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Platyceratidae from the Triassic St. Cassian Formation and the evolutionary history of the Neritomorpha (Gastropoda)

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With 3 figures

Kurzfassung: *Orthonychia alata* (LAUBE 1869) aus der obertriassischen St. Cassian Formation stellt den bisher jüngsten Vertreter der Platyceraten dar. Wie die paläozoischen Verwandten dieses Bewohners der tropischen Tethys lebten die Individuen der Art als Parasiten an Krinozoen. Die Merkmale der Larvalschale stellen *Orthonychia* in die Unterklasse der Neritomorpha innerhalb der Gastropoden. Aus der Geschichte der parasitischen Platyceraten ergibt sich, daß ihre herbivoren Vorfahren im Ordovizium gelebt haben. Damit ist der Nachweis eines hohen Alters der Neritomorpha als eigenständiger Gruppe der Gastropoden gegeben. Neritomorpha haben sich seit dem Ordovizium unabhängig von den anderen Unterklassen der Gastropoden (Archaeogastropoda, Caenogastropoda und Heterostropha) entwickelt. Ihre Entstehung ist nicht lange nach dem ersten Auftreten der Klasse der Gastropoden innerhalb der Mollusken erfolgt.

Abstract: *Orthonychia alata* (LAUBE 1869) represents the youngest known member of the Platyceratidae. It lived in the Late Triassic St. Cassian time, in shallow water of the Tethyan Ocean. Like its Paleozoic relatives it was a parasite on a crinozoan host. Features of the larval shell place *Orthonychia* in the Neritomorpha. The parasitic Platyceratidae represent a specialized group of the Neritomorpha which must have branched off from normal herbivorous neritomorph stock during the Ordovician. Neritomorpha thus represent a group of gastropods with an independant history ranging back into the older Paleozoic to the base of gastropod evolution.

Introduction

Modern parasitic molluscs on echinoderm hosts are represented by the species of the superfamily Eulimoidea (subclass Caenogastropoda). The history of this group can be traced back to the Upper Cretaceous. Older representatives are doubtful. Their systematic relation among the gastropods is somewhat unclear, but most probably they represent members of the order Ctenoglossa and have been derived from near the Janthinoidea. They are most similar to forms now seen in the Epitoniidae. The Ctenoglossa represent an old group with ancestors well established in Paleozoic time (BANDEL 1991a).

Paleozoic echinoderms also hosted parasitic gastropods. These were the Platyceratidae, which were supposed to have become extinct with Permian time (MEYER & AUSICH 1983). Platyceratid hosts were crinoids and blastoids (KOKEN 189; KEYES 1890; BOWSHER 1955). From turbiniform ancestors living in the Ordovician and representing simple trochospiral gastropods with holostomous aperture, limpet-shaped forms developed in the Silurian. These have been placed into the genera *Platyceras* CONRAD 1840 and *Orthonychia* HALL 1843.

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Ordovician platyceratids of the genera *Cyclonema* Hall 1852 and *Naticonema* Perner 1903 lived on crinoids but not fixed to a definite place on their host. By Devonian time they had become specialized to be attached to their host close to the anal opening (Horny 1964). Members of the genus *Platyceras* are found on their hosts only above the anal opening (Drevermann 1907; Wanner 1922; Meyer & Ausich 1983).

Usually the anal opening of the crinoid lies below the limpet. The limpets shell edge follows the morphology of the host body. Wanner (1922) believed that Permian *Platyceras* extended its proboscis with the mouth into the anal opening feeding on the tissue of the animal in a similar way as is known from the limpet-like modern eulimid *Thyca* that feeds on starfish.

Rollins & Brezinski (1988) were able to confirm Wanner's assumptions that *Platyceras* and *Orthonychia* were not just feeding on the faecal pellets of their host. They had uncovered rock layers in which a whole population of crinoids were embedded along with their parasites. And there crinoids without a parasite were larger than those carrying a platyceratid limpet. From this observation it can be deduced that platyceratids were not just commensals, but true parasites.

When the question of relationship of platyceratids to other gastropods is asked, a confusing picture arises from literature data. Koken (1896) considered *Platyceras* as Paleozoic branch of the Capulidae. He thought that this branch became extinct in Triassic time, while in his opinion modern capulids arose during Jurassic times. Wanner (1922) found *Platyceras* on Permian crinoids and accepted Koken's ideas. Wenz (1941), in contrast, considered platyceratids as convergent with capulids and not related to them at all. But his evidence is meagre. It consists only of the long time gap between last platyceratids which, in his opinion, lived in the Permian and capulids which according to him appeared in the Early Cretaceous.

Wenz (1941) thought that platyceratids belong to the Trochonematoidea, a predominantly Paleozoic group of gastropods with unclear status. Knight et al. (1960) divided the Trochonematidae of Wenz into several groups and placed the Platyceratidae in the Trochina Cox & Knight 1960 and thus near the Trochoidea and all slit-less trochiform archaeogastropods. Knight (1934) had considered also the Neritidae as possible ancestors and relatives of the Platyceratidae, mainly because the outer layer of the shell is calcitic. Knight (1934) envisaged a common ancestorhsip of the branches of gastropod groups with *Naticopsis* in one branch and *Platyceras* in the other branch. But this idea was not followed up by Knight et al. (1960).

Blastoids as well as most crinoids became extinct during the Permian-Triassic faunal crisis and platyceratids were considered to have become extinct at Mid-Permian time before the actual crisis (Wenz 1941; Knight et al. 1960; Meyer & Ausich 1983). But Platyceratidae, like some of the Paleozoic crinoids groups, survived the Permian/Triassic boundary as had been noted by Koken (1896) and forgotten since then. Only at the Triassic-Jurassic faunal change did Platyceratidae, probably together with their hosts, die out. Some other groups of gastropods not related to the Platyceratidae have also crossed the Permian-Triassic boundary to disappear at the end of the Triassic (Bandel 1991c).

The Triassic platyceratid *Orthonychia alata* (Laube 1869)

The genus *Platyceras* is based on the type *Platyceras vetusta* (Sowerby 1829) that was described clearly by Knight (1941). It lived in the Early Carboniferous in a shallow warm sea at what is now Queens County in Ireland. This limpet had a coiled juvenile shell. According to Knight et al. (1960), *Platyceras* is irregularly capuliform with no ornament except growth lines. A flattened inner side of the uncoiled whorl is not mentioned in the definition of the genus *Platyceras,* but their illustration shows this feature well (KNIGHT et al. 1960: fig. 153, 4a).

KNIGHT (1934) and WENZ (1941) distinguish two genera among the limpet-like platyceratids. *Platyceras* CONRAD 1840 with early whorls in contact and the last whorl free, and *Orthonychia* HALL 1843 with no part of the teleoconch closely coiled. This clear diagnosis was blurred somewhat by KNIGHT et al. (1960) who considered both types to represent subgenera of the genus *Platyceras,* together with some other forms such as the totally coiled species of *Visitator* PERNER 1991 and *Praenatica* PERNER 1903.

Orthonychia alata (LAUBE 1869)

Figs. 1, 2a–h, 3a

1869 *Capulus alatus* sp. nov. – LAUBE: 16, pl. 30, fig. 12.
1892 *Capulus? alatus* LAUBE – KITTL: 57.
1978 cfr. *Capulus alatus* LAUBE – ZARDINI: 39, pl. 24, figs. 3–7.

The holotype of LAUBE, housed in the Natural History Museum of Vienna (Nr. 1869/G 88), as well as seven specimens from the locality Campo near Cortina d'Ampezzo that had been collected by RINALDO ZARDINI, and 10 additional specimens collected since at the same locality were studied.

Fig. 1. Sketch of the larval shell of *Orthonychia alata* from St. Cassian Formation, Dolomites. The larval shell measures 0.3 mm in width.

Description: The small limpet (3 mm high and 1.5 mm wide) has a tightly coiled early ontogenetic shell (Figs. 1, 2a–f) and a teleoconch in which the whorls are not in contact. The apex of the limpet is formed by the larval and embryonic shell that consists of at least 2.5 whorls (Figs. 2a, 3a). These differ in shape, sculpture, and composition from the following limpet-like teleoconch. The whorls of the early ontogenetic shell are smooth and well rounded and tightly coiled so that subsequent whorls overlap the former ones. The earliest whorl is thus largely covered by the following whorl. The shape of the larval shell is spherical naticoid with dextral coiling and rapid expansion of whorl diameter. The margin of the shell of the fully grown planktotrophic veliger (pediveliger) is thickened and forms 6 thorn-like projections (BANDEL 1991b: fig. 3d). The larval shell measures about 0.7 mm in diameter and consists of aragonitic shell material with crossed lamellar structure.

The following teleoconch is a limpet with a horn-shaped shell twisted into a weak open dextral coil (Fig. 2a, b, g, h). While the outer portion of the whorl is evenly rounded, the inner side forms a broad groove, separated from the outside by sharp carinae (Fig. 2d, g, h).

The limpet-like shell formed directly after the pediveliger had settled on its host and finished metamorphosis. Shell additions of first increments of shell consist of a thick outer calcitic layer. The only sculpture consists of even collabral growth lines commonly raised to form an annulation. The groove on the inner shell side with its marginal carinae shows finer growth lines than the rounded outside (Fig. 2d). One half open whorl may be present in a fully grown shell of a maximum diameter of 3 mm.

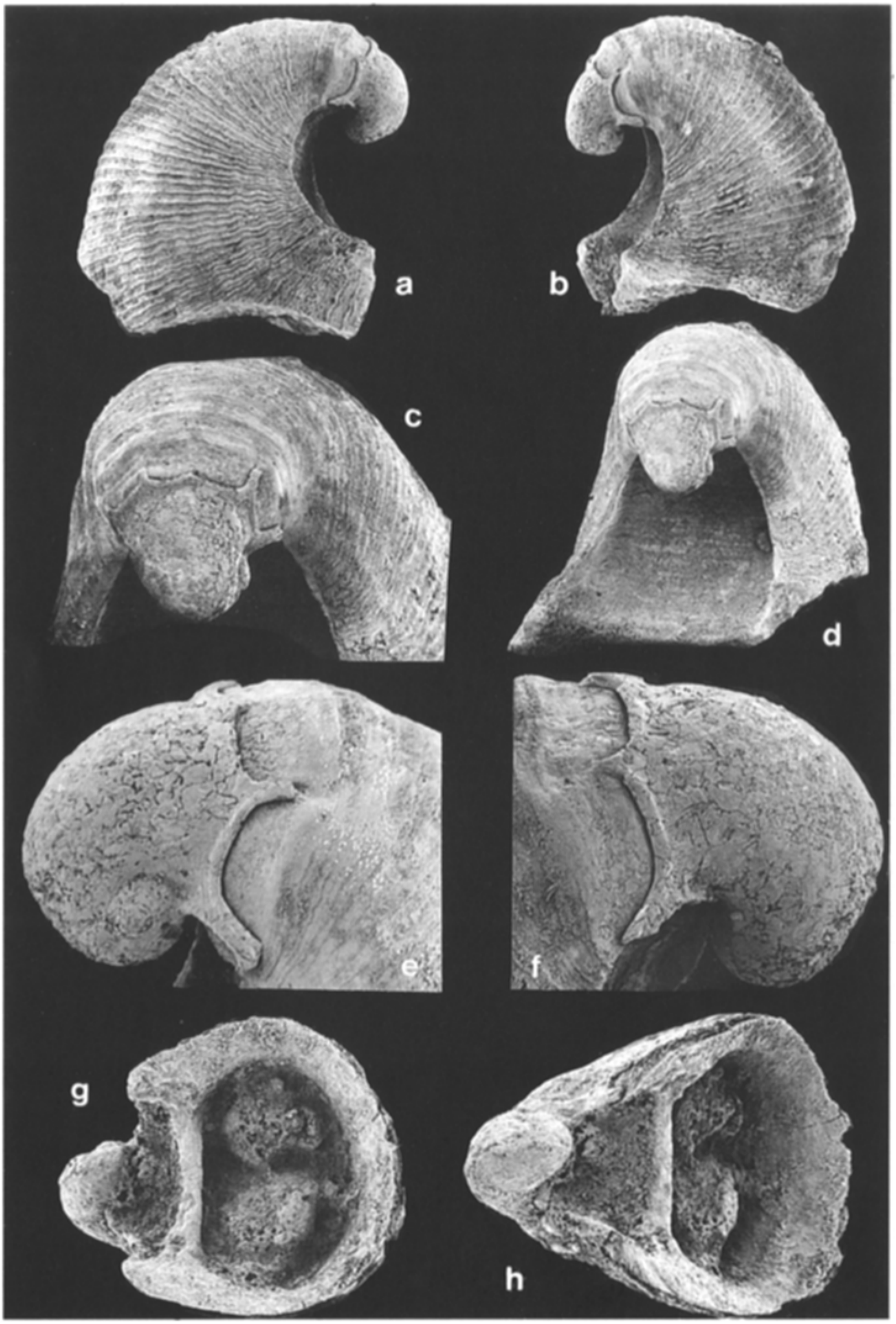
The shell of the teleoconch consists of a thick layer of foliated calcite. The protoconch, in contrast, is composed of aragonite in crossed lamellar structure. Only a very thin layer on the inner side of the limpet shell may have been aragonitic. The larval shell became sealed from the teleoconch and shell layers were deposited in it and closed it off from the interior of the limpet.

Discussion: In the literature, the shape of the protoconch of the genera *Platyceras* and *Orthonychia* remained somewhat mysterious. Yochelson (1956) described the earliest shell portions as ranging in shape from orthostrophic to vermiform and uncoiled. *Orthonychia alata* demonstrates, that the early whorls of platyceratids are normally coiled, as is the case with most gastropods (Bandel 1982). The larval shell is of aragonitic construction and may be dissolved during diagenesis. Such dissolution could explain Yochelson's (1956) observation of the presence of different kinds of embryonic shell types in the Platyceratidae. They could represent the most apical calcitic shell portions originally deposited within and following the aragonitic embryonic and larval shell.

The characteristic flattened groove on the inner face of the whorl of the teleoconch of *Orthonychia alata* can be noted also in other platyceratids described in the literature. Usually, authors did not describe it as quite as pronounced as it is in the Triassic species. A flattened inner whorl was noted by Tylor (1965) on the Carboniferous *Platyceras indianense* Miller & Gurley 1879. This flattening is connected with only one carina. Even closer in shape to that of *Orthonychia alata* are some of the Permian species described by Wanner (1922) from Timor. Here *Platyceras welteri* (Wanner 1922) and *P. sundaicus* (Wanner 1922) have a somewhat irregular, flattened inner side of the teleoconch accompanied my marginal carinae. A flattened inner whorl-face can be noted in the type species of the genus *Platyceras*, *P. vetustus* as reconstructed by Knight et al. (1960: fig. 153,4).

Shell structure of platyceratids in general seems to be dominated by a thick calcitic outer layer of the limpet (Carter & Hall, in prep.). Kriz & Lukes (1974) and Yochelson & Kriz (1974) even noted the preservation of color patterns on Devonian platyceratids, similar to those known from neritomorph gastropods of various ages, including the Late Triassic of the St. Cassian Formation (Tichy 1980).

Fig. 2. a–h: Aspects of the shell of *Orthonychia alata* from the Dolomites. a–f: Scanning pictures of the holotype. a, b: Lateral views of the about 3 mm high shell. c: Apical view with larval shell demonstrating its six apertural spines. The larval shell measures 0.3 mm in width. d: Broad groove on the inner side of the shell accompanied by marginal carinae. The base of the shell measures 2.7 mm. e: Apertural view of the larval shell that measures 0.7 mm in diameter. f: Umbilical view of the larval shell that is 0.7 mm wide. g: Small limpet shell from Campo seen from below with interior partly filled by sediment. The shell measures 1.6 mm across. h: Same specimen as in (g) seen from below demonstrating its dextral open coiling. The shell measures 1.6 mm across.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Comparison of the early ontogenetic shell of *Orthonychia alata* with that of fossil and modern Neritomorpha

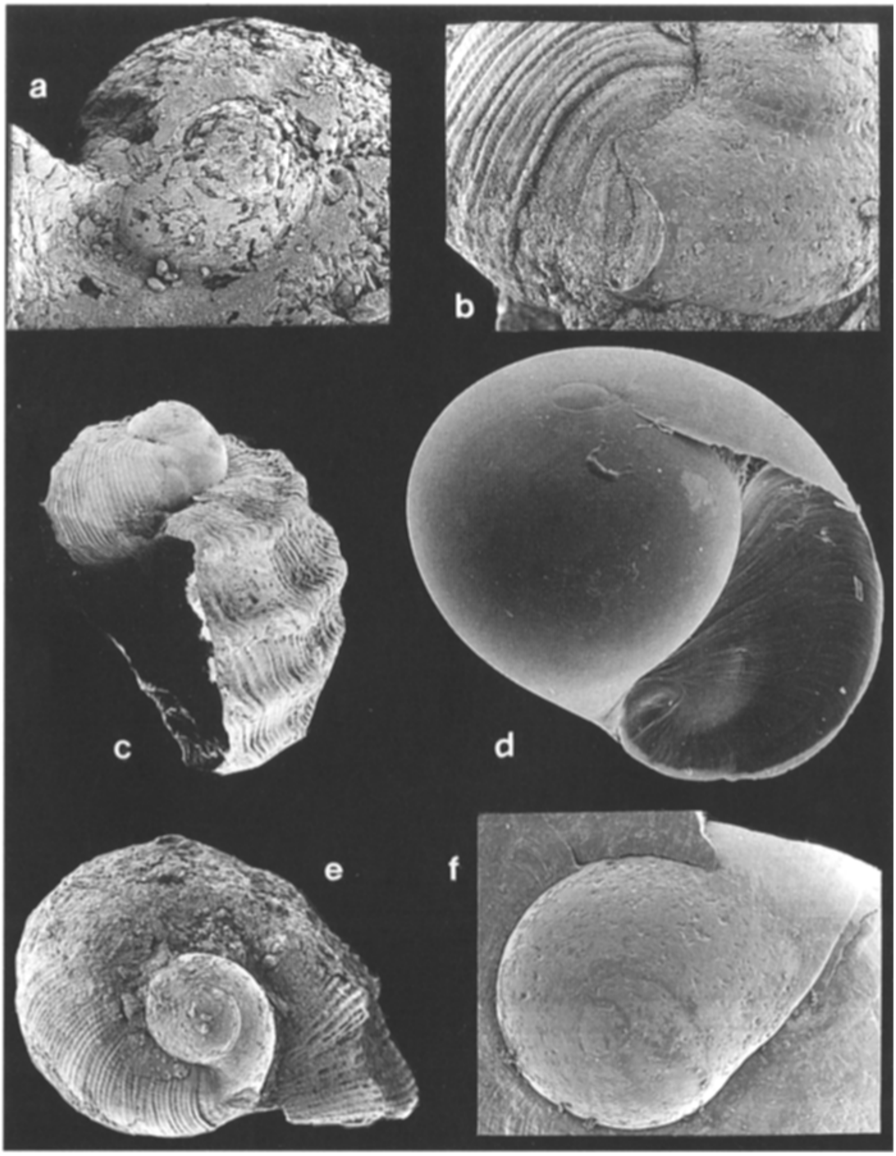
In Neritomorpha the larval shell that is produced by the free swimming larva after hatching from the egg capsule and before metamorphosis to a benthic snail is strongly convolute. Successive whorls partly or completely cover the whorls formed earlier on (BANDEL 1982: fig. 73, pl. 20, fig. 9, pl. 21, figs. 3–5, 10) (Fig. 3d, f).

Larval shells of modern representatives of *Smaragdia, Nerita, Neritina,* and *Phenacolepas* are very characteristic (Fig. 3d, f) and can be easily distinguished from shells produced by veliger larvae of other gastropod groups outside the Neritomorpha. No caenogastropod is known where smooth whorls of the larval shell overlap as much onto the embryonic shell and following whorls as in the Neritomorpha. The larvae of the Heterostropha also differ in this respect from the Neritomorpha and, in addition, usually twist from one (mostly sinistral) direction of coiling into another (mostly dextral) during late larval life.

Modern Neritomorpha, with the possible exception of *Neritopsis,* not only have rather convolute larval shells but also dissolve the inner walls of covered whorls (own observations on living larvae in the Red Sea during Meteor cruise 5, 1987; BANDEL 1991b).

Neritomorpha from the St. Cassian Formation hat lived contemporaneously with *Orthonychia alata* show convolute larval shells quite similar to those seen in modern representatives (Fig. 3b, c, e). Here some larvae show the smooth straight apertural outline of the fully grown veliger shell, while others have undulating margins (Fig. 3b, c, e). None are known that have spines at the margin of the pediveliger shell as is the case in *Orthonychia.* However, the larval shell of *Palaeonarica concentrica* (MÜNSTER 1841) shows almost three whorls with smooth surface and globular, convolute coiling. Here, the margin of the fully grown larval shell has a sutural projection of the apertural lip and a lobe on the flank followed by another projection in the middle of the whorl (Fig. 3b, c, e). On the covered anterior side of the apertural lip there is probably another lobe. Thus *Palaeonarica* larvae resemble those of *Orthonychia* but their apertural projections are much less developed. The margins of the aperture in the larval shell of *Delphinulopsis pustulosa* (MÜNSTER 1841) (at least 2.5 whorls) and *Neritopsis armata* (MÜNSTER 1841) (more than two whorls), both from the St. Cassian Formation, are straight and resemble the larval shells of modern neritids in this regard. *Neritopsis subornatus* (MÜNSTER 1841) from the St. Cassian Formation has well covered first whorls and 2.5 more larval whorls separated from each other by a well developed suture.

Fig. 3. a: The central portion of the larval shell of *Orthonychia alata* demonstrates the tight convolute coiling that is characteristic of Neritomorpha. Width of the illustrated shell 0.35 mm. b: The margin of the fully grown larval shell of *Palaeonarica concentrica* (MÜNSTER) from Stuores near St. Cassian is lobed in a similar way as is seen in *Orthonychia alata.* Detail of c. The apertural margin of the larval shell is 0.25 mm high. c: Side view of *Palaeonarica concentrica* from the Stuores locality near St. Cassian, St. Cassian Formation. The shell is 1.3 mm high. d: The fully grown veliger shell of a modern marine member of the Neritidae collected from the plankton of the Red Sea demonstrates the tight convolute coiling of the 0.6 mm wide shell. e: Apical view of *Palaeonarica concentrica,* a Triassic neritopsid from the Dolomites. Detail in b. The shell measures 1 mm across. f: The larval shell of a Pliocene *Smaragdia* from the Mediterranean Sea demonstrates the characteristic larval shell of the Neritomorpha with straight apertural margin. The larval shell measures 0.5 mm in maximum diameter. Le Puyet, southern France, collected by VON HACHT.



The shell of the planktotrophic veliger serves to distinguish neritomorphs from Archaeogastropoda on one side and Heterostropha (including Allogastropoda, Opisthobranchia and Pulmonata) and Caenogastropoda (including Ctenoglossa, Mesogastropoda and Neogastropoda) on the other side (BANDEL 1982, 1991b).

In a recent paper, HADFIELD & STRATHMANN (1990) discussed heterostrophic coiling occurring in the embryonic shell of Archaeogastropoda. They thought that having found embryonic shells with a slight sinistral twist within modern representatives of this group provides evidence for the minor value of protoconch morphology for taxonomic evaluation of fossil gastropods. However, Hadfield & Strathmann (1990) did not take into consideration that they had assembled data for archaeogastropods which actually deform their bilaterally symmetrical embryonic shell by force of the two retractor muscles of the embryo in coordination with the foot before they mineralize the shell and take up benthic life (Bandel 1982, 1986). They also had not noted that archaeogastropods, after deposition of the embryonic shell, construct the teleoconch directly and that a larval shell is not present within members of this subclass of the Gastropoda. The change from sinistral to dextral coiling in the subclass Heterostropha and the consistency of dextral coiling within the subclasses Caenogastropoda and Neritomorpha occurs within the larval shell and not the embryonic shell. This misunderstanding devaluates all far reaching conclusions on gastropod evolution by Hadfield & Strathmann (1990) since they are only based on observations of the morphology of the embryonic shell of archaeogastropods.

It is not yet clear to what extent larval shell morphology can be used to unravel the phylogeny of the neritomorphs. It is evident, however, that larval shells of the marine Neritomorphy differ from those of all other groups of gastropods that have a planktotrophic larva (Bandel 1982).

Conclusions

The Platyceratidae Hall 1859 are members of the gastropod group Neritomorpha as had been suggested by Knight (1934). While the history of platyceratids can be traced back into the Ordovician, that of the non-parasitic Neritomorpha is less clear. Many Paleozoic gastropod genera could belong to this group, but they all need confirmation. To trace the group back in time the early ontogenetic shell of fossil species must be studied. Shell structure may be an additional aid for correct systematic placement.

The larval shell of Platyceratidae is evidence of their place among the Neritomorpha. It differs from the early ontogenetic shell of the Archaeogastropoda which never have a shell that is produced by a planktotrophic veliger. It is also different from the Caenogastropoda with conical larval shell and from the Heterostropha with change of direction of coiling within the larval shell. The members of the subclass Neritomorpha, therefore, have had an independent evolution since at least Ordovician times which proceeded separately from that of the evolution of the other subclasses Archaeogastropoda, Caenogastropoda, and Heterostropha. The evolution of a planktotrophic larva in the Neritomorpha has probably occurred independently from that of the Caenogastropoda and Heterostropha, while Archaeogastropoda never developed larvae that feed on plankton.

Since Platyceratidae are shown to have neritomorph features, the subclass Neritomorpha can be differentiated into the following four orders: the aquatic Neritoina, the parasitic Platyceratina, the terrestrial Helicinina, and Hydrocenina. In the modern fauna, the Neritomorpha are represented by members of the superfamilies Neritopsoidea, Neritoidea, Hydrocenoidea, and Helicinoidea. Neritopsoidea are represented by two species of the genus *Neritopsis* in modern tropical seas, while Neritoidea encompass a large number of species within a number of genera living in marine, brackish, and fresh water environments. Among them are species with the characteristic neritid shell shape (a rounded short spire) as well as limpets. The Hydrocenoidea are represented by a number of species with very similar shape and living requirements and are mostly found among moist litter in areas with tropical or warm climate. While the shape of the embryonic shell 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. Its history might go back to the Early Mesozoic, but there is no fossil record. The terrestrial Helicinoidea have developed quite a number of species which are easily differentiated from those of the Hydrocenoidea (THOMPSON 1980). Fossil species have been described form strata as old as the Carboniferous (KNIGHT et al. 1960). However, these shells must remain doubtful due to convergence with the pulmonate Stylommatophora on one side and caenogastropod landsnails, especially among the Cyclophoroidea, on the other side (SOLEM 1983).

It is fairly safe to conclude, that Platyceratina probably evolved from ancestors close to Mesozoic and modern Neritopsoidea (Neritoina). The latter can be traced with confidence to the Late Paleozoic. While Neritoidea have come from the same source, the origin of the Platyceratina can be traced back to the Ordovician while that of the former can, at the moment, only be documented back to the Triassic (BANDEL 1988, 1991d). The origin of the terrestrial Hydrocenina and Helicinina is still unclear.

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