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Cretaceous volutid Neogastropoda from the Western Desert of Egypt and their place within the Neogastropoda (Mollusca)

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With 49 figures

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Abstract

Among modern Rachiglossa (Neogastropoda) the Volutidae are characterized by the mode of their early ontogeny that is always connected to much yolk consumption and a relatively large embryonic shell. Young hatch after completion of the metamorphosis crawling away from their spawn. The large size of their protoconch indicates that the four here newly described species *Caricella (Misrimelo) klitzschi*, *Misricymbiola chalmasi*, *M. conocoi*, and *Plicoliva (Misriplicoliva) bartheli* from the Maastrichtian of the Western Desert of Egypt hatched after a yolk-rich embryonic development had been completed. Their teleoconch shape relates them to modern members of the Volutidae. Shell-shape also resembles that of some members of the Cretaceous Pyrifusidae, especially species of the Volutoderminae. Most of the latter differ from Volutidae by having had a planktotrophic larva that was provided with a relatively small protoconch consisting of several whorls. The here described Cretaceous Volutidae are recorded from the southern shelf area of the Tethys Ocean on the African continent indicating that Volutidae may have originated here and from this area of their possible origin spread only by crawling young and not by free swimming larvae.

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Zusammenfassung

Unter den heute lebenden Rachioglossa (Neogastropoda) sind die Volutidae durch ihre Embryonal-Entwicklung ausgezeichnet, bei der immer viel Dotter aufgenommen wird und daher eine relativ große Embryonalschale gebildet wird. Die Jungtiere schlüpfen daher meist lange nach Abschluss der Metamorphose als kleine Kriechtiere aus ihren Gelegen. Die Größe des Protoconches belegt für die vier hier neu beschriebenen Arten *Caricella (Misrimelo) klitzschi*, *Misricymbiola chalmasi*, *M. conocoi* und *Plicoliva (Misriplicoliva) bartheli* aus dem Maastrichtium der westlichen Wüste in Ägypten, dass sie nach einer dotterreichen Embryogenese schlüpften. Die Gestalt ihres Teleoconches bringt sie mit heute lebenden Angehörigen der Volutidae in Verbindung. Auch die kretazischen Pyrifusidae und unter ihnen besonders die Angehörigen der Volutoderminae haben ähnliche Schalen, doch unterscheiden sie sich von den Volutidae dadurch, dass in ihrer Ontogenese meist eine planktotrophe Larve auftrat. Sie besitzen einen verhältnismäßig kleinen Protoconch, der aber mehreren Windungen umfasst. Die kretazischen Volutiden lassen sich zuerst vom südlichen Schelf des Tethys Ozeans belegen. Das legt nahe, dass die ersten Volutidae auch hier entstanden sind, und ihre Ausbreitung anschließend nur kriechend erfolgte und keine schwimmfähigen Larven mehr auftraten.

I. Introduction

Gastropods belonging to neogastropod family Volutidae represent a rather typical group that can be recognized as independent unit within the Neogastropoda (RIEDEL, 2000). Among its members the largest living marine gastropods occur with up to 500 mm large shells (WILSON, 1994, POPPE & GOTO, 1992). Volutids are large carnivores which usually prey upon worms and mollusks. They crawl with their large and broad foot and bury within soft sediment when resting. The edge of their mantle may be extended onto the shell when the animal is active and add shell material to the outside, sometimes forming a glaze on the shell surface. The operculum may be reduced in size or lost. The pallial cavity is oriented to the right and the siphon lies above the head. The exhalent opening is on the posterior edge of the long body whorl. Here it usually forms a canal at the posterior corner of the aperture. Typically the shell has columellar folds. Most species live on the continental shelves.

Among the taxa of Neogastropoda early ontogeny usually follows two different strategies (SIMROTH, 1895, THORSON, 1940, 1946, AMIO, 1963, THIRIOT-QUIÉVREUX, 1972, SHUTO, 1974, BANDEL, 1975a, 1976, 1982, and see references here). The first strategy is connected to relatively small and numerous eggs which are present within the shelter of an egg capsule. These develop into veligers that hatch and continue development as planktotrophic larvae which swim in the open sea for a more or less extended time feeding on small organisms. In this case an embryonic shell is formed within the egg capsule before hatching and a larval shell that grows during pelagic life is added to it. Both embryonic and larval shell together compose the protoconch. In the second strategy a lecithotrophic development occurs within the shelter of the egg capsule connected to more or less yolk consumption and the young hatch as crawling miniature adults. The growing embryo feeds either on liquid or granular yolk or on nurse eggs, in some cases on several of these food-sources which are contained within the egg capsules. In case of lecithotrophic development the protoconch is usually much larger, has a simplified outline, and no larval shell is developed. All species of the modern Volutidae, as far as known, develop mainly on liquid or granular yolk found in their egg capsules. Their protoconchs are usually very large (DARRAGH, 1988, POPPE & GOTO, 1992, RIEDEL, 2000).

Stem group representatives of several of the modern families of the Neogastropoda can be recognized quite well from Paleogene marine deposits. In case of the Cretaceous

species their exact place in the system of modern gastropods can rarely be ascertained (RIEDEL, 2000). Of many representatives of those species that have been regarded to present Neogastropoda from the Ripley Formation in northern Mississippi and southern Tennessee by SOHL (1964a,b) the protoconch has been studied (BANDEL & DOCKERY, 2003). Accordingly a morphology was found that commonly differs from that seen among the protoconchs of the modern Neogastropoda. But in case of the here described Maastrichtian species matters differ. Here large protoconchs resembling those of modern volutids like *Adelomelon* and *Cymbiola* are recognized and their teleoconchs resemble those of modern species as well (POPPE & GOTO, 1992). These shells from the Western Desert of Egypt had been collected by BARTHEL and HERMAN-DEGENS in the year 1971 (BARTHEL et al., 1981). QUAAS (1902), SERRA (1973) and ROSSI (1959) had described some species from the same or similar localities.

The studied specimen including the holotypes of the newly described species are deposited in the collection of the former SFB 69 in Berlin.

II. About the living Volutidae

The taxonomy of the Volutidae has been based mainly on the characteristics of the shell, and on the shape and number of the teeth of the radula. Both characters exhibit controversial trends (CERNOHORSKY, 1970, WEAVER & DUPONT, 1970, DARRAGH, 1988, LEAL & BOUCHET, 1989, POPPE & GOTO, 1992, RIEDEL, 2000, see further references here). Another feature utilized in the classification of modern Volutidae is geographic distribution (WEAVER & DUPONT, 1970, POPPE & GOTO, 1992). Also their occurrence in water of different depth and temperature has been utilized which appears to be of value within cold water species. POPPE & GOTO (1992) distinguished 43 modern genera, and about 500 living species of the Volutidae are thought to be in existence, mostly found in the southern Hemisphere. DARRAGH (1988) suggested that a third of all living species is found around Australia and they are common here at least since Mid-Tertiary times.

The shape and size of the protoconchs of Volutidae as aid in the identification at a generic level is of little use because it may be very variable. Even at the species level protoconchs show much variation in shape and size (POPPE & GOTO, 1992). The egg masses produced by species of the Volutidae varies quite a bit in size and shape. The egg capsules of *Voluta virescens* LIGHTFOOT, 1786 consist of about 1 cm wide attached shallow cupolas (BANDEL, 1976). A rod-like yolk concentration in their center surrounded by clear egg yolk provides food for only one or two embryos. They hatch after 30-38 days as miniature adult-like snails with their shell consisting of 2.5 whorls measuring 4.7 mm in height and 0.7 mm in width (BANDEL, 1975a, pl. 19, figs.2,3,8,9). The first whorl is ornamented by fine spiral lines, later the shell is smooth with growth lines as only ornament. Within the family Volutidae *V. virescens* hatches as rather small young compared with giant hatchlings like those of *Melo melo* LIGHTFOOT, 1786 with 30 mm large shell (AMIO, 1963).

Similar capsules as in case of *Voluta* are also produced by *Provocator pulcher* WATSON, 1882 from the southern Indian Ocean (ARNAUD & VAN MOL, 1979). They are 18 mm wide and 8 mm high and hold two to four embryos which develop during austral summer. Also *Cymbiola magnifica* (GEBAUER, 1802) from eastern Australia attaches its cupola-like egg-capsules to hard substrates (POPPE & GOTO, 1992). In case of *Odontocymbiola magellanica* (GMELIN, 1788) and *Adelomelon ancilla* (LIGHTFOOT, 1786) such egg capsules have a calcified wall (PENCHASZADEH & de MAHIEU, 1976). The few eggs within each capsule develop for a

period of up to three months in the shelter of the spawn before hatching as juveniles sometimes with a shell of about 10 mm in length.

Pachycymbiola brasiliana (LAMARCK, 1811) from the South American shelf has transparent ping-pong ball-like egg capsules (POPPE & GOTO, 1992). *Ericusa fulgetrum* (SOWERBY, 1825) produces circular eggs of about 25 mm in diameter which are deposited in the sand (POPPE & GOTO, 1992). *Melo amphora* (LIGHTFOOT, 1786) lays eggs with begin of the austral summer and young hatch a few months later. *Melo umbilicata* BRODERIP, 1826 also from Australia produces an egg-mass that consists of many capsules and has the shape of a pineapple. After hatching the miniature *Melo* buries itself in the sand for two months and begins feeding only afterwards (POPPE & GOTO, 1992).

Cymbium olla (LINNÉ, 1758) from the equatorial northeastern Atlantic broods 10 to 12 young until they hatch with rather large size (POPPE & GOTO, 1992). This type of development has been observed by MARCHE-MARCHAD (1968) and can here be confirmed on embryonic stages of shell growth observed from individuals that had been collected in Senegal. The embryos of *Alcithoe arabica* (GMELIN, 1788) feed on albuminous material secreted by the pallial oviduct (PONDER, 1970). All developments known also in case of the fossil species from Australia described by DARRAGH (1988) resulted in crawling young snails hatching from their egg cases and the embryonic shell usually larger than that noted in *Voluta* from Colombia (BANDEL, 1975a).

CLENCH & TURNER (1964) divided the subfamilies of the Volutidae on basis of the appearance of the salivary glands, the unpaired foregut gland and the shape of the radula. WEAVER & DUPONT (1970) based their classification of the Volutidae on radula morphology. Within the subfamily Athletinae the radula has three teeth in a row. The Volutinae have only one row of teeth in their radula and the teeth have more than 3 cusps. The Odontocymbiolinae have here only three cusps that are fang-like unlike those in the other subfamilies. In the Scaphellinae the median teeth are Y-shaped. WEAVER & DUPONT (1970) recognized 9 subfamilies among the recent species of the Volutidae. According to RIEDEL (2000) Volutidae are closely related to the Olividae, and the Marginellidae are closer to Volutidae s.s. than the Athletidae (=Athletinae). The radulae of many Volutidae and of the Marginellidae are characterized by the presence of only one tooth in each row. That of *Voluta* has a broadly triangular tooth with thickened margins. Such margins are also known for the radula of *Lyria* GRAY, 1847 which differs from that of the *Voluta*-relation in the number of cusps on the cutting edge. The central teeth of recently hatched individuals of *Voluta musica* LINNÉ, 1758 are similar to those of *Persicula* SCHUMACHER, 1817 and crescent shaped and it is only later in ontogeny that the *Voluta* tooth acquires its characteristic shape (BANDEL, 1984). According to CLENCH & TURNER (1970) *Odontocymbiola* has a radula with a bicuspid lateral tooth with a broad base. This genus resembles buccinid species in this respect when radulae as in *Melongena* SCHUMACHER, 1817 or *Vasum* RÖDING, 1798 are compared (BANDEL, 1984). BOUCHET (1990) found the Plicolivinae to have the radula with wishbone-shaped central tooth and comb-like lateral teeth. According to RIEDEL (2000) Plicolivinae BOUCHET, 1990 are more likely to be related to the Volutomitridae and the Athletinae to the Marginellidae rather than to the Volutidae.

III. Classification according to the anatomy

The neogastropods had according to the morphology of their radula been classified as *Rachiglossa* TROSCHEL, 1848 (=GRAY, 1852), *Nematoglossa* OLSSON, 1970, and *Toxoglossa* TROSCHEL, 1848. PONDER (1973) considered the Neogastropoda to represent a monophyletic group that he preferred to divide into the three superfamilies Muricoidea, Cancellarioidea, and Conoidea, which unite practically the same species as the above mentioned taxa suggested in literature. The first of these have a rachiglossate radula with three or one tooth in a row, the Cancellarioidea have the specialized nematoglossate radula (THIELE, 1931, Fig.422), and the third have a radula with 5 to 2 teeth in a row with development within the group culminating in poison injection needles as teeth (*toxogloss*) (see BANDEL, 1984 and RIEDEL 2000 for references). In the rachiglossan group PONDER (1973) noted that the elongation of the oesophagus during proboscis formation was provided by the dorsal wall of the buccal cavity. In the cancellariid group (*Nematoglossa*) the site of elongation lies in the mid-oesophagus, while in the *toxoglossans* the proboscis was formed by the elongation of the buccal tube. While the first two have a valve of Leiblein that aids in transport of food and liquids through the proboscis, the *toxoglossans* do not have such a valve. The absence of this valve was interpreted to have occurred secondarily (PONDER, 1973, DARRAGH & PONDER, 1998, KANTOR, 1996, RIEDEL, 2000). From the existing anatomical evidence it may also be permitted to interpret the *Toxoglossa* to have developed from ancestors which never had such a valve of Leiblein. This later organ had been interpreted, though, to represent the only plesiomorphic character that unites all Neogastropoda.

RIEDEL (2000) grouped the Neogastropoda by recognizing four groups. Of these the suborder Buccinina with Buccinoidea RAFINESQUE, 1815 and Columbelloidea SWAINSON, 1840 differs from the others by having no anal gland, which is present in all the others. The Turrina (= *Toxoglossa*) have no valve of Leiblein. RIEDEL (2000) also suggested that this valve has been lost secondarily. The Volutina with Mitroidea SWAINSON, 1831, Turbinelloidea SWAINSON, 1835, and Volutoidea RAFINESQUE, 1815 are considered to also include the Cancellariidae GRAY, 1853 (in the Mitroidea). RIEDEL (2000), therefore, interpreted the *Nematoglossa* with their rather peculiar radula to have developed secondarily. The fourth suborder, the Muricina hold the Muricoidea RAFINESQUE, 1815, and therefore only a part of the *Rachiglossa* of TROSCHEL (1856) (= *Stenoglossa* of THIELE, 1931) and also of the Muricoidea as interpreted by PONDER (1973, 1998).

KANTOR (1996) suggested that the Volutidae and here especially members of the Athletinae like *Volutocorbis* DALL, 1890 (possibly a subgenus to *Athleta* CONRAD, 1853) preserve the most conservative character within the Muricoidei (= *Rachiglossa* according to THIELE, 1931, WENZ, 1938, = *Muricea* according to PONDER, 1973, = *Muricoidea* according to PONDER & WARÉN, 1988) in regard to the construction of the snout. *Volutocorbis* has a short proboscis with the buccal mass lying at its base and glandular folds of the oesophagus (not a separate gland as is the usual case among the *Rachiglossa*). Volutidae have, thus, been suggested to represent in regard to their anatomy a basic design found among the Neogastropoda.

IV. Systematic description

Subclass Caenogastropoda Cox, 1959

The usual case in marine species of this subclass of the Gastropoda is the presence of a trochospirally and dextrally coiled larval shell attached to the embryonic shell. It differs in ornament and shape from the embryonic whorl as well as from the teleoconch and is usually formed during larval life in the plankton. It characterizes the Caenogastropoda from the other three extant gastropod subclasses, the Archaeogastropoda, Neritimorpha and Heterostropha (BANDEL, 1997). This larval portion of the protoconch can be substituted by a larger embryonic shell when the free larval phase of ontogeny is omitted by provision of embryonic feeding in the egg mass or in the shelter of the female (BANDEL, 1975a, 1982, see further references here). Sperm morphology (HEALY, 1996), osphradium and ctenidium (gill) construction (HASZPRUNAR, 1988) are among the anatomical features that also distinguish this subclass from the three other subclasses of the Gastropoda and thus support the differentiation with aid of the morphology of the early shell. Paleontological evidence indicates that this taxon of the Gastropoda has carried out independent evolution at least since Devonian time (BANDEL, 2002, see for references).

Superorder Latrogastropoda RIEDEL, 2000

Here the Neomesogastropoda BANDEL, 1991 and the Neogastropoda are included and the taxon is recognized since mid-Cretaceous time (RIEDEL, 2000 for references). Several larger superfamilies belonging within the frame of this taxon can be traced. Quite a number of data are noted from the Late Cretaceous, but apparently no taxon that can unequivocally placed here has been in existence before mid Cretaceous time (BANDEL, 1993, 1997, BANDEL, & RIEDEL, 1994).

Order Neogastropoda THIELE, 1929

The shell is provided with an anterior siphonal canal. Its composition with few exceptions is of aragonite and mainly of crossed lamellar structure. The protoconch of species with planktotrophic development is commonly provided with an apertural projection of the lower outer lip (sinusigera, see BANDEL et al., 1997 for additional references), and the embryonic shell measures usually more than 0.17 mm in diameter (BANDEL, 1975a). In the radula ribbon commonly only three teeth or one tooth are attached in each row. There is an anterior siphon, a more or less extended proboscis and the females have a pedal gland which aids in forming the horny egg capsule. Usually the mid gut gland that lies posterior of the buccal mass has its exit in front of the nerve ring that surrounds the gut in the region of the oesophagus and behind the buccal mass (RIEDEL, 2000, see references).

Suborder Rachiglossa TROSCHER, 1848

The ribbon of the radula has three teeth or one tooth in a row, rarely 5 as was recognized in some members of the Nassariidae by TROSCHER (1856), TROSCHER & THIELE (1865-1893) and BANDEL (1977, 1984), or the radula is missing altogether. The proboscis is provided with a valve (valve of Leiblein) that prevents regurgitation of consumed food during proboscis withdrawal. Distinct shell features that can be utilized to distinguish this taxon from others among some advanced Caenogastropoda, especially the Toxoglossa, are not known.

Superfamily Volutoidea RAFINESQUE, 1815

See Volutidae.

Family Volutidae RAFINESQUE, 1815

According to the data assembled by RIEDEL (2000, Fig.110) the shape of the shell of volutids is bucciniform, strombiform and bulliform and usually of relatively large size with an average of 5-20 cm in height. The inner lip of the aperture commonly bears columellar folds. All known species have lecithotrophic development with young hatching with one up to four whorls completed. The transition from protoconch to teleoconch may be quite indistinctly marked and the protoconch consists only of the embryonic shell and no larval shell. Development is completely within the egg capsule which contains yolk for extended development in its interior or, in rare cases, the embryos are brooded by the female. A direct development of most or all species of the volutids had also been suggested by THORSON (1950). The radula is triserial or uniserial and the central tooth has more than three cusps, always three cusps, or is Y-shaped.

Subfamily Caricellinae DALL, 1907

The teleoconch is fusiform and the protoconch consists of about one large rounded whorl forming a rounded or pointed apex of the shell. Ornament of the teleoconch is smooth or cancellate. The aperture is ovate and elongate, ending in a posterior canal and anterior siphonal canal. The inner lip exhibits three or four oblique plaits.

Remarks: WENZ (1938) considered Caricellinae to be the same as SCAPHELLINAE H. & A. ADAMS, 1858 and PONDER & WARÉN (1988) included them in the synonymy of Haliinae SISMONDA, 1842. Here it is preferred to use the taxon Caricellinae based on the fossil genus *Caricella* since well preserved material for comparison is available for this genus.

Genus *Caricella* CONRAD, 1835

Type species: *Caricella pyruloides* CONRAD, 1834 from the Eocene of Alabama as illustrated by DOCKERY (1980, Pl.17, Figs.7,8, Pl.77, Fig.3).

Description: The fusiform shell is provided with a protoconch that consists of only one or little more than one large rounded whorl with indistinct suture and rounded or pointed apex. Ornament of the teleoconch consists of spiral cords and fine axial ribs that begin at the end of the protoconch and form a cancellate pattern. In *Caricella* (*Caricella*) it features only the early teleoconch whorls and in *Caricella* (*Atraktus*) GARDNER, 1937 it is present also on later whorls of the teleoconch (DOCKERY, 1980, Pl.16, Fig.3, Pl.17, Figs.7,8). The inner lip of the aperture bears four columellar folds. The long siphonal canal is reflected.

Differences: *Caricella* (*Caricella*) closely resembles *Caricella* (*Misrimelo*) but differs from it by having a cancellate ornament of the early teleoconch whorls. Among the living species *Cymbiola* has rather similar shell shape (POPPE & GOTO, 1992).

Subgenus *Caricella* (*Misrimelo*) n. subgen.

The type to the subgenus is *Caricella* (*Misrimelo*) *klitzschi* n. sp., Late Cretaceous, Egypt.

Diagnosis: The large, pear-shaped shell consists of few whorls and has a short broadly conical spire. The initial whorls are enlarged and consist of little more than one whorl that forms a rounded knob on the spire. The teleoconch whorls are smooth, impressed along the

sutures and connect to a smooth rounded pillar of the short siphonal canal. The body whorl envelops the greatest portion of the previous shell and shell wall is thick. The aperture is ovate and elongate ending in a posterior canal and anterior siphonal canal. The inner lip exhibits three or four oblique plaits.

Derivatio nominis: Combination of terms with a shell resembling that of modern *Melo* and occurrence in Egypt, which is called Misr in Arabic.

Differences: *Caricella (Misrimelo)* is close in shape to *Caricella (Caricella)* but its teleoconch is smooth throughout while it is spirally ornamented or cancellate in the early whorls of *Caricella (Caricella)*, and throughout shell growth in *Caricella (Atraktus)*. The type of *Caricella (Misrimelo)* differs also by having only three columellar folds, while *Caricella (Caricella)* has four folds.

Caricella (Misrimelo) klitzschi n. sp.

(figs. 1 - 12)

Diagnosis: Like the diagnosis of the subgenus.

Description: The pear shaped, large shell with two and a half teleoconch whorls is 55 mm high and 3.6 cm wide. The initial whorls are enlarged and form a rounded knob on the spire that is about 6 mm wide and high. Whorls are contracted where they continue into the base of the siphonal canal. The body whorl envelops the greatest portion of the previous shell that has a maximum height of 85 mm and width of 60 mm. The shell wall is thick, especially along the sutures. The columellar lip exhibits three oblique plaits and the callus of the inner lip ends in a small depression parallel to the pillar axis. The fully grown shell has a callus pad on the inner lip near the posterior end of the outer lip.

Derivatio nominis: Named in honor of Prof. Dr. Eberhard KLITZSCH (Berlin) who has been guiding the SFB 69 (Sonderforschungsbereich of the DFG) that has been involved in the geological studies of Egypt for many years.

Type locality and stratigraphic position: Ammonite Hills in the Sand Sea of western Egypt (Conoco Chanal 20) and here the Maastrichtian *Overwegi* Beds with *Libycoceras* according to BARTHEL & HERMANN-DEGENS (1981).

Holotype: The individual illustrated in fig. 1 and reconstructed in figs. 9, 10 represents the holotype (no. 213), and there are 12 additional shells.

Differences: *Caricella (Misrimelo) klitzschi* is less rounded than the other known species that may belong to this subgenus from southern India, *C. (Misrimelo) pyriformis* (FORBES, 1846) which has four columellar plaits and no callus pad (STOLICZKA, 1868). *Caricella (Misrimelo) pyriformis* has an egg-shaped shell that consists of five whorls with short spire of broadly conical outline. The enlarged initial whorls form a rounded knob on the spire. The teleoconch whorls are smooth, impressed along the sutures, and somewhat contracted near the middle. The body whorl envelops the greatest portion of the previous

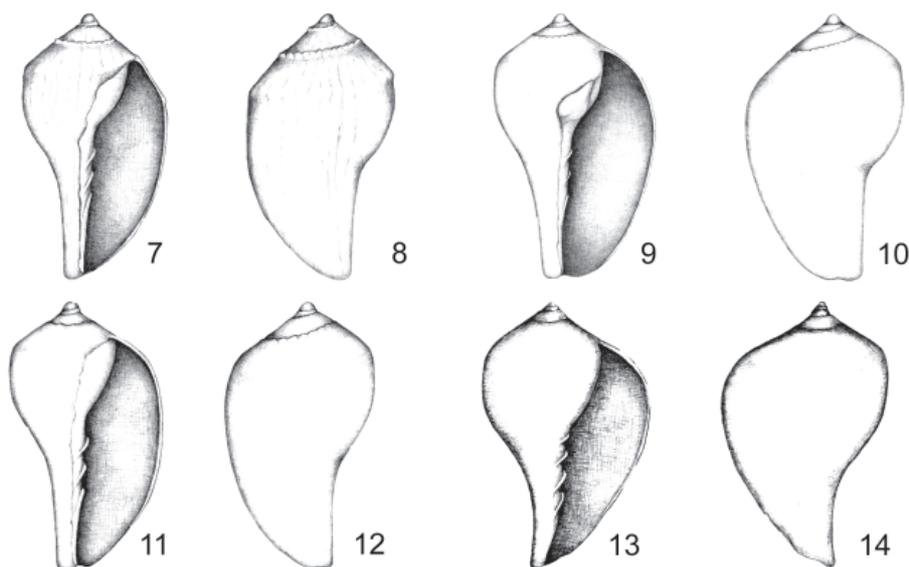
Figs. 1 - 6: *Caricella (Misrimelo) klitzschi* n. sp., from the Ammonite Hills in the Sand Sea of western Egypt (Conoco Channel 20) and here the Maastrichtian *Overwegi* Beds; **1:** Holotype (no. 213) is about 80 mm high. The fully grown shell has a callus pad on the inner lip near the posterior end of the outer lip; **2:** The 55 mm high and 36 mm wide individual (no. 13) exhibits the about 6 mm wide and round protoconch; **3:** The 85 mm high individual (no. 214) has the whorls contracted where they continue into the base of the siphonal canal; **4:** Same individual as in fig. 2, abapertural view. The pear shaped, large shell with two and a half teleoconch whorls is 55 mm high and 36 mm wide; **5:** The 40 mm high shell of a not fully grown individual (no. 209). The columellar lip exhibits three oblique plaits; **6:** Same individual as in fig. 5, abapertural view.



shell that has a maximum height of 95 mm and width of 65 mm. The thick shell has been covered by enamel, with growth lines visible only below this cover.

Remarks: Among modern genera *Pachycymbiola* IHERING, 1907 is quite similar to *Caricella* (*Misrimelo*) *klitzschi* in general shape. Especially *P. ferussacii* (DONOVAN, 1824) from the southern Atlantic shelf area of Argentina is similar in size. Members of modern *Cymbiola* like *C. nobilis* (LIGHTFOOT, 1786) that grows to 50 and 190 cm height are similar as well. The latter has a wide range from the intertidal to 70 m deep water along the Malay Peninsula to Borneo and the Philippines.

The young of *P. (Pachycymbiola) brasiliiana* LAMARCK, 1811 develop within pingpong-ball-like egg capsules. This species lives along the Argentinean coast and its egg masses may be washed to the beach when hatched (seen at the Rio de la Plata). The species is very similar to *Caricella demissa* (CONRAD, 1848) from the Oligocene of Mississippi (DOCKERY,

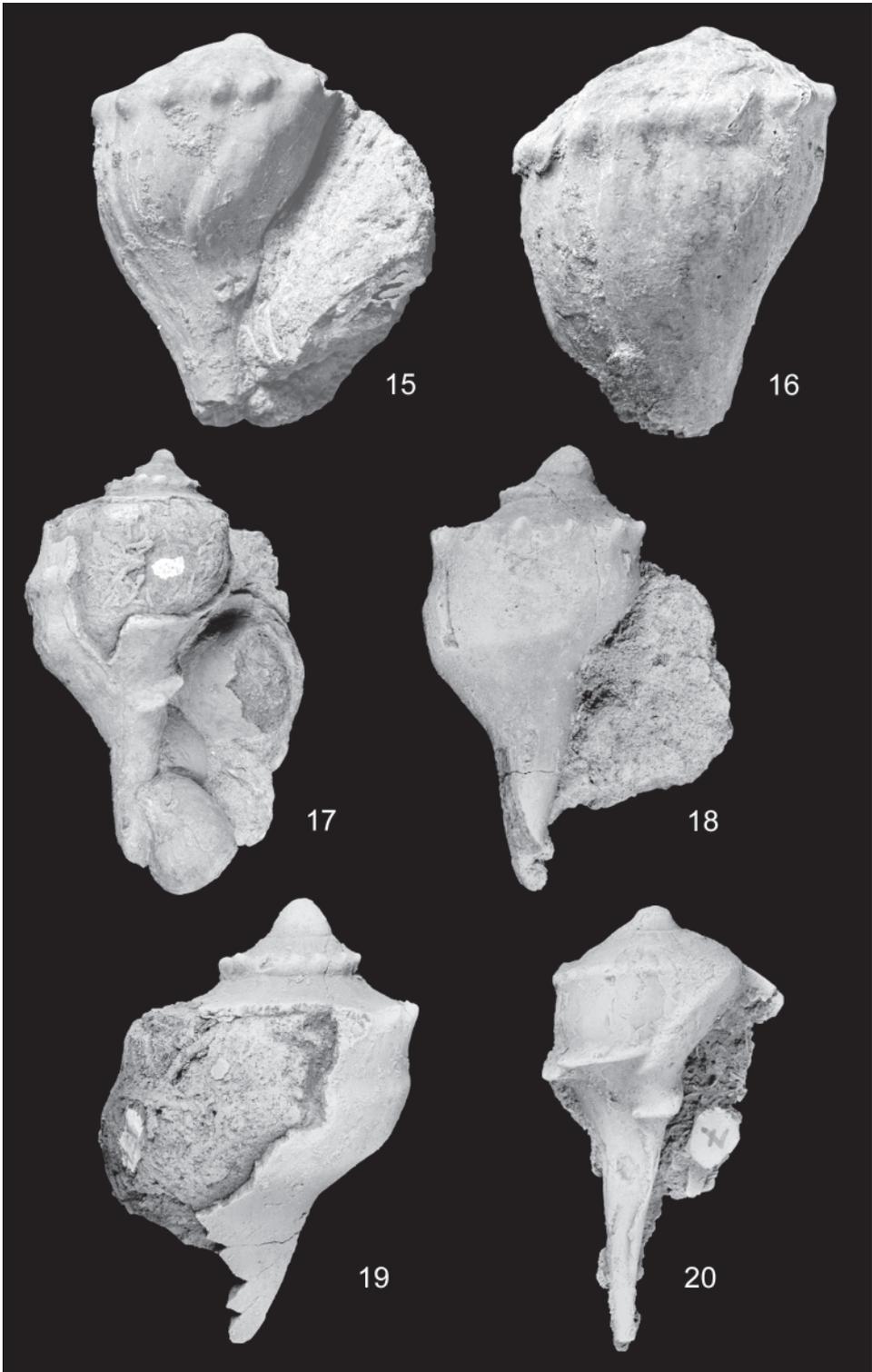


Figs. 7 - 12: *Caricella (Misrimelo) klitzschi* n. sp., from the Ammonite Hills in the Sand Sea of western Egypt (Conoco Channel 20) and here the Maastrichtian *Overwegi* Beds; **7:** Reconstructed shell (no. 211), about 60 mm high; **8:** Same as fig.7, abapertural view; **9:** Reconstructed shell with about 60 mm high shell (no. 213); **10:** Same as fig. 9, abapertural view; **11:** Reconstructed shell with about 60 mm high shell (no.13); **12:** Same as fig. 11, abapertural view.

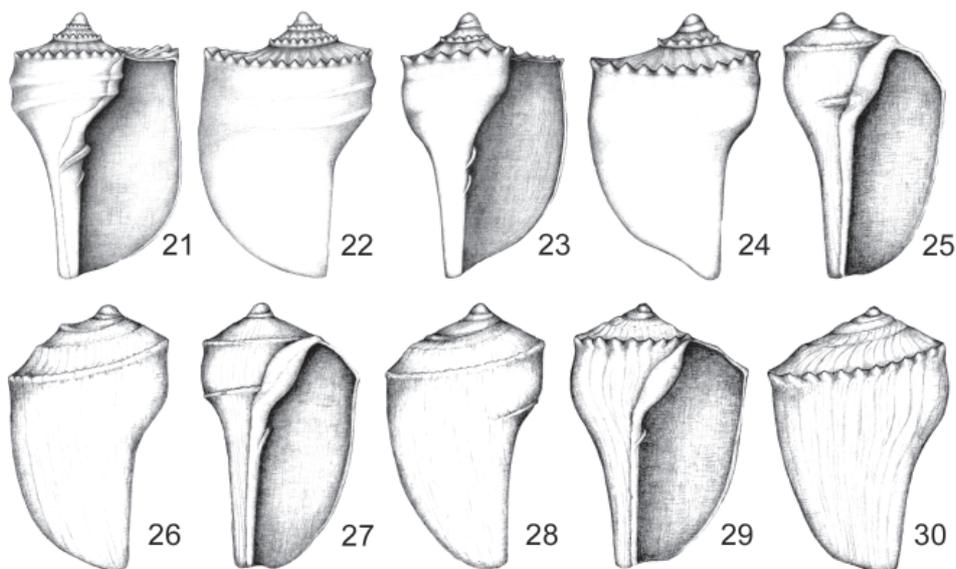
Figs. 13 - 14: The modern *Caricella subangulata* as comparison (about half size); **13:** Apertural view; **14:** abapertural view.

Figs. 15 - 19: *Misricymbiola chalmasi* (QUAAS, 1902), from Ammonite Hills in the Sand Sea of western Egypt (Conoco Channel 20) and here the Maastrichtian *Overwegi* Beds; **15:** Specimen (no. 33) with 35 mm high shell and well developed callus of the inner lip and inclined columellar folds; **16:** Same individual as in fig. 15, abapertural view; **17:** Specimen with 135 mm high shell. The inner lip bears three oblique folds that in the last whorl unite to one columellar swelling that is oriented at right angle to the axis of the spire; **18:** Specimen (no. 257) with the low conical spire that is stair-like and carries the large rounded protoconch that consists of about one whorl and is about 10 mm high and wide; **19:** Same shell of *Misricymbiola chalmasi* (QUAAS, 1902) as illustrated in fig. 34, abapertural view.

Fig. 20: *Misricymbiola conocoi* n. sp., holotype, from Ammonite Hills in the Sand Sea of western Egypt (Conoco Channel 20) and here the Maastrichtian *Overwegi* Beds; 45 mm high.



1980). Here the protoconch consists of two whorls, is smooth with a pointed apex and only about 1.5 mm high and wide. Transition into the teleoconch is abrupt and marked by the onset of spiral ribbons and axial ribs that form a net-shaped pattern and ornaments the next three whorls. Later whorls are smooth. In the type species to *Caricella*, *C. pyruloides* CONRAD, 1834 from the Eocene of the USA near the Gulf of Mexico, the protoconch closely resembles that of *C. (Misrimelo)* in having a button-like and rounded shape.

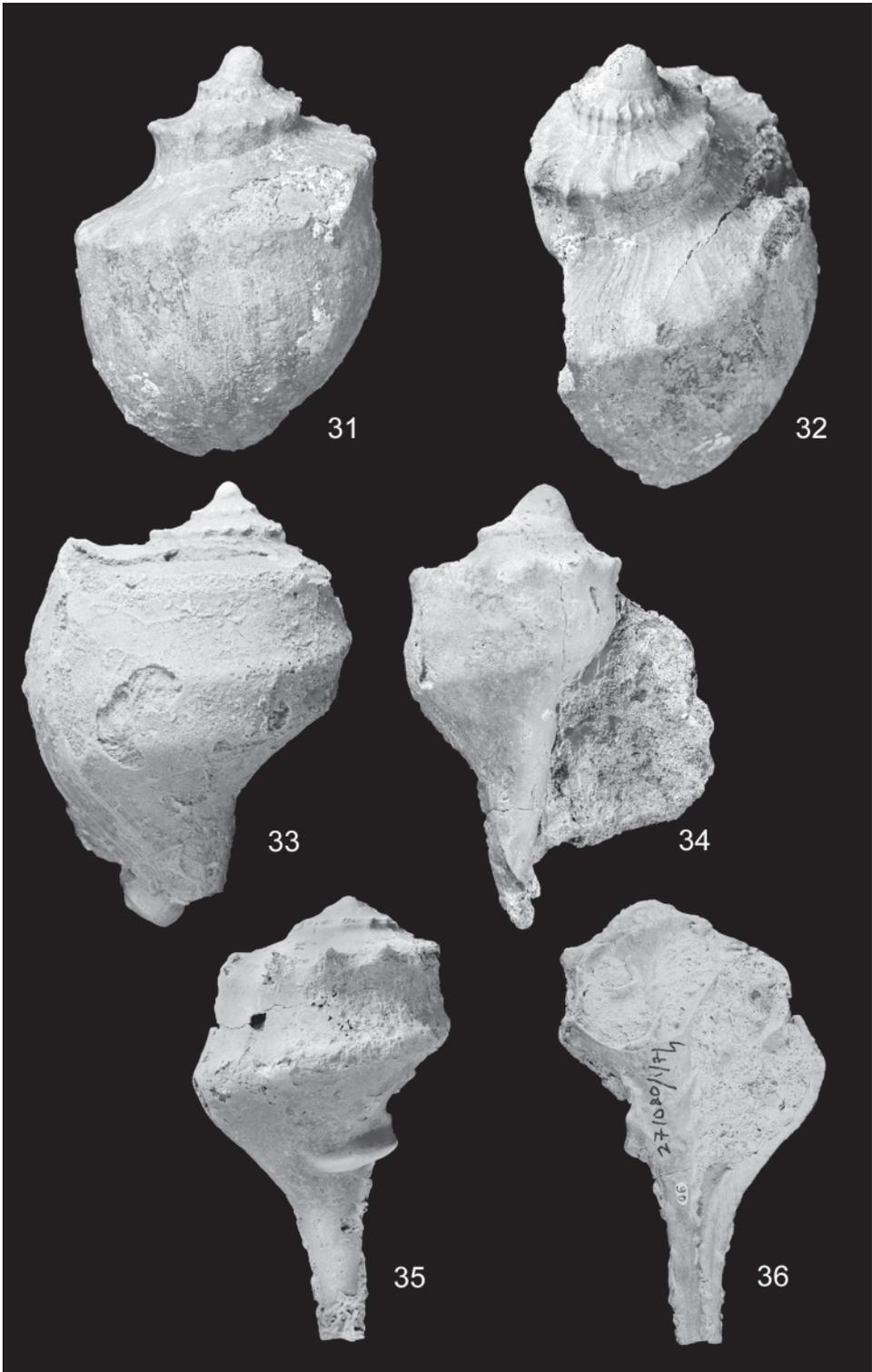


Figs. 21 - 24: *Misricymbiola chalmasi* (QUAAS, 1902), from Ammonite Hills in the Sand Sea of western Egypt (Conoco Channel 20) and here the Maastrichtian *Overwegi* Beds; **21:** Reconstructed from the specimen (no. 265) that is up to 155 mm high and 90 mm wide and whorls increase rapidly in diameter; **22:** Same shell as in fig. 21, abapertural view; **23:** The more juvenile shell (no.257) reconstructed from the specimen illustrated in fig. 34 has almost equal columellar folds; **24:** Same shell as in fig. 23, abapertural view.

Figs. 25 - 28: *Misricymbiola conocoi* n. sp. from Ammonite Hills in the Sand Sea of western Egypt (Conoco Channel 20) and here the Maastrichtian *Overwegi* Beds; **25:** Reconstructed from the individual (no.64) illustrated in figs. 37, 38. The shell is up to 50 mm high and 26 mm wide and whorls rapidly increase in diameter. The low conical spire with whorls separated by indistinct sutures carries a large rounded protoconch that consists of about one whorl and is about 5 mm high and wide; **26:** Same shell as in fig. 25, abapertural view; **27:** Holotype (no.7), reconstructed from the individual illustrated in fig. 20 and 55 mm in height; **28:** Same as in fig. 27, abapertural view.

Figs. 29 - 30: *Misricymbiola chalmasi* (QUAAS, 1902); **29:** Not fully grown specimen, reconstructed from the individual figured in fig.15; the shell would have been about 40 mm high; **30:** Same as in fig. 29, abapertural view.

Figs. 31 - 36: *Misricymbiola chalmasi* (QUAAS, 1902) from Ammonite Hills in the Sand Sea of western Egypt (Conoco Channel 20) and here the Maastrichtian *Overwegi* Beds; **31:** The low conical spire is stair-like and carries a large rounded protoconch that consists of about one whorl and is about 10 mm high and wide. The shell (no.15) is about 55 mm high; **32:** Same individual as seen in fig. 32, to show the large rounded protoconch. The angular periphery is ornamented by about 16 short, tubercular axial ribs, which feature only the upper peripheral corner; **33:** Same individual as in fig. 17, abapertural view. In the last whorl the side is more evenly rounded and only the upper corner remains while the two lower corners disappear; **34:** Specimen (no.257) with 75 mm high shell has the siphon well preserved; **35:** Specimen (no.90) with 150 mm high shell and the large final fold on the inner lip; **36:** Same specimen as in fig. 35, abapertural view, corroded.



Genus *Misricymbiola* n.gen.

Type species: *Misricymbiola chalmasi* (QUAAS, 1902) from the Late Cretaceous, Egypt.

Diagnosis: The pear-like large shell has a low conical spire with large rounded protoconch. The angular periphery may be ornamented by short axial ribs which do not continue onto the flattened sides of the whorl and onto the apical plane. The whorl flanks have up to two lower rounded corners and a constricted base which is extended into a supporting pillar of the long siphonal canal. The inner lip bears three oblique folds. In the body whorl the folds form a columellar swelling that is oriented at right angle to the axis of the spire.

Derivatio nominis: Combination of terms uniting shell-shape, resembling modern *Cymbiola* and the locality of its occurrence, Egypt which is called Misr in Arabic.

Differences: The rounded protoconch distinguishes *Misricymbiola* from *Turbinella* LAMARCK, 1799 which has a higher protoconch consisting of several whorls of which the first whorl is usually destroyed and the shell ends with a septum (BANDEL, 1975b). From *Caricella* (*Misrimelo*) distinguishes the shape of the teleoconch that resembles *Protobusyon* WADE, 1917 or *Hercorhyncus* CONRAD, 1868 among the late Cretaceous gastropods of Ripley Formation (SOHL, 1964). Both of the latter have much smaller protoconchs with more whorls and may be similar in size. The genus *Ptychoris* GABB, 1877 based on *Voluta purpuriformis* FORBES, 1846 that occurs in the Coniacian to Santonian Trichinopoly Group in the Ariyalur and Pondicherry areas of southeastern India resembles *Misricymbiola*. According to STOLICZKA (1868, Pl.6, Fig. 9), it is based on a rounded, spindle shaped, elongate ovate shell with a pointed spire that consists of six whorls the uppermost of which are smooth. The last whorl embraces more than two thirds of the previous whorls. It is evenly withdrawn toward the base that forms a solid column to the fairly long siphonal canal. The protoconch is rounded but not well known, and the young teleoconch has spiral lines. With advancing age the shell became more or less covered with an enamel that coated the spiral lirae. The aperture is enlarged ovate with a posterior canal next to the suture. Three folds feature the columellar portion of the inner lip. *Ptychoris* is closer to *Caricella* (*Misrimelo*) in shape than to *Misricymbiola* but differs from both by having a higher spire and an ornament of spiral liration. This ornament of fine spiral lirae resembles that of *Caricella* (*Caricella*), which differs in regard to its lower spire from *Ptychoris*.

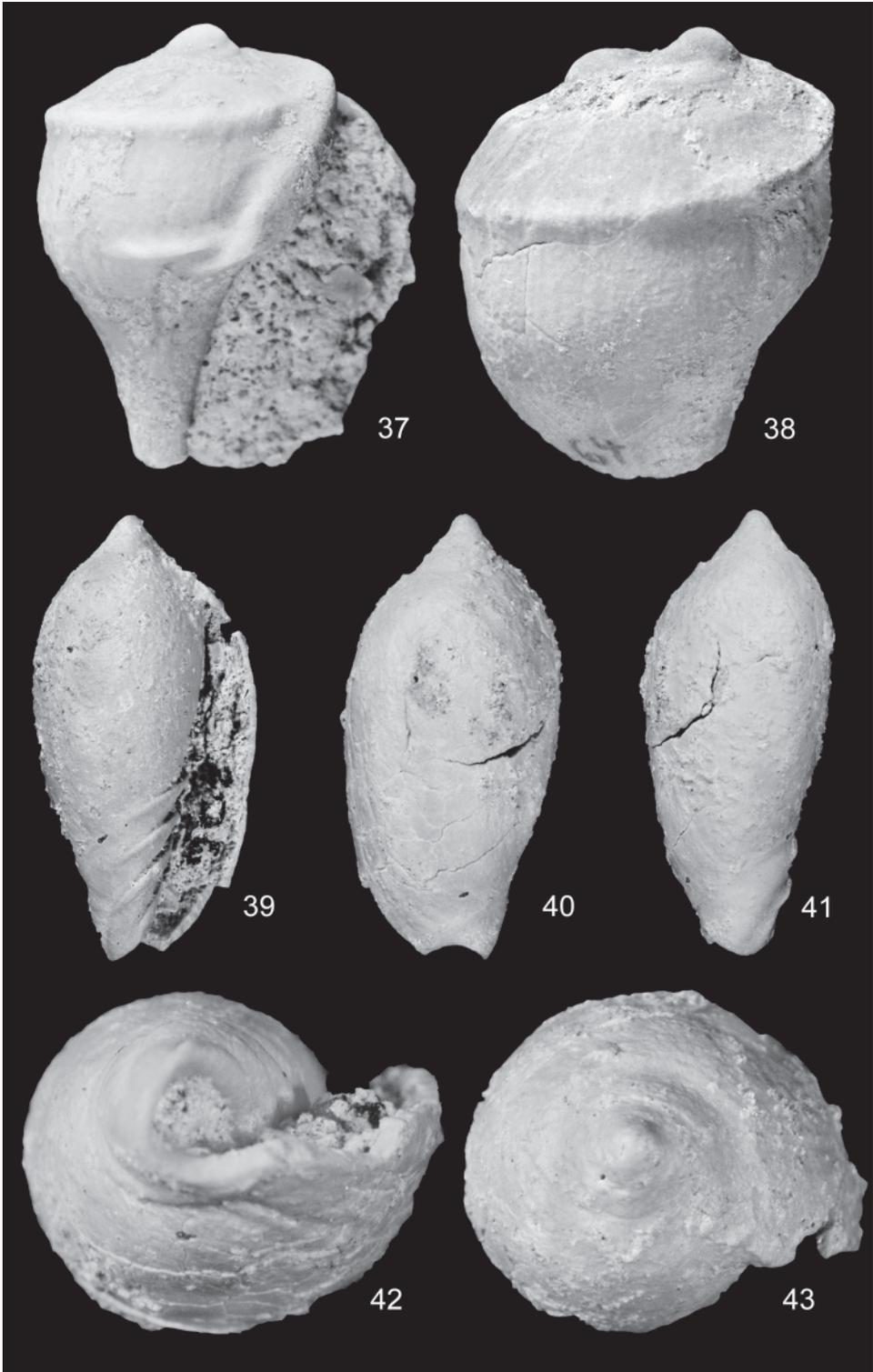
Misricymbiola chalmasi (QUAAS, 1902)

(figs. 15 -19, 21-24, 29-36))

Description: The large shell is up to 155 mm high and 90 mm wide and whorls increase rapidly in diameter. The low conical spire is stair-like and carries a large rounded protoconch that consists of about one whorl and is about 10 mm high and wide. With 2.2 teleoconch whorls the shell is 65 mm high and with one more whorl it has reached maturity. The angular periphery is ornamented by about 16 short, tubercular axial ribs which feature

Figs. 37 - 38: *Misricymbiola conocoi* n. sp., from Ammonite Hills in the Sand Sea of western Egypt (Conoco Channel 20) and here the Maastrichtian *Overwegi* Beds; **37:** Frontal view of specimen (no. 64) with the protoconch that consists of one whorl and is about 5 mm wide. The lower keel disappears on the body whorl; **38:** Same shell as in fig. 37, abapertural view.

Figs. 39 - 43: *Plicoliva* (*Misriplicoliva*) *bartheli* n. sp., from Ammonite Hills in the Sand Sea of western Egypt (Conoco Channel 20) and here the Maastrichtian *Overwegi* Beds; **39:** Holotype, with evenly olive-shaped shell of about 30 mm height and 15 mm in width; **40:** Same individual as in fig. 39, abapertural view; **41:** Same individual as in fig. 39, lateral view; **42:** Same individual as in fig. 39, umbilical view; **43:** Same individual as in fig. 39, apical view with smooth surface and rounded, rather large protoconch.



only the upper peripheral corner. Below it is a shallow concavity up to the median corner, a shallow convexity to the lower corner and a rapid decrease in width to the base. In the last whorl the side is more evenly rounded and only the upper corner remains while the two lower corners disappear. The inner lip bears three oblique folds that in the last whorl unite to one columellar swelling that is oriented at right angle to the axis of the spire.

Material: 7 individual shells were studied.

Comparison: Members of the family Turbinellidae SWAINSON, 1835 with large shells of fusiform shape and with columellar folds at about right angles to the shell axis are rather similar in teleoconch shape but protoconch shape differs. The genus *Turbinella* LAMARCK, 1799 with heavy, large, and fusiform shell has 3 or 4 strong folds on the columella. The type is *Xancus pyrum* LINNÉ, 1758 from India with an egg-mass consisting of pill-shaped capsules closely packed and attached to a long strand. Here the embryonic development is quite similar to that of *Turbinella angulata* (LIGHTFOOT, 1786) from the Caribbean Sea with the consumption of numerous nurse eggs and protoconch construction and shape very different from that of the Volutidae (BANDEL, 1975a, b).

Misricymbiola conocoi n. sp.

(figs. 20, 25 - 28, 37, 38))

Diagnosis: The protoconch consists of one whorl and is about 5 mm wide. The teleoconch reaches a size of 50 mm in height and 26 mm in width, consisting of three whorls. The angular periphery carries spiral keels that may be granulated. The sides are flattened and the basal corner is rounded. The aperture carries three folds on the inner lip of which only one is seen in the fully grown shell.

Description: The shell is up to 50 mm high and 26 mm wide and whorls rapidly increase in diameter. The low conical spire with whorls separated by indistinct sutures carries a large rounded protoconch that consists of about one whorl and is about 5 mm high and wide. With about 2 teleoconch whorls the shell is 40 mm high and with one more whorl is has reached maturity. The angular periphery is ornamented by a spiral keel and a second one forms the edge to the base. It may disappear or remain visible on the total or a part of one whorl. Below the flattened or slightly convex side there is either a weakly expressed lower corner or a well rounded transition to the base. This base continues into the siphonal pillar. The inner lip bears three oblique folds of which only one columellar swelling reaches the outside in the fully grown shell.

Derivatio nominis: Named for Conoco Company that aided K. Werner BARTHEL as well as our group with cars and in many other ways to carry out studies in the Cretaceous of Egypt.

Stratum typicum and stratigraphic position: Ammonite Hills in the Sand Sea of western Egypt (Conoco Channel 20) and here the Maastrichtian *Overwegi* Beds with *Libyoceras* according to BARTHEL & HERMAN-DEGENS (1981).

Holotype: The holotype represents the specimen (no.7) illustrated in fig. 20 and two more specimen were studied.

Differences: *Misricymbiola chalmasi* is larger and has more step-like spire than *M. conocoi*. The latter is also smaller in regard to the protoconch which measures only half of that of *M. chalmasi* in size. The fully grown teleoconch is also smaller and it has a more rounded shape.

Subfamily Plicolivinae BOUCHET, 1990

According to BOUCHET (1990) the radula of *Plicoliva* has rows of teeth with a wishbone-shaped central tooth and comb-like lateral teeth. BOUCHET (1990) noted so many differences in radular characters between *Plicoliva* and other volutids that he suggested to place *Plicoliva* separate from other Volutidae with similar shell in a subfamily by itself. RIEDEL (2000) placed *Plicoliva* closer to the Volutomitridae GRAY, 1854. He suggested that its radula, even though peculiar, is closer to that of the Volutomitridae than to that of the Volutidae. But RIEDEL (2000) also stated that the whole taxon Volutomitridae is of rather insecure affinity within the Rachiglossa, and probably closest in relation to the Volutidae.

Only two living species of *Plicoliva* are known, one from off Brazil and the other on the West African shelf on the opposite side of the Atlantic Ocean (POPPE & GOTO 1992). The subfamily Plicolivinae may thus represent a taxon besides the Athletinae that has 3 teeth in each row of the radula ribbon. Modern *Plicoliva* lives in 5 to 40 m deep water in sand and on rock (BOUCHET, 1990, POPPE & GOTO, 1992).

Genus *Plicoliva* PETUCH, 1979

Type-species: *Oliva zelindae* PETUCH, 1979 from off-shore Brazil.

Remarks: The shell is *Oliva*-like in shape, solid and glossy and has a columella with five strong columellar folds. *Oliva zelindae* represents a 30 mm long shell with smooth surface and solid glossy shell resembling a classic member of the genus *Oliva* BRUGUIÈRE, 1789, but is distinguished from it by the presence of five columellar folds. The radula also differs considerably from that of *Oliva* (compare BANDEL 1984 for *Oliva* & BOUCHET 1990 for *Plicoliva*).

Subgenus *Plicoliva (Misriplicoliva)* n. subgen.

The type to the subgenus is *Plicoliva (Misriplicoliva) bartheli* n. sp. from the Late Cretaceous of Egypt.

Diagnosis: The evenly rounded olive-shaped shell of about 30 mm height and 15 mm in width has a smooth surface with rounded, probably rather large protoconch. The spire is only one sixth or one fifth of total shell height and sutures are glazed over from the outside. The aperture is elongate and widest at its anterior side ending in a narrow posterior canal which represents a posterior notch that had been covered by shell glaze. The columellar lip has four strong oblique folds, the lower of which surrounds the siphonal notch.

Derivatio nominis: The name of the subgenus represents a combination of the genus name *Plicoliva* with the location of its origin, Egypt, which is Misr in Arabic.

Differences: *Plicoliva (Misriplicoliva)* from the Late Cretaceous differs from modern *Plicoliva (Plicoliva)* by the presence of only four instead of five columellar folds. *P. (Misriplicoliva)* is distinguished from *Myobarum* SOHL, 1964 by having a shorter spire and three instead of one fold above the strong ridge that surrounds the siphonal canal at the base of the columella. The later feature differentiates *P. (Misriplicoliva)* from *Liopeplum* DALL, 1890 and *Parafusus* WADE, 1918, which are callus covered from the outside and have a higher spire, as is also the case with *Volutomorpha* GABB, 1877 (SOHL, 1964). *P. (Misriplicoliva)* differs from *Ancillus* MONTFORT, 1810 that has a broad columellar fasciole which also features the broader *Ptychosyca* GABB, 1877 (SOHL, 1964).

Plicoliva (Misriplicoliva) bartheli n. sp.

(figs. 39 - 45)

Diagnosis: The 32 mm long and 16 mm wide *Plicoliva (Misriplicoliva)* has a shell that consists of at least 3.5 whorls of the teleoconch and has a large erect protoconch.

Description: As in the diagnosis. The protoconch is not well preserved and of rounded shape with about 1 mm in width. The evenly olive-shaped teleoconch of about 30 mm in height and 16 mm in width has a smooth surface with some growth increments near the aperture coated by callus, but still visible. The spire is only one fifth of total shell height. The sutures are shallow. The aperture is elongate and widest at its anterior side. The posterior canal is curved to the left. The columellar lip has four strong oblique folds, the lower of which surrounds the siphonal notch.

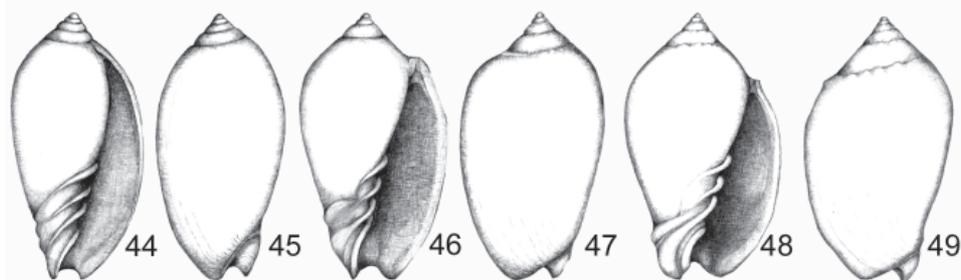
Derivatio nominis: Named in honor of Prof. Dr. K. Werner BARTHEL who was one of the collectors of the described fauna from the Sand Sea and a distinguished paleontologist.

Locus typicus: Conoco Channel 20 at Ammonite Hill locality in the Western Desert of Egypt (BARTHEL & HERMAN-DEGENS, 1981).

Stratum typicum: *Exogyra overwegi* beds with *Lybicoceras* (Maastrichtian) of the Western Desert, Egypt.

Holotype: Only two specimen were available for study of which the larger one (no.206) illustrated in fig. 39 represents the holotype.

Differences: The columellar folds are similar to those found in representatives of modern *Marginella* LAMARCK, 1799 which usually has a somewhat wider shell. Very similar in general shell shape and also apertural outline is *Hyalina* SCHUMACHER, 1817, but this modern genus has species which are usually much smaller in size. Marginellidae FLEMING, 1828 when fully grown usually have a glazed over protoconch. Modern *Oliva* and relation and *Olivella* SWAINSON, 1831 usually have a fasciolar band on the anterior portion of the



Figs. 44 - 45: *Plicoliva (Misriplicoliva) bartheli* n. sp. from Ammonite Hills in the Sand Sea of western Egypt (Conoco Channel 20) and here the Maastrichtian *Overwegi* Beds; **44:** Reconstructed from the holotype and the paratype. The aperture is elongate and widest at its anterior side ending in a narrow posterior canal with posterior notch. The columellar lip has four strong oblique folds, the lower of which surrounds the siphonal notch; **45:** Same individual, abapertural view.

Figs. 46 - 47: *Amoria zebra* (redrawn from POPPE & GOTO, 1992), modern shell; **46:** Apertural view, the shell is a little more than 50 mm high and differs only in regard to the posterior apertural notch from the shell of *Plicoliva*; **47:** Same shell as in fig. 46, abapertural view.

Figs. 48 - 49: *Cymbiola flavicans* redrawn from POPPE & GOTO (1992), modern shell; **48:** Apertural view, the shell is 60 mm high and differs in regard to the anterior ridges and the posterior notch of the aperture; **49:** Same shell as in fig. 48, abapertural view.

body whorl, which is not seen in *P. (Misriplicoliva)*. *Plicoliva (Plicoliva)* is very close in shape, size and the dimensions of the protoconch. It is, therefore, considered as closely related to *Plicoliva (Misriplicoliva)*, differing only in the number of columellar folds.

Remarks: The presence of *P. (Misriplicoliva)* in the Maastrichtian of Egypt explains the rather isolated position of modern *Plicoliva* among the Volutidae or Volutomitridae, which puzzled POPPE & GOTO (1992). The shallow sea that covered the modern Western Desert of Egypt at Late Campanian, Early Maastrichtian and perhaps also the Paleocene extended temporarily in a seaway across the whole African continent to West Africa and enabled faunal exchange from the Tethys to the expanding southern Atlantic Ocean at Late Cretaceous and Early Tertiary times (REYNOLDS et al., 1997). Modern *Plicoliva* may well represent off-springs of gastropods originating on the northern Gondwanian shelf. The further spreading of the Atlantic Ocean later separated the two still existing species of *Plicoliva* from each other. *Plicoliva* may, thus, represent an isolated taxon since at least the Eocene.

V. About the evolutionary history of the Latrogastropoda

Caenogastropod species belonging to the orders Neomesogastropoda and Neogastropoda (together they form the Latrogastropoda) have evolved since Mid Cretaceous time from still unknown ancestors. While most of the larger units of the Neomesogastropoda can be determined within the Cretaceous (BANDEL 1993, RIEDEL, 2000, see references here), the subunits (superfamilies, families) of the Neogastropoda are more difficult to trace back in time across the K/T boundary (see BANDEL & DOCKERY, 2001, 2003). Regarding the interpretation of evolution of the Neogastropoda two quite different opinions have been expressed in the literature.

One model stated that from Mid Cretaceous time onward almost all families of the Neogastropoda can be recognized (WENZ, 1938; SOHL, 1964a,b, 1987; TAYLOR & SOHL, 1962). TAYLOR & et al., (1980,1983) and TAYLOR & MORRIS (1988), for example, recognized from Albian rocks species that they considered to belong to the Muricidae, Buccinidae, Fasciolaridae, Melongenidae, and Mitridae, and from the Cenomanian stage onward they noted also members of the Volutidae and Cancellariidae.

The other model is that representatives of most of the characteristic families of the Neogastropoda are difficult to recognize in the Cretaceous, and that distinct groups are only rarely traced across the K/T boundary but that most of the units present today differentiated only during the Tertiary (BANDEL, 1993, 1997, 1999, BANDEL & STINNESBECK, 2000, BANDEL & DOCKERY, 2003). The definition of Neogastropoda as members of the Hypso-gastropoda representing a taxon that includes besides neogastropods also so called Neotaenioglossa such as Cassoidea, Littorinoidea and Ptenoglossa like Triphoridae, as suggested by PONDER & LINDBERG (1997, fig.5), can not be brought into accordance with the history of the groups concerned as has been extracted from the geological record (see BANDEL, 2002, for references).

BANDEL & DOCKERY (2003) suggested that such Late Cretaceous caenogastropods from the American Ripley Formation can be regarded to belong to the order Neogastropoda that have larval shells resembling in shape and size those found among modern neogastropods. These include the genera *Pseudorapa* HOLZAPFEL, 1888, *Pyrifusus* CONRAD, 1858, *Bellifusus* STEPHENSON, 1941, *Cryptorhytis* MEEK, 1876, *Pholidotoma* COSSMANN, 1896, *Drilluta* WADE,

1916, *Paleopsephaea* WADE, 1926, *Volutoderma* GABB, 1877, *Hercorhyncus* CONRAD, 1868, and *Pyropsis* CONRAD, 1860. All of these genera have species in the Campanian Coffee Sand and the Early Maastrichtian Ripley Formation of Mississippi and Tennessee with the protoconch preserved. It consists of a large (about 0.5 mm to 1 mm high) conical shell with a fairly large initial embryonic whorl (more than 0.15 mm across) that is well differentiated from the remaining protoconch, which usually consists of several whorls of larval shell (BANDEL, 1993). The larval part is smooth, bears a subsutural ridge or row of tubercles, and may or may not have a small median or anterior projection of the outer lip.

The superfamily Pyrifusoidea BANDEL & DOCKERY, 2001 consists of species with usually solid, medium-size to large shells (1-10 cm high) which are usually ornamented by spiral and collabral ribs. The aperture usually has a siphonal canal and a posterior notch or canal next to the suture on the outer lip. This notch gives rise to a subsutural ribbon. The shell of the living members of the Muricoidea RAFINESQUE, 1815 (= Muricina RIEDEL, 2000) commonly has a planktotrophic veliger with a more or less strongly ornamented protoconch and a pronounced projection of the outer lip. The teleoconch in Muricoidea and Buccinoidea RAFINESQUE, 1815 is mostly without the posterior notch of the aperture and the subsutural ribbon created by it. Based on the protoconch alone, no species of the Pyrifusoidea can be placed in any particular Recent neogastropod family, many of which have rather characteristic protoconch shapes (BANDEL et al., 1997, RIEDEL 2000).

The Pyrifusidae are based on the genus *Pyrifusus* CONRAD, 1858 with a siphon bearing, fusiform to pyriform shell that bears a collar below the suture as expression of a posterior notch of the outer lip of the aperture. Its protoconch is up to 1 mm high, has smooth rounded whorls with a basal apertural projection in the larval portion (BANDEL & DOCKERY, 2003). *Pyrifusus* based on *Pyrifusus subdensatus* CONRAD, 1858 from Owl Creek, Mississippi (SOHL, 1964a, pl.24, figs. 1-4) closely resembles species of genera like *Pseudorapa* HOLZAPFEL, 1888 from the Campanian Green Sand of Vaals (WENZ, 1938, figs. 3746, 3079) and *Bellifusus* STEPHENSON, 1941. Shell size in *Pyrifusus (Deussenia) gigantea* BANDEL & STINNESBECK, 2000 from the Maastrichtian Quiriquina Formation of Chile is more than 100 mm while the usual species of this genus from the Ripley Formation of the USA measure only up to 50 mm in height (SOHL, 1964a,b). Subfamilies included here are the Pseudorapinae BANDEL & DOCKERY, 2001, which have a pointed spire that is usually shorter than the last whorl, the Pyrifusinae BANDEL & STINNESBECK, 2000, with an even shorter spire, an inclined and often concave shoulder, and a large rounded body whorl, the Pholidotominae WENZ, 1938, with slender shell and spire as long or longer than the last whorl, the Beretrinae BANDEL & DOCKERY, 2003 with similar shell shape but elongate siphon, the Volutoderminae SOHL, 1964, with ovoid shape and commonly large shell, the Pyropsinae STEPHENSON, 1941, with rounded body and long siphon. Between all subfamilies transitional species connect so that it is somewhat arbitrary where to draw the lines of separation.

The Volutoderminae combine species with more or less *Voluta*-like shell that is more or less elongate fusiform and have a more or less high spire. Here whorls are constricted and may be shouldered. Ornament is by spiral cords and strong transverse ribs. The elongate aperture is narrow with a posterior notch, an extended broad siphonal canal and three, sometimes more and sometimes less, columellar folds on the inner lip. The protoconch consists of several whorls and is relatively small, probably formed by a planktotrophic larva. The genus *Gosavia* STOLICZKA, 1865 is of volutid or conoid shape, as is the more elongate *Volutoderma* GABB, 1877. SOHL (1964a,b) included *Volutoderma*, *Longoconcha* STEPHENSON, 1941, *Liopeplum* DALL, 1890, and *Volutomorpha*, GABB, 1877 in the Volutidae.

Ancestral representatives to the Cancellariidae and the Turridae (*Toxoglossa*) have been traced independently to the Santonian, with less secure data to the Cenomanian (see BANDEL & DOCKERY, 2003 for references). Members of the suborder *Toxoglossa* and possibly belonging to the family Turridae SWAINSON, 1840 have turrid shells with slender, high-spired to bi-conical shape, and their growth-lines show a well-developed subsutural or marginal posterior sinus. Commonly the protoconch of modern turrids is highly ornamented, but there are also smooth ones. Nothing of that type is known from the North-American Coon Creek fauna, and therefore the placement of the genera of the Amuletinae BANDEL & DOCKERY, 2003 in the Turridae is in doubt. Species of the Amuletinae have a slender turritiform shell that has a spire of about half of shell height and a long narrow siphon. The large smooth conical protoconch consists of several whorls and has a projection on the lower portion of the outer lip. The teleoconch has a wide subsutural or median sinus on the outer lip of the elongate aperture. The inner lip is smooth, and shell ornament consists of straight axial ribs and spiral ribs in variable arrangement. *Amuletum* STEPHENSON, 1941, and *Remnita* STEPHENSON, 1941 represent species from the Ripley Formation, which resemble modern *Toxoglossa* species of the subfamily Turrinae as interpreted by WENZ (1938). The teleoconch of *Amuletum* closely resembles that of a *Crassispira* SWAINSON, 1840, from the modern sea, but the protoconch is like that found in the Pyrifusidae.

Among the many species from the Ripley Formation of the USA members of the suborder Nematoglossa with the family Cancellariidae GRAY, 1853 are doubtful. The fusiform shells of those species suggested to belong here have a reticulated ornament, columellar and parietal folds on the inner lip of the aperture, and a truncate-conical to flat-topped protoconch. Cancellariids have a modified radula with distinctive, elongate teeth used to suck liquids, like blood, from fish or yolk from egg capsules. Due to the similarity in the shape of protoconchs of the Cancellariidae and Trichotropidae, a distinction of fossil species belonging to these widely different gastropod groups is difficult. The species connected to *Cancellaria* LAMARCK, 1799 and *Trigonostoma* BLAINVILLE, 1827 from the Late Cretaceous fauna do not present sound evidence for the presence of cancellariid (nematoglossan) neogastropods in the Ripley Formation.

The richly diverse members of the Rachiglossa, therefore, are difficult to detect among their potential Cretaceous representatives. The Neogastropoda, as we know them now, can be interpreted to represent the remnants of the Pyrifusidae that survived the Cretaceous/Tertiary faunal crises (BANDEL & STINNESBECK, 2000). This event had eradicated many transitional forms between groups of species with taenioglossate and rachiglossate radula which had been rather diverse in the Late Cretaceous.

VI. Summary and conclusions

One of the groups, though, that can be recognized to have been distinct already before the crisis is formed by the species with a large rounded protoconch from the Maastrichtian of the Western Desert in Egypt described above. They resemble the Eocene genus *Caricella* and the modern genera *Cymbiola* and *Plicoliva*. This could be interpreted as link connecting more modern genera with these Cretaceous species. The numerous volutids described by DARRAGH (1988) from the Australian Miocene all appear to have developed in a lecithotrophic way. It can be assumed that in the Maastrichtian of the shallow coastal Tethys on African (north-Gondwana) shores volutids developed which had the characteristic yolk rich embry-

ogenesis. These northern African species appear to be close to modern Volutidae as found in *Adelomelon* that lives along the southern shores of South America, *Cymbiola* that lives in South-East Asia and Australia and *Plicoliva* with species on both sides of the tropical Atlantic. On the other hand there is a connection to the Eocene of the Gulf coast and its *Caricella* type.

The impact on the faunal change-over connected to the Cretaceous-Tertiary boundary did, apparently, not eradicate especially such gastropods that had a non planktotrophic development, neither in the sea nor at land. The Volutidae appear to have acquired their modern characteristic of an exclusively lecithotrophic development latest during in the Maastriichtian and, thus, well before the change-over at the end of the Cretaceous. JABLONSKI (1986) indicated greater species longevity in Late Cretaceous mollusks that broadcast their larvae than in brooders, but found equal survivorship among brooders and broadcasters across the Cretaceous-Tertiary boundary. HANSEN (1980, 1982) supposed that Eocene neogastropods with planktotrophic larvae had broader geographic ranges, greater species longevities, and lower rates of extinction, than related species with lecithotrophic development. But later HANSEN (1987) also noted that larval ecology did not influence mollusk survivorship during the Eocene/Oligocene extinctions. Apparently with current knowledge about the matter it is wiser not to make general statements on survival or extinction in a crisis related to the mode of ontogeny in a group of gastropods.

BANDEL (1975a) had picked up and elaborated on the ideas of THORSON (1946, 1950) about distribution of species of gastropods in relation to the mode of their development and found no clear relation. Examples can be stated where species with lecithotrophic development are geographically widespread while others with planktotrophic development have a small distributional area and vice versa. Volutidae represent an example for survivorship from the Cretaceous to modern time and rather little change in the morphology of the species that lived then and that live now. On the other hand it appears as if most direct lineages that were constructed in literature between members of the Pyrifusidae and modern Neogastropoda interpreted to be closely related to them can not be supported. In this case the extermination of many species and genera at the K/T boundary may have affected the Pyrifusidae strongly, and thus species that usually had a long-term planktotrophic larva. Summing up models in which the mode of ontogeny is correlated to the fitness to survival over long times or to a faunal crisis have to be seen with great reservations. This is especially true in Gastropoda, where the fossil record is relatively good, but also convergence of shell shapes is very common and early ontogenetic shells are often not known, or, if known, have often been misinterpreted.

Volutidae as a taxon with modern *Voluta* and related genera like *Cymbiola*, *Cymbium*, and *Adelomelon* have been living on the shelf sea of the tropical Tethys Ocean during Late Cretaceous times. Volutidae due to their anatomical characters, as suggested by KANTOR (1996), appear to represent an early offshoot from the neogastropod branch that only later gave rise to most of the other families that can be clearly recognized today. It is also interesting that Volutidae appeared geographically at the northern shores of the disintegrating Gondwana Continent, while North America and Middle Europe have been dominated by the Pyrifusidae. No Cretaceous species of the volutids is known to have lived here in the Cretaceous. The ontogenetic mode of crawling young hatching provided members of the Volutidae to spread slowly and strictly by crawling on their foot. They still are much more common and richer in species in the southern than in the northern hemisphere. Convergence of shell shape created a confusing taxonomy in the past (WENZ, 1938) and has since been

considerably modified due to anatomical studies (KANTOR, 1996), but this still needs to be transported into the past. Many of the so-called volutids of the Tertiary need to be newly evaluated, especially by features of their protoconchs. The Cretaceous Volutoderminae (=Pholidotominae) *Volutoderma*, *Volutomorpha*, *Gosavia*, and *Beisselia* are not members of the Volutidae but of the Pyrifusidae and *Pholidotoma* and *Ficulopsis* STOLICZKA, 1868 are still of unknown relation.

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