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The history of *Theodoxus* and *Neritina* connected with description and systematic evaluation of related Neritimorpha (Gastropoda)

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With 315 figures

Contents

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Abstract

Theodoxus and *Neritina* are distinguished from each other by their ontogeny. While the *Theodoxus* relation hatches from its spawn as minature adult, *Neritina* and relation leaves its spawn as planktotrophic larva that will swim in the sea for a more or less extended period before its metamorphosis to a crawling young under the influence of fresh water. This difference in ontogeny can be recognized in the shape of the protoconch and history of both is traced to the Paleocene. Two subfamilies of the Nertininidae can, thus, be distinguishes, namely the Neritininae n. subfam. and the Theodoxinae n. subfam. The Jamaican *Fluvinerita* has a place among the Theodoxinae and, therefore, the paleobiogeographic range of the *Theodoxus* relation is much enlarged. Today its species live in Europe, Northern Africa, and the Middle East. Among living species of *Theodoxus* systematic differentiation is difficult and when fossil representatives are included the taxonomic separation of species is even more problematic. An explanation for this is suggested in local hybridisation, similar as is the case among modern species of *Neritina* occuring in the Indo-Pacific Ocean. Here transition between species are documented from Cebu (Philippines) and Bali (Indonesia) which include the "genera" *Clithon* as well as *Neritina* and its "subgenera". Interpretation of the evolution of the Neritoidea is not easy because of repeated convergence of shell shapes occurring at different times in different groups. Similar species as found among recent Neritoidea have been living in the tropical littoral zones in the Triassic, and during the Jurassic species adopted to the environment of coastal swamps. The Neritidae became quite recogniseable during the Cretaceous when smooth *Dontostoma* as well a spirally ribbed *Nerita* dwelled in tropical rocky littoral environments. A subdivision of the genus *Nerita* in subgenera is problematic since transitional species are the rule. Smaragdiidae have evolved mainly on and along with the marine sea grass. Their protoconch resembles that of the Paleogene Velatinae n. subfam. which evolved to quite characteristic shell shape and large shell dimensions. The Caribbean *Puperita* which evolved to quite characteristic shell shape and large shell dimensions. The Caribbean *Puperita* intermediates between Neritinae and Neritininae. *Calyptronerita* from the Eocene could represent an intermediate between Neritidae and Phenacolepadidae. Neritiliidae are an independant group that may be related to the Cretaceous *Schwardtina* and the terrestric Hydrocenidae, as is indicated when protoconchs are compared. Neritoidea characterised by dissolution of their inner shell walls in the larval shell as well as in the adult shell demonstrate within their genera *Theodoxus* and *Neritina* with many species commonly the occurences of hybrids, and similar tendencies may be discovered among members of the genera *Nerita* and *Smaragdia* as soon as they become more closely inspected. The distinction of species is rather difficult due to this process of hybridisation. Due to this proces a local distinction of species is rather difficult due to this process of hybridisation. Due to this proces a local geographic experssion is produced and rapid historical changes in faunal composition are possible. A better understanding of this process can help in the interpretation of paleobiogeography as is documented by the differences seen in the faunal composition of *Neritina* varieties from Bali, Cebu and Natal/Madagaskar.

Zusammenfassung

Theodoxus und *Neritina* erweisen sich als durch ihre Ontogenese voneinander getrennt. Während in ersterer eine fertige kleine Schnecke das Gelege verläßt, schlüpft bei zweiterer eine planktotrophe Larve, die erst nach längerem Aufenthalt im Meer unter Einfluß von Süßwasser metamorphisiert. Diese Entwicklungsunterschiede sind in der Gestalt des Protoconches erkennbar und bis ins Paläozän hinein zurückverfolgbar. Es ergeben sich daher Anhaltspunkte zur Trennung zweier Unterfamilien der Nertinidae, nämlich der Neritininae n. subfam. und Theodoxinae n. subfam. In letzteres Taxon könnte auch *Fluvinerita* einen Platz bekommen und damit den geographischen Bereich erweitern, der einmal von der *Theodoxus* Verwandtschaft besiedelt war. Denn *Theodoxus* lebt heute in Europa, Nordafrika und dem Nahen Osten, während *Fluvinerita* von Jamaika kommt. Unter heutigen Arten von *Theodoxus* ist die systematische Abtrennung schwierig, und wenn fossile Verteter miteinbezogen werden, wird eine taxonomische Trennung von Arten noch problematischer. Als Grund hierzu wird lokal unterschiedliche Hybridbildung angenommen und mit den Vorgängen verglichen, wie sie bei *Neritina*-Arten im Bereich des heutigen Indo-Pazifischen Ozean auftreten. Hier erweisen Übergänge besonders belegt von Cebu (Philippinen) und Bali (Indonesien), daß eine Vermischung von Arten auffritt, die teils verschiedenen Gattungen (*Clithon*), bzw Untergattungen von *Neritina* zugeordnete wurden. Die Aus-

deutung der Entwicklungsgeschichte der Neritoidea wird durch immer wieder ähnliche Schalengestalten erschwert, die zu unterschiedlichen Zeiten und in unterschiedlichen Verwandtschaftsgruppen entstehen konnten. Den heutigen Neritoidea ähnliche Arten traten schon im tropischen Litoral der Trias auf und schon während des Jura wurden Küstensümpfe besiedelt. Die Neritidae sind seit der Kreide erkennbar und besiedeln mit der glatten *Dontostoma* sowie der spiralig berippten *Nerita* vornehmlich Hartsubstrate im Gezeitenbereich tropischer Küsten. Eine Untergliederung von *Nerita* in Untergattungen erscheint wenig hilfreich, da Übergänge die Regel sind. Smaragdiidae sind marine Vertreter, die mit eine Reihe von modernen Arten vornehmlich das Seegras besiedeln und sich mit diesem zusammen eigenständig entwickelt haben. Ihr Protoconch verknüpft sie mit den paläogenen Velatinae n. subfam, die aber eine ganz eigenständige Schalengestalt und Dimension besaßen. Die karibische *Puperita* vermittelt zwischen Neritinae und Neritininae, und die eozäne *Calyptronerita* zwischen Neritidae und Phenacolepadidae. Die Neritiliidae erscheinen eigenständig und sind möglicherweise über Formen wie die kretazischen *Schwardtina* mit den terrestrischen Hydrocenidae verknüft, wie die Vergleichen der Protoconche andeuten. Neritoidea charakterisiert durch die Auflösung der inneren Schalenwände der Larvalschale wie des Teleoconches zeigen in ihren artenreichen Gattungen *Theodoxus* und *Neritina* weitgehende Tendenzen zur Hybridbildung und Ähnliches tritt vielleicht auch in der Gattung *Nerita* und *Smaragdia* auf. Dadurch ist die Artabgrenzung besonders erschwert und die spezielle Ausprägung der Arten gographisch sowie historisch mitbestimmt. Letzteres kann aber bei besserem Verständnis der möglichen Hybridbildungen auch zur Erhellung paläobiogeographischer Zusammenhänge genutzt werden, wie die Unterschiede der *Neritina* Varianten in Bali, Cebu und Natal/Madagaskar erweisen.

1. Introduction

Theodoxus is a gastropod of fresh water and belongs to the subclass Neritimorpha. Regarding shell shape it is very similar to *Neritina*, and has commonly been confused with it. *Neritina* in turn is clearly related to *Nerita*, and here also some confusingly similar species occur. But while *Nerita* lives under normal marine conditions on hard substrates within the intertidal regime in tropical and subtropical regions, *Neritina* dwells within or near the coast in the same climatic region where the influence of fresh water is very strong. All of these produce egg capsules of low dome shape that contains tens to several hundred eggs. In case of *Nerita* and *Neritina* all embryos usually develop into veligers and hatch for a more or less extended planktotrophic larval life (ROBERTSON 1971, 1976, SCHELTEMA 1971, RICHTER & THORSON 1975, BANDEL 1982, BANDEL et al 1997). In case of the Neritinidae that enter the estuarine areas with brackish water and even the fresh water this mode of development is usually retained, even though larvae have to be washed into the sea in order to survive (HOLTHUIS, 1995, BANDEL & RIEDEL 1998). In case of *Theodoxus* no free living larva is formed and the young develop within the egg capsule until hatching as crawling miniature adult (BANDEL 1982, Pl.21, Fig.6). Food for such a development stems from nurse eggs, which are devoured by only those few embryos, which develop. This evolution of purely fresh water neritinids may have occurred in the coastal swamps of the Tethys Ocean during the Paleogene (COSSMANN 1925). The adoption to living in fresh water throughout life by aid of nurse egg feeding in case of the genus *Theodoxus* resulted in a change of morphology of the early ontogenetic shell (BANDEL 1982, RIEDEL 1993). The ontogeny of *Theodoxus* has been described in detail by BLOCHMANN (1882) and was compared to that of *Neritina* by BANDEL (1982).

In this paper it will be shown that *Theodoxus* has been living in Europe since the Paleocene as had originally been suggested by COSSMANN (1925). The very earliest representative is very similar in shape of the early ontogenetic shell as well as that of the

teleoconch to modern *Theodoxus*. The question can, therefore, be asked, how it may actually be possible to distinguish species by their shell shape in case of this genus that has at least 60 millions years of history in Europe. Apparently it is extremely difficult to keep species of *Theodoxus* separated from each other that nowadays live from the Nile across the Near East to Turkey and Greece and from here east to the Caspian Sea and Volga River to the Sea of Azov, and to the west up the Danube south to Italy and North to the Baltic Sea, west to England, and from Morocco across the Apennine Peninsula to the Orkney Islands.

It is also difficult to distinguish *Theodoxus* from *Neritina*. The neritinid living along the eastern coast of Baha California, and in the coastal swamps of the Pacific Central America is commonly called *Theodoxus luteofaciatus* for example by Аввотт (1974) and Аввотт & DANCE (1982), while the survey of its protoconch reveals its relation to *Neritina* (see chapter 7.j) Thus, *Theodoxus* and *Neritina* have been commonly mixed up with each other. Their shells also resemble those of *Smaragdia* (see 11.e) and the fossil *Velates* (see chapter 12). Limpet-like representatives may be similar to members of the Phenacolepadidae or the fossil Pileolinae (see chapter 13). The terrestrial Hydrocenidae may be related to *Neritina* regarding the ontogeny but more probably to the Neritiliidae, that may live in the same environment as *Neritina*. They may be related to the fossil *Schwardtina* (see chapter 14).

2. What specifies the subclass Neritimorpha?

The most primitive of the living groups (subclasses) of the Gastropoda with a larval shell in addition to the embryonic one is represented by the Neritimorpha GOLIKOV & STAROBOGATOV 1975 (=suborder Neritopsina Cox & KNIGHT 1960; = superfamily Neritacea RAFINESQUE 1815 as used by KNIGHT et al. 1960). Neritimorpha are united by a radula of similar shape as found among the Rhipidoglossa MÖRCH 1865 (here used for archaeo-gastropods without inclusion of the Docoglossa TROSCHEL 1856 and Neritopsina), with a shell structure and gill similar to those of the Docoglossa. These later, which may also be called Patellogastropoda, are considered to represent the most primitive order of the subclass Archaeogastropoda by reasons of their anatomy (HASZPRUNAR 1985, 1988, PONDER & LIND-BERG 1997, SASAKI 1998). Regarding the mode of ontogeny of their early shell the Archaeogastropoda (Rhipidoglossa and Docoglossa alike) are the most primitive subclass of the living Gastropoda as demonstrated by BANDEL (1982). Neritimorpha are more advanced by having a planktotrophic larva or an equivalent intracapsular stage within their ontogeny.

When the paleontological record is consulted it appears that the older branch of the neritimorph lineage had a planktotrophic larva with openly coiled larval shell. This taxon lived in the time before the Mid-Devonian (BANDEL 1997, FRÝDA & BANDEL 1997) and became extinct with the end of the Paleozoic. Normally coiling protoconchs are seen from mid-Devonian time onward (BANDEL & HEIDELBERGER 2001). Since Carboniferous time the most usual ontogeny found among Neritimorpha has apparently included a larval stage during which the larval shell was secreted in tight convolute whorls around the embryonic shell (BANDEL 1982, 1992, 1988). During the Triassic the Neritoidea among them made their appearance (KITTL 1894, COSSMANN 1925) which are characterized by dissolving the internal walls of all whorls including those of the larval shell (FISCHER 1875, 1884, BANDEL 2000).

During their embryonic development within the shelter of the egg capsule Neritidae secrete a shallow concave and smooth primary shell. This shell detaches from the gland cells before it has grown to half a sphere and is mineralised by a layer of aragonitic calcium-

carbonate biocrystallites. The soft body connects to the shell only locally at spots on the inside of the shell to which later during the embryonic development the retractor muscle is fixed. Further shell growth is by accretion of shell increments formed by a free mantle edge. When the larva is ready to hatch, the embryonic shell resembles an egg with its slender upper part cut off obliquely (BANDEL 1982). During the following stage as planktonic larva a convolutedly coiled shell is secreted. The protoconch has commonly much of its early whorls hidden below the last one. The inner walls of the larval shell are resorbed (BANDEL 1992) with the result that the shell interior does not change much in shape but grows in size steadily.

Anatomically Neritimorpha represent an independent branch of the Gastropoda as had been recognized by TROSCHEL (1856), BOURNE (1909), THIELE (1935) and FRETTER & GRAHAM (1962). They observed that modern living forms have one, left kidney, a single left feather-like ctenidium (except in lung bearing forms), a heart with one or two auricles, internal fertilization, paired retractor muscles, and a rhipidoglossate radula. The ctenidium with filaments on both sides is attached only on its base and resembles the gill of *Acmaea*. This later docoglossate archaeogastropod is considered to represent the most primitive type found among modern gastropods (HASZPRUNAR 1985). The nerves connecting the ctenidia with each other and also the ctenidia themselves are different from those found in other gastropods groups and are therefore considered to have evolved not homologous to them (THIELE 1935).

The pallial complex of *Nerita* and *Neritina* consists of a left gill connected to a hypo-branchial gland and a right hypobranchial gland connected to a vestigial gill. This right gland is connected to a duct that allowed for internal fertilization and the production of egg capsules. Only the left duct serves as kidney. In most Archaeogastropoda, in contrast, the gonad discharges through the duct of the right kidney and external fertilization is practiced.

BOURNE (1909) stressed that the Neritimorpha have come from primitive gastropod stock which is supported by paleontological evidence due to which pre-mid-Devonian Neritimorpha and their stem group representatives with uncoiled embryonic shell and openly coiled larval shell (FRÝDA & BANDEL 1996, BANDEL 1997, BANDEL & FRÝDA 1999) range back to the early Ordovician and have thus developed independently from the rest of the Gastropoda since about 500 Million years. Based on cleavage patterns (BIGGELAER & HASZPRUNAR 1997) and on computer based cladograms (PONDER & LINDBERG 1997) arrived to similar conclusions as had BOURNE (1909) based on anatomical analysis and BANDEL (1982) based on the pattern of formation of the early ontogenetic shell.

3. Definition of the genus *Theodoxus* and the subfamily Theodoxinae

Superfamily Neritoidea RAFINESQUE 1815

The superfamily Neritoidea of the Neritimorpha, order Cycloneritimorpha BANDEL & FRÝDA 1999 is characterized by the dissolution of the inner shell walls in the teleoconch as well as in the protoconch (FISCHER 1884, WENZ 1938, BANDEL 1992).

Most Neritoidea have solid shells with outer calcite and inner aragonite layer. The flat callus covered innerlip of the aperture is provided with a collumellar edge that commonly bears teeth, folds or pimples. The operculum is calcareous and has usually a peg like projection that inserts into the muscle of the snail. The protoconch of all species with planktotrophic larva is spherical and has the inner walls resorbed. The inner walls of most teleoconchs are

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Most Neritoidea have solid shells with outer calcite and inner aragonite layer. The flat callus covered innerlip of the aperture is provided with a collumellar edge that commonly bears teeth, folds or pimples. The operculum is calcareous and has usually a peg like projection that inserts into the muscle of the snail. The protoconch of all species with planktotrophic larva is spherical and has the inner walls resorbed. The inner walls of most teleoconchs are

also dissolved. Species rich genera are *Nerita* and *Neritina*. The history of the Neritoidea is well established back into the late Triassic (KITTL 1894, COSSMANN 1925, ZARDINI 1978, 1985, BANDEL 1997).

GÖTTING (1974) suggested that within the Neritoidea there are about 200 species living nowadays, while ABBOTT & DANCE (1982) suggested that there are only about 50 species. WENZ (1938) included in the family Neritidae all neritimorphs with dissolved inner whorls. This taxon is here considered as superfamily ranging in time at least back to the Triassic. Within this family WENZ united species with rounded shell with such having limpet shape and such living in the sea and others living in the coastal swamps and in fresh water. But Neritoidea also include outside of species with limpet-like shell, rarely also such with elongate, planispirally coiled or button-like shell (BANDEL 2000).

Family Neritinidae n. fam.

Diagnosis: The family Neritinidae encompasses tropical coastal swamp species of the relation of *Neritina* with planktotrophic larvae and fresh water species of the relation of *Theodoxus* with nurse egg feeding and crawling young hatching from the egg case. The protoconch of species with free larva is convolutedly coiled and smooth or provided with fine collabral lines. The shell is usually smooth, has a very thin outer calcite layer and thick inner aragonite crossed lamellar layer composing its walls. The inner lip of the aperture forms a callus covered, flattened shelf and a columellar edge that commonly bears one larger denticle on its apical half and accompanying small denticles below and above, but may also be smoothly straight or concave. The operculum has a hinge on its inner columellar side consisting of a ridge that may or may not be accompanied by a peg or knob. Environmental requirement to the species of this family are brackish and fresh water conditions.

Remarks: As suggested by BANDEL (2000) this family unites those Neritoidea that are related to *Neritina*. It can be traced back into Jurassic time (COSSMANN 1925, BANDEL 1991, GRÜNDEL et al. 2000) (see chapter 9). Those species of the Neritinidae retaining the fully marine planktotrophic larva belong to the Nertininae, while those that have entered the fresh water with the larval stage abolished due to nurse egg feeding are united in the Theodoxinae.

Subfamily Theodoxinae n. subfam.

Diagnosis: This subfamily unites fresh water Neritinidae related to *Theodoxus*, which live without having a planktotrophic larva and by developing with the aid of nurse eggs exclusively. The protoconch consists of only the first whorl, which commonly has folded or wrinkled surface (figs.219-222). The embryonic shell is much larger than that of the Nertininae. The subfamily is based on the genus *Theodoxus* that has been living in Europe since at least Paleocene times.

Remarks: Most members of the Theodoxinae appear to have Europe as their centre of distribution, and perhaps location of origin. Species have been especially abundant within and at the margins of the Paratethys basin. Exceptional are those that have entered Northern Africa via the Nile and may have reached Ethiopia (BROWN 1980). The Jamaican *Fluvinerita* may have evolved parallel to *Theodoxus* a strictly fluviatile life, but is here interpreted to represent a relict species of a former wider distribution of *Theodoxus* (see chapter 5.c).

Genus *Theodoxus* MONTFORT 1810

The lowly coiled shell is usually smaller than 1 cm and consists of less than three whorls. Its operculum is D-shaped and has an internal ridge that may be accompanied by a knob that represents a projection that is almost vertical to the opercular ridge. Ridge and knob provide an articulation of the operculum with shell muscle and columellar lip. The genus *Theodoxus* can be characterized by its ontogeny with the aid of nurse eggs, which is reflected in the morphology of the early shell. The type-species of the genus is *Nerita fluviatilis* LINNAEUS 1758 (figs.1-7) which probably had originally been defined from individuals that were collected in the Main River in southern Germany. According to features of the operculum the two subgenera *Theodoxus* with no knob on the opercular hinge and *Neritaea* with knob are distinguished (BAKER 1923, THIELE 1929, JEKELIUS 1944, PAPP 1953). The knob is usually not present in case of *T. fluviatilis*.

The type species *Theodoxus fluviatilis* (LINNEUS 1758) is ornamented only by fine, commonly rather indistinct growth lines on its small semispherical shell (figs.1-7). The shell is commonly dark in colour with a pattern of yellow-white streaks, but colour pattern may be very variable (NEUMANN 1959a,b, 1960). The columellar plate may be white or yellow and may have a dark edge along the inner lip. The operculum is equipped with a ridge on the inner side supporting the attachment of the columellar muscle. The protoconch consists of one whorl that was produced within the egg capsule while nurse egg feeding and carried by the young hatching as crawling miniature adult. *T. fluviatilis* lives in Europe and also in Northern Africa (BROWN 1980). But these NW-African representatives have been placed in separate species by KRISTENSEN (1986) (see chapter 6.b).

Theodoxus is a characteristic gastropod of the fresh water that on first sight is very similar to the coastal *Neritina* and its relation. On second sight it differs from the basically tropical neritimorph genus *Neritina* and its closer relation by living in fresh water during its whole life, by having a distribution mainly within temperate climatic zones and, thirdly, by developing by aid of nurse egg consumption. *Theodoxus* spends its entire life within the same environment, which is commonly fresh water of rivers, creeks and lakes, sometimes brackish water as for example large portions of the coastal Baltic Sea and the Caspian Sea (see chapter 6.b). Usually *Theodoxus* lives on hard substrates, scraping food from its surface with the aid of the radula. Food consists of algae, but other crust forming organisms are also utilized since there are some populations that have been encountered in the dark cave environment (SCHÜTT 1963).

4. Definition of the genus *Neritina* and the subfamily Neritininae

Subfamily Neritininae n. subfam.

Diagnosis: The neritinine shells are usually glossy, hemispherical to limpet shaped with low spire and the last whorl forms most of the shell. The aperture is D-shaped and its inner lip expands on the former whorl with a more or less extensive callus pad. The shell is variably coloured and may display a wide variety of patterns. Ontogeny usually occurs in two steps. While the free swimming larvae live in the open ocean, after metamorphosis the benthic snail lives under brackish or fresh water conditions. Eggs develop in fresh water as well as in salty water and release swimming veligers. Some species have retardation in fresh

water in their development compared to such that have been deposited in areas with salinity change (estuaries) or brackish water conditions. They usually hatch as soon as they have reached the developmental stage of the planktotrophic veliger (figs.227,229,230). All embryos hatch as veligers and swim in the sea, but occasionally they develop within fresh water environment (HAYNES pers.com., BANDEL & RIOEDEL 1998).

The Neritininae are based on the genus *Neritina* in which the members including the type to the genus have a planktotrophic marine larva while the adults prefer to live in fresh water of creeks and rivers, within the zone of fresh water issuing from the ground in brackish or marine litoral environments and in the brackish intertidal zones. The shell is usually ovate in shape in case of *Neritina*, may have spines in its "*Clithon*" varieties, and is more or less limpet-like in case of *Septaria*. Usually ornament consists of variable coloration of dots, and lines and rarely fine spiral ribs. The outer calcite layer of the shell is thin and its bulk is composed of aragonitic shell with crossed lamellar structure.

Remarks: WENZ (1938) did not distinguish an own taxon for such Neritoidea (= Neritacea) - such as the Neritininae that had entered the coastal swamp region and the fresh water. A similar ecologic adaptation has been carried out within the Neritiliidae (*Neritilia*), which are not included within the Neritidae mainly due to differences in their radula (see chapters 8 and 14), and had been interpreted to represent a subfamily of the Neritidae by WENZ (1938).

Genus *Neritina* LAMARCK 1816

Description: The shell is ovate and similar to that of *Nerita*, but its outer calcite layer is thinner and smooth. The inner lip of the aperture has a smooth or weakly denticulate columellar edge and forms a simple callus pad on the outside of the former whorl. The operculum has a ridge-like curving rib and a more or less well developed peg that issues near the attachment end of this ridge. The genotype varies according to the author. Mostly it is considered to be represented by *Nerita pulligera* LINNEUS 1767 (figs.197-198) from no specific locality somewhere in the Indo Pacific (THIELE 1929, WENZ 1938), but COSSMANN (1925) suggested as genotype *Neritina zigzag* LAMARCK which probably is identical with *N. communis* QUOY & GAIMARD 1832 from the same Ocean (illustrated by ABBOTT & DANCE 1982) (figs-90-95).

Differences: *Neritina* is here interpreted to include *Clithon* from which it can usually be separated by the lack of spines on the shell (COSSMANN 1925). A distinction of *Clithon* as independent genus cannot be held up (see chapter 7. f, g, h). The outer lip of *Neritina* is not serrate or toothed as it is in some species of *Nerita*. The rounded shell and operculum sealing the aperture distinguishes from *Septaria* that has a limpet like shell, which is no longer, sealed by the reduced operculum. On the inner, columellar side of the operculum a rib and an additional peg are usually well developed.

The one type species to the genus *Neritina*, *N. pulligera* lives attached to hard sub-strate usually in running fresh water, for example in Matutinao River of Cebu (BANDEL & RIEDEL 1998). It has an ovate to semi spherical shell with rounded upper side and flattened lower side. Only one whorl covers earlier ones with the body whorl extending over the spire and covering it completely or almost so. The aperture is wide and ear-shaped. Its inner lip has a wide and flattened callus or a columellar edge with denticles among which one of the more apical ones is usually larger than the others. The ornament of the shell consists of fine colour pattern of zigzag or zebra lines, and the periostracum may have a more or less well developed spiral liration forming a reticulate pattern with regular growth increments. The shell measures up to about 2 cm in width and 1,5 cm in height. The operculum has the nucleus on the left handed base and from it issue radiating growth striae. A curving rib connected to a peg on its narrow end of the inside of the operculum serve as hinge and attachment to the columellar muscle.

Remarks: The anatomy has been described by STARMUHLNER (1969). The radula has also been illustrated by BAKER (1923), RIECH (1937), BRANDT (1974) and STARMÜHLNER (1983).

When the type species to *Neritina* suggested by COSSMANN (1925) is taken as the model, the description differs. *Neritina communis* as it is found on the intertidal mud flats and pebble beaches of Velar estuary at Porto Novo in Tamil Nadu (southern India) lives within brackish environment. The shell is of rounded outline and about 8 x 8 mm in size when fully grown with about three whorls of the teleoconch. The protoconch, like that of *N. pulligera*, is of round shape consisting of several convolute whorls. Transition to the teleoconch is marked by colour change and also change from purely aragonite composition to construction of a thin calcite layer below the periostracum underlain by a thick aragonite crossed lamellar layer. The well rounded spire exposes all whorls even though they overlap strongly onto each other. The callus of the inner lip is smooth and the columellar edge has one larger denticle in the apical portion, accompanied by more or less developed smaller denticles below and above, which may be missing. The ornament consists of a highly variable colour pattern on polished smooth background mostly of greenish grey, fine, zigzag or zebra lines and spiral ribbons on light background. The operculum has a solid hinge consisting of a thickened curving ridge and a stout peg at its attachment end. The later it oriented at right angle to the former.

Remarks: A more colourful variety of *N. communis* is documented by DANCE & ABBOTT (1982). This Indo-Pacific species closely resembles for example *N. luteofasciata* from the Pacific side of Central America and *N. virginea* in the Caribbean region regarding shape of the shell and living environment within changing salinities (see chapter 7.j).

5. Comparison of the early ontogeny of *Neritina* with that of *Theodoxus*

5.a Embryonic development of *Neritina*

Neritoidea in general fertilize their eggs internally and egg capsules surround them before they are deposited on hard substrates. The cupola-like egg capsules are reinforced by agglutinated material and usually hold many eggs (QUOY & GAIMARD 1835). In case of *Neritina puncticulata* (= *N. reclivata*) from Columbia 90 to 150 eggs are contained within a single bean-shaped egg capsule of about 1,3 mm length (fig.224). In the other species living in the Caribbean *Neritina virginea* the egg capsule is about 1 mm large and holds about 30-70 eggs. In both cases veligers hatch after about 20 days of development under tropical conditions (BANDEL 1982). A similar number of eggs ranging between 50 and 300 in each capsule were observed in species of *Neritina* and *Septaria* from Indopacific locations such as South Africa, West Africa and SE-Asia.

Among representatives of the Neritininae egg capsules are made of mucous organic material into which sand grains, faeces etc are agglutinated. The upper halve of the capsule is attached with a transparent organic ring to the lower halve which dissolves when the young are ready to hatch. During early cleavage in the 8 cell stage, the four posterior cells hold most of the yolk present within each embryo and are arrested in development. Through following stages of cleavage the yolk deficient anterior cells grow around these four cells forming the ectoderm and most of the entoderm. Four yolk- rich cells remain well visible until the embryo hatches from its egg capsule in *Neritina*. As soon as ectodermal cells have covered the yolk cells completely and the embryo has acquired a spherical shape the velum makes its appearance as apical prototroch with longer cilia on each side in a position of the velar lobes that form later during embryonic development.

At the time of formation of the shell gland and rudiment of the mantle neither anus nor mouth is present, but a slight trochospiral twist of the visceral mass indicates the presence of body torsion at this stage. At the veliger stage of the embryonic development a shallow

concave and smooth primary shell is secreted. As soon as mantle margin and shell detach from each other the shell is mineralised. It is now attached with the tissue of the soft body at the same place where later the retractor muscle connects to the interior of the shell, as soon as it is differentiated. Further growth of mantle cells around the visceral mass is connected with the secretion of shell growing in increments (this differs with growth of the embryonic shell in case of most Caenogastropoda and Heterostropha, see BANDEL 1975, 1982). Growth of the periostracal shell is connected to a mineralisation with aragonite crystallites on the inside of the shell. Between the edge of the mantle and the head- foot a groove forms, slowly increasing in size to develop into the pallial cavity. The muscle cells of the retractor muscle begin to function even before the shell has grown large enough to cover the whole body in case of *Neritina virginea* (BANDEL 1982). Before hatching the animal can withdraw into its shell and seal the aperture with an operculum. In general shape the embryonic shell resembles that of an egg with the upper part cut off obliquely (fig.227).

In the case of *Neritina virginea* the hatching veliger has a deep pallial cavity through which water is driven by a band of cilia entering the cavity along the neck leaving it along the roof of the cavity. In the case of *Neritina* and *Septaria* from Bali the pallial cavity has not developed far and is only represented by a narrow groove between mantle edge and the head-foot. The velum is equipped with a food groove ready to start the transport of planktonic food particles collected by the long cilia. Eyes are present within the velar lobes. Growth of shell stops when the visceral mass is covered and it is continued only after hatching from the egg capsule. When this hatching occurs in fresh water veligers survive more than two days in the freshwater as has been checked in Cebu (BANDEL & RIEDEL 1998). While the heart with functional two chambers is present in *Neritina virginea* and seen pulsating at the end of the pallial cavity, it has not yet developed in *Neritina turrita* and *N.* cf. *variegata* from Bali when it hatched from its egg capsule.
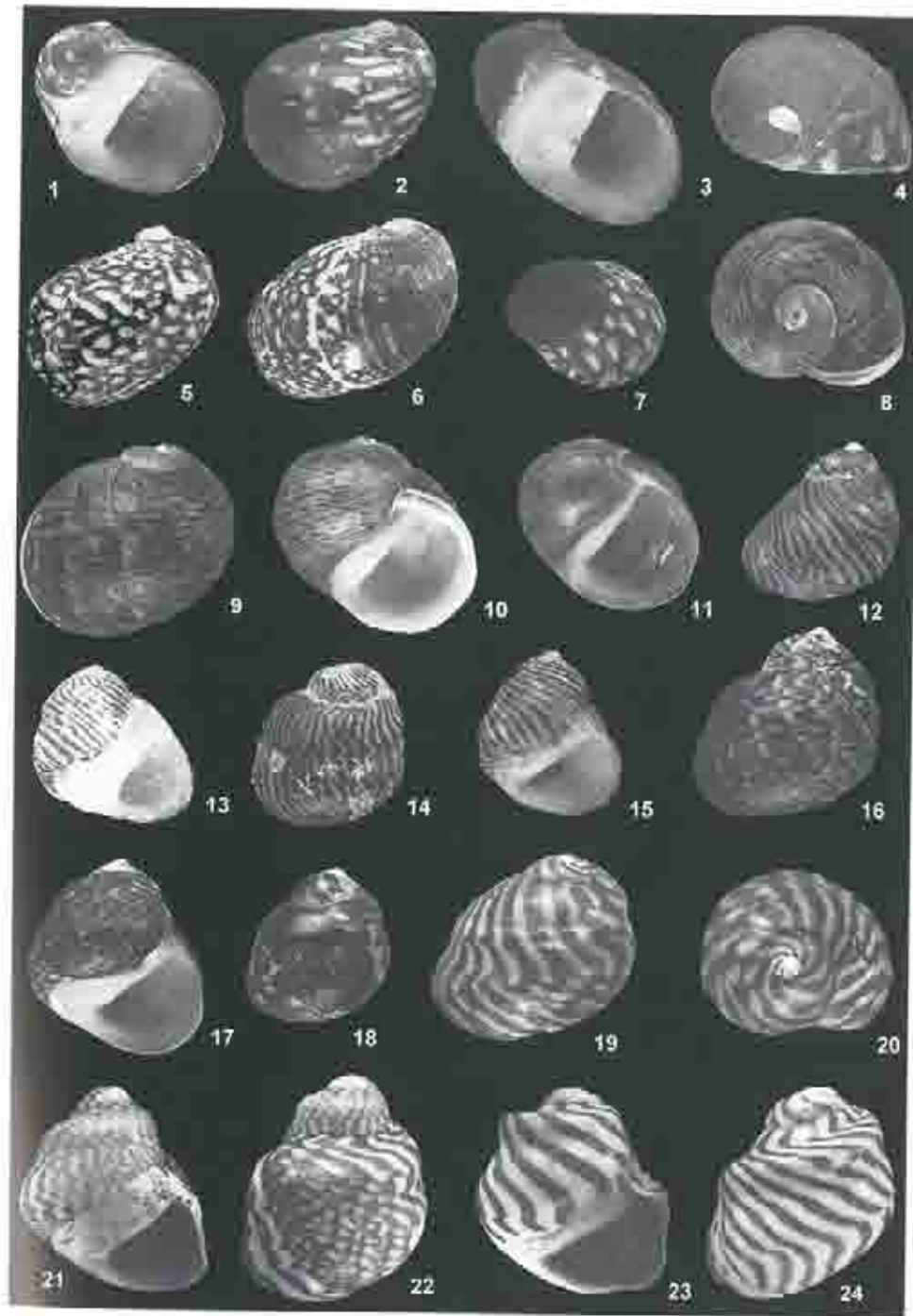
The hatched larva remains in the plankton for weeks and feeds on algal cells. During this time larval shell is added to the embryonic shell. It is globular to egg-shaped and in most species has a maximum diameter of about 0.4 to 0.6 mm, however, some protoconchs measure almost 0.8 mm across (figs.225-226). The initial embryonic whorl measures (interspecifically) 0.1 to 0.25 mm across. Externally, the suture of the embryonic and early larval whorl(s) is characteristically covered by later whorls, creating a convolute protoconch. Therefore the number of whorls is difficult to estimate, but formation of up to 2.5 larval whorls has been observed. The aperture is crescent-shaped, with the base comparatively broader. The outer apertural lip is thin and regularly rounded while the inner lip is thickened. In fully grown larvae the organic operculum seals the aperture of the protoconch. The size of the operculum

increases in a spiral, featured by axial growth increments, which, however, are confined to the external side. Internally, a tooth-like projection reinforces the nucleus. Larvae and their shells have been described by ROBERTSON (1971), SCHELTEMA (1971), LAURSEN (1981), BANDEL (1982, 1991b, 1992), BANDEL et al. (1997).

Larvae swim with the aid of a quadrilobated velum. The lobes are comparatively short, approximately matching the length of the conch. In it the retractor muscle is attached apically at the left side. It may withdraw the animal rapidly into its shell. All internal whorls are dissolved. The digestive gland shows dextral coiling in the apical portion reflecting the original dextral shell that has been transformed into a simple hollow sphere. The position of the heart is at the apical end of the pallial cavity. The heart has two chambers, a frontal one that sucks blood from the tissue of the mantle that surrounds the pallial cavity and a posterior one that pushes blood into the visceral mass and the head. The frontal digestive system is straight from the velum to the stomach and is only coiled up when the animal withdraws its head into its shell. The posterior portion of the digestive system is attached to the stomach on its apical portion and runs to the umbilical side of the aperture where the anus lies on the pallial side of the foot. Within the pallial cavity a current of water is kept going by a ribbon of cilia from the neck into the end of the cavity and from here on the roof to the shell margin.

In fully grown pediveligers a gill is present attached with its base at the end of the pallial cavity and projecting into it without being attached to its sides. Its attachment lies next to the heart. The velum of the pediveliger has four narrow lobes and during metamorphosis is resorbed. The foot is ciliated at its anterior end and broad in the pediveliger. The short tentacles are also ciliated and have eyes at their outer base with black pigment cups. A glandular ribbon runs from the apical portion of the visceral mass to the neck possibly representing a larval kidney.

During metamorphosis planktotrophic feeding with the ciliary action of the velum ends and benthic feeding with the radula supported snout begins. This transition is connected to a change in the construction of the shell morphology and structure. While the protoconch is mineralized by aragonitic biominerals, the teleoconch has an outer layer of calcitic construction succeeding the periostracum and only below that an aragonitic shell layer. The adult organization of the heart evolves jointly with the growth of the gill. The beat of the heart is reflected in pulsations running through the gill as well as along the tissues of the viscera. The position of the retractor muscle after metamorphosis has not changed. The anus lies within the pallial cavity and is connected to a ribbon of cilia leading to the mantle edge and transporting faecal pellets to the margin of the mantle. Here they fall off from the edge and transporting faecal pellets to the margin of the mantle. Here they fall off from the shell near the margin of the outer lip at the suture. This is part of the ribbon of cilia in the pallial cavity that can be noted in the veliger and is still present in the juvenile. It enters the cavity at the umbilical neck and runs through the whole cavity to the gill and from it up the pallial roof ending in a generally ciliated area at the sutural side of outer lip. In the active pallial roof ending in a generally ciliated area at the sutural side of outer lip. In the active animal water enters the pallial cavity over the head and leaves it at the lower side. The head carries the short snout with mouth and radula as well at the two long tentacles with bundles of sensing cilia distributed over them. The well developed eyes lie at their base. The stomach is found in the apical end of the shell near to the heart.

5.b Embryonic nurse egg feeding in *Theodoxus*

In case of *Theodoxus* pelagic larvae are eradicated from the ontogeny, as is the larval shell. Here life far from the sea and without access from the sea has become possible. The

egg capsules of *Theodoxus* consist of two halves, as is the case in *Neritina* and relation (BOURNE 1908). In the case of *Theodoxus* larval development has totally been restricted to the interior of the egg capsule by means of nurse egg feeding. *T. fluviatilis* from Northern Germany and the Baltic Sea as well as *T. jordani* from Jordan hatch as crawling young (BANDEL 1982, Pl.21, Fig.2,6). The protoconch is quite large (0,5-0,9 mm) and consist of a little less than one whorl (fig.219). With exception of the 0.2 mm wide apical cup the shell shows prominent growth lines and may show a pattern of radial wrinkles, very similar to what may be seen in the embryonic shell of *Hydrocena* and relation (see chapter 14.c) (figs.311-315). The protoconch grows in size during the embryonic consumption of yolk and is mineralized only after completion of this process.

Apparently Neritininae of the Indopazific tropics that usually enter the fresh water after metamorphosis may have sometimes an ontogeny without marine planktotrophic larvae (BANDEL & RIEDEL 1998). But in this case there is no nurse egg feeding involved and most probably single larvae entangled or surrounded by algal or bacterial growths on hard substrates in the river survive and continue to develop through the larval stage. HAYNES (personal communication) observed some kind of nest building of young after hatching in Fijian streams. BANDEL & RIEDEL (1998) supported this observation in Matutinao River of Cebu (Pilippines) (see chapter 7.g). But they did not find such a nest and did not observe how some of the larvae hatching from the egg capsules managed to remain in the river and develop here into a benthic juvenile, while the vast majority of their co-hatchlings were washed into the sea.

5.c What about *Fluvinerita* from Jamaica?

A flare in the picture of a uniform history among Neritinidae with lecithotrophic development to have occurred in the European-Near East region is presented by *Fluvinerita* that lives in mountain streams of Jamaica and apparently has direct development without planktotrophic larvae. The embryonic shell is quite large, consists of only one whorl and is characteristically wrinkled in its initial shell cup (fig.290). It is, therefore, a product of an embryo that developed its shell while devouring much yolk. The young hatched from the egg capsule as crawling snail. The embryonic shell indicates a development within the shelter of the egg capsule until crawling young hatch with the protoconch having a little less than one whorl and wrinkled surface, as is the case within the genus *Theodoxus*.

Neritina (Fluvinerita) alticola PILSBRY 1932 (= *Neritina tenebricosa* C.B. ADAMS 1852) has the type from Black River in Jamaica. According to RUSSELL (1941, Pl.2, Figs.1,2) *Fluvinerita* differs from *Theodoxus fluviatilis* by having a more rounded shell shape (he did not compare with *Theodoxus jordani* or other species of *Theodoxus*) and it has the same type of operculum with ridge but not with peg at its inner columellar side. In different mountain rivers of Jamaica *Fluvinerita* lives exclusively in fresh water and in up to 1000 m height.

Fluvinerita alticola has a roundish dark coloured shell that consists of about 2,5 whorls of the teleoconch all of which are exposed on the rounded apex (figs.8-11), succeeding on a protoconch, which apparently consists of a non-planktotrophic shell (fig.290). It is a cup-like initial portion with concentric growth lines and a constriction at the twist to the aperture of the embryonic shell. Coloration of the teleoconch is variable consisting of spiral streaks and radial zigzag patterns. The egg capsules are of neritinid type without calcareous inclusions in the cupola portion of the lid. The inner lip callus is simple, even, smooth and not broad. Its columellar edge is straight simple with no concave ends or furrow and no denticles.

It is not clear what relation exists of *Fluvinerita* to other Neritidae or Neritinidae. If it represents a member of the Theodoxinae, which is here suggested, its living place on an

Antillean island is peculiar and needs explanation. *Theodoxus* and relation has apparently never been recognized from North America, but may have occurred in South America. NUTTALL (1990, Figs.9-25) described from the Pebasian strata *Neritina ortoni* CONRAD 1871 that lived in or marginal of the large Amazon Lake that existed in the Late Miocene. Its shell may be a little angular and consists of about 2,5 whorls succeeding the protoconch that is unknown. Ornament is quite variable, and it differs from modern Caribbean species of *Neritina* mainly by the operculum which is lacking a peg, as is the case in *Fluvinerita*; and the members of the *Theodoxus fluviatilis* group. *Neritina ortoni* also occurs in the Cuenca area in Ecuador where that large Amazonian lake may have had a connection to the Pacific Ocean, before the Andes began to rise in the late Miocene. If this fossil species can be shown to represent a member of the genus *Theodoxus*, the Theodoxinae may have had a much wider distribution at Miocene times than they have nowadays (see chapter 9.c).

6. *Theodoxus* from the Paleocene to the recent

6.a The oldest known *Theodoxus*, *T. fabulus*.

Theodoxus fabulus (BRIART & CORNET 1887) has a shell of rounded outline with the aperture almost circular and is almost as high as the total shell. Sutures are quite distinct and accompanied by a flattening of the shoulder that grades in the rounded flanks. This slight depression next to the suture is present only on the body whorl and is not developed in the early teleoconch. The actual shell opening is semicircular; and the callus of the inner lip is not very wide and bears a shallow groove in its centre. The columellar lip has slightly concave shape with a wide low thickening in its upper part, which in juveniles consists of a broad and low denticle. In a fully-grown individual with 10 mm wide and 9 mm high shell the spire is low and has a rapid increase in whorl diameter. The teleoconch consists of 2.5 to 3 whorls. Ornament is by brown zigzag lines that show some deformation along spiral bands. The protoconch consists of only a little more than 1 whorl with 0.55 mm in width and a pattern of spirally arranged rows of grooves crossed by collabral lines. The transition into the teleoconch is quite indistinct and the initial shell portion measures almost 0.2 mm across (figs.222-223).

The specimens are from the Montien (Calcaire de Mons) of Mons in Belgium (BRIART & CORNET 1887, GLIBERT 1973). It had originally been described as *Neritina fabula*, was suggested to be placed with *Theodoxus* by COSSMANN (1925) due to its similar shell shape with modern *T. fluviatilis*. GLIBERT

Figs. 25-26: *Theodoxus doricus* (NEUMAYR 1869), 25: from the Kos Formation of the Pliocene of Greece with extremely elongate shell shape, 26: with 9 mm high shell in apertural view.
Figs. 27-31: *Theodoxus danubialis* (PFEIFFER 1828), 27: from the Danube near Komarom (Hungary) with checkered colour pattern and 6 mm high shell, 28: with zigzag colour pattern and 10 mm high shell, 29: apical view, 30: with apertural view and axial stripes, 31: seen from behind.
Figs. 32-35: *Theodoxus* (*Neritaea*) *jordani* (SOWERBY 1832), 32: from the spring and creek at Pella in the northern Jordan Valley has a dark rounded shell of 6 mm in width, 33: apical view, 34: apertural view, 35: with totally black shell.
Figs. 36-40: *Theodoxus* cf. *jordani*, 36: from the Pliocene of Ghor Canal near Abu Habil in Jordan with striped colour pattern and 7 mm in height, 37: same shell in apertural view, 38: apical view, same as 39 in apertural view, 40: with checkerboard colour pattern.
Figs. 41-48: The 6 mm high shell of *Theodoxus* from the Pontian of a sandpit near Papkesi at the eastern Lake Balaton in Hungary is a white colour morph of a number of varieties shown in 42-57: 42: with light spiral ribbons, 43: with regular spiral ribbons, 44: dotted variety that could be determined as *Theodoxus soceni* JEKELIUS 1944 since it has a rounded shell that is ornamented with brown triangles or dots pointing forwards and present on light background, 45: with colouration reflecting a mixture of spiral stripes and zigzag-pattern, 5 mm high shell, 46: white background and fine, somewhat irregular spiral stripes, 5 mm high shell, 47: with fine, braching spiral ornament, 6 mm high shell, 48: specimen that could be determined as *Theodoxus prozlatarici* JEKELIUS 1944 with small (6 mm high), round shell with colouration of a median white spiral ribbon on brown background.
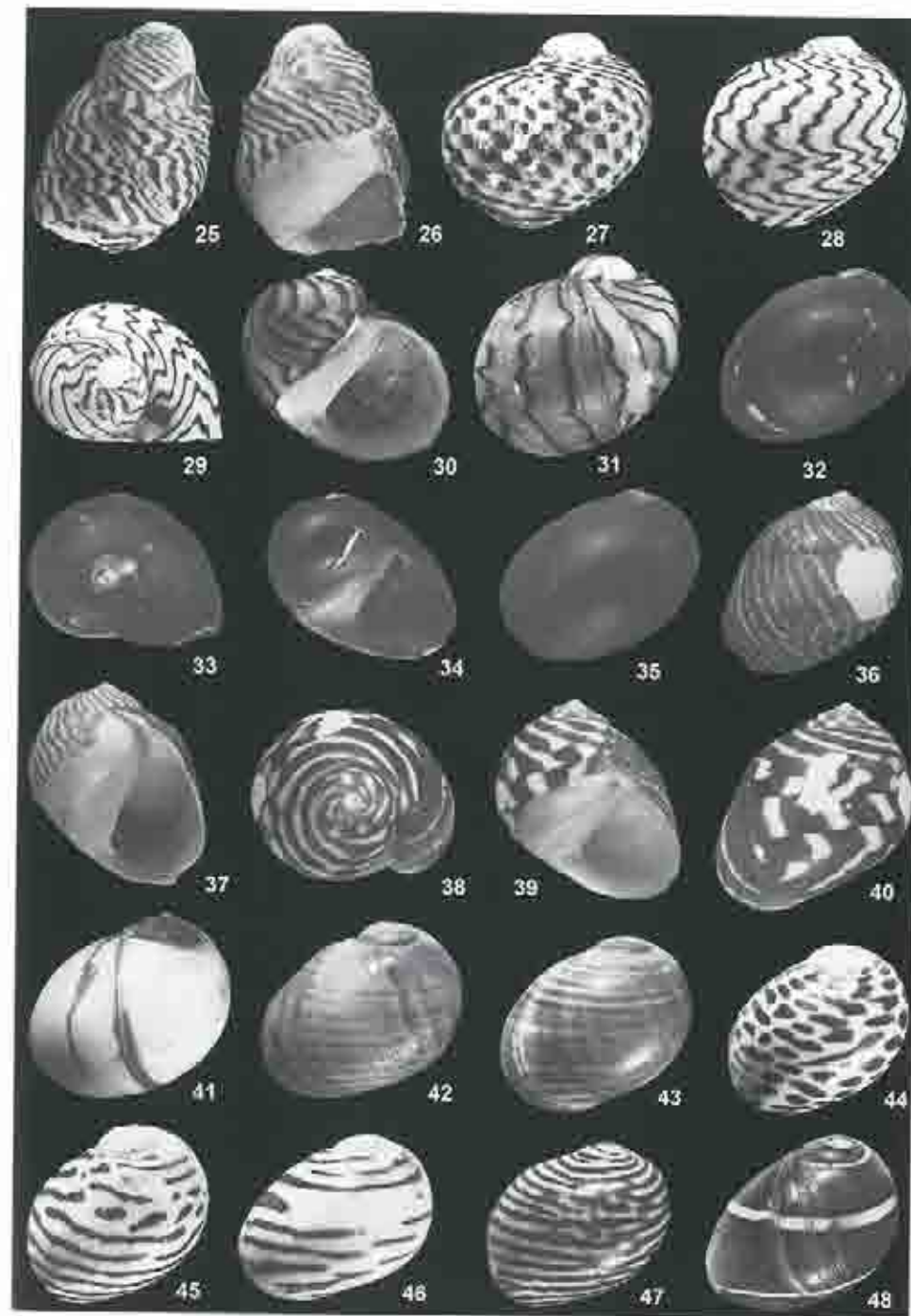
(1973, Pl.2, Fig.10) called it *Theodoxus (Vittoclithon?) fabulus* relating it to the group around *Neritina meleagris* LAMARCK supposedly living in Sumatra (WENZ 1938, Fig. 1033). Actually *N. meleagris* is a species of the *Neritina virginea* group and lives in the Caribbean Sea (RUSSELL 1941) (see chapter 7.j). This recent species represents a form with the typical planktotrophic larval phase within its ontogeny and may be similar or the same as what is called here *Neritina communis* (see chapter 4). But the early ontogenetic shell of *Theodoxus fabulus* clearly indicates a development connected to nurse egg feeding that is reflected by the morphology of the protoconch. The shape of the teleoconch as well as its size is very close to that of modern *Theodoxus fluviatilis* as had been noted by COSSMANN (1913, Pl.3, Figs.54-56, 1925). Actually it is closer in shape to modern *Theodoxus jordani* (see below). But *T. fabulus* from the Paleocene of Belgium could just as well be included within the genus *Fluvinerita* as it occurs in Jamaica.

6.b Living *Theodoxus*

Theodoxus fluviatilis from the Baltic Sea and from fresh water lakes in northern Europe is an inhabitant of the fresh water without intermittent marine larval stage present. NEUMANN (1960) demonstrated experimentally that *T. fluviatilis* tolerates large salinity changes and reproduces successfully from normal fresh water to salinities reaching 15 gram of sea-salt in one litre of water. *Theodoxus fluviatilis* usually has only a ridge on the inner side of the operculum to which the columellar muscle attaches. It lives in W- Europe and in western North Africa (BROWN 1980), while *Theodoxus jordani* has a slender peg pointing toward the columellar lip in addition to the ridge of the operculum and occurs in SW Asia.

BAKER (1923) confirmed these two species or groups of species of *Theodoxus* as had originally been suggested by ROTH (1855). One of these is centred on *Theodoxus fluviatilis* (LINNEUS 1758); and the other around *Theodoxus jordani* (SOWERBY 1832). The first was placed by BAKER (1923) into the subgenus *Theodoxus (Theodoxus)* suggesting to differ from the second belonging to the subgenus *Theodoxus (Neritaea)* ROTH 1855 by features of the teeth of the radula as well as by having only a ridge (*T. (Theodoxus)*) or ridge and apophysis (= peg) (*T. (Neritaea)*) added to it on the columellar side of the operculum. THIELE (1929) and WENZ (1938) also adopted this classification of ROTH (1855).

Theodoxus fluviatilis (LINNEUS 1758)

The shell succeeding the protoconch consists of only up to 1,5 whorls or a little less. *T. fluviatilis* demonstrates a broad spectrum of colour morphs (NEUMANN 1959a,b, 1960).

T. fluviatilis from a pond near the mouth of river Neretwa into the Adriatic Sea in Croatia has a light brownish colouration of the shell while the members of the population studied from the Oder river in eastern Germany is almost black commonly with white dots. In both the shell has maximally 1,5 whorls of the teleoconch and a rather delicate internal ridge on the operculum hinge without a peg (figs.1-7). While the Croatian individuals are only about 6 mm in size those from the Oder measure around 8 mm in maximal width.

T. fluviatilis lives in rivers, hiding under stones or wood by day, foraging at night on plants and detritus. It also occurs in canals and the littoral region of lakes. The animals are limited to hard water, and they tolerate a moderate to high salinity, up to 17 ppm in the Loch of Stenness, Orkney (GRAHAM 1988) and in the Baltic Sea. As BONDESEN (1940) had noted *T. fluviatilis* also lives in water of almost North Sea quality and is found in the Baltic Sea in up to 16 ppm. In brackish water 50 to 70 eggs are present within each capsule while in fresh water up to 150 eggs are found (BONDESEN 1940, GRAHAM 1988, own observations in the Baltic Sea). Breeding begins in late spring with spawning in summer. Females lay capsules on wood and stones or the shells of other animals. It was assumed by BONDESEN (1940) that under more marine conditions *Theodoxus fluviatilis* may develop in a similar way as is found in *Neritina*. But own experiments that were carried out in the field (Baltic Sea) and the aquarium (Hamburg) revealed no differences. Animals living under almost marine conditions developed as those in fresh water, only by nurse egg feeding and young never hatched as free-swimming veliger.

Theodoxus danubialis (PFEIFFER 1828)

Ornament of the shell in *T. danubialis* commonly consists of coarser axial zigzag colour patterns than usually seen in *T. fluviatilis* and triangular dots as found among the latter is usually not present in the former. But colour patterns may also be similar. The overall impression in case of *T. danubilis* is a less fine ornamental pattern as seen in *T. fluviatilis* (BODON & GIOVANNELLI 1995, Pls.1 and 2). Their illustrations also demonstrate a more oval shape of the shell in case of *T. fluviatilis* and a more globular one in case of *T. danubialis*. This difference was also documented by graphs of shell measurements. Checked with the specimen collected from the Oder and the Danube these results of BODON & GIOVANNELLI (1995) can be supported, in that *T. fluviatilis* never has a teleoconch that exceeds 1,5 whorls succeeding the protoconch (Oder), while in *T. danubialis* grows to about 2 whorls (Danube). This later species lived from Kehlheim to the delta, but according to FRANK (1984) is no longer living in Germany since 1963 and will be encountered only from Austria downstream. Its size lies around 12-14 mm in width and 10-12 mm in height (figs.27-31).

Regarding differences in operculum morphology BODON & GIOVANNELLI (1995, Figs.1-22) demonstrated that the ridge on the inner side of the operculum in case of *T. danubialis* is less wide and less spoon shaped, as is that of *T. fluviatilis*. Both have only a ridge without additional peg. BODON & GIOVANNELLI (1995) analysed *T. danubialis* in detail mainly based on populations from Northern Italy where it locally lived together with *T. fluviatilis*.

SCHÜTT (1988) described from the river Save in Croatia a form of *T. danubialis* with angled whorl as had been noted in earlier literature as *Theodoxus danubialis carinatus* (SCHMIDT 1847). Living animals at that locality showed only a weakly developed keel similarly as had been described by MARTENS (1879).

According to SCHÜTT (1986) Central Europe has three species of *Theodoxus*, these being *T. fluviatilis, T. danubialis* and *T. transversalis* (C. PFEIFFER 1828), and SCHÜTT & SESEN (1989) stated that there are even 4 species living in Central Europe, which can be distinguished by shell shape and colour pattern. This includes *T. prevostianus* (PFEIFFER 1828) supposedly a relict species now living in several warm springs of Austria, Hungary and Romania. According to FRANK (1984) *T. transversalis* has disappeared in the Danube, where it used to live together with *T. danubialis* from which it is distinguished by smaller size (less than 10 mm). According to the illustration by GEYER (1909, Pl.10, Figs.23,24) *T. transversalis* is exactly of the same shell shape as *T. fluviatilis*, but differs by having a spirally striped colouration. But such a colouration lies clearly within the varieties noted by NEUMANN (1959a,b) to occur within the population of *T. fluviatilis* as it lived in the river Werra. NEUMANN could stabilize the different colour patterns by culturing and selecting races. Thus, selective breeding could separate individuals with spiral ribbons, with axial stripes and with drop-like colour patterns from each other.

A small sized variety of *T. danubialis* lives in Zmeica Lake of Romania in brackish water and measures up to 6 mm maximum diameter. It has a very regular colour pattern of black more or less regular radial lines on white or yellowish background (material provided by Bogdan MARINESCU, Bucharest). This light coloured variety of *T. danubialis* in size and shape is very close to *T. prevostianus* as encountered in huge numbers in the creek in Bad Vöslau next to the thermal spring and connected swimming pool. Here the shell is black, consists of two whorls of the teleoconch and has an operculum like *T. danubialis* with the ridge a little twisted up, contrasting to this feature in *T. fluviatilis* from the Oder, where the ridge is similar in dimension but not twisted up. The shell is only about 5 mm in maximum diameter. *T. prevostianus* from the warm springs near Oradea (Petea) in western Romania, studied from material supplied by B. MARINESCU, also has a dark shell sometimes with very well expressed spire. It has the same general shape and number of whorls but is smaller than *T. danubialis* from the Danube near Budapest.

KROLOPP (1977) noted in regard to the species of *Theodoxus* from late Pleistocene sediments of the Carpathian arc that they are quite different from those of the early Pleistocene. He suggested that of former species of *Theodoxus* only *T. transversalis* survived in rivers while *Theodoxus prevostianus* survived the climatic change only in warm water thermal springs. KORMOS (1905) discussed *Theodoxus*

from Püspökfürdo (=Bischofsbad, = Petea near Oradea) and noted that several varieties described by BRUSINA (1902) of *T. prevostianus* may actually represent independent species. This opinion is not followed here. The small collection provided by B. MARINESCU indicates that a little more oval individuals, little smaller individuals, and such with a little bit more elevated spire are present as well as some colour varieties. KORMÓS (1905) actually suggested that *T. adelae* (BRUSINA 1902) of the ancient Oradea springs and associated lakes gave rise to *T. prevostianus*, while *T. gizelae* (BRUSINA 1902) from the same locality evolved into *T. fluviatilis*. This represents a most unlikely scenario, and more likely is that the warm springs of Oradea at different times and localities gave rise to different morphological expressions of the same species *T. danubialis*.

SCHÜTT & SESEN (1989) suggested that three species of *Theodoxus (Theodoxus)* live at different localities in Anatolia, these being *T. doriae* ISSEL 1865, *T. heldreichi* MARTENS 1879 and *T. syriaca* BOURGUIGNAT 1852. Of these *T. heldreichi* is characterized as being close in shape to *T. fluviatilis* and *T. saulcyi* (BOURGUIGNAT 1852), and *T. (Neritaea) anatolicus* (RÉCLUZ 1841) differs from these only in regard to the operculum that has a ridge and a peg (SCHÜTT & SESEN 1992). According to JAECKEL et al (1958) there are also *Theodoxus pallasi* (LINDHOLM 1924) from brackish water of the Black Sea, *T. varius* (MENKE 1888) living in Albania, and *T. euxinus* (CLESSIN 1885) from Bulgaria and the Dobrudscha (Romania) living in SE Europe.

Theodoxus meridionalis (PHILIPPI 1836)

According to BODON & GIOVANELLI (1995) in Italy aside from *T. fluviatilis* and *T. danubialis* also a third species is living in Sicily. This *T. meridionalis* also lives in Tunisia (KRISTENSEN 1986) and has a large knob at the base of the opercular ridge. Such a feature is also found in *T. anatolicus* and *T. varius* (ROSSMÄSSLER 1835) that live in Greece, Turkey and the Near East (SCHÜTT 1986, DAGAN 1971). According to BODON & GIOVANELLI (1995) the connection that may exist between these three is not fully elucidated. KRISTENSEN (1986) analysed North African representatives of *Theodoxus* and found differences between these and *T. fluviatilis*. He suggested that a *T. numidicus* (RÉCLUZ 1841) differs from *T. fluviatilis* by the lack of a distinct spire (more rounded apex) and less rectangular aperture. A *T. maresi* (BOURGUIGNAT 1864) was also interpreted to be distinct in sometimes having a peg next to the opercular ridge. Such a peg was utilized to distinguish a third species *T. meridionalis* that

Figs. 49-57: *Theodoxus* from the Pontian of Papkesi near Lake Balaton (Hungary) with different spirally striped colour morphs (49-57), the shell is 6 mm high, 50: a morph that could be determined as *Theodoxus eugenii* JEKELIUS 1944 with round shell and 4 dark and 4 white ribbons, 51: with more puplish pattern, 52: morph that could be determined as *Theodoxus vetranici* (BRUSINA 1902) with round shell ornamented by dark spiral lines on light background, 53: with ornament of few regular spiral ribbons on white background, 54: with more pronounced spire and splitting spiral stripes, 55: with evenly rounded spire and splitting of spiral stripes connected to an interrruption in growth, 56: with splitting spiral spire and splitting of spiral stripes similar as in fig.55 but in coarser pattern, 57: with well rounded spire and very regular spiral ornament, 6 mm high.

Figs. 58-60: *Puperita pupa* (LINNÉ 1767) from the Caribbean Sea (Curacao from tidal pools) 58: with smooth, 9 mm high shell ornamented with black stripes on white background, 59: apertural view. 60: apical view.

Figs. 61-63: *Puperita tristis* (d'ORBIGNY 1842) representing a variety of *P. pupa* that has a pattern of black background with small white dots, 61: shell from Curacao, 8 mm high, 62: seen from the side. 63: apical view.

Figs. 64-66: *Ninnia geticus* MARINESCU from the late Miocene of Romania (Jaszofen Valley) with 15 mm in width, in side view (64, 65), and in apertural view (66).

Fig. 67: Operculum of *Neritina gagates* LAMARCK 1822 seen from the inner side and with 15 mm in maximal diameter. Umzamba estuary, South Africa

Figs. 68-71: *Neritina gagates* LAMARCK 1822 68: from the estuary of the South African Umzamba River seen in apertural view with 20 mm high shell, 69: with light shining through the shell the fine pattern of dark zigzag bands below the dark periostracum appears, 70: in side view with light shining through it and 23 mm height, 71: in side view with light shining through it and 20 mm height
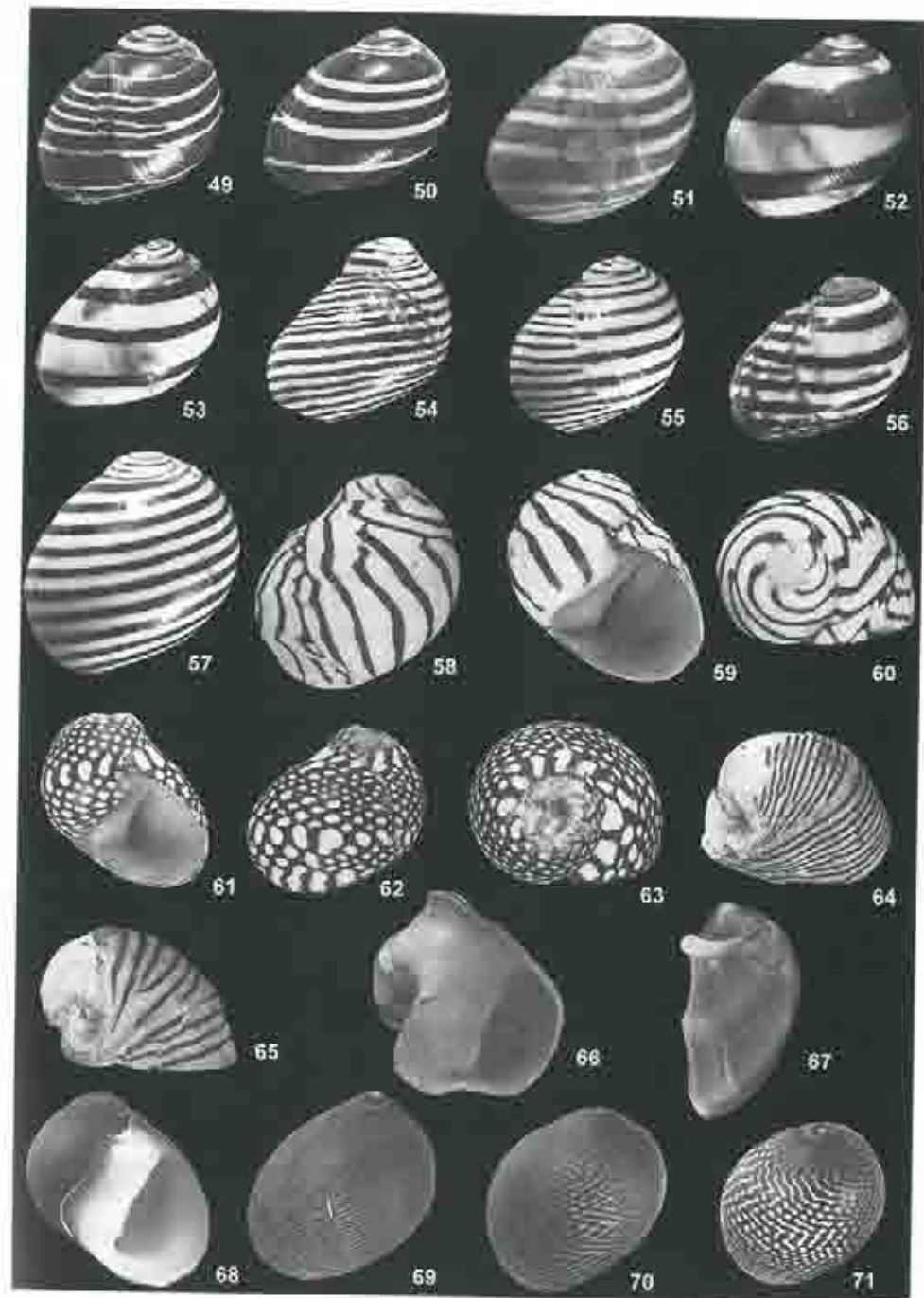
lives in Tunisia as well as in Sicily. KRISTENSEN (1986) concluded that only these three species live in Northwestern Africa and no *T. fluviatilis*.

JEKELIUS (1944) and PAPP (1953, Pl.1) studied the opercula of individuals of some *Theodoxus* populations living in Europe. According to PAPP (1953) *T. fluviatilis* is characterized by an operculum with internal ridge and a more or less reduced peg. Of all *T. fluviatilis* studied from river Oder, some of northern and eastern Germany and from Croatia the operculum never had a peg and was provided only with a ridge. But it was noted by JEKELIUS (1944) and PAPP (1953) that the subgenera *T. (Neritaea)* with peg and *T. (Theodoxus)* without peg based on this character are not stable. This discussed this character in detail and found transitions from peg bearing individuals to such without peg within the same Pliocene population (see chapter 6.c). A similar result was obtained by ROTH (1982, 1984) in case of recent species analysed from different localities between Danube and Jordan. She noted rather large variability among the living representatives of *Theodoxus jordani* regarding the size and form of the projections of the opercular hinge.

Theodoxus (Neritaea) jordani (SOWERBY 1832)

The type to *Theodoxus jordani* and the subgenus *T. (Neritaea)* as illustrated by WENZ (1938, Fig.1038) lives in the river Jordan, and nowadays also in the northern Ghor Canal between Yarmouk river mouth and Zerqa river mouth. From dredging in the canal near Abu Habil (Jordan) a fauna of several hundred individuals of all sizes was recovered (spring 2001) (figs.12-20).

In the specimen of the population from the Ghor Canal the embryonic shell composes the first whorl and is clearly set off from the teleoconch by its usually uniform, commonly white colouration. The teleoconch consists of about 2,5 whorls; as is the case in *Theodoxus* from Pella spring nearby (see below) but colouration and shape differ considerably. With the onset of the teleoconch the most common pattern of colouration seen is that of somewhat irregular, commonly zigzag shaped dark ribbons on light background. About 4 to 7 such broad ribbons commonly feature the first teleoconch whorl. But there are also totally black as well as totally white colour morphs. The most characteristic feature of the first teleoconch whorl is the appearance of a distinct but not always well developed flattened apical side of the whorl with more or less well developed corner. The shape of a shell with one teleoconch whorl is hemispherical with rounded apex and flattened base. The shell is wider than high. The inner lip is smooth; callus covered and has a straight columellar edge without denticles.

In the second whorl of the teleoconch the relative height of the whorl increases and whorl sides flatten more or less. In many individuals the shoulder corner develops into a rounded ridge and a depression is found below it. In other individuals no such ridge is present and the sides are more or less flattened. With the second whorl of the teleoconch completing the shell, it is higher than wide (up to 10 mm high and 9 mm wide). The callus morphology of the inner lip changes to more rounded bulging form and the columellar edge appears evenly concave. The colour pattern of axial ribs may continue but ribs may also fuse marginally to form a pattern of white dots or fuse totally to turn into uniform black. There are also mixtures of such colourations or, after renewed shell growth, one-pattern changes into the other. A total transition in shapes between individuals that have been named *T. orontis* and *T. jordani* by SCHÜTT (1987 Pl.2, Figs.1,2) is developed. The first represents the variety with a depression on the whorl side, and the second the variety with somewhat flattened sides of the last whorl.

The operculum is provided with a ridge and a peg representing a solid structure on the inner side next to the columellar margin as illustrated by DAGAN (1971, Pl.2, Figs.1,2). It is quite like that of the roundish and low variety of *Theodoxus* from Pella.

Remarks: *Theodoxus groyana* from the Pliocene of Italy as described by GIROTTI & ESU (1974) has a little more rounded whorls, but otherwise closely resembles *Theodoxus* from the Ghor Canal. The Pliocene *Theodoxus orontis* BLANCKENHORN 1897 as described by SCHÜTT (1987) from deposits in the Orontis valley cannot be considered as ancestral to *T. jordani* as assumed by SCHÜTT since exactly such individuals are common within the population now living in the Ghor Canal. The individuals with strongly developed corner and depression below it look very similar to *Theodoxus doricus* from

the Kos Formation on the Island of Kos (material collected by E. VOIGT and here compared). This species has been described and interpreted in detail by WILLMANN (1991) (see chapter 6.c).

Theodoxus jordani (= *T. macrii* RÉCLUZ 1841) from Pella resembles those individuals that can be found in springs and clean creeks in Jordan (figs.32-35). It is a black roundish *Theodoxus* that has been collected with several hundred individuals from the spring at Pella in the region of the northern Jordan Rift near the town Mashara in Jordan. According to BLANCKENHORN (1897) this form of *T. jordani* could be placed with *T. anatolica* (RÉCLUZ 1854), and a very similar form from Pliocene deposits in Syria was called *T. orontis* BLANCKENHORN 1887. According to ROTH (1984) it also received the name *Theodoxus macrii*. The spring, pool, and creek of Pella have since (2000) been destroyed, but populations of other springs in the region of northern Jordan are similar in character. The number of clean springs in Jordan still containing population of *Theodoxus* is unfortunately decreasing. The shell consists of 2,5 whorls of the teleoconch added to the embryonic shell. Shell height is up to 5 mm and its width is slightly larger. The callus formed by the inner lip is smooth as is its columellar margin that is slightly concave in its apical portion. Shell colouration is uniformly black, and in juvenile shells a fine spiral liration is seen when the light is shining through the shell. Whorls are smooth and well rounded. The operculum was studied from more than 200 individuals of different sizes and was found to be rather uniform regarding the ridge and peg forming the hinge on its inner side. The grown individuals produced numerous egg capsules attached to stones and the shells of other gastropods. The species prefers water of good quality and is very sensitive to pollution (BANDEL & SALAMEH 1981).

Theodoxus jordani develops no larvae but has the same type of ontogeny, as is the case in *T. fluviatilis* (figs.220-221). The embryonic development is totally concluded within the shelter of the egg capsule. The young hatch as crawling miniature adults having developed from nurse eggs. This species occurs originally in all clean springs and creeks in Jordan south to the Dead Sea area, and according to the analysis carried out by DAGAN (1972) also in similar settings in Israel.

The differences between *T. jordani* (= *T. macrii*) as those found in Pella and *T. fluviatilis* as noted from the river Oder is quite distinct, even though both appear similar on first sight due to their basically black colouration. The peg on the operculum distinguishes clearly as does the number of whorls found added to the embryonic shell. While there is no peg in addition to the ridge in case of *T. fluviatilis*, there is always one in the hinge of *T. jordani*. While there are never more than 1,5 whorls of the teleoconch in *T. fluviatilis*, there are about 2,5 whorls in case of *T. jordani*.

Remarks: According to TCHERNOV (1973, Pl.1, fig.1) and HOROWITZ (1979) *T. jordani* occurred unchanged from the base of the Pleistocene to recent times in different fresh water localities in the Jordan Rift. According to SCHÜTT (1983) *T. jordani* is the same species in the Orontes and Jordan area. This species can according to SCHÜTT (1983) be differentiated from the species *T. anatolica* RÉCLUZ 1841, *T. nilotica*, and *T. mesopotamica* MOUSSON 1874, while TCHERNOV (1975) considered all these to represent the same species, but ecophenotypes of them, which has been supported by ROTH (1984). She had noted that two types of radula morphologies appear to be present in this species as if two distinct populations had mixed. TCHERNOV (1975) thought that *Theodoxus jordani* had been living in fresh water as early as the Oligocene and had come to Israel, Palestine, Jordan and the Lake of Galilee (Lake Tiberias) from Europe (Sarmatian Province). An earlier theory had been phrased by KOBELT (1904) who suggested that *Theodoxus (Neritaea)* came from tropical Africa, while *Theodoxus (Theodoxus)* arose in Europe even as far back in time as Jurassic. But this idea is not supported by the observation that *Theodoxus* species with shape of the shell and typical features of the opercular hinge lived in Germany and France during mid-Tertiary times.

For example *Theodoxus subangularis* (SANDBERGER) (collected and provided for study by D. KADOLSKY) from the "Cerithium Schichten" of Flörsheim in Hessen (late Oligocene) had been placed within the *Neritina* relation. But it represents of *Theodoxus* rather similar to *T. jordani* with protoconch consisting of one large, more than 0,4 mm wide first whorl. The operculum has the characteristic cow-horn like shape of a hinge provided with ridge and peg. The first whorl of the teleoconch has a flattened shoulder and well-rounded sides. There are 2,5 whorls of the teleoconch until the shell is fully-grown.

The late whorls are rounded and colouration consists of white dots in brownish background but also stripes. The callus of the inner lip is simple and the columellar edge is smooth or delicately dented.

Another rather similar species *Theodoxus matheroni* (WENZ) (determined by D. KADOLSKY) from Venelles near Aix-en-Provence in southern France and here the "Formation du Gypse d'Aix" has a similar protoconch. Here the early teleoconch whorls are rounded. There are more than two whorls of the teleoconch before the individuals of this species were fully-grown. Colour patterns also consist of white dots on brown background. The operculum resembles that found in the *Clithon* group of *Neritina* and of the *T. jordani* relation. These two quite similar species of *Theodoxus* from central Germany and southern France indicate that species similar to modern *T. jordani* existed in the mid-Tertiary times wide spread in Europe.

TCHERNOV (1975) had found colourless morphs in subterraneous surrounding of *T. jordani*, as was also observed by ROTH (1982) in Lake Tiberias and by SCHÜTT (1963) in case of *Theodoxus subterrelictus* from Dalmatia. White morphs also occurred among the population encountered to live in the Ghor Canal in spring 2001. HELLER (1979) observed that colouration might act as protection from molluscivore fish or crabs in Israel. Even though many varieties of shell colours are found in the individuals from Lake Tiberius and the vicinity DAGAN (1971) interpreted that they all belong to the same species in Israel. According to TCHERNOV (1975) *T. jordani* represents the same species or a very close relative to *Theodoxus meosopotamica, T. euphratica* MOUSSON 1874, *T. cinctilla* MARTENS 1874 and lives everywhere in the region from Turkey, Mesopotamia to the Nile (but see below). Its colour in Israel is very variable and there is a transparent variety living in a cave of Ein Nur near the Sea of Galilee in warm water of a spring. SCHÜTT (1984) also noted 14 synonym taxa to *Theodoxus jordani* (SOWERBY 1932). He found the species to be common in the Orontes, the Jordan and the coastal rivers of Palestine, Israel and Lebanon. But he considered that in the central Euphrates lives another species, and that the Nile is also inhabited by another species.

Figs. 72-73: *Neritina "Clithon" cornonata* (LEACH 1815) with globular shell that has a small spire and body whorl coating former whorls and in this individual without spines, the shell from Mnyameni estuary is about 12 mm high. 73: apical view.

Fig. 74: Operculum of *Neritina "Clithon" coronata* seen from the inner side and with a maximum diameter of 6 mm from the Umzamba iver, South Africa. It belongs to individual of 76-77.

Figs. 75-77: *Neritina "Clithon" coronata* from Umzamba estuary with 17 mm high shell (75), 76: with 15 mm high shell, 77: with light shining through and displaying a colour pattern of triangles.

Fig. 78: *Neritina auriculata* LAMARCK 1816 from Umzamba River estuary with shell of semi-spherical shape with flattened base and rapid increase in shell diameter so that a grown specimen has only little more than one teleoconch whorl. Maximum diameter 23 mm.

Fig. 79: Operculum of the specimen in 78 seen from the inner side with maximum diameter of 12 mm.

Figs. 80-81: *Neritina pulligera* (LINNE 1758) from the Mnyameni River with oval, semi-spherical shell with rounded upper side and flattened lower side. The juvenile shell measures 6 mm in width, 81: with light shining through the shell and displaying the ornamental pattern.

Figs. 82-83: *Septaria porcellana* (LINNE 1758) with symmetrical, cap-like shell from Mnyameni estuary (South Africa) with about 9 mm long shell. The light shining through the shell brings out colour pattern. 83: seen from the apical side.

Fig. 84: Operculum of *Septaria borbonica* (BORY DE ST. VINCENT 1803) with 11 mm in maximum diameter and seen from the inner side coming from an individual with 31 mm large shell from Umzamba estuary.

Figs. 85-87: *Septaria borbonica* (BORY DE ST. VINCENT 1803) with view on the outer side and light shining through the shell and illuminating the ornamental pattern. Maximum diameter 20 mm of this limpet from Umzamba estuary, South Africa.

Figs. 88-89: *Septaria porcellana* (LINNE 1758) with symmetrical, cap-like shell belonging to a juvenile from Umzamba estuary (South Africa) with about 10 mm long shell, 89: from the apical side and with light shining through it, so the ornamental pattern is better visible.

Figs. 90-93: *Neritina communis* (QUOY & GAIMARD 1832) from the Velur estuary in Tamil Nadu, southern India. The shell measures about 8 x 8 mm. In figs. 91-93 colour morphs of this species with similar shell size are shown, 91: with uniform zigzag pattern. 92: with zigzag and arrow-head pattern and colour ribbons, and 93: with spiral ribbons of zebra pattern.
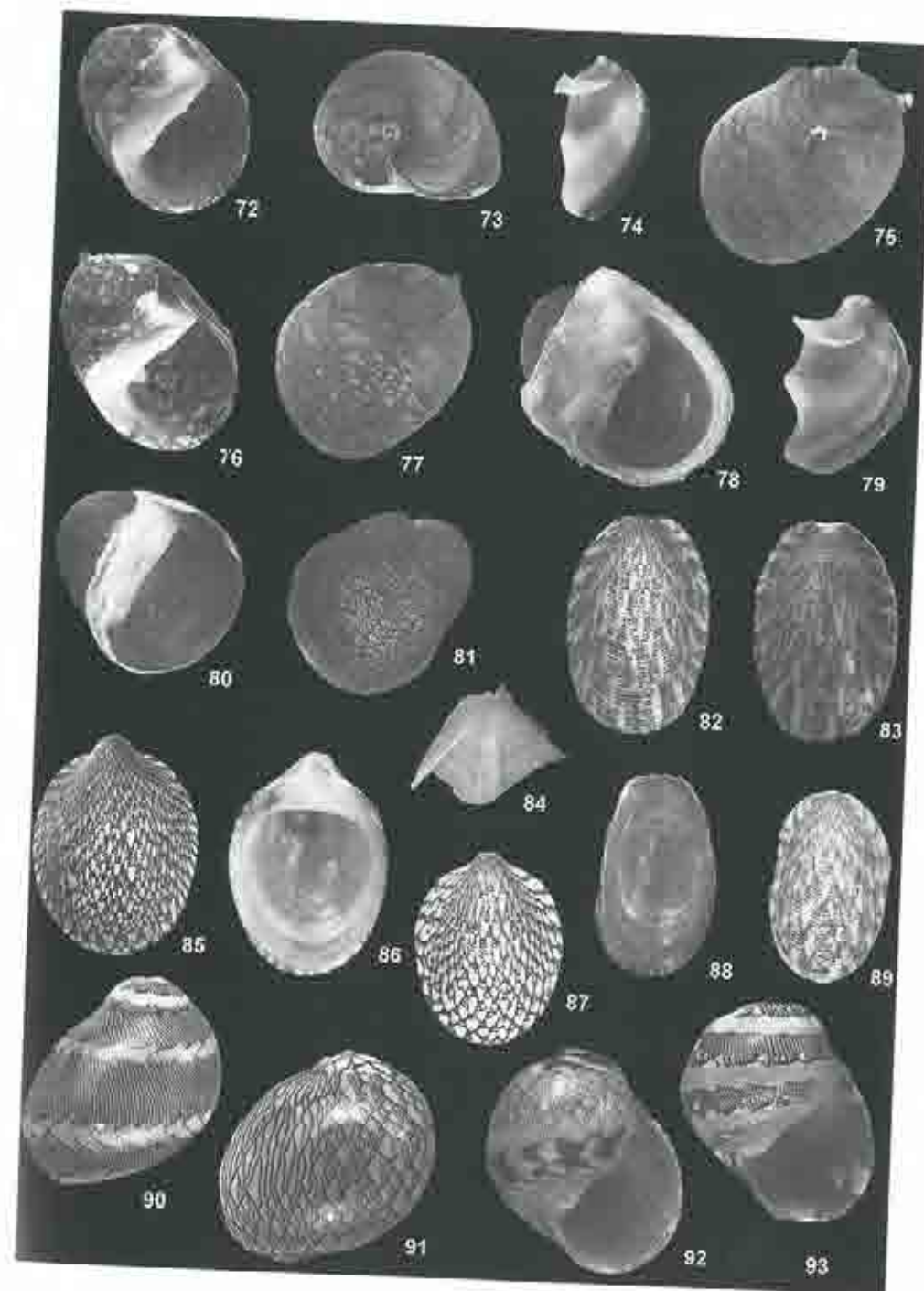
Theodoxus niloticus (Reeve 1856)

According to Brown (1980) a close relative or variety of *T. jordani* is represented by *Theodoxus niloticus* from the river Nile. According to Brown (1980) the shell is hardly distinguishable from that of *T. fluviatilis*, but the operculum supposedly is different by having a peg and a rib (*T. fluviatilis* has only the rib and no peg Brown 1980, Figs.15a,b, 16b,c). The shell is variably coloured with almost white forms as well as almost black ones and finely striped ones in zigzag patterns. Its habitat is from Luxor to the delta of the Nile and abundant in the extinct fauna of the Faiyum depression and it may occur further up the Nile in Ethiopia. Specimen collected from the Nile near Cairo were analysed regarding operculum and radula. The operculum of these individuals had only the ridge and no peg, as is the case in *T. fluviatilis*. *Theodoxus* from the Nile having about 1,5 whorls of the teleoconch, and a little more than 2 whorls when fully grown to 7 mm in width, therefore, does not belong in the relation of *T. jordan* but is a *T. fluviatilis* or very similar to it.

Theodoxus liturata (Eichwald 1841) (=astrachanicus Starobogatov 1994)

Anistratenko et al. (1999) described 7 species of *Theodoxus* that are interpreted to occur in the area of the Black Sea and the Sea of Asov. To do so they studied again the types of *Nerita fluviatilis* and chose a lectotype that is of low shape with dark background colouration and bears rows of light dots (about 10). This lectotype was utilized to distinguish the other species presented in that publication. *Theodoxus danasteri* (Lindholm 1808), since their shell shape is generally very similar to each other. *Theodoxus danasteri* (Lindholm 1808), for example, is illustrated with irregular collabral lines as ornament and a shell that is a little more oval (lower apex) than the *T. fluviatilis* lectotype. *Theodoxus euxinus* (Clessin 1885) has a slightly shorter shell but more irregular lines as ornament. *Theodoxus sarmaticus* (Lindholm 1901) also has white dots on dark ground and the shell appears to be of lower shape. *Theodoxus subthermalis* Issel 1865 appears to be just like *T. sarmaticus* in shape and ornament but may have a little lower shell. *Theodoxus velox* Anistratenko 1999, presented only as drawing, is apparently without colour marks, and a *Theodoxus dniestroviensis* is also documented that looks like *T. fluviatilis* but has spiral light ribbons as ornament.

Theodoxus astrachanicus can be evaluated from material collected in summer 2000 from Astrachan down the Volga River into the northern portion of the Caspian Sea. Here shells are around 5 mm wide and 4 mm high and consist of only one whorl that succeeds the protoconch. They have thus 0,5 whorls of the teleoconch less than is normal in *T. fluviatilis*. Otherwise the shell is of similar shape and size. Ornament consists of zebra pattern of brown or black stripes on light background. These lines may be almost straight, they may have zigzag pattern or they may be interrupted into dots. Also uniform white to yellowish specimen are common in the northern Caspian Sea, while in the Volga delta region below Astrachan individuals are usually striped. Commonly the axial colour pattern shows a recess on the side of the whorl, which appears as if there was a rib, while actually the flank is evenly convex.

T. astrachanicus has as only constant difference to *T. fluviatilis* in fully grown specimen one whorl instead of 1,5 whorls of the teleoconch. According to Dybowski (1888, Pl.2. Fig.10); Grimm (1876) had described *T. liturata* in detail. *T. liturata* = *astrachanicus* lives on rocks and wood in the Volga River. The colouration of all individuals is here quite similar with dense pattern of brown axial stripes which usually have an irregularity at the periphery which creates the impression of a ridge, while the shell here actually forms an even bend. The animals attach well to the substrate by their low somewhat oval shell. Here their egg capsules are common and attached to the rocks on which they dwell. This species also lives within the northern Caspian Sea and was encountered in large numbers among the shell debris found on the shore of Chemchusny Island that lies next to the border between Russian and Kazakhstan. In this shallow part of the sea changes of salinity between 5 and 10 ppm occur. From *Vallisneria* piled up on the beach shells remain after the plants have been devoured mainly by amphipods. *Theodoxus* here is represented by the same species as found in the Volga Delta but they are smaller in size and lighter in colouration. Here forms with dots and totally white individuals are common.

6.b. Some *Theodoxus* in the Pliocene

Theodoxus from the Pliocene of the Ghor Canal near Abu Habil on the Jordanian side of the Northern Jordan Rift Valley can be compared with other fossils found in deposits of more or less the same time in Greece, Spain and Hungary. The shell of these fossils closely resembles those individuals of *T. jordani* that live next to the fossil occurrence on the sides of the Ghor Canal within this canal which contains water from river Yarmouk and occasionally also from the Sea of Galilee which is utilized for irrigation on the Jordanian side of Jordan River. The shell consists of the embryonic whorl and 2,5 whorls of the teleoconch (figs.36-40). It is ornamented with brown axial stripes or checkerboard pattern with brown and white, quite similar to many individuals of *T. jordani* from the canal (figs.12-20). The inner lip covers a strong callus forming a convex cussion with a concave and smooth columellar edge. Until the begin of the last whorl the shell is hemispherical. In the last whorl of the teleoconch shell height increases reaching 8 mm with 6 mm in width. The side of the last whorl is somewhat flattened.

Practically no difference can, therefore, be noted between *T. jordani* from the Ghor Canal and the *Theodoxus* that lived in the lake that existed in the same geographical position during the late Pliocene. Tchernov (1973, Pl.1, fig.1) had noted a similar *Theodoxus* that lived in a lake at the locality where now Yarmouk River issues into the Jordan River and in which Erq al-Ahmar Formation was deposited. He found this species to represent the same that has been described as *Neritina karasuna* Mousson 1874 (Blanckenhorn 1897) and *Neritina orontis* Blanckenhorn 1897 from the Pliocene of the Orontis Basin.

According to the description of Blanckenhorn (1897) both species differ from each other as much as the varieties of *Theodoxus* seen nowadays in the springs of Jordan on one side (*T. karasuna*) (figs.32-35) and the Ghor Canal (*T. orontis*) (Figs.12-20) on the other side. A species with similarly high last whorl and depression on the side was also determined as *T. orontis* Blankenhorn 1897 (Schütt 1988, Pl.2, Fig.9) from Pliocene deposits in the Orontes valley. They also are close to individuals in modern populations of *T. jordani* from the Sea of Galilee, illustrated by Heller (1993). The species name for this variety of a slightly higher shell with constriction, therefore, is not needed as was suggested by Tchernov (1973).

Also specimen of *Theodoxus doricus* (Neumayr 1869) from the Kos Formation of the Pliocene of Greece had shells with similar ornament and shape (based on material collected by E. Voigt) (figs.21-26). According to Willmann (1981) *Theodoxus hellenicus* represents an important stratigraphical marker in the Pliocene deposits of Kos and Rhodes. Willmann (1981) suggested that it developed from *Theodoxus doricus* by forming depressions on the sides of its whorls. According to Willmann's (1981) interpretation also subspecies evolved here as isolated morphotypes, which later on may have mixed again forming hybrids. These subspecies of *Theodoxus doricus* were interpreted to have become transformed into different morphologies, which later mixed their characters again, interpreted as subsequent bastardisation. Bukowski (1893, Pl.7) described from the Pliocene lacustrine deposits of Rhodes and Kos the three species *T. pseudomicans* (Bukowski 1893), *T. fontannesi* (Neumayr 1879), and *T. hellenicus* (Bukowski 1893), which are distinguished from each other by a more or less high spire with rounded to convex sides. Bukowski noted that all three species have a broad overlap in shape. He also remarked that compared with *Theodoxus* of similar age but different geographic occurrence there is also close similarity, for example with *T. micans* (Fuchs 1877) from the Greek mainland and *T. doricus* from eastern Kos. Actually most of the shapes and colourations noted by Bukowski (1893) are still realized in modern *T. jordani* as it occurs in the catchment of the Jordan River. The profusion of species names available for this gastropod that can be called *T. jordani* and has lived in the region for the last 3 Million years, thus, confuses matters more than it can enlighten.

The species described by Rust (1997) as *Theodoxus trilophosensis* Rust 1997 differs by having fewer whorls and lower shell shape. Unfortunately Rust gave no differential diagnosis, so that it remains unclear what characterizes this fossil species and distinguishes it from *T. fluviatilis* or from other representatives of *Theodoxus* as still live in Greece (Schütt 1986). *T. trilophosensis* from the Neogene of the North-Aegeanan area demonstrates variation of ornamental pattern, and Rust suggested, that striped morphs were more common in brackish environment, while dark morphs had been living

in fresh water. RUST (1997) supported his data by relying on the experiments that had been carried out by NEUMANN (1959a,b) with *T. fluviatilis*. But RUST (1997) also compared his data with those of GRÜNEBERG (1976) on *Clithon (Pictoneritina) oualaniensis*, but did not take into consideration that this later species is only very distantly related to *Theodoxus*, has a planktotrophic marine larval stage, and different living environment (see chapter 7.g).

Compared with *Theodoxus* from the Pliocene of the Ghor Canal near Abu Habil in Jordan the Greek Pliocene *Theodoxus trilophosensis* appears to be a little more rounded and consist of one whorl less when fully grown. Most interesting is here the shape of the apophysis on the inner side of the operculum. RUST (1997, Fig.10) documented that within a single population of this late Neogene species from Greece near Thessalonici the operculum projection graded from individuals without second peg as in modern *T. fluviatilis* to individuals with peg as in modern *T. jordani*. He connected his observation with changes in the intensity of crab predation. Here the individuals belonging to one species would have changed from the subgenus *Theodoxus* with only the ridge into the subgenus *Neritaea* with ridge and peg within the same locality through time. But it may be a change that occurred not so much in reaction to increased predation by crabs but due to hybridisation of forms with *Neritaea* operculum with such of *Theodoxus* operculum. JEKELIUS (1932) has already noticed such variation in operculum construction in case of *Theodoxus semiplicatus*, and ROTH (1984) observed similar variation and a broad morphological spectrum in case of *Theodoxus jordani*.

ESU & GIROTTI (1974) discussed the validity of generic names such as *Neritina, Theodoxus, Clithon, Smaragdia, Calvertia,* and *Puperita* and came to the conclusion that the genus *Neritina* is best used for this "species" of Villefranchian *Theodoxus*. This species from Italy appears to fall in the same range of shapes as can be noted for the Jordanian *Theodoxus*. In difference to modern *Neritina (Theodoxus) fluviatilis*. ESU & GIROTTI noted the presence of a small peg on the inner side of the operculum, which they considered to be absent in the living form. ESU & GIROTTI (1974) did not utilize the early ontogenetic shell in their discussion, which actually represents the best character of the shell to distinguish *Neritina* and *Theodoxus*. These authors had still regarded *Theodoxus* as subgenus to *Neritina*, the other subgenus being *N. (Neritaea)* ROTH 1855. ESU & GIROTTI (1974) considered the modern *Theodoxus jordani* and species from Greece to represent members of the subgenus *N. (Neritaea)*, and *Theodoxus danubialis/fluviatilis* to represent the subgenus *N. (Theodoxus)*. The transition observed to occur between the characteristic differences of these taxa noted in detail by RUST (1997) indicates that there can only one taxon *Theodoxus* and that this can not be seen as subgenus to *Neritina* and that it should be considered the same as *Neritaea*.

WILLMANN (1980) noted that two species of *Theodoxus* must have lived side by side in a late Neogene lake at Crete (Greece). Of these *Theodoxus spratti* (JENKINS 1864) has a shell shape rather similar to that found in *T. jordani* living in the Ghor Canal of Jordan. WILLMANN noted many colour morphs that had by other authors been considered to represent independent species. ANAPIOTIS (1976) recognized *Theodoxus crenulatus, T. semiplicatus* and *T. mariae*, species that had been described from

Figs. 94-**97**: *Neritina communis* (QUOY & GAIMARD 1832) from the Velar estuary in Tamil Nadu, southern India. The shell is about 8 x 8 mm and ornamented by regular spiral ribbons, 95: has a change in ornament from dark ribbons and zigzag pattern to finely striped radial pattern.
Figs. 96-99: *Neritina afra* SOWERBY 1841 from the estuary near Limbe (Cameroon) with 8 mm high shell. 96: showing delicate colour pattern; 97: with dotted colour ornament, 98: apertural view and coarse teeth on the columellar plate, 99: with drop-like patterns.
Figs.100-103: *Neritina rubricata* MORELET 1858 from the underside of wet logs in the beach drift of the uppermost tidal zone at Douala (Cameroon), 100: with 7 mm high shell, seen in apertural view, 101: of the same shell displaying a pattern of ornamented ribbons, 102: apertural view with shell that has a more dull coloration, 103: seen from behind with spiral color ribbons.
Figs. 104-107: *Neritina luteofasciatus* (MILLER 1879) from the Gulf of California, Bahia Concepción with about 10 mm high shell with inclined axial stripes as ornament (104), 105: same shell seen from behind, 106: with finely reticulate patterns in brown and grey In apical view, 107: seen from behind,
Figs. 108-113: A species from the estuary of the Matutinao River (Cebu) that appears to be a mixture of *Neritina communis* and *Neritina "Clithon"* with colour varieties in 108-115 (type 4). The shell is about 12 mm high.
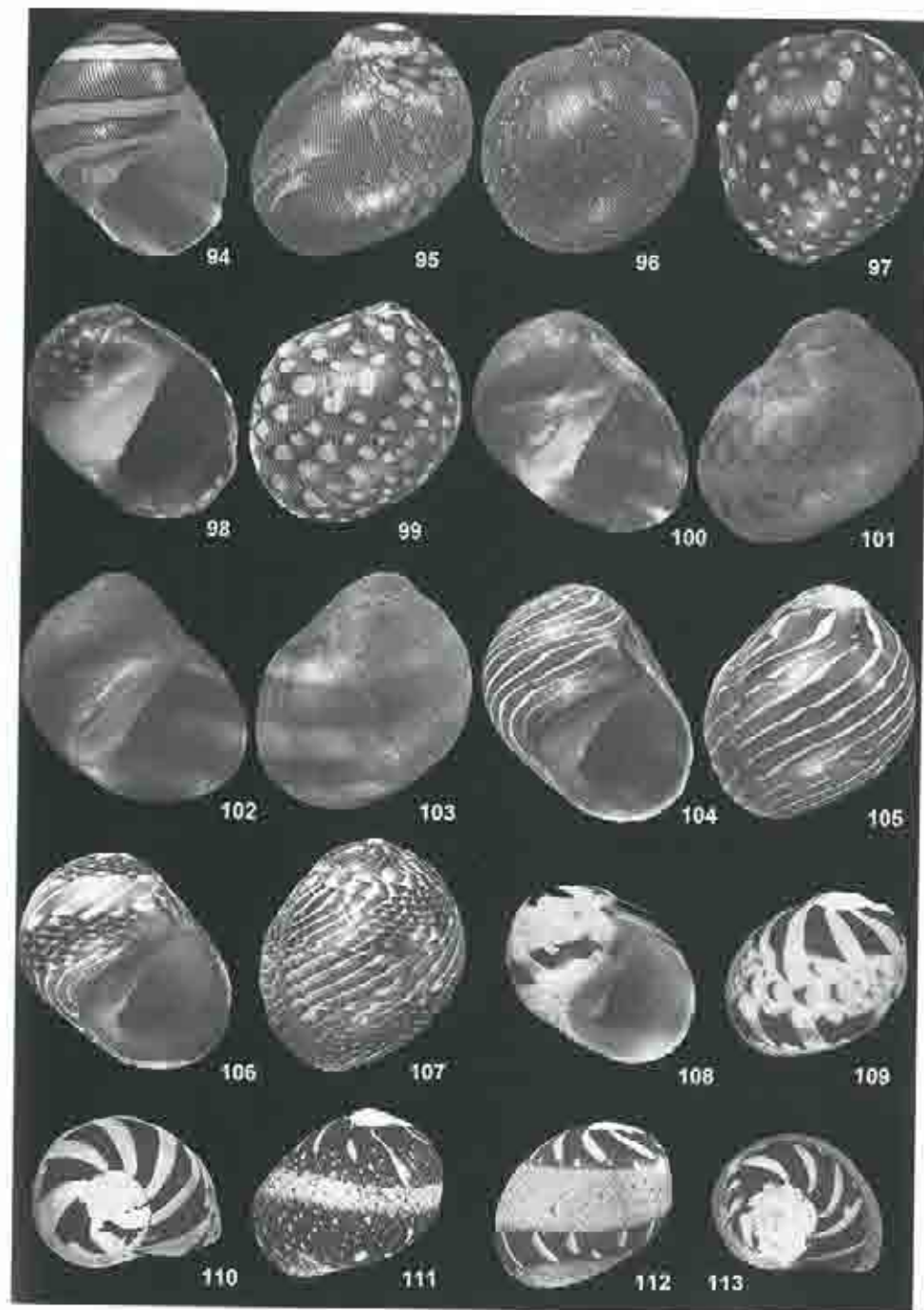
the late Miocene Lake Pannonian by JEKELIUS (1944) and PAPP (1953). The other species, according to WILLMANN (1980), is *Theodoxus abnormis* (JENKINS, 1864) that has two spiral keels separated from each other by the concave side of the last whorl of the adult. While the keel right below the suture is weak that on the edge to the base may be rather strong and even develop spines (WILLMANN 1980, Figs.2 c-g). In this regard *T. abnormis* resembles to some extend the shouldered varieties of *Theodoxus danubialis* rediscovered by SCHÜTT (1988) in Croatia, but the later being related to *T. danubialis* and not *T. jordani*, as the former. *Theodoxus spratti* and *Theodoxus abnormis* have co-occurred for some time in the lake clearly distinguished, and thus did not hybridise, and according to WILLMANN's (1980) model were thus independent species. But this is a dangerous assumption, since living *Theodoxus jordani* from the Sea of Galilee form varieties with such elongated whorl and even a groove on the side (HELLER 1993), but also low rounded forms sometimes without mixing.

From the Andalusian Pliocene of Arenas del Rey and Fuensanta in the Granada Basin BANDEL et al (2000) described shells belonging to *Theodoxus fluviatilis*. The shell of these forms that lived in a large lake consists of 2,5 whorls (first whorl representing the protoconch) measures only 7 mm in maximum diameter with 5 mm in width and 4 mm in height when placed on the apertural plane. The colour pattern consists of light triangles with their pointed portion towards the outer lip. The protoconch consist of an about 0,3 mm wide whorl that consists of a semi globular cup with a narrow apertural collar added to it. It resembles the protoconch of *Theodoxus jordani* as illustrated by RIEDEL (1993) but is a little smaller and has a relatively larger apical cup.

So apparently both *Theodoxus* (*Theodoxus*) as well as *Theodoxus* (*Neritaea*) quite similar to modern *T. fluviatilis* and *T. jordani* were present in the Pliocene of Europe. The observations of RUST (1997) indicate that species that could be placed in both subgenera interbred in the lake, which assembled the deposits, studied by him. The resulting species had an operculum intermediating from one to the other subgenus. This would support the assumption of WILLMANN (1981) that characteristic "species" as for example the keeled *T. helenicus* interbred with more simply shaped "species" coming in from other sources and thus lost their peculiarities of shell form.

6.d An inflation of *Theodoxus* species in the late Miocene

From Sarmatian, Pannonian and Pontian beds (Late Miocene) of the Lake Pannon, which lay in the Central Paratethys Basin, many species of *Theodoxus* have been described. In the collection of the Hungarian Geological Survey in Budapest about 50 species are catalogued from this region that have been considered as represent independent taxa. BRUSINA (1874, 1884, 1897, 1902) described many species and subspecies from the Balkan, mainly Croatia. Others have been described by FUCHS (1877), PAPP (1953, 1954), STRAUSZ (1966), LÖRENTHAY (1902, 1906, 1911) and others. PAPP & THENIUS (1954) noted 4 species of *Theodoxus* to co-occur within the beach deposits of the Pannonian Lake in the Vienna Basin near Vösendorf. According to PAPP (1985) 18 species and subspecies are known from the Vienna Basin of which only 7 have also been recognized from the Pannonian of Soceni in Romania, where 12 species have been differentiated by JEKELIUS (1944).

In his review on the Pannonian fauna of the Vienna Basin PAPP (1985) mentioned only 4 species, *Theodoxus postcrenulatus*, *T. intracarpaticus*, *T. loebersdorfensis*, and *T. zografi*. Their illustrations document that it is mainly the colour pattern, secondarily the size of the shell that is used to distinguish species. When the descriptions and illustrations of JEKELIUS (1944) are consulted it is also the shape of the shell that has been used to distinguish species. PAPP (1953) based his species mainly on colour patterns, which by comparison with recent species and in the light of experiments carried out by NEUMANN (1959a,b), must be considered to be highly variable within a species. All these species can, thus, also be regarded to represent variants of one or a few species. Since the number of whorls of the teleoconch of adult individuals is usually not mentioned in descriptions, comparison with

recent species is difficult. But some colour varieties are characteristic to populations. Here that of Tihany and Papkesi near Lake Balaton (Hungary) was analysed in more detail (figs.41-57).

CSATO (1993) suggested that the history of a lake in the Pannonian Basin began with the Tortonian about 10 Million years ago and ended in the Messinian crisis about 5 Million years ago. Lake Pannon at late Miocene time was a brackish sea that was usually closed to the world oceans (MATYAS et al. 1996). During the Pontian period about 7 to 5 Million years ago this brackish Lake Pannon and its surrounding rivers, lakes and swamps occupied the area around the modern Lake Balaton. MATYAS et al (1996) analysed the shells of bivalves belonging to the *Congeria* and the *Limnocardia* relation, both restricted to the lake proper and not found in its fresh water intercalations. These data suggest a salinity of the Pannon Lake of about 5 ppm. *Theodoxus* from Tihany can be dated since here lake deposits containing it have become covered by a basalt that has an age of about 7 Million years (MÜLLER 1985). This species could be placed close to *T. eugenii* JEKELIUS 1844 and was called *Theodoxus radmanesti* (FUCHS) by MÜLLER (1985, Pl.1, Figs.1,2) and *T. vetranici* by BARTHA (1956). From Tihany and Papkesi many individuals (more than 1000) were extracted from the sediment and colour morphs were separated from each other (figs.41-57). Most individuals have black spiral ribbons on white background. The number of such ribbons is variable ranging from about 4 to 10. At growth interruptions a sudden change may occur regarding ribbon number, for example by doubling it. There are also numerous individuals in which the background is dark grey and ribbons are white. Also shells may have brown ribbons on white background or white ribbons on brown background. Sometimes a zigzag pattern is still recognizable when ribbons consist of elongate dots (fig.44). Dotted varieties were named *T. soceni* by BARTHA (1955) when collected at Varpalota (Hungary) and *T. crenulatus varpalotensis* BARTHA, 1956. In addition some shells have a uniform colouration of grey, brown or white.

Among all these colour varieties the shell shape is the same. About 2,5 whorls of the teleoconch succeed the white embryonic whorl. Increase of whorl diameter is regular, and the spire is low, with some variation regarding the size of the spire. More irregular growth lines in the last quarter whorl characterize the fully-grown shell. Shell size is usually around 5 mm in width and 4 mm in height. The columellar lip of the aperture has a fine crenulation of dentition of up to 10 denticles of which the apical ones are a little larger. The callus pad is simple with rounded margin. The operculum resembles that of *T. jordani* with ridge and peg.

According to PAPP (1954) Sarmatian deposits from the Vienna Basin contain the most ancient species of *Theodoxus* of the western part of Lake Pannon region, living together with *Neritina*. This is *Theodoxus postcrenulatus* PAPP 1953 (PAPP 1985, Pl.30, Figs.1-3) that is supposed to have evolved from the Tortonian *Theodoxus crenulatus*. PAPP (1953, 1985) suggested that *T. crenulatus* might represent an ancestral species to the richly diverse *Theodoxus* assemblages noted in the deposits of the Pannonian sea or its coastal regions. Its columellar lip is weakly dented to crenulated and the shell has a maximum size of 13 mm. The type of this species is from Württemberg. According to BARTHA (1956) *T. crenulatus* closely resembles modern *T. danubialis* and also the fossil *Theodoxus semiplicatus* with zigzag pattern and this species was reported from the Pannonian of Tab and Varpalota near Lake Balaton as well as earlier Miocene deposits from other localities in Europe. But these speculations are problematic since very similar *Theodoxus* has been living in Europe for example at Oligocene time as proven in case of *T. matheroni* and *T. subangulatus* (see chapter 6.b).

During the Sarmatian about 11,5 million years ago the salinity of the sea dropped and the marine fauna disappeared to a large extent (PAPP 1963). PAPP (1954) suggested that the brackish Sarmatian sea in its marginal portions of estuaries and coastal swamps was settled by a fauna consisting of two species of *Melanopsis* with varieties, one species of *Neritina*, one of *Theodoxus* and one of the bivalve *Congeria*. When the sea changed its salinity toward fresh water the dreissenids with *Congeria*, the neritids with *Theodoxus*, the melanopsids with *Melanopsis* and some cardiids supposedly managed to adapt to the environment, while all the other molluscan groups disappeared and became extinct. But this scenario needs not to be realistic since all these groups, perhaps with exception of some cardiids had representatives living in fresh water before the existence of Lake Pannon and connected rivers and

ponds in the region of the Paratethys basin. In case of *Melanopsis* this has been documented by BANDEL (2000).

From Soceni in Romania JEKELIUS (1944) described the species of *Theodoxus* from the Sarmatian to the Pontian deposits. He discussed possible differences in shell shape, especially those of the columellar edge of the inner lip of the aperture and the shape of the inner side of the operculum. JEKELIUS came to the conclusion, that regarding shell features all recognized species should be considered to belong to the same genus and subgenus *Theodoxus* with the characters of the shell not very useful to differentiate them well. But even though recognizing this JEKELIUS distinguished 10 different *Theodoxus* taxa only in the Sarmatian deposits, of which 9 were considered to represent species. In the Pannonian he recognized 12 species with only little overlap to the species from the Sarmatian.

The *Theodoxus* species of Soceni according to JEKELIUS (1944) are arranged according to their general shape in a list below. The 19 species from Soceni, of which several can be variants of each other, appears to be a round globular group, a small ovoid or elongate group and the lonely limpet *Ninnia*. (see chapter 7.1.).

Theodoxus crenulatus (KLEIN 1853): Round shell, dark background, and light irregular of triangular dots (JEKELIUS 1944, Pl.5, Figs.1-3; PAPP 1954, Pl.5, Figs.4, 5).

Theodoxus soceni JEKELIUS 1944: Rounded shell, light background, brown triangles with points forwards, dark dots point backwards (JEKELIUS 1944, Pl.5, Figs.7-26 (Sarmatian), Pl.42, Figs.27-33 (Pontian), Pl.5, Figs.27-28 (Pannonian), PAPP 1954, Pl.5, Figs.6-10 (Sarmatian).

Theodoxus prozlatarici JEKELIUS 1944: Small, round shell, median white spiral, brown background (JEKELIUS 1944, Pl.5, Fig.38, Sarmatian).

Theodoxus vetranici (BRUSINA 1902): Round shell, spiral dark lines, and light background (JEKELIUS 1944, Pl.42, Figs.1-3, Pontian).

Theodoxus eugenii JEKELIUS 1944: Round shell, zigzag pattern in dark 4 ribbons, and 4 white ribbons (JEKELIUS 1944, Pl.42, Figs.6, 7).

Theodoxus turislavicus JEKELIUS 1944: Small round shell, fine spiral, zigzag lines (JEKELIUS 1944, Pl.42, Figs.17-21, Pontian).

Theodoxus banaticus JEKELIUS 1944: Oval shell, irregular to triangular dots, brown background, median ribbon (JEKELIUS 1944, Pl.5, Figs.29-37, Sarmatian).

Theodoxus carasiensis JEKELIUS 1944: Small oval shell, large brown dots, light background or opposite (JEKELIUS 1944, Pl.6, Figs.1-15).

Theodoxus tortuosus JEKELIUS 1944: Small oval shell, dense brown zigzag-lines, light background (JEKELIUS 1944, Pl.6, Figs.16-21 (Sarmatian), Pl.42, Figs.14-16 (Pontian); PAPP (1954, Pl.5, Fig.11 (Sarmatian and Pannonian)).

Figs. 114-115: A species from the estuary of the Matutinao River (Cebu) that appears to be a mix of *Neritina communis* and *Neritina* "*Clithon*" (type 4) with colour varieties in 109-115. The shell is about 12 mm high.

Figs. 116-121: *Neritina communis* from the mangrove of Areao (Cebu, Philippines) with about 8 mm high and wide shell, seen from the side (116), 117: apical view, 118: with more uniform coloration in apical view, 119: seen from the side, 120: with different colour morph, 121: apertural view.

Figs. 122-125: *Neritina piratica* RUSSELL 1940 from the mangrove flats of Tolu in Columbia (Caribbean Sea) with regular zig-zag pattern and 23 mm high shell.

Figs. 126-129: *Neritina* cf. *variegata* (LESSON 1832) from supratidal mud flats in the mangrove near Lovina, Bali, Indonesia with zigzag pattern of different type and about 20 mm high shell.

Figs. 130-131: *Neritina turrita* (GMELIN 1790) from supratidal flats near Kuta, Bali, Indonesia with 30 mm high shell and characteristic zebra-striped pattern.

Figs. 132-133: *Neritina turrita* (GMELIN 1790) from supratidal flats near Lovina Beach, Bali, Indonesia with 25 mm high shell and characteristic zebra-striped pattern.
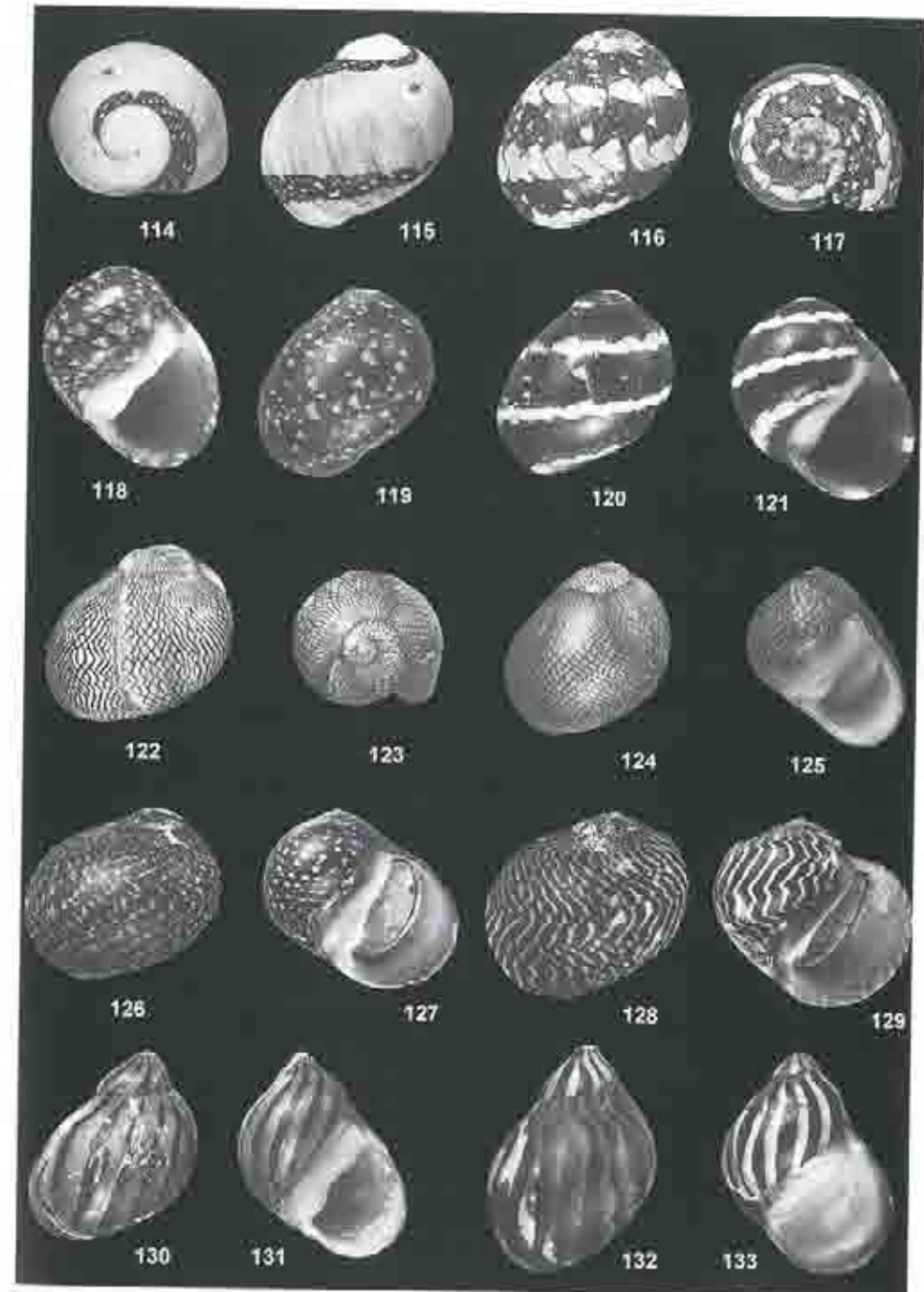
Theodoxus politioanei JEKELIUS 1944: Oval shell, brown spiral lines, light background (JEKELIUS 1944, Pl.6, Figs.22-32, Sarmatian).

Theodoxus intracarpaticus JEKELIUS 1944: Oval shell, rounded light dots, brown background (JEKELIUS 1944, Pl.41, Figs.1-24 (Pontian)).

Theodoxus perlongus JEKELIUS 1944: Small oval shell, indistinctly spiral (JEKELIUS 1944, Pl.42, Figs.4, 5, Pontian).

Theodoxus dacius JEKELIUS 1944: Small oval shell, zigzag-pattern in spiral ribbons (JEKELIUS 1944, Pl.42, Figs.8-11, Pontian), resembling that of *T. prozlatarici* from the Sarmatian.

Theodoxus zlatarici (BRUSINA 1902): Small oval shell, 2 spiral ribbons of large white dots, dark background (JEKELIUS 1944, Pl.42, Figs.12, 13, Pontian).

Theodoxus mariae (HANDMANN 1887): Small oval shell, zigzag lines of dark dots (JEKELIUS 1944, Pl.42, Figs.22-24, Pannonian, PAPP 1953, Pl.3, Figs.9-12).

Theodoxus politus JEKELIUS 1944: Elongated shell, light brown to grey (JEKELIUS 1944, Pl.6, Figs.1-15, Sarmatian).

Theodoxus petralbensis JEKELIUS 1944: Small elongate shell, fine wavy lines, similar to *T. zografi* BRUSINA 1902 (JEKELIUS 1944, Pl.42, Figs.25, 26, Pontian).

Theodoxus timisensis JEKELIUS 1944: Elongate shell, very dense zigzag-lines or dots (JEKELIUS 1944, Pl.5, Figs.4-6).

Ninnia soceni JEKELIUS 1944: Flattened semi-limpet shell, granular surface, ornament like *T. soceni,* shape like *Ninnia martensi* (BRUSINA 1897) (see figs.64-66).

From the Pannonian of the Vienna Basin PAPP (1953) described quite a number of *Theodoxus* species and subspecies many of which closely resemble *T. crenulatus* in shell shape. But apparently the ornament consists dominantly of spirally arranged dots or light triangles, which merge into zigzag patterns. Of the 18 different taxa that were distinguished by PAPP (1953 Pl.1, Figs.1-32, Pl.2, Figs.1-16) eleven were regarded as species, the others as subspecies. In regard to general shell shape there is a difference of more rounded shapes as present in *Theodoxus postcrenulatus and T. brenneri,* more ovoid shape in *Theodoxus intracarpaticus, T. soceni, T. turislavicus, T. eugenii, T. zoographi* etc. *Theodoxus loebersdorfensis* HANDMANN 1887 (PAPP 1953, Pl.2, Figs. 29-23, 1985) is described to differ only by the operculum that has no apophysis (even though PAPP had noted that this is a highly variable character). PAPP distinguishes 3 subspecies of this form, one of which could be *T. pitari* BRUSINA (PAPP 1953, Pl.2, Figs.16-20).

7. Examples of the modern Neritininae

Neritininae are found in the coastal swamps of all tropical regions. The existing species of *Neritina* have been divided into subgenera by BAKER (1923) basically based on differences in shell shape and in shape of the teeth of the radula. BAKER suggested the 4 subgenera *Neritina, Neripteron, Vitta, and Vittina.* According to THIELE (1929) there are 5 subgenera of the genus *Neritina, Neritina* s.s., *Vitta, Neripteron, Vittina* and *Neritona.* WENZ (1938), in addition, splitted *Neripteron* into *Neripteron* s.s. and *Clypeolum.* CUNNINGHAM VAUGHT (1989) considered the following 11 subgenera of *Neritina: Neritina (Neritina), Neritina (Clypeolum)* RÉCLUZ 1842, *Neritina (Nereina)* CRISTOFORI & JAN 1832, *Neritina (Neripteron)* LESSON 1830, *Neritina (Neritona)* MARTENS 1869, *Neritina (Provittoida)* BAKER 1923, *Neritina (Vittoida)* BAKER 1923, *Neritina (Vittina)* BAKER 1923, *Neritina (Vitta)* MÖRCH 1923, *Neritina (Pseudonerita)* BAKER 1923, and *Neritina (Dostia)* GRAY 1847. While *Clithon* was suggested to represent a subgenus to *Theodoxus* by THIELE (1929) which is still utilised by ABBOTT & DANCE (1982), WENZ (1938) considered it an independent genus with the subgenera *Clithon (Clithon), C. (Vittoclithon)* BAKER 1923, *C. (Pictoneritina)* IREDALE 1936, *C. (Alinoclithon)* BAKER 1923 and *C. (Neritioclithon)* BAKER 1923.

The resulting system is quite confusing and does not reflect true relations among the different species in existence today, as was documented by HAYNES (2001). HAYNES based her opinion on the analysis of one of the richest nertininid fauna in existence living around the Fiji Islands. It will be shown in the following chapters, that species belonging to different subgenera most probably form hybrids with each other, which indicates their close relation to each other. They can, therefore, be placed in different species only with reservations, certainly not into different subgenera or even independent genera such as *Clithon.*

7.a Generalities about modern Neritininae

Neritina, the related *Clithon* as well as its limpet-like relatives *Septaria* usually settle in the coastal environment, arriving here after a planktotrophic larval stage. Larvae metamorphose either where water is brackish, or where the influenced of fresh water is present. From here many species enter the fresh water by crawling upstream. In all species that have been studied in this regard early ontogeny after hatching from the egg capsule is connected to a larval phase during which the individual is a planktotrophic veliger that swims in the sea feeding on phytoplankton. The only exception to this life in the open sea is still mysterious, as described below (chapter 7.g, figs.254-256). Only when this stage of life ends with metamorphosis to the benthic young, the individual may enter fresh water and spend all its further life within this environment

The characteristic species of *Clithon* are distinguished from *Neritina* by the presence of spines on the shell (COSSMANN 1925) and, sometimes, by the morphology of the ridge and peg on the inner side of the operculum. But, apparently, there are hybrids connecting members of both genera, which, therefore, are no natural units. *Septaria* differs by having limpet-like shell connected to the reduction of the function of the operculum. *Theodoxus* is very similar to *Neritina* regarding the shape of the teleoconch but differs in the dimension and shape of its protoconch that reflects the early ontogeny, which has no planktotrophic veliger and, therefore, no larval shell. *Theodoxus* also differs by living in fresh water or weakly brackish water for all its life.

BROWN (1990) suggested, that the subgroups of *Neritina* are not soundly based. A similar opinion has been expressed by HAYNES (1990, pers. comm.). She had noted that the subgeneric differentiation as found in literature confuses matters more than it helps in clarifying the evolutionary history of the *Neritina* relation. HAYNES also suggested that there might only be 10 to 11 species of *Neritina,* which are found in the huge area of the tropical Pacific between Java - New Guinea - Solomon Islands - Fiji region and fewer species in the North and East Pacific, the Indian Ocean and the Caribbean Region. But also according to HAYNES (2001) there are 24 species of neritinines (including *Septaria* and *Clithon*) in Fijian streams, 16 in Samoa and 8 in French Polynesia (POINTIER & MARQUET 1990). Also 8 (with *Neritilia* 9) were encountered in a river in Cebu (Philippines) (BANDEL & RIEDEL 1998) (but see chapter 7.g). From Australia SCOTT & KENNY (1998) report the occurence of only 4 species.

STARMÜHLNER (1993) noted the occurrence of 15 species in the Tonga-Samoa region of the SW Pacific including one species that was described as *Puperita* and one as *Neritilia*. On the Island Ovalau situated 17 km off the larger island Viti Levu, Fiji there are 17 species if neritinines found in the two streams that were analysed by HAYNES (1988). A high number of species (about 25) was encountered in streams of New Caledonia (POLLABAUER 1986). Apparently the region of the Fiji Islands and of New Caledonia represents the centre of diversity in modern Neritininae. Taiwan and Japan have 15 species (KOMATSU 1986), which probably are mostly the same as those species encountered to the east of these occurrences in the Pilippines (see chapter 7.g), and largely resemble species as found in Indonesia (see chapter 7.h).

According to HAYNES (2001) splitting of the genus *Neritina* into many subgenera is not very useful in understanding biogeography and evolution of the nertininids. She suggested different lineages of *Neritina*, for example one representing the relation of *Neritina auriculata*, that connect to the Hawaiian species especially those with extended outer lip and to *Neritina latissima* from the Pacific Central America (but see chapter 7.m). Another group would be formed by *Neritina turrita* and *N. variegata* from the Indopacific, which appear to be distantly related to the *Neritina virginea* group of the Caribbean region (see chapter 7.j). *Clithon* s.s. and *Septaria* are found only in the Indo-Pacific region and are absent from the Caribbean, Central American, and West African regions.

Here some of these lineages are traced. In the chapters 7.b, 7.c, 7.e, and 7.f special attention is given to the neritine fauna of the estuaries of the Umzamba and Mnyameni Rivers at the border between the Northern Cape Province and southern Natal at the coast of the Indian Ocean. These river mouths are strongly influenced by the daily tides which is responsible for about 1,5 m of change in water level. During low tide much of the estuarine water leaves the pond into the sea through a deep canal in the sand bar. At the end of low tide the estuarine area is mostly taken by fresh water. At high tide water enters the estuary and a large pool forms that is about 3 km long in case of the Umzamba estuary. At its upstream end the intertidal regime clearly ends with the begin of normal fluviatile fresh water conditions. This is indicated by the first appearance of basommatophoran gastropods of lymnaeid and planorbid species. *Phragmites* reeds are found here and further downwards *Scirpus* reeds are common with *Bruguiera* bushes with knobbly elbow-like projections forming small mangrove forest patches. Three species of *Neritina*, (*N. gagates*, *N. pulligera*, *N. auriculata*) are present here, besides one species of *Clithon* and two species of *Septaria* and one species of *Neritilia* which are described further below (chapters 7.b; 7.c; 7.e; 7.f; 7.i;14.a).

Figs. 134-135: *Neritina turrita* (GMELIN 1790) from supratidal flats near Lovina Beach, Bali, Indonesia with 25 mm high shell and characteristic zebra-striped pattern.
Figs. 136-137: *Neritina ("Clithon") cf. nucleolus* (MORELET 1856) from the estuarine intertidal region near Lovina Beach, Bali, Indonesia with side and apertural view and 12 mm in height.
Figs. 138-149: *Neritina cf. corona* (LINNÉ 1758) from the estuarine intertidal region near Lovina Beach, Bali, Indonesia, 138: with spine bearing 12 mm wide shell, 139: seen in apical view, 140: with banded variety, 141: with dotted variety, 142: with less spinous shell of 15 mm in width, 143: apical view, 144: with few spines, 145: in apertural view, 146: with rounded shell and uniform colouration, 147: with ornament of arrows and one spine, 148: apical view, 149: with regularly dotted and rounded shell. Figs. 150-153: *Neritina "Clithon" corona* (LINNÉ 1758) from near Port Moresby, New Guinea with convolutely coiled shell of 20 mm in height and spineless morphs (150-151) and spine bearing shells (152-153).
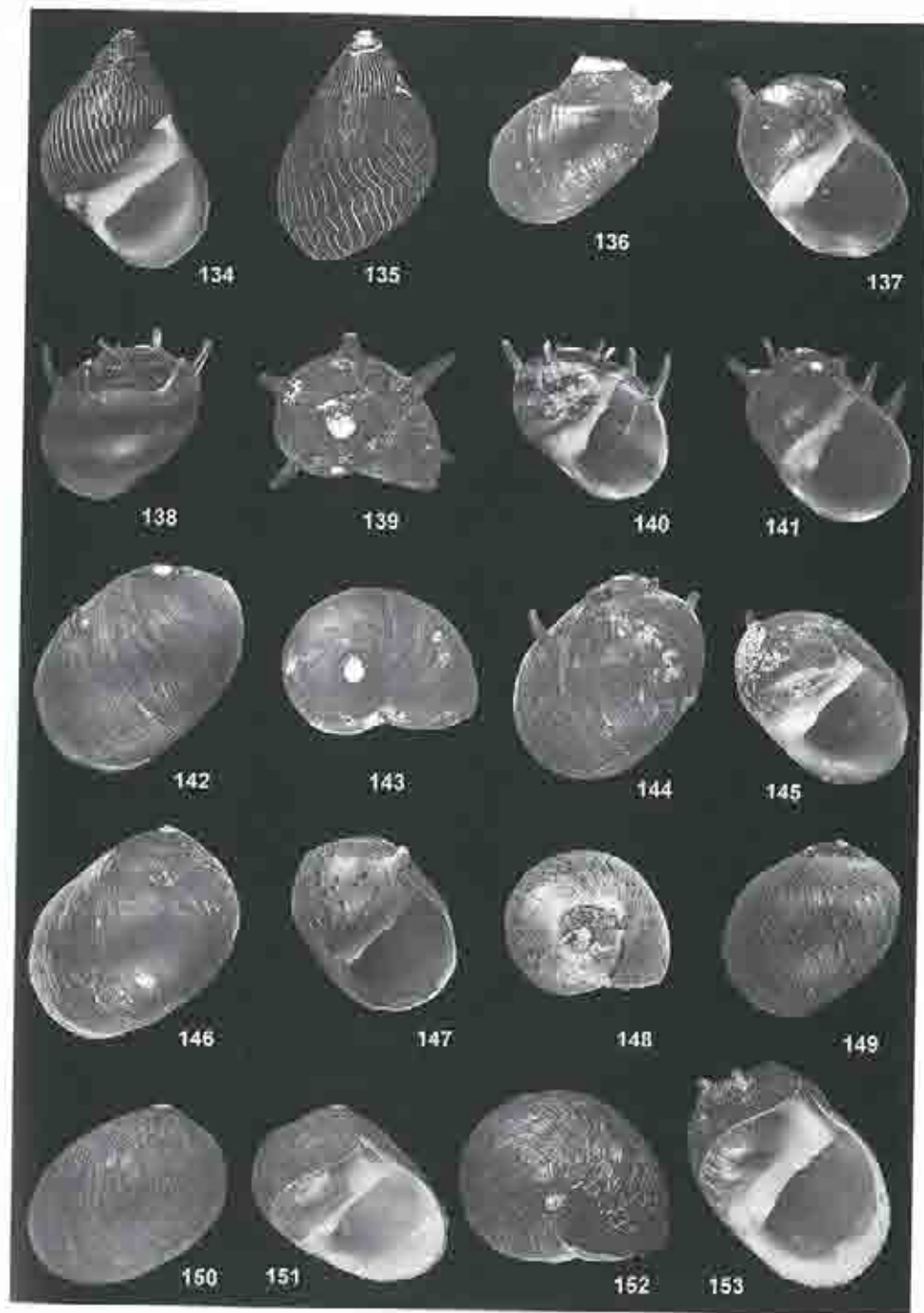
7.b The group of the genotype of *Neritina, N. pulligera,* with rapid whorl growth

According to WENZ (1938) the genus *Neritina* is based on *Nerita pulligera* from the Indo-Pacific. It has an ovate shell with thin outer calcitic layer and smooth surface. Growth of the teleoconch is with rapid increase in shell diameter and ends with less than two whorls. The inner lip of the aperture is smooth or weakly denticulate. The operculum has a long ridge connecting the rib and peg. Among the characteristic species of the *N. pulligera* group the shell consist of only about 1,5 whorls of the teleoconch, is lower than wide, plane along the aperture and the shelf of the inner lip. The snails are, thus, quite well adapted to hold onto hard substrates.

Neritina pulligera (LINNAEUS 1758) from the Umzamba River is found on rocks in the estuary next to its upstream end. The oval, semi-spherical shell with rounded upper side and flattened lower side has only the last whorl of the teleoconch visible covering the protoconch and about one half juvenile teleoconch whorl. The upper edge of the outer lip of the aperture extends over the spire, coating it. But there is usually a pit here where the protoconch and shell near to it has become dissolved. The aperture is wide and ear-shaped. Its inner lip forms a wide shiny shelf that may be tinted with bluish-black, while yellowish orange may form a semicircle around the aperture. There are 6 to 15 fine denticles present in a central concavity of the columellar lip. The ornament of the shell consists of a fine pattern of zigzag or zebra lines of brown and black on greenish or brownish background, better visible on younger specimens than on older ones. The periostracum is black and the pattern comes out with light shining through the shell. The ornament may also be a pattern of triangular patches and it varies from individual to individual and even within different stages of shell growth. The fully-grown shell measures 12 mm in width and 6 mm in height. The operculum has the nucleus on the left-handed base and from it issue brown blackish radiating growth striae. The outside is yellow-brownish and the outer margin in reddish brown and of horny consistency. The rib and a peg on the inner side of the operculum are strongly developed.

Nertina pulligera is found at the end of estuaries in Umzamba and neighbouring rivers. Within its group *N. pulligera* lives most widely distributed in the Indo-Pacific from the African Coast to the Philippines and the tropical Pacific Islands. BROWN (1980, Fig.16 d-f) noted the African occurrence of *N. pulligera* from South Africa to Kenya, and its presence from Madagascar was documented by STARMÜHLNER (1969, Figs.73-77; 1976, Pl.11, Figs.104-110). Here shells may grow to about 22 mm in width and 15 mm in height.

Individuals were collected from a spring forming a lake in the limestone at the coast near Toliara (SW Madagascar) in the year 2000. Here *N. pulligera* lives together with *N. auriculata* and it is very difficult to distinguish the two species, which appear to merge with each other. So there is a total transition between these (see chapter 7.c).

A specimen from the Kawasan River in Cebu collected by BANDEL & RIEDEL (1998) reached a maximum width of almost 30 mm and a height of about 24 mm. Here the operculum has a very distinct ridge and peg. According to HAYNES (2001) *Neritina pulligera* is separated from the rest of the non-winged species of *Neritina* by presenting only the last whorl of the teleoconch in addition to several characters of the male genital system. Its long penis resembles most that found in the *N. auriculata* group. With its long spermatophore it differs from all others.

N. pulligera resembles other Indo-Pacific species such as *Neritina canalis* SOWERBY 1825 and *Neritina petiti* RÉCLUZ 1841 regarding shell shape and penis and sperm morphology. These later two species live from New Guinea to the Polynesian Islands (BENTHEM-JUTTING 1963, STARMÜHLNER 1976, Pl.11, Figs.94-95; 1993, Fig.47). In addition to these two, STARMÜHLNER (1969, 1983) considered to be closely related to *N. pulligera* and to belong in the same evolutionary group also *Neritina asperulata* RÉCLUZ 1855 living from the Philippines everywhere in the tropical Pacific all the way to Samoa, *Neritina porcata* GOULD 1847 and *Neritina squamipicta* (RÉCLUZ 1843) with the same distribution (see chapter 7.h). Including *Neritina pulligera* these species also occur in New Caledonia, where according

to POLLABAUER (1986) *Neritina macgillivrayi* (REEVE 1855) can be included in this group even though its shell has quite a bit flatter shape (RIECH 1937, STARMÜHLNER 1976). STARMÜHLNER (1993) suggested that *Neritina (Neritina) canalis, N. (N.) petiti* and perhaps also *N. (N.) porcata* from Samoa and Tonga in the SW Pacific belong to the relation of what has been determined as *N. pulligera* in many regions of the Indo-Pacific by other authors.

7.c The group of *Neritina auriculata,* with lips of the aperture expanding

The characteristic shell feature of the *N. auriculata* group is the ear-like extensions of the outer lip, which join the plate-like inner lip callus to form a D-shaped basal plate (fig.78). The sub genotype is *N. taitensis* LESSON 1830 from Tahiti, which is perhaps the same as *N. auriculata* according to POINTIER & MARQUET (1990) and STARMÜHLNER (1993), but not according to Hayes (2001) (as *N. tahitiensis*). According to THIELE (1929) the shell of the subgenus *Neritina (Neripteron)* LESSON 1830 has a flattened apertural side and more or less widened outer lips. This subgenus, thus, resembles that of *Neritina* s.s. in general shell shape but has become even more limpet-like by extending both ends of the outer apertural lip. According to HAYNES (2001) *N. auriculata* belongs to the winged branch of the neritinid evolutionary tree and has a very similar species in the Hawaiian *N. vespitina* SOWERBY 1855. Both have a thin operculum, which separates from the Hawaiian *N. cariosa* (see below in 7. m). All three together differ from *N. dilatata* BRODERIP 1832 only regarding the spermatophore shape see 7.m).

In case of *Neritina auriculata* LAMARCK 1816 from Umzamba River estuary (figs.78-79) the shell is of semi-spherical shape with flattened base and rapid increase in shell diameter so that a grown specimen has only little more than one whorl succeeding the usually corroded protoconch. The suture is furrow-like. The outer lip of the aperture ends in two wings, the apical of which is the largest. Among growth stages and also among individuals these wings of the outer lip are quite variable in shape. Ornament consists of greenish-brown spiral lines and delicate spiral granular grooves and ridges crossed by collabral growth lines. The later form hemi-circles in the rounded whorl, which is enlarged only on the front and the sides while the end of the inner lip plate is etched into the shell. Thus, older individuals have a corroded and flattened early whorl where it contacts the inner lip. The aperture is wide, half-moon-shaped with wide inner lip to which the wings of the outer lip are added marginally. The shell is thin on the outer lip, which has a sharp margin. The callus of the inner lip has an orange tinge and some grooves near the central columellar margin. This margin of the inner lip is shallowly concave and has 7 to 20 minute denticles. The shell is up to 24 mm in length and 10 mm in height.

Very similar specimen, also reaching this height and width were encountered in the spring lake of the carst cave Sarodrano south of Toliara in Madagascar. But while some of the fully-grown individuals here have the characteristic wing-like lip (figs.196, 202), others do not form it and resemble *N. pulligera* forming a total transition between both species. In contrast to the suggestion by HAYNES (2001) to place *N. pulligera* closer to the members of the *N. turrita* group, the transitional forms found in this carstic spring in Madagascar indicate that it may actually form hybrids with *N. auriculata* (figs.196-202). Thus, both species are closely related. When the about 150 specimen collected from that spring lake in the limestone at about high tide level are compared with each other transitional morphs bridge relatively typical *N. pulligera* of shell sized up to 19 mm in width and 14 mm in height with winged *N. auriculata* with shell width up to 20 mm and height only reaching 9 mm. Within the typical *N. auriculata* individuals with fully developed wing-like outer lip occur in sizes between less than 10 mm while others reach this shape only after having grown to more than 15 mm in width. In Bali similar sizes were encountered, but growth in *N. auriculata* is more regular than was observed in Madagascar (figs.203-206). In the Matutinao River of Cebu *N. pulligera* grows to much larger size of 30X22 mm (BANDEL & RIEDEL 1998). The early teleoconch of *N. auriculata* as well as *N. pulligera* from Sarodrano spring is commonly covered by a fine spiral ornament, which later disappears. Juveniles may have a felt like periostracum (STARMÜHLNER 1969). These *Neritina* morphs from Sarodrano

spring lake in their extremes represent typical *Neritina auriculata* with wing-like outer lip and typical *N. pulligera* with high shell. Apparently they represent the result of interbreeding of members of both species.

In Cebu and Bali both *N. pulligera* and *N. auriculata* were not observed in transitions. In Bali both species migrate from the uppermost estuarine environment into fresh water springs. They live in pools, creeks or rivers which usually are not be reached by the sea, not even at spring tides. The operculum is of semilunular shape with outer median ridge in its centre. Its columellar side is sinuous, the yellow nucleus lies at the right hand base, and its colour is greyish black with a reddish-yellow outside edge. The peg on the inner side has a rounded top, the rib is sickle shaped and there is a median furrow.

According to RIECH (1937) the shell of *N. auriculata* is quite variable. *N. auriculata* has been described from quite different places in the Indo-Pacific region (BUTOT 1955; STARMÜHLNER 1969, 1970, 1976, Pl.9, Figs.64,65, Pl.10, Figs.76-79, 82-85; POINTIER & MARQUET 1990, Pl.1, Figs.6,7; BANDEL & RIEDEL 1998, Fig.7,k). The last whorl encloses the earlier whorls as in *N. pulligera*, but the aperture margin is distinctly expanded in *N. auriculata*, and increase in whorl width is more rapid. This extended upper columellar area as well as the teleoconch that consist of only one whorls and a wide columellar area according to HAYNES (1988, 2001) characterize the species which closely resembkles *N. vespitina* from Hawai (see 7.m).

According to PÖLLABAUER (1986) *N. auriculata* differs from *N. lecontei* (RÉCLUZ 1853) only in regard to the operculum. *N. dilatata* differs from *N. lecontei* mainly in regard to the number of denticles on the columellar lip (PÖLLABAUER 1986), with 3 instead of 1 large denticles besides smaller ones. *N. taitensis* in New Caledonia lives in the brackish estuary near its mouth and differs extremely little from the others. It is thus quite evident that the four species of the *N. auriculata* relation of New Caledonia are very close to each other (PÖLLABAUER 1986).

In the centre of diversity of the Indopacific *Neritina* that includes places like Fidji Islands and New Caledonia, both species are further differentiated into morphs or closely related species that appear to be largely not interbreeding with each other. So apparently in the centre of diversity the different units of the species group *N. auriculata / N. pulligera* behave like "good" species while on the periphery of their occurrence they hybridize and thus merge with each other. Apparently *N. pulligera* does not occur in French Polynesia (POINTIER & MARQUET 1990) while it is represented in its typical shape in Tonga and Sumoa (STARMÜHLNER 1993, Pl.9, Fig.44).

In case of *Pseudonerita* BAKER 1923 and *Neritodryas* MARTENS 1869 fine spiral ribs ornament the shell (WENZ 1938, Fig.1044, HAYES 2001, p.53)), which distinguishes it from the more usual case

Fig. 154: *Neritina* cf. *corona* (LINNÉ 1758) from the estuarine intertidal region near Lovina Beach, Bali, Indonesia with spine bearing 14 mm wide shell.
Fig. 155: Apical view of *Neritina "Clithon" corona* (LINNÉ 1758) from near Port Moresby, New Guinea with convolutely coiled shell of 20 mm in width with spine bearing shell as in figs.152-153.
Figs. 156-158: *Neritina "Clithon"* with dark background and white arrow-shaped dots from the estuary of Matutinao River on Cebu, Philippines with 14 mm high shell. 156 and 157 of the same shell, and 158 with smaller dots.
Figs. 159-162: *Neritina ("Clithon")* cf. *bicolor* (RÉCLUZ 1843) (morph 7) from a tidal creek of the mangrove at Arcao, Cebu, Philippines with 13 mm high shell. 159 and 162 and 160-161 represent the same shell seen from different sides, with differently sized white dots.
Figs. 163-165: *Neritina ("Clithon")* of morph 2 from the estuarine portion of Matutinao River on Cebu with 7 mm wide and high shell (163-164) and 11 mm high shell (165)
Figs. 166-168: *Neritina ("Clithon")* of the coarsely ribbed type of morph 3 with 15 mm high shell and spines from the estuarine portion of Matutinao River, Cebu.
Figs. 169-172: *Neritina ("Clithon")* of morph 3 from the purely freshwater middle part of Matutinao River of spine bearing shells with a black subsutural ribbon and 12 mm high shell.
Fig. 173-175: *Neritina ("Clithon")* of morph 3 from Matutinao River above the estuary with 16 mm high shell
Figs. 176-177: *Neritina ("Clithon")* of morph 1 from the upper Matutinao River and 15 mm high shell (similar to 178-180).
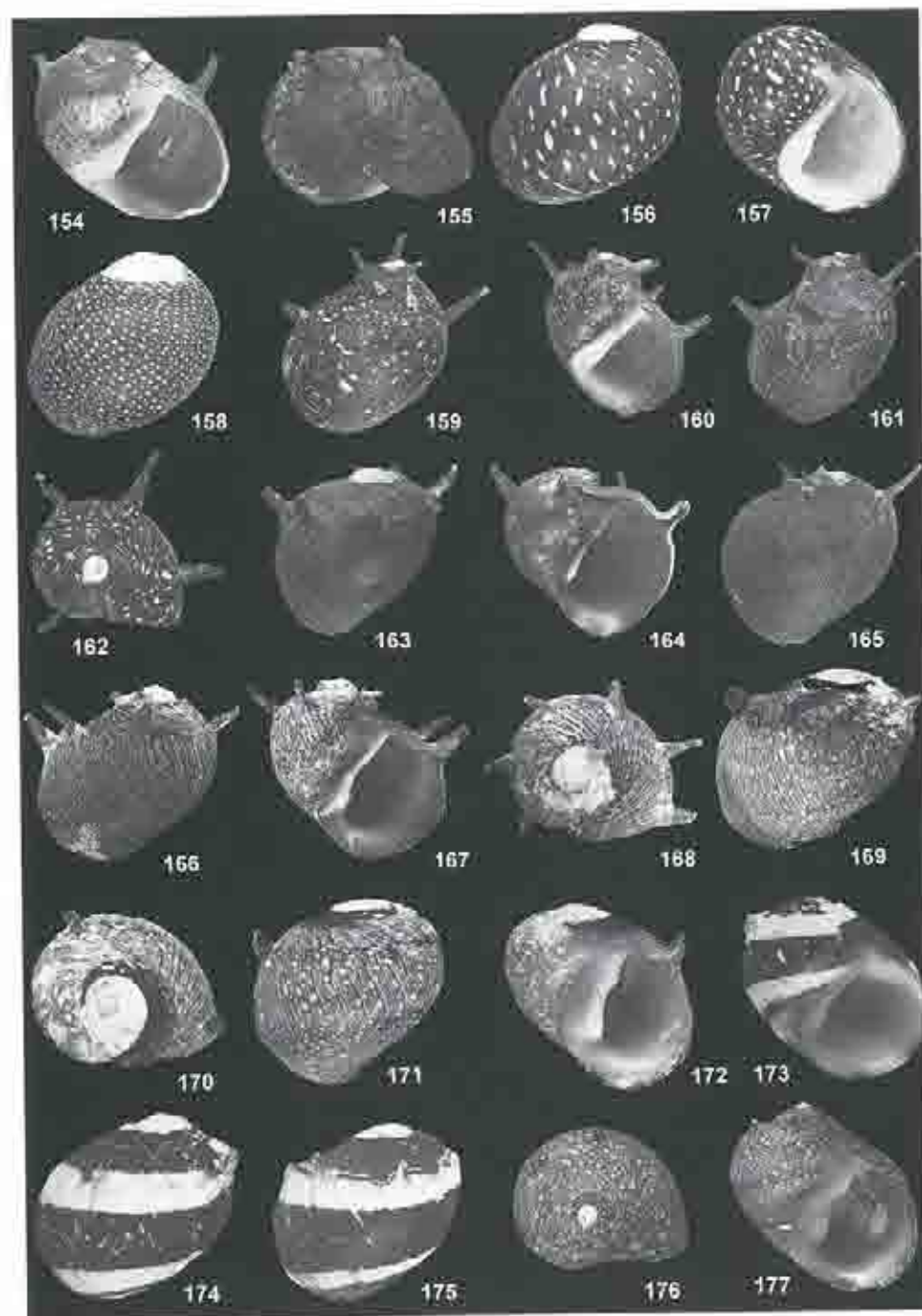
in *Neritina* where the shell is smooth. But juveniles of *N. pulligera* commonly have also fine spiral ornament. *Pseudonerita holoserica* GARRETT 1872 from Viti Island has ovoid nertinid shape with rapid increase in shell diameter and 1,5 teleoconch whorls. Its ornament is of spiral striae in tight arrangement, actually representing rounded spiral ribs separated by narrow deep furrows. The inner lip is slightly concave and delicately serrated with 7 to 9 to 12 equal low denticles continuous in the internal side of the edge as ridges. The outer lip has no denticles within and is thick and smooth. The inner lip callus is thick and smooth. *Pseudonerita obtusa* (REEVE 1856) from the Philippines may represent a similar species, and BANDEL & RIEDEL (1998, Fig.4) noted a *Neritina* sp. of similar shape from Matutinao River in Cebu, but smooth shell surface (Figs.248, 253).

The genus *Neritodryas* MARTENS 1869 according to THIELE (1929) is also considered separated from the genus *Neritina*. Besides *Neritodryas cornea* (LINNÉ 1758) there are a few species that live above water in coastal forests of the Indo-Pacific. In case of *Neritodryas subsulcata* (SOWERBY 1836) the semi-spherical shell is a bit wider than high and has an ornament of spiral ridges separated by narrow spiral grooves crossed by fine growth lines. Colouration is dark olive to dark brown to black. The inclined aperture has a white columellar callus with finely denticulate inner lip. (STARMÜHLNER 1976, Pl. 9, Figs. 62,63, HAYNES 2001). The radula of *Neritodryas subsulcata* as shown by STARMÜHLNER (1976) resembles that of *N. cornea* described by BAKER (1923) and RIECH (1937). The species occurs from the Nicobares across the Indonesian and Philippine Islands to the tropical Pacific Islands and is characterized as fresh water species. POLLABAUER (1986) reported one species of *Neritodryas chimmoi* (REEVE 1856) from New Caledonia living about to up 500 m upstream in rivers and creeks. The species of both these ornamented genera *Pseudonerita* and *Neritodryas* need to be studied in more detail before their relation with *Neritina* can be interpreted.

7.d The group of the genotype to *Neritina* suggested by COSSMANN (1925), *N. zigzag*.

In pure populations of many individuals *Neritina communis* (QUOY & GAIMARD 1832) is found in the Velar estuary in Tamil Nadu, southern India (figs.90-95). Here the spire of the shell is rounded and coiling is quite convolute but with the whorls remaining visible. There are about 3 whorls of the teleoconch, and the shell is about 8 x 8 mm when fully grown. Very similar individuals are found in the mangrove environment of Cebu (see chapter 7.g). In the last half whorl relative shell height increases, but it remains more of rounded shape than is seen in *N. oualaniensis* with more elevated spire.

Neritina oualaniensis (LESSON 1831) on Rarotonga Island (Cook Islands, Polynesia) (figs.185-189) lives on the intertidal pebble beach in such places where fresh water springs form pools and little creeks. During low tide they move within the fresh water puddles, and they also place their spawn here to the underside of rocks. During high tide the normal seawater covers them. The shell consists of the typical protoconch with several strongly convolute whorls and more than 2,5 but less than 3 whorls of the teleoconch. The size reached is about 10 mm in height and almost 9 mm in width, and the whorls of the teleoconch. The size reached is about 10 mm in height and almost 9 mm in width, and the apex appears pointed with all whorls well visible. Colouration is dark with zigzag patterns and light triangles. The inner lip is similar as seen in a population collected at the mouth of Matutinao River in Cebu (BANDEL & RIEDEL 1998, Fig.7,L,N,M). Here the shell is about 5 mm wide and 5 mm high and consists of 3 whorls of the teleoconch succeeding the protoconch. A very similar species, perhaps the same, was determined as *Neritina canalis* SOWERBY 1825 by POINTIER & MARQUET (1990, Pl.1, Figs.3-5) from French Polynesia. But in difference it is characterized as living in the upper part of rivers, which does not agree with the ecology of *N. oualaniensis* from Rarotonga. More like the species from Rarotonga is *Clithon faba* (SOWERBY 1836) as it occurs in Taiwan and lives in the estuarine region (KOMATSU 1986, Fig.3).

The spire is much lower and the columellar margin usually more dented than in a little *Neritina* from Bali that is here called *N. cf. roissyana* (WENZ 1938, Fig.1050). In small freshwater puddles within the gravel beach of northern Bali (Indonesia) *N. cf. roissyana* with pointed spire and *Littorina-*

like shape is found together with forms just like *N. oualaniensis* as found in Cebu. But while the later population consists of individuals with the same shell shape and, thus, is pure, in Bali a total transition between these two species is developed.

N. oualaniensis has been placed in the genus *Clithon* MONTFORT 1810 (WENZ 1938), and here the subgenus *Clithon (Pictoneritina)* BAKER 1923. *Neritina roissyana* in contrast was placed within the genus *Neritina*, and here the subgenus *N. (Vittina)* BAKER 1923. If both species form hybrids, as appears to be the case in Bali (see chapter 7.h), than they cannot be placed very far from each other taxonomically as was suggested by BAKER (1923), but they have to be at least members of the same subgenus. ABBOTT & DANCE (1982) even preferred the genus *Theodoxus* in describing *Neritina oualaniensis*, which makes confusion complete. *Neritina roissyana* as illustrated by STARMÜHLNER (1993, Pl.9, Fig.46) is not the same species as that determined as *N. cf. roissyana* from Bali, but probably the same that has been determined as *N. turrita* here (see chapter 7.e), following the good illustration of *N. turrita* as presented by ABBOTT & DANCE (1982).

Neritina communis from the Indian Velar estuary closely resembles in shape *Neritina luteofasciatus* (MILLER 1879) from the Gulf of California, which is here considered to be related to the *Neritina virginea* group (see chapter 7.j).

7.e The group of *Neritina gagates,* with rounded to long oval shell and several whorls

Neritina gagates LAMARCK 1822 is a common gastropod in the transition from seawater to fresh water in the South African Umzamba River Region (figs.67-71) as well as on the northwestern coast of Madagascar. The about 3 cm high and 2.6 mm wide shell is of dark appearance with blackish-brown periostracum that overlies a fine pattern of dark zigzag bands on a yellowish brown ground colour. The solid shell with globular spire shows 2.5 whorls succeeding the larval shell and whorls are rapidly increasing in diameter. The last whorl makes up four fifth of the total height and is slightly shouldered. The aperture is yellowish green to white bluish on the inner side of the outer lip and at the border to the columellar area the callus is yellow to orange with an orange spot near the base. The columellar lip bears few to about 15 denticles. The operculum is semilunular with polished external surface and fine fan-like growth striae. The nucleus has a yellow spot and the remaining outside is dark brownish, black with a reddish brown outer horny edge. The inner surface of the operculum is shiny callus and has a broad short double peg with rounded thickened top. The median rib is a slightly curved ridge (fig.67).

N. gagates has been described by REEVE (1855), MARTENS (1879), TRYON (1888), STARMÜHLNER (1969,1983), and BROWN (1980), and its radula by BAKER (1923) and STARMÜHLNER (1983, Fig.10). Its shell is much higher and has more whorls of the teleoconch as are present in *N. pulligera* and *N. auriculata* that live together with *N. gagates* in the Mnyameni and Umzamba estuaries of South Africa.

In *Neritina turrita* (GMELIN 1790) the early whorls remain well visible when the shell grows due to its more elongate shape. The fully grown shell consists of about 4 whorls in addition to the protoconch (figs.130-135). The last whorls occupy two thirds of shell height. Colouration consists of inclined black lines that lie on yellow greenish background creating a zebra pattern (ABBOTT & DANCE 1982). Specimen from Lovina Beach on the northern shore of Bali and from the estuary in the mangroves of southern Bali may reach a size of 3 cm in height and 2,5 cm in width. Animals transferred into the aquarium in Hamburg lived here for several years in brackish water and continued to produce egg capsules. The operculum of *N. turrita* is equipped with a strong ridge with the peg projecting to form another ridge or a strong knob. Among different individuals this peg forms a knob or a ridge, demonstrating the variability present here.

N. turrita lives from India to New Caledonia and throughout the tropical Pacific Islands, and according to STARMÜHLNER (1976, Pl.9, Figs.66-70) varieties in ornament and shell shape resulted in a splitting into several species. According to POLLABAUER (1986) *N. turrita* closely resembles *N. roissyana* (RÉCLUZ 1841) with egg-shaped shell that shows an ornamental pattern of zigzag lines and has all its whorls well exposed (if not corroded). *N. roissyana* according to STARMÜHLNER (1993, Fig.46) lives from the coasts of Australia to the south Pacific Islands to New Caledonia (see chapter 7.h). It is similar to *Neritina turtoni* (RÉCLUZ 1843) (STARMÜHLNER 1976, Pl.9, Figs. 71,72) from Fiji. According to HAYNES (2001) *N. turrita* is also very close to *Neritina variegata* (LESSON 1830) differing from the later by having a slight spire. But *N. turrita* can be distinguishes from *N. variegata* by its much higher shell with more pointed spire (figs.130-135), and the *N. turrita* from Fiji illustrated by HAYNES (2001, p.39) is here considered to represent a *N.* cf. *variegata*.

From French Polynesia POINTIER & MARQUET (1990, Pl.1, Figs.1,2) drescribed such a short form of *Neritina turrita*. It is quite the same species that is here called *N. variegata* (figs.126-129), and it is living in the high tide region of the estuary as is also similar to that seen in Bali (see chapter 7.h).

While *N. variegata* supposedly represents the subgenus *N. (Vittoidea)* BAKER 1923 its apparent relative *N. turrita* is close in shape to *N. roissyana*. The later according to WENZ (1938) represents the type to the subgenus *N. (Vittina)* BAKER 1923. But this subgeneric distinction is misleading as is supported by the transitions observed to occur between *N. turrita* and *N. variegata* in Bali (see chapter 7.h). RIECH (1937) noted transitions from *N. turrita* to *N. communis* (QUOY & GAIMARD) (= *N. waigiensis* (LESSON)) and *N. ziczac* (SOWERBY) (= *N. coromandeliana* SOWERBY). But in this case it needs to be confirmed whether *N. communis* of the determination offered by RIECH is the *N. communis* that has been recognized from the Velar estuary in India.

STARMÜHLNER (1976, Pl.9, Figs.3-75; 1993, Figs.45, 65) characterized *Neritina variegata* as having fine spiral micro-sculpture on the smooth shell that has very variable colour patterns. These may commonly be zigzag-like and in general the colour is dark brown to black. About three whorls (2,5 according to POLLABAUER 1986) are visible on the fully-grown shell. *N. variegata* occurs from the eastern Gulf of Bengales (Nicobares) to the Philippines, New Caledonia, to the Pacific Islands as far as Tahiti (STARMÜHLNER 1992, 1993).

N. variegata from Bali reaches a size of 2,2 cm in width and height when fully grown with more than three whorls succeeding the protoconch (figs.226-228). The colouration is from course zebra pattern to fine zebra or zigzag-lines to dotted black or total black, grading in that regard into forms resembling *N. gagates* on one side (dark) (figs.68-71) and *N. turrita* (zebra pattern) (figs.130.135). Regarding the living environment on Bali *N. variegata* and *N. turrita* prefer the uppermost tidal zone and here move much above water (see chapter 7.h). HAYNES (pers. com.) suggested to connect the species of the *N. turrita*, *N. variegata* group from the Indopacific to the similar Caribbean group around the species *Neritina virginea* and *Neritina punctulata*. She found that the last two have a simple penis, while that of the other three (*N. variegata*, *N. turrita* and *N. gagates*) may be folded. *N. turrita* and *N. variegata* jointly are said to differ from *N. gagates* by having a differently shaped spermatophore.

7.f Spiny shells of *Clithon* and difference to *Neritina*

COSSMANN (1925) distinguished species of the genus *Clithon* MONTFORT 1810 from *Neritina*, *Neripteron* and *Theodoxus* by having spines. He suggested that *Neritina brevispina* LAMARCK = *N.*

Figs. 178-180: *Neritina ("Clithon")* of morph 1 from the upper Matutinao River with 15 mm high shell.
Figs. 181-184: *Neritina ("Clithon")* of morph 2 from the upper Matutinao River with coarsely ribbed greenish variety and 18 mm high shell.
Figs. 185-189: *Neritina* cf. *oualaniensis* with 9 mm high shell from fresh water puddles in the beach of Rarotonga, Cook Island.
Figs. 190-193: *Neritina* cf. *porcata* from Matutinao River with 12 mm high shell.
Figs. 194-195: *Neritina vespitina* SOWERBY 1849 with 15 mm wide shell from Hawaii.
Figs. 196: *Neritina auriculata* from the carstic spring Sarodrano south of Toliara (Madagascar) with 20 mm wide shell in apertural view with widely expanded wings of the inner lip.
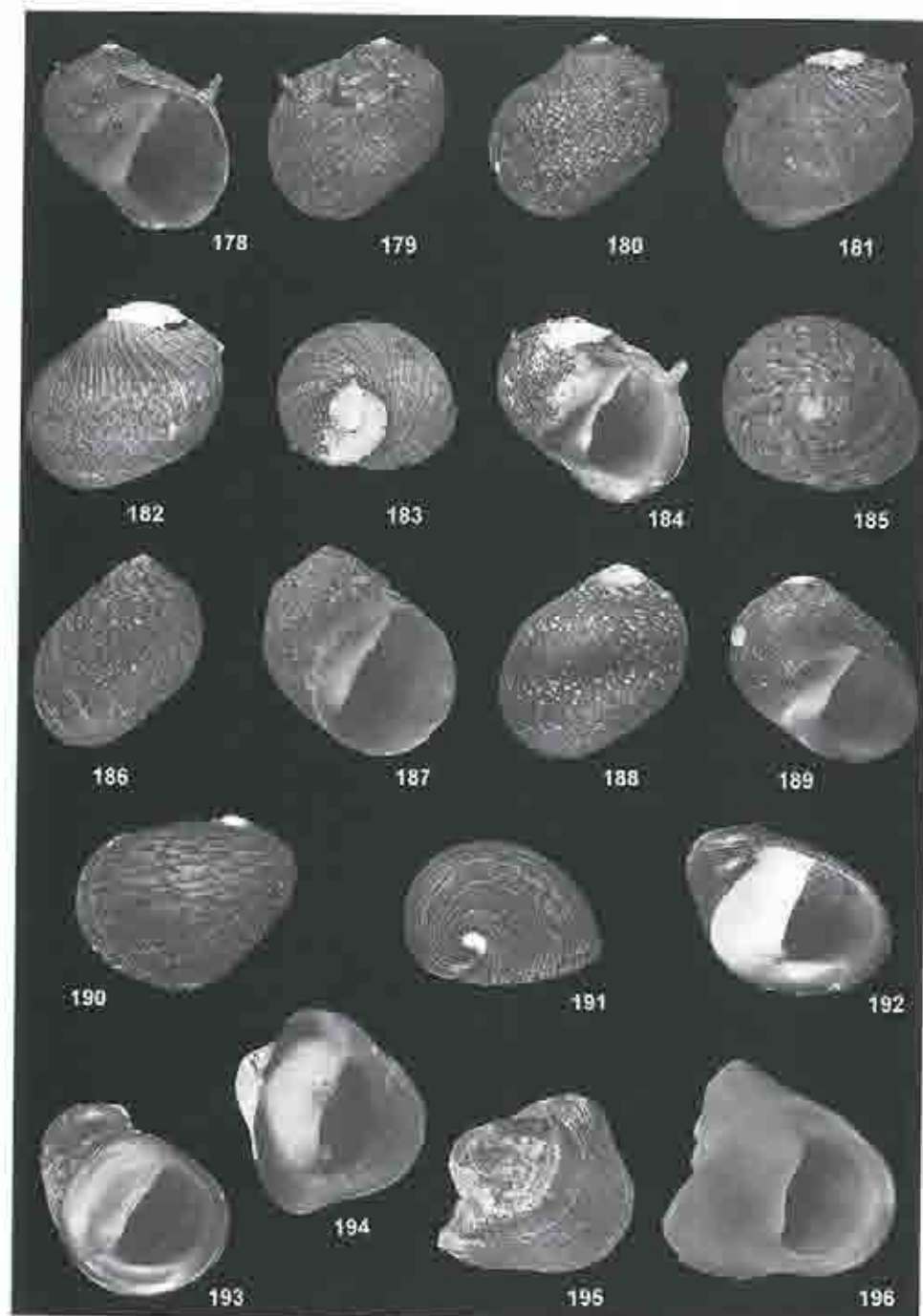
corona LINNÉ 1758 should be a characteristic species of the genus. It has been noted that actually a total transition from spine-bearing *Clithon* to smooth *Neritina* can be recognized (see chapters 7.g; 7.h). Within this taxon there are species, which have individuals with spines and such without spines. THIELE (1929) considered *Clithon* to represent a subgenus of *Theodoxus* following suggestions of BAKER (1923).

The type species of the genus is *Nerita corona* LINNAEUS 1758 from Asian rivers. The more characteristic species of *Clithon* form spines, which in the case of *C. corona* are produced by all individuals of the transition zone from marine to fresh water environment while individuals in pure fresh water may produce no spines (BANDEL & RIEDEL 1998). *Clithon corona* lives only in such creeks that can be reached from the sea (STARMÜHLNER 1984), but this species has been interpreted to not cross the Indian Ocean and being found only in its eastern portion. According to BROWN (1980) members of the genus *Clithon* have not, until now, been reported from Africa, but only in Madagascar. This observation is changed here by specimen found in the eatuary of the Umzamba River and Mnyameni River in the south of the coast of Natal in South Africa.

Neritina "Clithon" cornonata (LEACH 1815)

Description: The shell is globular, solid and has a small spire with 2,5 whorls that succeed the protoconch (figs.72-77). The largest individual encountered is 18 mm high and 19 mm wide. The last whorl is slightly to strongly shouldered and may, or may not, have two to four hollow spines. Coarse growth lines may form sinuous grooves seen as wrinkles on the upper whorl flank and as simple straight growth striae and the lower whorl and base. They are crossed by very fine spiral striae. The ornament has an olive green background with light green and mottled bands on it. The aperture is oblique, broad semilunular. The callus is white with a bluish or greenish tinge. The columellar area carries one broad prominent denticle on the upper third and sometimes another one in the lower part and 3-6 smaller denticles in a concavity between them and sometimes some denticles (0-5) above them too in a lesser concavity. The operculum has a shallow groove over the exterior surface and a corresponding low ridge on the backside ending in the hinge teeth (fig.74). The granulose outside has a dark brown nucleus and yellowish pink colour. The interior surface is yellow with dark brown margin.

Neritina coronata differs from the other neritinids from South Africa by having a corner and/or spines on the upper flank of its whorls. *N. coronata* lives only in the Madagascan sub region (STARMÜHLNER 1983) with *Clithon longispina* (RÈCLUZ, 1841) representing a synonym. It is practically impossible to distinguish *N. coronata* from some of the varieties formed by *Neritina "Clithon"* in the Indosnesian and Philippinian regions (see below).

7.g Transitions observed among species of *Neritina* and *N. "Clithon"* in Cebu

In the mangroves near Arcao and in Matutinao River at Cebu (Philippines) seven species could be determined. All these have transitional forms between each other, but they also occur in pure or almost pure populations which consists of numerous individuals. The fauna of Matutinao River from the begin of the estuary to its springs from limestone was described by BANDEL & RIEDEL (1998). Neritimorph gastropods occur from the mouth of the rivers estuary in the beach to about 1,5 km upstream. Here different morphs of *Clithon* cf. *corona* in addition to four species of *Neritina* (*N. oualaniensis* in the river mouth, *N. pulligera* in the fresh water portion of the river, the uncommon *N.* cf. *porcata* upriver (figs.248, 253), and *N. dilatata* as cf. *auriculata* from the estuary), three species of *Septaria*, and one species of *Neritilia* were encountered by BANDEL & RIEDEL (1998). Of the *C.* cf. *corona* group two additional morphs are found in mangroves on the Island of Cebu, especially noted near the town of Arcao.

In a reevaluation within the *Clithon* cf. *corona* group quite different morphs of roundish shape can be distinguished which could be placed into different species of *Neritina "Clithon"* but within the river merge into each other. Going downriver an area of boulders, which compose the substrate of the river below the effluence of a power plant has many individuals of two varieties (figs.176-184). They live on the rocks for about 400 meters downstream. Here boulders create a series of short waterfalls, cascades and pools and thus a diverse pattern of currents. One morph of *N. "Clithon"* has reddish colouration, the other is usually greenish-olive. Both have shells reaching a size of 22 mm in height and width and they consist of more than 4 whorls. In the reddish variety many individuals have obviously carried out their whole ontogeny in these river surroundings by some still a little mysterious larval development within a thicket of algal or bacterial growth on rocks (figs.254-256). This has been observed by HAYNES (written communication) and confirmed by BANDEL & RIEDEL (1998). In their living environment several hundred egg capsules found in this uppermost occurrence of *Neritina* and *Septaria* in the river were opened by BANDEL & RIEDEL (1998), and they encountered only developments towards small veliger larvae of which 100 to 300 leave one capsule when hatching.

Among the specimen of the reddish morph (*N. "Clithon"* sp.1) of which about 50 were collected and analysed some were juveniles and had grown to the size of only 2 to 2,5 whorls of the teleoconch. These whorls are angular and from the early ones to the last whorl they continue to construct with this shape until they are fully grown which is with about 4 whorls of the teleoconch. Growth pattern is usually connected to strong growth increments and the surface is usually granulated, with the colour pattern reflected in granulation (figs.182, 184). This pattern commonly consists of fine axial lines which zigzag and form small triangles with their point toward the aperture. Triangles are commonly raised above the surface. Consulting the study of POLLABAUER (1986) that deals with species from New Caledonia, the description of *Clithon pritchardi* (DOHRN 1861) would fit here. Especially the triangular dots raised from the surface of the whorls to form pustules appear characteristic. Such morphs are very rarely found in the lower portions of theMatutinao river and in its estuarine region (figs.166-167).

The olive-green modification (*N. "Clithon"* sp. 2) of this upper river fauna has a similar colour pattern consisting of fine triangles, mostly raised to form pustules. But in this morph no juvenile shells have been encountered and 5 individuals were found to have a dark subsutural ribbon, as is characteristic for those individuals that have migrated upriver (see below). Most shells carry somewhat irregular spines on their more or less prominent shoulder (figs.176-181).

In the Matutinao River the upper population of *N. "Clithon"* is separated from an about 500 m long lower course of the river above the estuary by a sandy bend with few individuals. This represents a dividing zone and the fauna below it consists mainly of more or less fully-grown individuals. Here about 120 specimen collected and analysed fall into two morphs. Most are spinous, and they have coarse growth increments commonly forming irregular axial ridges. The olive-grey varieties among them do not differ much from the same colour form (*N. "Clithon"* sp. 2) further upriver. But the other morph (*N. "Clithon"* sp. 3) is characterized by white and black broad spiral colour ribbons (figs.168-175). Their size range is from 10 to 22 mm in width and height and all have rather rugged growth increments. According to the descriptions of POLLABAUER (1986) they could be placed with *Clithon nucleus* (MORELET 1856). POINTIER & MARQUET (1990, Pl.2, Fig.4) placed similarly coloured individuals from Tahiti with *Clithon spinosus* (SOWERBY 1845).

In the estuarine portion of the Matutinao River that extends about 500 m upriver from the seashore the greatest variety within this species is observed in addition to all growth stages. Very young individuals can best be found on rocks in the uppermost estuary. They settle with an almost globular larval shell that surrounds the embryonic shell to a large extend. It measures 0,4 to 0,45 mm in diameter and has about 30 very delicate axial ridges on the final half of the last whorl. The protoconch consists of at least 2,5 convolute whorls (figs.246, 250, 259). In most cases the ontogeny of the teleoconch is characterized by three changes in growth (allometry). The first whorl succeeding the larval shell is rounded and increases the shell to about 1,5 mm in width and height. At beginning there is a small umbilicus, which becomes closed as the callus of the flattened inner lip forms fig.244).

Colouration is of fine axial lines. At the second whorl of the teleoconch the evenly rounded whorl side changes into one with a rounded corner and a less well rounded apical side. All individuals of about 4 mm size have that corner of the whorl. After about 1.5 whorls have formed, the first spine may be formed (fig.243). It is a rounded gutter open to the front when it lies in the aperture. When it moves back it becomes a closed hollow spine with frontal suture. Its base is evenly coated over by shell deposits so there remains no trace of it seen from the inside of the shell. The second teleoconch whorl may have no spine or up to 6 of them and the corner is prominently developed. With formation of the third whorl in most cases of the more than 300 individuals studied the shoulder is eliminated and whorls are rounded again. The shell size is about 5 mm in width and height. The columellar lip of the aperture is characteristically dented with one larger denticle in the apical portion and 4-5 smaller ones below that.

There are two morphs in the estuarine portion both of which are very common and usually quite distinct from each other by colouration. Both grow to about 15 mm in width and height and consist of a little more than 4 whorls of the teleoconch. Usually there are no spines and all former spines have been dissolved by the successive whorls, which overlap the shoulder of former whorls. One variety (N. "Clithon" sp.4) has a subsutural dark ribbon of variable thickness and consistence of more or less densely arranges axial stripes (figs.108-115). Below it a light colour band is present, which may be almost uniformly yellowish or may be covered by fine or coarse zigzag or arrow patterns. Below it there is usually another dark spiral band, and a light band occupies the base. The callus of the inner lip has not changed much, but its columellar edge may have small denticles also above the larger denticle. Variability is high, and colour ranges from yellow to yellowish-brown to grey and reddish. The colour ribbons do not appear before the third whorl of the teleoconch

The other morph (N. "Clithon" sp.5) with similar shell shape is uniformly olive-grey to brownish-black with fine mottled pattern below, usually consisting of arrows in axial lines (figs.163-165). While the first morph with the subsutural ribbon appears to be not found in New Caledonia, the second could be placed with Clithon olivaceus (RECLUZ 1842) as described by POLLABAUER (1986).

In addition to these two dominant morphs the estuarine portion of Matutimo River has colour morphs that are black with white, or yellow dots of triangular shape (figs.156-158). Other morphs have not carried out the change from spine bearing to non-spine bearing whorls and still have the

Figs. 197-198: *Neritina pulligera* with 20 mm wide shell from the carstic spring Sarodrano south of Toliara (Madagascar) with 20 mm wide shell, seen from the side (197) and with expanded base (198).
Figs. 199-202: *Neritina auriculata* from the carstic spring Sarodrano south of Toliara (Madagascar) with 12 mm wide shell seen from the side (199) and from the base (200), and the same in the second individual (201-202).
Figs. 203-206: *Neritina auriculata* from spring lake of northern Bali with 26 mm wide shell, the teleoconch is only one whorl (203), with two unequal wings (204, 206), and concave callus of the inner lip (206).
Fig. 207: *Nerita fulgurans* GMELIN 1791 with 18 mm high shell from the shore of Santa Marta, Colombia, Caribbean Sea.
Fig. 208: *Neritina violacea* (GMELIN 1791) with 20 mm wide shell from the mangrove of the Velar estuary in Tamnil Nadu, southern India.
Fig. 209: *Nerita squamulata* with 23 mm high shell from the shore of Cebu, Philippines.
Figs. 210: *Nerita versicolor* GMELIN 1791 with 25 mm high shell from the shore of Curacao, Caribbean Sea.
Fig. 211: *Nerita undata* LINNÉ 1758 with 24 mm high shell from the shore of Port Sudan, Red Sea.
Fig. 212: *Nerita tessellata* GMELIN 1791 with 20 mm high shell from Curacao, Caribbean Sea.
Fig. 213: *Nerita peloronta* LINNÉ 1758 with 22 mm high shell from the shore of Curacao, Caribbean Sea.
Fig. 214: *Nerita plicata* LINNÉ 1758 with 22 mm high shell from the shore at Bali, Indonesia.
Fig. 215: *Nerita albicilla* LINNÉ 1758 (cf. *textilis*) with 20 mm wide shell from the shore of Cebu, Philippines.
Fig. 216: *Nerita atramentosa* REEVE 1855 with 20 mm high shell from mangrove roots at the edge of the sea at Sydney, East Australia.
Fig. 217: *Nerita planospira* ANTON 1839 with 18 mm high shell from the shore of Aqaba, Red Sea.
Fig. 218: *Nerita undata* with 26 mm high shell from the shore of Port Sudan, Red Sea.

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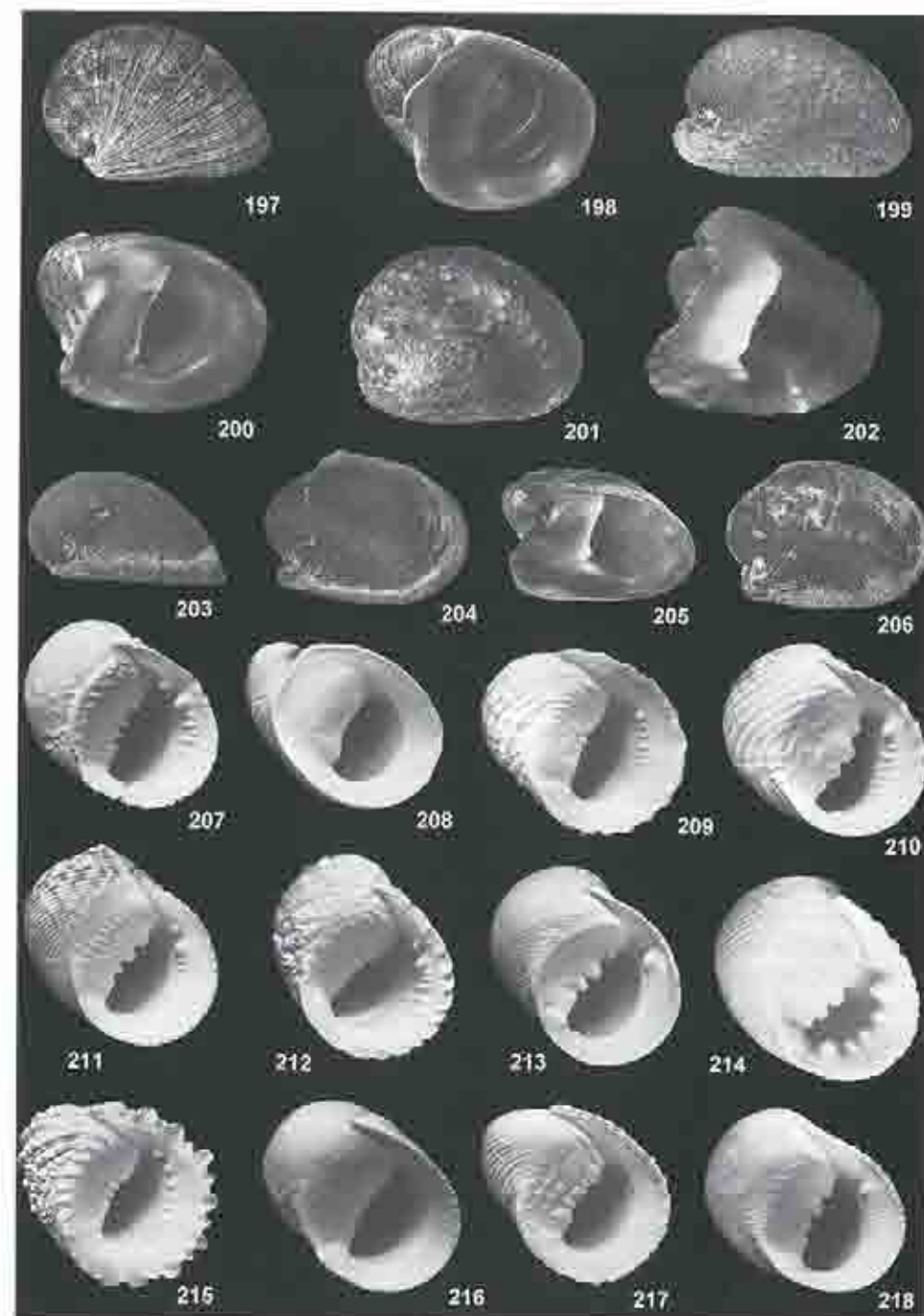
corner and spines in the fourth whorl of their teleoconch. These are rare, however, of the colour varieties dark-olive and reddish mottled, but usually with smooth shell. Those with slightly tuberculate shell and strong growth ridges also occur (figs.166-167), similar as is described in case of individuals from Tonga and Samoa by STARMÜHLNER (1993, figs.40,41) and determined as *Clithon corona*.

The Matutinao morph with subsutural dark colour band clearly grades into a species (*N. "Clithon"* sp.6) that lives in the mangrove flats of Cebu and was collected in larger number (more than 100 individuals) near Arcao (figs.116-121). It could be placed in the species *Neritina communis* as illustrated by ABBOTT & DANCE (1982) and consists of 3 whorls of its teleoconch when 7 mm high and wide. Here shell growth has no allometric interruptions and proceeds from the protoconch onwards with regular growth and evenly rounded whorls as well as with variable but similar colour pattern of fine axial lines and pointed arrow and sometimes spiral ribbons. The operculum is formed just like that of the Matutinao river *N. "Clithon"* varieties (*N. "Clithon"* sp. 1-5).

The colour morph with white dots on black surface resembles a species that could be named *C. bicolor* (RÉCLUZ 1843) according to the description given by POLLABAUER (1986), and *Clithon diadema* (BRODERIP, 1832) as shown by HAYNES (2001) from Fiji. A very similar individual included within (*N. Clithon spinosus* was illustrated by POINTIER & MARQUET (1990, Pl.2, Fig.6) from Tahiti. This form (*N. "Clithon"* sp.7) lives in large numbers and almost all individuals (about 100 were collected and analysed) of similar shape and colouration at tidal creeks connecting the sea with a small mangrove at Arcao (figs.169-162). After the first whorl of the teleoconch all dark colour patterns fuse forming a black background colour in which white or yellow triangular dots are included. On the second teleoconch whorl spines appear, and there may be up to 8 spines on one whorl. These are very long and delicate and they continue to be present up to the last whorl of the maximally 16 mm wide and 14 mm high shells with about 3 whorls of the teleoconch (figs.136-141). Their colour pattern is quite like that seen in some morphs of a non-spinous form in the estuary of the Matutinao River, but coiling differs. This species usually grows in such a way that spines of the former whorls are not resorbed. Thus, the spire is more exposed, and all spinous whorls are preserved. While most individuals have this spinous form, a smooth surface and black colour with light arrow dots, there are a few individuals with lower spire and spines of the early whorls resorbed and others with colour pattern of fine grey zigzag lines and some with granular surface pattern.

In all the seven discussed forms, that could be placed into different species and occur in rather large populations of similar morphs, the operculum is basically the same, even though there may be some variation in the cow horn like internal ridge. These variations are not connected to the different shell forms, but to growth stages and regard the thickness of the two projections.

If species should be distinguished, these could be characterized as:

1. Reddish mottled with triangular granulation and teleoconch cornered throughout (upper Matutinao River) (figs.178-180).

2. Greenish and greyish mottled, teleoconch cornered throughout, smooth shell and spiny (upper to lower Matutinao River) (figs.181-184).

3. Spiny angular shell with coarse growth increments and spiral dark and white colour ribbons (lower river Matutinao above estuary) (figs.169-175).

4. Shell with subsutural dark ribbon and corner in the early teleoconch and here also spines while later teleoconch is smooth and rounded (estuarine Matutinao River)(figs.108-115).

5. Shell like 6 but olive dark coloration. (estuarine Matutinao River) (figs.163-165).

6. Shell rounded and evenly curving without spines (mangrove flats Arcao) (figs.116-121).

7. Spiny angular shell with black with light arrows as coloration and all spiny whorls preserved (from intertidal creek in Arcao) (figs.159-162).

From a similar environment of short rivers in New Caledonia POLLABAUER (1986) distinguished 6 different forms, 5 of these as belonging to the species *C. corona*, *C. nucleolus* MORELET 1856, *C. pritchardi* (DOHRN 1861), *C. bicolor* (RÉCLUZ 1843), and *C. olicaceus* (RÉCLUZ 1842). Among the *Clithon* species of the Pacific Islands from New Guinea to Tahiti STARMÜHLNER (1976) described the 7

different species, *C. corona*, *C. diadema* (RÉCLUZ 1841), *C. olivaceus*, *C. squarrosa* (RÉCLUZ 1842), *C. rarispina*, (MOUSSON 1848), *C. spinosus* (SOWERBY 1845), *C. chlorostomus* BRODERIP 1832. Four species of *Clithon* were recognized by STARMÜHLNER (1993) from the Tonga and Samoa Islands, while according to POINTIER & MARQUET (1990) only *Clithon spinosus* occurs in French Polynesia.

In the eastern portion of the Indo-Pacific Ocean from Indonesia increasingly so towards the Oceanic Islands like Fiji and New Caledonia *Neritina "Clithon"* appears to become more confusing and split into many species with very similar shell, which are difficult to distinguish. These species of *Neritina "Clithon"* appear to be rather close to each other and they are difficult to differentiate by conchological means. They also have rather similar radulae and are similarly constructed regarding male and female genital systems and spermatophore shape (HAYNES 2001). When the general shell shape is taken into consideration among the spiny *Clithons C. corona*, *C. coronata* have about 4 whorls of the teleoconch. A *C. spinosus* from Museum material in London has only 1,5 teleoconch whorls and therefore belongs to different group. Here observations on the fauna of Bali may be included, where transition to species with more rapid shell increase and thus a wider shell occurs (see below).

7.h *Neritina "Clithon"* and *N. turrita* transitions in Balinese estuaries

When little rivers and creeks in Bali are entering the sea they demonstrate a neritininid fauna in which quite a number of different species or races of *Neritina-Clithon* are encountered that appear to merge with each other locally. In front of a small river just to the west of the village Sangsit near Singaraja a population is encountered consisting of a small sized littoriniform species that could be called *Neritina* cf. *roissyana* (*Neritina* 1) (fig.229) (This species does not represent the *N. roissyana* of STARMÜHLNER (1993) that resembles *N. turrita* as described here). *N.* cf. *roissyana* lives where fresh water seeps through gravel beds of the beach forming puddles within the intertidal zone. The increase in whorl diameter is very regular and remains constant to the fully-grown specimen. The shell is about 7 mm high and 5 mm wide. The inner lip ends in a columellar edge that has one larger denticle in its more apical portion and may be smooth below and above or have small tubercules or undulations here. The rather large protoconch is succeeded by 4 whorls of the teleoconch. Ornament is grey with very fine dark axial stripes that may zigzag and form narrow elongate triangles, which are pointing towards the aperture.

The operculum carries on the inner side next to the columellar corner a ridge that bifurcates into a rounded ridge point and a solid peg. This is quite the same in another species with small shell size, but low spire that could be placed near *Clithon=Neritina* cf. *oualaniensis* (LESSON 1831) (*Neritina* 2). Here the shell is about 5 mm wide and 5 mm high and consists of 3 whorls of the teleoconch succeeding the rounded and projecting protoconch. Increase in whorl diameter is regular throughout growth of the teleoconch. Small triangles and fine dark lines on grey background dominate the ornamental patterns. Apertural features closely resemble those of *N.* cf. *roissyana* into which it appears to grade. Populations in which one or the other of these two species appear to dominate are very close to each other in the seaward position of the river mouth where the fresh water puddle present at low tide are washed with sea water at high tides. *N.* cf. *oualaniensis* resembles *Clithon faba* (SOWERBY 1836) as described by KOMATSU (1986, Fig.3) from Taiwan. It could also be identical with a species from the estuary of Tonga and Samoa that was determined as *Puperita* (*Heminerita*) *amoena* (GOULD 1847) by STARMÜHLNER (1993, Pl.6, Fig. 26, Pl.9, Fig.39). It closely resembles *Clithon oualaniensis* as described and illustrated by HAYNES (2001) from Fiji.

There is also a total gradation observable towards a lower and more ovoid shaped form or species that could be called *Neritina* cf. *porcata* (GOULD 1847) (*Neritina* 3). This rather small form measures about 5 mm in width and 3 mm in height and resembles a young of the ovoid variety of the spiny *Clithon* or a wide form of *N.* cf. *oualaniensis*. A similar species found in the Matutinao river from Cebu (figs.248, 253) was not involved in the interbreeding of species (see above) observed here among other species. In Bali both *N.* cf. *porcata* and *N.* cf. *oualaniensis* co-occur, the later more toward the beach the former more within the estuary. Ornamental pattern of *N.* cf. *porcata* consists of small triangles rather similar to *N.* cf. *oualaniensis* but there are also uniformly dark, greenish or

brownish individuals as well as such with broad spiral ribbons. Colours in general are more brownish and greenish than grey. The teleoconch consists only of 1,5 whorls with rather rapid and regular increase in shell width. Even in small individuals the protoconch is usually dissolved and there is a deep pit in the apex. There appears to be a transition to the low *Clithon cf. nucleolus* (*Neritina* 4). Species with a larger shell but also wider than high shape from Samoa and other Pacific islands have been determined as *Neritina* (*Neritina*) *canalis* SOWERBY 1825 and *N.* (*N.*) *petiti* RÉCLUZ 1841.

Within the intertidal estuarine regions *Clithon cf. nucleolus* (MORELET 1856) has a rather variable shell (figs.136-137) that in shape is similar to the small elongate oval *N.* cf. *porcata*, and in coloration totally grades into the spherical *C.* cf. *corona* with shiny and commonly greenish shell. *C.* cf. *nucleolux* has the first teleoconch whorl without spines (figs.232, 234) and from the second whorl onwards there may be 1 to 6 spines on each whorl and there appear to be about 2,5 teleoconch whorls until the individuals are grown with about 5 mm wide shell. Spines are usually long and commonly open gutter-like and appear well below the suture on a more or less well-developed shoulder. The shell is variably coloured between dark yellowish to greenish and violet, and patterns commonly consist of fine arrow points, which are oriented towards the aperture. But there are also individuals of uniform coloration or fine axial stripes or spiral bands.

As in the more spherical form that could be placed with *C.* cf. *corona* (LINNÉ 1758) (*Neritina* 5) (figs.138-149) the first teleoconch whorl usually forms a dark subsutural ribbon and a low depression next to it. The aperture shows a thick columellar area, that is wrinkled and demonstrates 5 to 6 denticles at its inner lip of which the upper (apical) is represented by an rounded larger tooth. The semi lunar operculum is smooth on the outside with a shallow groove crossing the surface that

Fig. 219: The embryonic whorl of *Theodoxus fluviatilis* from the mouth of the Neretwa river in Croatia is about 0,8 mm wide.

Figs. 220-221: The embryonic whorl of *Theodoxus jordani* from Jordan measures 0,5 mm in its first whorl and has typical initial growth line pattern. The juvenile hatches with about one whorl as indicated by growth intermission (221). (Adult shells see figs.12-20).

Figs. 222-223: *Theodoxus fabulus* (BRIART & CORNET 1887) from the Paleocene of Mons in Belgium has a 0,7 mm wide embryonic shell (222) that is ornamented by wrinkles and folds and the juvenile shell as in *Theodoxus* (223) is 2 mm high.

Fig. 224: An opened and upturned egg capsule (less than 2 mm wide) of *Neritina* holds the embryos with shell of about 0,15 mm in diameter and about ready to hatch (from Cebu).

Figs. 225-226: Veliger shells of neritoideans from the Plankton of the southern Red Sea that belong to larvae about ready to metamorphose. They measure about 0,6 mm in diameter.

Fig. 227: The embryonic shell of hatching *Neritina piratica* from Colombia (Caribbean Sea) with the cup like first shell and its growth line pattern. The shell is 0,15 mm wide.

Fig. 228: The protoconch of *Nerita undata* (LINNÉUS 1758) from the Red Sea (Port Sudan) is about 0,5 mm in diameter.

Fig. 229: The protoconch of *Neritina* cf. *roissyana* from Lovina Beach (Bali, Indonesia) is 0,6 mm wide with strongly overlapping, convolute larval whorls.

Figs. 230-231: The 0,5 mm wide protoconch (230) and 1,6 mm high juvenile teleoconch (231) of *Neritina turrita* or *N.* cf. *variegata* from the Lovina Beach estuary in Bali (Indonesia).

Fig. 232: Juvenile shell of *Neritina* "*Clithon*" from Lovina Beach (Bali, Indonesia) of 1,5 mm in height.

Fig. 233: Juvenile shell with 1,3 mm high shell of *Nerita tricarinata* (see 280) from the Eocene of the Paris Basin with the end of the protoconch and first teleoconch.

Fig. 234: *Neritina* "*Clithon*" from Bali with 0,3 mm wide protoconch.

Figs. 235-236: *Neritina pulligera* from Lovina Beach, Bali with operculum sealing the shell that displays the larval operculum (235), 236: with juvenile shell of 2,2 mm width.

Figs. 237-238: *Neritina auriculata* seen from the side (237) and in apertural view (238) with 3 mm wide shell from Lovina Beach, Bali.

Fig. 239: *Smaragdia* from Port Sudan (Red Sea) with 0,7 mm large protoconch.

Fig. 240: The detail to 242 with the almost 0,7 mm wide protoconch of *Smaragdia* from the Mediterranean Pliocene with 2,5 whorls and marginal ridge of pediveliger shell.

Fig. 241: *Smaragdia* from Bali (sea grass beds in NW lagoons) with much of the larval shell covered by the teleoconch, 0,6 mm of it are visible.

Fig. 242: *Smaragdia* from the Pliocene of Le Puyet, Nice (Mediterranean Sea), same shell as in 240.
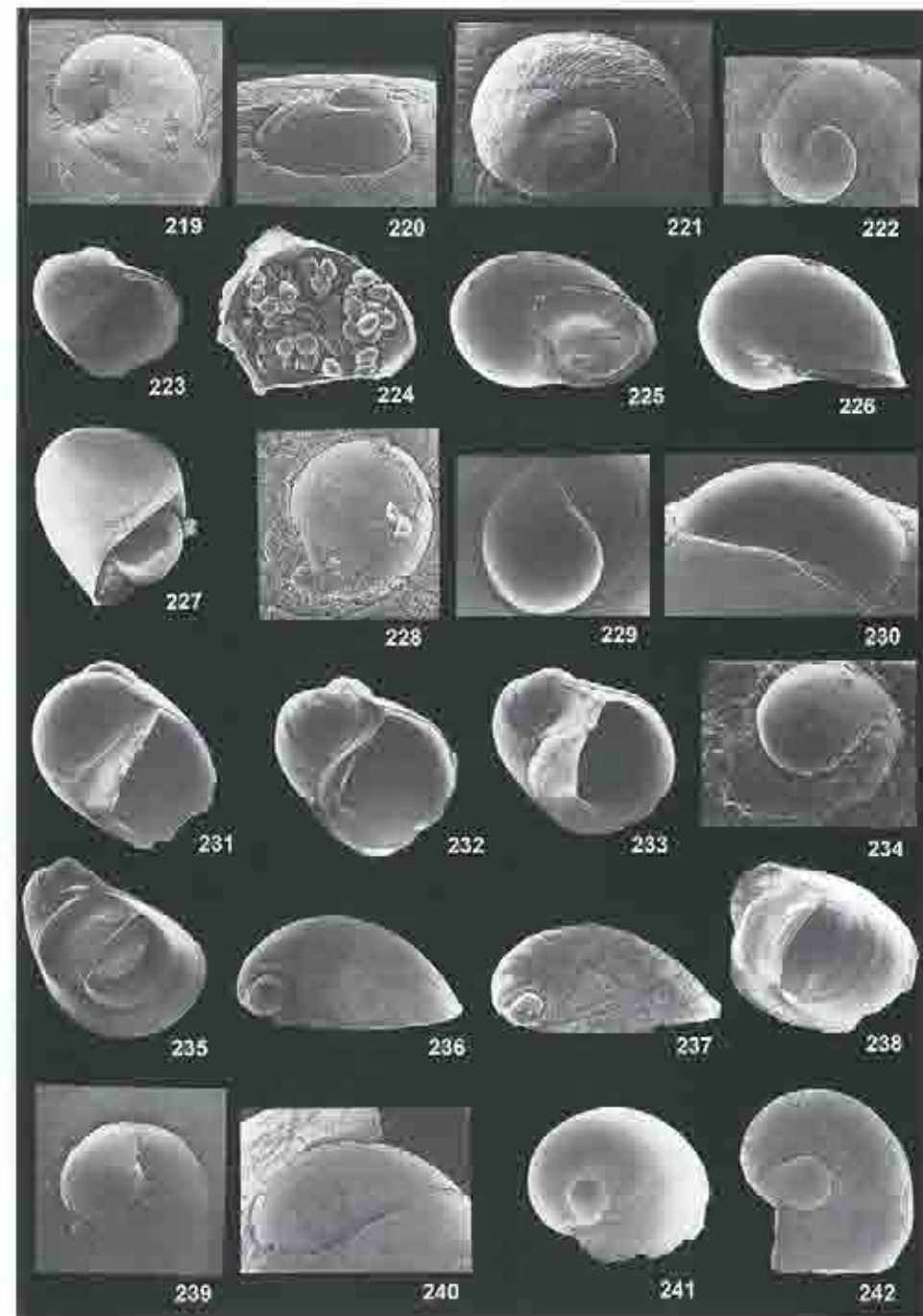
corresponds with a lower ridge on the back surface. A ridge with two horn-like projections forms the hinge. While the ovoid C. cf. *nucleolus* appears to remain within the intertidal regime and has small shells, the C. cf. *corona* is more variable and extends with some varieties far upstream growing to 15 mm x 15 mm large individuals. These large individuals have four or even a little more than 4 whorls of the teleoconch and usually strongly corroded apex. Individuals found upstream of the intertidal regime in the creeks of Bali may have a shell that is ornamented with axial wrinkles as would be the case in *Clithon* cf. *pritchardi* (DOHRN 1861) observed in about 15 mm wide and 12 mm high and fully grown individuals from the estuary of Lovina more commonly than in the Sangsit estuary. Extremes may move far upstream and reach a size of 25 mm in height and 20 mm in width.

Even though *Neritina* cf. *porcata* and spine-less *Clithon* cf. *nucleolus* sometimes resemble individuals of *Neritina pulligera* with similar semi-spherical shell, a pattern of fine spiral liration was present only in the latter. The operculum of the three different species is rather similar and has rib and peg strongly developed. In Bali also no transition is noted between *N. pulligera* on one side and *N. auriculata* (figs.203-206) on the other which both occur together, for example, in a fresh water spring well above the sea in a temple east of Singaraja (unlike a similar environment Madagaskar (see chapters 7.b, 7.c) where both mix).

In the estuarine area there may be many individuals without spines that are difficult to distinguish from *Neritina* cf. *communis* (*Neritina* 6) with ornament of the shell consisting of yellow spiral ribbons and ribbons ornamented with axial dark lines. All whorls are visible in the low and rounded apex and there is usually a shallow depression below the suture, as is found in the spine bearing C. cf. *corona*. Whorl increase is very regular. Even though there are many individuals of this smooth form it is not in separate population to the spine bearing forms (figs.138-149). The later have individuals with rounded apex and spines of former whorls resorbed, and others with the spire more exposed and with spines apex and spines of former whorls preserved. A whorl may have 0-10 spines. The original subsutural depression of the former whorls preserved. A whorl may have 0-10 spines. The original subsutural depression of the former whorls preserved. A whorl may remain indistinct or be transformed into a ridged shoulder bearing spines and could be determined as *Clithon* cf. *diadema* (RÉCLUZ, 1841) consisting of more than 4 whorls which a weakly shouldered below the suture. This shoulder bears the spines, which are especially well developed in juvenile individuals. But here in Bali no population was observed in which a spiny *N.* *"Clithon"* with spines of former whorls dissolved could be separated from a population were these spines remained exposed and undissolved, as is the case in Cebu.

On muddy surfaces between vegetation and below mangrove bushes in the supratidal and extreme high tidal estuary with more or less regular influence of sea water the large and conspicuous shiny smooth *Neritina turrita* (GMELIN 1790) (*Neritina* 7) may be found with elongate conical shell that consists of 4 whorls of the teleoconch which including the protoconch are all visible and of which the last makes up two thirds of shell height (figs.130-135). The shell is up to more than 3 cm high and more than 2 cm wide. As ornamental pattern inclined black lines lie on yellow greenish smooth and shiny background. The columellar lip of the aperture is concave and below and above a median larger denticle smaller denticles are developed. *N. turrita* was collected from hard muddy surfaces in the region of extreme high tide in the mangrove environment along small rivers in Sangsit and Lovina (northern Bali) and near Petitengel Temple west of Kuta in southern Bali. ABBOTT & DANCE (1982) illustrated a *N. turrita* as found in Bali, while a *N. turrita* from Tahiti illustrated by POINTIER & MARQUET (1990) is quite like *N.* cf. *variegata* from Bali. STARMÜHLNER (1993, P.9, fig.46) described and illustrated a *Neritina* of similar shape, ornament and size of *N. turrita* in Bali and determined it as *N. (Vittina) roissyana* living in estuarine regions from the coast of Australia to the Fiji Islands and Samoa.

Neritina cf. *variegata* (*Neritina* 8) is also quite large and has a more slow increase in shell height (figs.126-129) and is more commonly encountered in Bali, but in the same environment as *N. turrita*. *N.* cf. *variegata* (LESSON 1832) has the shell as wide as high (up to 2,5 cm) and whorl width increases regularly during growth (figs.230-231). There are about 4 whorls of the teleoconch, which are ornamented in a similar manner as found in *N. turrita*. Usually dense black lines are found on yellowish background. These lines may be simple, widely spaced, and zigzag, or they fuse to form a pattern of drop like dots between them. Lines may also be so close to each other to almost fuse and form a black shell. Just below the suture the whorl is slightly concave and further on the sides it is well rounded.

The colour of the operculum varies between light yellowish orange to black. A very fine pattern of dense spiral liration features the shell surface. The operculum of *N. turrita* as well as *N.* cf. *variegata* resembles that of *"Clithon"* by having two horn-like pegs at each end of the ridge. Obviously, both in Lovina as well as near Sangsit the low *N.* cf. *variegata* and the high *N. turrita* grade into each other. Both have similar colouration pattern. Their mode of live commonly outside of the water and the smooth appearance of the shell distinguishes from *Neritina "Clithon"* in the field. KOMATSU (1986, Figs.7-10) distinguished intermediate shell types as seen in Bali among Taiwanese *Neritina*. Of these *N. turrita* is just like that in Bali. What is called *N.* cf. *variegata* in Bali was further subdivided into the three species *N. variegata*, *N. parallela* (RÖDING 1798) and *N. plumbea* SOWERBY 1855. The individuals determined as *N. variegata* by KOMATSU closely resemble those described with the same species name by STARMÜHLNER (1993) from Samoa. The *Neritina turrita* and *N. turtoni* RECLUS 1843 described by HAYNES (2001) from Fiji living in similar enviroment would be included with *N.* cf. *variegata* of Bali.

A very similar shell shape is found in *Neritina* cf. *squamipicta* (RÉCLUZ 1832) (*Neritina* 9), which differs from *N.* cf. *variegata* by having the suture covering the whorls of the spire and by a more uniform dentition of the columellar edge. Coloration may be extremely similar and a transition may be well possible. Such a transitional individual was noted at Lovina estuary and appears to connect with *N. "Clithon"*. The shell of *N.* cf. *squamipicta* is hemispherical seen from the side with last whorl coating over and thus hiding all former ones. The inner lip callus is simple and smooth and the columellar lip is dented. The shiny smooth shell of fully-grown individuals measures about 1,5 cm in width, is slightly higher and consists of more than three teleoconch whorls which cover each other from first whorl to the last succeeding the protoconch. The colour pattern is shiny dark brown with large drop-like to triangular dots. A totally brown but otherwise very similar shell was called *Clithon olivaceus* (RECLUS 1843) by HAYNES (2001) from Fiji streams. Transition in shape and coloration appears to exist also to *N.* cf. *variegata*, even though fully developed individuals of *N.* cf. *squamipicta* can easily be distinguished by the covered spire and the uniformly dented edge of the inner lip. This species was found in Sangsit, Lovina and near Kuta, but more rarely than others. A very similar species with the apex covered up by succeeding whorls and individuals with and without spines were named *Clithon corona* by STARMÜHLNER coming from Port Moresby in New Guinea (figs.150-153, 155)..

In Bali transitions were noted to occur from:

Neritina 1: with littoriniform small shells and living place in freshwater puddles in the intertidal beach, to

Neritina 2: with rounded small shells of similar coloration and similar living mode, and from here to

Neritina 3: with small ovoid shells further up into the estuary, to

Neritina 4: with ovoid shell and spines and remaining in the estuary (figs.13-137), while

Neritina 5: with spherical shell with or without spines moves upstream into the fresh water (figs.138-140). Compared with Cebu the *N. "Clithon"* with reddish mottled triangular granulation and teleoconch cornered throughout is rarely present among the *N. "Clithon"* varieties in the creeks above the estuary. The same can be stated regarding the greenish and greyish mottled *N. "Clithon"* with teleoconch cornered throughout, smooth shell and spiny that appears to represent the large specimen that have moves upstream furthest in Bali. These varieties also include the spiny angular form with coarse growth increments and spiral dark and while colour ribbons. But all these *N. "Clithon"* morphs (1-3 in Cebu) are not found in larger and almost pure populations, as is the case in Matutinao River in Cebu.

Neritina 6: represent a smooth variety of *Neritina* 5 living in the estuary (figs.142-146) that closely resembles Nr. 6 of Cebu.

Neritina 7: is the high spired large *N. turrita* that lives on muddy supratidal ground (figs.130-135), clearly merging with

Neritina 8: with low spired axially striped forms of the same environment (figs.126-129), which again appears to grade into

Neritina 9: with similar shape but former whorls of the spire covered by succeeding whorls.

Not represented in Bali were the varieties 4 with strong allometric growth of the estuarine Matutinao River and the spiny angular shell with black with light arrows as coloration and all spiny whorls preserved (No. 7 from intertidal creek in Arcao, Cebu).

Thus the *Neritina* races of Bali to some degree resemble those of Cebu, but they have a rather distinct own character by including transitions to the small forms of the beach (1 and 2) and the oval forms such as *N.* cf. *porcata* (3). There is also a good chance that the *N. turrita–N.* cf. *variegata* is involved in the hybridisation here as well, which was not observed in Cebu. Among the Balinese species or morphs of the *Clithon* cf. *corona* group, *C.* cf. *corona* can be distinguished from *C.* cf. *pritchardi* by its smooth shell surface. In Cebu there is apparently a mix with the dotted and spiny *C.* cf. *bicolor*, which was not encountered in Bali.

All shells with exception of 249 illustrated on this plate are from Mututinao River, Cebu, Philippines.

Fig. 243: Juvenile shell with 2 mm in diameter of *Neritina* "*Clithon*" with the first spine.

Fig. 244: Juvenile shell with first whorl of the teleoconch and about 1,5 mm high shell from *Neritina* "*Clithon*".

Fig. 245: Juvenile shell with 4 mm in height of *Neritina oualaniensis* from the entrance of the estuary with protoconch in 247.

Fig. 246: The rounded protoconch measuring about 0,45 mm in width and consisting of 2,5 whorls of *Neritina* "*Clithon*" is settled by boring organisms which typically destroy this organic and aragonitic portion of the shell during further growth of the snail.

Fig. 247: Protoconch of *N. oualaniensis* is almost 0,5 mm wide, has a ridged margin of the pediveliger shell and strongly convolute whorls.

Fig. 248: Apertural view of the shell of *Neritina* sp. (*N.* cf. *porcata* in BANDEL & RIEDEL 1998) shown in Fig. 253 with the operculum in place.

Fig. 249: Side view of the juvenile *Smaragdia* from the sea grass environment of north Bali with 1 mm high shell and about 0,5 mm high roundish protoconch.

Fig. 250: The protoconch of *Neritina* "*Clithon*" is about 0,45 mm wide and consists of 2,5 whorls of which the last is ornamented by fine axial lines.

Figs. 251-252: The protoconch of *Neritina pulligera* measures about 0,4 mm across and consists of more than 2 whorls (251) and the juvenile shell is shown with 2,4 mm in maximum diameter (252).

Fig. 253: die view of *Neritina* sp. of the same species as in 248 with 3,3 mm in maximal shell width.

Figs. 254-256: *Neritina* "*Clithon*" with protoconch indicating development of the larva in the river Mututinao (254), with 3 mm wide shell, that in 255 shows a corroded protoconch of about 0,32 mm in diameter (smaller than that of marine larvae, see 246, 250, 259), 256: with juvenile shell with 3 mm in diameter.

Figs. 257-258: Side view of the juvenile *Neritina auriculata* with 1,2 mm in basal width and the protoconch with 0,35 mm in width and about 2 whorls (257), and protoconch that consists of a little more than 2,5 whorls and measures about 0,4 mm in diameter.

Fig. 259: The protoconch of *Neritina* "*Clithon*" measures about 0,45 mm.

Fig. 260: Juvenile shell of *Neritina auriculata* with 1,2 mm wide base (detail in 263).

Fig. 261: Apertural view of a young *Septaria* with about 3 mm long shell.

Fig. 262: Apical view of a 2,2 mm long juvenile *Septaria*.

Fig. 263: The protoconch of *Neritina auriculata* (detail to 260) is about 0,4 mm wide.

Fig. 264: The protoconch of *Septaria* with about 0,4 mm in width is directly succeeded by the limpet like teleoconch.

Figs. 265-266: The juvenile *Septaria* is almost 3 mm in maximal width (265), and its protoconch is well rounded, convolute and about 0,4 mm wide (266).
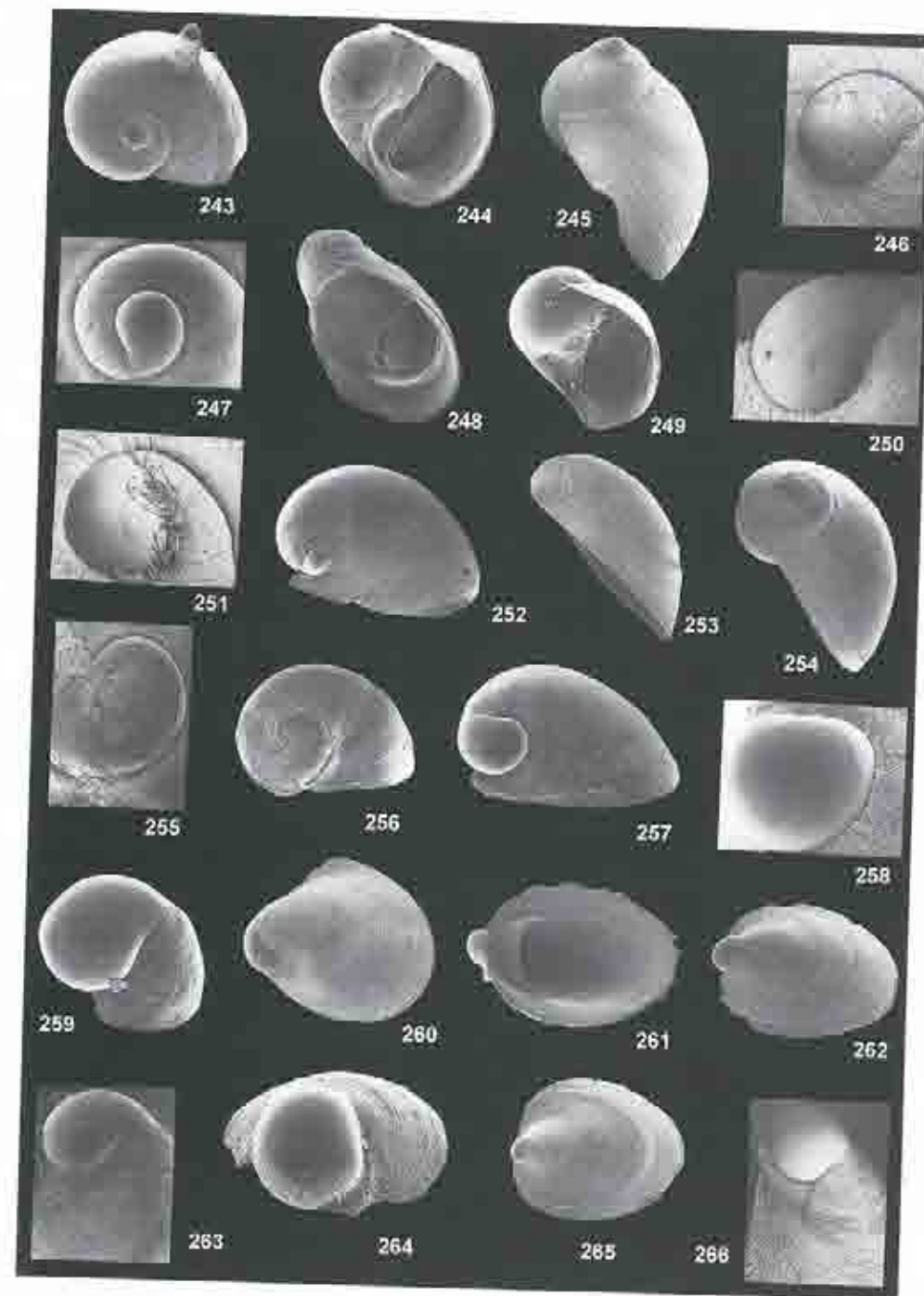
7.i Sandal shells of *Septaria* FÉRUSSAC 1807

Septaria holds limpet-like neritininids that have a narrow septum separating the body portion with the foot from the visceral mass. The genotype is *Patella borbonica* BORY DE ST. VINCENT 1803 from Reunion Island. From the estuary of the Umzamba River *Septaria porcellana* comes far up into the actual river above the estuary. In the intertidal area where the river runs rapidly at low tide, both *S. porcellana* and *Septaria borbonica* are characteristic. They were more common in the headwater at the Umzamba than in that of the Mnyameni and were absent in the Umtamvuna River, just north of the Umzamba River.

Septaria borbonica (BORY DE ST. VINCENT 1803)

Description: The symmetrical, cap-like shell has an apex that overlies the posterior edge of the shell and points backwards to the right. It is corroded at its basal portion, even though the outer lip is raised above it from juveniles of 6 mm shell diameter onward to the fully grown 32 mm long ones. The posterior margin is almost straight, the anterior rounded. The inner shelf is narrow and has an almost straight and smooth columellar edge. A network of triangles and rounded dots along with wavy dark lines ornaments the shell on yellowish or greenish background. This ornament is quite variable but rather characteristic (figs.85-87).

The operculum is kept in a pocket between shell and foot and is of quadrate shape with nucleus in marginal position. It lies hidden and enclosed between the upper side of the foot and the lower side of the visceral mass (fig.84). It function is no longer to close the aperture, but it serves as shelf separating foot and visceral mass and connects to the reduced inner lip.

Remarks: The shape of the aperture is more rounded than that of *S. porcellana* and the inner lip is straighter than in the later, which is more rounded convex. The operculum differs by having much more substance than that of *S. porcellana*. The shell is more solid in composition than in *S. porcellana* and it pattern of ornament consists of shorter triangles.

Septaria porcellana (LINNEUS 1758)

Description: The symmetrical, cap-like shell has an apex that reaches over the posterior edge of the shell and is corroded on its base. The shell is quite thin and lenticular oval reaching a length of 22 mm and width of 15 mm. The posterior and anterior margin of the outer apertural lip is rounded as well as the columellar edge of the inner lip. The ornament of the shell is seen also on the inner shell surface since shell is thin and translucent. Ornament consists of a pattern of collabral lines and radially arranged lenticular elongated triangles crossing up to ten of these lines. Ornament is quite variable but keeps this general pattern (figs.88-89). The operculum has lost its function and is thin and brittle. It lies hidden and enclosed between the upper side of the foot and the lower side of the visceral mass.

Remarks: These two very similar species *Sepataria borbonica* and *S. porcellana* can be differentiated from each other by the ornamental pattern of the shell, the shape of the aperture, curvature of the inner lip and composition of the operculum. The shell of *S. borbonica* is usually wider than that of *S. porcellana*, but this cannot be noted in all individuals. The shell is usually thinner in *S. porcellana*, but this is also only observable among individuals of one locality since it depends on the chemistry of the water. The pattern of ornament in *S. porcellana* has longitudinal spindle-like triangles, while those in *S. borbonica* are short and not crossed by collabral lines. The inner lip in *S. porcellana* is more concave than that in *S. borbonica*, but this feature is variable among individuals. The same holds true in regard to the rounded outline of the posterior outer lip, which is always present in *S. porcellana* and found in unusual or juvenile individuals of *S. borbonica*. The operculum in *S. borbonica* is much more solid than that in *S. porcellana*, but both are hidden below the shell. According to HAYNES (1994) *S. borbonica* and *S. porcellana* can also be distinguished by their reproductive systems.

Septaria has several rather similar species, which can be distinguished by the shape and the position of the early teleoconch, the shape and size of the inner lip and the shape of the aperture as a whole. *S. borbonica* has oval shape and a rounded or almost straight inner lip, while the inner lip of *S. porcellata* is of more rounded outline and the shell is more slender. Both have the early whorls in apical

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position in front of the posterior lip of the aperture and eroded at the base. More eroded and further extending is the early coiled portion in *S. sanguisuga* REEVE 1856 (HAYNES 2001).

HAYNES (1994) noted that at least 44 species of *Septaria (Navicella)* have been described and can be studied on their type specimen in London, Geneva and Paris. But shell shape is rather variable and HAYNES (1991) discovered that with the morphology of one shell type that would be placed with *S. porcellana* there were four different genital systems, indicating that different species have rather similar shells. The genital system in *S. suffreni* (SOWERBY 1841) from Fiji was found to be very close to that of *Neritina* while in *S. bougainvillei* (RÉCLUZ 1841) from Fiji it has become most simplified and, thus, altered in regard to the conditions found in *Neritina*. Thus, HAYNES (1994) expressed the opinion that shell shape, colour, pattern of ornament and shape of operculum is poorly diagnostic character for placing *Septaria* specimen into a certain species.

According to STARMÜHLNER (1983) *S. borbonica* is characteristic to the Madagascan Province and has a very similar species from the northern margin of the Indian Ocean to the Pacific Islands and here between New Guinea and Tahiti in *S. porcellana*. According to HAYNES (1994) the genital system of *S. borbonica* from Mauritius and Madagascar resembles that of *S. porcellana*. Here ornament is quite variable (STARMÜHLNER 1976, Pl.13, Figs.132-138). PÖLLABAUER (1986) found in New Caledonia 5 species of *Septaria*, *S. porcellana*, *S. bougainvillei* (RÉCLUZ 1841), *S. sanguisuga* (REEVE 1856), *S. janelli* (RÉCLUZ 1841) and *S. suffreni* (RÉCLUZ 1841) which can best distinguished from each other by their anatomy.

HAYNES (1991) suggested an evolution to have occurred within the genus *Septaria* leading from species in which males and females are of the same size so such where males are smaller and finally to species in which the small individuals act as male and when grown transform into females. Regarding protoconch morphology *Septaria* does not differ from *Neritina* (BANDEL 1991b, Pl.2, Figs.5,6, BANDEL & RIEDEL 1998, Figs.4,7) (figs.261-262, 264-266, 292, 296).

7.j The Central American and Caribbean group on both sides of the Isthmus of Panama

According to the classification adopted by THIELE (1929) the common Caribbean species *Neritina virginea* (LINNÉ 1758) represents the type species to the subgenus *Neritina (Vitta)* MÖRCH 1852. It is characterized by a smooth shell with rounded or pointed apex and more than three whorls of the teleoconch succeeding the protoconch. The subgenus was interpreted by WENZ (1938) to hold species like *N. virginea* from the Caribbean Sea as well as the *Neritina* species from West Africa. According to RUSSELL (1941) there is a whole group of species living in the Caribbean Sea that resemble *N. virginea*. He distinguished 7 species of which 6 where placed in the subgenus *N. (Nereina)* CRISTOFORI & JAN 1832 and only *N. punctulata* LAMARCK 1816 was seen as member of the subgenus *N. (Neritina)* LAMARCK 1816. WENZ (1938) in contrast placed the later into the subgenus *N. (Nereina)*, and *N. virginea* in *N. (Vitta)*.

Neritina virginea shows a wide variety of ornaments on its shell, which to a certain degree reflect the salinity of its living environment. The saltier the environment of growth the more colourful is the shell. In brackish and fresh water shells are greenish-grey, while in salinities raised above normal purplish and red colour are common (BANDEL & WEDLER 1987). *N. virginea* was kept in the aquarium in Bonn for more than 5 years. The animals can stay alive in fresh water as well as in brackish water and reproduce here. The teleoconch of *N. virginea* and the very similar *Neritina puncticulata* LAMARCK 1822 (ABBOTT & DANCE 1982) = *Neritina clenchi* RUSSELL 1940 (ABBOTT 1974, Fig.530) have a teleoconch consisting of more than three whorls of which all remain visible in the apical shell portion. *N. virginea* is more pointed in its spire than *N. clenchi* and remains smaller (around 1 cm in height and width) while the later grows to twice that size. Both prefer environments with brackish water, even though members of this species will survive well under marine conditions in very protected environments. Large populations are found on muddy and sandy bottoms as well as on mangrove roots and stems

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within the tidal zone in estuarine areas in the Caribbean Sea at Columbia. While *N. virginea* lives among the roots of the mangrove within the tidal zone in estuaries. *N. clenchi* lives within the mangrove forest on decaying leaves and muddy bottom and on the beach of mangrove ponds in Columbia (BANDEL & WEDLER 1987).

RUSSELL (1941) noted that regarding the cusps on the teeth of the radula *Neritina virginea* grades into *N. reclivata* (SAY 1822) and that into *N. clenchi* (=*N. puncticulata*). *N. reclivata* or *N. clenchi* RUSSELL 1940 by ABBOTT (1974) was observed to live in a fresh-water spring on the Gulf of Mexico in Florida that issues into the beach. RUSSELL (1941) also noted that these three species prefer increasingly fresher water for their living environment, with *N. virginea* in the brackish estuary and *N. clenchi* moving upstream into in the rivers. The species described by RUSSELL (1941, Pl.3, Figs.5,6) as *Neritina piratica* RUSSELL 1940 from the Caribbean Sea at Nicaragua was encountered in the mangrove of Tolu in Columbia (figs.122-125). The rounded shells of this species consist of four whorls of the teleoconch succeeding the protoconch and is about 2,5 cm high and a little less wide. It differs from *N. virginea* that lives in the same area but at more exposed position by its larger size and finer ornamental pattern. The other species recognized by RUSSELL (1941) are *N. meleagris* LAMARCK 1822 from Santo Domingo and *N. zebra* (BUQUIERE 1792) from French Guinea. All of these are similar to each other and it is only *N. punctulata* LAMARCK 1816 that has a subpatelliform shape and only 1,5 whorls of the teleoconch.

What has been named *Theodoxus luteofasciatus* MILLER 1879 by ABBOTT (1974, Pl.3, 531, ABBOTT & DANCE 1982, p.55) (= *Neritina picta* SOWERBY 1832) representing a *Neritina* from the Gulf

Figs. 267-270. *Semineritina mammaria* (LAMARCK 1804) from the mid Eocene of the Paris Basin (Saffrée). The juvenile shell is 2,5 mm high (267), 268: apical view of the protoconch with 0,8 mm width and almost 3 whorls, 269: protoconch seen from the side with undulating end of the larval shell and 0,9 mm in height, 270: with juvenile, 1,5 mm high shell.

Fig. 271: The same as in 278 seen from the side with protoconch of *N. tricarinata* contained in the early teleoconch and about 0,7 mm high.

Fig. 272: Protoconch of *Semineritina mammaria* in the juvenile shell measuring 0,8 mm across. Same locality and age as in 267

Fig. 273: The protoconch of *Velates schmiedeliana* CHEMNITZ 1886 from the mid-Eocene of Dudar in Hungary measures 4,6 mm in diameter and is later covered to a large extent (274-275).

Fig. 274: *Velates schmiedelianus* in detail of fig.275 with the protoconch as it lies in the apex of the teleoconch and consists of about 2,5 shell whorls.

Fig. 275: As 274 in apertural view of the *Neritina*-like juvenile shell of *Velates* of 1,2 mm in height.

Fig. 276: Protoconch with onset of teleoconch of *Velates* sp. from the Eocene of Saffree in the Paris Basin. The protoconch is 0,4 mm high and ornamented by axial lines.

Fig. 277: Cf. *Neritoplica* from Saffrée(Middle Eocene of the Paris Basin).

Fig. 278: Apical view of juvenile shell of *N. tricarinata* (same shell as in 271 and see 280) with the large protoconch of 0,8 mm in diameter and more than three whorls.

Fig. 279: Shell of a juvenile neritinid (same as in 277).

Fig. 280: Juvenile *Nerita tricarinata* LAMARCK from the Eocene of the Paris Basin at Saffrée in France with 3,7 mm high shell. Same as specimen in figs.271, 278

Fig. 281: Juvenile shell of *Neritoplica montensis* BRIANT & CORNET 1887 in apertural view measures 3,7 mm in height; figs.283-285 represent the same species from the Paleocene of Mons in Belgium.

Fig. 282: Protoconch of the same species as in 277 and 279

Fig. 283: As in 281 the protoconch measures 0,5 mm across. Collection of the Natural History Museum in Brussels, Nr. 168444.

Fig. 284: The protoconch of *N. montensis* measures 0,5 mm across and consists of about 2,5 whorls from the Calcaire de Mons, Belgium.

Fig. 285: Apical view of *N. montensis* with 3 mm wide juvenile shell (see 280, 283, 284).

Figs. 286-287: Limpet shell of smooth "phenacolepadid" from the Oligocene (Chattian) of Glimmerode near Kassel. The teleoconch measures about 2 mm in diameter (286) and the protoconch is 0,25 mm wide (287).

Figs. 288-289: Same genus as in figs.286, 287 but from the Recent lagoonal sediment of Lizard Island, NE-Australia, with 2,5 mm wide shell (289) holding the somewhat inclined protoconch with 0,4 mm width in its visible portion.

Fig. 290: Protoconch of *Fluvinerita alticola* from Jamaica consisting of almost one wrinkled whorl with about 0,6 mm in diameter. (adult shells in figs.8-11).
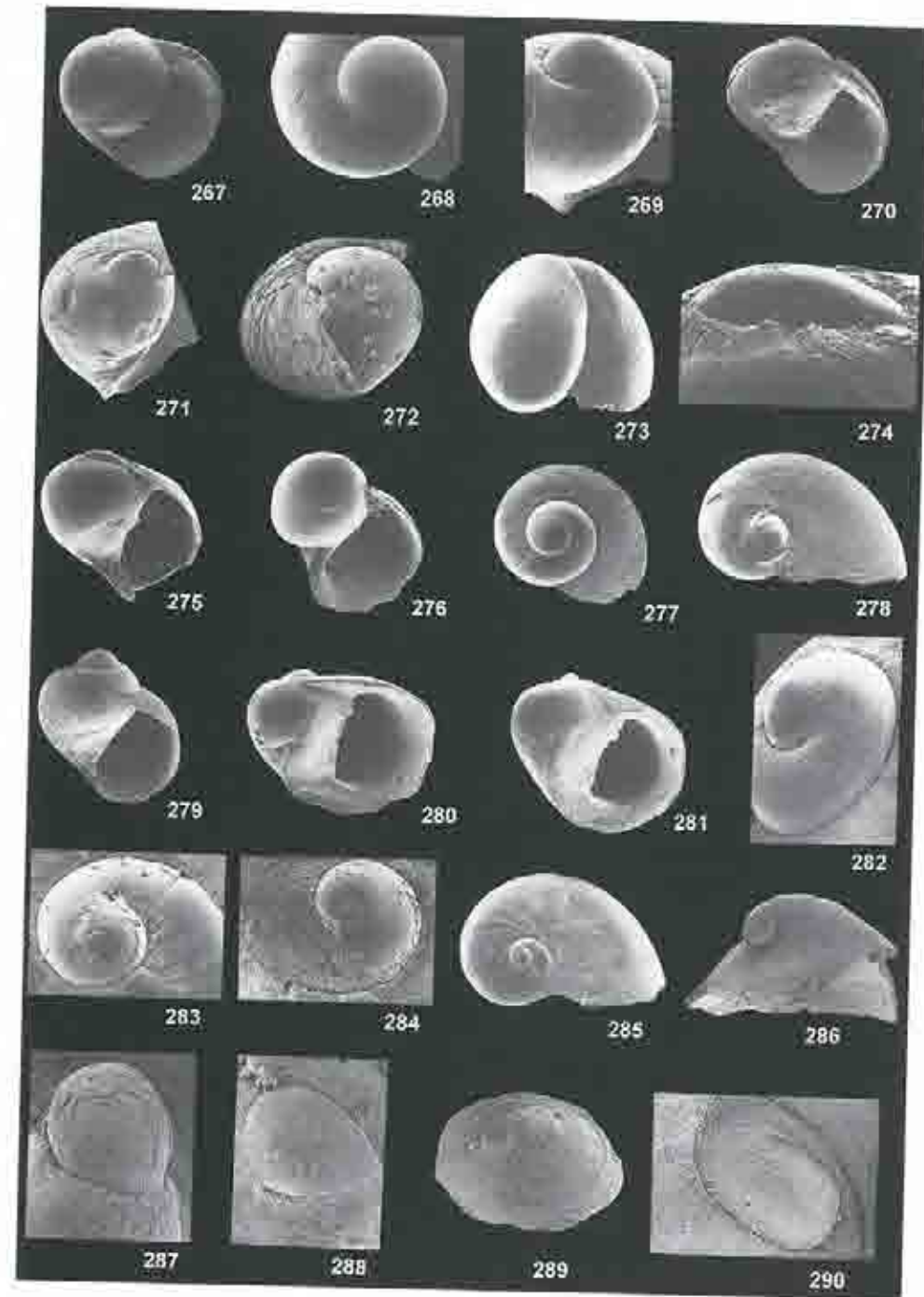
of California has a very similar shell to that of N. *virginea*. Individuals from Puerto San Carlos living in fresh water near the beach the shell is about 10 mm large, glossy-smooth round shell and with a colour pattern of oblique stripes of grey black, yellow and white. Colour patterns of specimen collected on sandy bottom in Bahia Concepción (by Steffen KIEL) are quite variable with axial elements predominating but forming more spacious to finely reticulate patterns usually in the coloration of brown and grey (figs.104-107). The number of whorls is like that of the Caribbean *N.virginea* with more than three succeeding the protoconch, which is clearly that of a planktotrophic larva. *N. luteofasciata* had been placed in the subgenus *N. (Vittoclithon)* BAKER 1923.

According to WENZ (1939) *Neritina (Neripteron)* is split into *N. (Neripteron)* s.s. based on the Indopacific *N. tahitiensis* from Tahiti and *N. (Clypeolum)* based on *N. latissima* from the Pacific side of Nicaragua. *N. latissima* BRODERIP 1833 from the Pacific coast of Panama according to HAYNES (pers. com.) has a different type of spermatophore as found within the *N. virginea* relation, a thin operculum and otherwise similar features and also smooth shell. According to ABBOTT & DANCE (1982) *N. latissima* occurs from Mexico to Ecuador in the fresh water dominated part of estuaries and its early shell has several whorls of the teleoconch before the outer lip of the teleoconch greatly increases in size forming a wing-like extension. It is here interpreted that *N. latissima* represents a winged offshoot of the *N. virginea* relation. The Pacific side of Central America has been in contact with the Caribbean Sea some three million years ago and there has been extensive exchange of fauna before that time (KEIGWIN 1978).

7.k West African *Neritina*

BROWN recognized 8 species of *Neritina* from West Africa that live within the coastal swamps and estuarine regions of rivers from Senegal to Angola. Among these the two species *Neritina oweniana* (WOOD 1828) and *Neritina tiassalensis* BINDER 1955 are large, reaching almost 3 cm in maximum diameter. Of these *N. oweniana* has a shell with wing-like outer lip when fully grown. It lives in nearly normal fresh water (BROWN 1980, Fig.17a, b) and was found 27 miles upstream the mouth of Congo River. The fairly large shell (up to 28 mm width) has two wing-like projections of the outer lip when is fully grown. It lives in nearly normal fresh water in rivers from Liberia to Angola (western Africa). The operculum has a good-sized peg.

The rather similar species *Neritina tiassalensis* with large shell (more than 2 cm in diameter) has similar shape to the juveniles of *N. oweniana* but lacks the extended aperture. It lives in streams and was found even 80 km inland in rapids of the Bandama River of the Ivory Coast. In contrast *Neritina cristata* MORELET 1864 has a shell with a widely expanded aperture and a ridge on the upper surface of the whorl. According to BROWN (1980, Fig.17g) this species should occur in Cameroon. A *Neritina* that can be considered neither *N. oweniana* nor *N. tiassalensis* or a mixture of both was encountered high up the estuary of the Sanaga River near its confluence with TwaTwa River. The species has been taken to Hamburg alive and is still living in the Aquarium after three years. Some of them have evolved into winged individuals, others have remained without wings. Whorls of the teleoconch coat the protoconch over and also cover each other so that not much more than the last whorl is visible. The final shell shape is that of a low hemisphere with about 2 cm in maximum width and 1 cm in height.

Neritina afra SOWERBY 184 (figs.96-99) was reported as abundant in torrential streams of up to 200-300 m above sea water in Ile du Prince (African West Coast) (BROWN 1980, Fig. 18d,e). BANDEL & KOWALKE (1999) noted *Neritina afra* in the brackish estuary of rivers near Limbe (Cameroon) with up to 14 mm high and 13 mm wide shell and low though distinct spire and coarse teeth on the columellar plate. A dark greenish-brown colour sometimes with large yellowish patches features the outside while the columellar plate has an orange tinge. Individuals of this species were encountered in the *Nipa*-mangrove as well as in estuarine pools of small rivers below Mount Cameroon. Freshly metamorphosed young were found in great numbers in the transition from the estuarine to the fresh water environment and near springs in the gravel bed of the beach. Dull coloured individuals occur commonly in the upper tidal flats in and outside the mangrove swamps wherever fresh water seeps out of the ground.

Juvenile individuals of *N. afra* are more colourful than older ones and thus resemble *N. glabrata* from the Sanaga Delta of Cameroon. But members of both species can well be distinguished by small differences in the shape of the teeth of the radulae (BANDEL & KOWALKE 1999, Fig.2). Even though both *N. afra* and *N. glabrata* have the same number of teleoconch whorls (2,5) *N. afra* is three times larger, due to a more rapid increase in whorl diameter during growth. The shell of *N. afra*, therefore, appears to be relatively less globular and more flattened at its apertural side

Another species of this group from Cameroon was noted by *Neritina rubricata* MORELET 1858 (similar or the same as *Neritina adansoniana* (RÉCLUZ 1841)) that is described to measure up to 13 mm in height and 12 mm in width (BROWN 1980, Fig.17d-f). Near Douala in the mangroves it was found to live on the underside of wet logs in the beach drift of the uppermost tidal zone (figs.100-103). Here individuals were never larger than 6 mm and about as high as wide. The dull coloured shell has a prominent spire in contrast to *N. afra* and *N. glabrata* and a toothed columellar margin. The first whorl of the teleoconch totally cover-over the protoconch and there are 2,5 whorls of teleoconch when in the last whorl the suture is inclined revealing more of the spire. Thus, there is a clear allometric growth at first of extreme convolution coating the globular protoconch and later a more spacious growth with higher last whorl. *N. rubricata* can also be distinguished by radula characteristics (BANDEL & KOWALKE 1999, Fig.2). According to MANDAHL-BARTH (1973) and BROWN (1980, Fig.17d-f) *N. rubricata* occurs from Gambia to Cameroon. This species lives and is active in moist environment far up the beach and rests when covered by water.

The individuals of *Neritina glabrata* SOWERBY 1849 from Cameroon have an up to 7.5 mm high and 8.5 mm wide smooth shell with low spire and evenly rounded last whorl. Most fully-grown individuals remain below 5 mm in size. The teleoconch whorls coil convolutely so that they cover each other and part of the protoconch. But usually the protoconch is corroded so that there is a pit in the apex, and of the 2,5 whorls of the teleoconch only the last one is visible. While shells with two teleoconch whorls are of evenly rounded shape, the last half whorl creates a more oval appearance by being higher than the others. Ornament is highly varied (PILSBRY & BEQUAERT 1927, BROWN 1980, Figs.18b,c). Individuals from the Sanaga Delta may be bright yellow, jet black or reddish brown and there are also a rather large variety of ornaments consisting of stripes and dots in several colours (BANDEL & KOWALKE 1999). *N. glabrata* is very common on the beach in the coastal lagoon at the Sanaga River delta of Cameroon. It occurs from Gambia to Angola (BROWN 1980) and is more colourful and has a less expanded spire as well as a narrower aperture than is the case in *N. afra*. Also the place in the coastal environment of *Neritina glabrata* differs from that of the other species, being more beach sand and beach rubble with water seeping through in contrast to sandy muddy mangrove flats in the uppermost tidal regime as in *N. afra*. Bright coloration and place in the estuary near to the sea resembles the Indo-Pacific *Clithon oualaniesis* as described by BANDEL & RIEDEL (1998).

When these West African species of *Neritina* are seen as a group they can be distinguished from other biogeographic groups by the coiling mode and composition of the whorls of the teleoconch. Whorls overlap usually to cover most or all of the protoconch and earlier shell portions, and there are 2,5 whorls of the teleoconch. In these African coastal environments there is usually a lack of dissolved carbonate in the water and shell erosion is, therefore, quite strong and rapid. The interior of the African Conti0nent next to the western African coast usually consists of crystalline and eruptive rocks and very little limestone and marls. The results can be seen very well when the shells of the gastropods living in profusion in the coastal swamps and rivers are viewed. Of the shells collected by us (BANDEL & KOWALKE 1999) most have the early whorls corroded, and in case of the nerites the aragonite protoconch is dissolved and that remaining pit in the apex has become deeper and larger during life when open to the influence of the environment. Thus it is certainly of convenience and a positive selective factor when during shell growth earlier shell portions become covered, as is the case in all West African *Nertina* species to a large extent.

While BROWN (1980) distinguished 8 species from the West African coast, BANDEL & KOWALKE (1999) found only four in Cameroon between Mount Cameroon and Sanaga river mouth that could clearly be distinguished. While *N. glabrata* and *N. rubricata* represent only one type and are probably "pure" species, *N. oweniana* appears to show a mix with *N. tiassalensis*, and *N. afra* could also represent a mix of two "species", one of them of a little more rounded shape and the other with a little more flattened shell (see also ADENOGE et al. 11969

7.1 Convergence of *Theodoxus* (*Ninnia*) with *Neritina violacea*

The limpet-like *Ninnia* BRUSINA 1902 is based on the living *Ninnia schulzei* (GRIMM 1877) in the Caspian Sea could well be the offshoot of limpet-like species from the Pliocene of Abchasia. Here the subgenera of *Theodoxus* according to WENZ (1938) *Neritonyx* ANDRUSSOV 1912, *Brusinaella* ANDRUSSOV 1912, *Ninniopsis* Tomlin 1930 appear to be related or could even be members of the one rather variable species (figs.64-66). Apparently they are related to the Pannonian species *Ninnia soceni* JEKELIUS 1944 which according to JEKELIUS

Fig. 291: *Phenacolepas hamillei* (FISCHER 1857) from the Caribbean Sea near Santa Marta Colombia, with about 3,5 mm wide shell, protoconch in 293.

Fig. 292: Limpet-like neritimorph that is close to *Septaria* but also to *Phenacolepas*, the same as in 296 and 299. The shell is 4 mm wide at its base, Port Essington, Australia, Australian Museum Nr.C162447.

Fig. 293: *Phenacolepas hamillei* from the Caribbean Sea with about 0,5 mm high protoconch (detail to 291).

Fig. 294-295: *Phenacolepas arabica* RUEPP from the EDLAUER collection (58000) Naturhistorisches Museum, Wien. Maximal width is 2,4 mm, 295: with protoconch of 0,5 mm in size and consisting of several convolute whorls.

Fig. 296: As in Fig. 292 with 4 mm wide base.

Fig. 297: Protoconch with 0,9 mm in diameter of *Calyptronerita* from Villers in the Paris Basin representing the detail to Fig.300.

Fig. 298: Detail to 301 with 0,5 mm wide protoconch half covered by the teleoconch.

Fig. 299: Detail to fig.282 and 296 with 0,45 mm wide protoconch.

Fig. 300: *Calyptronerita* with 3 mm wide juvenile shell from the Eocene of the Paris Basin (detail in Fig. 297).

Fig. 301: *Phenacolepas arabica* of the collection EDLAUER (57996) with 1,8 mm wide shell.

Fig. 302: *Neritilia rubida* from Samoa (Coll. Naturhistorisches Museum, Wien) with 2,2 mm wide shell.

Fig. 303: *Neritilia* from the Pliocene of Le Puyet near Nice (Mediterranean Sea) in apical view as is shown in fig. 305.

Fig. 304: The detail to 307 of *Neritilia rubida* with the protoconch that is about 0,25 mm wide and displays radial and spiral ornament on its larval shell.

Fig. 305: The same shell as in 303 in upertural view with the juvenile shell of *Neritilia* holding the 0,35 mm wide protoconch with ornament of spiral striation.

Fig. 306: Operculum of *Neritilia rubida* from Bali (302) with excentric nucleus and peg projecting from its columellar side. It is 1,2 mm wide in outer view.

Fig. 307: A 1,2 mm wide juvenile shell of *Neritilia rubida* from the estuary of Matutinao River on Cebu, Philippines.

Fig. 308: The protoconch of *Hydrocena* (*Georissa*) *williamsi* GODWIN AUSTEN 1889 from the mountain forrest of Bali is about 0,4 mm wide.

Fig. 309: *Hydrocena* (*Georissa*) *saritta* BEUS from the Coll. EDLAUER of the Natural History Museum in Wien, Nr.5394 with about 2 mm high shell. Protoconch in 314.

Figs. 310-311: *Hydrocena* (*Georissa*) *rubescens* with about 2 mm high shell from coll. KLEMM of the Naturhistorisches Museum, Wien, 30611, 311: shows the protoconch with about 0,3 mm in height, detail see 315.

Fig. 312: *Hydrocena* (*Georissa*) *chrysacme* from the Coll in the NHM Wien with 0,35 mm wide protoconch.

Fig. 313: Hydrocenid from Vietnam with a 0,4 mm wide protoconch on the ornamented teleoconch whorl.

Fig. 314: Protoconch of *H. saritta* (309) is 0,4 mm wide.

Fig. 315: The protoconch of *Hydrocena* (*Georissa*) *rubescens* measurs 0,3 mm across in the same shell as in 310.
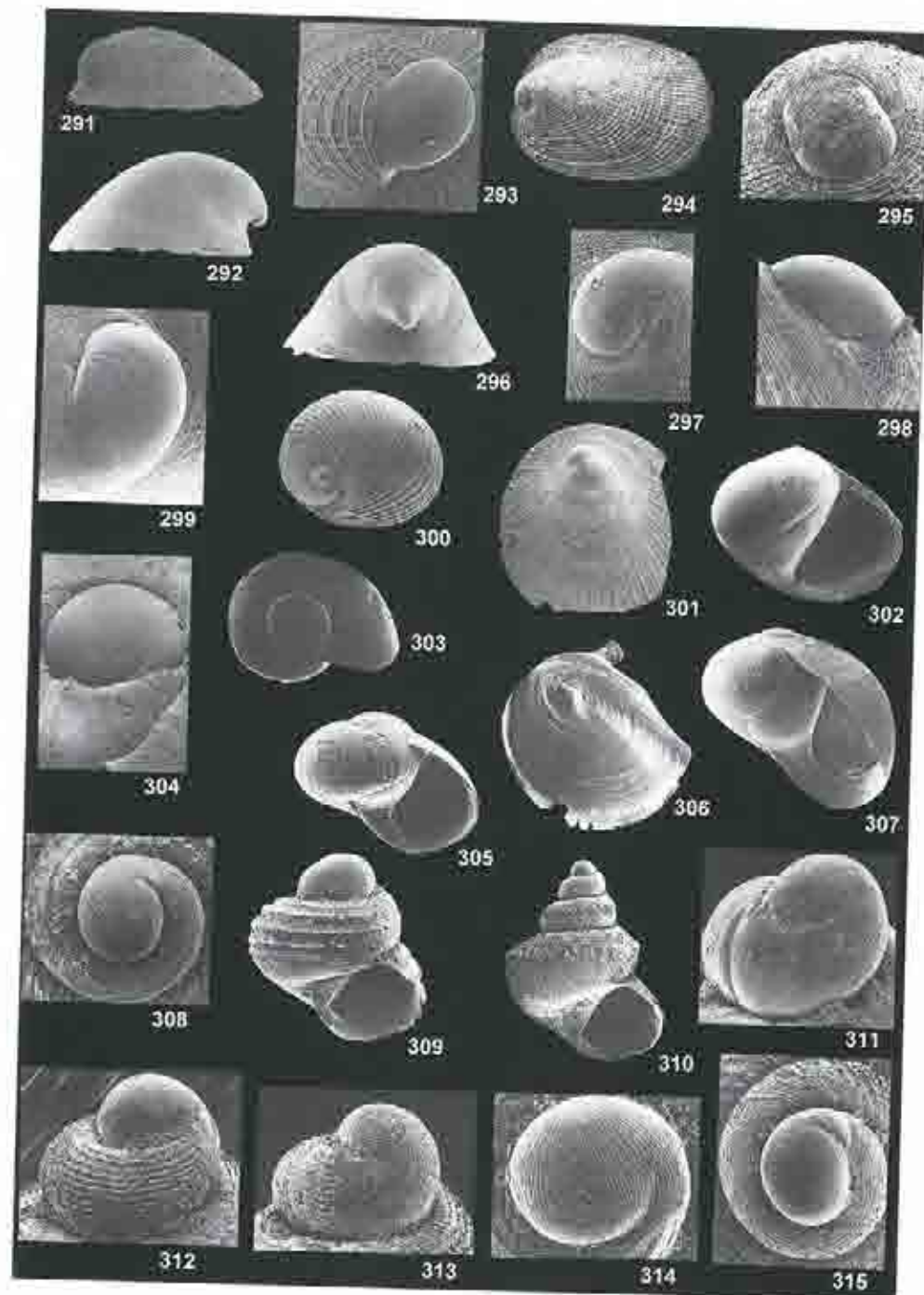
(1944, Pl.42, Figs.34-37) has a flattened shell with broad aperture and a spiral ridge. This ornament resembles that of *Theodoxus soceni* and JEKELIUS suggested transitions from *Ninnia* to this species in the fauna of Soceni. The surface of the shell is wrinkled which differs from that of *Ninnia martensi* (BRUSINA,1897) from Markusevec where the surface is smooth.

Ninnia schulzii living in the Caspian Sea is larger than *Theodoxus liturata* that also lives here. Its aperture has an expanded outer lip uniting with the callus of the inner lip in a straight line. The recent species appears to have a higher spire (DYBOWSKI 1888, Pl.2, Fig.9) than the fossil *Ninnia geticus* (F. MARINESCU) from the Maeotian (Late Miocene) of Romania from Jazofea Valley. The later was studied on material provided by Bogdan MARINESCU (Bucharest). The shell consists of at least 1,5 whorls of the teleoconch and has an aperture that measures 1,5 cm in width and about 1 cm along the coiling axis, which is almost parallel to the plane formed by the aperture. The shell has irregular growth lines as ornament and coloration by axial black stripes on white background.

Ninnia geticus representing a close relative to *Theodoxus* has a shell that is quite similar to that of *Neritina auriculata*, which has a relatively lower shell but very similar apertural outline. *Ninnia* differs from *Neritina* by having the lecithotrophic ontogeny of *Theodoxus*.

The modern *Neritina violacea* (GMELIN 1791) from SE-Asian mangrove environment (fig.208) differs from *Ninnia* by having a pelagic larva. It was collected in southeastern India as well as in eastern Java. *N. violacea* (= *N. crepidularia* LAMARCK 1822) lives along tidal channels in the mangrove near Porto Novo in Tamil Nadu (south-eastern India). The about 2 cm large limpet has its apex directed sideways in posterior position. The teleoconch consists of only a little more than one whorl with even increase in diameter. The outer lip surrounds the inner lip that forms an interior shelf well below the increase in diameter. The outer lip surrounds the inner lip that forms an interior shelf well below the surface of the aperture. This inner lip is covered by thick callus, evenly inclined and smooth. Its concave columellar edge is finely denticulate in its central portion bearing 10-14 denticles. The calcitic outer shell layer is thin as is generally the case in *Neritina* and *Septaria*. The operculum is smooth and has two internal denticles, but of intermediate shape between *Neritina* and *Nerita*. Like *Nerita* a tissue attachment scar takes the area between the projecting ridge and the roundish peg. Also the edge is serrated.

Individuals from Goa housed at the Natural History Museum at London are very similar to *Neritina (Dostia) violacea* (GMELIN 1791) from Thailand and could very well represent the same species. This could also be the same with *Neritina (Dostia) melanostoma* TROSCHEL 1837 from the Indo-Malaysian region and the Philippines. In Java *N. violacea* was encountered in the mangrove formed in the swamps of the Brantas River to the east of Surabaya. The animals are very tough and survived several years of living in a small aquarium in Hamburg with brackish water and wet rocks feeding only on algal crusts growing there and occasional by grain flakes. The species is also found in Fiji (HAYNES 2001).

WENZ (1938) distinguished the subgenus *Neritina (Dostia)* GRAY 1847 from *Neripteron* and characterized it by a strongly widened outer lip and selected *Nerita crepidularia* LAMARCK 1822 from SE Asia as type. CUSHING WOODS & SAUL (1986) described a species of *Neritina (Dostia)* from the Campanian of California as *Neritina (Dostia) cuneata* GABB 1864. They noted that it differs from *Velates* in the mode of coiling and in the configuration of the inner lip, which is finely toothed and broadly sulcate like *N. (Dostia) violacea*. While there is much callus in *Velates perversus* the callus is deposited thinly across the deck and is thick around the labral rim in Neritina *(Dostia)*.

Tomostoma DESHAYES, 1823 is based on *Tomostoma neritoides* (DESHAYES, 1823) from the mid-Eocene at Chaussy in the Paris Basin (COSSMANN 1925, Pl.7, Figs.10-12). It is a thin limpet-shaped shell that carries the apex on the posterior half and has a large septum. The aperture has an inner lip with a central sinus bordered by two rounded denticles on both sides. The ornament consists of growth lines and shell surface is smooth. The outer lip forms a continuous rim around the aperture. STRAUSZ (1966, Pl.4, Figs.3,5,9) described a shell less and the inner lip that is slightly concave septum. STRAUSZ (1966, Pl.4, Figs.3,5,9) described a shell less than 4 mm large with apex near the shell margin as *Pileolus (Tomostoma) dudariensis*. This small shell based on a single individual from the Nummulitic sandstone of Lutetian age (Eocene) from Dudar

could well represent a young specimen of *Tomostoma neritoides* from the rocks of similar age and facies found in the Paris Basin. The inner lip profile of *T. neritoides* is sulcate and resembles that of *Neritina (Dostia)*. The shell is a limpet and could be interpreted to present an early representative of the *Septaria* lineage. But the inner lip profile of *T. neritoides* is strongly crenulated and lies well below the shell margin resembling that of *Neritina (Dostia)*. The concave shape of the inner lip, the tight aperture and the dented columellar margin resemble conditions as seen in case of *Pileolus*, while the smooth shell resembles that of *Neritina*. Even though *Tomostoma neritoides* resembles *Septaria*, it does not appear to come from a *Neritina pulligera* of *N. auriculata* relation with wider apertures and not from the Cretaceous *Pileolus* with radial ornament (BANDEL & KIEL in press). It may therefore very well represent an independent lineage of limpet-like neritids.

This indicated that limpet-like shapes have formed repeatedly and cap-like neritoids have arisen convergently among different lineages. This has been demonstrated in case of the Triassic *Pseudorthonychia* resembling Paleozoic *Orthonychia* and of Jurassic to Cretaceous *Pileolus* (BANDEL & FRÝDA 1999, BANDEL 2000).

7.m The winged *Neritina*, results of convergent evolution in different lineages

The Hawaiian *Neritina granosum* SOWERBY 1825, *N. vespitina* SOWERBY 1825 (figs.194-195) and *N. cariosa* (WOOD 1928) have the aperture of the adult individuals expanded much like the west African *N. oweninana*, the Central American Pacific *Neritina latissima*, and the Indo-Pacific *Neritina auriculata* (figs.196, 199-202). ABBOTT & DANCE (1982) placed all these geographically widely separate species according to the characteristic shape of their adult aperture in the genus *Clypeolum* RÉCLUZ 1842. BAKER (1923), in contrast, had interpreted *N. cariosa* to represent the type to the subgenus *N. (Alinoclithon)*, accordingly WENZ (1938) placed it as subgenus with the genus *Clithon*. All *Neritina* species with wing-like outer lips such as *N. latissima*, *N. taitensis* (= *N. auriculata*) and *N. oweninana* had been placed in the subgenus *N. (Neripteron)* LESSON 1830 by THIELE (1929). WENZ (1938) placed winged species from Central America (*N. latissima*) and West Africa (*N. oweninan*) in the subgenus *N. (Clypeolum)*, and only those from the Indo-Pacific (*N. taitensis* and *N. auriculata*) in the subgenus *N. (Neripteron)*. HAYNES (2001) related *N. latissima* to the Hawaiian *N. granosa* and *N. neglecta* PEASE 1860, and all these to the Indopacific *N. auriculata*, *N. dilatata* BRODERIP 1832, *N. tahitiensis* (= *taitensis*), including the Hawaiian *N. vespitina*.

When studied in the context of the other species of *Neritina* that live within the same biogeographic province a different picture emerges. It than appears that these species can be related to different groups of *Neritina* some of which are best distinguished from each other by the number of whorls that are produced before the aperture expands. But also other features noted in comparison to the species living near them are of help.

The group around *N. auriculata* clearly includes *N. taitensis*, and *N. dilatata*. The last of these, *N. dilatata*, from the syntype housed in the Natural History Museum at London, like *N. auriculata* demonstrates a teleoconch consisting only of one whorl. But it is also closely connected to other Indo-Pacific species around *N. pulligera* with only about one whorl of the teleoconch (see chapter 7.c). *N. oweniana* is best seen in context with the other West African members of the genus *Neritina*. Within this group much or all of the early whorls of the teleoconch are covered with the succeeding whorls. In addition, the wing like apertural widening develops only in adult individuals, while juveniles have no apertural wings.

There are 4 endemic species of *Neritina* in Hawaii of which *N. neglecta* PEASE 1860 has no wings and consists of about 1,5 whorls succeeding the protoconch. HAYNES connected it to the very characteristic *N. granosa* SOWERBY 1825 that lives in fresh water of the mouth of streams. This species has not only wings but also a very granulated shell (HAYNES 2001). Like *N. neglecta* it has no peg on the inner side of the operculum. *N. cariosa* (WOOD 1928) differs in regard to its mode of life in brackish water and it has, like *N. vespitina* a peg and a ridge on its operculum. Especially *N. vespitina* from Hawaii resembles *N. auriculata* from the Indo-Pacific (compare figs.194 and 196).

According to the illustration of Abbott & Dance (1982) *Neritina latissima* (Broderip 1833) widens its shell only at the end of an ontogeny similar to that of the West African *N. oweniana* and contrasting to *N. auriculata* (figs.257-258, 260). The operculum resembles that of *N. virginea*, and it is quite likely that *N. latissima* has evolved from that group including *N. virginea* from the Caribbean Sea and *N. luteofasciata* from the Gulf of California. Specimen studied from the Museum of Natural History in London demonstrated that the post larval shell consists of about 1,5 whorls of normal coiling mode before the lips of the aperture expand widely forming lobed margins. In the Caribbean Sea another species, *Neritina punctulata* Lamarck 1816, has reduced the numbers of whorls to 1,5 (Russell 1941, Pl.4, Figs.3,4) to acquire a more limpet like shape, but without widening the aperture with extended wing like lips, as is the case in *N. latissima*. Thus, it appears as if the Panama region has evolved independently winged species with related species living in the Caribbean Sea. Separation of the two faunal provinces has occurred with the closure of the Panama Seaway only about 3 Million years ago.

Apparently *Neritina* species with expanded lips have evolved from non-expanding species independently in the Central American region, the West African region, and the Indopacific. From the later the Hawaiian branch could have evolved, and in that case *N. neglecta* has returned to non-winged shape from *N. auriculata* like ancestors.

8. A short review of radula features

Troschel (1856, Pl.16, Figs.1-12, Pl.18, Figs.1-8) characterized the rows in the neritimorph radula as having a single central tooth succeeded on each side by one large intermediary tooth and two tiny second and third intermediary teeth. The next in each row is the pair of solid lateral teeth. The lamellar marginal teeth form an arced lateral brush on the sides of each row. It is especially these marginal teeth that relate the neritimorph radula with the rhipidoglossan radula of the archaeogastropod Vetigastropoda. Fretter (1965) noted that in the neritids the rhipidoglossan radula has the lateral teeth nearest to the marginals enlarged and most powerful, while the marginals have great freedom for their rotary movement as they sweep up loosened particles on the backstroke of the radula. When *Nerita* is about to feed the snout is extended. As the mouth opens the tip of the odontophore advances and the broad radula ribbon is stretched out. The odontophore begins to recede from the moment it is fully protruded the scraping and brushing of the radula teeth are synchronized with closing the mouth.

Thiele (1929) characterized the radulae of the 6 families of the Neritoidea as follows:

Neritopsidae: In the long radula ribbon there are no central teeth; three intermediary teeth of similar shape are small and slender and bear cusps on their frontal edge. The lateral teeth are large and of rounded triangular shape with a broad rounded and smooth cutting edge. The numerous marginal teeth have long stalks and one part is dented and the other not on their cutting edge. The radula of *Neritopsis* was described by Fischer (1875) and again Warén & Bouchet (1993). The radula has the central tooth and also the three laterals reduced to thin membranes. It is thus probably not close to the original neritimorph condition.

Neritidae: The central tooth is small and of the intermediary teeth the inner pair is broad and elongated and there are two much smaller further intermediary teeth. The lateral tooth is large, mineralised and solid with cutting and scraping edge. As Baker (1923) noted it usually shows considerable wear. The marginal teeth are simple and have a slender stalk and an upturned point. They fan out during biting and sweep in material scraped by the mineralised fourth lateral pair. According to Hickman (1984, Fig.10) the fourth tooth in each row (counting from the central in lateral direction) is the dominant tooth in the neritoid condition. Numerous radulae of Neritidae have been figured by Komatsu (1986). Own observations on the radulae of *Nerita fulgurans, N. peloronta, N. albicilla, N.*

undata, N. tessellata, and *N. versicolor* revealed that the morphology of the teeth is very similar to each other. Usually the broad cutting edge of the lateral tooth is smooth and there are between 30 and 35 marginal teeth present. There exist considerable variability within the teeth present in the radulae of one species, especially when different ontogenetic stages are taken into consideration.

According to Baker (1924), Fretter (1965, 1984), Hickmann (1984), and Warén & Bouchet (2001) the Phenacolepadidae have a multiangular top quadrate small central tooth with rounded corners and simple frontal cutting edge. The first intermediary tooth is twice as wide as long and bears a dented cutting edge on its anterior portion. There are three intermediary teeth of smaller size and each having a dented cutting edge. The lateral tooth has several larger denticles and a large cutting edge. It appears to be smaller than is the case in *Nerita.* The marginal teeth are numerous and have dented cutting edges and long stalks. These lateral teeth have a spoon-like cutting edge and lateral flange.

The radula of the Neritiliidae has been described by Baker (1923) and Starmühlner (1976, 1983, 1993). In *Neritilia rubida* (Pease 1865) a central tooth is missing. There is only one intermediate tooth with lenticular form, inclined anterior edge and a short outer lappet. The lateral tooth has an inclined cutting edge with 12 to 14 denticles and a rounded outer basal projection. The marginal teeth are widened at their anterior end a carry 4-5 denticles here. There are slight differences in the numbers of cusps on the teeth that distinguish the species (Bandel & Kowalke 1999, Fig.2).

In the naked Titiscaniidae the central teeth or also missing. The intermediate teeth form only two pairs of rows with the inner tooth wide at the base and narrow at the top having a pointed cutting edge here and the outer intermediate tooth a bit larger but without cutting edge. The lateral tooth has a simple rounded cutting edge a widened median part and a pointed posterior portion. The marginal teeth count more than 100 in each row and are long stalked and undented.

In the land-living Hydrocenidae and Helicinidae the central and intermediary teeth are reduced (Bourne 1908, Scott & Kenny 1998, Fig.15, 76d). In the Hydrocenidae also the lateral teeth are strongly reduced in size and the marginal teeth are numerous. In Helicinidae central teeth are still present (Scott & Kenny 1998, Fig.15.77C,D)

Neritina was divided into subgenera by Baker (1923), according to differences he noted in the radula. This differentiation is suggested to be unnatural by Haynes (2001). She suggested that radula shape is not a very reliable character, since being quite variable even within a single species. Own radula studies carried out on different *Neritina* species support Haynes, and differences among species are very difficult to state. Binder (1957) demonstrated variations also to occur in the radulae of West African species.

When the radula of *Nerita* is compared with that of *Puperita* as was carried out in case of *P. pupa* from Curacao, Caribbean Sea, it is revealed that in the later the central tooth is a little more broadly square but otherwise teeth are very similar and closely resemble those especially of *Nerita undata. Neritina piratica* from Columbia, *Neritina gagates* from South Africa, *Neritina communis* from SE India, and diverse members of the *Neritina "Clithon"* group from Cebu and Bali have been compared with each other. When single radulae are studied small differences can be noted among species. Regarding comparison with *Nerita* differences are more obvious since the lateral tooth is usually dented in case of *Neritina*, while it is smooth in case of *Nerita*. Also small differences were noted in comparison with two species of *Septaria* from Natal. But a closer inspection of the variety within one species, *Neritina communis* from the Velar estary in SE India, revealed that these small differences noted between species might have little meaning. Here 25 radulae were analysed with the aid of the scanning electron microscope. The result showed a large variety to be present regarding central tooth width-length relation as well as a variable number of cusps present on the cutting edge of the lateral teeth. Also the relative length-width relation of the innermost pair of the intermediate teeth varies. But these differences are exactly those that could be utilized- and have been applied in literature- to distinguish different species among of *Neritina* and *Septaria*.

The conclusion can be drawn that within the Neritimorpha the radula can be utilized well as character in the description of larger taxonomic units, while it usually is not very useful in defining species or even groups of related species. This preliminary analysis of the radulae of about 25 species

of neritids with the aid of the scanning electron microscopy indicates that the fine differences noted by BAKER (1923) to distinguish subgenera among the Neritininae are difficult to support. Variability noted among individuals within a single species in contrast indicates that many of the radula data found in literature and used to distinguish species of *Neritina* may be misleading.

9. Paleontological evidence for the history of *Neritina*

Triassic nertinids may look rather similar to modern *Nerita* and *Neritina*. To all present knowledge they have lived in the shallow tropical sea. During Jurassic time they entered the coastal swamps. For example in the estuarine environment in which the late Jurassic Guimarota beds in Portugal were deposited (Oxfordian or Kimmeridgian according to BRAUCKMANN 1978) was also the living place for a small neritinid snail with characters similar to those of modern *Neritina*. The largest difference lies in the shape and extends of the inner lip callus. This feature appears to represente the only difference from modern *Neritina* and its relation (BANDEL & KIEL in prep.). The small (about 4 mm maximum diameter) smooth and semispherical nertitid shell consists of about 3 whorls of the teleoconch that is ornamented by two spiral colour ribbons consisting of pointed triangles that point towards the aperture. The protoconch is spherical and the inner walls of the shell are totally dissolved. This small neritoid lived in an estuarine environment together with *Ptychostylus guimarotensis* BANDEL 1991 and *Melampoides jurassicus* BANDEL 1991, the latter of which represents an ellobiid archaeopulmonate (BANDEL 1991). In possibly a similar environment *Neritina liassica* DUNKER occurred that has been found in the sandstones of the Lias near Halberstadt. Its *Neritina*-like ovate and smooth shell with variable colour patterns preserved is also not dented on its columellar edge. COSSMANN (1925) has suggested the presence of *Neritina*-like species to occur since Bathonian time and their shell features resembling that of *Neritodomus*.

From the Paleocene the species *Neritina montensis* BRIANT & CORNET 1887 is known (GLIBERT 1973) (figs.282, 283-285).

Description: The rounded little shell from the Paleocene of the Calcaire de Mons in Belgium (Mons) has a short almost flattened spire and a large last whorl that is smooth and shiny. Ornament consists of brown lines that form a widely spaced zigzag pattern on the smooth background of the shell surface. The aperture takes up most of the flattened base and consists of a semi-lunar opening and a large flattened callus of the inner lip, surrounded by the outer lip in a similar manner, as is the case in *Neritina pulligera*. The columellar lip has two upper larger denticles, and a number of small indistinct denticles on the lower portion. The protoconch measures about 0,5 mm across and consists of at least 2,5 whorls of which only the last one remains visible on an uncorroded shell. The last whorl overlaps onto the former whorls, hiding them. The globular protoconch is smooth and has a simple hemicircular aperture (figs.283-284).

Differences: *Neritina montensis* according to GLIBERT (1973) may be included within the genus *Neritoplica* OPPENHEIM 1892. But it differs from *Neritoplica uniplicata* representing the type to the genus *Neritoplica* by its more triangular shape, while the later is of globular shape (COSSMANN 1913, Pl.3, Figs.59-62). From *Theodoxus fabulus* coming from the same locality it differs by having a dented columellar lip and a protoconch that was produced by a planctotrophic larva and, thus, consists of 2.5 whorls. *Theodoxus*, in contrast has a protoconch of only one whorl (fig.222) produced during lecithotrophic ontogeny within the shelter of the egg capsule. *N. montensis* is distinguished from most members of the genus *Neritina* by the protoconch in which the last whorl enwraps all former ones (figs.283-284). In most cases of modern *Neritina* allmost all whorls are visible, even though whorls overlap considerably. The larval shell of *Smaragdia* has a similar overlap.

Neritina montensis was described also by COSSMANN (1913, Pl.3, Figs.59-62) and GLIBERT (1973, Pl.2, Fig.9) from the Paleocene. It resembles *Neritoplica* that encompasses species with smooth

neritinid shell with an oblique, semicircular aperture. It has a strong fold on the posterior columellar edge of the inner lip that continues into the interior of the shell. Some weak denticles may be present below. The genotype by subsequent designation is *Neritoplica uniplicata* (SOWERBY) (=*Neritoplica globulus* (DESHAYES) from the upper Paleocene of the Paris Basin (WENZ 1938, Fig.1031). OPPENHEIM (1892) noted that Recent neritinids never show a strong columellar fold like *Neritoplica*. He regarded this feature as primitive and considered *Neritoplica* as a link between Recent *Nerita*, the Neritininae and Cretaceous *Deianira*. But when compared with modern neritinids it becomes evident that spine-less *Neritina "Clithon"* of the *C. corona* group such as found in rivers of SE Asia is extremely similar to the Paleocene *N. montensis* regarding all features seen on the shell (see chapter 7.f, g, h). *Neritoplica* appears to have lived along the shore during the Late Cretaceous (KOWALKE & BANDEL 1996, Pl.1, Fig.1) (BANDEL & KIEL in prep.), and it may have entered the coastal swamps at that time.

During the Eocene several species of *Neritina* were living in coastal swamps along the Tethys Ocean, such as *Neritina lutea* ZITTEL 1862 found in the Bakony mountains at Dudar in Hungary. Here the spire consists of 2-3 whorls of the teleoconch and there is a slight concavity on the upper side of the whorls below the suture. The inner lip consists of a hemispherical callus pad and a finely dented columellar edge. The posterior margin has a stronger denticle apically and 5-6 weaker ones below. The ornament of the smooth shell consists of broad spiral stripes and numerous light brown dots arranged spirally all over the shell surface along with fine collabral stripes.

The studied specimen come from the brackish water clay of the Dudar coal mine. Their shell is about 1 cm high and wide. The material from Dudar indicates, that the inner lip in the adult differs from that of the juvenile. While the callus forms a wide thickened pad in the adult and the columellar edge is almost smooth, the inner lip of the juvenile is flat and the columellar edge dented. The protoconch is formed by a rounded shell, quite as is the case in a planktotrophic larva.

It seems that *Neritina lutea* is the same as *Neritina passayana* DESHAYES 1866 with the colouration sometimes dominated by spiral stripes, and in other individuals by dots (DESHAYES 1866, Figs.11-13, COSSMANN 1925, Pl.7, Figs.20, 24). According to SZÖTS (1953) *N. lutea* occurs at Gant with its sedimentary transition from shallow marine deposits to such of the coastal swamp. Also from the Eocene of Hungary a species very close or the same as *Neritina passayana* from the Paris Basin was described as *N. dudariensis* STRAUSZ 1966 (KESCSKEMETI-KORMENDY 1972, Pl.4, Figs.13-18; BARTHA & KECSKEMETI-KORMENDY 1963, Pl.21, Figs.7,8). This species from the Dorog Basin to the north of Budapest was also figured by OPPENHEIM (1892, Pl.31, Fig.13) and STRAUSZ (1966, Pl.4, Figs.6-8). KECSKEMETI-KORMENDY (1972) noted that the typical *N. dudariensis* is higher and the apex more raised and the denticles of the inner lip are less developed. STRAUSZ (1966, Pl.4, Figs.6-8) considered *N. dudariensis* a different species from *Neritina dutemplei* (DESHAYES) as illustrated by COSSMANN & PISSARRO (1910-1913, Pl.5, Figs. 39-40) because of unidentified differences on the columellar lip. From *Neritina consobrina* FÉRUSSAC as illustrated by DESHAYES (1824-1837, Pl.19, Figs.5, 6) it differs by having the concave upper shell flank in the penultimate whorl. But all of these "species" may belong to the same species having lived in different parts of the coastal swamps of the Tethys Ocean during Mid Eocene times.

According to COSSMANN (1925) there were quite a number of rather similar species of *Nertitina* that lived during the Eocene of Europe, and similar ones also occurred in different species in the Oligocene and Miocene here, before temperatures dropped below their requirements. Most of the illustrations provided show species resembling *Neritina communis* and relation among the living species with rounded shell and columellar lip bearing one larger denticle in its more apical part.

9.a A *Neritina* or *Theodoxus* from the Oligocene of New Zealand

The species *Neritina pomahakaensis* (FINLAY 1924) according to BEU & MAXWELL (1990) has a 8-10 mm high globosely shell that has a depressed spire which is corroded in most specimens. The protoconch is smooth and cap-shaped and teleoconch consists of 2-2.5 whorls that are slightly flattened or weakly concave adapical, convex below with the last whorl capacious. There is no sculpture apart from growth lines and weak spiral striae. Shell colour pattern consists of narrow

brown to grey zigzag stripes on paler background. The aperture is large and ovate with the inner lip oblique and almost straight produced laterally to form a moderately wide thin septum (inner lip callus), bearing a single low fold near the adapical end, otherwise smooth. The operculum is ovate with smooth outer face, paucispiral with subterminal nucleus and a curved apophysis emerging opposite the nucleus on the inner side.

This late Oligocene species from New Zealand was described as belonging to *Neritoplica* because of the single columellar denticle present. It is therefore not considered to belong to *Neritina* or *Theodoxus*. But such a denticle is characteristic to many living species of these genera, so that this argument is of little value. BEU & MAXWELL (1990) consider the species to be close to *Neritoplica subornata* (ORBIGNY 1850) from the Paleocene of French fresh water deposits. *N. pomahakaensis* is the only representatives of *Neritina* or the like in the New Zealand Tertiary. It appears together with *Melanopsis* in New Zealand in the Oligocene within estuarine swamp fauna.

It would be highly interesting to know its protoconch since its occurrence together with *Melanopsis* suggests relation to other fresh water species that lived along the shores of the Tethys Ocean (BANDEL 2000).

10. Comparison with older neritoids

In the Late Triassic St. Cassian Formation of the Dolomites the genus *Trachynerita* KITTL 1894 with the species *Trachynerita quadrata* (STOPPANI 1858-60) belongs to the Neritoidea since it has the inner wall of its shell dissolved. Here the family Protoneritidae KITTL 1899 would be available to place *Platychilina* KOKEN 1892, *Protonerita* KITTL 1894 and *Trachynerita* KITTL 1894 from the late Triassic in a higher taxon. But COSSMANN (1925) correctly observed, that it would be quite difficult to distinguish this taxon from taxa used to place later members of the Neritoidea with similar shell shape.

T. quadrata has a 0,4 mm wide protoconch with simple apertural margin and clearly including a planktotrophic larval shell. It is succeeded by 2,5 whorls of the teleoconch with angular whorls and step-like shape of the dull spire. Its only ornament consists of growth lines and colour pattern of zigzag marks. The aperture is egg-shaped with narrow inner lip and simple, thin outer lip with a central callus thickening. The similar *Trachynerita nodifera* KITTL 1895 has nodular anterior and posterior edges, is otherwise similar. It protoconch is smaller (about 0,3 mm in diameter), and the shell is also only a little more than 2 mm high when fully grown and having 2,5 whorls. *T. quadrata* has been illustrated by ZARDINI (1985, Pl.3, Fig.9a) as *Naticopsis zitteli* (pers. comm. Annette SCHWARDT).

The genus *Neritaria* KOKEN 1892 with *N. mandelslohi* (KLIPSTEIN 1843) also from the St. Cassian Formation has a large protoconch measuring about 0,6 mm in diameter and consisting of almost three whorls with a finely reticulate ornament and a row of nodes near the suture. The teleoconch consists of 1,7 whorls and is globular in shape when the shell measures 2,6 mm in height and 2,7 mm in width. Sutures are indistinct and ornament is that of collabral elements that may be indistinct or quite distinct axial ribs. In addition there may be zigzag and spiral colour patterns. The aperture is semicircular and oblique with a callus pad at the umbilical portion of the inner lip and a denticle on the apical portion within the outer lip. The operculum is paucispiral and thin and has a smooth surface. *Neritaria neritina* (MÜNSTER 1841) from the same Triassic strata differs regarding the denticle on the outer lip of the aperture and a smoother protoconch having only axial ribs and a larger size of almost 1 mm in diameter with more than 3 whorls. In the globular teleoconch the inner lip has a thick callus that forms a hump in the umbilical region. The columellar edge has a central denticle and a second broad anterior denticle. SCHWARDT (in prep.) also noted a species of the genus *Neritaria* from the St. Cassian Formation that is of more lenticular shape with more tightly coiled whorls and also two denticles on the columellar edge of the callus covered inner lip.

Neritininae resemble in general shell shape species of the Jurassic genera *Neritoma* and *Neridomus* (=*Neritodomus* as renamed by FISCHER 1885) according to COSSMANN (1925) and WENZ (1938). *Neritoma*

MORRIS 1849 has a spherical smaragdiform thick shell of globose shape and obliquely oval in outline and about as high as wide. The sutures between whorls are shallow. The inner lip of the aperture is thick diminishing the aperture, and the columellar according to WENZ (1938, fig. 1009) carries a median denticle and the genus is based on *Neritoma sinuosa* (SOWERBY 1818) from the Upper Jurassic of Boulogne sur Mer.

Neridomus MORRIS & LYCETT 1851 represents a genus of fully marine species growing to a size of 1-2 cm. The type is *Nerita hemisphaerica* MORRIS & LYCETT from the Bathonian (mid-Jurassic) according to COSSMANN (1925). In difference to the latter *Neridomus* (=*Neritoma*) has a smooth callus of the inner lip. KASE (1984) described *Neritoma* (*Neridomus*) from the Early Cretaceous as globose shells with whorls embracing each other almost entirely. The aperture is auriform in outline, and the inner lip thickened and simple as had also been suggested by ALLISON (1955). WENZ (1938) considered both these smooth Jurassic neritoids to belong to the same genus and to represent subgenera with the indentation of the lip characterizing *Neritoma* (*Neritoma*) and distinguishes it from *Neritoma* (*Neridomus*) MORRIS & LYCETT 1851 with otherwise similar spherical shell shape (according to WENZ 1938).

HUDLESTON (1884, Pl.9, Figs.4-6; 1894, Pl. 28, Figs.11-12) considered Jurassic species to represent a subgenus to *Nerita (Neridomus)* and described *Neridomus tumidula* (PHILLIPS 1829), which may be the same species as that considered as type (*Nerita hemisphaerica* ROEMER according to MORRIS & LYCETT (1851) from the Middle Jurassic of England (WENZ 1938. Fig.1008). This species is the same or very similar to *Neridomus anglica* COX & ARKELL 1950. COSSMANN (1885) described several Mid-Jurassic species from France, all of which are quite similar and fit in the diagnosis of *Neritoma* (*Neridomus*) with smooth columellar edge of the callus pad of the inner lip of the aperture. COSSMANN (1925) considered *Neritoma nuda* (PIETTE) as neo-genotype since it displays the undented columellar edge, which is usually not preserved in the type species and the other species belonging to this genus.

Jurassic nerites therefore appear to represent two differing types of columellar edges, one smooth and the other provided with a denticle. *Lissochilus* PETHO 1882 represents a genus with cancellate ornament of the shell (COSSMANN 1925). They could represent relatives of the Triassic genera of which *Trachynerita* has a simple smooth columellar edge while that of *Neritaria* has a denticle in its posterior portion.

Species like *Neritoma* (*Neridomus*) *dolichostoma* (COSSMANN 1907) occur in the Mid-Cretaceous of Japan (KASE 1984, Pl.10, Figs. 9, 10) as well as in the Urgon facies of the early Cretaceous of France (COSSMANN 1907, Pl.6, Figs.18, 20; 1916, Fig.22; 1925, Pl.6, Figs.22, 23). This species has an about 2 cm wide and high shell and a wide bulging callus of the inner lip and a smooth columellar edge. Ornament of the rounded and smooth whorls consists of zigzag colour bands. It is also similar to *Neritoma woodfordi* ALLISON 1955 from the Albian of Baja California (KASE 1984, ALLISON 1955).

The genus *Lyosoma* WHITE 1880, based on *Lyosoma powelli* WHITE 1876 from the Middle Jurassic of Wyoming (WENZ, 1938, Fig.1019) has the inner lip not preserved (KNIGHT et al. 1960). Here the last whorl of the teleoconch has oblique lamellar axial folds as ornament. The genotype according to SOHL (1965) has a smooth inner lip, which distinguishes from *Otostoma* with coarsely dented inner lip. In the description of *Lyosoma* by WENZ (1938, Fig. 1019) the inner lip has a denticulate columellar edge while in his illustration this edge appears to be smooth and not dented. If SOHL (1965) is correct, and the inner lip is smooth, *Nerita costifera* PIETTE illustrated by COSSMANN (1885, Pl.27, Figs.59, 60) could also be placed here from the French Mid Jurassic, marine beds. HUDLESTON (1894, Pl.9, Figs.7-9; 1894, Pl.28, Figs.6-9) described three very similar species, as *Nerita pseudocostata* ORBIGNY 1849, *N. costulata* DESHAYES 1838 and *N. subrugosa* HUDLESTON 1894 from the Mid-Jurassic of England, which could be considered to belong to *Lyosoma*. Here the up to 1 cm large subglobular shells are ornamented by regular axial ribs, and the aperture is simple, like that of *Neridomus*. The smooth and simply straight columellar lip and thin outer lip distinguish clearly from genera like *Nerita, Dontostoma, Otostoma* and *Neritoplica*.

In the late Cretaceous *Otostoma* ARCHIAC 1859 that includes such taxa as *Corsania* VIDAL 1918 and *Desmieria* BAYLE 1904 is a common neritinoid (BANDEL & KIEL in press) that has a characteristic

pattern of ornament, which appears to be restricted to Cretaceous times, in contrast to the observations of COSSMANN (1925).

11. Comparison with the Neritidae

11.a Recent Neritinae of the genus *Nerita*

Spiral ribs usually ornament the roundish shell of species of the neritines, more rarely they are smooth or axially ribbed. The shell has a low spire, enveloping body whorl, and inner walls are resorbed. The protoconch is smooth and consists of several aragonite whorls, is globose and involute (BANDEL 1982, Pl.21, Fig.3) (fig.228). The aperture is of semicircular outline with denticulate or smooth columellar edge of the inner lip and often a crenulated interior of the outer lip but, sometimes also a smooth inner side of outer lip. The teleoconch is composed of a relatively thick outer calcite layer, which is underlain by an inner aragonite layer with crossed lamellar structure. A planktotrophic larva has usually enlarged the protoconch with smooth whorls in strongly convolute arrangement. As in the teleoconch inner walls are resorbed in the protoconch as well (BANDEL 1992). Here the shell consists of very thin organic periostracum underlain by aragonite mineral deposits.

The modern genus *Nerita* LINNÉ 1758 with ovate to hemispherical solid shell with low spire and enveloping body whorl has the aperture usually with denticulate columellar septum and crenulated interior of the outer lip. The inner walls are resorbed. The flat callus of the inner lip commonly bears teeth, folds or pimples and extends over much of the base. The operculum is calcareous and usually carries a projection on its inner side next to the columellar lip in which inserts into the muscle of the snail. This hinge consists of a flattened projection extending to the side that is supported by a basal thickening and connected to a lateral ridge. Below this ridge a patterned muscle scar is present. All *Nerita* species as well as *Dontostoma* have a similar opercular hinge. It differs from that of *Puperita* and *Neritina* that have more knob-like pegs at their hinge.

The globose protoconch is smooth and consists of several whorls, which are of strongly involute coiling (figs.225-226). The genotype is *Nerita peloronta* LINNÉ 1758 from the Caribbean Sea (WENZ 1938) (fig.213).

Only species that have a spiral ornament of ribs are here included in the genus *Nerita*. According to COSSMANN (1925) the genotype of *Nerita* is *N. senegalensis* GMELIN 1791 that lives on the West African coast. It is similar in shape to the Pacific *N. atramentosa* REEVE 1855 from Australia to New Zealand (ABBOTT & DANCE 1982), which differs by reaching about double size. The relatively large *N. peloronta* (about 4 cm high) and the relatively small *N. senegalensis* (about 1 cm high) taken together represent quite well the range of shapes present within the genus *Nerita* in total (figs.213, 216).

The genus *Nerita* has been split into several subgenera. Only those subgenera proposed by THIELE (1929), WENZ (1938) and VERMEIJ (1984) that have a spiral ornament are here considered to belong the genus *Nerita*. When outside of the designated type species to the subgenera other species of the genus are included in the comparison transitions from one subgenus to the other become obvious. These regard the presence or absence of callus ridges and tubercules of the inner lip of the aperture, the number and size of the columellar denticles, the crenulation or denticles present or absent in the outer lip, the covering of the spire due to a more or less convolute coiling mode, and the presence or absence of pustules on the operculum. Thus, the distinction of subgenera is of doubtful use among the living species and may be just as misleading as is shown to be the case within the genus *Neritina* (see chapter 7.). When fossil species from the Tertiary were to be included, this picture becomes even more confused and more subgenera would have to be created.

The subgenera suggested by WENZ (1938) amounted to four, while VERMEIJ (1984) recognized nine. Of these later only those with a spiral ornament are considered here to compose the genus *Nerita*. So there are 8 subgenera that can be characterized as follows:

1.) *Nerita* (*Nerita*) has a low spire, a smooth inner lip callus, and characteristically is the columellar edge with two large denticles. On the outer lip a large posterior and a small anterior denticle are present with small denticles between them (fig.213). The operculum is tuberculated.

Remarks: *Nerita* (*Nerita*) is based on the rather large (4x4 cm) *N.* (*N.*) *peloronta* with more than three whorls of the teleoconch and a concave inner lip callus and smooth columellar margin that is slightly concave bearing two larger denticles of which the posterior one is the larger, and there is a posterior groove. The large denticles of the outer lip lie in front of the operculum if it is withdrawn. The subgenus *Nerita* (*Nerita*) is represented by only one species from the Caribbean Sea (ABBOTT 1974, Pl.3, Fig.519, BANDEL & WEDLER 1987) (fig.213).

2.) *Nerita* (*Theliostyla*) MÖRCH 1852 has low spire, and characteristically is a granulated inner lip callus. The columellar edge bears 4 small teeth, and on the outer lip a larger posterior denticle and row of small denticles are present. The operculum is granulated.

Remarks: *Nerita* (*Theliostyla*) with the type species *N. albicilla* LINNAEUS 1758 from the Indo-Pacific has a low semi-egg-shaped shell with almost flat apex and a little more than two teleoconch whorls (fig.215). The inner lip callus is granulated and the outer lip dented within sometimes a larger denticle in posterior position.

A species from the Gulf of Aqaba that closely resembles *N. planospira*, belonging to the subgenus *N.* (*Ilnerita*), has the callus smooth and the columellar edge almost so, while shell shape and ornament is like that of *N. albicilla*. The columellar lip is centrally slightly concave and, in case of *N. albicilla* has 4 small teeth in this depression. At the apical end of the columellar edge there is a gutter-like depression connected to a smooth callus ribbon. Ornament usually consists of well-developed spiral ribs. The operculum is granulated on the outside. It differs from *N.* (*Nerita*) by not having the two posterior strong denticles on the columellar inner lip and small teeth on this lip. The callus of the inner lip is covered with granules as is the case in *N. tesselata* (fig.212).

N. (*T.*) *senegalensis* GMELIN 1791 from the Cameroonian coast forms only about two whorls of the teleoconch. Here the aperture closely resembles that of *N. albicilla*, while spiral ribs are less distinct, and the shell is smaller (about 12 mm instead of 24 mm). But the West African *N. senegalensis* closely resembles *Nerita atramentosa* REEVE 1855 from Western Australia (ABBOTT & DANCE 1982). Specimens of this later species, that represents the type of the subgenus *N.* (*Melanerita*), were collected in a mangrove near Sydney are double as large, but otherwise closely resemble *N. senegalensis*.

From the middle Miocene of Hungary Strausz (1966, Pl.53, Figs.17-19) described *Neritina plutonis* BASTEROT 1825 that very closely resembles the *N. cf. planospira* living on pebbles and rock surface in the intertidal region of the Gulf of Aqaba, but may have a few more spiral ribs. (15-20) instead of 9-12 found in the living one. In both, the living and the fossil from the Paratethys, the rib on the peripheral edge is the largest, as is the case in *N. planospira* from the edge of the mangrove on Cebu.

N. (*Theliostyla*) resembles *N.* (*Melanerita*) in shape, ornament and lip features, but the inner lip callus is more concave in *N.* (*Melanerita*). According to WENZ (1938, Fig.1024) the subgenus *N.* (*Theliostyla*) holds several species and according to CUSHING-WOODS & SAUL (1986, Fig.6; 13, 16, 17) it occurs in the Palaeocene of California. This fossil species looks quite similar to *N. planospira* living in the mangrove of Cebu. The protoconch is of characteristic shape to the genus (SASAKI 1998, Fig.78a,b). It measures more than 0,5 mm in width and height.

3.) *Nerita* (*Heminerita*) has a visible spire, and characteristically a smooth inner lip callus, the columellar edge with low denticles, and a smooth outer lip. The operculum is granulated with smooth margin.

Remarks: *Nerita* (*Heminerita*) MARTENS 1887 (3) based on *N. pica* GOULD 1850 = *N. japonica* DUNKER 1859 from Japan has a indistinctly to distinctly spirally corded shell with visible spire, but roundish to egg shaped shell outline in size to 1-1,5 cm. Whorls are 2,5 after the typically rounded protoconch, and they are all well visible. *N.* (*Heminerita*) *guamensis* QUOY & GAIMARD 1834 belonging here is a relatively high spired shell with almost 3 whorls of the teleoconch, about 1 cm height and ornament of spiral ribs. But here the operculum is smooth and flat. The columellar edge of the inner lip

is slightly concave, and there are no or simple rounded denticles, variable with different individuals of the same species. The apical canal on the inner lip is well developed and there is a thick callus ribbon near the suture connected to it. A similar species with about 2,5 teleoconch whorls lives next to the mangrove in Rarotonga (Cook Islands) of the Pacific. It has an operculum with smooth exterior surface.

N. (Heminerita) forms a group of relatively small species of *Nerita*, which resemble *N. (Heminerita) insculpta (Cymostyla)* save for the smooth callus and greatly reduced lip dentition. *N. (Heminerita) insculpta (Cymostyla)* save for the smooth callus and greatly reduced lip dentition. *N. (Heminerita) insculpta* Récluz 1841 from the Marshall Islands as well developed spiral ornament, but also a pustulous operculum and low rounded denticles on the inner lip callus. Thus there appears to be transition to other *Nerita*. This is also the case with all black *Nerita (Heminerita) morio* Sowerby 1833 from the Easter Islands, which closely resembles the Cameroonian *Nerita senegalensis* in shape, size and ornament, but has smooth inner and outer lip.

4.) *Nerita (Cymostyla)* has short, pointed upright spire, and characteristically the inner lip callus with branching folds. The columellar edge bears two or three teeth, and the outer lip is denticulated with the most the apical denticle being the largest. The operculum is granulated.

Remarks: *Nerita (Cymostyla)* Martens 1887 is based on *N. undata* Linneus 1758 from the tropical Indo-Pacific with about three whorls of the teleoconch and well developed pointed spire (figs.211, 218). Apically to the large denticle of the aperture and near the suture there is a low apical canal with narrow callus ribbon that is deposited on the inner lip callus. This later feature resembles *N. (Linneria)= Dontostoma*. Wenz (1938) suggested to unite *N. (Cymostyla)* with *Nerita (Ritena) N. (Linneria)= Dontostoma*. Wenz (1938) suggested to unite *N. (Cymostyla)* with *Nerita (Ritena)* Gray 1858 in the same subgenus. Apparently *N. (C.) undata* is present in Mombasa, Port Sudan, Bali, and the Philippines representing a common and large species of the intertidal rocky shore. The number of large denticles on the apical portion of the outer lip is somewhat variable ranging from 1-3. *N. (Cymostyla)* is differentiated from *N. (Ritena)* by the columellar edge. Its protoconch is illustrated in fig.228.

From the mid-Miocene of the Paratethys Strausz (1966, Pl.54, Fig.1) described *Nerita undata pseudoplicata* Strausz, 1960 that closely resembles the living *N. undata*. The fossil species differs in having fewer spiral ribs of the ornament (18 instead of 30), otherwise resembles modern *N. undata*, but not *N. plicata* which has different apertural features. It also shows similarities with *Nerita fulgurans* Gmelin 1791 from the Caribbean Sea (fig.207).

5.) *Nerita (Ritena)* has rounded and projecting spire, a ridge covered inner lip callus. Characteristically the columellar edge bears 3-4 strong teeth, and the outer lip is strongly dented, with large denticle apically, second large one anteriorly and 3-4 folds between them. The operculum is smooth and concave when young and tuberculated later.

Remarks: *Nerita (Ritena)* is based on *N. plicata* Linnaeus 1758 from Central America (Wenz 1838, Fig.1023) with a little more than three whorls of the teleoconch. It occurs widely in the Pacific and specimen from Bali and Cebu are just like it. The shell has strong spiral cords and a strongly toothed aperture. Cossmann (1925) suggested here the subgenus *N. (Pila)* Klein 1758 for this strongly ornamented species from the Indo-Pacific. The inner lip callus has a pattern of folds that is similar to that found in *N. (Cymostyla) undata* but also to *N. versicolor* (fig.210). But in contrast to the former the columellar edge is convexly rounded and carries 3-4 strong teeth (fig.214). Fully-grown specimens appear to have a fully tuberculated operculum. Individuals from Bali, Rarotonga and Mombasa appear to belong to the same species.

6.) *Nerita (Melanerita)* has low and rounded top, and characteristically a concave and granulated inner lip. The columellar edge bears 2-3 denticles, and the outer lip is serrated and has two large denticles apically. The operculum is pustulated.

Remarks: *Nerita (Melanerita)* Martens 1887 (6) has the type species *N. nigra* Martens 1889 (= *N. atramentosa* Reeve, 1855) from southern Australia (fig.216). *N. (Melanerita) melanotragus* occurs from New Zealand to Tahiti, from Bali to Hawaii and South Australia. It is a rock clinger with flat and concave inner lip deep down. Whorl dimension increases rapidly so that very little apertural area of former whorls remain visible, or they are totally concealed by the last whorl. The large shell like that

of *N. tessellata* Gmelin 1791 from the Caribbean Sea is usually dark (fig.212). The inner lip is concave with an apical ridge that forms a groove before meeting the outer lip. The columellar lip has two angular ridges on both sides of the 2-3 median denticles. The outer lip has two large denticles apically and a serration besides that on the inner side. Here the spire remains well visible and is exposed.

N. (Melanerita) shares many features common with *N. (Theliostyla)*, and may in part represent a group of cool-water species of *N. (Theliostyla)* in which the external sculpture, callus sculpture, and lip dentition have become reduced (fig.212). In the Caribbean *Nerita tessellata* Gmelin 1791 the lip dentition is not reduced, as is also the case in the type species. It is also similar to *N. (Cymostyla)*, but differs by having a concave inner lip callus and an etched margin next to the callus. This large feature is the most characteristic part of the subgenus *N. (Melanerita)*. The species *N. (Melanerita) ocellata* Le Guillou 1841 is from Bali. Here the inner lip callus and the columellar edge are a little smoother than in the type species.

7.) *Nerita (Ilynerita)* has a characteristically flattened apex with a peripheral angulation. The inner lip is strongly pustulose with the columellar lip bearing three large denticles. The operculum is smooth.

Remarks: *Nerita (Ilynerita)* Martens 1887 (7) is characterized by a flattened apex, and one apical spiral rib developing into a crenulated ridge that may or may not form an angulation on the outer lip. There are strong spiral cords on the outer surface of the shell. It has a strongly pustulose callus with few large irregular tubercules on it and on the inner lip a deep apical sutural canal. The columellar lip is more straight than that of *N. (Melanerita)*, but otherwise very similar with three solid central denticles. Type species and only species of the subgenus is *N. planospira* Anton 1839 from the Indo-Pacific (fig.217). Abbott (1974) considered the subgenus to be the same as *N. (Theliostyla)*. The subgenus occurs all around the Indo-Pacific from India to New Caledonia, the Philippines, Indonesia, and the Fijis.

8.) *Nerita (Amphinerita)* is low and rounded, and has characteristically the inner lip weakly tuberculated and the columellar edge with low tubercules. The operculum is partly granulated and has a smooth margin.

Remarks: The subgenus *Nerita (Amphinerita)* Martens 1887 (8) with the type species *N. umlaasiana* Krauss 1848 from South Africa (Baker 1923, Wenz 1938, Fig.1025) owns an operculum like that of *N. olivaria* Le Gillou 1841 with two granulated regions separated by a longitudinal line on the outer surface. Seen from the side the spire is not visible, the ornament consists of very fine spiral lirae, and the shell may appear smooth on the type species. The callus and the columellar edge of the inner lip are only weakly tuberculated. The operculum differs in *N. (Amphinerita) articulata* Gould from Indochina, with fine spiral ornament and uniformly granulated operculum. This large species that lives from Indochina to Australia has a simple inner lip callus, a well-developed subsutural groove on that callus, a slightly concave columellar lip with four denticles on its central portion.

Resume: All these species have a very characteristic place in the ecology of mostly tropical shores. Their usual habitat is hard substrates in the littoral zone of warm seas.In the Pacific realm they live together with *Dontostoma*. Onto the hard substarte they usually also deposit their egg capsules which are of cupola-like shape (Bandel 1982). Their lid–like convex upper part is reinforced by calcareous spherules, which have been produced by the female. In Columbia it was observed that *Nerita versicolor* has between 50 and 100 eggs in each egg capsule, and all of them develop into a veliger within more than two weeks and hatch. The same can also be stated for *Nerita tessellata, Nerita peloronta,* and *Nerita fulgurans*.

Vermeij (1984) speculated on the relationships among the subgenera of the genus *Nerita*. He suggested that the smooth *N. (Linnerita)* (in part *Dontostoma*) is closely allied to *N. (Amphinerita)* and furthest removed from *N. (Ritena)*. It was assumed that the clade including *Linnerita* and *Amphinerita* is of relatively recent origin, since these are confined in the modern fauna to the Indo-West-Pacific, and have no known fossil species outside that region (contrary observations see Bandel & Kiel in prep). *N. (Cymostyla)*, *N. (Ritena)*, and *N. (Theliostyla)*, on the other hand, are interpreted to have Tethyan (c.f. Pacific) distributions, which is interpreted to imply a more ancient origin for these usually

strongly sculptured nerites. N. (Melanerita) shares many features common with N. (Theliostyla), and may represent a group of cool-water species of the later clade, in which the external sculpture, callus sculpture, and lip dentition have become reduced. N. (Heminerita) representing a group of small sized species which resemble N. (Cymostyla) save for the smooth callus and greatly reduced lip dentition have been interpreted to be progenetic derivatives of the N. (Cymostyla) stock, which are now found chiefly on islands in the Indo-West-Pacific region. WENZ (1938), in contrast, interpreted this taxon as subgenus to Puperita. VERMEIJ (1984) found the relations of the monospecific N. (Ilynerita) and N. (Nerita) confined respectively to the Indo-West- Pacific and Caribbean regions remaining unclear.

Actually all these assumptions expressed by VERMEIJ (1984) are quite unsafe in the light of the more ancient species that have been found in the Late Cretaceous (BANDEL & KIEL in prep.). Species resembling Dontostoma and Nerita have been living in the Tethys Ocean more than 70 million years ago and they settled a continuous coast stretching from America to Asia across Europe. They were also present in the Southern Hemisphere as is evidenced by species from South Africa.

The ecology of Nerita and Dontostoma is quite the same all over the worlds Oceans. Tropical rocky shores usually have 2 to 4 species living side by side, but usually one in highest splash water position and the others in differing positions below, sometimes connected to the proximity of tidal pools. WELLS (1978) noted in the Admiralty Gulf of NW Australia that Nerita reticulata KARSTEN 1789 (= Nerita signata LAMARCK 1822) is highest up to the shore with broad overlap with Nerita undata and Dontostoma polita mixed in with smaller numbers. Similarily the shores of the Red Sea house D. polita in middle position and N. undata above the median splash zone and Nerita albicilla within the splash zone. In the Caribbean region Nerita tessellata lives in the lower intertidal zone, in overlapping rage with N. fulgurans. The splash zone is preferred by N. peloronta and N. versicolor of which only the very large individuals move highest up (BANDEL & WEDLER 1987).

11.b Some Neritinae from the Eocene

In a group of Nerita species from the Eocene of Europe several have a low shell with three to five strong spiral ribs. The juvenile shell of what appears to be a Nerita tricarinata LAMARCK was studied coming from the locality Saffrée in the Paris Basin (COSSMANN 1925, Pl.6, Figs.18,41,42). The protoconch has an embryonic shell that measures about 0,12 mm in diameter and is surrounded and partly concealed by more than one whorl of larval shell. The whole protoconch measures about 0,7-0.8 mm in width and height (figs.271, 278). A slight collabral growth line ornament is developed, and the apertural margin is weakly sinuous. The teleoconch features three strong spiral keels between which numerous smaller ones appear with later whorls (fig.280). There are four whorls in the fully-grown shell. The inner lip is flattened, and its callus cover granulations. The columellar edge is granulated with the upper and the lower denticle larger and the ones in between on a slightly concave edge.

According to SZÖTS (1953, Pl.2, Figs.1,2) a similar species occurs in Gant (Hungary) and was also illustrated by OPPENHEIM (1896, Pl.5, Fig.8) and DAINELLI (1905, Pl.1, Figs.12,13). Nerita pentastoma DESHAYES 1866 differs by having more spiral ribs. It has an essentially smooth shell between the main spiral keels, as is the case in N. tricarinata, while these are filled with fine riblets in Nerita heberti. Nerita pentastoma according to COSSMANN (1925, Pl.6, Figs.18, 41,42) has a close relative in Dalmatia, which he called Nerita dainellii COSSMANN 1925. A species figured by KECSKEMETI-KÖRMENDY (1972, Pl.3, Figs.10-12, Pl.4, figs. 1-3) from the Eocene of the Dorog Basin is also of this group. In Neritina heberti SZÖTS 1953 the protoconch is smooth and rounded, and with begin of the teleoconch the shell bears four keels and becomes more and more flattened apically. In this apically flattened zone there are three or four finely granular spiral riblets, of which also some appear during shell growthon the sides. With four whorls the shell is fully-grown and measures about 7 mm in height and 9 mm in width. The slightly concave columellar edge is granulated with the upper and the lower denticle larger and the ones in between. According to SZÖTS (1953, Pl.2, Figs.3-5) this species is close to N. pentastoma. Specimens from Dorog are about 6 mm high and 8 mm wide (KECSKEMETI-KÖRMENDY 1972, Pl.4, Figs.4,8).

11.c Semineritina and Dontostoma.

The genus Semineritina COSSMANN, 1925 based on S. mammaria (LAMARCK 1804) from the Middle Eocene of the Paris Basin (COSSMANN 1925, Pl.6, Figs.37, 38) differs from most other Neritinae by shell shape and convex columellar lip. The shell is of rounded shape and ornamented by fine axial ribs. The inner lip of the aperture bears subequal rounded denticles (fig.267). The protoconch consists of several convolute whorls, which overlap only so much, that all remain well visible (figs.268-269). The genus was called Seminerita (not Semineritina) by WENZ (1938, Fig.1026). The even denticulation on the columellar lip and the relatively wide open coiling of the globular protoconch distinguish this species from Neritina which has uneven denticulation on the columellar lip and the whorls of the protoconch more strongly convolute and disguising each other. Semineritina mammaria with semispherical shell has fine collabral growth increments and a thickened inner lip callus that plugs the umbilicus. Its aperture is of semilunular shape with numerous rounded denticles on the inner lip. The protoconch measures 0.8 mm across and consists of almost 3 whorls, which strongly overlap but are all visible. The studied shells (figs.267-270. 272) were collected near Saffree.

Semineritina resembles with Mesoneritina YEN 1946 that is based on the early Cretaceous M. nebrascensis (MEEK & HAYDEN 1862) and represents also a genus with smooth shell and narrow callus of the inner lip, but with smooth columellar edge. A new species of Mesoneritina is described by BANDEL & KIEL (in prep.) from the Santonian of Hungary with small globular neritinid shell that has a smooth surface and an ornament of zigzag pattern and dots. The aperture has a comparatively narrow callus ribbon of the inner lip with smooth columellar edge, and simple outer lip. In the low spire the protoconch is that formed by a planktotrophic larva. Mesoneritina differs from Semineritina by having a smooth shell and a smooth columellar edge of the inner lip of the aperture. In addition Mesonertina has lived in estuarine brackish environment, while Semineritina lived in the shallow open sea. Neritina has a broader callus of the inner lip and the columellar edge has denticles, while that of Mesoneritina is smooth.

The genus Dontostoma KLEIN 1753 is characterized by a Nerita-like shell with ornament of collabral wrinkles or ribs and no spiral sculpture. The outer lip is weakly dented within or smooth, and the columellar lip bears 3 to 5 teeth in its central part, which is slightly concave. The callus of the inner lip is smooth or weakly transversely wrinkled. The outside of the operculum is smooth and has a raised ridged or granulated rim. The hinge on the inner columellar side of the operculum closely resembles that found among Nerita with wedge-like projecting ridge and marginal lamella with serration on the raised edge. The muscle attachment is seen as terraced spot between wedge and ridge.

The type of Dontostoma is Nerita polita LINNAEUS 1758 from the tropical Indo-Pacific, that according to COSSMANN (1925) was placed in the subgenus N. (Ritena) GRAY 1858. Dontostoma compared with Puperita reveals that the later has no axial ornament, and compared with Nerita by having no spiral ornament. If the ornament is considered a generically distinctive character, Dontostoma= N. (Linnerita) can be interpreted to represent an independent genus by its own. It could be connected to the Tertiary Semineritina. Puperita comes close and is also living on the rocky shore in tidal pools. But while the opercular hinge in Dontostoma is quite similar to that of Nerita, this hinge in case of Puperita more resembles that of Neritina. SAUL & SQUIRES (1997) described two Cretaceous species from California to belong here, or rather a smooth "Amphinerita". But their Nerita (Amphinerita) eos SAUL & SQUIRES 1997 from the Early Cretaceous has a smooth columellar edge of the inner lip, thus, represents a similar shell as is found among Jurassic Neritidae, for example the Neritoma relation.

The taxon Nerita (Linnerita) VERMEIJ 1984 had already been distinguished from the taxon Nerita (Nerita) as Dontostoma KLEIN 1753, in HERRMANNSEN 1845. It was characterized has having a low spire and, in contrast to Nerita s.str., no spiral sculpture but rather collabral sculpture that consists of closely spaced wrinkle-like ribs which are almost collabral in their arrangement. The subgenus was based on Nerita polita LINNAEUS 1758. Related species such as N. antiquata RÉCLUZ 1853 from the Philippines, N. doreyana QUOY & GAIMARD 1834 also known from the intertidal zone of the Indian

Ocean and *N. orbignyana* RÉCLUZ 1841 (Red Sea) all live in the Indo-West-Pacific region and may represent varieties of the same species, *Dontostoma polita* (see ABBOTT & DANCE 1982). According to VERMEIJ (1984) the collabral wrinkles of *Linnerita= Dontostoma* are best developed in *N. antiquata*. A mid-Miocene species belonging here is *Nerita gigantea* BELLARDI & MICHELOTTI 1840 as noted by STRAUSZ (1966, Pl.50, Figs.1,2) from the Paratethys. This up to 3 cm sized shell is smooth and closely resembles the living *Dontostoma polita*. Even the two teeth present on the inner side of the outer lip occur in modern varieties of this species as was shown by ABBOTT & DANCE (1982).

11.d Comparison with *Puperita*

Among the modern members of the subfamily Neritinae there are three genera with a smooth rounded shell that have rather special ecological requirements. Of these subgenus *Nerita (Puperita)* GRAY 1857 with the type *Puperita pupa* (LINNE 1767) from the Caribbean Sea lives in tidal pools in the rocky shore. It has a smooth shell ornamented with zebra-like stripes on white background (figs.58-60). The aperture has a smooth inner lip callus and the columellar edge has small denticles which start posterior of the centre with an indistinct larger denticle and a number of small ones (about 5) succeeding from a smooth portion near the posterior edge. The operculum is smooth on the outside and has a rib on the inside that is accompanied by a peg, which may be reduced (RUSSELL 1941).

Specimens from Nassau (Bahamas) and from Curacao were found to lives in tidal pools within the spray and splash zone. The fractured shell demonstrates a relatively thick outer calcite layer, and the bulk of the shell is formed by the aragonite inner crossed lamellar layer. The aperture and the smooth operculum are light yellow. The opercular hinge is here cow-horn like with a knob-like end of the ridge and a similar knob-like peg. The egg capsules of *Puperita* are like those of *Nerita* attached to the rock within the living environment and from them hatch planktotrophic veliger larvae. *P. pupa* lives in tidal pools in the rocky shore, in which they live submerged even though they may contain rather warm and salty water after extended sunshine or after rains quite diluted sea water. Since shell shape and ornament closely resembles that of some *Neritina*, *Puperita* was considered to represent a member of the genus *Neritina* by COSSMANN (1925) while WENZ (1938) considered it as independent genus. RUSSELL (1941) stated that *Puperita* does not entirely exhibit the characters of either the genus *Neritina* or those of *Nerita*.

In the Caribbean Sea there is also a *Puperita tristis* (ORBIGNY 1842) (figs.61-63) that has the same shape as *P. pupa*, but differs regarding its coloration that is in a pattern of black with small white dots (ABBOTT 1974, Fig. 526 a). According to RUSSELL (1941) *Puperita pupa* and *P. tristis* at places appear to mix. This can be confirmed by rare occurrences of *P. tristis* within the population of *P. pupa* collected at Curacao. *Puperita japonica* according to (HABE 1960) has 2,8 to 4 mm large egg-capsules, holding calcareous granules in their cover as found among the *Nerita* species (BANDEL 1982). From these capsules all young hatch as veligers. The protoconch of *Puperita bensoni* (RÉCLUZ 1850) was described by SASAKI (1998, Figs.78 c-d). It is globular and about 0,4 mm in diameter and smooth in contrast to the early teleoconch that has fine spiral lirae. Such fine spiral liration was used by WENZ (1938) in order to distinguish the smooth subgenera *P. (Puperita)* and the spirally delicately ornamented *P. (Heminerita)* (MARTENS 1887).

Puperita differs from *Nerita* by having a smooth shell and a cow horn-like hinge on the operculum without muscle scar. This later character also distinguishes from *Dontostoma*. The living environment is splash pool without influence of fresh water, and the thicker calcite outer layer of the shell distinguishes from *Neritina*. Larger size and living environment separates from the sea grass living *Smaragdia*. Regarding the shape of the teeth of the radula *Puperita* is closer to *Nerita* than to *Neritina* (see chapter 8).

11.e Comparison with the Smaragdiinae

The subfamily Smaragdiinae BAKER 1923 with the characteristic genus *Smaragdia* ISSEL 1869 has a small glossy shell that is smooth and obliquely ovate in shape. It is usually coloured in green with red flecks or stripes. The type is *S. viridis* (LINNÉ 1758) from the Mediterranean Sea. *Smaragdia* is considered to represent its own subfamily due to slight differences in radula morphology with *Nerita* and others. The genera *Smaragdia* and *Tanzaniella* are included. *Smaragdia viridis* has a small glossy smooth shell that is ovate oblique in shape. The inner lip callus is rounded, thick and convex, sometimes with a depression near the umbilical region, and there is a dented columellar edge. This edge is quite variable, and there may be hardly any denticle visible, or there may be up to 8 of them. Sometimes these denticles are well developed especially the basal and most apical one is expressed. A Pliocene representative of possibly the same species comes from SE-France (figs.240, 242).

Smaragdia from the Caribbean Sea consists of a 6 mm wide and 4 mm high shell of ovoid outline that consists of about 1,5 whorls of the teleoconch that succeed the rounded protoconch. Colouration is pea-green often with chalk-white zigzag bars and sometimes brown lines. It lives on turtle grass (ABBOTT 1974, BANDEL & WEDLER 1987). In Bali sea grass is settled by two different species of *Smaragdia* that can be distinguished easily by the size of their protoconch. The one with larger protoconch is a bit more roundish in shape and both have not quite two whorls of the teleoconch succeeding the protoconch (figs.241, 249). Regarding the teleoconch colouration is extremely variable and shell shape may be very similar to *Smaragdia* from the Caribbean Sea. According to SCOTT & KENNY (1998) four species of *Smaragdia* are known from Australia.

Tanzaniella LUPU 1979 also has a small shell of up to 2 mm height and 2.5 mm width with oblique aperture and simple columellar lip. The operculum is thick and has fine radial striations. It bears a single tooth on its inner side by which it clutches at the leg muscle. The type is *Neritina souverbiana* MONTROZIER 1883 from the Tanzanian shore. *Tanzaniella* is said to differ from *Smaragdia viridis* in regard to the number of the central teeth of the radula, which also differs from that of *Theodoxus* and *Nerita*. The shell closely resembles that of *Smaragdia* and it may prove very difficult to distinguish from *Smaragdia*.

In *Smaragdia* the cupola-shaped egg capsules have transparent walls, the greenish eggs almost matching the colour of the sea grass on which they are attached. *Nerita* secretes very similar egg capsules, however, aragonite or calcite spheres reinforce the capsule membrane and mask the eggs (BANDEL 1982). The egg capsule of *Smaragdia viridis* was found to contain about 100 eggs, which develop into hatching veligers within 16 days.

COSSMANN (1925) included *Smaragdia* as subgenus with the genus *Neritina* and suggested its presence from the late Cretaceous onwards, but the only species that looks like a modern *Smaragdia* appeard to be *N. expansa* REUSS 1856 (= HÖRNES 1856) from the Mid Miocene of the Paratethys (COSSMANN 1925, Pl.6, Figs.26-27). This *Neritina expansa* was redescribed by STRAUSZ (1966, Fig.35e,f), and it carries the characteristic tuberculation of the columellar edge with the largest denticle near the base. Specimens collected from mid-Miocene deposits at Varpalota in Hungary have an about 6 mm wide shell consisting of a little more than 2,5 whorls of the teleoconch and a rounded rather large protoconch that projects from the apex. The denticles on the columellar edge are very variable and ornament consists of delicate lines forming triangles, very similar as is the case in the modern Balinese species. But the shell of *S. expansa* from the Miocene is of more roundish shape, has a little larger teleoconch with more whorls.

Puperita and *Smaragdia* represent neritid species that resemble *Nerita* regarding their living environment, but in regard to shell shape they are closer to *Neritina*. As is the case in the later in *Smaragdia* egg capsules are purely organic. *Velates* could have arisen from smooth ancestral forms that also gave rise to *Smaragdia*, since it also lived in the normal marine environment. The resemblance

of the protoconch of *Velates* with that of *Smaragdia* could thus be explained (figs.273, 278 compared with 249). Tertiary species belonging to *Neodesmieria* and *Semineritina* may fill the gap.

The genus *Neodesmieria* MAGNE & VERGNEAU-SAUBADE 1974 is based on a semi globular shell of about 8 mm height and a little more width is smooth and has three visible whorls. The aperture is oblique has a thick inner lip callus and the columellar lip is smooth. The genus *Neodesmieria* is based on a single individual from the Oligocene of the Aquitaine with the type *Nerita sanctistephani* COSSMANN & PEYROT 1917.

Smaragdia appears to be represent a group of Nertioidea co-evolving with sea grass beds and occurs in all warmer seas on the globe. In contrast to *Nerita*, *Smaragdia* lives on that angiosperm turtle grass, in depths from the low water line down to more than 10 m, the green colour of its shell providing perfect camouflage. Sea grass evolved during the Cretaceous and was present already at Late Cretaceous time.

12. The Velatinae n. sufam.

Diagnosis: The shell in general outline is limpet shaped with a nearly flattened base and an evenly rounded top. The callus plate of the inner lip bulges strongly projecting from the basal plane and extends across the basal corner forming a crescent shaped callus rim on the side opposite to the outer lip of the aperture. The aperture is narrow with a rounded anterior portion and a narrow channelled apical portion. The columellar edge of the inner lip is more or less evenly dented, and there is a narrow furrow next to the inner side of the outer lip on both ends. The outer lip is thickened and smooth. The apex lies posteriorly and sideways. The protoconch is egg shaped, higher than wide, with the last whorl covering most of the former shell (figs.273-274). Its ornament consists of a fine collabral lineation. Only the very juvenile teleoconch is *Neritina*-like (figs.275) and the flattened base appears soon after metamorphosis. The subfamily is based on the genus *Velates* from which its name is derived.

Differences: In contrast to limpets of the Neritinae and Nertitininae the outer lip of the Velatinae does not form the base of the shell but the base is formed by callus of the inner lip.

The genus *Velates* MONTFORT 1810 according to COSSMANN (1925) is based on *Neritina schmiedeliana* CHEMNITZ 1786 which probably the same species as *N. conoidea* LAMARCK. According to WENZ (1938) this is also the same as *Nerita perversa* GMELIN from the Eocene of the Paris Basin.

The teleoconch of *Velates* may grow to large size (12 cm diameter) and acquires limpet-like shape (STRAUSZ 1966, Pl.4, Figs.1,4, Pl.23, Figs.6-9, Pl.24, Figs.1-3). While the juvenile shell is of low-spired naticid shape it changes during growth into patelliform adults by the addition of callus. *Velates* is rounded above and flattened below, but the base is not that of a limpet, since the callus of the inner lip forms a pad that bulges from the basal plane. This callus pad also extends across the basal edge onto the sides where the foot of the active animal lay. This contrasts to other neritioidean limpets where the outer lip of the aperture forms most or all of the contact between shell and substrate (BANDEL 2000). Thus, *Velates* can be placed neither in the Neritinae nor in the Neritininae or the Cretaceous Otostoma ralation (BANDEL & KIEL in prep). Its protoconch is that of a planktrotrophic larva (figs.273, 276) similar to that of the small sized Smaragdiinae, thus, they as well as the Theodoxinae with lecithotrophic development are also no alternative. Therefore they are placed in a subfamily by themselves to include the genus *Velates*.

The genus *Velates* holds some very characteristic large sized species found predominantly in Eocene shallow sea deposits. CUSHING-WOODS & SAUL (1986) found growth stages of *V. perversus* to include the change from tightly coiled juvenile whorls with naticiform shape and few teeth on the columellar edge of the inner lip to the reduced-coiled adult whorls with patelliform shape and exten-sive callus. According to CUSHING-WOODS & SAUL (1986, Figs.6, 1-3,8) the type is from the Paleocene of Vigny in France. COSSMANN's (1925, Pl.7, Figs.22, 23) *Velates schmiedelianus* is quite the same as the individuals here studied from Eocene of Dudar in Hungary.

Velates schmiedelianus from Dudar was analysed in detail. Here the juvenile shell with protoconch and one whorl of the teleoconch has all shell interior including that of the embryonic and larval shell united to form a uniform cavity with all internal walls dissolved. The last whorl of the protoconch is large and covers most of the former shell (fully-grown protoconch) is egg-shaped, about 0,4 mm wide and 0,5 mm high. The narrow aperture is in front enlarged into a collar like pediveliger-lip (figs.273, 276). There is very fine collabral step-like ornament on the last whorl as can be found among some protoconchs of modern *Neritina* and relatives (BANDEL & RIEDEL 1998).

In juveniles with low-spired naticid shell shape the columellar teeth on the edge of the inner lip are well developed (fig.275). Later on they may be more variable in shape. Transformation into patelliform adults occurs within juvenile growth stages after formation of about 1,5 teleoconch whorls by the addition of callus. Adult shells reach a size of 10 to 12 cm in width. In this large shell the spire is largely concealed by succeeding whorls and glazed over. In fully-grown individuals there are more than three whorls of the teleoconch. The base is plane or more commonly convex and covered by a thick callus, which results in a non-limpet typed apertural surface. The outer lip is not surrounding the whole base here, as would be the case in other typical neritoidean limpets such as *Pileolus* or *Septaria*. In addition the bulge of the callus projects over the shell margin creating a convex basal plane.

The uncertainty regarding the type to *Velates* is not very important in regard to the systematic placement, since all mentioned species are very similar to each other. Thus, *Velates* has at least three different species that can be distinguished clearly by shell shape, size, apex position, and probably also the shape and dentition of the columellar inner lip. According to CUSHING-WOODS & SAUL (1986) typical *Velates* with expanded thick callus covering the apertural face is known only from the Paleogene. They named the rather similar species *Velates noetlingi* COSSMANN & PISARRO 1909, *V. balkanicus* BONTSCHEFF 1897, *V. vizcainoensis* CUSHING-WOODS & SAUL 1986, and *V. californicus* VOKES 1935.

CUSHING-WOODS & SAUL (1986) and SAVAZZI (1992) suggested that *Velates* lived on firm to moderately soft bottom in slightly deeper water than most modern neritids. Only one exception should be noted among the modern Neritidae and that is *Smaragdia* (but see chapter 15). Regarding behavior great differences must be stated to exist between these genera. *Smaragdia* lives on the blades of the seagrass in shallow water to about 15 m of depth. *Velates* is usually found together with large foraminifera of the *Nummulites* type and has thus also lived in well-illuminated shallow seawater of areas with sandy bottom, perhaps also covered by sea grass. But it certainly did not live on the blades but may have been feeding from them as well. Shells of *Velates schiedelianus* grown to a size of about 12 cm in width resemble closely those illustrated by CUSHING-WOODS & SAUL (1986, Fig.5,16 and 5,18) with the name *Velates californicus* from the Early Eocene of California. This later species as well as *Velates noetlingi* from the Eocene of the Paris Basin is very close to *V. schmiedelianus* from Dudar and may even represent the same species. *V. vizcainoensis* is of more rounded shape and also has a convex inner lip margin (CUSHING-WOODS & SAUL (1986, Figs.5,8-5,14). According to these authors *Velates perversus* from the Paleocene has the apex higher up on the shell and also a rounded shape in front, while that of *Velates schmiedleinanus* is angular here and thin.

The protoconch of *Velates* is more egg-shaped than that of *Neritina*, but both show parts of the early whorls still uncovered by later whorls, as is also the case in *Smaragdia*. In *Tomostoma* the shell remains of smaller size, is thin walled, limpet-shaped and carries the apex acentrically on the posterior half, which differs from *Velates* that carries the apex at the side (STRAUSZ 1966, Pl.4, Figs.3,5.9). Also the patelliform shell of *Tomostoma* and has a broadly oval basis which is entirely formed by the outer lip that has grown around the margin, while the inner lip of *Velates* is formed by a thick callus pad that bulges and extends over the basal corner. CUSHING-WOODS & SAUL (1986) cited VOKES (1935) in stating that *Nerita umzambiensis* and *N. kaffraria* from Late Cretaceous Umzamba Formation of South Africa differ from *Velates*, which is confirmed by BANDEL & KIEL (in prep.).

13. The limpet family Phenacolepadidae

13.a Modern Phenacolepadidae

The genus *Phenacolepas* PILSBRY 1891 has been the name giving taxon on which this group of neritimorph limpets is based. The Phenacolepadidae PILSBRY 1895 represent a modern family of neritimorph limpets present with a number of species several of which live on the blades of sea grass (BANDEL & WEDLER 1987), or in cryptic environments within reefs (WARÉN & BOUCHET 2001). Nothing has remained of the inner lip or its derivates in the cap-like shell that is usually low and small (figs.294, 295, 298, 299, 301). The history of this group appears to range back to the Eocene (WENZ 1938). The shape of the radula clearly places this group of limpets with the *Nerita*-relation (THIELE 1929). HICKMAN (1984, Fig.10) illustrated the radula of *Nerita undata* jointly with that of *Phenacolepas osculans* and noted great similarity.

In case of specimen that could be studied at the collection of the Smithsonian Museum in Washington, it was noted that a species determined as *Phenacolepas cytherae* LESSON 1831 from near Ceylon consists of a very regular cup-like shell of 1-2 cm in diameter with oval, almost round aperture and central a little backward placed apex. Another one determined as *Phenacolepas mirabilis* is rather similar but even larger. In the genus *Hyalopatina* with *Hyalopatina rushii* (DALL 1889) the shell forms a rather flat cap that is almost smooth with an tuberculate periostracum and small globular protoconch of the *Nerita* type. It is seen from the inside of the shell that the inner walls of the protoconch are totally dissolved and this cavity is continuous into the general shell cavity. This genus is more shallow cup-like than the other Phenacolepadidae, and its ornament is smooth. *Phenacolepas pulchellus* LISCHKE is rather low and carries the apex near the back, the aperture is oval and there are radial ribs that form granules with the growth lamellae. The same species has been studied under the name *Cinnalepeta pulchella* (LISCHKE 1871) and SASAKI (1998, Fig.86) found a radula very similar to that of *Phenacolepas*. SASAKI (1998, Fig. 86) and BANDEL (1991a) noted the globular multispiral protoconch in undetermined species of the later genus from the Pacific. *Phenacolepas cancellatus* PAESE from near Hawaii is similar and also *Phenacolepas hamilei* from Florida and the Caribbean Sea. Of this later species the larval shell has been analysed and illustrated (BANDEL 1982) (figs.291, 293).

In regard the incorporation of the protoconch into the conical teleoconch Phenacolepadidae differ from the patellids. Here the larval shell is integrated into the limpet by having all internal walls dissolved away, while in patellomorphs the embryonic shell is closed off, as soon as there is a small limpet-teleoconch, and usually it is lost afterwards. In phenacolepadids the protoconch becomes a used portion of the teleoconch. The metamorphosed pediveliger first forms a *Pileolus*-like first juvenile shell with wide aperture before there is growth all around the limpet margin. In the Patellogastropoda the shell cup with continuous lower margin succeeds the protoconch consisting of the archaeogastropod-typical whorl of the embryonic shell right away.

Smooth neritimorph limpets resembling *Septaria* on one side (figs.292, 296, 299) and a flat *Phenacolepas* on the other side (figs.288, 289) live in Australian tropical shallow waters, and have been present during the Oligocene in Europe in similar environment as well (figs.286-287).

13.b The potentially ancestral phenacolepadid *Calyptronerita*

From the Eocene of Villers in the Paris Basin a small shell of what could be determined as *Calyptronerita* LE RENARD 1980 demonstrates transitional features from *Nerita*-like shells to such of *Phenacolepas*. The documented shell (Pl.14 Figs.297, 300)) consists of a little more than one teleoconch whorl added to the smooth and well rounded protoconch. This protoconch is quite large measuring about 0,9 mm in maximal diameter. In it the last whorl of the larval shell extends over the earlier whorls to a large degree and sutures are very indistinct. But a central apical convexity of about 0,25 mm in diameter represents earlier larval whorls as

well as the embryonic shell, which are coated over (fig.297). The transition to the teleoconch is sudden and with straight margin. Teleoconch whorls increase in width rapidly during growth, and the shell with one whorl of the teleoconch is more than 3 mm in width. With a further half whorl it would reach about 6 mm in diameter. Ornament of the teleoconch consists of a rather regular pattern formed by collabral ribs crossed over by fine spirally arranged lirae. There are about 40 axial ribs counted in one whorl and about 50 fine spiral ribs crossing them. The resulting pattern is very close to that seen in *Phenacolepas hemphili* living in the Caribbean Sea (figs.291, 293).

According to DOLIN & RENARD (1980, Pl.1, Fig.9) the type to the genus *Calyptronerita* is *C. dolinorum* LE RENARD, 1980 from the Auversian of the Paris Basin. The shell is, when fully-grown limpet-like with the inner lip below shell margin and concave, and shell shape resembling that of a *Calyptraea*. A relation is suggested with *Vergnesia* DELPEY 1940 from the Late Eocene of the Paris Basin (KNIGHT et al. 1960, Fig. 184, 1a,b) where the inner lip is even more like that found in *Septaria* and the teleoconch more limpet-like. The type species of *Calyptronerita* measures 14 mm in width, so that it is not at all clear whether the here documented species belongs to it or not, since it appears to have only about half size.

14. Neritiliidae and possible relations

The family Neritiliidae SCHEPMAN 1908 is distinguished by features of the radula (THIELE 1929). In the name-giving genus *Neritilia* the radula differs from that of *Nertina* and relation by having no central teeth (BAKER 1923, RUSSELL 1941, STARMÜHLNER 1976, BANDEL & KOWALKE 1999). The operculum has only a simple marginal ridge (fig.306), in contrast to *Neritina* (STARMÜHLNER 1993, Pl.7, Fig.37). The central genus of this taxon is *Neritilia. Pisulina* was placed in the Smaragdiinae by THIELE (1929) and WENZ (1938), but it actually belongs in the Neritiliinae and has the same type of radula as was documented by KANO & KASE (2000a, Fig.12). Also the protoconch is distinctive. In species with free larval stage it bears spiral liration in its final whorl (BANDEL & RIEDEL 1998, KANO & KASE 2000a).

14.a *Neritilia* and relation

Neritilia is represented by a few species, which usually live in the estuarine environment, and here mostly in places where continuously fresh water conditions can be entered. This ecology was observed in case of *Nertitilia rubida* in Cebu (BANDEL & RIEDEL 1998) (fig.304, 307), and in Bali (own observations 1991, 1999). It has been described from the Caribbean Sea in case of *Neritilia succinea* (RÉCLUZ 1841) by RUSSELL (1941), and from Western Africa and here *Neritilia monoeli* DOHRN 1866 in the end of streams coming from Mount Cameroon (BOETTGER 1905, BANDEL & KOWALKE 1999). *Neritilia consimilis* MARTENS 1879 was found in streams of Islands of the Indian Ocean (STARMÜHLNER 1976, BROWN 1980) and its occurrence in South Africa is described below.

All species of *Neritilia* MARTENS 1879 are small (about 2-5 mm), have an obliquely egg-shaped, subglobular shell that is smooth and has a semicircular oblique aperture. The inner lip consists of a narrow callus and smooth columellar inner margin. The operculum of *Neritilia* has a simple apophysis (fig.306). The protoconch of species with planktrotrophic larva is spirally lirated (BANDEL & RIEDEL 1998, KANO & KASE 2000a, Fig. 10) (fig.304). The genotype is *Neritina rubida* PEASE 1865 from Tahiti (fig.302). According to POINTIER & MARQUET (1990, Pl.2, Fig.3) *N. rubida* from French Polynesia is the same with *N. hawaiiensis* KAY 1979.

BANDEL & RIEDEL (1998) found that veligers of *N. rubida* from Cebu hatch with a shell diameter of about 0.11 mm. The veligers have to cope with freshwater for only a short distance until they reach the estuary or hatch at the estuary proper respectively. They probably remain free-swimming larvae and feed in the marine plankton for several weeks. The veligers develop a multispiral globular shell, which measures about 0,3 mm across when the larva is ready to metamorphose. Spiral rows of pits produce a characteristical ornament (BANDEL & RIEDEL 1998, Fig.6A-B). Metamorphosis occurs preferably in the upper reaches of the estuary from where most individuals migrate into the freshwater and only few remain in the brackish influence. Migration is sometimes supported by larger gastropods, the shell of which may be used as carriers by the minute *Neritilia*.

Neritilia consimilis (MARTENS 1879)

Individuals from the South African coast have a small shell. With 1,7 whorls of the teleoconch that measures only about 2 mm in width and 1,5 mm in height. The shape is oval egg-like with convex apical side and in juvenile stage of yellowish coloration while older individuals are brownish or have a black outer layer that formed due to subsequent deposition of ironoxides. The aperture is semicircular and wide with non-dented columellar lip. The callus of the inner lip is wide and shiny and the operculum is thin with reddish inner and outer side. A thin ridge-like appendage is present which extends over the edge.

Neritilia was noted in the upper reaches of the Umzamba estuary and the same environment in the Mnyameni River to the south of Umzamba River, both in Transkei (northern Cape Province). Here it lives in the river from just above the reaches of the highest tides to the begin of true estuarine conditions, where at low tide the water remains standing. Its small egg capsules are attached on the lower side of rocks, together with sponge crusts.

Differences: According to STARMÜHLNER (1993, Pl.14, Figs.158,159,160)) the shells of *Neritilia consimilis* are obliquely elliptical and not transversely ovate as in *Neritilia rubida*. The aperture of *N. consimilis* is oblique and semi-elliptical, but not extended as in *N. rubida*. STARMÜHLNER (1983) considers *N. consimilis* and *N. rubida* to be closely related species but distinct from each other even though they live in exactly the same type of environment. In case of *Neritilia manoeli* the shell is larger measuring up to 3.5 mm in height and 4 mm in width but otherwise shell features are the same (BANDEL & KOWALKE 1999). The Caribbean *Neritilia succinea* (RÉCLUZ 1841) is relatively large (up to 5,5 mm wide and 5 mm high), consists of 2,5 whorls and its radula is quite like that of the other species of this genus (RUSSELL 1941, Fig.4). Own material from Guadeloupe demonstrates that the shell is transversely ovate, as described in case of *N. rubida*. According to STARMÜHLNER (1976) the genital system of *Neritilia rubida* is quite different from that of *Neritina*, as had already been noted by ANDREWS (1937).

A *Neritilia panamensis* MORRISON from Rio Juan Diaz near Panama City with wide aperture shows only growth lines and is smooth (housed at the Smithsonian Museum in Washington). The inner lip has no dentition and the shell appears to be punctate especially below the callus of the inner lip. The embryonic shell is well differentiated from the adult shell. *Neritilia succinea* of Alligator Pond in Jamaica is similar to the species from Panama and also is punctate, but the embryonic shell is very smooth and hidden below the juvenile whorls. It lives in lakes and rivers near the sea. In Hawaii *Neritilia hawaiiensis* has been reported (KAY 1979, Fig.19k.l) from Makalawena Pond.

Neritilia also lived in the Mediterranean Sea during the Pliocene as documented by a little shell extracted from sediments of that age exposed near Nice, SE France (figs.303, 305). A species from the late Oligocene of Greece was described by HARZHAUSER & KOWALKE (2001). But these authors created a rather problematic addition to the Neritiliinae with their new genus *Agapilia* HARZHAUSER & KOWALKE 2001. Its type species is defined to be represented by *Nerita picta* FÉRUSSAC 1825 from the Aquitanian (Late Oligocene) of southern France. This species according to COSSMANN (1925) is common and polymorph, occurring up into the Miocene, and it is obviously larger than any modern *Neritilia*. HARZHAUSER & KOWALKE 2001, Fig.2, 5-10) illustrated *Agapilia picta* with individual from the Oligocene of Agapi as shell that is a little wider than high. But unfortunately they included at least two different species within their new genus (Fig.2, 5-8 and Fig.2, 9-12) of which the proposed type species is not

a member of the Neritiliidae. STRAUSZ (1966, Pl.49, Figs.13-17) described *Neritina picta* (FÉRUSSAC 1825) from the mid-Miocene of the Paratethys as roundish to laterally flattened *Neritina* with variable coloration that grew to a size of about 1 cm. Its columellar lip has the characteristic features of *Nertina* with a large apical denticle and smaller ones below it. PAPP (1954) had noted its wide variation in shell shape and ornament from the Sarmatian brackish water environment of the Paratethys. The *Neritilia*-like species from Greece, in contrast, is preserved with protoconch that has the features of *Neritilia* especially the ornament of spiral rows of pits. So in spite of the taxonomic confusion created by HARZHAUSER & KOWALKE (2001) they demonstrated the occurrence of *Neritilia* in the brackish water fauna of the Oligocene of the Mediterranean Sea.

Genus *Pisulina* NEVILL & NEVILL 1869

Pisulina had been placed with the Smaragdiinae by THIELE (1929) and WENZ (1938). HERBERT & KILBURN (1991) distinguished *Pisulina* from other neritimorphs by having the axis of coiling of the protoconch differing from that of the teleoconch. *Pisulina* actually belongs in the Neritiliinae as was documented by KANO & KASE (2000a). According to these authors the globose neritiform shell is smooth. The inner lip of the aperture consists of a smooth callus and has a projection with one tooth in the type species, and 3-7 teeth on its columellar edge in the other species. The outer lip is smooth. The inner walls are resorbed. Several spiral ribs ornament the protoconch. The teleoconch consists of less than four whorls. The thin operculum is semicircular with an apophysis near the base of the inner margin and smooth paucispiral outer side. It consists of an outer corneous layer with smooth surface and an inner calcareous layer with growth lines and a long ridge.

The type is *P. adamsiana* NEVILL & NEVILL 1869 from Sri Lanka. Its protoconch has been illustrated by SASAKI (1998, Fig.78,g,h). It is about 0,5 mm in diameter and of globular shape with whorls strongly overlapping onto each other. The species was found by (KANO & KASE 2000) to live in the tropical and subtropical Indo-Pacific mostly in submarine caves. The 6,5 mm wide and 6,7 mm high shell is thick, globose to obliquely ovate with a robust quadrangular projection on its inner lip. The protoconch is globular more than 0,2 mm in diameter and ornamented by 3 or 4 spiral ridges and microscopic pits. Such a multispiral protoconch is also present in *P. subpacifica*, with smooth embryonic shell that is largely involved with the larval shell that bears four or five spiral ridges and many minute pits. The inner walls of the protoconch are resorbed. (KANO & KASE 2000a) found 6 species the oldest of which is of Miocene age.

Within this genus *Pisulina* the species *P. biplicata* THIELE 1925 from Okinawa has non-planktotrophic development and simplified embryonic shell (KANO & KASE 2000a, Fig.5). This marine species that lives within submarine caves has, thus, a similar development as found in *Theodoxus*, but in the marine environment. *P. biplicata* in contrast to *P. adamsiana* has 3-5 blunt teeth on its inner lip and a paucispiral protoconch. The cave dwelling *Pisulina maxima* KANO & KASE 2000 is relatively large with 12 mm wide and 10 mm high shell and also paucispiral protoconch. (KANO & KASE 2000a).

According to these authors the operculum of *Pisulina* differs from that of all other Neritimorpha. It is paucispiral, calcified on its interior surface, bears an apophysis without peg but the nucleus lays centrally (not acentric like in others). While other neritoids have only 0,7 volutions *Pisulina* has more than one succeeding the embryonic/larval one (KANO & KASE 2000, Figs.8,9). They found living animals on the walls of shallowly submarine caves of the tropical Indo-Pacific between Hawaii and the Philippines.

Also the genus *Pisulinella* KANO & KASE 2000 belongs into this relation. The type species is *Pisulinella miocenica* from the Miocene of Eniwetok Atoll (KANO & KASE, 2000b). According to these authors the genus resembles *Pisulina* and has 3-4 teeth at the margin of the inner lip of the aperture. The outer lip has weak denticles on its inner side. The protoconch has spiral striae like that in *Pisulina* and *Neritilia*. *Pisulinella* differs from *Pisulina* by having tubercules on the outer lip and a shallow groove on the callus of the inner lip, both of which are present neither in *Neritilia* nor in *Pisulina* (KANO & KASE 2000). The difference between *Pisulina* and *Neritilia* lies in the denticles present on the edge

of the inner lip. *Pisulinella* differs in having also denticles on the inner side of the outer lip, when fully grown, while the other two are here smooth.

14.b. *Schwardtina* BANDEL & RIEDEL 1994

The type species of *Schwardtina* is *Helix cretacea* TAUSCH 1886 from the Ajka coal deposits of Senonian age in the Bakony Mountains of Hungary. It has an around 2 mm large shell with globular shape that resembles *Hydrocena* in its general morphology. The about 3 smooth whorls of the teleoconch with a spire angle of about 50° have all internal walls including the columella resorbed. The simple aperture has a thickened inner lip that covers the umbilical region.

Schwardtina cretacea according to BANDEL & RIEDEL (1994 Pl.1, Figs.1-6) has a characteristic egg-shaped and inflated protoconch that is about 0,4 mm wide and 0,25 mm high and an ornament of irregular punctuation. The initial shell cap is demarcated by a circular groove and has a diameter of 0,12 mm. In the centre of the initial cap lies a circular region ornamented by minute pits. The last whorls of the teleoconch occupy 3/4 of the total height. The aperture has a sharp outer lip and a broad inner lip that is thickened to form a callus. The protoconch of *Schwardtina* is typical for non-planktotrophic species with inflated embryonic shell that is succeeded by the teleoconch and not by a larval shell. The protoconch type, in combination with the resorption of the columella, is diagnostic for aquatic Neritoidea (BANDEL 1982). However, a similar teleoconch among the neritimorphan gastropods is only known from the terrestrial genus *Hydrocena*, which is still unknown from Mesozoic deposits.

14.c Hydrocenidae TROSCHEL 1856

The members of the terrestrial genus *Hydrocena* PFEIFFER 1847 have been classified as order Hydrocenina TROSCHEL, 1856 and superfamily Hydrocenoidea TROSCHEL 1856 and family Hydrocenidae. This family holds only the one genus *Hydrocena* according to THIELE (1929), with subgenera such as *H.* (*Chondrella*), *H.* (*Georissa*), and *H.* (*Georissopsis*). Hydrocenidae dissolve their inner shell walls (WENZ 1938) as is the case among Neritidae, but they have become lung breathing land snails. Their operculum resembles that of the Neritiliidae, and the radula resembles that of the Neritidae in general, but has special features (SASAKI 1998, Fig.90). On the inner side of the operculum muscle attachment is supported by one digitiform apophyis (SCOTT & KENNY 1998, Fig.17, 76 B, C). Species commonly are very similar to each other differing only in ornament, with some species spirally lirated while others have a smooth shell (CLIMO 1973). They are most common on limestone and here among moist litter in areas with tropical or warm climate. While the shape of the embryonic shell (figs.308-315) indicates a close relation to the Neritoidea (BANDEL 1982, SASAKI 1998) the occurrence of the Hyrocenoidea in the Old World as well as the New World and its range from New Zealand- Australia to Europe- Asia provides evidence for a Pangean origin. Hydrocenoid history might go back to the Early Mesozoic but there is no fossil record. Only one species is found in Africa, and that is *Hydrocena nilotica* BENSON from South Africa.

The subgenus *Hydrocena* (*Hydrocena*) PFEIFFER, 1847 has a shell ornament consisting only of growth lines. The subgenus *Hydrocena* (*Georissa*) BLANFORD, 1864 in contrast has a shell ornament that consists of spiral ribs. For example the species *Hydrocena* (*Georissa*) *williamsi* GODWIN AUSTEN 1889 from Bali is a very common snail on and under litter in the forest on the mountains within the slopes of the large crater lakes. It lives in continuously moist mountain forests in Bali and can be encountered sometimes with a dozen individuals of this tiny species on the lower side of one rotting leave. The shell is small measuring only about 2,5 mm in height and 1,8 mm in width with 3,5 whorls (VERMEULEN & WHITTEN 1998, Fig.15). Ornament consists of spiral ridges on the last whorl varying in number (fig.308). Its embryonic shell measures about 0.4 mm in width and height and is ornamented

by ribs. In other species the shape and size of the shell is similar, but ornament differs somewhat (figs.309-315)

The other terrestrial group of the Neritimorpha are the Helicinoidea that have developed quite a number of species, which are easily differentiated from those of the Hydrocenoidea (THOMPSON 1980). Fossil species have been described from strata as old as the Carboniferous (KNIGHT et al. 1960). However, these shells must remain doubtful due to convergence with the pulmonate Stylommatophora on one side and caenogastropod landsnails especially among the Cyclophoroidea on the other side (SOLEM 1983).

15. Neritimorphs in the exotic environment of the seeps and hot vents in the deep sea

The normal living environment of Neritidae is the shore, commonly the intertidal regime. Even *Smaragdia* and *Phenacolepas*, which prefer the sea grass beds, are somewhat exceptional. But much more deviating from the "normal" living environment are some species that have moved into the deep sea and here to hydrocarbon seeps and hydrothermal vents.

The genus *Bathynerita* CLARKE 1989 based on *B. naticoidea* CLARKE 1989 lives on oil seeps and hydrothermal vents in 500 to 700 m depth in the Gulf of Mexico (CLARKE 1989). The about 1 cm large smooth and simple shell with rapid increase in shell diameter is equipped with an operculum that carries an internal peg and is smooth with only growth lines and spiral nucleus near the anterior inner edge. The aperture is widened to such a degree that the shell can almost be considered to belong to a limpet, but the operculum still seals the aperture a little behind the outer apertural edge of the mouth. The apex is always corroded and succeeded by 1-1,5 teleoconch whorls of about equal width and height. It has a characteristic radula (WARÉN & BOUCHET 1993). Its columellar edge is smooth and usually concave, with a narrow callus of the inner lip, almost smooth and simple. The outer shell layer is of calcite and smooth, with only growth increments as apparent ornament, but also rather indistinct spiral ornament present as well. It probably is a simplified *Nerita* on the merge to become a limpet. Its ontogeny includes planktotrophic larvae, which hatch from typical neritid egg-capsules that apparently, in contrast to shallow water *Nerita*, have no calcarous spherules in their lid portion (WARÉN & BOUCHET 2001, Fig.30).

The genera *Shinkailepas* OKUTANI 1989 and *Olgasolaris* BECK 1992 are Phena-colepadidae, which have evolved to live in deep water next to hydrothermal exhalations feeding on bacterial crusts (OKUTANI et al. 1989, BECK 1992, 1997, WARÉN & BOUCHET 2001). Their radula closely resembles that of *Phenacolepas* (BECK 1992, WARÉN & BOUCHET 2001). They represent species with limpet like shell and with the cancellate ornament of *Phenacolepas*. But in contrast to the later the shell has pores. The protoconch is of the *Nerita*-type (BECK 1992, Pl.1, Fig.6, Pl.5, Fig.1).). As is characteristic to these the whorls of the larval shell of *Olgasolaris tollmanni* BECK 1992 are tightly coiled so that BECK had the misleading impression that the protoconch was reduced in morphology, while it actually represents the typical neritid shape. Such typical shape is present in case of *Shinakolepas briandi* WARÉN & BOUCHET 2001 that has a 0,8 mm large protoconch consisting of several whorls (WARÉN & BOUCHET 2001, Fig.32f). The radula is very similar to that of *Phenacolepas* (FRETTER 1984, OKUTANI et al. 1989, HICKMAN 1984, BAKER 1923, BARNARD 1963, THIELE 1909, BECK 1992). *Shinkailepas tufari* BECK 1992 according to BECK (1982 Pl.2, Fig.4) is described as having crossed lamellar structure and nacre in one shell, which is clearly a mistake, since the figured shell-structure is that of the inner callus cover which on first sight resembles nacre but actually is composed of the scaly layer (BANDEL 1979, 1990) as it commonly is found among different gastropods with dominantly crossed lamellar structure. (BECK 1992) noted that the radula places this genus within the *Phenacolepas* relation, but for hot vent species he suggested the subfamily Shinkailepadinae OKUTANI & OHTA 1988. BECK (1997) speculated that Phenacolepadidae including the Shinkailepadinae of the hot vents in the deep ocean were related to the fresh water species of *Septaria* and *Neritina* (*Clypeolum*), and he also speculated that the

rhipidoglossan Neomphaloidea, Peltospiridea, Lepeto-driloidea and Clypeosectoidea have derived from the same ancestral archaeogastropod group from which the *Nerita*-group came. But these speculations are unlikely to be correct. *Olgasolaris* is a typical phenacolepadid genus that occurs in a rather unusual environment of hot vents, but had its origin among shallow water relatives.

16. Conclusions

The similarities found in shape and composition of the shell of *Neritina* on one side and *Theodoxus* on the other indicates that both are related. The living environment preferred by these also documents this relation. But since, as shown here, *Theodoxus* has an independent history ranging back for more than 60 Million years its characteristic ontogeny including nurse egg feeding is considered a subfamily character. Ontogeny by nurse egg feeding, thus, distinguishes the Theodoxinae from the Nertininae, which have a planktotrophic larva. Both together are united within the Neritinidae and thus in a family that is distinguished from the Neritidae by an independent history ranging back well into the Mesozoic Era, perhaps to the Jurassic and thus for about 150 Million years. But there is also a strong possibility that *Neritina* and the Nertinidae may connect with the Jurassic-Cretaceous Neritoidea of the *Neritoplica* relation (BANDEL & KIEL in prep.). Members of this genus still lived in the fully marine environment during the late Cretaceous.

Life in the coastal swamps in brackish and commonly fresh water conditions distinguishes the Neritinidae from the Neritidae while ontogeny as planktotrophic marine larva with basically the same shell or protoconch type unites them.

Within the Neritidae the relation of *Nerita* can be traced back to the mid Cretaceous forming the Neritinae. They have their special ecology, which is the rocky tropical shore and similar surrounding such as the roots on the seaward side of mangrove forests. Apparently *Smaragdia* has branched off from these or their stem group when sea grass became available and adaptation to living on its blade-like leaves formed the Smargdiinae. Here probably quite a number of species evolved which still need to be differentiated in more detail. A good and useful character to distinguish species is here supplied by the shape and size of the protoconch.

Most Neritinae have a spirally arranged shell ornament, and it may well be that axially ornamented and smooth species such as *Dontostoma* and *Puperita* can be proven to have a history that reaches far back in time. The shell composition with relatively thick calcitic outer layer, the shape of the columellar lip with denticles in a median depression, and the mode of life in the fully marine coastal environment of splash pools brings *Puperita* closer to *Dontostoma* than to *Neritina*. This is despite the fact that the black zigzag ornament on white background and the general shell shape closely reminds of *Neritina*. The construction of the hinge of the operculum reminds of *Neritina* more than of *Nerita* and *Dontostoma* while the radula is close to that of *Nerita*.

During the Paleogene the large sized and peculiar *Velates* evolved and after Eocene time became extinct again, forming the extinct subfamily Velatinae. They are distinguished by their size and the callus covered flattened base, as well as having a peculiar shape of larval shell. This protoconch is much more similar to that of *Nerita*, *Smaragdia* and *Nertina* as is the protoconch of the *Neritilia* relation. Here also the radula differs so that the whole group including *Neritilia*, *Pisulina* and *Pisulinella* are considered to represent their own taxon, quite distinct from the Neritidae, which would, therefore, represent the Neritiliidae. A

possible transition from Neritiliidae could exist to the *Hydrocena* relation of minute land snails via such Cretaceous species as for example in *Schwardtina*. But this later relation is still quite speculative and it would be good to have more information on fossils species and also on the ontogeny of modern *Hydrocena*.

The large amount of species that have been described for *Theodoxus* from the Neogene of the Paratethys Basin, as well as the confusing database on especially the Indopacific species of *Neritina* can find an explanation when the process of hybrid formation is here involved. In both cases meeting of species depends on factors that are independent of the activities of the involved species. In case of *Neritina* it is chance currents that carry veliger larvae from the estuary of one island or continent to the next, and in *Theodoxus* it is the reshuffle of catchment areas of rivers and the rearrangement of inland seas that allows migration and meeting of species. In this study it is shown that some species hybridised with each other when meeting in one region while more or less the same did not mix there genes and remained separated in another region. Why this is so is quite unknown. But the process of evolution is clearly influenced by the possibility of interbreeding. Evolutionary pathways in space and time are more difficult to recognize when such sudden exchanges of genetic material occur between species that had a more or less extended history in geographically distant and distinct regions.

Neritina and *Theodoxus* are not the only taxa of gastropods in which hybrids appear to be in important factor that has to be taken into account when their evolutionary history is reconstructed. A similar influence was discovered in the relationship of *Melanopsis* (BANDEL 2000) and is expected also among genera like *Thiara*, *Melanoides* and *Tarebia* of the Cerithioidea (Caenogastropoda) of fresh water and estuaries. The result would be a net-like interrelation among related species during the evolutionary process in time connected with the usual branching in a bush-like manner as is considered the "normal" mode in which evolution from one to the next species proceeds.

Neritoidea traced back to the Triassic appear to have been living mostly at the shore or near to it. But as well as managing to settle land and fresh water, some have adapted to the rather different conditions of deep water hot vents and oil seeps.

Acknowledgements

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An annotated catalogue of fossil Ripiphoridae, taxonomic notes, and the description of a new genus and species from Baltic amber (Coleoptera: Ripiphoridae: Ripidiinae)

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With 15 figures

Contents

Abstract

Pauroripidius gen. nov. (Ripiphoridae: Ripidiinae) is described from Baltic amber. It is uniquely characterized by eight-jointed antennae with the distal five antennomeres uniflabellate and it shares with some extant ripidiine genera the reduction of the maxillary palpi to an unjointed, knob-like protuberance. The type species is *Pauroripidius groehni* sp. nov. It is possible that a previously described copal specimen is generically identical with *Pauroripidius* gen. nov. Should this prove true, *Pauroripidius* gen. nov. may contain as yet undiscovered extant species. All records of subfossil and

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