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Living fossils among tiny Allogastropoda with high and slender shell from the reef environment of the Gulf of Aqaba with remarks on fossil and recent relatives

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With 71 figures

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**Abstract**

Among the minute, slender, many whorled gastropods from the fringing reef in front of the marine station at Aqaba (Jordan) a number of species are difficult to place among the better known taxonomic units, but can be documented to have a long history with little change reaching far into the past. The small *Donaldina* from the Carboniferous and Permian closely resembles Recent *Murchisonella*. Recent *Graphis* has its counterparts in Triassic *Cristalloella* and Jurassic *Urloella* and *Rotfanella*. *Ebala* has changed little since the Triassic and resembles the Late Paleozoic *Streptacis*. The characters of the Jurassic *Falsoebala* can be recognized in living species and has a certain representative from the Eocene of Hungary. Recent *Cima* and *Hemiaclis* have protoconchs that place them closer to Carboniferous Streptacidae and Mesozoic Tofanellidae than to modern groups such as Pyramidellidae or Eulimidae which they resemble in regard to the shape of their adult shell. *Murchisonella*, *Ebala* and *Graphis* have species or counterpart genera that lived 150 to 300 Million years ago. Thus, these genera represent true living fossils among the members of the subclass Heterostropha, order Allogastropoda. The new species *Cima urdunensis*, *Cima gantensis*, *Murchisonella arabica*, *Murchisonella cebuana*, *Ebala communis*, *Falsoebala hungarica*, *Hemiaclis aqabensis*, and *Graphis pacifica* are described.

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### Zusammenfassung

Unter den kleinen hochgetürmten Schnecken aus dem Saumriff vor der Meerestation von Aqaba (Jordanien) befinden sich eine Reihe von Arten, die nur schwer einer der bekannteren taxonomischen Einheiten zuzuordnen sind, jedoch eine weit in die Vergangenheit zurückreichende Geschichte aufweisen. So läßt sich die rezente *Murchisonella* mit *Donaldina* aus dem späten Paläozoikum vergleichen. *Ebala* könnte gut in die Verwandtschaft von *Streptacis* aus dem Karbon passen und besitzt zahlreiche Arten aus dem Mesozoikum. *Falsoebala* aus dem Jura ist noch in heutigen Arten erkennbar, und hat eine sichere Art im Eozän. *Graphis* ist leicht mit *Cristalloella* aus der Trias und besonders eng mit *Urlocella* und *Roffanella* aus dem Jura verknüpfbar. *Hemiaclis* läßt sich noch nicht einer anderen, älteren Gattung zuordnen, ist jedoch im Bau des Protoconches den mesozoischen Tofanellidae (Allogastropoda) ähnlicher als hinsichtlich der Adultschalengestalt ähnlichen modernen Caenogastropoden. Auch *Cima urdunensis* ähnelt eher einer karbonischen oder triadischen Streptacidae als einer modernen Pyramidellide. Die beschriebenen Schnecken sind am ehesten den Allogastropoda zuzurechnen. Unter ihnen haben heute lebende Arten von *Murchisonella*, *Graphis* und *Ebala* fossile Gegenüber, die ihnen so stark ähneln, daß sie als lebende Fossilien betrachtet werden können, die sich seit 300-150 Millionen Jahren kaum verändert haben. Die neuen Arten *Cima urdunensis*, *Cima gantensis*, *Murchisonella arabica*, *Murchisonella cebuana*, *Ebala communis*, *Falsoebala hungarica*, *Hemiaclis aqabaensis*, *Graphis pacifica* werden beschrieben.

### I. Introduction

Among the tiny marine gastropods that have traditionally been placed with the Pyramidellidae and the Aclididae, species of the genera *Murchisonella*, *Ebala*, *Hemiaclis* and *Graphis* live on and within the small reef that lies in front of the marine station of Aqaba (Jordan). As had been noted by COSSMANN (1895), the protoconch of the genera which he placed in the Aclisidae (= Aclididae Sars, 1878 and of most other authors) are a little "awkward" and sometimes resemble those of the pyramidellids in being flat on the top of the shell and having a different direction of their axis of coiling. THIELE (1931) placed more weight in the absence of a radula and had the genera *Murchisonella*, *Graphis* and *Aclis* in the family Aclididae, *Ebala* in the family Pyramidellidae of his Stirps Aglossa. WENZ (1939) changed Aglossa into Pyramidelloidea (= Gymnoglossa and Aglossa). He united here the usually small sized parasites on echinoderms (Eulimidae = Melanellidae) with parasitic species living on mollusks and worms (Pyramidellidae) with the Aclididae. The Aclididae have a small shell with similar elongate shape but their mode of life is still unknown. A similar arrangement with Aclididae between Epitoniidae and Eulimidae and *Ebala* with reservations in the Pyramidellidae was also suggested by SMITH (1998) and PONDER & DE KEYZER (1998) in the classification adopted for Australian mollusks.

KOLLMANN & YOCHelson (1976) attempted to trace the evolution of the Heterostropha (Opisthobranchia) into the Carboniferous. In their study the Opisthobranchia were interpreted as subclass of gastropods as had been suggested by KNIGHT et al. (1960). This taxon was interpreted to contain as one superfamily also the Pyramidelloidea ORBIGNY, 1840. Herein included were genera such as *Donaldina* and *Streptacis* with type species from the Carboniferous. HASZPRUNAR (1985b) distinguished an own taxon of the Heterostropha, the Allogastropoda, which have since been documented to have carried out an independent evolution from other gastropods ranging back to the Devonian (FRYDA & BLODGETT, 2001; BANDEL & HEIDELBERGER, 2002, BANDEL, 2002).

Modern gastropods with a shell fitting into the diagnosis of *Donaldina* live among coralline algae in the environment of tropical coral reefs (BANDEL, 1991, 1994). Specimens

belonging to the Donaldinidae can be found in the modern genus *Murchisonella* or *Schwengelia*. These taxa were found in shallow water of the Caribbean Sea among coral rubble of shallow bays, transported from the reef into deeper water near Cebu in the Philippines (BANDEL, 1991, figs.7a,b). They were collected alive from shallow coral reefs at Lizard Island in the Great Barrier reef of Australia (BANDEL, 1996). *Murchisonella* was considered a member of the Aclididae by THIELE (1931, fig.229), but ABBOTT (1974, fig.1466) interpreted these to belong to the genus *Schwengelia*, a synonym of *Murchisonella*.

*Streptacis* on the other side was noted to resemble in many ways the modern *Ebala*, a tiny gastropod with the protoconch twisted off quite conspicuously (GRAHAM, 1988, fig.270). *Ebala* and its relatives are usually placed within the Pyramidelloidea and here the family Pyramidellidae which represent a taxon with a very large number of species usually living as parasites on marine mollusks and worms. While the main radiation of the species of the Pyramidellidae appears to have occurred since the late Cretaceous (SOHL, 1964, DOCKERY, 1993), the tiny *Ebala* is also regularly found in Jurassic and Triassic marine deposits (BANDEL 1994, 1996, SCHRÖDER, 1995, GRÜNDEL, 1998, KAIM, 2004). The animal of *Ebala* was studied by WARÉN (1994, figs. 1D-F) who found a complicated jaw apparatus that distinguishes it well from Pyramidellidae and from other Heterostropha.

According to BANDEL (1996) living individuals of *Donaldina/Murchisonella* on Lizard Island had two prominent ciliated tentacles on its mantle edge, extending from the subsutural sinus in the outer lip of the aperture. The cilia of the frontal pallial tentacle are continuous with a ciliated band that crosses the entire mantle cavity. On the head lie small simple eyes close to each other, and flattened triangular tentacles are covered by cilia and extend to the sides. Between the tentacles two ciliated mouth lobes lie above the mouth which probe the substrate when the animal is active. They carry sense cilia on their frontal end. The propodium is also densely ciliated. When the little snail moves, the foot proceeds continuously and rapidly while the shell is dragged behind and periodically pulled forward in short jerks by periodical contraction of the retractor muscle. The foot carries a large transparent operculum that is able to seal the aperture tightly.

Within the Aclididae, FRETTER & GRAHAM (1982) discussed the genus *Cima* and found the animal of *Cima minima* to have no snout but a proboscis that may be protruded, and that contains a radula. Since most of the Eulimidae and of the Pyramidellidae have no radula, *Cima* does not fit here. WARÉN (1993) suggested an independent taxon, the Cimidae to place *Cima* and related forms.

Usually *Graphis* is assigned to the Aclididae. According to Smith (1998) this placement was apparently doubted by BOUCHET & WARÉN (1986), only the genus *Aclis* will remain in the family Aclididae. The uniting factor had been characters of the protoconch (COSSMANN, 1895) which was noted to be unusually broad. FRETTER & GRAHAM (1982) noted that *Graphis* differs from *Aclis* not only in shell shape and ornament but also that of the body such as the presence of a tentacle on the mantle edge on the right. Moreover, in contrast to *Cima* the animal of *Graphis albida* has a snout on its head, and each tentacle bears an eye.

This study documents that some of the tiny gastropods which nowadays live within the environment of tropical reefs have a very long history of evolution during which their shell shape changed very little. Although these species are not uncommon in shallow marine environments, due to their small size they have usually been overlooked. Many changes have occurred in the environment that surrounds them during their existence in time. In case of *Murchisonella*, even the large faunal turn-over from the Paleozoic to the Mesozoic had little impact. Very similar species belonging to the *Donaldina* relation lived quite

commonly in shallow water environments of tropical seas during the Carboniferous and Permian. Their characteristic protoconch closely resembles that found in *Cima*. However, *Cima* lacks spiral ornament and the subsutural sinus is less strongly developed. Both genera can be interpreted to be members of the Streptacidoidea, Donaldinidae, and belong to groups in which the protoconch lies flatly on top of the teleoconch. The protoconch of *Ebala* is similar, but its smooth initial shell is sinistral in its early portion and becomes planispiral before begin of the teleoconch. The coiling axis deviates strongly from that of the teleoconch. Members of this genus have been living on the tropical reef flat in the Triassic, and are well documented since then. They lived and live from the very shallow reef lagoon to deeper shelf environments, and they are quite similar to Late Paleozoic species of the genus *Streptacis*. Characteristically, the whorls of the protoconch are quite detached from those of the teleoconch.

While *Cima*, *Murchisonella* and *Ebala* have a protoconch that does not change direction of coiling, that of *Graphis* is sinistral at first and later twists into the dextral coiling mode, i.e. the change of coiling direction occurs within the protoconch and not the transition to the teleoconch. Such shell shapes in species with small and elongate teleoconch are represented in the fossil record since the late Triassic (BANDEL, 1995, 1996). Smooth protoconchs of that type are found in members of the Tofanellidae with several species known from Triassic, Jurassic and Cretaceous rocks. Some species of the Tofanellidae have a larval shell with the outer lip bearing a projection, others have protoconchs with simple and straight outer lip. Among the latter *Rotfanella* from the Jurassic can hardly be distinguished from the modern *Graphis*, except for its age. *Graphis* is well separated from *Aclis* which could be a caenogastropod. Whether *Hemiaclis* is related to *Aclis* still needs to be evaluated. Regarding protoconch shape *Hemiaclis aqabaensis* described below appears to represent a member of the Tofanellidae. But the faint ornament on the larval shell is not known from any tofanellid species so far, including *Graphis*.

The modern species that can be included in the families Donaldinidae, Ebalidae, and Tofanellidae are representatives of ancient taxa. Their fossil history exceeds the age of the reef community in which they are found today (e.g. fringe reef of Aqaba). Reef types have since changed even several times, reef building organisms such as corals have changed in composition, importance as frame builders and even in mineralogy. Thus, the shallow water community from the Late Triassic, in which Tofanellidae, Donaldinidae and Ebalidae occur, were quite different from those of today (e.g. FÜRSICH & WENDT, 1976). Almost all of the co-occurring mollusks have been exchanged since then several times. Since the mid Cretaceous, a whole set of new gastropod predators has evolved, especially the very active naticids that prey on them. For example, sea grass has since changed the bottom substrate of the lagoon. Apparently the small species here described were not strongly effected by these and many other changes. One could argue, that such unusually small sized gastropods represent rather specialized species belonging to larger groups which have more “normal” sized species, but apparently this is not the case. The small size of these gastropods is a characteristic feature that has been present in this group for the last several hundred million years. *Cima*, *Murchisonella*, *Ebala* and *Graphis* can be considered to represent living fossils even more than *Pleurotomaria*, which is usually considered as the typical example among gastropods (HICKMAN, 1984).

## II. Systematic descriptions

### Subclass: Heterostropha FISCHER, 1885

The subclass Heterostropha (=Heterobranchia) represents all those gastropods that have a sinistral larval shell (protoconch) and a dextral teleoconch with a change in coiling at metamorphosis or during larval life, or such species that had ancestors with such ontogeny. In rare cases this tendency left to right coiling is reversed. They include the orders Allogastropoda and Euthyneura.

### Order: Allogastropoda HASZPRUNAR, 1985

The order includes shell bearing Heterostropha such as Streptacidoidea, Pyramidelloidea, Mathildoidea, Architectonicoidea, Nerineoidea and Valvatoidea. It probably represents a paraphyletic taxon that includes all Heterostropha which are not Euthyneura (= Opisthobranchia and Pulmonata).

### Superfamily Streptacidoidea KNIGHT, 1931

Streptacidoidea (=Streptacididae of KNIGHT et al. (1960)) have high spired shells with sinistral protoconch, often rounded sinus in the outer lip of the aperture high on the whorl and simple oval outline of the aperture. Their ornament consists of growth lines and/or spiral lines or ribs. The protoconch is a discoid (initially sinistral) whorl that caps the spire flatly or is deviated. Streptacidoidea are considered to hold the families Streptacididae, Donaldinidae, and Ebalidae, all of which have genera that lived at least in the Early Mesozoic (Triassic) some in the Late Paleozoic (see BANDEL 1996, 2002 for references).

### Family Streptacididae KNIGHT, 1931

The representatives of the Streptacididae have high and slender shells with many whorls with a sinus on the apical outer lip. The protoconch is flattened disc-shaped and left-coiled and may be situated flatly or obliquely upon the teleoconch. The teleoconch is ornamented by fine curving growth lines and there may be fine spiral lines. Its whorls are rounded, sutures are impressed, and there is no open umbilicus. The outer apertural lip is sinuous with a sinus below the suture and an lobe near its center. The columellar lip is short and arched.

Representatives of this ancient group (see BANDEL, 2002 for references) with characteristic shell shape and size still exist and are represented by the modern species of the Ebalidae.

### Genus *Cima* CHASTER, 1898

The type species to the genus is *Odostomia minima* JEFFREYS, 1858 illustrated by FRETTER & GRAHAM (1982, figs.293, 294) and GRAHAM (1988, fig.216). The minute columnar shell has a blunt apex with globular protoconch. The aperture is oval with wide sinus in the upper portion of the outer lip. The rounded whorls are smooth and there are only growth lines.

Remarks: Also species of the genus *Pherusa* JEFFREYS, 1869, which according to THIELE (1931) is a synonym of *Pherusina* NORMAN, 1888, are similar. GRAHAM (1988, Fig.218) described the type *Pherusa gulsonae* (CLARK, 1850) from the Atlantic occurring from

Madeira to England. Its shell is almost cylindrical, small with 6-7 rounded whorls. The apex is rounded and the outer lip of the aperture has a deep anal sinus. The base is averted to form a trough. The shell is only 2 mm high. It closely resembles *Cima* and has a wide apertural notch.

Regarding the shape of the teleoconch *Cima urdunensis* and *Cima gantensis* resemble an early Jurassic species described by SCHRÖDER (1995, Pl.10, figs.15-17) and later placed in the genus *Usedomella* by GRÜNDEL (1998). (see Pl.1, figs.12-15). Here the protoconch differs by having one more whorl in which the initial left coiling changes into dextral coiling.

*Cima urdunensis* n. sp.

(figs. 1 - 5)

**Diagnosis:** The minute shell has a blunt apex which holds a left coiled protoconch consisting of one whorl. The whorls of the teleoconch are rounded and ornamented by somewhat irregular growth lines. The aperture is oval and may or may not have a subsutural sinus.

**Derivatio nominis:** This *Cima* come from the Jordanian (Urdun in Arabic) coast of the Red Sea.

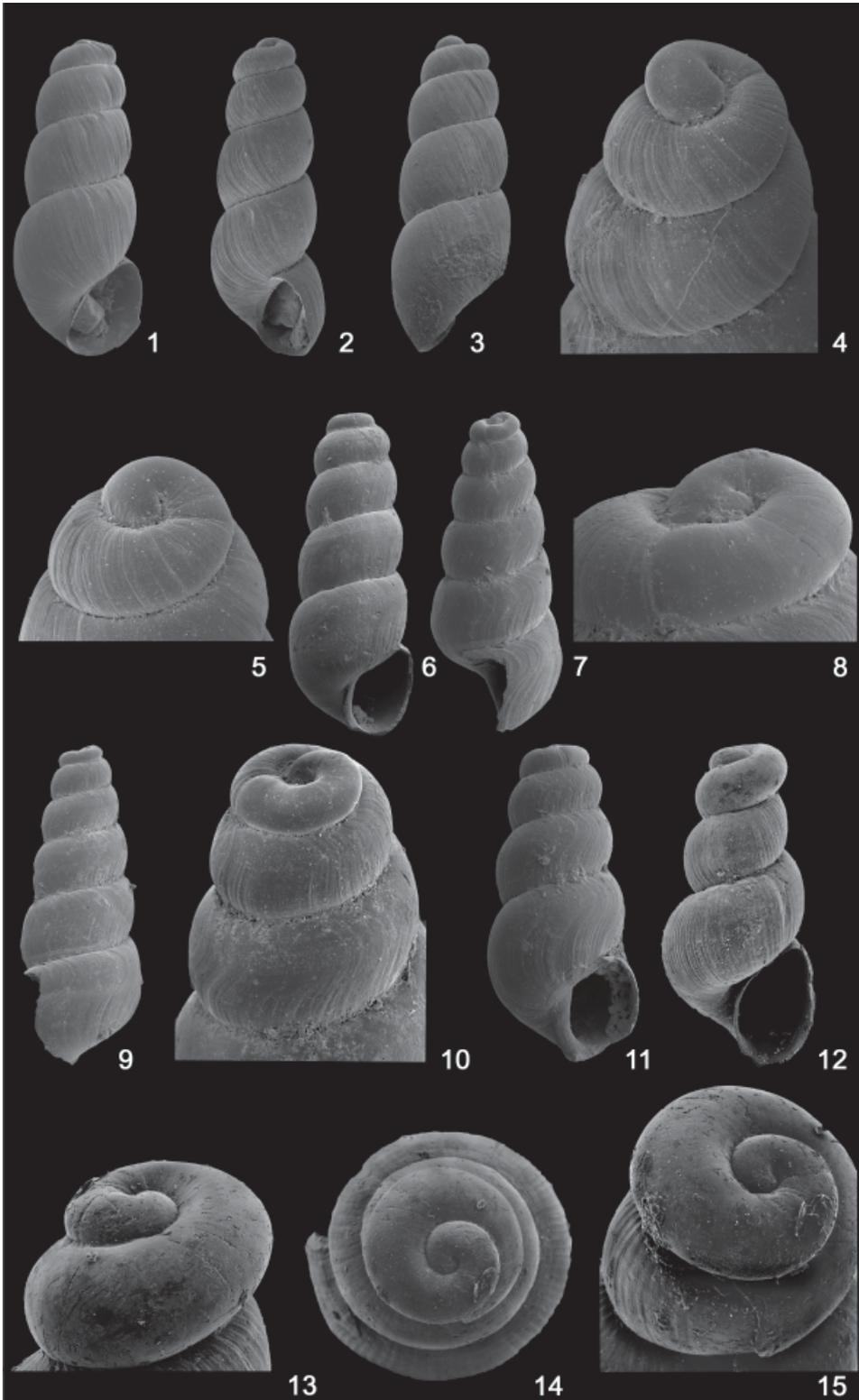
**Material:** Several shells from the base of the small fringing reef in front of the marine station at Aqaba. The species lives in shallow water of 0,5 to 3 m of depth within the frame of the reef. The holotype is the figured shell (fig.1). It is deposited in the collection of the Geological-Paleontological Institute and Museum, University Hamburg.

**Description:** The small and delicate shell has a high spire, columnar shape with blunt apex. There are about 5 whorls which are well rounded and have a deep suture. The ornament consists only of growth lines which reflect a somewhat sinuous course of the outer lip. The aperture is oval and rounded. The protoconch consists of about one planispiral whorl. The protoconch measures about 0,14 mm across and the teleoconch with 5 whorls is a little more than 1 mm high. The shell is opaque white and transparent.

**Remarks:** *Cima urdunensis* may represent a donaldinid with lecithotrophic development, since there are folds on the initial part of the protoconch. It differs from *Hemiaclis* with similar teleoconch shape by the protoconch, which here is not coiling into the right within the protoconch. The protoconch is smaller and lies more plane on the top of the teleoconch as is the case in *Cima minima* JEFFREYS, 1858 as known from southern England (GRAHAM 1988, fig. 216).

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**Figs. 1-5:** *Cima urdunensis* n. sp.; **1:** Holotype, from the reef flat of Aqaba, Red Sea; shell about 1 mm high; **2:** Shell a little less than 1 mm high, growth lines simple or with shallow subsutural sinus; **3:** Shell almost 1mm, seen from behind; **4:** Protoconch with one about 0.14 mm wide whorl of the embryonic shell well distinguished from the whorls of the teleoconch; **5:** The protoconch of this individual has a wrinkled initial portion of the embryonic shell and measures 0.14 mm across. **Figs. 6-11:** *Cima gantensis* n. sp.; **6:** Holotype with a little more than 1 mm high shell from the mid-Eocene of Gant in Hungary; **7:** Shell, in slightly inclined position exposes the growth line pattern with well developed sinus below the suture; **8:** Protoconch, flat, consisting of almost 1.5 whorls with about 0.15 mm in diameter; **9:** Fully grown shell, 1.2 mm high, the sinus in the outer lip of the aperture well developed, and the protoconch is flattened; **10:** Protoconch, with a sinistral initial portion and is planispiral at transition to the teleoconch. It measures 0.15 mm across; **11:** A shell with the growth line pattern well developed, simple aperture and flat protoconch. The shell is 0.8 mm high. **Figs. 12-15:** *Usedomella schroederi* GRÜNDEL, 1998 from the Early Jurassic as described by SCHRÖDER (1995, Pl.10, fig.15-17) with the protoconch having a sinistral embryonic whorl and the change into dextral coiling within the larval shell. Shell is about 0.75 mm high; **13:** Detail of fig. 12, with sinistral first whorl and transition into dextral coiling; **14:** Detail of fig.12 as in SCHRÖDER (1995, Pl.10, fig.17) apical view; **15:** Larval shell ends with sinuous apertural margin, as shown by SCHRÖDER (1995, pl. 10, fig. 16).



*Cima gantensis* n. sp.

(figs. 6 - 11)

Diagnosis: The flat protoconch consists of almost 1,5 whorls and has a left coiled embryonic whorl. Dextral coiling begins within the first whorl of the teleoconch. The shell is about 1,2 mm high with 5 rounded whorls of the teleoconch. The aperture is oval and has a sinus in the apical part of its outer lip. Ornament consists only of fine growth lines.

Derivatio nominis and material: This *Cima* has been extracted from the marl of the quarry at Gant in Hungary and is called according to its type locality. The rocks have been deposited during the middle Eocene near to the margin of a costal swamp in shallow marine waters (own observations in the field).

Holotype: Illustrated on fig. 6, represents the holotype and is deposited in the collection of the Geological-Palaeontological Institute and Museum, University of Hamburg.

Description: Characteristic of the species is the sinus in the apical part of the outer lip, and the donaldinid protoconch. The latter measures only about 0,15 mm across: The left coiled embryonic whorl ends with onset of growth lines and continued into the flatly coiled larval whorl that ends with a thickened margin of its rounded aperture. This thickening distinguishes the protoconch well from the teleoconch. The teleoconch consists of five well rounded whorls which form the slender shell, measures only about 1,2 mm in height and 0,4 mm in width. Whorl diameter increases slowly during growth. The almost round aperture has its columellar lip a little thickened by an outwards twisting rim and the outer lip curves to form an umbilical lobe and a subsutural sinus.

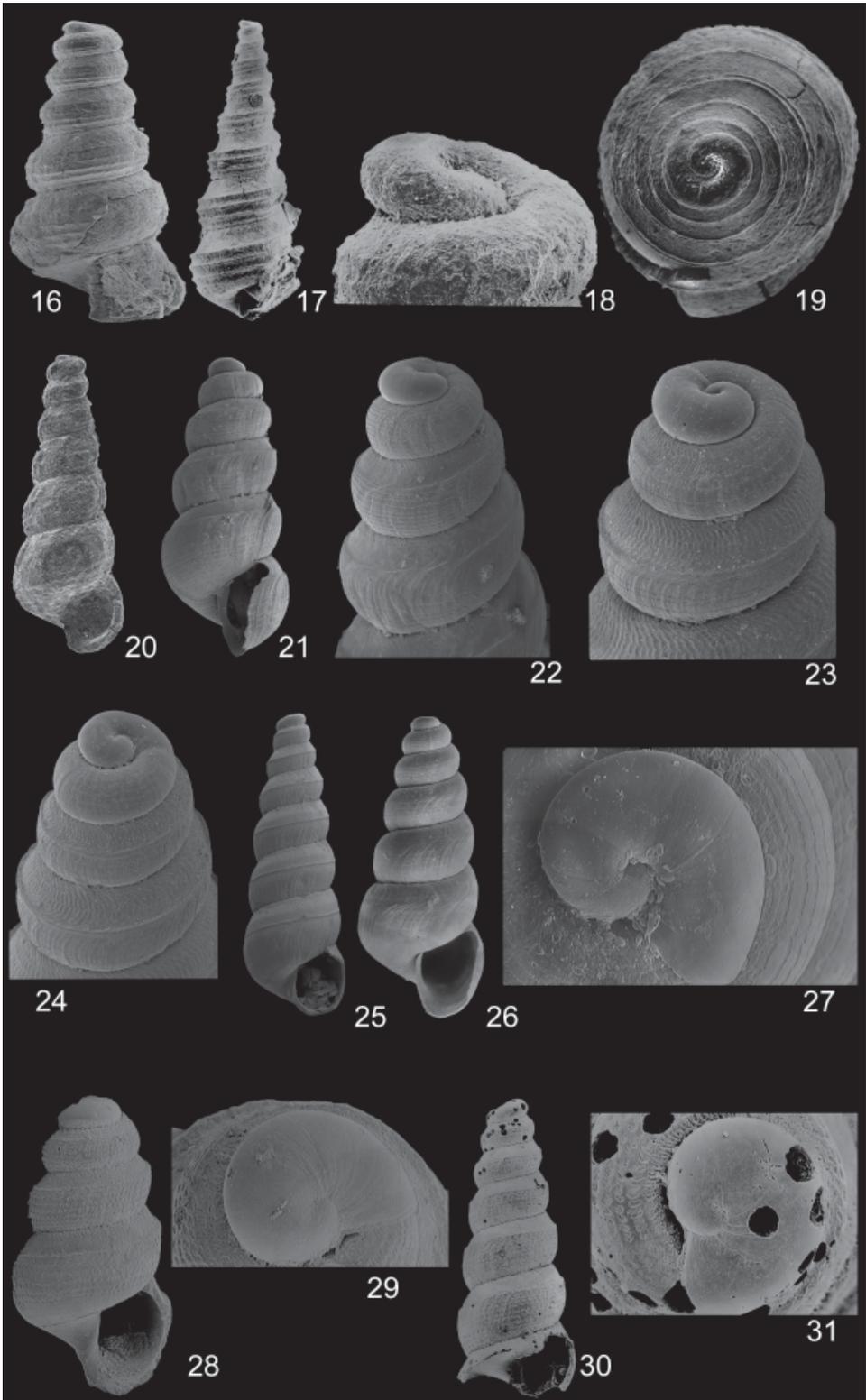
Remarks: *Cima gantensis* is very close in shape to *Cima urdunensis* and differs from it by having a protoconch consisting of 1,5 instead of one whorl and by a more pronounced subsutural sinus in the outer lip of the aperture in teleoconch whorls.

Family Donaldinidae BANDEL 1994

In members of the Donaldinidae the teleoconch usually has a wide oblique shoulder and is ornamented by spiral ribs (BANDEL, 1996, 2002). The protoconch is sinistrally coiled

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**Fig. 16:** *Donaldina stevensana* (MEEK & WORTHEN, 1866) from the Late Carboniferous of the USA as in BANDEL (2002, pl 1, fig. 12) with about 2 mm high shell. **Figs. 17-19:** *Donaldina ohioensis* BANDEL, 2002; **17:** Shell from the Late Carboniferous of Ohio with about 3 mm high shell; **18:** Protoconch (as in fig.17) with a flat a slightly sinistrally coiled shell of about 0.12 mm in diameter closely resembles that of *Murchisonella* in shape and orientation; **19:** Apical view of the shell in figs. 17-18, showing the flat protoconch on the teleoconch with apical shoulder, and spiral ornament on the sides as seen in *Murchisonella*. **Fig. 20:** *Donaldina media* BANDEL, 2002 from the Late Carboniferous of Texas, USA with about 1.7 mm high shell resembles modern *Murchisonella*. **Figs.21-25:** *Murchisonella arabica* n. sp.; **21:** Juvenile shell from Aqaba with about 2 mm high, having the subsutural sinus on the outer lip well developed; **22:** Apical portion of a shell with shoulder and side with lobe reflected in growth-line pattern with the illustrated shell portion, about 1mm high; **23:** Protoconch, consisting of a little more than one smooth rounded whorl that changes from slight sinistral coiling at begin to planispiral coiling, and measures 0.15 mm in diameter; **24:** Teleoconch, with a flattened apical ramp, growth lines tracing the outline of the subsutural sinus. The flat protoconch is about 0.15 mm in diameter; **25:** Holotype, from the fringing reef at Aqaba with 1.8 mm high shell. **Figs. 26-27:** *Murchisonella* sp. **26:** Shell from the sea grass covered lagoon at Lizard Island, Great Barrier Reef, Australia, shell about 1.5 mm high; **27:** Detail of fig.26, with the protoconch similar to that seen in fig. 31 but larger measuring almost 0.2 mm in diameter, also the shoulder of the teleoconch less distinctly developed. **Figs. 28-31:** *Murchisonella cebuana* n. sp.; **28:** Juvenile shell from off-shore Cebu City, Philippines, about 1 mm high and ornamented by characteristic spiral rows of pits; **29:** Detail of the shell in fig. 28, with the flat protoconch, about 0.15 mm in width; **30:** Holotype, shell about xx high and ornamented of rows of pits; **31:**Detail of the shell in fig.30 with a protoconch having the initial portion of the slightly sinistral embryonic shell covered by the larval shell, protoconch measures 0.15 mm across.



without changing into dextral coiling. The family is based on the genus *Donaldina* KNIGHT, 1933 representing a shell with high spire that is ornamented with spiral threads confined generally to the lower part of the whorl. It is based on the Carboniferous genotype *Donaldina grantonensis* (DONALD 1898) from Scotland (see BANDEL 2002 for references).

#### Genus *Murchisonella* MÖRCH, 1875

The type is *Murchisonia* (*Murchisonella*) *spectrum* MÖRCH, 1875 from the Caribbean Sea (THIELE, 1931, fig.229, WARÉN, 1994). BANDEL (1996) noted tentacles on the mantle edge in *Murchisonella* from the Barrier reef area of Australia (figs. 26, 27), which distinguish the genus from similar small ones with high spire, such as those belonging to the species-rich Pyramidellidae.

Remarks: *Donaldina* from the Late Paleozoic, as described by Yoo (1988, 1994) was also interpreted by WARÉN (1994) to be quite similar to modern *Murchisonella*. The species of *Donaldina* described by BANDEL (2002) from the Carboniferous of the USA reflect this similarity (figs. 16-20 and here illustrated again) in regard of ornament of the teleo-conch as well as shape of the protoconch.

#### *Murchisonella arabica* n. sp.

(figs. 21 - 25)

Diagnosis: The protoconch consists of one smooth, rounded planispiral whorl with initial part rounded and smooth. The teleoconch has a broad, flattened, sloping shoulder ending in a peripheral spiral rib and is formed behind a subsutural sinus of the outer lip of the aperture. The sides are weakly rounded with ornament of curving collabral lines and sometimes spiral grooves. The base is rounded and without open umbilicus.

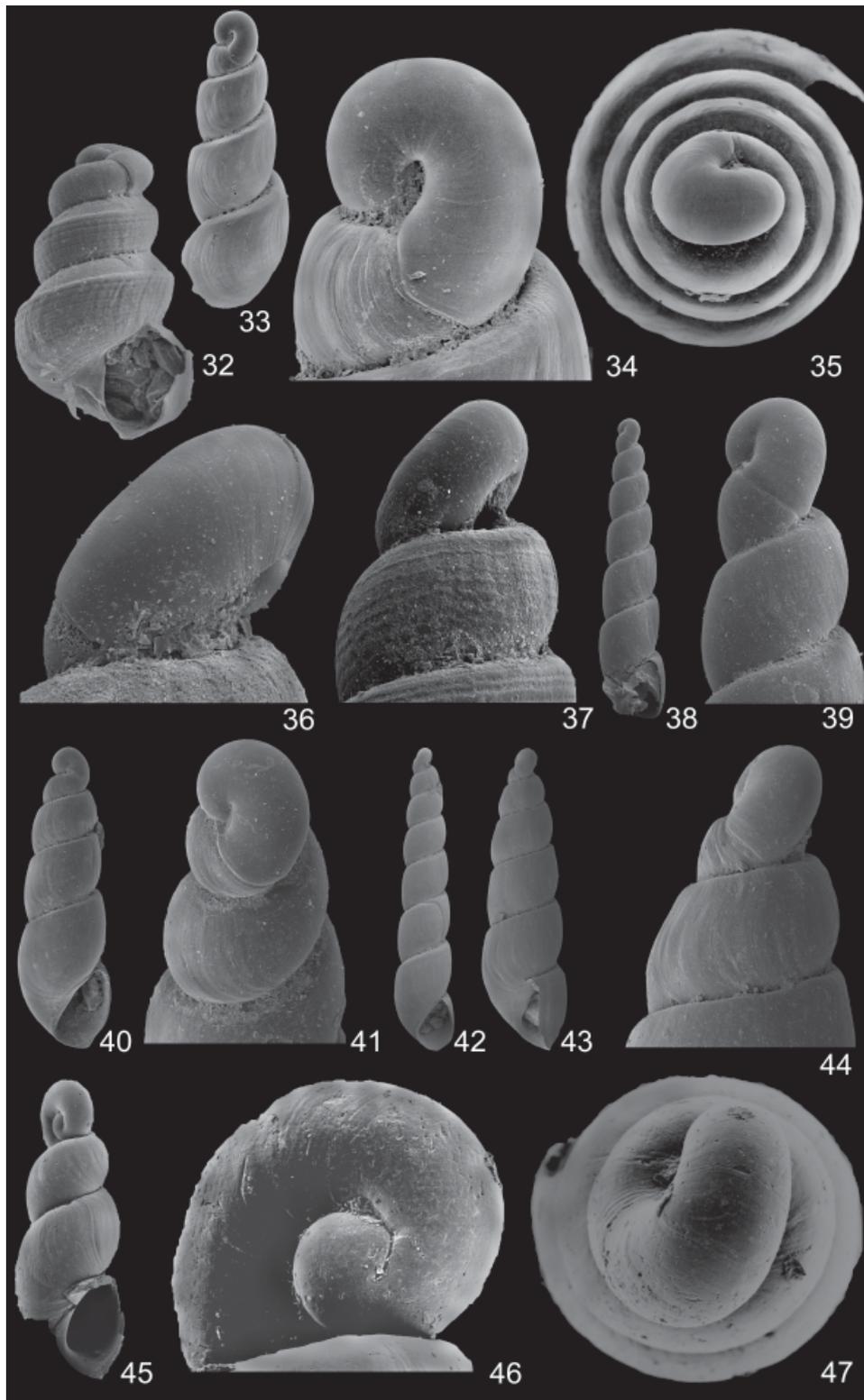
Derivatio nominis: This *Murchisonella* is from the Arabian shore of the Red Sea and named accordingly.

Material: Several shells from the fringing reef in front of the marine station in Aqaba with that illustrated in fig.25 representing the holotype, housed in the Museum of the Geological and Paleontological Institut of the University Hamburg.

Description: The species is as in the diagnosis with protoconch measuring about 0,15 mm in diameter (figs. 22-24) and the teleoconch with broad flattened shoulder (figs.

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**Fig. 32:** *Murchisonella floridana* (BARTSCH, 1911) from the Caribbean Sea near Santa Marta, Colombia; juvenile shell of about 0.6 mm in height. **Figs. 33-35:** *Ebala* sp., **33:** Shell from off-shore Cebu City, Philippines with 0.9 mm long shell has more curving growth lines than *Ebala communis* and a more prominent whorl shoulder; **34:** Protoconch as in fig. 33, measuring almost 0.2 mm in diameter and resembles that of *Ebala liassica* in size and shape; **35:** Apex as in fig.33, documents a slight deviation from 90° formed by the axis of coiling of the protoconch with that of the teleoconch. **Figs. 36-44:** *Ebala communis* n. sp; **36:** Protoconch from Aqaba is almost planispiral, sinistral and about 0.15 mm in diameter; **37:** Transition of the protoconch to the teleoconch from Aqaba, from left to right coiling and detached from the first whorl of the teleoconch, here with ornament of spiral lines; **38:** Almost fully grown shell from the shallow lagoon of Aqaba, 1.6 mm long; **39:** Detail of fig. 38, with the transition from the sinistral protoconch to the dextral teleoconch; **40:** Juvenile shell from Aqaba, with about 1 mm long shell with simple aperture; **41:** Umbilical view of the protoconch whorl from Aqaba, with the concealed initial part. Protoconch diameter of about 0.15 mm; **42:** Holotype, from the shallow lagoon of the reef flat at Aqaba Marine Station, with 2.2 mm long shell; **43:** Juvenile shell from Aqaba, with 1.4 mm long shell appearing to be less slender than the fully grown one; **44:** Detail of fig. 43, with transition from protoconch to teleoconch. **Figs. 45-47:** *Ebala liassica* SCHRÖDER, 1995 from the Jurassic, **45:** Conch closely resembling the modern species, but its protoconch is larger (the shell is about 0.6 mm high); **46:** Protoconch as illustrated by SCHRÖDER (1995, Pl.10), fig. consists of about 1.5 whorls and is 0.19 mm wide; **47:** Protoconch axis of coiling and that of the teleoconch (detail of fig.45) form an angle of 90° with each other.



23, 24). The shoulder is ornamented by evenly curving growth increments as well as wrinkles and tubercles arranged along them. Below the peripheral spiral rib bordering the shoulder the sides are ornamented by evenly forward curving growth lines and fine lines following them (fig. 22). A fully grown shell with nearly 7 whorls of the teleoconch measures almost 2 mm in height.

Differences: *Murchisonella arabica* differs from the *Murchisonella cebuana* as described below and previously illustrated by BANDEL (1991, Pl.8, figs.5,11) from Cebu in having a less tightly coiled protoconch and in the ornament of the teleoconch not consisting of rows of pits. The shoulder of *Murchisonella arabica* is relatively wider and the sides appear to be more evenly rounded. A *Murchisonella* sp. (figs. 26, 27) from Lizard Island in the Australian Barrier Reef appears to be a little broader and with even more rounded whorls.

*Murchisonella cebuana* n. sp.

(figs. 28 - 31)

Diagnosis: The protoconch consists of one smooth planispiral whorl with initial part covered. The teleoconch has a flattened sloping shoulder ending in a peripheral spiral rib. The side is ornamented by 6-7 spiral rows of pits. The base is rounded and without open umbilicus. The teleoconch has a broad, flattened, sloping shoulder ending in a peripheral spiral rib and borders a subsutural sinus of the outer lip of the aperture. The sides are weakly rounded with ornament of curving collabral lines and sometimes spiral grooves. The base is rounded and without open umbilicus.

Derivatio nominis: The described shells are from Cebu, Philippines, and named accordingly.

Material: The holotype is illustrated on fig. 30, deposited in the collection of the Geological-Palaeontological Institute, University of Hamburg. It comes from material described by BANDEL (1991) that has naturally been washed from a reef platform into deeper water.

Description: The shell is as indicated in the diagnosis and has an about 0,15 mm wide protoconch (figs. 29, 31). The later is smooth with simple growth lines. Only the half covered embryonic shell has some grooves and ridges in its early portion. A shell with 8 whorls is less than 1,5 mm high. The ornamental pattern of the teleoconch is characteristic, resembling that of *Murchisonella* sp. from the shallow lagoon of the Barrier Reef area of Lizard Island, Australia (figs. 26, 27), but here the protoconch is a little larger and the whorls of the teleoconch are more rounded.

Genus *Schwengelia* BARTSCH, 1947

The species *Schwengelia floridana* (BARTSCH, 1911) on which this genus is based (ABBOTT, 1974) can probably be included in the genus *Murchisonella*. The genera *Schwengelia* and *Murchisonella* are no separate units. Since *Schwengelia* BARTSCH, 1947 was proposed later than *Murchisonella*, the latter should be used. It is also possible that the type to the genus *Murchisonella* is actually this species.

*Murchisonella floridana* (BARTSCH, 1911)

(fig. 32)

Description: The elongate turreted shell has a sloping strong shoulder ending in a spiral cord. The sides are rounded and ornamented by several spiral cords, of which four remain uncovered by succeeding whorls. This species illustrated by ABBOTT (1974, fig.1466)

was originally described as *Aclis floridana*. The protoconch of an individual from the Caribbean Sea near Santa Marta is flatly coiled, consists of more than one whorl, and has a simple rounded aperture (fig. 32). It is quite similar to that of the species of *Murchisonella* from the Pacific, described above.

Differences: *Murchisonella floridana* is very close in shape and ornament to *Murchisonella arabica* but has lower whorls and a more angular edge between shoulder and rounded sides. *Murchisonella cebuana* differs by the characteristic ornament of rows of pits. This later ornament is also present in *Murchisonella* sp. collected from Lizard Island, NE Australia.

#### Family Ebalidae WARÉN 1994 (=Ebalidae BANDEL, 1994)

This family of the superfamily Streptacidoidea has the protoconch sinistrally coiled and smooth. Transition into the dextral teleoconch occurs at contact between protoconch and teleoconch. Within the Pyramidellidae, there are similar species but they are usually larger in size and bear more sculpture. According to WARÉN (1994), the Ebalidae differ from the Pyramidellidae in having a complicated jaw apparatus.

#### Genus *Ebala* LEACH, 1847

The type species is *Ebala nitidissima* (MONTAGU, 1803) that lives in the Mediterranean Sea and the Northern Atlantic Ocean (FRETTER et al. 1986, figs.439,440).

The small (1-2 mm) slender, cone shaped shell consists of 6-8 whorls of the teleoconch with a convex profile and deep marked oblique sutures. The aperture is oval and a little pinched at its posterior end. The spindle is straight and smooth. The protoconch consists of sinistral almost planispiral whorls forming almost a right angle with the teleoconch.

According to GRAHAM (1988, fig.270), *Ebala nitidissima* is a small, 2,5 mm long animal with the shell having an oblique upstanding apex and 6-8 post-larval whorls with convex profile and deep sutures. With exception of growth lines and very fine spiral lines, the surface of the shell is smooth. The protoconch consists of two nearly planispiral whorls. The aperture is oval and the columella simple. According to THORSON (1946), the young hatch from 0,1 mm large eggs after about 6 days with a 0,12 mm large shell. The head bears two triangular tentacles which are heavily ciliated. There are two eyes and anterior to the tentacle lies a short flattened region. *Ebala* lives in 5-50 m depth from unknown food source (GRAHAM, 1988).

#### *Ebala communis* n. sp.

(figs. 36 - 44)

Diagnosis: Slender shell with up to 7 whorls of the teleoconch and 2 mm in height. Whorls are a little angular at their posterior side. Ornament consists of curving growth lines and more or less distinct fine spiral lines. The protoconch consists of about 1.3 almost planispiral whorl that is detached from the teleoconch. The change from the left into the right coiling mode occurs within the first part of the teleoconch. The axis of coiling forms an angle of about 45° with that of the adult shell.

Derivatio nominis: This species is very common on the reef flat at Aqaba.

Material: Several shells and with the one in fig. 42 representing the holotype, which is deposited in the of Museum of the Geological-Palaeontological Institut, University of Hamburg. Animals were found living among stones in the lowermost inter-tidal area of the lagoon covered by dense algal growth and the area with sea grass. The type locality is the fringing reef in front of the marine station at Aqaba.

Description: *Ebala communis* from Aqaba is a little more than 1 mm long with 5 whorls of the teleoconch (figs. 40, 43) and 2 mm with 7 whorls (figs. 38, 42). The upstanding apex consists of less than 1,5 whorls of the protoconch and is almost planispiral and left coiled and measures about 0,15 mm in diameter (figs. 36, 37, 39, 44). Its whorls are smooth and rounded and they are attached to the teleoconch with inclination and axis of coiling deviating strongly with the apex inclined toward the anterior (figs.36-37). The left coiling of the first whorl is documented by displaying the rounded initial part on the apex ( fig. 36) and having it half covered on the umbilical side (fig. 41).

The post-larval whorls of the teleoconch are angular with deep sutures, narrow shoulders, and flattened sides. With exception of sinuous growth lines and very fine spiral lines (fig. 37) the surface of the shell is smooth. The aperture is oval, wider in front, and the columella simple. The ornament of fine spiral lines is well developed, indistinct or absent. Growth lines may reflect the presence of a subsutural sinus on the outer lip, which may also be very indistinct. The shell is translucent white.

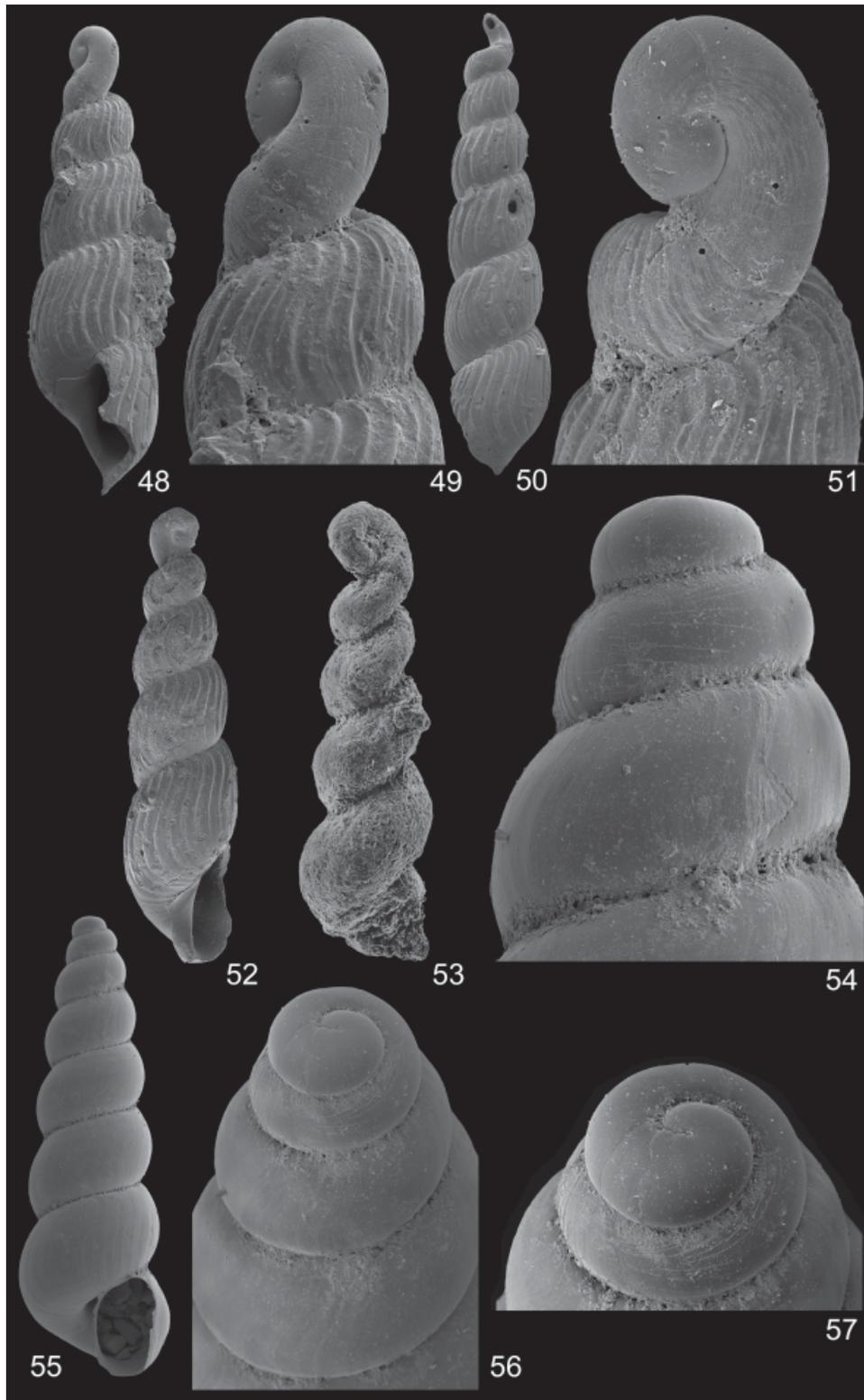
Remarks: *Ebala communis* differs from *Ebala nitidissima* by having a more angular outline of the whorls of the teleoconch and fewer whorls of the protoconch. It could represent a species with vast distribution in the tropical Pacific, since very similar shells were found near Satonda in Indonesia. The species illustrated by BANDEL (1991, Pl. 8, fig. 1) from Cebu has a more upright protoconch, well expressed shoulders, and rounder whorls (figs. 33-35). It is, thus, more similar to *Ebala nitidissima* than to *Ebala communis*.

The Triassic *Ebala cassiana* BANDEL, 1996 has a protoconch of 1.5 lowly coiled whorls forming an angle of almost 90° with the smooth teleoconch that consists of whorls as high as wide separated from each other by inclined sutures. A shell of 2 mm length has a maximum width of 0,7 mm and consists of 4,5 whorls of the teleoconch. The simple low sinistral, spiral protoconch of *Ebala cassiana* resembles protoconchs as are found among species of modern *Ebala* and Carboniferous *Streptacis* (fig. 53). It differs from the large almost planispiral protoconch of *Cassianebala* BANDEL, 1996, by having more than two ornamented whorls. The protoconch of *Loxebala* BANDEL, 1996, in contrast, coils around the same axis as its teleoconch and changes from left to right coiling within the larval shell portion. In *Ebala cassiana* almost 90° deviation occurs between axis directions, and change from left to right coiling occurs as in modern *Ebala* in the earliest teleoconch.

*Ebala liassica* SCHRÖDER, 1995 (SCHRÖDER, 1995, Pl.10, figs.18-21), here reproduced on (figs. 45-47) from the Early Jurassic, is very similar to *Ebala cassiana* and also to *Ebala* sp. living off shore from Cebu (figs. 33-35). From the Late Cretaceous KIEL & BANDEL, (2001, Pl.1, figs.15-17) described *Ebala gruendeli*. A Jurassic form with sinuous growth line pattern was named *Falsoebala* by GRÜNDEL (1998, Pl.3) which otherwise is quite similar to *Ebala*. Illustrations of *Falsoebala procera* GRÜNDEL, 1998 from the mid-Jurassic mixed

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**Figs. 48-52:** *Falsoebala hungarica* n. sp., from mid-Eocene marls from Gant in Hungary: **48:** Shell about 1.6 mm high; **49:** Detail of fig. 48, with smooth and erect protoconch, about 0.18 mm high; **50:** Shell, 1.6 mm high with more than five whorls of the teleoconch; **51:** Protoconch smooth, sinistral, almost planispiral and quite detached from the teleoconch, about 0.18 mm high; **52:** Holotype, a little more than 1 mm high and not fully adult. **Fig. 53:** *Streptacis whitfieldi* MEEK, 1871 from the late Carboniferous of Texas as illustrated by BANDEL (2002, Pl.1, fig.1) with 1.1 mm high shell. **Figs. 54-57:** *Hemiaclis aqabaensis* n. sp., **54:** Detail of fig.55 with the initial whorls of the shell and the protoconch comprising the first two whorls with fine spiral lines on the second whorl; **55:** Holotype, 1.6 mm high, with details in figs. 54, 56, 57. From the fringing reef at the marine station of Aqaba; **56:** Detail of fig.55, with flat embryonic whorl and the larval whorl of the protoconch. First whorl measures 0.13 mm across; **57:** Detail of fig. 56, with the embryonic whorl with initial sinistral portion and dextral ornamented larval shell composing the protoconch.



with those of *Ebala communis* from the modern reef lagoon would be difficult to hold apart. This would be even more so in case of *Ebala* sp. from Cebu that has more strongly developed curving growth lines. The protoconch of *Falsoebala procera* is a little larger and its embryonic part is ornamented by a groove-ridge pattern.

#### Genus *Falsoebala* GRÜNDEL, 1998

According to GRÜNDEL (1998), this genus has a shell shape as in *Ebala*, but with well expressed subsutural sinus. He based the genus on *Falsoebala compacta* GRÜNDEL, 1998 from the mid-Jurassic (GRÜNDEL, 1998, Pl.3, figs.27-32). This species has a relatively smooth shell surface, while *Falsoebala costata* GRÜNDEL, 1998, also from the mid Jurassic, has collabral ribs which reflect the curving outline of the outer lip of the aperture. Here, a species from the mid-Eocene shallow marine near shore deposits of Gant in Hungary is described, which suggests that *Falsoebala* survived into the Tertiary.

#### *Falsoebala hungarica* n. sp.

(figs. 48 - 52)

Diagnosis: The teleoconch has the shape and size of *Ebala* but an ornament of regular sinuous, collabral ribs which reflect a broad subsutural sinus on the outer lip of the aperture. The protoconch is smooth and almost planispiral coiled to the left. Its transition to the teleoconch represents the transition to the right coiled shell.

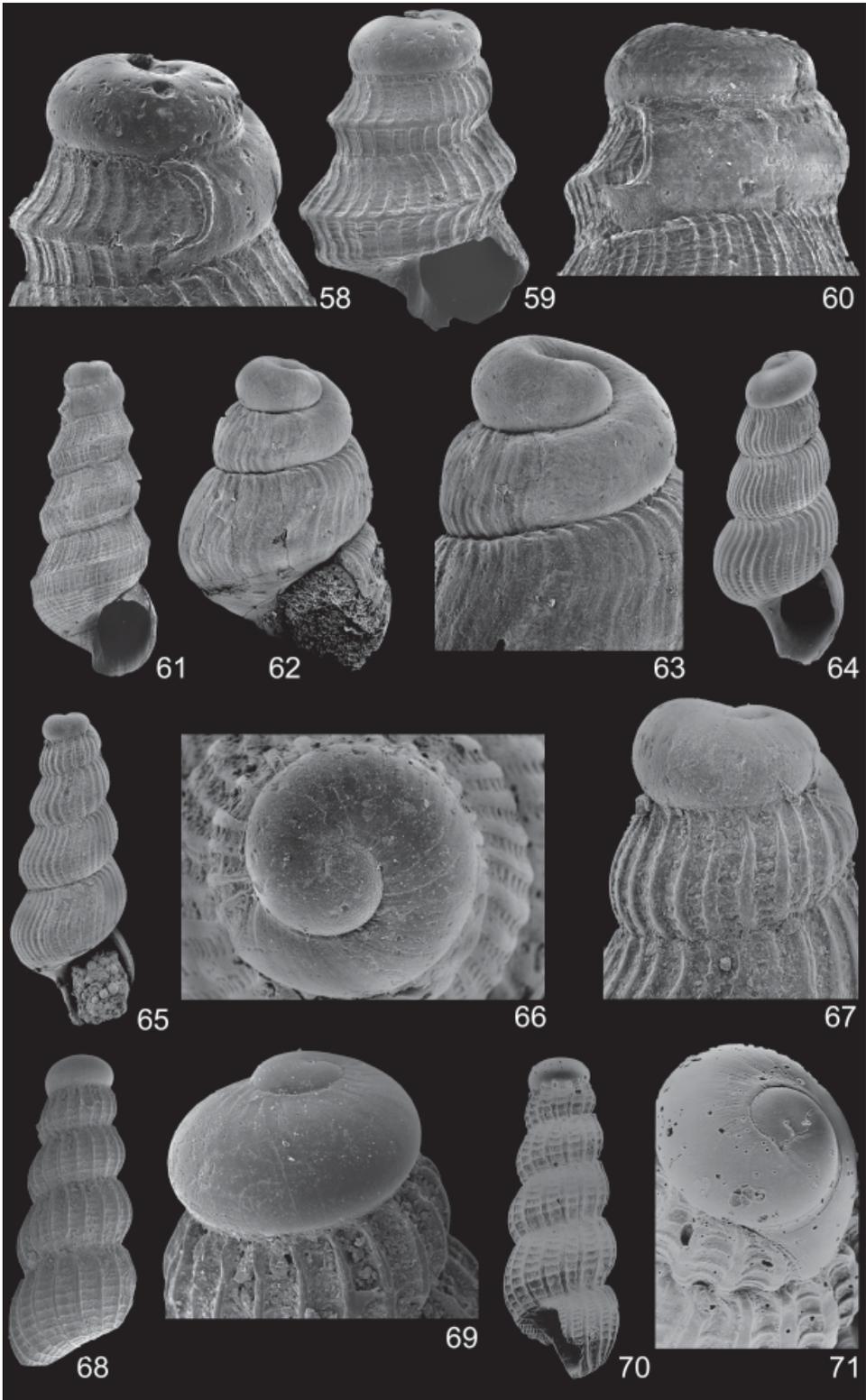
Derivatio nominis and locus typicus: *Falsoebala hungarica* comes from Gant in Hungary (Hungaria) and from a stone quarry that has been described in detail by Szöts (1953). The shells are from a layer in the middle height of the quarry where shallow marine deposits are intercalated with such of a coastal mangle forest (own observations).

Material: Several shells were studied and the specimen on fig. 52 represents to holotype, deposited in the collection of the Geol.-Palaeont. Inst.and Mus., University of Hamburg.

Description: The coiling axis of the protoconch deviates from that of the teleoconch by almost 90°. It is totally detached and only its apertural margin is in contact with the first whorl of the teleoconch (figs. 49-51). Similar as in the Jurassic *Falsoebala costata* GRÜNDEL, 1998, about 30 collabral ribs may be found on each whorl and they are even more strongly developed (figs. 48-50, 52). The same number ribs is variable in *Falsoebala hungarica* and there may be less than 20 such ribs. With 6 whorls of the teleoconch the shell is about 1,3 mm high.

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**Figs. 58-61:** *Wonwalica minuta* SCHRÖDER, 1995; **58:** Shell with a diameter of about 0.2 mm, from the early Cretaceous of Poland as described by SCHRÖDER (1995); **59:** Juvenile shell, detail of fig.58, protoconch with a well developed apertural projection, and flattened above; **60:** Protoconch, detail of fig.61; **61:** Holotype, a juvenile shell from the early Cretaceous (Valanginian) of Poland is 0.9 mm high. **Figs. 62-63:** *Urlocella* cf. *minuera* GRÜNDEL, 1998 as illustrated by SCHRÖDER (1995, Pl.10, fig. 9) from the middle Jurassic; **62:** Shell 0.7 mm high, bearing the smooth tofanellid protoconch; **63:** Detail of fig.62, also illustrated by SCHRÖDER (1995, Pl.10, fig.11) with the simple curving apertural margin of the fully grown protoconch set off from the teleoconch ornamented by growth lines. The protoconch resembles that of the genus *Graphis*. **Figs. 64-67:** *Graphis albida* (KANMACHER, 1798); **64:** Shell about 1 mm high, from the Pliocene of Nice; **65:** Shell about 1.3 mm high, from Pliocene marls of Nice (southern France); **66:** Detail of fig.65, with the embryonic shell with granulated surface ornament submerged with its initial portion below the larval shell. Protoconch measures about 0.7 mm across; **67:** Detail of fig.65, with the flattened smooth protoconch. **Figs. 68-71:** *Graphis pacifica* n. sp.; **68:** Holotype, from the fringing reef at Aqaba, with 0.75 mm shell; **69:** Detail of fig.68, with the bulbous protoconch measuring a little more than 0.2 mm in diameter; **70:** Shell from off-shore Cebu City, Philippines with 1.4 mm high shell; **71:** Protoconch detail of fig.70, with bulbous shape and submerged initial portion of the embryonic whorl; measuring about 0.2 mm across.



#### Family Aclididae Sars, 1878

The shell is elongate, minute, slender and many whorled. The protoconch is flat on top and relatively wide and bulbous (ABBOTT, 1974). The adult shell is usually small and has few characters (BOUCHET & WARÉN, 1986). The dominant genus is *Aclis* with ornament of fine spiral ribs on the teleoconch. A family Aclisidae COSSMANN, 1895 was suggested which was considered to hold the genera *Aclis*, *Graphis* and *Stilbe* with subgenera. COSSMANN (1895) included species with slender elongate, many whorled shells which are smooth or ornamented but all have a peculiar protoconch that is wide but dextral. He considered this family to intermediate between Janthinoidea (Scalidae-Epitoniidae) and Turritellidae on one side and the Pyramidellidae on the other. This interconnection was also based on the shape of the protoconch of the Aclisidae (= Aclididae) and he also noted a similarity with the Mathildidae in this respect. He noted the appearance of this group since the Paleocene, although some older fossil gastropods from the Devonian and Carboniferous are similar. However, these are considered to belong to the Loxonematidae and Murchisoniidae. According to FRETTER & GRAHAM (1962) and GRAHAM (1988) even *Graphis*, *Pherusina*, *Cima* and *Hemiaclis* belong here. PONDER & WARÉN (1988) placed the Aclididae with the Ctenoglossa GRAY, 1853 and here with the superfamily Janthinoidea LAMARCK, 1810, as one of its three families, the Epitoniidae BERRY, 1910, Janthinidae LAMARCK, 1812 and Aclididae. SMITH (1998) placed Aclididae near the Epitoniidae and within the Janthinoidea following the classification of PONDER & WARÉN (1988). The shape of the protoconch in *Hemiaclis*, *Graphis* and *Cima* clearly documents that this place in the system is not correct for the here discussed members of these genera.

#### Genus *Aclis* LOVÉN, 1846

The type species is *Aclis supranitida* (WOOD, 1842) (= *Aclis minor* BROWN, 1827) from the eastern Atlantic Ocean including the Mediterranean (WENZ 1939, fig.2424, GRAHAM, 1988, fig.212).

*Aclis minor* has a small slender conical shell with about 10-11 rounded semitransparent whorls. The aperture is small and oval. The outer lip is angular at front and the umbilicus is open. The base has a narrow umbilicus. The protoconch has about 4 smooth whorls and is about 0,5 mm high with the initial whorl rather swollen and the boundary to the adult shell marked (FRETTER & GRAHAM, 1982). The teleoconch is as high as 6 mm and is ornamented by more or less well developed spiral ribs on shiny surface. The larvae are not known. According to Sars (1878), the radula is ptenoglossate. BOUCHET & WARÉN (1986) noted in *Aclis minor* that the foot has lateral lappets which cover the base of the shell when the animal is crawling.

#### Genus *Hemiaclis* Sars, 1878

The type as chosen by Sars (1878) is *Aclis (Hemiaclis) ventrosa* (FRIELE, 1874) (FRETTER & GRAHAM 1982, fig.288; GRAHAM 1988, fig.215) which lives in the eastern north Atlantic. The shell consisting of many whorls, is high conical, smooth and glossy and about 5 mm high. The whorls are rounded and the last whorl occupies not more than one third of shell height. The aperture is oval and there is a narrow umbilicus.

#### Genus *Hemiaclis aqabaensis* n. sp.

(figs. 54 - 57)

Diagnosis: In contrast to *Aclis* the teleoconch is smooth, and in contrast to *Hemiaclis ventrosa* the shell is more slender. The protoconch consist of an involute embryonic shell

and one whorl of rounded dextral larval shell with ornament of fine inclined lines. Transition from protoconch to teleoconch is marked only by growth lines and end of ornament.

Derivatio nominis: Called after Aqaba that lies near the type locality. This species is found in a few individuals from the fringing reef in Aqaba.

Material: The holotype is the illustrated individual (fig. 55) from the small reef in front of the marine station in Aqaba. It is deposited in the Museum of the Geological and Paleontological Institute, University of Hamburg.

Description: *Hemiaclis aqabaensis* is a slender, about 1,6 mm high, glossy, delicate shell with well rounded whorls without any ornament. The aperture is oval with the broad subsutural sinus in the outer lip. The umbilicus is open and small. The shell consists of 7 whorls (fig. 55). The protoconch has an embryonic shell of about 0,13 mm in diameter similar to that of *Murchisonella* or *Graphis* in shape and, in the larval shell, the right coiling mode is present, as well as a fine ornament of oblique lines of tubercles (figs. 54, 56, 57). The protoconch measures about 0,2 mm in height and width and consists of about two whorls. The protoconch is not markedly heterostrophic, but with plane first whorl.

Remarks: The shell resembles that of *Aclis walleri* JEFFREYS, 1867 as described by GRAHAM (1988, fig.214). *Aclis walleri* consists of 10 whorls and is 4 mm high. According to GRAHAM the body of this species is like that of the type species of *Aclis* and its biology and mode of life is unknown.

#### Family Tofanellidae BANDEL, 1995

According to BANDEL (1995), this family holds species with small, slender, turritelliform shell that have spiral and collabral ornament with spiral ribs or keels dominating. Whorl flanks are angular or convexly flattened. The aperture is angular or rounded and provided with a short, shallow anterior canal. The shape of the protoconch provides the distinctive feature of this family. Its embryonic whorl is left coiled and immersed in the apex of the larval shell. The rounded whorls of the larval shell gradually change from left coiling to plane coiling and finally to dextral coiling. The margin of the aperture of the protoconch is usually thickened, and a hook-like projection of the outer lip may or may not be present. The larval shell is smooth or indistinctly ornamented by straight growth lines and axial or spiral lines.

The Tofanellidae are based on *Tofanella* BANDEL, 1995 from the late Triassic St. Cassian Formation of the Dolomites, Alps. GRÜNDEL (1998) suggested to split the taxon into the subfamilies Tofanellinae and Usedomellinae, but the genera held herein contain species which are sometimes very difficult to place in one genus or the other or to a representative of one subfamily or the other. These subfamilies may, therefore, not be very useful.

#### Subfamily Tofanellinae BANDEL, 1995

The protoconch ends with a median projection of the outer lip (larval hook). The whorls of the teleoconch may have a keel, and their flanks are commonly angular. Ornament consists of coarser axial ribs and fine spiral ribs. Triassic genera included are *Tofanella* and *Cristalloella*. Species belonging to *Cristalloella* can be traced through the Jurassic into the Cretaceous and very similar ones were also called *Wonwalica* by SCHROEDER (1995) and placed in *Cristalloella* by KAIM (2004). GRÜNDEL (1998) placed in the Tofanellinae the genera *Camponaxis* BANDEL, 1995, *Cristalloella*, *Tofanella*, and *Wonwalica* SCHRÖDER, 1995.

The genus *Cristalloella* BANDEL, 1995 includes species with slender, small shell with many whorls bearing a keeled flank and fine axial ribs crossed by spiral lines. The smooth protoconch is sinistral in coiling in its top with the first whorl immersed in the dextral final whorl, which has a thickened margin. The type species is *Cristalloella cassiana* BANDEL, 1995 from the late Triassic of the southern Alps. *Cristalloella parva* BANDEL, GRÜNDEL & MAXWELL, 2000 comes from Jurassic of New Zealand. Here the protoconch consists of 1,5 whorls, is a bit more than 0,2 mm wide and high, has wrinkles in its larval portion and a thickened simple margin. The teleoconch whorls have the characteristic triangular outline produced by the median keel and numerous fine growth lines which trace the oblique shape of the outer lip. The genus *Wonwalica* SCHRÖDER, 1995 proposed to include *Cristalloella*-like species from the Jurassic and Cretaceous according to KAIM (2004) can be regarded as synonym. This is based on *Wonwalica minuta* SCHRÖDER, 1995 from the early Cretaceous of Poland (figs. 58-61) with teleoconch shape and ornament that is extremely similar to that of *Cristalloella cassiana* from the St. Cassian Formation, from which it only differs by the protoconch consisting of only 1,5 whorls and not two whorls. GRÜNDEL (1998, Pl.1, figs.1-3) placed here *Wonwalica spiralocostata* GRÜNDEL, 1998 from the Callovian of northern Germany that also has a hooked margin of the outer lip of its protoconch.

#### Subfamily Usedomellinae GRÜNDEL, 1998

The genus *Usedomella* GRÜNDEL, 1998 is based on a mid Jurassic species *Usedomella laevigatoidea* (GRÜNDEL, 1993) which has a teleoconch resembling that of *Ebala* connected to a protoconch as found in *Graphis* among modern species or *Tofanella* among fossil ones. The embryonic whorl is left coiled and within the larval shell the coiling mode changes into dextral, ending in a simple aperture without projection of the outer lip. Such a gastropod, *Usedomella schroederi* GRÜNDEL, 1998, from the Jurassic had first been documented in open nomenclature by SCHRÖDER (1995, Pl.10, figs.15-17) (here figs. 12-15). The protoconch distinguishes *Usedomella* from *Cima* where the whorls of the protoconch do not turn into dextral coiling mode, and it is only the first whorl of the teleoconch that is dextrally coiled, while the protoconch changes from left only into plane coiling mode. According to GRÜNDEL (1998) the *Graphis* species illustrated by BANDEL (1991, Pl.8, fig.6) from the Philippines (figs. 70, 71) belongs in his subfamily. This can be supported because species of *Rotfanella* GRÜNDEL, 1998, if found in the Recent fauna and not in the Jurassic, would have to be placed within the genus *Graphis*.

*Camponaxis* BANDEL, 1995 based on *Camponaxis lateplicatum* (KLIPSTEIN, 1843) from the Late Triassic St. Cassian Formation of the Alps has the teleoconch ornamented by axial ribs that may or may not be crossed by spiral lines of smaller size than the ribs. The protoconch is of tofanellid type with a sinistral embryonic shell and twists into dextral coiling well within the larval shell. BANDEL et al., (2000) included the Jurassic *Camponaxis zardiniensis* BANDEL, GRÜNDEL & MAXWELL, 2000 from New Zealand in this genus and placed the genus with the Usedomellinae. Even the genus *Urlocella* GRÜNDEL, 1998 based on the Jurassic *Urlocella minuera* GRÜNDEL, 1998 (GRÜNDEL, 1998, Pl.1, figs. 11-13, Pl.2, figs. 14-16, 1999, Pl.1, figs.12-13) is placed here. It has sinuous growth lines and fine collabral axial ornament crossed by fine spiral lines which in later whorls disappear (fig. 62, 63). The protoconch is smooth and closely resembles that of *Graphis pacifica* n.sp. also with simple apertural margin of the larval shell (see also KAIM, 2004 in case of “*Chrysallida*” *minuera*). KAIM (2004) treated *Urlocella* GRÜNDEL as synonym of *Chrysallida* CARPENTER, 1856. *Chrysallida* sensu KAIM (2004) also belongs to this group, since the protoconch turns into

the right coiling mode with its larval shell, which is clearly not the case in members of the Pyramidellidae. *Odostomia (Chrysallida)* CARPENTER, 1857 is represented by a modern pyramidellid with the typical protoconch of the group, which is coiled to the left until it contacts the teleoconch. Therefore, KAIM's (2004) choice for a synonym is not followed here.

Even the genus *Rotfanella* GRÜNDEL, 1998 with the type species *Rotfanella rotundata* GRÜNDEL, 1998 from the mid-Jurassic (Callovium) resembles *Camponaxis* in protoconch shape and arrangement and in ornament of the teleoconch. In case of *Rotfanella herrigi* GRÜNDEL, 1999 and the very similar *Rotfanella weissi* GRÜNDEL, 1999 from the mid Jurassic (GRÜNDEL, 1999, Pl.2, figs.1-11), the teleoconch closely resembles that of *Graphis pacifica* n. sp. described below, and only the protoconch distinguishes by having 0,5 whorls less. An *Urlocella* from the Jurassic or *Rotfanella* with more strongly developed ornament of the teleoconch also from the Jurassic, if living nowadays would have to be placed in the genus *Graphis*, in respect to features of the morphology of the shell. *Urlocella* can be treated at synonym to *Graphis*, since only time distinguishes both genera from each other.

#### Genus *Graphis* JEFFREYS, 1867

The type is *Turbo albidus* KANMACHER, 1798, according to COSSMANN (1912), but according to THIELE (1931) it is *Aclis (Graphis) unica* (MONTAGU, 1803), which, fortunately, according to GRAHAM (1988, fig. 217) is synonym of *Turbo albidus*. It lives in the eastern North Atlantic as well as in the Mediterranean Sea (FRETTER & GRAHAM, 1982, fig.290).

The small (2mm high) needle-shaped shell has a blunt bulbous apex. Two whorls belong to the protoconch and are smooth. Teleoconch whorls are convex with sutures well expressed and there are 7-9 of them. The ornament consists of many delicate axial ribs with spiral ridges in the intervening spaces. The aperture is rounded and small. The protoconch according to COSSMANN (1895) is globular and deviating. It consists of two smooth whorls which are separated by drastic change in ornament from the first whorl of the teleoconch. The protoconch is 0,13 mm high and 0,065 mm wide (FRETTER & GRAHAM, 1982). According to GRAHAM (1988, Fig.217) *Graphis* is a hermaphroditic gastropod that has no radula and probably sucks body liquid from some unknown organisms. There is a tentacle on the mantle edge (FRETTER & GRAHAM, 1982).

Remarks: The genus *Graphis* has been placed by WENZ (1938) within the family Aclididae SARS, 1878, and these into the superfamily Pyramidelloidea. According to THIELE (1931) and WENZ (1939) members of the Aclididae are represented by small slender conical shells with smooth, dextral protoconch, and sometimes attached to the teleoconch a little inclined. The rounded whorls meet in deep sutures and may be ornamented in different way. Even the aperture varies in shape among the genera. Usually it is egg shaped and has a continuous margin. The columella is thin and the operculum organic and has few whorls. THIELE (1931) and WENZ (1939) placed the genus *Aclis* LOVÉN, 1846 with the subgenera *Aclis* as well as *Murchisonella* MÖRCH, 1875 and also *Graphis* JEFFREYS, 1867 here. In case of *Graphis*, WENZ (1939) considered a first occurrence from the Danian, that is the oldest Paleogene, and modern species are reported from the Mediterranean Sea and the Atlantic Ocean. ABBOTT (1974) accepted this taxonomic placement and also considered *Graphis* to represent a subgenus to *Aclis*. VAUGHT (1989) suggested *Graphis* to represent a independent genus of the Aclididae but regarded *Murchisonella* (= *Murchisoniella* FISCHER, 1884) as representing its subgenus. FRETTER & GRAHAM (1982) suggested that *Graphis* may not be closely related to *Aclis* and that it does represent not even a member of the Aclididae,

because of shell morphology and the presence of a foot tentacle. This latter interpretation is here confirmed by the documentation of *Graphis*-like species that lived in the Jurassic and related genera such as *Camponaxis* that occurred in the Late Triassic.

*Graphis albida* (KANMACHER, 1798)

(figs. 64- 67)

The here described shells are from the Pliocene of Nice in southern France and were collected by the late Ulrich von HACHT. The locality is a clay pit at Peyrol. The narrow tall conical shell consists of 9 to 10 whorls and has an apical angle of about 15°. The apex is bulbous and the whorls are increasing in diameter in a very regular way and have curved sides. The protoconch consists 1,7 whorls of which the left coiled embryonic portion is ornamented by a groove and pit pattern (fig. 66). The end of the 0,12 mm wide embryonic shell is indicated by the begin of growth lines and the change into dextral coiling mode. The larval whorl is smooth with growth lines reflecting a simple outer lip of its aperture. The protoconch is about 0,2 mm wide and almost the same in height (figs. 66-67). The embryonic shell appears partly covered by the larval shell which has a simple, slightly concave aperture, quite opposite to the outer lip of the teleoconch that is slightly convex.

The ornament of the teleoconch begins abruptly and consists of about 30 flexuous, collabral ribs per whorl. In addition, the teleoconch is ornamented with finer spiral ridges which are confined to the area between the ribs and weak at the base. Sinuous axial ribs and spiral ridges produce a pattern of slightly elongated cancellation. The aperture is oval and its outer lip curves smoothly to the base of the columella, showing a small anal sinus and a slight peripheral bulge. The columella is thin and nearly straight, and there is no umbilicus (figs. 64, 65).

Remarks: In the description of *Graphis albida* by FRETTER & GRAHAM (1982), the dimensions of the protoconch have to be corrected (not 0.065 mm width and 0.13 mm height) and it does not consist of two whorls but a little less. COSSMANN (1912) recorded the occurrence of *Graphis* from the Eocene of the Paris Basin.

*Graphis pacifica* n. sp.

(figs. 68 - 71)

Diagnosis: This *Graphis* has about 18 axial ribs on each whorl of its teleoconch which have smaller spiral ridges between them. The protoconch is almost as wide as the first whorl of the teleoconch, has the characteristic shape of the genus and consists of two whorls.

Derivatio nominis: It occurs from Aqaba to at least the Philippines, that is in much of the Pacific Ocean and is named accordingly.

Material: Two individuals from the fringing reef in Aqaba and several ones from near Cebu City in Cebu. The holotype is illustrated on fig. 68 and housed in the collection of the Geological-Palaeontological Institute and Museum, University of Hamburg.

Description: *Graphis pacifica* from the Gulf of Aqaba (Pl.5, figs. 68, 69) and from the Pacific Ocean near Cebu (figs. 70, 71) has the same general shape of the shell as in *Graphis albida* but the ornament of oblong cancellation is a bit wider. There are about 15 axial ribs and between them 8 spiral ridges visible on the whorl sides. The protoconch consists of almost two whorls of which the embryonic shell measures only about 0.08 mm across and the larval shell is 0.35 mm wide and 0.28 mm high. Here the embryonic shell is clearly covered with its apical end by the larval whorl.

*Graphis pacifica* from Aqaba lives among algae in the very shallow lagoon on the top of the fringing reef in Aqaba.

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