Fig. 2 with the whole protoconch visible that is of similar height as width, consisting of a little more than two whorls and measuring about 0.3 mm across.

Fig. 4: *Amaurellina* sp. as in Fig. 2 and Fig. 3 with the almost 3 mm high juvenile shell that carries the protoconch on its apex from the Eocene of Damery, Paris Basin.

Fig. 5: The protoconch of *Crommium* sp. from the Eocene of the Paris Basin (Damery) has a protoconch reflecting a planktotrophic larva very much of the same type as observed in *Amaurellina* from the same locality (Fig. 3). The ornament of the larval shell also consists of collabral lirae reflecting the sinuous outline of the outer lip. The protoconch is wider (0.3 mm) than high.

Fig. 6: After metamorphosis the growth line pattern of the protoconch of *Crommium* sp. changed from sinuous to simple (same shell as in Fig. 5). The juvenile shell is about 1 mm high.

Fig. 7: The fully grown shell of *Natalites herberti* n. sp. is 1.5 cm wide and high, subglobose with round profile. The broadly lanceolate aperture has a narrow posterior canal forming a notch of the outer lip at its onset on the former whorl. The siphonal canal is narrow, deep and twisted to the left. The umbilicus is open with the columellar lip reflexed on the right side and bordered by a carina on the other side.

Fig. 8: Shell of Fig. 7 seen from behind with the sinuous collabral growth laminae of the ornament. Holotype from Umzamba river mouth in the northeastern-most Cape Province of South Africa (Pondoland, northeastern Transkei).

Fig. 9: *Schizobasis kilburni* n. sp. seen from behind with lowly rounded shell. Holotype.

Fig. 10: The same as Fig. 9 in apertural view has the shell a little wider (23 mm) than high (21 mm). The ornament consists of 5 strong nodose spiral cords. There is a narrow, curving siphonal canal that is strongly bent back and pressed against the shell base. Umzamba river mouth in the northeastern-most Cape Province of South Africa.