

## Notes on the evolution and higher classification of the subclass Neritimorpha (Gastropoda) with the description of some new taxa

Klaus BANDEL & Jiří FRÝDA

with 3 text-figures and 3 plates

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Neritimorpha represent a subclass of the Gastropoda that regarding its anatomy is close to the Archaeogastropoda, regarding its ontogeny it resembles more the Caenogastropoda. Ontogenetic development includes a larval phase during which a planktotrophic veliger may produce a larval shell. The members of the new order Cycloneritimorpha have a larval shell that is tightly coiled and rounded. The representatives of the other new order Cyrtoneritimorpha have a hook-like openly coiled protoconch. Recognition of these two new taxa splits seemingly well established Palaeozoic gastropod groups like the Platyceratoidea which apparently are polyphyletic. The protoconch shape is evidence for teleoconch convergence between a Carboniferous *Orthonychia* and the Triassic *Pseudorthonychia* n. gen. Neritimorpha existed from Ordovician onward first with the Cyrtoneritimorpha and later the still extant Cycloneritimorpha with an overlap in time of occurrence from the Devonian to the Permian.

Neritimorpha stellen eine unabhängige Unterklasse der Gastropoda dar, deren anatomische Merkmale jenen der Archaeogastropoda ähneln, während der Verlauf ihrer Ontogenese mehr dem der Caenogastropoda gleicht. Die Ontogenese der Neritimorpha schließt eine Larvalphase ein, in deren Verlauf eine planktotrophe Larve ausgebildet sein kann, die dann eine eigene Larvalschale ausscheidet. Innerhalb der Ordnung Cycloneritimorpha n. ord. wird eine Larvalschale ausgeschieden, die eng gewunden ist und rundliche Gestalt besitzt. Bei den Cyrtoneritimorpha n. ord. ist hingegen der Protoconch offen hakenartig gebogen. So gut bekannte paläozoische Gruppen wie die Platyceratoidea scheinen jeweils beiden Unterklassen zuzufallen. Auf jeden Fall ist die karbonische Gattung *Orthonychia* trotz fast identem Teleoconch nicht mit der triassischen Gattung *Pseudorthonychia* n. gen. zu vereinen, sondern konvergent entstanden. Cyrtoneritimorpha bestehen vom Ordovizium an, vom Devon bis zum Perm lebten sie mit den Cycloneritimorphen gemeinsam, und seit der Trias existieren nur noch die Cycloneritimorpha.

Addresses of the authors: Prof. Dr. Klaus BANDEL, Universität Hamburg, Geologisch-Paläontologisches Institut und Museum, Bundesstraße 55, D-20146 Hamburg, Germany, e-mail: <bandel@geowiss.uni-hamburg.de>. – Jiří FRÝDA, Czech Geological Survey, Klarov 3/131, 118 21 Praha 1, Czech Republic, e-mail: <fryda@cgu.cz>

### Introduction

Neritidae have several anatomical characters that distinguish them quite well from other gastropods (see FRETTER & GRAHAM 1962 for data and references). Their radula resembles that of the Archaeogastropoda (TROSCHEL 1856), and they have, therefore, usually been placed close to these or within these to representing one of their families or superfamilies. This was so even though their differences to usual types of archaeogastropods as found among the Trochoidea s.l. and Pleurotomarioidea s.l. had been stated quite early (BOURNE 1908). WENZ (1938) interpreted the Neritacea (= Neritoidea) to represent one of several superfamilies of the order Archaeogastropoda. KNIGHT et al. (1960) considered them to belong to the order Archaeogastropoda and here the superorder Neritopsina with mainly the Neritacea (= Neritoidea).

The taxon Neritimorpha was established by GOLIKOV & STAROBOGATOV (1975) as a new superorder of the subclass Pectinibranchia BLAINVILLE, 1814 of the class Gastropoda. In this frame, the Neritimorpha unite the superfamilies Neritoidea, Hydrocenoidea, Titiscanioidea, and with question mark also Cocculinoidea. This latter group of the cocculinids had already been placed with some reservations next to the Neritacea by THIELE (1931-35), and here it is still found in modern accounts on gastropod classification as that of PONDER & LINDBERG (1997). SALVINI-PLAWEN & HASZPRUNAR (1987) placed the Neritopsina (= Neritimorpha) in the Archaeogastropoda. Later, HASZPRUNAR (1993) again suggested to place the Neritimorpha and the architaenioglossate groups (Cyclophoroidea and Ampullarioidea) to the Archaeogastropoda which he considered to be a paraphyletic taxon.

BANDEL (1992b, 1997) used differences in the ontogeny of Gastropoda to distinguish different subclasses. These differences are reflected in the shape of the early ontogenetic shell which can be studied in living as well as in fossil species. Here, the development of the Neritimorpha is characterized by a typical, strongly convolute protoconch that includes a larval shell, quite in contrast to that of the Archaeogastropoda (including the orders Vetigastropoda and Docoglossa). This kind of neritimorph early ontogenetic shell is observed in fossil record from the Middle Devonian time onward. The independent position of the Neritimorpha was also noted recently by BIGGELAAR & HASZPRUNAR (1996) who characterized the large gastropod taxa according to the first cleavage patterns of their embryos. Accordingly, it was suggested that the Neritimorpha differ from the Docoglossa and Vetigastropoda and also from the Architaenioglossa. The later is placed close to other Caenogastropoda due to their ontogenetic pattern and the features of their radula. Thus, their conclusions are quite consistent with the concept of the Neritimorpha of BANDEL (1982) and BANDEL & GELDMACHER (1996).

In the modern Neritimorpha, the superfamilies Neritopsioidea, Neritoidea, Hydrocenoidea, and Helicinoidea are united. Of these, the Neritopsioidea have survived with only a few species in the tropical seas. Apparently, their refuge lies in submarine caves as found in coral reefs of the Indo-Pacific (KASE & HAYAMI 1992). The Neritoidea form the bulk of the marine, brackish and freshwater species found today. The Hydrocenoidea represent a rather uniform group of small sized land snails, and the Helicinoidea are a group of lung breathing, usually tropical land snails that show many shapes and sizes, but their relation to the Neritimorpha is quite unresolved (THOMPSON 1980).

The oldest undoubted evidence for the characteristic, strongly convolute early shell of the subclass Neritimorpha is known from the Triassic St. Cassian Formation (BANDEL 1992a). Up to now there is no absolutely safe evidence for the Palaeozoic representative of the subclass Neritimorpha that is based on the protoconch. One possible exception could be an ornamented larval shell from the Late Carboniferous of Germany described by HERHOLZ (1992) that very closely resembles the larval shell of *Naticopsis* from the Late Triassic St. Cassian Formation of the Alps (BANDEL 1992a, SCHWARDT, pers. comm.). Also there is the information on *Naticopsis* from the Early Carboniferous of Australia with a protoconch of about 1,5 smooth, tightly coiled whorls (YOO 1994). The family Plagiothyridae KNIGHT, 1956 represents a potential member of the subclass Neritimorpha (KNIGHT et al. 1960), and they had quite a number of species that lived during mid-Devonian and Carboniferous times.

Some Palaeozoic members of the superfamilies Neritoidea and Platyceratoidea were considered to be potential representatives of the Neritimorpha by BANDEL (1992a). Beside the general shell shape the presence of the thick calcitic outer shell layer is consistent with this placement. The thick calcitic outer layer of the members of the Carboniferous genus *Orthonychia* was described by BATTEN (1984a). Also the findings of the preserved colour patterns on Devonian platyceratids (YOCHELSON 1956; KRÍŽ & LUKEŠ 1974; YOCHELSON & KRÍŽ 1974; own observations) suggested the presence of the calcitic outer layer to be generally present among the platyceratids s.l.

## New model of classification of the subclass Neritimorpha

The discovery of the well preserved early shells in the members of the Palaeozoic superfamily „Platyceratoidea“ shows that this group unites gastropods with at least two types of protoconchs: a strongly convolute type among those that lived from the Triassic onwards and an openly coiled, fish hook-like type in a number of species occurring from the Ordovician to the Permian. In case of the Triassic members of the „Platyceratoidea“ with the here newly named genus *Pseudorhynchia* the protoconch is clearly of the type known among extant Neritimorpha (pl. 2 figs. 1-4). In case of the Carboniferous members of the „Platyceratoidea“ represented by *Orthonychia parva* (SWALLOW, 1858) the protoconch is of the same type (pl. 2 figs. 5-8) as found among older Palaeozoic gastropods of neritimorph shape here newly described as members of the family Vltavellidae. Both these types may, thus, be traced in the fossil record for more than 200 million years, and the changes noted in their shape within some genera and groups during this time are very minor. We, therefore, consider this character of the protoconch morphology to have a very high-level taxonomic significance. For this reason, we propose to divide the subclass Neritimorpha in two separate orders, Cycloneritimorpha and Cyrtoneritimorpha.

### Cycloneritimorpha n. ord.

**Diagnosis:** The members of this order of the Neritimorpha have a strongly convolute larval shell (BANDEL 1982: fig. 73; pl. 20 fig. 9; pl. 21 figs. 3-5, 10; 1992: figs. 1-3; BANDEL & RIEDEL 1998: figs. 4-7; BANDEL et al. 1997: fig. 1A, B, C) and here pl. 1 figs. 1-8; pl. 2 figs. 1-4.

**Comparison:** The members of the order Cycloneritimorpha n. ord. are distinguished from those of the order Cyrtoneritimorpha n. ord. in having a strongly convolute larval shell, while that of the later is openly coiled. The modern Cycloneritimorpha are represented by the superfamilies Neritopsioidea, Neritoidea, Hydrocenoidea, and probably also the Helicinoidea.

**Remarks:** Species belonging to the order Cycloneritimorpha n. ord. may be traced from the Recent back to at least the Triassic (i.e., more than 200 million years) where the strongly convolute larval shell of the Neritidae and Neritopsidae was documented by BANDEL (1992a). These data have since been confirmed and elaborated upon by SCHWARDT (pers. comm.). She found that about half of the more than 30 species of Neritimorpha that lived in the reefs of the Late Triassic Tethys Ocean now exposed in the Italian Dolomites belong to the Neritopsioidea and the other half to the Neritoidea. Neritopsioidea are probably also present in the Carboniferous as indicated by YOO (1994) and even in the mid-Devonian as found by HEIDELBERGER (pers. comm.). Most probably some genera which are usually considered to represent members of the family Platyceratidae like *Praenatica* PERNER, 1903 and *Visitor* PERNER, 1911 but also at least some species that are considered to belong to *Platyceras* CONRAD, 1840 as well as the Palaeozoic members of the families Neritopsidae and Plagiothyridae also belong to the order Cycloneritimorpha n. ord. If these observations can be confirmed, the order Cycloneritimorpha n. ord. has existed since late Early Devonian time and, thus, for about 400 million years.

PONDER & LINDBERG (1997) suggested that the shared protoconch morphology seen in the vetigastropods and the cocculinids is plesiomorphic and that of the neritopsines derived from that ancestral type. The initial neritopsine larval shell could be, according to their understanding, a highly modified one, because of intracapsular development with the incremental growth phase pushed back onto the mineralization stage. But this unusual interpretation, whatever it may actually express, does not take into account that it is not the neritopsine larval shell that can be interpreted as the modified case, if the cocculinids were really related to the Neritopsina (= Neritimorpha). On the contrary, the cocculinids would have to be the modified ones with strongly simplified protoconch of only one whorl. We know from all gastropod groups which have the potential of a planktotrophic larval stage that those species that have no planktotrophic larva simplify their early ontogenetic shell. This has been documented in many cases and is also evident within the Neritidae (BANDEL 1982, see here for references). The lecithotrophic development as found among the Neritimorpha is documented here with the neritopsid *Neritopsis parisiensis* (pl. 1 figs. 3, 4), the neritid *Theodoxus jordani* (SOWERBY, 1932) (pl. 1 fig. 8), and the hydrocenid *Georissa* BLANFORD, 1864 (pl. 1 fig. 7). All these have protoconchs that differ strongly from the protoconchs of archaeogastropods, like that of *Cocculina*. If PONDER & LINDBERG (1997) suggest an opposite development to explain their supposed close relation between cocculinids and neritids, they should present evidence for such unusual embryonic reversal.

The close relation that exists between the way in which ontogeny proceeds to the mode in which phylogeny occurred is known since HAECKELS (1874) observations, and this is certainly also the case in the Gastropoda. So, if there are two totally different modes of ontogenetic development, one with the potential of a shell bearing larva and the other without, than this must have consequences in taxonomy and systematic placing of the groups involved. Cocculinids have the mode of development observed in the Archaeogastropoda as defined by BANDEL (1991, 1997) including also the Docoglossa. These have no planktotrophic veliger, and they form no or only very little shell in addition to the primary shell before onset of the teleoconch (BANDEL 1982, 1998). Neritidae, in contrast, hatch from their spawn with at least the primary shell completed. Only afterwards they form a larval and, thus, secondary shell. Their ontogeny is more extended than that of the cocculinids before the teleoconch program is initiated in shell growth. It can, thus, be concluded that cocculinid and neritid relations are not closer than archaeogastropod and neritimorph relations in general.

### Superfamily Neritopsioidea RAFINESQUE, 1815

According to WENZ (1938), Neritopsioidea are characterized by their inner walls which are not resorbed, as it is the case in the Neritoidea, and by the calcareous operculum that is not spirally arranged as in the Neritidae.

#### Family Neritopsidae GRAY, 1847

**Description:** The globular shell has a little protruding spire and large last whorl. The inner lip of the aperture is broad and smooth and is formed by a broad callus. The inner walls of the shell are not resorbed, and the operculum is not spiral.

**Remarks:** BATTEN (1984b) expressed the opinion that during the Triassic seven species of the genus *Neritopsis* GRATELOUP, 1832 were present, during the Jurassic and Cretaceous there were 80 species and in the Tertiary 11 species. *Neritopsis*, according to BATTEN (1984b), is derived from the Permian genus *Trachydomia* MEEK & WORTHEN, 1866. Since mid-Devonian, 14 genera belonging to that group have formed which supposedly lived mostly during the time span Permian/Triassic. Since the begin of the Tertiary only representatives of *Neritopsis* have survived. This genus is based on the type-species *Neritopsis moniliformis* GRATELOUP, 1832 from the Miocene of the Paris Basin. It has a medium sized shell with a moderately protruding obtuse spire. Its last whorl is globose with evenly convex flanks. The orbicular aperture has a moderately thickened concave inner lip. Here, a quadrangular depression is present at its middle into which the opercular edge is fitted. The sculpture consists of thick granulated spiral cords that may be intersected by axial ribs and form reticulate ornament. The operculum is solid and trapeziform with a quadrangular projection at the adaxial side. The protoconch is simple and smooth.

The protoconch can be that of a planktotrophic larva as is the case in the individual of *Neritopsis radula* LINNÉ, 1857 from the Indo-Pacific Ocean (Mauritius) (pl. 1 fig. 1, 2) or can be formed by individuals that hatch ready to metamorphose as was the case in *Neritopsis parisiensis* DESHAYES, 1864 from the Eocene of the Paris Basin (pl. 1 figs. 3, 4). The difference between these two lies in the number of whorls that are present. In case of the planktotrophic *N. radula* the protoconch consists of more than two whorls, while in case of the lecithotrophic *N. parisiensis* it consists of a little more than one whorl.

The superfamily Neritopsioidea contains the Neritopsidae, but probably also two families with rather peculiar teleoconch, as are the Pseudorthonychiidae n. fam. and the Cortinellidae BANDEL, 1998, both from the St. Cassian Formation of the Dolomites (Italian Alps). While the latter has a planspirally coiled small teleoconch, that of the former is cap-like in shape.

#### Family Pseudorthonychiidae n. fam.

**Diagnosis:** The family is composed of gastropods with a tightly coiled neritimorph larval shell composed of aragonite and a platyceratiform horn-like teleoconch that is largely composed of a thick calcitic outer shell layer. The genus on which the family is based is *Pseudorthonychia* n. gen. from the Late Triassic of the Dolomites (Italian Alps).

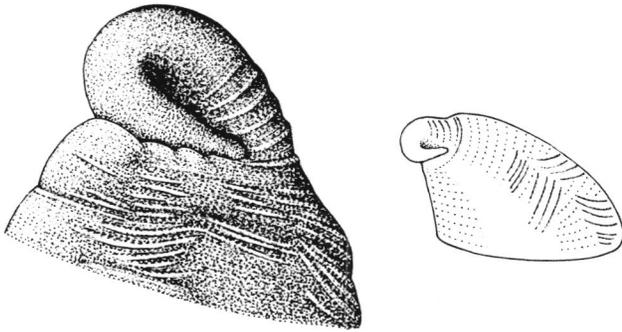
**Remarks:** The Palaeozoic parasitic gastropods united in the family Platyceratidae have also been considered by BANDEL (1992a) to belong to the subclass Neritimorpha based on his discovery of a neritimorph protoconch attached to the Triassic *Orthonychia alata* (LAUBE, 1869). But since a closer relative of the type species of *Platyceras* presented by *Orthonychia parva* has non-neritimorph type of protoconch (as shown below), *Pseudorthonychia* has to be placed in a different taxon, as proposed here.

#### *Pseudorthonychia* n. gen.

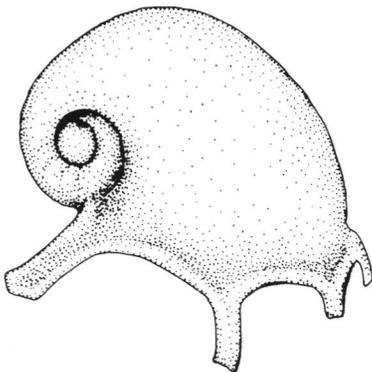
**Type species:** Triassic *Capulus alatus* LAUBE, 1869 from the St. Cassian Formation.

**Diagnosis:** The *Orthonychia*-like cap-like teleoconch is connected with a closely coiled protoconch of the neritimorph type. The convolutedly coiled smooth larval shell has apertural thorns and ends abruptly against the rough teleoconch.

**Comparison:** The characteristic larval shell with 6 thorn-like projections (BANDEL 1992a: figs. 1, 2) (pl. 2 figs. 2-4) may easily distinguish this tentatively monotypic genus from the Palaeozoic genus *Orthonychia* HALL, 1843 which has an openly coiled fishhook-like early whorl (see below) (pl. 2 figs. 5-8, pl. 3. figs. 1, 2). *Pseudorthonychia* resembles *Platyceras* and *Orthonychia* in the shape and construction of the teleoconch, but differs from these by having the protoconch of the *Neritopsis* type with closely coiled spherical larval shell.



Text-fig. 1: Drawing of *Orthonychia parva* (SWALLOW, 1858) from the Pennsylvanian (Late Carboniferous) of Saint Louis (Missouri, USA).



Text-fig. 2: The protoconch of *Pseudorthonychia alata* (LAUBE, 1869) is coiled and provided with apertural spines, shown in a sketch of a fully grown pediveliger shell.

***Pseudorthonychia alata* (LAUBE, 1869) n. comb.**

Pl. 2 figs. 1-4

According to BANDEL (1992a: figs. 1, 2 a-h, 3a) and ZARDINI (1978: pl. 24 figs. 3-7) *Pseudorthonychia alata* is a small limpet (3 mm high and 1.5 mm wide) with tightly coiled early ontogenetic shell and teleoconch with whorls not in contact. The apex of the limpet is formed by the larval and embryonic shell that consists of at least 2.5 whorls. These differ in shape, sculpture and composition from the following limpet-like teleoconch. The protoconch measures

0.7 mm in diameter, is spherical to naticoid in shape with smooth, well rounded and strongly convolute whorls. The earliest whorl is largely covered by the following whorl. The margin of the shell of the fully grown planktotrophic veliger (pediveliger) is thickened and forms 6 thorn-like projections. The teleoconch is horn-shaped forming a weak open half dextral coil. The outer lip of the aperture is evenly rounded while the inner lip is concave forming a broad groove behind it, separated from the outside by sharp carinae. Shell additions to the aragonitic protoconch consist of thick calcitic growth increments of the limpet shaped teleoconch. Ornament consists of even collabral growth lines.

**Remarks:** *Pseudorthonychia alata* from the Late Triassic St. Cassian Formation near Cortina d'Ampezzo demonstrates the characteristic inner flattening accompanied by marginal carinae (pl. 2 fig. 3). A similar shape was noted by TYLER (1965) in the Carboniferous *Platyceras indianense* MILLER & GURLEY, 1879 having a groove that runs from the apertural margin to the apex of the shell. TYLER suggested this species to represent a new subgenus *Euthyrhachis* TYLER, 1965, that was suggested to differ from *Orthonychia* s.s. from the Early Carboniferous by this keel accompanied groove. It is, therefore, evident that there exists a close convergence in teleoconch shape regarding *Orthonychia* and relatives from the Carboniferous and Permian, and *Pseudorthonychia* n. gen., while the protoconch clearly distinguishes both taxa. Caution is suggested, though, since the shape of the protoconch of many of the Carboniferous and Permian platyceratids is still unknown.

**Superfamily Neritoidea RAFINESQUE, 1815**

Most representatives of the family Neritidae RAFINESQUE, 1815 have solid shells with outer calcitic and inner aragonitic layers. The inner lip usually forms a large callus that covers more or less the base, and its columellar edge commonly bears teeth and folds. The operculum is calcareous and usually has a peg-like projection which inserts into the muscle of the snail. The protoconch of all species with planktotrophic larva is rounded in shape. The inner walls of the protoconch are resorbed and also the inner walls of most teleoconchs are usually dissolved. The genera *Nerita* and *Neritina* have many species. The history of the group is well established back into the Late Triassic.

BANDEL et al. (1997: fig. 1, A-C) presented a generalized description of the early ontogenetic shell of Neritidae. Accordingly, the larvae are able to swim with the aid of a quadrilobated velum. This velum is not lost by detachment but is resorbed when metamorphosis is triggered off. The larval shell is globular to egg-shaped and varies specifically in diameter from about 0.5 to 0.8 mm in different taxa when they are ready to metamorphose. The initial embryonic whorl measures (interspecifically) 0.1 to 0.25 mm across. The number of convolute whorls is difficult to estimate, but up to 2.5 larval whorls have been observed. Neritid larval shells have also been described by ROBERTSON (1971), SCHELTEMA (1971), LAURSEN (1981), BANDEL (1982, 1991, 1992a, b), BANDEL & RIEDEL (1998), and here in pl. 1 figs. 5, 6.

The Neritoidea hold families like the Neritidae and Neritiniidae with the genus *Neritina* LAMARCK, 1816 and its relations. The family Deianiridae with the Cretaceous *Deianira* STOLICZKA, 1859 belongs here (BANDEL & RIEDEL 1994: pl. 2 figs. 1-6, pl. 3 figs. 1-8), as well as the Neri-

tiliinae BAKER, 1923 with *Neritilia* MARTENS, 1879 representing minute species living in estuaries (BANDEL & RIEDEL 1998: fig. 6A, B), others, like the limpet family Phenacolepadidae PILSBRY, 1891 based on the genus *Phenacolepas* PILSBRY, 1891, are found on sea grass but also in the deep sea (CLARKE 1989; BECK 1992).

Members of the family Hydrocenidae TROSCHER, 1856 with species of *Hydrocena* PFEIFFER, 1847 are land snails. It is uncertain, whether or not representatives of the Hydrocenidae are related to the Neritidae. Their protoconch is that of a lecithotrophic neritimorph as is illustrated in case of *Georissa* (pl. 1 fig. 7). Whether or not the representatives of the superfamily Helicinoidea THOMPSON, 1980 (order Helicinina THOMPSON, 1980) that holds several families of terrestrial gastropods are related to the Neritoidea is uncertain. THOMPSON (1980) suggested that the Helicinoidea are no relatives of the Neritoidea, and NAKAMURA (1986) found a different number of chromosomes, 18 pairs instead of 11-14 pairs in the Neritidae.

### Cyrtoneritimorpha n. ord.

**Diagnosis:** The neritimorph teleoconch shape includes naticiform (*Vltaviella*-type) to completely disjunct (*Orthonychia*-type) forms all of which are associated with the characteristic, openly coiled, fishhook-like protoconch (KNIGHT 1934: pl. 25, YOCHERSON 1956: pl. 23 figs. 27-29, FRÝDA & MANDA 1997: pl. 9; here: pl. 2 figs. 5-8, pl. 3 figs. 1-8).

**Comparison:** The characteristic fishhook-like protoconch distinguishes the members of the order Cyrtoneritimorpha n. ord. from that of the order Cycloneritimorpha n. ord. The latter have a strongly convolute larval shell. The straight primary shell connected to the hook-like larval shell distinguishes Cyrtoneritimorpha n. ord. from members of the superfamily Peruneloidea FRÝDA & BANDEL, 1997. The latter also had openly coiled protoconchs, but their embryonic or primary shell is openly coiled with dextral trend. Also, gastropods united in the subclass Euomphalomorpha have an openly coiled early shell (BANDEL & FRÝDA 1998). But protoconchs of Cyrtoneritimorpha n. ord. differ from those of the Euomphalomorpha in being trochospirally coiled instead of planispirally coiled. They also are distinguished by their fishhook-like shape with much smaller initial shell portion contrasting to the bulbous, egg-shaped early shell of the Euomphalomorpha.

**Remarks:** Species of the Cyrtoneritimorpha n. ord. have lived from the Early Ordovician to the Late Permian. The characteristic protoconchs are known from the Ordovician (BOCKELIE & YOCHERSON 1979, DŽIK 1994), and the Silurian (FRÝDA 1998a, b). Connected to their teleoconchs they are known from the Devonian (FRÝDA & MANDA 1997), the Carboniferous (KNIGHT 1934), and the Permian (YOCHERSON 1956). The characteristic protoconch retained its fishhook-like shape for 250 million years and, thus, this shell character must be considered as very significant for higher taxonomy. We found two distinct groups among the Cycloneritimorpha n. ord. which we establish as families, the Orthonychiidae and the Vltaviellidae.

Cyrtoneritimorph als well as perunelomorph protoconchs are relatively common in some Early Ludlowian carbonate layers of the Prague Basin (FRÝDA 1998a, b). Usually, the shells represent fully grown protoconchs at the

stage in which the onset of the teleoconch would follow and, thus, the spirally grown shell in case of the Vltaviellidae. The small size of the initial portion of the protoconch and its cup-like rounded shape indicates that it represents the shell of the veliger hatching from the egg-mass. Modern species that belong to the primitive Caenogastropoda and have an ontogeny that includes a planktotrophic larva hatch with a shell of about 0,1 mm in size (BANDEL 1975). Taxa of the Neritimorpha with a similar development also have about the same size when they are hatching (BANDEL 1982). In the later case this shell is only weakly curved, resembling an egg with its top cut off slightly obliquely. This shape resembles that found in the embryonic shell of the cyrtoneritimorph species as well (pl. 2 fig. 8; pl. 3 fig. 8). The following shell in modern species with planktotrophic development is usually a tightly and spirally coiled larval shell (pl. 1 figs. 2, 5, 6).

In contrast, Early Devonian and older representatives of the Cyrtoneritimorpha n. ord. display spiral coiling with whorls touching each other in the teleoconch only. The larva produced an openly coiled shell. When the amount of shell produced by the ancient larva is compared with that secreted by a modern species with planktotrophic larva, the difference lies only in the mode of coiling, but not in the amount of tubular shell that is added to the embryonic shell during larval life. When metamorphosis to benthic life occurs, the embryonic shell has been surrounded by one to two larval whorls.

The shells found in the Kopanina Formation (Ludlow) of the Prague Basin represent fully grown larval shells as they would be ready to metamorphose from pelagic to benthic life (pl. 3 fig. 8). If these openly coiled larval shells would be wrapped tightly around the embryonic shell they would have the dimensions found among modern neritimorphs with a larval shell. Planktotrophic gastropod larvae need to find the correct type of environment to be able to metamorphose successfully. But many larvae have to change their life style from the pelagic mode to the benthic mode in an environment in which the benthic snail can not survive. But during transition and metamorphosis the shell is solidly calcified in order to provide the benthic young with a fitting exoskeleton for survival. This solid calcification of the shell is a prerequisite for a high fossilization potential. In modern deep sea sediments larval shells of animals actually having their living environment in the shallow sea are commonly found together with the shells of typically pelagic animals like pteropods or globigerinids. Obviously, gastropods with planktotrophic larvae in Ordovician to Devonian times behaved in a similar way, calcified their shells to be capable to cope with a benthic life, which in the wrong place did not continue but end, therefore, before teleoconch could be added. Once formed many such shells could fossilize since they were calcified. We find layers with the larval shells of benthic gastropods very common but of species that actually conducted their adult life somewhere else. The occurrence of numerous fully grown protoconchs of cyrtoneritimorph gastropods and the absence of the adults belonging to these as is found in several Early Ludlowian rocks of the Prague Basin can, thus, be explained.

Up to now, only very few of the early shells (protoconchs) can be combined with a teleoconch taxon. Among them are the Carboniferous *Orthonychia parva* (SWALLOW, 1858), the Permian *Orthonychia* sp., both from North America, and the Devonian *Vltaviella reticulata* FRÝDA &

MANDA, 1997 from the Prague Basin. These three momentarily are the only species known to have a cyrtoneritimorph protoconch (KNIGHT 1934, YOCHELSON 1956, BANDEL 1997, FRÝDA & MANDA 1997), but it is expected that many more of them will eventually be discovered.

Orthonychiidae n. fam.

**Diagnosis:** Shells are openly coiled and cap-like with a fishhook-like protoconch of the Cyrtoneritimorpha.

**Type genus:** *Orthonychia* HALL, 1843.

**Comparison:** Shells of members of Orthonychiidae differ from those of the Vltaviellidae by their completely disjunct coiling.

**Remarks:** Very rarely Palaeozoic gastropods are preserved with their protoconch still complete. Exceptions are the Carboniferous *Orthonychia parva* (SWALLOW, 1858) (see KNIGHT 1934: pl. 25 fig. 1), and the Permian *Orthonychia* sp. (see YOCHELSON 1956: pl. 23 figs. 27-29). As noted by YOCHELSON (1956: 259) the same type of protoconch may also be present in the Permian *Orthonychia bowsheri* YOCHELSON, 1956. In the majority of shells, the protoconch is lost and a blunt apex is preserved only, as was noted in many representatives of *Orthonychia* species that have been studied by the authors in different collections. YOCHELSON (1956) correctly suggested that this openly coiled, fishhook-like protoconch represented a free swimming or at least free moving stage during the life of the *Orthonychia*, which lived attached as parasite on crinoids.

*Orthonychia parva* (SWALLOW, 1858) from the St. Louis outlier of the Des Moines group in the Pennsylvanian of Missouri in USA has the typical larval shell, as is shown in pl. 2 figs. 5-8 and pl. 3 figs. 1, 2. It is some 0.6 or 0.7 mm in maximum diameter with the embryonic shell about 0.1 mm long and 0.06 mm wide. A constriction delimits this embryonic shell from the larval shell (pl. 2 fig. 8). The larval shell is conical for the first 0.45 mm and from there it curves into an even spire with a rather rapid increase in whorl diameter. Before the larval shell ends six axial ribs ornament the shell, the last one forming the margin of the pediveliger (pl. 2 fig. 8, pl. 3 fig. 2). With the onset of the teleoconch the shell width increases to grow as a cap-like shell (pl. 2 figs. 5-7, pl. 3 fig. 1).

Vltaviellidae n. fam.

**Diagnosis:** The teleoconch is small, globular and naticiform and connected to an openly coiled, cyrtoneritimorph protoconch.

**Type genus:** *Vltaviella* FRÝDA & MANDA, 1997.

**Comparison:** Presently only the genus *Vltaviella* can be placed in the family Vltaviellidae, since protoconch morphology of many other species possibly belonging here are not yet known. On the other hand, many protoconchs are known to which the teleoconchs still have to be discovered. *Orthonychia parva* also has the cyrtoneritimorph protoconch, but its teleoconch is disjunctly coiled and limpet-like. Species of the naticiform genera *Praenatica* and *Cancellator* from the Silurian and Devonian appear to have closely coiled early whorls and, thus, seem to have a non cycloneritimorph protoconch. If this can be confirmed, they do not belong to either the Orthonychiidae or Vltaviellidae.

The relatively common occurrence of protoconchs of cyrtoneritimorph-type in the fossil record (BOCKELIE & YOCHELSON 1979, DŽIK 1994, FRÝDA & MANDA 1997) suggests that there should be many more taxa in that systematic unit, which have not yet been recognized due to their preservation, that does not allow to study the first whorl of the shell.

*Vltaviella* FRÝDA & MANDA, 1997

**Diagnosis:** The small, globular, naticiform shell has an openly coiled initial whorl. The initial part of the first whorl is formed by an elongate cup with a diameter of about 0.06 mm at its apex and 0.10 mm at the end of the protoconch and the start of the dextral teleoconch. The diameter of the opening between the inner sides of the first whorl is about 0.30 mm. The teleoconch consists of at least three whorls which are rapidly expanding in diameter. Ornament consists of spiral and collabral elements that form a regular reticulate pattern. The outer apertural lip is oblique.

**Type species:** *Vltaviella reticulata* FRÝDA & MANDA, 1997 from the early Lochkovian (Early Devonian) of the Prague Basin (pl. 3 figs. 3-6).

**Remarks:** The naticiform shell shape of *Vltaviella* resembles those found commonly among members of the Neritoidea, but the characteristic shape of the protoconch distinguishes it from all known gastropod genera. Similar protoconchs are expected to occur on other Paleozoic gastropod species but up to now it is recognized in *Vltaviella reticulata* only (FRÝDA & MANDA 1997: pl. 2). The protoconch shape is quite constant, and numerous protoconchs were found without being attached to their teleoconchs in the same beds. This suggests a high mortality that occurred when the openly coiled protoconch was succeeded by the closely coiled teleoconch (FRÝDA 1998a, b). Since this was the stage of metamorphosis in which larval life changed into benthic life such a mortality is understandable and can also be observed among modern species in the same transitional phase of life, where freshly settling larvae are highly endangered by death.

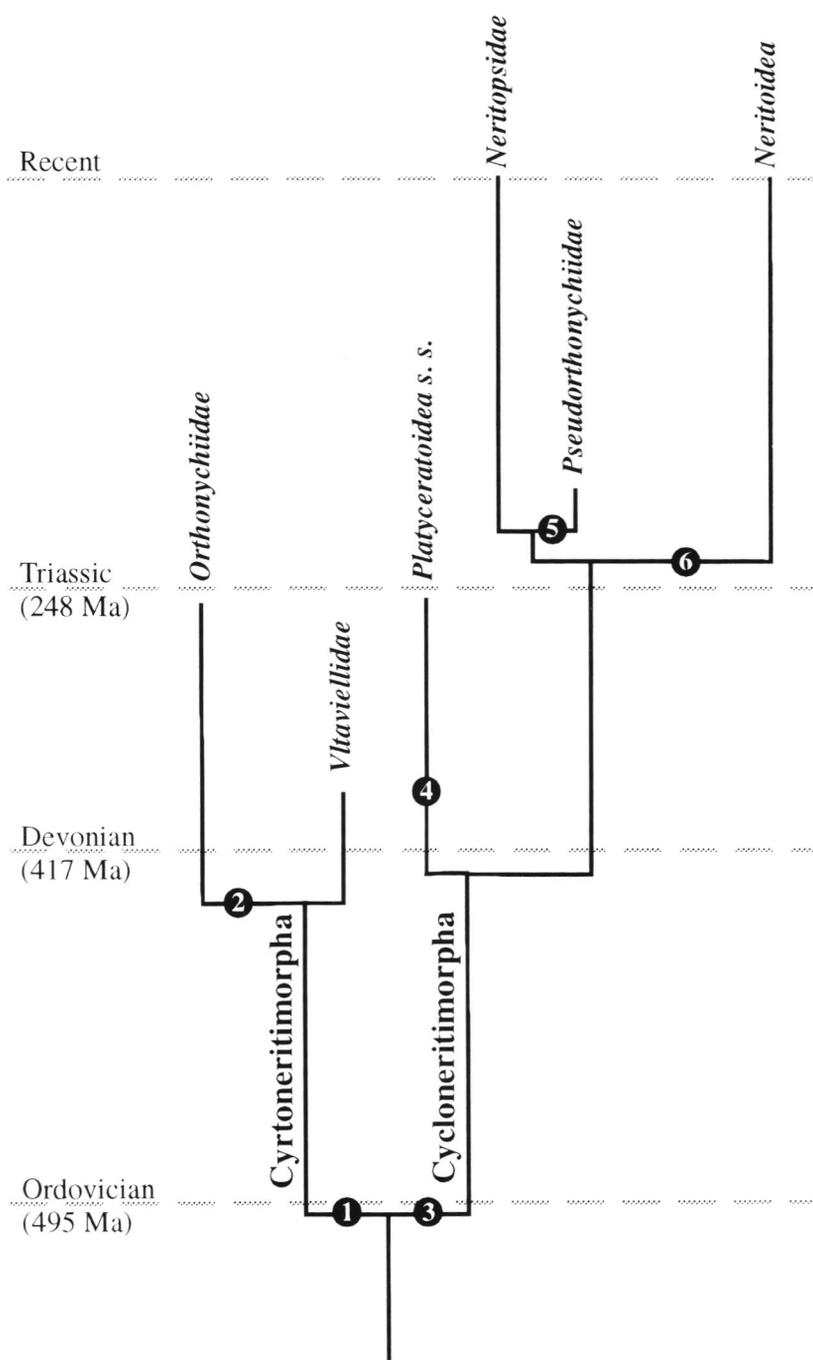
The protoconch of *Vltaviella reticulata* resembles in shape that of *Orthonychia parva* but is more regularly curving and has a non ornamented larval shell. The transition into the teleoconch is more indistinct, since there is no change in the type of increase in whorl diameter (pl. 1 figs. 5-7).

Unresolved Neritimorpha:

Superfamily Platyceratoidea HALL, 1859

**Remarks:** KNIGHT et al. (1960) placed the superfamily Platyceratoidea together with the superfamilies Microdomatoidea, Anomphaloidea, Oriostomatoidea, and Trochoidea in the suborder Trochina COX & KNIGHT, 1960 of the Archaeogastropoda.

The genus *Platyceras* is based on the type species *Platyceras vetusta* (SOWERBY, 1829) that was described clearly by KNIGHT (1941). It lived during the Early Carboniferous in a shallow warm sea the deposits of which are now exposed in Queens County, Ireland. The protoconch is not preserved in the holotype of *Platyceras vetusta* as was noted by WENZ (1938: fig. 480). KNIGHT (1941: pl. 88 fig.



Text-fig. 3: The cladogram depicts the assumed course of evolution of the Neritimorpha. It started out with a hypothetical neritimorph ancestor that developed an openly coiled larval shell (1) during the early Ordovician. The Vltaviellidae represent those species of the Cyrtoneritimorpha that have a normally, dextrally coiled teleoconch. An unknown group of these developed limpet-like forms (2) that survived with the Orthonychiidae up the Permian end-crisis. During the Ordovician or Silurian a group began to coil the protoconch in a tight convolute helicospire (3) forming the Cycloneritimorpha branch of the Neritimorpha. Possibly with the Platyceratoidea s. s. a branch of limpet-like parasites developed (4) during the early Paleozoic, which in contrast to the Orthonychiidae may have had a coiled protoconch. The Neritopsidae represent Cycloneritimorpha that have survived from Devonian to modern times with little change. During the Triassic the Pseudorthonychiidae developed with convergent limpet-like teleoconch to that of the Orthonychiidae and Platyceratoidea, but with a neritopsid protoconch (5). During late Paleozoic or early Triassic the internal walls of protoconch and teleoconch were dissolved giving rise to the Neritoidea (6).

1a-d) chose a paratype that clearly shows the tightly coiled juvenile whorls, but not the protoconch. KNIGHT (1934) and WENZ (1938) distinguish two genera among those platyceratids that are limpet-shaped, *Platyceras* CONRAD, 1840 with the 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 somewhat blurred by KNIGHT et al. (1960) who considered both types to represent subgenera of the genus *Platyceras*, together with some other forms like the totally coiled species of *Visitor* PERNER, 1911 and *Praenatica* PERNER, 1903. In case of the latter two it is not really safe to assume that they have

carried out the parasitic mode of life on pelmatozoans that is connected to Platyceratidae s.s. *Praenatica* occurs rather commonly in the reefoid and lagoonal Early Devonian limestones of the Prague Basin and grew to large size. It may well have lived like modern *Nerita* by scraping algal growths from hard substrates.

KNIGHT et al. (1960) considered the Platyceratoidea to represent an independent superfamily of the Trochina and, thus, the suborder of the Archaeogastropoda which bear most non-slit-bearing species. Within their frame they included also families like Holopeidae that contain genera like *Araeonema* KNIGHT, 1933 and *Yunnania* MANSUY, 1912 which have been demonstrated to represent Archaeogastropoda with nacreous shell layer and can be considered close to the modern Trochoidea (BANDEL 1993). The same applies to species of the Carboniferous Microdomatidae and the Triassic Anomphalidae which have turned out to represent nacreous archaeogastropods (BANDEL 1993). Also, the Early Devonian *Holopea kettneri* FRÝDA & BANDEL, 1997 has an archaeogastropod protoconch. Other members of the family Holopeidae like *Gyronema* ULRICH & SCOFIELD, 1897 and *Rhabdotocochlis* KNIGHT, 1933 are better

placed in the subclass Archaeogastropoda as was suggested by BANDEL & GELDMACHER (1996).

Many members of the platyceratids had a rather specialized life on pelmatozoans. Ordovician platyceratids of the genera *Cyclonema* HALL, 1852 and *Naticonema* PERNER, 1903 have been found to have settled on different portions of the pelmatozoan body, while from Devonian onward they have usually been found attached to the anal opening of the Crinozoan (MEYER & AUSICH 1983). The later authors had the opinion that platyceratids were coprophagous and, thus, just represented commensals and no parasites. But ROLLINS & BREZINSKI (1988) noted on Lower Carboniferous crinoids that those specimen serving as host to *Platyceras* were smaller than those free of the gastropod. They concluded that platyceratids, therefore, represented parasitic gastropods. The rich diversification of the platyceratids reflects the species richness of the crinoids during Palaeozoic time and their decline resulted in the disappearance of the parasitic snails. Even pelagic crinoids like the free floating crinoid *Scyphocrinites* has its parasite with *Orthonychia elegans* (ZITTEL, 1881) according to HORNY (1964).

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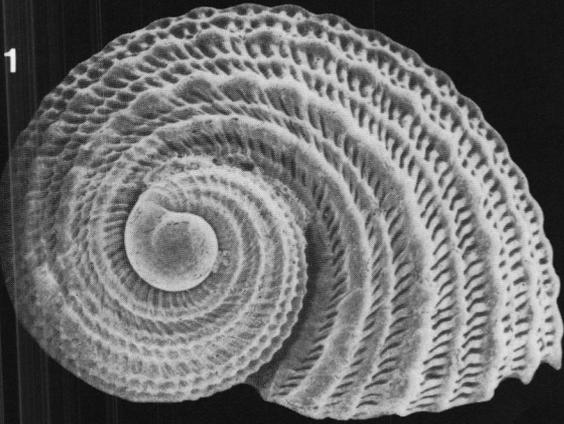
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## Plate 1

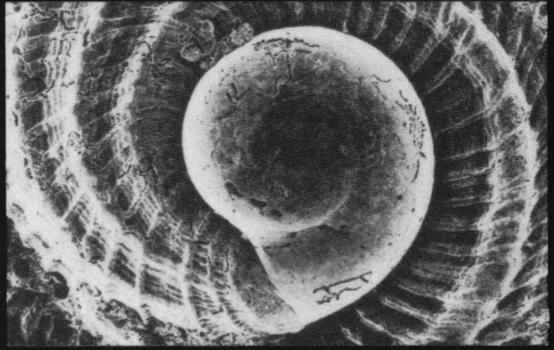
### Gastropoda of the subclass Neritimorpha

- Fig. 1: Apical view of the juvenile teleoconch of *Neritopsis radula* LINNÉ, 1857 from Mauritius in the Indo-Pacific Ocean. The shell measures 3 mm across.
- Fig. 2: The detail to fig. 1 of *Neritopsis radula* shows its 0.55 mm wide protoconch that consists of more than two whorls of tightly convolute shell.
- Fig. 3: Apical view of a 3 mm wide juvenile shell of *Neritopsis parisiensis* DESHAYES, 1864 from the Eocene of the Paris Basin with protoconch seen in detail in fig. 4.
- Fig. 4: The same *Neritopsis parisiensis* as in fig. 3 with the 0.4 mm wide protoconch that consists only of about one whorl and has been formed during a lecithotrophic embryogenesis.
- Fig. 5: The juvenile shell of *Neritina* LAMARCK, 1816 from an estuary of Bali (Indonesia) has a 0.4 mm wide smooth protoconch consisting of 3 whorls which are so tightly coiled that they cover each other to a large degree.
- Fig. 6: The rounded protoconch of *Neritina* LAMARCK, 1816 from an estuary of Cebu (Philippines) is well distinguished from the teleoconch and bears a last rounded marginal addition to its shell formed by the fully grown veliger. The shell is ornamented by fine axial striation and consists of 3.5 whorls that overlap onto each other strongly.
- Fig. 7: The protoconch of *Georissa* BLANFORD, 1864 from forest litter near Manila (Philippines) measures 3.5 mm across and is the result of a yolk-rich embryonic development, due to which the shell became simplified.
- Fig. 8: The shape of the initial 0.25 mm wide first whorl of the protoconch of *Theodoxus jordani* (SOWERBY, 1932) from a freshwater spring in Jordan reflects its lecithotrophic development due to nurse-egg feeding.

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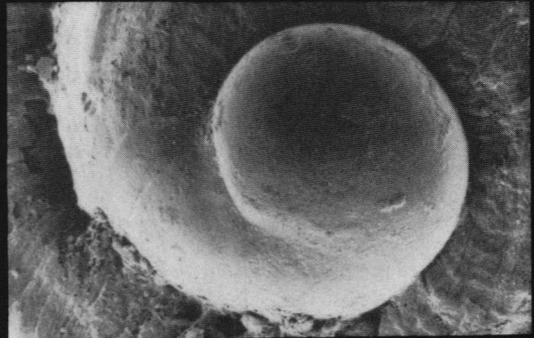
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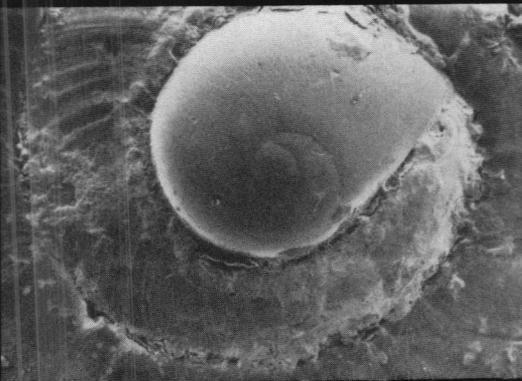
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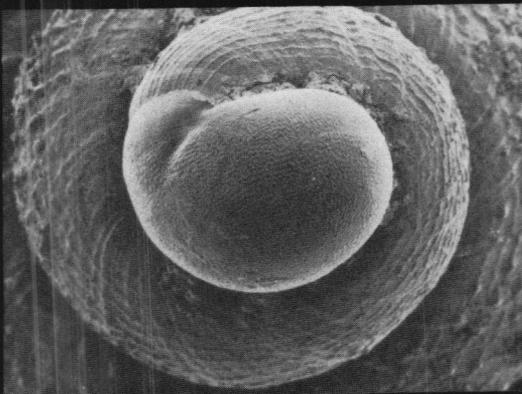
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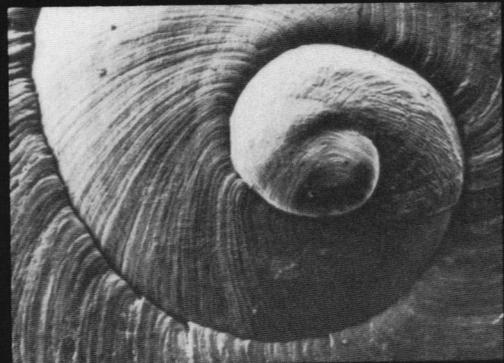
6



7



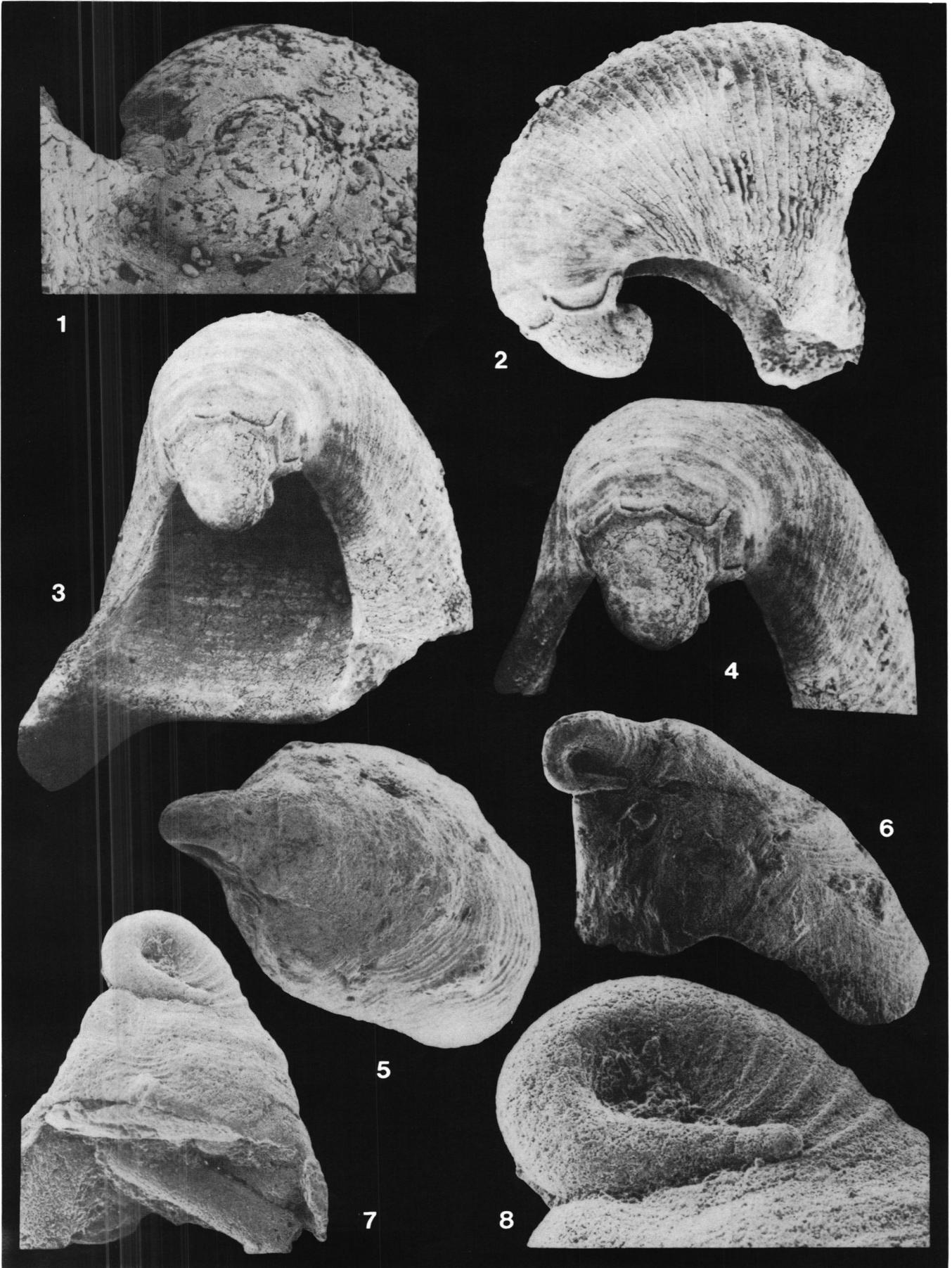
8



## Plate 2

### Gastropoda of the subclass Neritimorpha

- Fig. 1: The protoconch of *Pseudorthonychia alata* (LAUBE, 1869) n. comb. is shown as detail to fig. 2. The tightly coiled larval shell measures 0.2 mm in diameter of its first whorl.
- Fig. 2: *Pseudorthonychia alata* (LAUBE, 1869) n. comb. from the Late Triassic St. Cassian Formation in side view of the same specimen that is shown in figs. 3 and 4.
- Fig. 3: *Pseudorthonychia alata* from the Italian Dolomites of Cortina d'Ampezzo seen in apical view with the protoconch above the concave posterior shell front. The shell is 5 mm high.
- Fig. 4: The same shell of *Pseudorthonychia alata* as in figs. 1-3 with the protoconch bearing spines at its apertural edge and a width of about 0.5 mm.
- Fig. 5: Apical view of *Orthonychia parva* (SWALLOW, 1858) from the St. Louis outlier of the Des Moines group in the Pennsylvanian of Missouri. Apical view of 3 mm wide shell.
- Fig. 6: *Orthonychia parva* with the same shell as in fig. 5 seen from the side. The protoconch forms a hook on the cap-like teleoconch.
- Fig. 7: *Orthonychia parva* from the same locality as in fig. 1 with individual seen from the posterior side with the protoconch (detail in fig. 8) placed on the rounded cap-like teleoconch. The juvenile shell is 1.7 mm high.
- Fig. 8: *Orthonychia parva* has a rounded embryonic shell, a conical early larval shell and an axially ornamented late larval shell. The protoconch measures about 0.7 in largest diameter.



### Plate 3

#### Gastropoda of the subclass Neritimorpha

- Fig. 1: *Orthonychia parva* (SWALLOW, 1858) from the St. Louis outlier of the Des Moines group in the Pennsylvanian of Missouri. Lateral view of 2 mm wide shell.
- Fig. 2: *Orthonychia parva* with the same shell as in fig. 1 seen with the hook-like protoconch in detail.
- Fig. 3: Holotype of *Vltaviella reticulata* FRÝDA & MANDA, 1997 from the *Monograptus uniformis* graptolite biozone of the Lochkov Formation (Early Devonian) of the Prague Basin. The shell is 2.5 mm wide.
- Fig. 4: Oblique view of the same shell as in fig. 3 showing the reticulate shell ornamentation and openly coiled protoconch.
- Fig. 5: Oblique view of the paratype of *Vltaviella reticulata* with the openly coiled first whorl that is 0.7 mm wide.
- Fig. 6: Apical view of the same shell as in fig. 5
- Fig. 7: Isolated protoconch of *Vltaviella reticulata* with the open coiling visible. The maximum diameter of the shell is 0.7 mm.
- Fig. 8: Cyrtoneritomorph protoconch from the lower part of the Kopanina Formation (Late Silurian, Ludlow) of the Pague Basin. The shell measures 0.7 mm in largest diameter.

