The new family Cortinellidae (Gastropoda, Mollusca) connected to a review of the evolutionary history of the subclass Neritimorpha

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With 9 figures

Abstract: The Cortinellidae n. fam. are based on the genus *Cortinella* BANDEL, 1989 with the type *Euomphalus aries* LAUBE, 1868 from the Late Triassic St. Cassian Formation and represent an independent lineage of the Neritimorpha, Cycloneritimorpha as is indicated by its characteristic tightly coiled protoconch that is connected to a small planispirally coiled teleoconch consisting of an aragonitic, crossed lamellar shell. *Cortinella* dissolved internal walls in the protoconch which places it in the superfamily Neritoidea. The evolute planispiral shape of the teleoconch of Cortinellidae occurs only once in the known evolutionary scenario of the Neritimorpha and is thus of high taxonomic value characterising the new family.

Zusammenfassung: Die Cortinellidae n. fam. gründen sich auf die Gattung *Cortinella* BANDEL, 1989 mit der Typusart *Euomphalus aries* LAUBE, 1868, einer klein-wüchsigen, planispiralig aufgerollten Schnecke der späten Trias der St. Cassian Formation der Dolomiten. Sie repräsentieren eine eigenständige Entwicklungsreihe innerhalb der Unterklasse Neritimorpha, Überordnung Cycloneritimorpha mit völlig aragonitisch und vornehmlich aus Kreuzlamellen aufgebauter Schale. Die Auflösung der Innenwände des Protoconches stellt *Cortinella* in die Überfamilie Neritoidea. Die ungewöhnliche planispiraligen Gestalt der Cortinellidae ist bisher nur in dieser Familie innerhalb der Neritimorpha bekannt.

1. Introduction

The genus *Cortinella* was newly described (BANDEL 1988, 1993) when it became evident that neither shell structure nor size and shape of the proto-conch were similar to those of the genus *Brochidium*, to which its species had been placed before (KOKEN 1889, KITTL 1894, ZARDINI 1978). Even later the protoconch of *Cortinella* was found in more perfect preservation. Only then it was realised that the protoconch is actually not of the type that is charac-teristic for the Archaeogastropoda and also for *Brochidium*, but that it has the shape and composition of the early ontogenetic shell that is characteristic for the Neritimorpha (BANDEL 1982, 1994, 1997).

Marine Neritimorpha, in contrast to the Archaeogastropoda, usually have in their early ontogeny a planktotrophic development as pelagic veliger larva. During their early development the embryo secretes a primary shell that forms a wide open bowl. An egg-shaped secondary shell with growth increments is added before the veliger hatches from the egg case. This secondary embryonic shell is characteristic and differs from that of most archaeogastropods and those caenogastropods and heterostrophs with plank-tonic larva where the embryonic and primary shell usually are one and the same. The mantle of the neritimorph embryo, in contrast, detaches from the shell margin before the embryonic shell is completed. This shell of the initial veliger larva is mineralised by aragonitic crystallites which are added to the organic shell wall on the inside of the shell (BANDEL 1982). The Archaeogastropoda, in contrast, mineralise their early shell by aragonitic crystallites that grow into the organic primary shell.

The embryonic shell of a neritimorph resembles an egg with its upper portion cut off obliquely. To it during the larval stage a convolutedly coiled shell is secreted in which succeeding whorls cover much of their preceding ones. The whorls of the larval shell may, therefore, overlap strongly onto each other. In modern neritimorph species with planktonic larva the protoconch is, thus, strongly convolute. Much surface of the former whorls are hidden below the last one. Larval shells of living Neritidae have been described by BANDEL et al. (1997) and BANDEL & RIEDEL (1998) from several different species. The fully grown larvae swim with the aid of a quadrilobated velum. The larval shell is globular to egg-shaped and in most species has a maxi-mum diameter of about 0.5 to 0.6 mm, rarely almost 0. 8 mm across. The initial embryonic whorl measures (interspecifically) 0.1 to 0.25 mm across. The protoconch is always smooth in appearance, the ornamentation confined to faint spiral striation and axial growth increments. Only part of the visceral mass of the larva is coiled, due to the dissolution of internal shell walls. The suture of the embryonic and early larval whorl may be covered by later whorls so that the number of whorls is difficult to estimate, but up to 2.5

larval whorls occur. The aperture is crescent-shaped with thin and regularly rounded outer lip and thickened inner lip. The organic operculum seals the aperture of the protoconch. It is coiled and shows as many whorls as the shell. Such protoconchs have also been described by ROBERTSON (1971), SCHELTEMA (1971), RICHTER & THORSON (1975), LAURSEN (1981), BANDEL (1982, 1991, 1992 a).

The hatched larva remains in the plankton for weeks and feeds on algal cells. This contrasts with the larvae of the archaeogastropods which may swim in the Plankton, but do not feed from it and rely only on the yolk reserves that are provided from the egg throughout their pelagic existence. All Archaeogastropoda only have a primary shell (= protoconch I) that is not succeeded by a larval shell, but directly by the teleoconch (BANDEL 1982, SASAKI 1998, PAGE 1997, COLLIN & VOLTZOW 1998). Fossil Neritimorpha can be recognised as well on these peculiarities of their protoconch. Neritimorpha were, therefore, considered to represent an independent subclass of the Gastropoda (BANDEL 1982, 1992 a, 1997).

When a protoconch of similar morphology as found among modern Neritimorpha was discovered to be attached to the teleoconch of *Cortinella*, it became evident that this Triassic genus represents a member of the Neritimorpha. Before, it had been placed tentatively with the Trochomorpha, a non slit branch of fossil Archaeogastropoda with uncertain relations to modern groups (BANDEL 1993, BANDEL & GELDMACHER 1996). While the protoconch is good evidence for such a placement in the gastropod system, the teleoconch is rather unusual when compared with those known to occur within the extant and fossil Neritimorpha.

2. Systematic classification of the genus *Cortinella*

Subclass	Neritimorpha GOLIKOV & STAROBOGATOV, 1975
Superorder	Cycloneritimorpha BANDEL & FRÝDA, 1999
Order	Neritoina RAFINESQUE, 1815

Superfamily	Neritoidea RAFINESQUE, 1815
Family	Cortinellidae n. fam

Diagnosis: Members of this family have a neritimorph protoconch that is connected to a planispirally coiled shell. Inner walls in the protoconch are dissolved. The shell wall consists of aragonitic biocrystallites arranged in crossed lamellar structure. The family is based on the genus *Cortinella* from the Late Triassic (early Carnian) St. Cassian Formation of the Dolomites near Cortina d'Ampezzo.

Difference: Neritopsidae GRAY, 1847 and Naticopsidae MILLER, 1889 have a trochispiral shell that is connected to a protoconch in which in contrast to that of

the Cortinellidae the inner walls are not dissolved. The protoconch of the Triassic Naticopsidae, also in contrast, is ornamented by axial and spiral elements (pers. comm. ANNETTE SCHWARDT). Carboniferous representatives have a tightly coiled early shell which is otherwise not well known (YOO 1994). The teleoconch of Cortinellidae, in contrast, is planispirally coiled. Neritidae also have the protoconch with internal walls dissolved and their teleoconchs are usually lowly trochiform of more or less globular shape. In several lineages they evolved a cap-like shell form, as in the *Pileolus* SOWERBY, 1823, *Phenacolepas* PILSBRY, 1891 or *Septaria* FÉRUSSAC, 1807 relation. But there is no other branch of the Neritimorpha known that has evolved planispirally coiled shells as is the case in the Cortinellidae.

According to BOGGILD (1930) the outer layer of the shell in Neritidae is usually calcitic and inner layer consist of aragonitic crossed lamellae. But even though this structural composition is commonly found within the Neritimorpha, it is not so everywhere in the group. For example the terrestrial species (Hydrocenidae, Helicinidae) are all totally aragonitic in composition as are the marine limpet-like Phenacolepadidae. The inner aragonitic layer in all fossil and Recent Neritimorpha that have been analysed so far is confirmed to be always crossed lamellar in structure (BANDEL 1990). Cortinellidae can, thus, be added to those Neritimorpha that have an aragonitic crossed lamellar shell without calcitic layers.

Genus   *Cortinella* BANDEL, 1988

Description: The shell is planispirally and slightly dextrally coiled and consists of only little more than one teleoconch whorl with a maximum of 3 mm in width. The diameter of the whorl increases rapidly. The apertural margin of the fully grown teleoconch may be somewhat irregular in outline. The protoconch measures about 0.5 mm in width and 0.3 mm in height. It is lowly dextrally coiled with rounded apex and narrow umbilicus. Its ornament consists of fine radial ribs on the apical side which end on the rounded flanks. These are smooth at their base. The innermost, embryonic whorl is egg-shaped and ornamented by growth lines. It is covered to a large extent by the whorls of the larval shell which overlap much onto each other and have rounded sides. At its aperture the protoconch is wide and thickened with its outer lip having a very shallow sinus apically and another sinus umbilically. All internal walls are dissolved. The teleoconch consists of only a little more than one whorl that is strongly ornamented with collabral axial ribs and numerous fine spiral lirae crossing them. The structure of the shell is composed predominantly of crossed lamellar layers of aragonitic composition. The type is *Euomphalus aries* LAUBE, 1868 from the St. Cassian Formation.

Differences: When gastropods with similarly small shape and planispiral coiling from the St. Cassian Formation are compared, *Cortinella* has a more rapid increase in shell diameter than *Brochidium* KOKEN, 1889, *Sorapisella* BANDEL, 1993 and *Triadoskenea* BANDEL, 1993 (BANDEL 1993, Pl. 3, figs. 5, 9; Pl. 4, figs. 1, 3, 4). The most distinctive difference, though, is found in the construction and shape of the protoconch. It consists of less than one whorl of the archaeogastropod type in the latter, while it is a neritimorph shape with a larval shell of several whorls in *Cortinella*. This feature also distinguishes *Cortinella* very clearly from the early non-slit teleoconch whorls of *Wortheniella* SCHWARDT, 1992 and *Rolandomphalus* SCHWARDT, 1992 which are planispirally coiled. Here, during later stages of teleoconch growth, a selenizone formed and the shell became trochispirally coiled (SCHWARDT 1992). *Cortinella* is distinguished from *Brochidium cingulatum* (MÜNSTER, 1834) by the protoconch, less rapid increase in whorl diameter as well as shell composition (BANDEL 1993, Pl. 2, figs. 8, 9, Pl. 3, figs. 4, 10). It has no calcitic outer shell layer but consists of crossed lamellar structure throughout.

Species   *Cortinella aries* (LAUBE, 1868)   Figs. 1-3

Synonomy: see BANDEL (1993).

Description: The shell is as noted in the genus *Cortinella*. The teleoconch consists of 1.2 to 1.5 whorls with 3 mm in maximum diameter. Whorls overlap only slightly with each other on their inner sides. Ornament consists of continuous axial ribs which curve backwards near the apex and near the umbilicus. The aperture is thickened and of circular outline (ZARDINI 1978, Pl. 8, fig. 9, 1985, Pl. 4, fig. 7; BANDEL 1988, Pl. 6, fig. 4, Pl. 7, figs. 1-3, 1993 Pl. 3, figs. 5, 9, 1994, Pl. 2, fig. 13). The protoconch consists of more than 2.5 tightly coiled whorls and measures about 0,5 mm in width and height.

Species   *Cortinella acutecostatum* (ZARDINI, 1985)   Figs. 4-8

Synonomy: see BANDEL (1993).

Description: The first teleoconch whorl has 12-18 strong and straight axial ribs which continue from the back to the umbilicus. On the later whorl ribs are lamella-like with shallow sinus on the flattened flanks (BANDEL 1993, Pl. 3, figs. 3, 6). Teleoconch size is 2-3 mm. There are up to 18 collabral, varix-like axial ribs on one whorl with numerous fine spiral lirae crossing them. The former varices sometimes are somewhat irregular. The protoconch consists of more than 2.5 whorls and measures 0.55 mm in width and 0.33 mm in height with a thickened apertural margin. With the exception of fine radial ribs on the apical side which end on the rounded flanks it is

smooth. Protoconch shape is as described for the genus. In the juvenile teleo-conch the inner lip covers the inner whorls, while it detaches in fully grown individuals from the whorls of the younger shell and the aperture becomes uninterrupted. It retains a slight inclination indicating a slight dextral twist in the coiling of the shell.

Differences: Regarding size of teleoconch and shape of protoconch *Cortinella aries* and *C. acutecostatum* are close to each other. They differ regarding the ornament of the teleoconch, that has more and lower axial ribs in *C. aries* and fewer and higher ones in *C. acutecostatum*. *Brochidium campense* ZARDINI, 1978 probably represents a variety of *C. aries*.

Remarks: Fully grown individuals of *C. aries* and *C. acutecostatum* may have an irregular apertural margin (ZARDINI 1985, Pl. 3, figs. 4, 5), which indicates that the animal was sessile and attached to some kind of irregular surface. To this rugged surface they pulled down their shell margin when they were disturbed. *Cortinella* chose such habitat right after its meta-mophosis from larval live similarly as is found among modern Calyptrae-oidea LAMARCK, 1809 such as *Hipponix benthophilus* (DALL, 1889) that lives attached to the spines of large cidarioidean sea urchins (BANDEL & RIEDEL 1994 b) or the small sized fossarids and vanikorids that live in miniature caves in reefs (BANDEL & KOWALKE 1997).

The Paleozoic *Spirina* KAYSER, 1889 with the type *S. brilonensis* KAYSER, 1889 from the Middle Devonian of Brilon in the north-eastern "Rheinisches Schiefergebirge", Germany is of generally similar shell shape as that of *Cortinella* (KNIGHT 1941, Pl. 84, fig. 4). Several species lived in Late Silurian time in the area of the Barrandium near Prague in Bohemia. *Temno-spira* PERNER, 1903 with the type species *Brochidium monile* PERNER, 1903 from the Late Silurian of the Barrandiums also resembles *Spirina* and *Corti-nella* (KNIGHT 1941, Pl. 85, fig. 2). *Spirina* and *Temnospira* grew to much

Fig. 1-3. *Cortinella aries* (LAUBE, 1868) in apical view (fig. 1) with shell measuring 1,2 mm across shows the smooth first whorls of the rounded protoconch and the ribbed teleoconch; (fig. 2) with shell measuring 1,4 mm in diameter in umbilical view; (fig. 3) seen from the side with the protoconch helically coiled while the teleoconch is planispirally coiled in the 1,2 mm wide shell.

Fig. 4-5. *Cortinella acutecostatum* (ZARDINI, 1985) with juvenile shells with 1,2 mm in diameter in umbilical (fig. 4) and apical (fig. 5) view has the rounded helically coiled protoconch succeeded by the plansipirally coiled teleoconch.
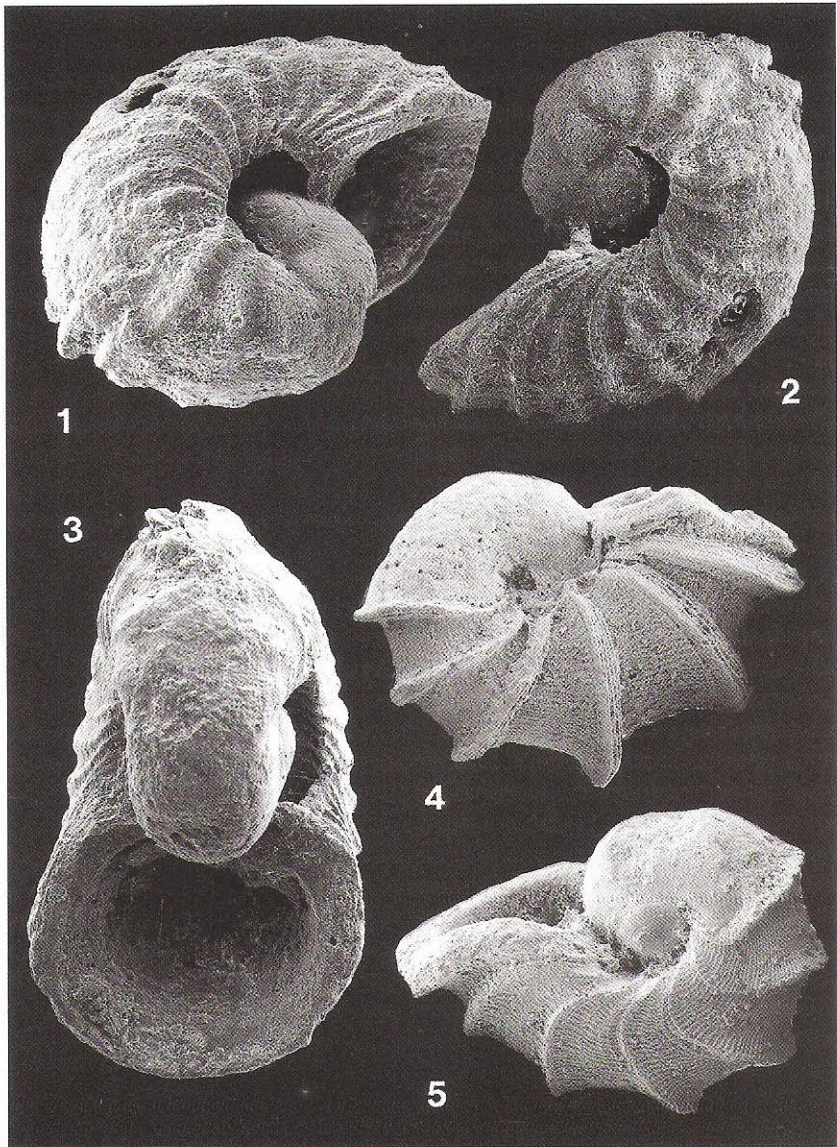
Fig. 1-5 (Legend see p. 116)

larger size than is noted in *Cortinella*. But since the protoconch of neither *Spirina*, nor *Temnospira* is known, their place in the system of the Gastropoda must remain open.

3. Cortinellidae and Neritimorpha in general

Neritimorpha have commonly been considered to represent archaeogastropods especially due to their complex rhipidoglossate radula (TROSCHEL 1856, TROSCHEL & THIELE, 1865-1893). The similarity of radula features induced THIELE (1929) to classify Neritoidea with the Archaeogastropoda. WENZ (1938) and KNIGHT et al (1960) accepted this position in the taxonomic system and it has since been assumed to be correct in most more recent classification schemes (SALVINI-PLAWEN 1980, HASZPRUNAR 1988, 1993, GRAHAM 1988, PONDER & LINDBERG 1996, 1997). But BOURNE (1908, 1911) had considered the *Nerita*-relation to be of very ancient stock. He found that Neritidae represent modified representatives of a primitive stock that has special characters peculiar to themselves and which can not be found among the Archaeogastropoda and the Caenogastropoda. His opinion was repeated by YONGE (1947) and referred to by FRETTER & GRAHAM (1962). According to the latter, modern living species have as specialities among others a single left feather-like ctenidium (except in lung bearing forms), and internal fertilisation. MORTON & YONGE (1964) suggested as additional distinguishing characters the production of egg capsules and connected to that a complex ontogeny. This specific embryonic development of the Neritidae had been described in detail by BLOCHMANN (1882) and was confirmed by BANDEL (1982). According to BIGGELAAR & HASZPRUNAR (1996) the early development of the embryo of the Neritimorpha placed them in quite a different position from trochoidean Archaeogastropoda, that, they should be considered to represent an independent gastropod unit. Thus, they had arrived at similar conclusions regarding another early ontogenetic feature of the Neritimorpha as had been suggested by BANDEL (1982) based on the protoconch shape and formation.

This protoconch of Neritimorpha is very distinctive and can also be recognised in a fossil species without doubt. Here whorls overlap and the egg-shaped embryonic shell has growth lines. This unique mode of development of the neritoid larval shell (BANDEL 1982, 1991, 1992a) differs from that of the Caenogastropoda with less tight coiling and growth-line-less embryonic shell. It also differs from that of the Heterostropha with their sinistral protoconch that is otherwise similar to that of the caenogastropods.

Even though PONDER & LINDBERG (1997) recognised that differences in ontogenetic pathways reflect biological distance between taxa, they suggested that Cocculinidae represent the closest relatives to Neritidae
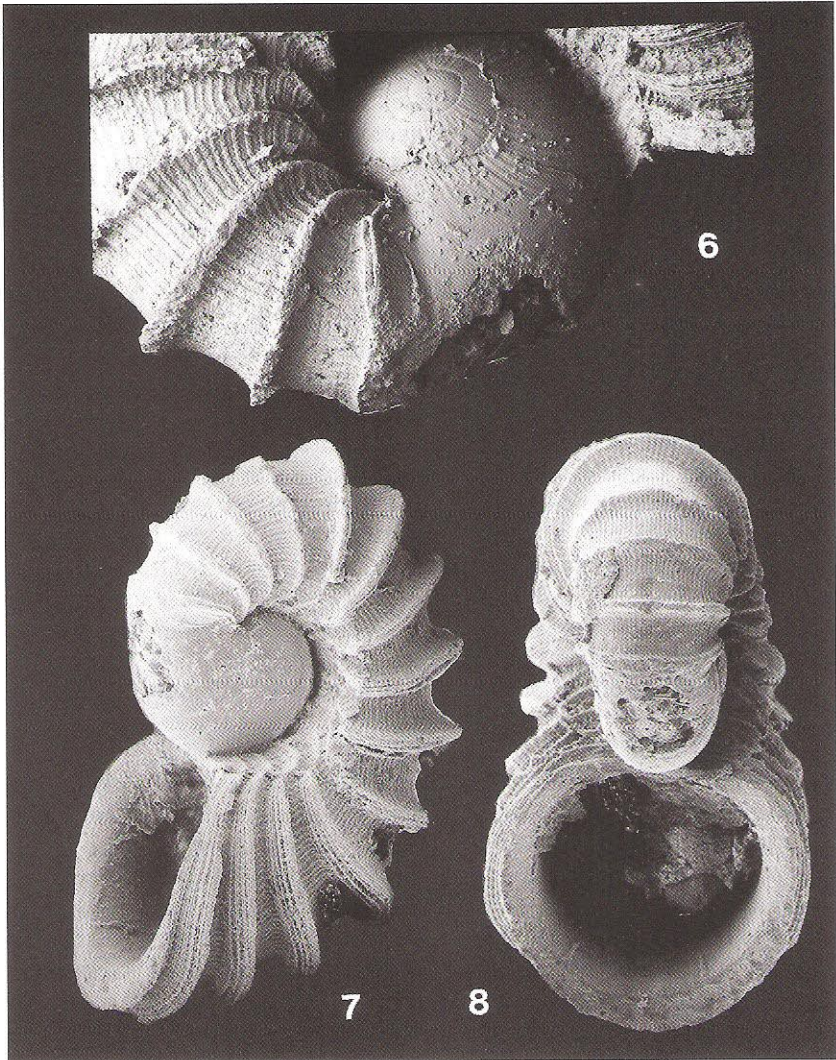
Fig. 6-8. *Cortinella acutecostatum* (ZARDINI, 1985) with the delicately ornamented larval shell tightly coiled around the embryonic shell and well differentiated from the teleoconch (protoconch about 0,55 mm across); in umbilical view with 1,2 mm wide shell (fig. 7) and in apertural view with rounded aperture and width of shell about 1,2 mm (fig. 8).

among the gastropods, here following the assumptions of THIELE (1929). They offered the model that the initial neritopsine larval shell could be highly modified due to intracapsular development. In this way, they argued, it may have developed from a shell as is present in the cocculinids. Since neritimorphs with intracapsular embryonic development are known, for example in case of *Theodoxus* MONTFORT, 1810 and the Hydrocenidae (BANDEL 1982, 1997, SASAKI 1998) this idea cannot be based on any known ontogeny. Cocculinidae obviously have an embryonic shell that is like that of other Archaeogastropoda as can be gathered from illustrations and descriptions of such protoconchs by MARSHALL (1986), HASZPRUNAR (1988), and McLEAN (1988, 1989). The ontogeny of the Cocculinidae follows a similar pathway as that of Vetigastropoda and Docoglossa.

The ontogeny of the Neritimorpha, in contrast, is more complex and indirect. It includes a stage of a planktotrophic larva. As in Caenogastropoda and Heterostropha this larval stage may be transformed to yolk feeding within the egg capsule until a crawling young may hatch. The split-off between ontogenies leading to the Neritimorpha on one side and the Archaeogastropoda on the other side occurred at a very early stage in gastropod evolution, probably during late Cambrian or early Ordovician time (BANDEL & FRÝDA 1999). The idea of THIELE (1929), WENZ (1938) repeated by PONDER & LINDBERG (1997) about a sister-group-relationship between *Patella* and *Nerita* is correct but these sisters lived 500 Million years ago.

The morphology of the protoconch, if interpreted correctly, reflects the different stages of ontogeny. These have to be analysed in modern species, may perhaps sometimes be difficult to believe if not seen by personal inspection, but after all, can be tested and, thus, falsified. This approach is suggested in further evaluation of archaeogastropod early ontogeny rather than a general doubt about biomechanical evidence (PONDER & LINDBERG 1997, p. 100). Any method of elucidation of the evolution within a complex and ancient group as the Gastropoda, thus, also should include the analysis of the early ontogenetic shell. It has to be carried out with careful evaluation of all shell-secreting and shell-calcification features. Otherwise independent groups and differing strategies are not kept well separated and the result will be confusion. This activity can not be substituted by theoretical approaches but only by experiments.

4. Systematic classification of the Neritimorpha including fossil data

Subclass   Neritimorpha GOLIKOV & STAROBOGATOV, 1975

Living Neritimorpha contain the aquatic order Neritoina RAFINESQUE, 1815 and the two terrestrial orders Helicinina THOMPSON, 1980 and Hydrocenina

TROSCHEL, 1856. Recently it was demonstrated by BANDEL & FRÝDA (1999) that Neritimorpha have a more complex evolutionary history than was assumed. From Ordovician to Devonian times neritimorphs developed by forming an openly coiled shell when in the ontogenetic stage of a planktonic larva switching to normal helicospiral coiling when benthic life began and while secreting the teleoconch. They, thus, have a hook-like protoconch and are placed in an independent superorder Cyrtoneritimorpha by themselves. While they appear to have been the only neritimorphs present in Ordovician and Silurian time, during the Devonian coiled protoconchs are found (HEIDELBERGER & BANDEL 1999). Only few species survived to the late Permian that belong to the Cyrtoneritimorpha. From Devonian to Recent neritimorphs usually have a tightly coiled protoconch, and these represent the superorder Cycloneritimorpha. The marine species of both of these have usually a larval shell that reflects the presence of an extended period of their ontogeny that was occupied by a planktotrophic veliger.

5. Cladogram (Fig. 9) to illustrate what can be gathered from the fossil record up to date including an explanation

The model includes the idea that Platyceratoidea HALL, 1859 ranging back in time to the Ordovician represent the closest relatives to those Paleozoic gastropods (BANDEL 1992 a) that can with little doubt be included in the Neritimorpha (discussion see BANDEL & FRÝDA 1999). But of these only the Orthonychiidae BANDEL & FRÝDA, 1999 and Vltaviellidae BANDEL & FRÝDA, 1999 are provided with a fish hook-like protoconch (1) of the Cyrtoneritimorpha as shown by FRÝDA & BANDEL (1997). The limpet shape has been developed secondarily with *Orthonychia* HALL, 1843 (2), probably from the Silurian onward up to the Late Permian. They lived on crinozoans as did also the relatives of *Platyceras* CONRAD, 1840 which perhaps belong to the Cycloneritimorpha. In the latter case it would be a convergent group to the Orthonychiidae. As suggested by BANDEL (1997), the larva was plankton-feeding and constructed similar to the modern veliger. As their modern coiled counterparts they mineralized and became fit to be preserved during diagenesis with and right after metamorphosis to benthic life.

It is supposed that the earliest recognisable members of the Neritopsoidea RAFINESQUE, 1815 lived with several genera in the Mid Devonian carbonate platform environment, commonly the coral stromatoporoid reef and associated reef-lagoon. The origin of the Cycloneritimorpha BANDEL & FRÝDA, 1999 with coiled protoconch (3) is still unknown regarding the time of first occurrence and the closest relative. Plagiothyridae KNIGHT, 1956 are middle Devonian to early Carboniferous Cycloneritimorphs, based on the middle Devonian *Plagiothyra* WHIDBORNE, 1892, *Dirachis* WHIDBORNE,
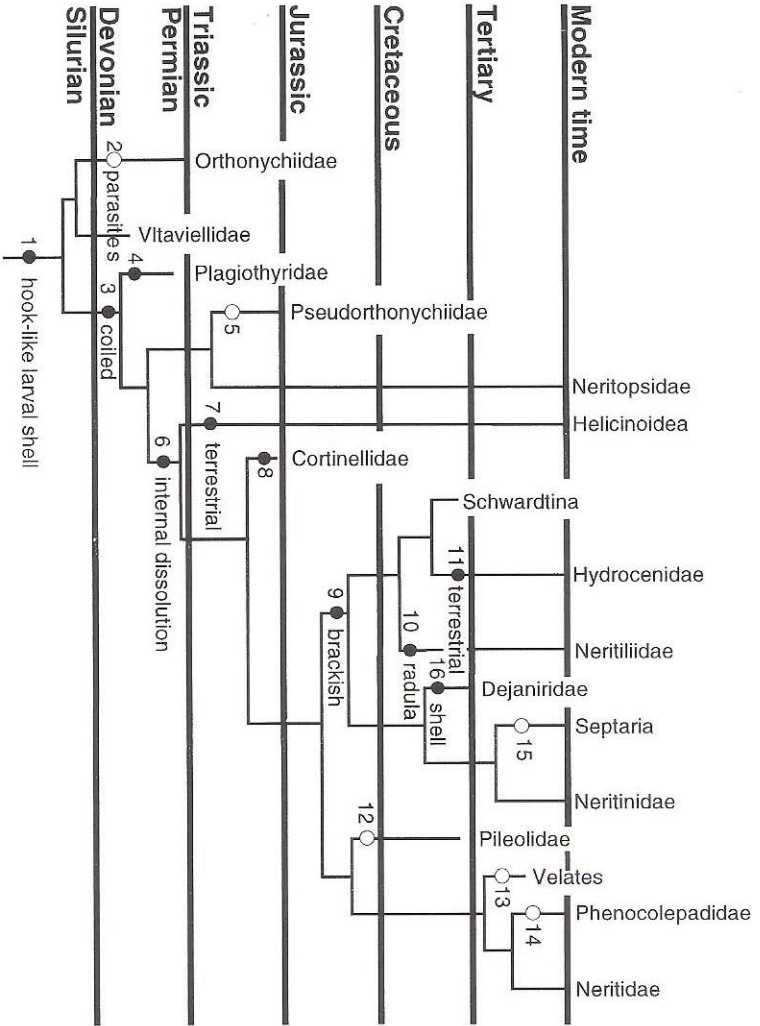
Fig. 9. Cladogram of a model of evolution of the Neritomorpha within the time from the Silurian to the Recent. The numbers are explained in chapter 5.

1891 and *Nerrhenia* HEIDELBERGER & BANDEL, 1999. The later has a simple, coiled protoconch with rounded whorls but less globular shape as is usually found among later species of the Neritimorpha (4). Their protoconchs appear to be of globular shape and convolutely coiled as is the case in a *Naticopsis*- like species from the Carboniferous (HERHOLZ 1992) and is recognised in *Naticopsis* species in the Triassic (SCHWARDT pers. communication). *Naticopsis* from the Early Carboniferous of east Australia has a tightly coiled protoconch (YOO 1994) but the fossil does not allow to determine where the protoconch ends and where the teleoconch begins. A convergent genus to the *Platyceras* of the Paleozoic time developed with the Pseudorthonychiidae BANDEL & FRÝDA, 1999 in the Triassic from neritopsid ancestors (5).

Neritopsoidea are characterised by retaining their inner walls and not resorbing them as is the case in the Neritoidea (WENZ 1938). Also their calcareous operculum is not spirally arranged as in the Neritidae. Species belonging to the family Neritopsidae GRAY, 1847 have a globular shell with little protruding spire and large last whorl. The inner lip of the aperture is broad and smooth. *Neritopsis* GRATELOUP, 1832 is based on the type *Neritopsis moniliformis* GRATELOUP, 1832 from the Miocene of the Paris Basin and is very close to the living *Neritopsis radula* GRAY, 1842 (BATTEN 1984).

Whether the characteristic internal dissolution of the protoconch (6) and also usually the teleoconch already began during the Carboniferous or within the Triassic is still unknown. The time of origin of the Neritoidea is, thus, still unknown. Definite poof is present for the Late Triassic (BANDEL 1992, SCHWARDT in prep.). SOLEM (1983) assumed that there may be Carboniferous Helcinoidea THOMPSON, 1980, certainly Early Cretaceous ones in the USA, and there have been species living in Europe by Late Cretaceous time (HRUBESCH 1965). They developed a terrestrial life with lung and strongly lecithotrophic ontogeny (7) (BOURNE 1911, THOMPSON 1980). The Cortinellidae branch with planispiral coiling (8) of the teleoconch have a neritid protoconch.

The Neritidae RAFINESQUE, 1815 can be traced through Mesozoic times and most species have the characteristic neritid shell shape (a rounded short spire). Most Neritidae have solid shells with outer calcitic and inner aragonitic layer. The columellar edge of the inner lip of the aperture commonly bears denticles or folds. The operculum is calcareous and has usually a peg-like projection. The protoconch of all species with planktotrophic larva is spherical and has the inner walls resorbed. The inner walls of most teleoconchs are also dissolved. Species rich genera are *Nerita* LINNÉ, 1758 and *Neritina* LAMARCK, 1816. The history of the family Neritidae is well established back into the Late Triassic.

With Jurassic time the brackish water and the estuarine area was settled by Neritoidea of the Neritinidae RAFINESQUE, 1815 branch (9). Relatives of the genus *Neritina* (Neritinidae) live in the brackish water of streams issuing into the sea, of Mangrove forests in estuarine conditions and in fresh water near to the sea. Whether this original adaptation also included the Neritiliidae BAKER, 1923 (10) with modem *Neritilia* MARTENS, 1879 with its unusual radula morphology (BANDEL & KOWALKE 1999), or not, is unknown. The fossil *Schwardtina* BANDEL & RIEDEL, 1994 from the Santonian could represent a member of the neritiliids, but similarities in protoconch ornament (BANDEL & RIEDEL 1994a) (11) make a relation to the terrestrial Hydrocenidae TROSCHEL, 1856 plausible. Nothing is known about the fossil history of the small sized terrestrial Hydrocenidae TROSCHEL, 1856 which are found mostly in tropical surroundings throughout the world. While the shape of the embryonic shell (*Hydrocena* PFEIFFER, 1847 in BANDEL 1992b, Fig. 9, SASAKI 1998, Fig. 87) indicates a close relation to the Neritoidea the occurrence of the Hydrocenoidea in the Old World as well as the New World and its range from New Zealand-Australia to Europe-Asia provides evidence for a Pangean origin.

With the *Pileolus*-relation (Pileolidae) the limpet shape developed (12) during late Jurassic time from *Nerita*-like ancestors in fully marine development of reef and beach environment (MUSTAFA & BANDEL 1992). Later in the Early Tertiary from *Neritina*-like ancestors the *Velates*-group formed limpets (13) that lived in the equivalent of the sea-grass environment of modern times in tropical warm water lagoons in southern Europe as well at the western north American shore (CUSHING WOODS & SAUL 1986). Another independent group of limpets derived perhaps from *Smaragdia*-like relation of sea grass living species is the small sized Phenacolepadidae THIELE, 1929 (14) and some of its species have since settled on such exotic place at hydro-sulfide smokers on hot vents in the deep sea (BECK 1992). They arrive here as planktotrophic veliger with characteristic spherical protoconch of the marine Neritoidea. This is very evident when the larval shells illustrated by BANDEL (1982, Pl. 21, figs. 7, 8) for *Phenacolepas* PILSBRY, 1891 from the sea grass environment in the shallow Caribbean Sea are compared with those figured by BECK (1992, Pl. 5, figs. 1, 2) of *Olgasolaris* BECK, 1992 from the hot vent environment in the deep sea of the Western Pazific Ocean.

In the brackish and estuarine environment the *Neritina*-relation has developed since Mid-Tertiary time the limpets of *Septaria* FÉRUSSAC, 1807 (15), still interconnected to their origination by shape of the early ontogenetic shell (HAYNES 1994, BANDEL & RIEDEL 1998). *Septaria* can be related to the *Neritina*-group of nerids which commonly live in fresh water after metamorphosis and swim in the open sea during their larval stage of ontogeny

(BANDEL & RIEDEL 1998, and see there further lit). An unusual shell with angular shape and largely shell filled teleoconch connected to a nonnal neritine protoconch (16) has developed in the Late Cretaceous Dejaniridae, probably from *Neritina*-like ancestors (BANDEL & RIEDEL 1994a). Within the *Titiscania* BERGH, 1890 relation naked neritimorphs evolved which nowadays live in littoral environment in Mauritius and other Pacific Islands of which it is assumed that they belong to the Neritiopsidae because of similarities in radula shape (WENZ 1938).

The history of the Cycloneritimorpha branch of the Neritimorpha ranges back to the Mid-Devonian and probably can be connected to that of the Cyrtoneritimorpha (partly Platyceratoidea) as suggested by BANDEL (1992a) and supported by BANDEL & FRÝDA (1999). Neritimorpha have, thus, carried out an evolution quite separate from that of the other Gastropoda since 500 million years, with Cycloneritimorpha since 350 million years. From an ecological point of view many areas have been settled ranging from the deep sea and here the hot vents (BECK 1992, CLARKE, 1989) to the land, from the sea to the fresh water, with especially rich speciation in the tropical shallow water carbonate environment since Devonian time (Neritopsidae, Neritidae), the estuarine and tropical brackish water environment since the Jurassic (Neritinidae, Neritiliidae) and the limestone based tropical terrestrial environment since the Cretaceous (Helicinidae, Hydrocenidae).

References

BANDEL, K. (1982): Morphologie und Bildung der frühontogenetischen Gehäuse bei conchiferen Mollusken. – Fazies, **7**: 1-198; Erlangen.

– (1988): Repräsentieren die Euomphaloidea eine natürliche Einheit der Gastropoden? – Mitt. Geol.-Paläont. Inst. Univ. Hamburg, **67**: 1-33; Hamburg.

– (1990): Shell structure of the Gastropoda excluding the Archaeogastropoda. – In: CARTER, J. G. (Ed.): Skeletal Biomineralization: Patterns Processes and Evolutionary Trends **I**: 117-134; New York, (Van Nostrand Reinolds).

– (1991): Ontogenetic changes reflected in the morphology of the molluscan shell. – In: SCHMIDT-KITTLER, N. & VOGEL, K. (Eds.): Constructional Morphology and Evolution: 211-230; Berlin (Springer).

– (1992a): Platyceratidae from the Triassic St. Cassian Formation and the evolutionary history of the Neritomorpha (Gastropoda). – Paläont. Z., **66**: 231-240; Stuttgart.

– (1992b): Evolution der Gastropoden aus biologischer und paläontologischer Sicht. – Veröff. Übersee-Mus., Naturwiss. Bremen, **11**: 17-25, Bremen.

– (1993): Trochomorpha aus der triassischen St. Cassian Formation (Gastropoda, (Dolomiten). – Ann. Naturhist. Mus. Wien, **95**: 1-99; Wien.

BANDEL, K. (1994): Comparision of Upper Triassic and Lower Jurassic gastropods from the Peruvian Andes (Pucará Group) and the Alps (Cassian Formation). – Palaeontographica, **233A**: 127-160; Stuttgart.

– (1997): Higher classification and pattern of evolution of the Gastropoda. A synthesis of biological and paleontological data. – Cour. Forschungsinst. Senckenberg, **201**: 57-81; Frankfurt.

BANDEL, K. & FRÝDA, J. (1999): Notes on the evolution and higher classification of the subclass Neritimorpha (Gastropoda) with the description of some new taxa. – Geologica et Palaeontologica, **33**: 219-235, 3 pls.; Marburg.

BANDEL, K. & GELDMACHER, W. (1996): The structure of the shell of *Patella crenata* connected with suggestions to the classification and evolution of the Archaeogastropoda. – Freiberger Forschungsh., **C 464**: 1-71, 15. pl.; Freiberg.

BANDEL, K. & KOWALKE, T. (1997): Systematic value of the larval shell of fossil and modern Vanikoridae, Pickworthiidae and the genus *Fossarus* (Caenogastropoda, Mollusca). – Berliner geowiss. Abh., **E 25**: 31-29; Berlin.

– (1999): Helgoländer Wiss. Mitt., im Druck.

BANDEL, K. & RIEDEL, F. (1994a): The Late Cretaceous gastropod fauna from Ajka (Bakony Mountains, Hungary). A Revision. – Ann. Naturhist. Mus. Wien, **96A**, S. 1-65, 1994; Wien.

– (1994b): Classification of recent and fossil Calyptraeoidea with a discussion on neomesogastropod phylogeny. – Berliner geowiss. Abh., **E 13**: 329-367; Berlin.

– (1998): Ecological zonation of gastropods in the Matutinao River (Cebu, Philippines), with focus in their life cycles. – Annls. Limnol., **34**: 171-191.

BANDEL, K., RIEDEL, F. & WEIKERT, H. (1997): Planctonic gastropod larvae from the Red Sea: A Synopsis. Ophelia, **47**:151-202; Helsingör.

BATTEN, R. L. (1984): *Neopilina, Neomphalus,* and *Neritopsis,* living fossil molluscs. – In "Living Fossils" N. R. ELDREDGE, ed. 218-224.

BECK, L. A. (1992): Two new neritacean limpets (Gastropoda: Prosobranchia: Neritacea: Phenacolepatidae) from hydrothermal vents at Hydrothermal field 1 "Wienerwald" in the Manus back-Arc Basin Bismarck Sea, (Papua New Guinea). – Ann. naturhist. Mus. Wien (B), **93**: 259-275; Wien.

BIGGELAAR, J. A. M. VAN DEN, HASZPRUNAR , G. (1996): Cleavage patterns and mesentoblast formation in the Gastropoda: an evolutionary perspective. – Evolution, **50**: 1520-1540; Los Angeles.

BLOCHMANN, F. (1882): Über die Entwicklung der *Neritina fluviatilis*, Müll.. – Z. wiss. Zool., **36**: 125-174; Leipzig.

BOGGILD, O. B. (1930): The shell structure of the molluscs. – Kongel. Danske Vidensk. Selkabs Skrifter, Naturvid. Math. Afd., **9**: 213-326; Kopenhagen.

BOURNE, G. C. (1908): Contributions to the morphology of the group Neritacea of aspidobranch gastropods. Part I. The Neritidae. – Proc Zool. Soc. London, **1908**: 810-887; London.

– (1911): Contributions to the morphology of the group Neritacea of aspidobranch gastropods. Part II. The Helicinidae. – Proc. Zool. Soc. London, **1911**: 759-809; London.

CLARKE, A. H. (1989): New molluscs from under-sea oil seep sites off Louisiana. – Malacology Data net 2: 122-134.

COLLIN, R. & VOLTZOW, J. (1998): Initiation, calcification, and form of larval "Archaeogastropod" shells. – J. Morphol., **235**: 77-89.

CUSHING WOODS, A. J. & SAUL, L. R. (1986): New Neritidae from southwestern North America. – J. Paleont., **60**: 636-655; Tulsa.

FRETTER, V. & GRAHAM, A. (1962): British prosobranch molluscs, their functional anatomy and ecology. – 755 pp. London, Roy. Soc.

FRÝDA, J. & BANDEL, K. (1997): New Early Devonian gastropods from the *Plectonotus* (*Boucotonotus*) - *Palaeozygopleura* Community in the Prague Basin (Bohemia). – Mitt. Geol.-Pal. Inst. Univ. Hamburg., **80**: 1-57; Hamburg.

GRAHAM, A. (1988): Molluscs: prosobranch and pyramidellid gastropods. – Synopses of the British Fauna, (N. S.), **2**: 1-662; London.

HASZPRUNAR, G. (1988): On the origin and evolution of the major gastropod groups, with special reference to the Streptoneura. – J. Molluscan Stud., **54**: 367-441; London.

–   (1993): The Archaeogastropoda. A clade, a grade or what else?. – Amer. Malacolog. Bull., **10**: 165-177; Houston, Texas.

HAYNES, A. (1994): Reproductive strategies in the freshwater genus *Septaria* (Neritidae). Malacolog. Rev., Suppl., **6**: Molluscan Reproduction, 1994,:1-7.

HEIDELBERGER, D. & BANDEL, K. (1999): Micromorph gastropoda from the Middle Devonian (Givetian) limestone of the Soetenich Syncline (Eifel). – Mitt. Geol.-Pal. Inst. Univ. Hamburg., **83**: 129-162, 46 figs.; Hamburg

HERHOLZ, M. (1992): Mikromorphe Gastropoden aus dem rheinisch-westfälischen Steinkohlerevier (Oberkarbon). – N. J. Geol. Paläont., Mh., **1992**: 242-256; Stuttgart.

HRUBESCH, K. (1965): Die santone Gosau-Landschneckenfauna von Glanegg bei Salzburg, Österreich. – Mitt. Bayer. Staatssamml. Paläont. Histor. Geol., **5**: 83-120, 6 pls.; München.

KITTL, E. (1894): Die Gastropoden der Schichten von St. Cassian der südalpinen Trias.Teil III. – Ann. k. k. naturhistor. Hofmus., **9**: 144-277; Wien.

KNIGHT, J. B. (1941): Paleozoic gastropod genotypes. – Bull. Geol. Soc. Amer., Spec. Pap., **32**: 1-510, 96 pls.; New York.

KNIGHT, J. B., BATTEN, R. L. & YOCHELSON, E. L. (1960): I: Mollusca. – 1169-1351, In: MOORE, R. C. (Ed). Treatise on Invertebrate Paleontology. Univ. Kansas Press; Lawrence.

KOKEN, E. (1889): Über die Entwicklung der Gastropoden vom Cambrium bis zur Trias. – N. Jb. Min., Geol. Palaeont., suppl. vol., **6**: 305-484, pls. 10-14; Stuttgart.

LAURSEN, D. (1981): Taxonomy and distribution of teleplanic prosobranch larvae in the North Atlantic. – Dana-Report (Copenhagen) 89: 1-43, 3 pls.; Copenhagen.

MARSHALL, B. A. (1986): Recent and Tertiary Cocculinidae and Pseudococculinidae (Mollusca: Gastropoda) from New Zealand and New South Wales. – New Zealand and New South Wales. – New Zealand J. Zool., **12**: 505-546.

MCLEAN, J. H. (1988): New archaeogastropod limpets from hydrothermal vents, superfamily Lepetodrilacea. Part I: Systematic description. – Phil. Trans. R. Soc. Lond., (B), **319**: 1-32; London.

McLean, J. H. (1989): New archaeogastropod limpets from hydrothermal vents, new family Peltospiridae, new superfamily Peltospiracea. – Zoologica Scripta, **18**: 49-66;

Morton, J. E. & Yonge, C. M. (1964):Classification and structure of Mollusca. – In: Wilbur, K. M. & Yonge, C. M. (Eds.): Physiology of Mollusca **1**: 1-58; London & New York (Academic Press).

Mustafa, H. & Bandel, K. (1992): Gastropods from lagoonal limestones in the Upper Cretaceous of Jordan. – N. Jb. Geol. Paläont., Abh., **185**: 349-376; Stuttgart.

Page, L. R. (1997): Ontogenetic torsion and protoconch form in the archaeogastropod *Haliotis kamtschatkana*: Evolutionary implications. – Acta Zoologica, **78**: 227-245, Stockholm.

Ponder, W. F. & Lindberg, D. (1996): Gastropod phylogeny - Challenges for the 90's. – In: Taylor, J. D. (Ed.): Origin and evolutionary radiation of the Mollusca: 135-154; Oxford (University Press).

–   (1997): Towards a phylogeny of gastropod molluscs: an analysis using morphological characters. – Zool. J. Linnean Soc., **119**: 83-265; London.

Richter, G. & Thorson, G. (1975): Pelagische Prosobranchier-Larven des Golfes von Neapel. – Ophelia, **13**: 109-163, 20 pls.; Helsingör.

Robertson, R. (1971): Scanning electron microscopy of planktonic larval marine gastropod shells. – The Veliger, 14 (1): 1-12, 9 pls.; Berkeley.

Salvini-Plawen, L. v. (1980): A reconsideration of the systematics in the Mollusca (phylogeny and higher classification). – Malacologia, **19**: 249-278; Philadelphia.

Sasaki, T. (1998): Comparative anatomy and phylogeny of the Recent Archaeogastropoda (Mollusca: Gastropoda). – The University Museum, University Tokyo, Bull., **38**: 1-223; Tokyo.

Scheltema, R. (1971): Larval dispersal as a means of genetic exchange between geographically separated populations of shoal-water benthic marine gastropods. – Biol. Bull., **140**: 284-322.

Schwardt, A. (1992): Revision der *Wortheniella*-Gruppe (Archaeogastropoda) der Cassianer Schichten (Trias, Dolomiten). – Ann. Naturhist. Mus., **94**: 23-57; Wien.

Solem, A. (1983): Lost or kept internal whorls: Ordinal differences in land snails. – J. Molluscan Stud., suppl., **12 A**: 172-178; London.

Thiele, J. (1929): Handbuch der systematischen Weichtierkunde. – Jena, Gustav Fischer.

Thompson, F. G. (1980): Proserpinoid land snails and their relationships within the Archaeogastropoda. – Malacologia, **20**: 1-33; Ann Arbor.

Troschel, F. H. (1856): Das Gebiss der Schnecken zur Begründung einer natürlichen Classification. – 1-252, Erster Band, Nicolaische Verlagsbuchhandlung; Berlin.

Troschel, F. H. & Thiele, J. (1865-1893): Das Gebiss der Schnecken zur Begründung einer natürlichen Classification, **2**: 409 pp., Nicolaische Verlagsbuchhandlung, Berlin.

WENZ, W. (1938): Gastropoda, I. – 1639 pp. – In: SCHINDEWOLF, O. H. (Ed.): Handbuch der Paläozoologie, **6**; Berlin.

YONGE, C. M. (1947): The pallial organs in the aspidobranch Gastropoda and their evolution throughout the Mollusca. – Philos. Trans. Royal Soc. London, B, **232**: 443-518; London.

YOO, E. K. (1994): Early Carboniferous Mollusca from the Tamworth Belt, New South Wales, Australia. – Rec. Austral. Mus., **46**: 63-120; Sydney.

ZARDINI, R. (1978). Fossili Cassiani (Trias Mediosuperiore) Atlanti dei Gasteropodi della Formazione di S. Cassiano Raccolti della Regione Dolomitica Atorno a Cortina d'Ampezzo. – 1-58; Cortina d'Ampezzo.

– (1985): Fossili Cassiani (Trias Mediosuperiore) Atlanti dei Gasteropodi della Formazione di S. Cassiano Raccolti della Regione Dolomitica Atorno a Cortina d'Ampezzo. – 1-16; Cortina d' Ampezzo.

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