

Higher classification of Paleozoic gastropods inferred from their early shell ontogeny

Vyšší klasifikace paleozoických gastropodů
odvozená z ontogeneze jejich rané schránky
(Czech summary)

(7 text-figs.)

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The presence of six natural groups (Amphigastropoda, Archaeogastropoda, Mimospirina, Cyrtoneritimorpha, Euomphalomorpha, and Perunelomorpha) were revealed among Silurian and Devonian gastropods of the Prague Basin (Czech Republic) on the basis of their protoconch morphology. The nature of the early shells in the core genus *Bellerophon* demonstrates that the Amphigastropoda does not belong to the subclass Archaeogastropoda and that it forms a long-lived (Cambrian through Triassic), independent molluscan group. The very small size of the bilaterally symmetrical early shell of *Bellerophon* (Amphigastropoda) indicates the presence of a planktotrophic larval stage. The higher taxonomic position of the Cambro–Devonian Mimospirina, uniting the Paleozoic gastropods with sinistrally coiled shells bearing a large sinistrally coiled, non-archaeogastropod protoconch, is still open. The discovery of archaeogastropod-type protoconchs in Early Devonian gastropods indicates that the Archaeogastropoda have had the same early ontogenetic pattern for at least 400 Ma (Devonian to Recent) and represent a very old, independent gastropod group. The Early Ordovician–Late Permian members of the order Cyrtoneritimorpha (Neritimorpha) with their characteristic fish hook-like protoconch probably gave rise to the modern Cycloneritimorpha (Neritimorpha). The Euomphalomorpha with a cyrtoconic and planispiral openly coiled protoconch form an independent gastropod group, known only from the Paleozoic (Cambrian–Permian). The Early Ordovician–Early Devonian members of the order Perunelomorpha, with an open, trochospiral protoconch, evolved larvae which secreted their typical larval shell. The Perunelomorpha may represent an ancestral group of the Caenogastropoda and Heterostropha. The uncoiled protoconchs found in Cyrtoneritimorpha, Euomphalomorpha and Perunelomorpha represent a very old shell feature. The higher gastropods (Caenogastropoda, Heterostropha, and Neritimorpha), as well as the extinct Euomphalomorpha, may have evolved from a common ancestor with an uncoiled tubular shell, and thus, not directly from the Paleozoic Archaeogastropoda and/or Amphigastropoda.

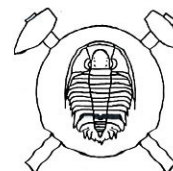
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Introduction

The higher classification of Paleozoic gastropods has traditionally been based only on the evaluation of their teleoconch characters (Wenz 1938–1944, Knight et al. 1960). Unfortunately, as shown by many studies of living gastropods, the similarities in their teleoconch characters are often a result of shell shape convergence in unrelated gastropod groups. Thus, the morphological characters of teleoconchs have only limited or no significance for the higher classification of gastropods. In contrast to Paleozoic gastropods, the classification of modern gastropods has also used their anatomical and biochemical characters, as well as data on their early shell ontogeny (e.g., Haszprunar 1988; Golikov – Starobogatov 1975; Ponder – Lindberg 1997). The zoological classification of modern gastropods can also be used successfully for fossil gastropods of Cenozoic and Mesozoic age. However, the Paleozoic gastropod fauna seems to be very different from that of the post-Paleozoic. These differences have been emphasized by the number of extinct higher taxonomic categories like the Bellerophontina, Macluritina, Euomphalina, and Paragastropoda, which have been established for Paleozoic gastropods. The relationships of these megataxa to extant gastropod groups are uncertain and often mysterious. Recent gastropods have been placed in one of four gastropod megataxa

(=subclasses), Archaeogastropoda, Neritimorpha, Caenogastropoda, and Heterostropha. Each of these modern subclasses may be characterized by its typical early shell ontogeny. This character is the most important and often only undoubted key for their determination in the fossil record.

On-going work on Silurian and Devonian gastropods, focused also on their protoconch morphology, has revealed important new data for their higher classification (Frýda 1995, 1997, 1998a–e, 1999a, b; Frýda – Bandel 1997; Frýda – Blodgett 1998; Frýda – Manda 1997; Bandel – Frýda 1996, 1998, 1999). These data were obtained mainly by detailed study of rich gastropod material coming from Devonian strata of the Czech Republic, Germany and Alaska. My own research on these gastropods has shown that localities belonging to the *Plectonotus* (*Boucotonotus*) – *Palaeozygopleura* Community (Frýda – Manda 1997) of the Prague Basin have provided the most important data hitherto about the nature of protoconchs in Devonian gastropods. In this paper, present-day higher classification of the Paleozoic gastropods is discussed on the basis of these new data. The presence of six natural groups (Amphigastropoda, Archaeogastropoda, Mimospirina, Cyrtoneritimorpha, Euomphalomorpha, and Perunelomorpha) were revealed among Silurian and Devonian gastropods of the Prague Basin. These groups are discussed below in detail.



Amphigastropoda – extinct group of Paleozoic molluscs

Historical review

During the last 60 years much new data about bellerophontiform molluscs, as well as about their shells with well preserved muscle scars, were published (see Horný 1992, Peel 1991a, b, and Wahlman 1992 for review). However, interpretation of these data has divided paleontologists, who have variously argued that bellerophontiform molluscs were untorted, exogastrically oriented monoplacophorans, or torted, endogastrically oriented gastropods, or a polyphyletic combination of both (see Horný 1992, Peel 1991a, b, and Wahlman 1992). In this short historical review I have noted only some important opinions which are discussed below on the basis of new data presented here.

Paleozoic symmetrical univalved molluscs belonging to *Bellerophon* and related genera were placed in Amphigastropoda by Simroth (1906). Later Wenz concluded that the Tryblidiacea with their cap-shaped shells and six or eight symmetrical pairs of muscle scars were not fossil Patellacea, but very primitive gastropods ancestral to Amphineura and Bellerophontacea. For this reason Wenz (1940, 1943) placed *Cyrtionella* together with *Tryblidium*-like and *Bellerophon*-like molluscs into the new subclass Amphigastropoda. Wenz thus emended the Amphigastropoda of Simroth, who had used this name only for bellerophontid molluscs. Wenz also placed the subclass Amphigastropoda together with the subclasses Prosobranchia (=Streptoneura) and Euryneura in the class Gastropoda and suggested that the molluscs united in the subclass Amphigastropoda were untorted.

Knight (1947) published his findings of the muscle scars in the genera *Sinuities* and *Bellerophon* and interpreted them as evidence that these genera were torted gastropods. He also agreed with Wenz's conclusion that the genus *Cyrtionella* and its relatives were untorted molluscs like the Tryblidiacea. Knight (1952) and Knight and Yochelson (1958) discussed and summarized the theories on phylogeny of primitive molluscs. This conception was used later by Knight et al. (1960) in the "Treatise on Invertebrate Paleontology" where bellerophontid molluscs were placed within the suborder Bellerophontina Ulrich and Scofield, 1897 of the order Archaeogastropoda Thiele, 1925. The Bellerophontina have been considered to be torted, in contrast to *Cyrtionella* and its relatives which were placed in the order Tryblidioidea Lemche, 1957 of the Monoplacophora.

Horný (1965) divided the class Monoplacophora into two subclasses: Tergomya and Cyclomya. Tergomya contain monoplacophorans having a cap-shaped or spoon-shaped shell with several (generally 5–8) pairs of dorsal muscles arranged in a circle, the anterior apex located outside the circle; no apertural sinus is present. Tryblidiida Lemche, 1957 is the only order placed into this subclass. According to Horný, the subclass Cyclomya inclu-

des two orders: Archinacellida Knight and Yochelson, 1958 and Cyrtionellida Horný, 1963.

Yochelson (1967) summarized the opinions on the classification of monoplacophorans and bellerophontiform molluscs and he expressed doubt that it would be possible to find an absolute criterion for the distinction of torted bellerophontiform gastropods and "cyclomyan" monoplacophorans.

On the basis of the discovery of symmetrically-disposed multiple muscle scars in the Devonian bellerophontiform species *Sinuitopsis acutilira*, Rollins and Batten (1968) noted that such a character as a sinus or slit can no longer be considered as always anterior, and thus provide evidence for torsion in fossil archaeogastropods. According to these authors, sinus-bearing cyclomyans were quite possibly the direct ancestors of the primitive archaeogastropods (i.e., the Bellerophontina). Rollins and Batten (1968) also changed the diagnosis of the subclass Cyclomya and proposed assigning some genera with a sinus or slit on the dorsum to this group. Thus, the earlier undoubted character for distinction of torted bellerophontiform gastropods and "cyclomyan" monoplacophorans (such as the presence of multiple muscle scars as is interpreted today by some authors) was definitely rejected. Rollins and Batten (1968) suggested that bellerophontiform and pleurotomarioidean gastropods originated from Cambrian "cyclomyan" monoplacophorans, and that the same mechanism also occurred later during the Ordovician and Devonian, and therefore gastropods represent a polyphyletic group.

Runnegar and Jell (1976) criticized the usage of muscle scar pattern as an important character for classification of the class Monoplacophora and they proposed a new classification. The Monoplacophora were divided into three orders: Cyrtionellida, Tryblidiida, and Bellerophontida.

Yochelson (1978) analyzed and criticized the classification proposed by Runnegar and Jell (1976) and suggested that the Bellerophontoidea originated from the Pleurotomarioidea. He also considered the helcionellids to be a separate class of the Mollusca. This opinion was later followed by Peel (1991a), who established a new class Helcionelloida for them.

Salvini-Plawen (1980) analyzed the higher taxonomy of the Mollusca and also discussed the taxonomic position of bellerophontiform molluscs. He mentioned that planispiral coiling of the shell is a typical character of untorted molluscs (such as Cephalopoda). Salvini-Plawen suggested that the dorsal sinus is a shell character which developed in bellerophontiform molluscs earlier than torsion (the primary character of the Gastropoda). Thus the presence of a dorsal sinus in bellerophontiform molluscs could not be taken as evidence for torsion of their soft body. Bellerophontiform molluscs are considered by him to be untorted molluscs. Salvini-Plawen (1980) established a new class Galeroconcha which includes orders Tryblidiida and Bellerophontida. Tryblidiida are divided

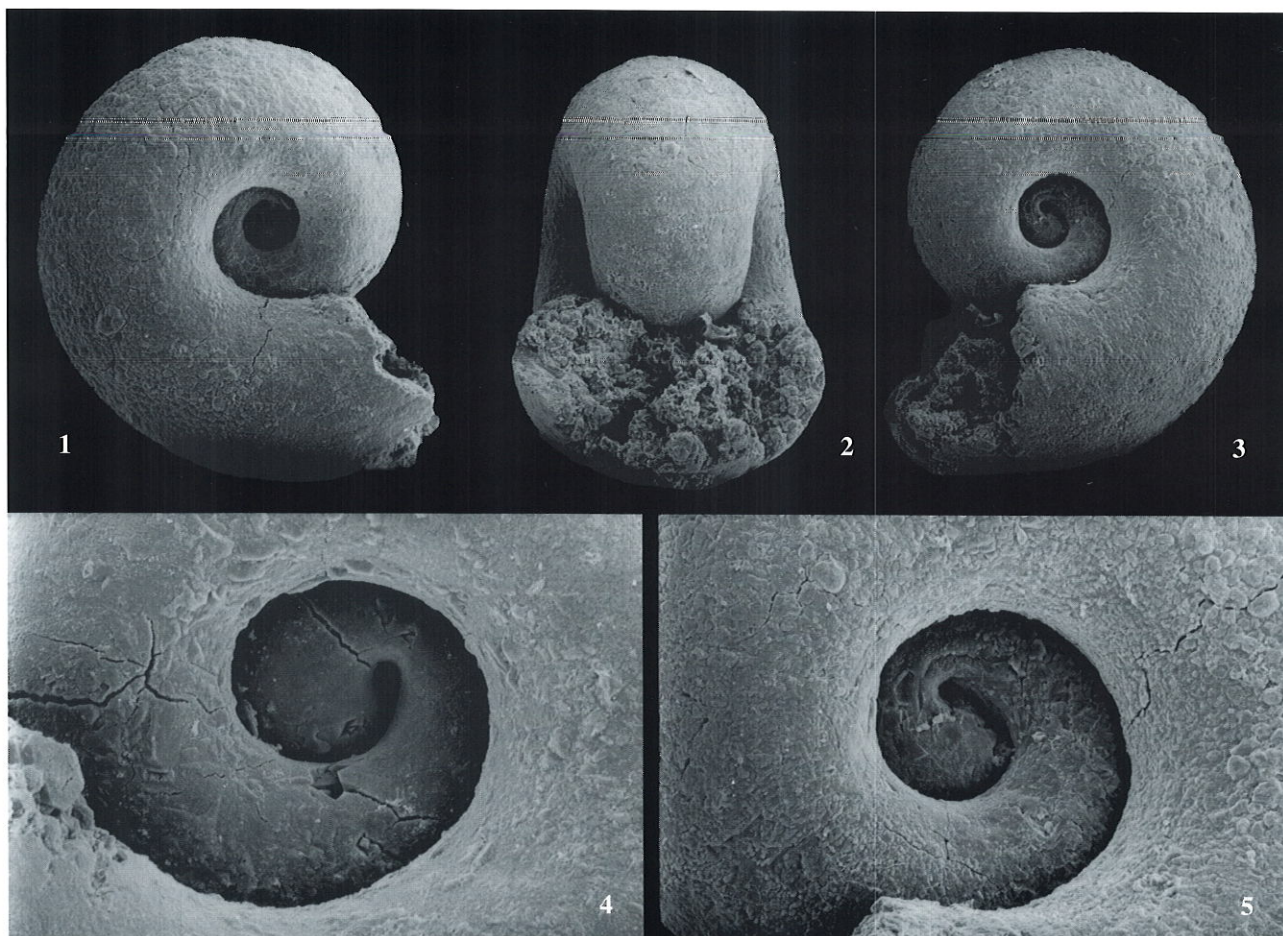


Fig. 1. The early shell of *Bellerophon* cf. *scaber* (PERNER, 1903) from the Kopanina Formation (early Ludlow, Late Silurian) of the Prague Basin. 1–3, 5 – specimen CGU JF 618; 1 – lateral view, x118; 2 – apertural view, x118; 3 – lateral view, x115; 5 – detail view of fig. 3, x325; 4 – detailed view of protoconch; specimen CGU JF 619, x370.

into three suborders: Tryblidiina, Cyrtionellina, and Archinacellina. The order Bellerophontina includes the suborders Sinuitopsina, Helcionellina, and Bellerophontina. Salvini-Plawen (1980) also criticized the classification published by Horný (1965). *Tergomya* were considered to be Tryblidiina and *Cyclomya* to belong to the Bellerophontida.

Peel (1980) interpreted a muscle scar pattern in his new genus *Sylvestrosphaera* from the Silurian of England to be the result of the reduction of muscle attachment sites in retractile monoplacophorans by muscle fusion. He also suggested that the reduction in the number of pairs of muscle scars was a natural consequence of life in a narrowly coiled, cone-shaped shell typical of retractile and non-retractile isostrophic monoplacophorans. According to Peel, monoplacophorans with only one pair of muscle scars may occur and in such situation it could be impossible to distinguish monoplacophorans and gastropods on the basis of muscle scar patterns alone. Runnegar (1981), concurring with Peel (1980), pointed out that the number of muscle scars depends only on the shell shape and style of life. Runnegar (1981) considered all bellerophontiform molluscs to belong to the class Monoplacophora.

According to Dzik (1981) the “cyclomyan” monoplacophorans and bellerophontiform gastropods are closely related. He synonymized the order Cyrtionellida with the Bellerophontida. The class Monoplacophora was divided in three subclasses: Amphigastropoda, *Tergomya*, and *Coniconcha*.

A detailed analysis of the higher taxonomy of bellerophontiform molluscs was published by Harper and Rollins (1982). According to these authors the muscle scars in univalve molluscs are among the least reliable criterion for assessment of their phylogenetic position. Bellerophontoideans and “cyclomyan monoplacophorans” belong according to them to the class Gastropoda. Harper and Rollins (1982) mentioned that muscle symmetry is known to occur in such a wide range of unrelated forms (Monoplacophora, some Archaeogastropoda and some Mesogastropoda); hence, it is not a phylogenetic attribute. Also as stated by these authors, “muscle segmentation and fusion within a set of muscles can be as much a factor of distribution of connective tissue as pseudometamerism”. They mentioned their observation of species of the gastropod genus *Acmaea* Eschscholtz commonly having segmented scars. Harper

and Rollins (1982) concluded that “muscle multiplicity is yet another phylogenetic placebo” and that muscle scar patterns are almost useless by themselves for determining systematic placement of the higher category levels.

Yochelson (1984) pointed out that the Bellerophontoidea and Murchisonioidea belong to the suborder Pleurotomariina Cox and Knight, 1960 and he also suggested eliminating the suborder Bellerophontina because it includes the Helcionelloidea, which are neither bellerophontoideans or gastropods. According to Yochelson (1984) the Bellerophontoidea originated from pleurotomarioideans.

Peel (1986) discovered muscle scars in *Porcellia woodwardi* (Sowerby, 1829) from the Carboniferous of England. He noted that this species possessed two muscle scars and that these were located at approximately corresponding positions on the upper and basal whorl surfaces. According to Peel the similar positions of the muscle scars in *Bellerophon* and in *Porcellia* reflect morphological convergence of their shells and can not contribute to solving the question of the systematic position of *Bellerophon*.

Peel (1991a, b) established two classes: the Tergomya and Helcionelloidea, uniting untorted symmetrical univalved molluscs. Members of the class Tergomya Peel, 1991b (= Tergomya Horný, 1965 + Cyclomya (in part) Horný, 1965) are considered to be exogastric molluscs in contrast to the Helcionelloidea which are interpreted to include endogastrically coiled shells.

The above short historical overview of the classification of bellerophontiform molluscs has revealed the principal problems. Poor knowledge of the soft body of these molluscs has provided sufficient space for many, often contradictory, speculations. In addition, the significance of some shell characters for the higher classification of these molluscs has been overestimated. The interpretations of muscle scars as well as that of further shell characters in terms of functional adaptation have also provided contradictory opinions. Thus, at present there is no generally accepted classification of bellerophontiform molluscs.

How to solve the confusion in higher classification of Paleozoic symmetrical univalved molluscs?

Naturally there are no reliable instructions on how to solve the problem. Our limited knowledge of the soft-part morphology of these molluscs is based mainly on interpretations of such shell characters as their muscle scar pattern, the presence of a dorsal slit, and the shape of their aperture. As shown above, none of these characters alone could solve the confusion. Thus, only detailed revision and evaluation of all available data should clarify it. In this context it should be mentioned that the morphology of the early shell represents an important character which has not been hitherto used in studying the relationships of Paleozoic symmetrical, univalved molluscs.

This high-level taxonomically significant character has been utilized many times in different groups of the class Gastropoda.

Protoconchs of Paleozoic symmetrical univalved molluscs

The genus *Bellerophon* and related bellerophontiform genera were placed by Knight et al. (1960) into the suborder Bellerophontina Ulrich and Scofield, 1897 of the order Archaeogastropoda Thiele, 1929. As shown by Bandel (1982, 1992) the protoconch of members of the Archaeogastropoda consists of a little less than one whorl and it is succeeded by the teleoconch. There is no additional larval shell that is constructed by a planktotrophic veliger as may be present in species of other extant gastropod subclasses (Neritimorpha, Caenogastropoda and Heterostrophia). The early archaeogastropod protoconch is formed by a bilaterally symmetrical, unmineralized shell. During transition to the benthic stage the protoconch is mechanically deformed and subsequently mineralized (Bandel 1982). New data show that the Archaeogastropoda had the same type of protoconch for at least 400 Ma (Devonian to Recent; Frýda 1998a–e, Frýda – Bandel 1997; Frýda – Manda 1997). Thus, protoconch shape has provided a good criterion for the recognition of Archaeogastropoda in the fossil record. The morphology of the early shells of *Bellerophon* and related bellerophontiform genera may be used for testing the relationships of bellerophontiform molluscs to fossil and living Archaeogastropoda.

Unfortunately our knowledge of the early shell in extant Monoplacophora is still poor. Lemche and Wingstrand (1959) wrongly described and figured a protoconch of *Neopilina galathea* as a helicoid protoconch. According to Haszprunar and Schaefer (1997) the neopilinid protoconch is known only in small species and it is bowl shaped. The shell apex of these living Monoplacophora shows two distinct zones (Warén, 1988; Urgorri – Troncoso, 1994). This fact may indicate the existence of a true larval shell (i.e., protoconch II; Haszprunar – Schaefer, 1997). According to Warén (in Haszprunar – Schaefer, 1997) it is not known how the protoconch of neopilinids is lost after metamorphosis.

Dzik (1981) described and figured early shells of the bellerophontiform genera *Sinuitopsis* and *Modestospira* which are bilaterally symmetrically coiled. The early shell of *Modestospira* sp. from the Ordovician of Poland is formed by only the first half of the whorl which is smooth and has a diameter of about 0.4 mm. The later shell bears the characteristic ornamentation of the adult shell. The same shape of the early shell was found by Frýda (1988) in *Modestospira mergli* from the Ordovician strata of Bohemia.

Horný (1993) described the early shell of a cyrtoneilid species *Neocyrtolites advena* (Perner, 1903) [= *Cyclocyrtoneilla advena* (Perner, 1903)] in which he found a slightly different shell ornamentation than in the adult shell. This may suggest the existence of a true larval shell



Fig. 2. Archaeogastropoda – Cirroidea. 1 – apertural view of *Alaskiella medfraensis* from the late Early Devonian (Emsian) of the west-central Alaska, x25; 2, 3 – *Alaskacirrus bandeli* from the late Early Devonian (Emsian) of the west-central Alaska, 2 – apertural view, x50, 3 – oblique view of concave apical depression formed by the umbilicus of dextrally coiled initial portion of shell, x30; 4 – *Pernerircirrus sinistorsus* from the Late Silurian of the Prague Basin (Bohemia), apical view, x4; 5 – *Barrandecirrus filiformis* from the *Prionopeltis archiaci* – *Atrypodea modesta* Community (late Ludfordian, Ludlow, Silurian; Prague Basin), apical view of the sinistral coiled teleoconch with deeply concave apical depression formed by the umbilicus of dextrally coiled initial portion of shell, x8.

in cyrtoneid molluscs. A sharp peak in the size-frequency distribution in *Kokenospira estona* (Koken, 1889) for shells having about three whorls was found by Dzik (1978), who interpreted it as an effect of the increase of mortality during hatching and/or metamorphosis (Dzik, 1981). The above-mentioned data may also suggest the existence of a true larval shell in some bellerophontiform molluscs. Nevertheless, no data about the early shell of the core genus *Bellerophon* and its closely related genera have hitherto been available.

My systematic effort to find bellerophontid shells with a well preserved early shell have recently been successful (Frýda 1998a, b; Bandel – Frýda, in prep.) Several bellerophontid shells with protoconch were found in early Ludlovian rocks (Silurian) of the Prague Basin. These small shells belong to *Bellerophon*, but because they are

juvenile, the exact species determination is difficult. The general shape of these juvenile shells cannot be distinguished from that of *Bellerophon scaber* (Perner, 1903) which is hitherto only known from late Wenlockian strata of the Prague Basin. The shells figured here as *Bellerophon* cf. *scaber* (Perner, 1903) are found in slightly younger (early Ludlow) strata and they most probably belong to *Bellerophon scaber* (Perner, 1903). Recently Horný (1994, 1996) described muscle scars in *Bellerophon scaber* (Perner, 1903), which are similar in general shape and position to muscle scars described in *Bellerophon* by Knight (1947); thus, Horný considered them to demonstrate undoubted evidence of the gastropod affinity of this mollusc.

The early shell of *Bellerophon* cf. *scaber* is bilaterally symmetrical and its size is very small (fig. 1). The diameter of the beginning of the first whorl is only about

0.05 mm. In addition, the typical deformation of the protoconch which occurs in members of the Archaeogastropoda is not developed. Thus, according to its shape and size of the early shell, *Bellerophon* cf. *scaber* does not belong to the subclass Archaeogastropoda. More detailed evaluation of this discovery is under preparation (Bandel – Frýda, in prep.)

Class level position of Bellerophon

As shown above, *Bellerophon* and related genera cannot be considered to belong to the subclass Archaeogastropoda where they were previously placed by many authors (e.g., Knight et al. 1960; Peel 1991a, b; Ponder – Lindberg 1997). In addition, newly discovered early shells of *Bellerophon* differ from those of sinuate cyrtoneurids (like *Sinuitopsis*; Dzik, 1982) as well as from living neopilinids (Haszprunar – Schaefer, 1997). Thus, these data suggest that bellerophonitiform molluscs probably represent a polyphyletic group. On the basis of protoconch type, *Bellerophon* and related genera are considered to form an independent group of molluscs (Frýda 1998a, b) and the name Amphigastropoda Simroth, 1906 may be used for it as suggested earlier by Bandel – Geldmacher (1996). Unfortunately, none of above-mentioned shell features can resolve the question whether *Bellerophon* and related genera (Amphigastropoda) were Gastropoda or Monoplacophora (= Tryblidiida). If torsion of their soft body can be demonstrated by future study, then they must be placed in the class Gastropoda as a separate subclass. If the opposite state can be determined (i.e. untorted state of the soft body), then the Amphigastropoda will probably form a separate class of Mollusca.

Mimospirina

The taxon Mimospirina was established by Dzik (1983) as a new suborder of the Archaeogastropoda uniting members of extinct families Clisospiridae Miller, 1925 and Onychochilidae Koken, 1925. Opinions on their higher taxonomic position as well as on their relationships have often changed (see Wenz 1938; Knight et al. 1960; Horný 1964; Golikov – Starobogatov 1975; Peel 1975, 1986; Wangberg-Eriksson 1979; Frýda – Rohr 1999, in prep.).

McLean (1981) suggested that the members of the superfamilies Macluritoidea and Clisospiroidea do not belong to his suborder Euomphalina but represent lineages apart from this group. Later, Dzik (1983) on the basis of his study of the early shell ontogeny of the genus *Mimospira*, proposed separating both the Clisospiridae and Onychochilidae from the suborder Macluritina and established a new suborder Mimospirina for them. On the other hand, Linsley and Kier (1984) on the basis of a functional analysis, proposed uniting the Onychochiloidea (including Clisospiridae and Onychochilidae), Macluritoidea, and possibly the Euomphaloidea in a new order Hyperstrophina of a new class Paragastropoda. The class

Paragastropoda has been considered to represent untorted molluscs. However, the quite different early shell ontogeny of members of the Onychochiloidea and Euomphaloidea (Dzik 1983; Frýda 1989, 1995; Bandel – Frýda 1998; Frýda – Rohr, in prep.) suggests that the class Paragastropoda is an artificial group with no zoological validity. Also Dzik's (1983) interpretation of Mimospirina as a group belonging to the Archaeogastropoda is invalid. The large smooth protoconch of the Mimospirina, consisting of more than one whorl (Dzik 1983; Frýda 1989, 1995; Frýda – Rohr, in prep.), differs from that of the Archaeogastropoda.

Ponder and Lindberg (1997, p. 203) speculated that ancestors of Heterostropha may have arisen from a lineage with hyperstrophic dextral (i.e. sinistrally coiled) shells. They suggested that such an ancestor could have been amongst the Macluritoidea, and "sinistral hyperstrophic" Ordovician *Mimospira* is mentioned as their possible example. However, there is no evidence that Ordovician *Mimospira* and related genera belonging to the superfamily Onychochiloidea were "sinistral hyperstrophic". In addition, there is no data about the protoconchs of any members of the superfamily Macluritoidea. The teleoconch shapes of macluritoidean gastropods are far from those of the early Heterostropha of Early Carboniferous age. In summary, the Cambro-Devonian Mimospirina (Clisospiridae and Onychochilidae) definitely do not belong to the Archaeogastropoda. The higher systematic position of these molluscs, with a sinistrally coiled shell bearing a large sinistral protoconch, is still open.

Archaeogastropoda

Among Paleozoic gastropods, the members of the subclass Archaeogastropoda have been considered to be the most common gastropod group. Redefinition of this group by Bandel (1982), based on their early shell ontogeny type, has provided a good criterion for their determination in the fossil record. According to the teleoconch morphology, the oldest presumed Archaeogastropoda are known from the Late Cambrian (Knight et al. 1960). However, the oldest undoubted evidence for their occurrence based on their typical protoconch type comes from the Early Devonian (Frýda – Bandel 1997; Frýda – Mandá 1997; Frýda 1998a–d, 1999). The discovery of archaeogastropod-type protoconchs in these Early Devonian gastropods indicates that the subclass Archaeogastropoda has had the same early ontogenetic pattern for at least 400 Ma (Devonian to Recent) and represents a very old, independent gastropod group.

Classification of Paleozoic Archaeogastropoda

The concept of the subclass Archaeogastropoda has been changed many times and different usage may be found in the most recent scientific studies (Haszprunar 1993; Bandel – Geldmacher 1996; Ponder – Lindberg 1997).



Fig. 3. Archaeogastropoda – Murchisonoidea. 1 – *Murchisonia (Murchisonia) pragensis* from the Praha Formation (Pragian, Early Devonian, Prague Basin), apertural view, x30; 2–4 – Givetian (Middle Devonian) species of *Murchisonia (Murchisonia)* from the Paffrath area (Bergisches Land, Germany), 2 – lateral view of *Murchisonia (Murchisonia) "bilineata"*, x2; 3 – apertural view of *Murchisonia (Murchisonia) "bilineata"* with spiral cords of fine nodose, x0.8; 4 – lateral view of *Murchisonia "archiaci var. coronata"*, x2; 5, 7 – apical and lateral views of *Murchisonia (Murchisonia) holynensis* showing the protoconch of archaeogastropod type, 5 – x37, 7 – x85; 6 – lateral view of juvenile shell of *Murchisonia (Murchisonia) holynensis*, x37.

Knight et al. (1960) considered a majority of the Paleozoic gastropods to belong to the Archaeogastropoda. This concept was developed only on the basis of evaluation of the teleoconch shell characters in Paleozoic gastropods. Recent studies (Frýda – Bandel 1997; Frýda – Manda 1997; Frýda 1998a, b, c; Bandel – Frýda 1998, 1999) have shown that the presumed Paleozoic archaeogastropod family-level taxa unite gastropods belonging to different gastropod subclasses. In addition, some shell characters such as the presence or absence of a slit, considered to be important high-level characters for the classification of Paleozoic archaeogastropods, have very limited significance (Bandel – Frýda 1996; Bandel – Gel-

dmacher 1996). Thus, among the Paleozoic archaeogastropods there are large taxa uniting forms with shells having or lacking slits like modern members of the Seguenzioidea or Scissurelloidea (Marshall 1983; Bandel 1998). In fossil members of the Archaeogastropoda the development of such a shell character as a slit that generates a selenizone probably occurred several times. In addition, slit-bearing forms have probably lost this feature several times in different lineages; thus, this shell character cannot be used for suborder-level diagnosis (cf. Knight et al. 1960). In many cases a fossil archaeogastropod can only be placed within a morphogroup and a relationship cannot be established to a surviving species or group. In such

cases, Bandel – Frýda (1996) and Bandel – Geldmacher (1996) suggested that they should be included in a group of the Trochomorpha or the Selenimorpha. To sum up, the present classification of the Paleozoic Archaeogastropoda is artificial and a new one, possibly less artificial, should be established on the basis of detailed, specimen-based studies of all available characters including also some new shell characters like the nature of the protoconch and shell structure.

In the following paragraphs, problems of the present-day classification of the Paleozoic Archaeogastropoda are illustrated using the phylogenetic models of superfamilies Cirroidea, Murchisonoidea and Loxonematoidea.

Cirroidea

The extinct superfamily Cirroidea unites the Mesozoic Cirridae and the Paleozoic Porcellidae (Bandel 1993). The oldest representatives of the Cirroidea are known from the Paleozoic, the oldest representatives of the Porcellidae from the Silurian (Frýda 1995, 1997) and the Cirridae from slightly younger, Emsian (Early Devonian) strata (Frýda – Blodgett 1998). The stratigraphic range of the superfamily Cirroidea is at least from Silurian to Cretaceous and so spans an interval of about 350 million years duration. The unusual change in shell coiling (from dextral to sinistral) during their early shell ontogeny is a character which is unknown among the rest of the Archaeogastropoda. Thus, the Cirroidea may represent an independent, long-lived order of the subclass Archaeogastropoda (fig. 2). According to Bandel (1993), members of the family Porcellidae bearing a slit evolved during the Triassic into members of the Cirridae that lacked a slit. However, the discovery of *Alaskacirrus bandeli* Frýda and Blodgett, 1998, coming from the late Early Devonian (Emsian) of Alaska has changed our view on the early phylogeny of the family Cirridae, the members of which were hitherto known only from Mesozoic strata. Similarly, unusual shells of Early Devonian *Pavlodiscus yochelsoni* Frýda, 1998 from of the Prague Basin show some resemblance to members of the Porcellidae (planispirally coiled teleoconch and dextrally coiled early shell), but in contrast they bear no selenizone. The discovery of these gastropods (*Alaskacirrus* and *Pavlodiscus*) has suggested that the family Cirridae separated from the family Porcellidae at least since the Early Devonian, much earlier than was suggested by Bandel (1993). On the other hand, both these genera may also represent dead-end branches of the Paleozoic Cirroidea. Thus, it is necessary to focus our studies on the evolution of this superfamily and find new data to test the above mentioned evolutionary models.

Murchisonoidea

In contrast to Cirroidea, the superfamily Murchisonoidea (fig. 3) unites Paleozoic gastropods which occur very commonly. Unfortunately, the protoconch of the type spe-

cies of *Murchisonia*, *Murchisonia bilineata*, from the Givetian (Middle Devonian) of Germany is still unknown and so the higher taxonomic position of superfamily Murchisonoidea is questionable. However, several species of *Murchisonia* and closely related taxa from the Lochkovian, Pragian and Emsian (Early Devonian) of the Prague Basin have an archaeogastropod-type protoconch (Frýda – Manda 1997, Frýda 1999, unpubl. data). The discovery of these protoconchs is very important for an evaluation of their higher taxonomic position. The Murchisonoidea were placed in the subclass Caenogastropoda in some recent gastropod classifications (e.g., Ponder – Warén 1988). Nevertheless, the discovery of archaeogastropod-type protoconchs in Early Devonian species suggests that the Murchisonoidea belong to the subclass Archaeogastropoda. For a definitive solution of the higher taxonomic position of the latter superfamily, it is necessary to obtain new data about the Middle Devonian core group of the genus *Murchisonia*.

Loxonematoidea

The superfamily Loxonematoidea unites Paleozoic gastropods which are also occur commonly (fig. 4). Knight et al. (1960) placed this superfamily, including the families Loxonematidae, Palaeozygopleuridae, Pseudozygopleuridae, and Zygopleuridae, within the Caenogastropoda. This opinion on the position of this extinct superfamily was also followed by Taylor and Sohl (1962) and Ponder and Warén (1988). On the other hand, Golikov and Starobogatov (1975) placed the Loxonematoidea, together with the superfamilies Aclidoidea, Pyramidelloidea, and Nerineoidea, into the order (=subclass) Heterostropha. The initial part of the shell in the core genus *Loxonema* Phillips, 1841 is still unknown. Bandel (1991) suggested that Loxonematoidea represent a polyphyletic group and tentatively placed Loxonematidae together with his new family Polygyrinidae into the Mesogastropoda (Caenogastropoda). Members of the families Pseudozygopleuridae, Zygopleuridae, and Protoculidae (Zygopleuroidea Bandel, 1991) have larval shells or simplified shells that reflect lecithotrophic development and thus they belong without doubt to the subclass Caenogastropoda. In contrast, the Early Devonian members of the families Loxonematidae (*Katoptychia* and *Stylonema*) and Palaeozygopleuridae (*Palaeozygopleura*) had a large archaeogastropod-type protoconch and thus no larval shell formed during their ontogeny (Frýda – Bandel 1997; Frýda unpubl. data). For this reason, the members of the family Palaeozygopleuridae and at least some Loxonematidae do not fit into the Caenogastropoda, but appear to be members of the subclass Archaeogastropoda. The very slender, high-spired shells of *Loxonema* or *Palaeozygopleura*-type represent an unusual teleoconch character among the members of the subclass Archaeogastropoda. This character together with their archaeogastropod-type protoconch places these gastropods in their own order Sty-

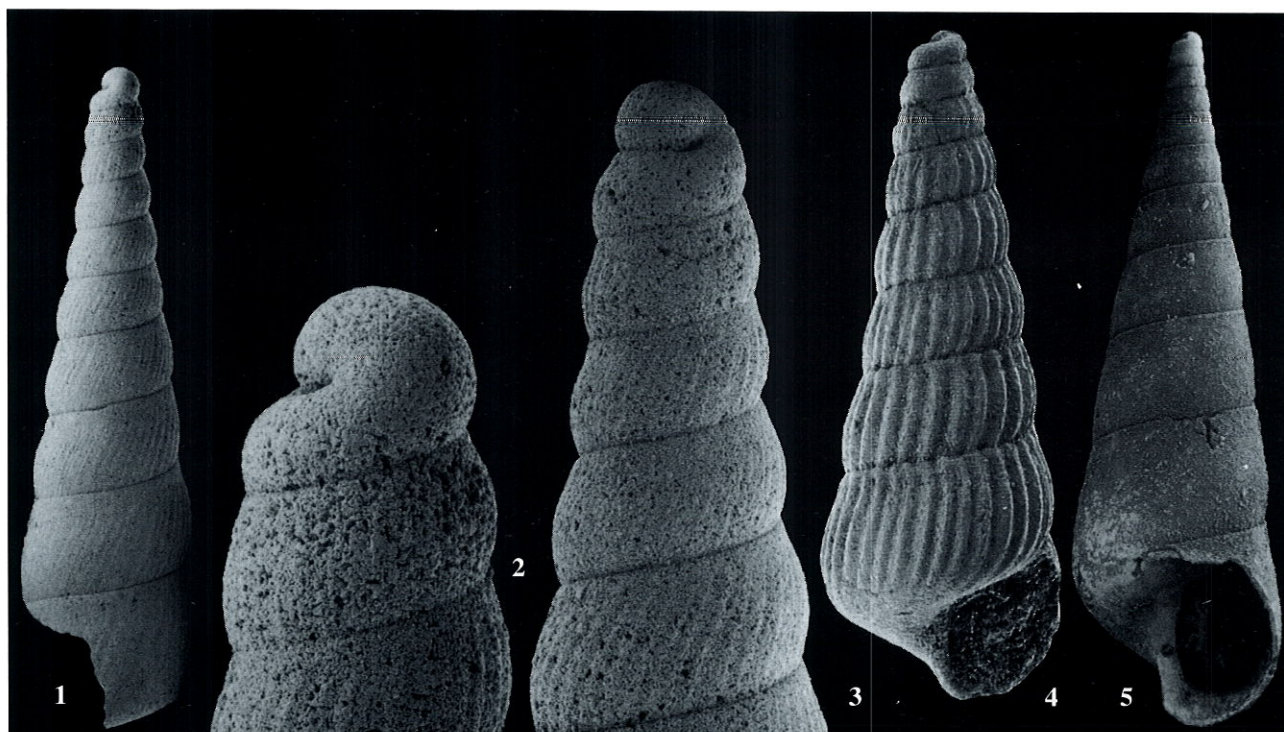


Fig. 4. Archaeogastropoda – Loxonematoidea. 1–3 – *Palaeozygopleura (Bohemozya) kettneri* from the uppermost part of the Třebotov Limestone (Daleje-Třebotov Formation; late Emsian, Early Devonian; Prague Basin), 1 – lateral view, x14; 2, 3 – detailed views of early whorls, 2 – x60, 3 – x43; 4 – *Palaeozygopleura (Palaeozygopleura) alinae* from the Praha Formation (Pragian, Early Devonian, Prague Basin); lateral view, x20; 5 – *Katoptychia holynensis* from the uppermost part of the Třebotov Limestone (Daleje-Třebotov Formation; late Emsian, Early Devonian; Prague Basin), lateral view, x9.

logastropoda Frýda and Bandel, 1997. The extinct superfamily Loxonematoidea probably unites the members of two gastropod subclasses, the Archaeogastropoda and Caenogastropoda, and so has no zoological validity. If it is true, then this fact has an important influence on all present models of the early evolution of the subclass Caenogastropoda (Bandel 1991, 1997; Ponder – Lindberg 1997; Nützel 1997).

Neritimorpha

The taxon Neritimorpha was established by Golikov and Starobogatov (1975) as a new superorder of the subclass Pectinibranchia. According to them the Neritimorpha unites the superfamilies Neritoidea, Hydrocenoidea, Titiscanioidea, and possibly also the Cocculinoidea. Salvini-Plawen and Haszprunar (1987) placed the Neritopsina (=Neritimorpha), together with the Docoglossa, Cocculiniforma, Vetigastropoda, Segueziina, and Architaenioglossa, in the Archaeogastropoda which they considered to be a paraphyletic group. Later, Haszprunar (1993) again suggested placing the Neritimorpha and the architaenioglossate groups (Cyclophoroidea and Ampullarioidea) in his concept of the Archaeogastropoda. Bandel (1992) considered the Neritimorpha to represent an independent subclass characterized by a typical, strongly convolute protoconch. Recently the independent position of the Neritimorpha was also noted by Biggelaar and Haszprunar (1996), who characterized this large gastropod taxon by its cleavage patterns. The results of this study suggests that the Neritimor-

pha forms a gastropod group which is far removed from the Docoglossa (= Patellogastropoda) and Vetigastropoda.

Protoconch of fossil Neritimorpha

The oldest undoubted evidence for the characteristic, strongly convolute early shell of extant Neritimorpha is known from the Triassic St. Cassian Formation (Bandel 1992, 1997). On the basis of the discovery of a neritimorph protoconch in the Triassic *Orthonychia alata* (Laube 1869), Bandel (1992) considered the Paleozoic parasitic gastropods of the family Platyceratidae to belong to the subclass Neritimorpha. Besides their general shell shape, the presence of a thick calcitic outer shell layer (Batten 1984) often bearing colour bands (Yochelson 1956; Kříž – Lukeš 1974; Yochelson – Kříž 1974; Frýda unpubl. data) seems to be conformable with this view. However, new discoveries of well-preserved early shells in the members of the family Platyceratidae (Frýda 1998 a, b) show that this group unites gastropods with at least two protoconch types: 1.) a strongly convolute type and 2.) an openly coiled, fish hook-like type. Both these types may be traced in the fossil record for more than 200 million years and the changes in their shape during this time were insignificant (Frýda 1998a, b, c; Bandel – Frýda, in press). This character has been considered to have very high-level taxonomic significance and for this reason, the subclass Neritimorpha has been divided into two separate orders, the Cycloneritimorpha and Cyrtoneriti-



Fig. 5. Cyrtoneritimorpha. 1 – cyrtoneritimorph protoconch from the Kopanina Formation (early Ludlow, Late Silurian; Prague Basin), x90; 2–5 – *Vltaviella reticulata* from the *Monograptus uniformis* graptolite Biozone (Lochkov Formation; early Lochkovian, Early Devonian; Prague Basin), 2 – protoconch of *Vltaviella reticulata*, x65; 3 – oblique view of juvenile shell, x38; 4, 5 – lateral and oblique views showing a reticulate ornamentation, 4 – x25, 5 – x28.

morpha (Frýda 1998a, b, c; Bandel – Frýda 1999, in press). The order Cycloneritimorpha is characterized by a strongly convolute protoconch and may be traced from the Recent back to at least to the Carboniferous. The “placyceratids” with openly coiled, fish hook-like protoconchs form the order Cyrtoneritimorpha. The members of this order may be traced, according to their characteristic fish hook-like protoconch, from the Early Ordovician to the Late Permian, and thus, existed for about 250 million years (Frýda 1998a, b, c; Bandel – Frýda 1999, in press). A sharp increase in mortality during the early shell ontogeny in some Cyrtoneritimorpha, as in *Vltaviella* Frýda and Manda, 1997 (fig. 5), may suggest the presence of a planktotrophic larval stage in this group.

From the above-mentioned facts it is quite evident that the presumed Paleozoic members of the subclass Neritimorpha unites two gastropod groups, the Cycloneritimorpha and Cyrtoneritimorpha, differing by the shape of their protoconchs. The relations of these neritimorph groups to each other, as well as their relations to other gastropod groups are still mysterious (Bandel – Frýda 1999, in press). New detailed studies of the early shells of presumed Paleozoic Neritimorpha may shed new light on the origin of this gastropod subclass.

Euomphalomorpha

Koninck (1881) established his family Euomphalidae for Early Carboniferous gastropods having a planispiral or low trochospiral shell in which the whorls only just touch or overlap very little with each other. Later, Koken (1889) considered the euomphalid gastropods to be related with the members of the Pleurotomarioidea because he observed a morphological convergence among both groups. He thus concluded that the Pleurotomarioidea and the Euomphaloidea arose from the same stock. Wenz (1938) placed the family Euomphalidae, together with the families Omphalocirridae, Platyacridae, Cirridae, Oriostomatidae, Poleumitidae and Macluritidae, within the superfamily Euomphalacea (= Euomphaloidea). All members of the Euomphaloidea were considered by Wenz to belong to the Archaeogastropoda. Yochelson (1956) interpreted the Euomphaloidea to have been derived from the Macluritoidae in the Early Ordovician and he placed three families, Euomphalidae, Helicotomidae and Omphalotrochidae in this superfamily. This concept was followed by Knight et al. (1960). McLean (1981) considered the deep-sea, hot vent limpet *Neomphalus* McLean, 1981 to represent a living species of the Euomphaloidea. For this reason McLe-

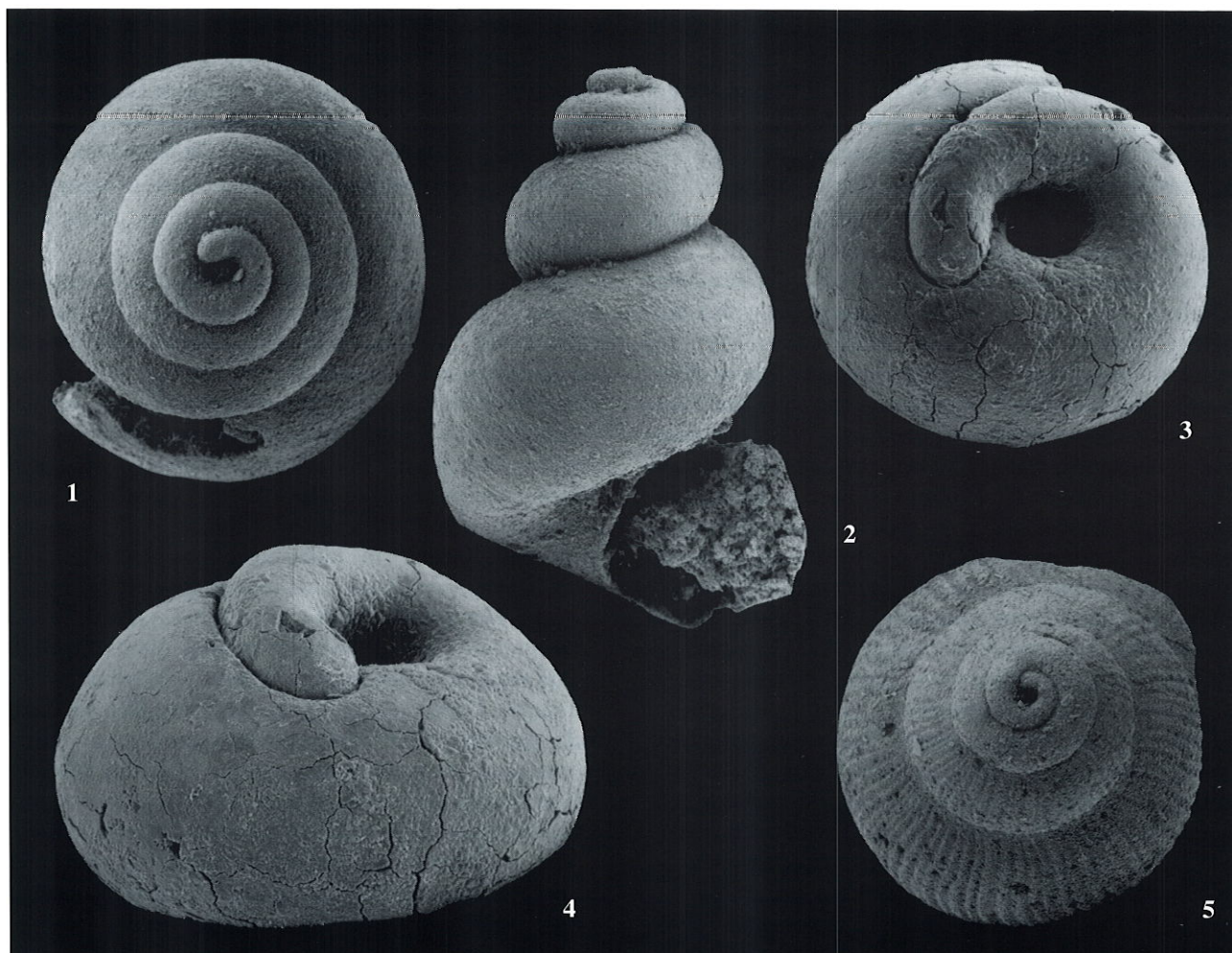


Fig. 6. Perunelomorpha. 1, 2 – *Perunela bohémica* from the Praha Formation (Barrandov; Pragian, Early Devonian; Prague Basin); 1 – apical view showing the openly coiled first whorl, x42, 2 – lateral view, x36; 3, 4 – perunelomorph protoconch from the lower part of Kopanina Formation (early Ludlow, Late Silurian; Prague Basin), 3 – apical view, x140; 4 – oblique view, same shell as in fig. 3, x180; 5 – apical view of *Zenospira pragensis* showing an openly coiled early whorl, x42.

an (1981) placed his genus *Neomphalus* in a new superfamily Neomphaloidea of a new suborder Euomphalina. The suborder Euomphalina, uniting members of the modern Neomphaloidea with the Paleozoic Euomphaloidea, was considered to belong to the Archaeogastropoda. Linsley and Kier (1984) proposed uniting the Onychochilacea (including Clisospiridae and Onychochilidae), Macluritacea, and Euomphalacea (with question mark) into a new order Hyperstrophina of a new class Paragastropoda.

Protoconch of Euomphalus and the related genera

Bandel and Frýda (1998) found a cyrtconic and planispiral, openly coiled protoconch in the Devonian and Carboniferous genera *Euomphalus*, *Straparollus*, *Serpulospira*, *Phymatifer*, *Schizostoma*, and *Nodeuomphalus* that form the core group of the superfamily Euomphaloidea Koninck, 1881. The protoconch is openly coiled and carries a bulbous, oblique initial egg-shaped portion. The protoconch forms an open half coil with a thickened end and smooth surface. This character

distinguishes Euomphaloidea from members of the other four extant subclasses of the Gastropoda: the Archaeogastropoda, Neritimorpha, Caenogastropoda and Heterostrophia. For this reason, Bandel and Frýda (1998) placed the Euomphaloidea in the new subclass Euomphalomorpha. The Euomphalomorpha are considered to be an independent gastropod group, known only from the Paleozoic (Cambrian–Permian).

Perunelomorpha

On-going studies focused on the protoconch morphology of Silurian and Devonian gastropods (Frýda 1998a–c; Frýda – Bandel 1997; Frýda – Manda 1997) has revealed the presence of gastropod shells having a very unusual, openly coiled early whorl. This feature distinguishes them from living and fossil members of large gastropod megataxa like the Archaeogastropoda, Euomphalomorpha, Neritimorpha (Cycloneritimorpha and Cyrtoneritimorpha), Caenogastropoda and Heterostrophia. For this reason, these gastropods have been placed in a new order Perunelo-

morpha based on the superfamily Peruneloidea which unites two families, the Perunelidae and Chuchlinidae (Frýda – Bandel 1997; Frýda 1998a–c). A typical feature of the perunelomorph gastropods is a strong increase of the mortality rate during early shell ontogeny, which was observed in their Silurian members (Frýda 1998a, c). This feature suggests the presence of a planktotrophic larva stage in the perunelomorph gastropods.

The higher taxonomic position of the order Perunelomorpha is still a mystery. Paleozoic gastropods with asymmetrically coiled shells may be placed in one of the five gastropod subclasses: Archaeogastropoda, Euomphalomorpha, Neritimorpha, Caenogastropoda, and Heterostrophina. Archaeogastropoda have, in contrast to Perunelomorpha, a protoconch that has been pulled into a spiral shell with characteristic lateral folds, and have no planktotrophic larvae (Bandel 1982). As shown above, Amphigastropoda (*Bellerophon* and related taxa) also had a quite different protoconch than the Perunelomorpha. For this reason, the order Perunelomorpha cannot be placed in these subclasses. Gastropods belonging to the Perunelomorpha have an openly coiled early shell as do the members of the subclass Euomphalomorpha, but they differ from the latter by two features. Firstly, Perunelomorpha have trochospirally (not planispirally) coiled early shells unlike the Euomphalomorpha. Secondly, Perunelomorpha have a smaller and less bulbous initial shell portion than is found in any euomphalomorph gastropods studied so far (Bandel – Frýda 1998). The members of the Cyrtoneuritimorpha, also having openly coiled protoconchs, differ from Perunelomorpha by their fish hook-like protoconchs.

Members of the order Perunelomorpha can be traced from the Early Ordovician to the Early Devonian (Bockellie – Yochelson 1979; Dzik 1994; Frýda – Bandel 1997; Frýda – Manda 1997; Frýda 1998a–c) and so had a duration of about 100 Ma. Unfortunately, only very few perunelomorph protoconchs can be connected with a teleoconch. Nevertheless, the discovery of a new rich fauna from the Silurian and Devonian of the Prague Basin shows that the members of the order Perunelomorpha were a very common gastropod group (Frýda, unpubl. data).

A new model of gastropod evolution

On the basis of protoconch morphology, the presence of six natural groups (Amphigastropoda, Archaeogastropoda, Mimospirina, Cyrtoneuritimorpha, Euomphalomorpha, and Perunelomorpha) have been recognized among Silurian and Devonian gastropods.

The Amphigastropoda (*Bellerophon* and the related genera) are considered to be a long-lived (from Cambrian to Triassic), independent molluscan group. The discovery of early whorls in the core genus *Bellerophon* seems to be consistent with a model published by Naef (1911), Salwini-Plawen (1980), and Bandel and Geldmacher (1996) that the Amphigastropoda represent gastropods in which torsion of the soft body occurred, only af-

ter complete embryogenesis when the shell was mineralized. However, the question of whether the Amphigastropoda were torted or untorted molluscs is still open. Nevertheless, the protoconch of *Bellerophon* definitely demonstrates that the Amphigastropoda do not belong to the subclass Archaeogastropoda in contrast to many present-day classifications (e.g., Knight et al. 1960; Peel 1991a, b; Ponder – Lindberg 1997).

The members of the subclass Archaeogastropoda also represent an ancient gastropod group. There is unambiguous evidence for the same pattern of early ontogeny of the Archaeogastropoda for at least the last 400 million years (from the early Lochkovian to the Recent). Bandel (1982, 1992) and Bandel and Geldmacher (1996) showed that the primary shell of Archaeogastropoda is deformed before it was mineralized. The torsion of the visceral mass also occurs after the formation of the bilaterally symmetrical shell. Recently the independent position of the subclass Archaeogastropoda was also suggested by Biggelaar and Haszprunar (1996) who found quite different cleavage patterns and timing of mesentoblast formation in this group in comparison with those in subclasses Neritimorpha, Caenogastropoda and Heterostrophina. All these facts together with evidence for the same pattern of early ontogeny in the Archaeogastropoda during the last 400 million years (Frýda – Manda 1997) suggest that this group represent a very old, independent gastropod group.

The members of the subclass Euomphalomorpha and the orders Cyrtoneuritimorpha and Perunelomorpha had an openly coiled early whorl. As noted by Bandel and Frýda (1998) the shell structure of Euomphalomorpha may suggest connection to the Neritimorpha. However, until now we have no evidence for the existence of a true larval shell in the extinct subclass Euomphalomorpha, in contrast to the members of Cyrtoneuritimorpha and Perunelomorpha. The members of the order Cyrtoneuritimorpha are considered to belong to the subclass Neritimorpha. The same teleoconch shape, thick calcitic outer shell layer and presence of true larval shell are considered to be "evidence" for the linkage of the Paleozoic Cyrtoneuritimorpha and extant Neritimorpha (= Cycloneuritimorpha). On the other hand the gastropods belonging to the order Perunelomorpha, also developing a planktotrophic larval shell, may represent an ancestral group of the younger gastropod subclasses, such as the Caenogastropoda and Heterostrophina (Bandel 1997, Frýda 1998a–c). The similarity of teleoconch shapes of the Devonian Perunelomorpha (*Zenospira* and *Chuchlina*; Frýda – Bandel 1997; Frýda – Manda 1997) with those of the oldest undoubted Caenogastropoda and Heterostrophina (Kollmann – Yochelson 1976; Yoo 1988, 1994) as well as the presence of a planktotrophic larval stage in all these groups is evidence for linkage of the Paleozoic Perunelomorpha and extant Caenogastropoda and Heterostrophina. In addition, an uncoiled planktotrophic larval shell was present in some Carboniferous caenogastropods (e.g., *Globozyga mediocris*; Nützel 1997, Pl. 34 A–C).

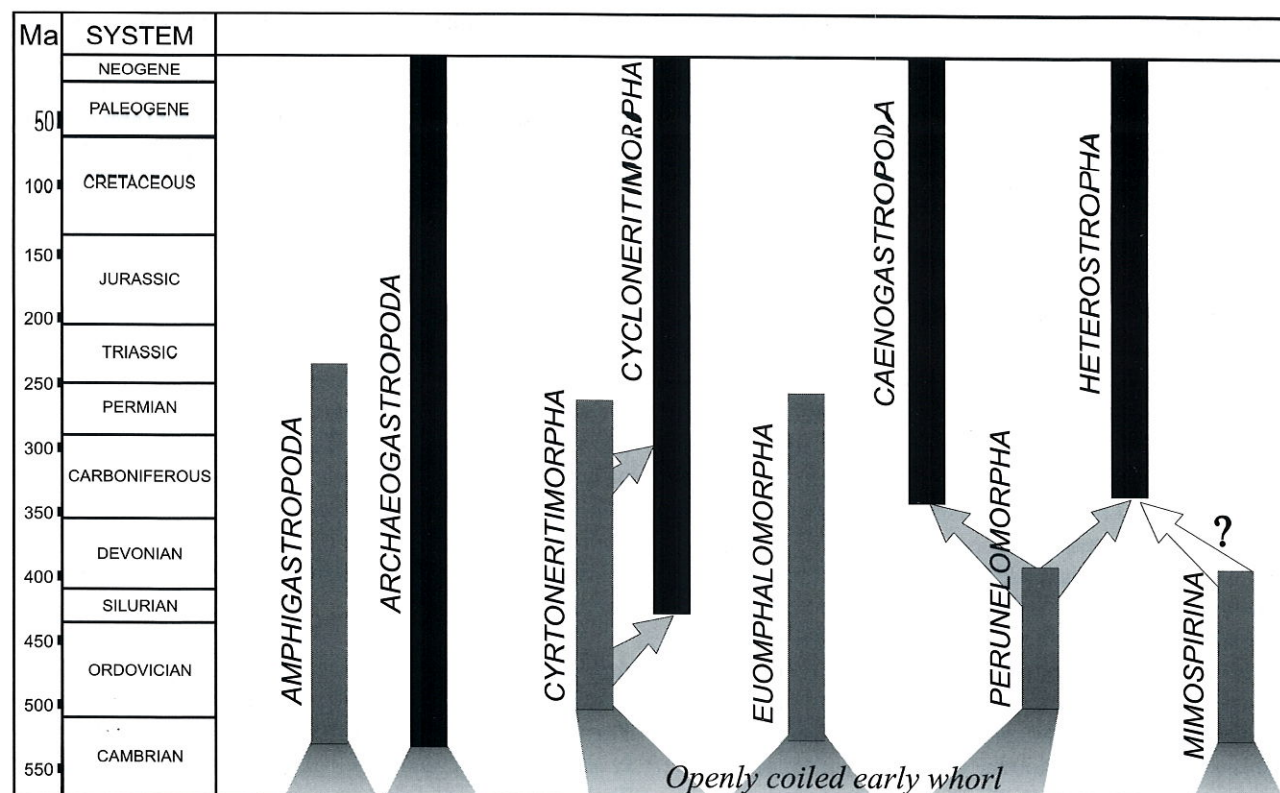


Fig. 7. Model of the relationship of major gastropod groups and their stratigraphic ranges. Arrows indicate probable connections between lineages (see text).

Is uncoiling a plesiomorphic shell character of the higher gastropods?

As shown above, an uncoiled protoconch was recently found in several, long-lived groups of Paleozoic gastropods (Cyrtoneritimorpha, Perunelomorpha, and Euomphalomorpha; Frýda – Bandel 1997; Frýda – Manda 1997; Bandel 1997; Bandel – Frýda 1998, 1999; Frýda 1998a, b, c). The Ordovician–Permian Cyrtoneritimorpha with uncoiled, fish hook-like protoconchs probably gave rise during the Paleozoic (?Silurian) to the modern Neritimorpha with a strongly convolute protoconch. On the other hand, the Ordovician–Devonian Perunelomorpha may represent the ancestral group of Caenogastropoda and/or Heterostropha. The Euomphalomorpha, also having an uncoiled protoconch, forms an independent gastropod group, known only from the Paleozoic, which may be related to the Neritimorpha (Bandel – Frýda 1998). Thus, uncoiling of protoconchs found in the above-mentioned groups may represent a very old shell feature (Frýda 1998c). In contrast to these groups, the latter feature is not known among the members of the subclasses Archaeogastropoda and Amphigastropoda (*Bellerophon* and related taxa). The above mentioned data suggest that the higher gastropods (Caenogastropoda, Heterostropha, and Neritimorpha) as well as the extinct Euomphalomorpha may have evolved from a common ancestor with an uncoiled tubular shell (fig. 7), and thus, not directly from

the Paleozoic Archaeogastropoda and/or Amphigastropoda, which is in contrast to most of the recent phylogenetic schemes (see Ponder – Lindberg 1997 for review). If this is true, then present-day models of the early phylogeny of the class Gastropoda must be changed.

Problems of proposed model

Naturally, the still very poor knowledge of Paleozoic gastropods remains the main problem with the model of gastropod evolution proposed here. During the last 5 years, systematic and on-going studies of early shell ontogeny of Silurian and Devonian gastropods have multiplied by several times our data about this taxonomically important shell feature (Frýda 1995, 1997, 1998a–e, 1999b; Frýda – Bandel 1997; Frýda – Blodgett 1998; Frýda – Manda 1997; Bandel – Frýda 1996, 1998, 1999). Interpretation of all the above cited references, as well as new data, will be a very good source for future tests of different models of gastropod evolution. Recent discovery of an unusual Early Devonian limpet, *Pragoscutula wareni* Frýda, 1998, is a typical example of such data. The shells of this fossil, bearing a closely and dextrally coiled protoconch of about 1.5 whorls, represent the oldest (and first Devonian) evidence for a closely coiled, non-archaeogastropod and non-amphigastropod protoconch type. The significance of this discovery for the model proposed here is under study (Frýda 1999, in prep.).

Conclusions

1. The nature of the early shells in the core genus *Bellerophon* demonstrates that this genus (and thus also the Bellerophontoidea, **Amphigastropoda**) does not belong to the subclass Archaeogastropoda. In addition, the early shells in *Bellerophon* differ from those of sinuate cyrtoneilids as well as from living neopilinids. The very small size of the bilaterally symmetrical early shell of *Bellerophon* (Amphigastropoda) indicates the presence of a planktotrophic larval stage forming this shell. A non-archaeogastropod type protoconch in *Bellerophon* testifies against the hypotheses of Yochelson (1978, 1984) and McLean (1984). Thus, *Bellerophon* and related genera (Amphigastropoda) are considered to represent an extinct, long-lived (from the Cambrian to the Triassic), independent molluscan group.

2. The higher taxonomic position of the Cambro–Devonian **Mimospirina**, uniting the Paleozoic gastropods with sinistrally coiled shells bearing a large sinistrally coiled, non-archaeogastropod protoconch, is still open. Nevertheless, the nature of the early shells in *Mimospira* demonstrates that the Mimospirina do not belong to the subclass Archaeogastropoda. In addition, the large size and shape of early shell in *Mimospira*, consisting of more than one whorl, suggests the presence of a larval stage during which the larval shell was formed. Quite differing morphologies of the early shells in members of the Mimospirina and Euomphaloidea argue against the zoological validity of the class Paragastropoda.

3. The discovery of archaeogastropod-type protoconchs in some Early Devonian gastropods indicates that the subclass **Archaeogastropoda** has had the same early ontogenetic pattern for at least 400 Ma (Devonian to Recent) and that it represents a very old, independent gastropod group.

4. The members of the order **Cyrtoneritimorpha** (Neritimorpha) may be traced according to their characteristic fish hook-like protoconch from the Early Ordovician to the Late Permian and thus about 250 million years. In the Paleozoic (Devonian?) this neritimorph group, with a typically openly coiled larval shell which developed during a planktotrophic stage, probably gave rise to the modern Cycloneritimorpha (Neritimorpha) characterized by a strongly convolute protoconch. The latter group may be traced from the Recent back to at least the Carboniferous.

5. The cyrtoneilic and planispirally openly coiled protoconch of *Euomphalus* and related taxa (Euomphalomorpha) distinguishes them from members of the other four extant subclasses of the Gastropoda (Bandel – Frýda 1998). The subclass **Euomphalomorpha** forms an independent gastropod group, known only from the Paleozoic (Cambrian–Permian). The non-archaeogastropod type of protoconch in Euomphalomorpha testifies against the zoological validity of suborder Euomphalina (McLean 1981), which was proposed to unite the members of modern Neomphaloidea (Archaeogastropoda) with the Paleozoic Euomphaloidea.

6. The members of the order **Perunelomorpha**, with an open, trochospiral protoconch, can be traced from the Early Ordovician to the Early Devonian and so the group existed for about 100 Ma. The Perunelomorpha evolved planktotrophic larvae which secreted their typical larval shell. This fact, together with the similarity of teleoconch shapes in Devonian Perunelomorpha and the oldest undoubted Caenogastropoda and Heterostropha of Carboniferous age, suggests that the Perunelomorpha may represent their ancestral group.

7. The uncoiled protoconchs found in **Cyrtoneritimorpha**, **Euomphalomorpha** and **Perunelomorpha** may represent a very old shell feature. This fact suggests that the higher gastropods (Caenogastropoda, Heterostropha, and Neritimorpha), as well as the extinct Euomphalomorpha, may have evolved from a common ancestor with an uncoiled tubular shell, and thus, not directly from the Paleozoic Archaeogastropoda and/or Amphigastropoda.

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References

- Bandel K. (1982): Morphologie und Bildung der frühontogenetischen Gehäuse bei conchiferen Mollusken. – *Fazies*, 7, 1–198.
- (1991): Über triassische "Loxonematoidea" und ihre Beziehungen zu rezenten und paläozoischen Schnecken. – *Paläont. Z.*, 65, 3–4, 239–268.
- (1992): Platyceratidae from the Triassic St. Cassian Formation and the evolutionary history of the Neritimorpha (Gastropoda). – *Paläont. Z.*, 66, 3–4, 231–240.
- (1993): Evolutionary history of sinistral archaeogastropods with and without slit (Cirroidea, Vetigastropoda). – *Freiberg. Forsch.*, C450, 41–81. Freiberg.
- (1997): Higher classification and pattern of evolution of the Gastropoda. – *Cour. Forsch.-Inst. Senckenberg*, 201, 57–81.
- (1998): Scissurellidae als Modell für die Variationsbreite einer natürlichen Einheit der Schlitzbandschnecken (Mollusca, Archaeogastropoda). – *Mitt. Geol.-Paläont. Inst. Univ. Hamburg*, 81, 1–120. Hamburg.
- Bandel, K. – Frýda, J. (1996): *Balbinipleura*, a new slit bearing archaeogastropod (Vetigastropoda) from the Lower Devonian of Bohemia and the Lower Carboniferous of Belgium. – *Neu. Jb. Geol. Paläont., Hefte* 6, 325–344.

- (1998): Position of Euomphalidae in the system of the Gastropoda. – Senckenberg. Lethaea., 78, 1/2, 103–131. Frankfurt.
- (1999, in press): Notes on the evolution and higher classification of the subclass Neritimorpha (Gastropoda) with the description of some new taxa. – *Geologica et Palaeont.*
- Bandel, K. – Geldmacher, W. (1996): The structure of the shell of *Patella crenata* connected with suggestions to the classification and evolution of the Archaeogastropoda. – *Freiberg. Forsch.*, C 464, 1–71. Freiburg.
- Batten, R. L. (1984): The calcitic wall in the Paleozoic families Euomphalidae and Platyceratidae (Archeogastropoda). – *J. Paleont.*, 58, 5, 1186–1192.
- Biggelaar, J. A. M. – Haszprunar, G. (1996): Cleavage patterns and mesentoblast formation in the Gastropoda: an evolutionary perspective. – *Evolution*, 50, 4, 1520–1540.
- Bockellie, T. G. – Yochelson, E. L. (1979): Variation in a species of “worm” from the Ordovician of Spitsbergen. – *Särtrykk av Norsk Polarinstitutt, Skrifter*, 167, 225–237.
- Dzik, J. (1978): Larval development of hyolithids. – *Lethaia*, 11, 293–299.
- (1981): Larval development, musculature, and relationships of *Sinuitiesis* and related Baltic bellerophonts. – *Nor. Geol. Tidsskr.*, 61, 2, 111–121.
- (1982): Larval development and relationships of *Mimospira*; a presumably hyperstrophic Ordovician gastropod. – *Geol. Fören. Förh.*, 104, 3, 231–239.
- (1994): Evolution of “small shelly fossils” assemblages of the Early Paleozoic. – *Acta Palaeont. Pol.*, 39, 3, 247–313.
- Frýda, J. (1988): A new species of *Modestospira* (Gastropoda) from the Ordovician of Bohemia. – *Věst. Ústř. Úst. geol.*, 63, 4, 227–232. Praha.
- (1989): A new species of *Mimospira* (Clisospiridae, Gastropoda) from the Late Ordovician of Bohemia. – *Věst. Ústř. Úst. geol.*, 64, 4, 237–241. Praha.
- (1995): Shell ontogeny of some Lower Paleozoic gastropods and its significance for higher taxonomy. – Twelfth International Malacological Congress, Vigo, 305–306. Vigo.
- (1997): Oldest representatives of the superfamily Cirroidea (Vetigastropoda) with notes on their early phylogeny. – *J. Paleont.*, 71, 5, 839–847.
- (1998a): Classification and Phylogeny of Devonian Gastropods. – Thesis, Universität Hamburg, 1–187. 28 Pls., Hamburg.
- (1998b): Some new and better recognized Devonian gastropods from the Prague Basin (Bohemia). – *Věst. Čes. geol. Úst.*, 73, 1, 41–49. Praha.
- (1998c): Did the ancestors of higher gastropods (Neritimorpha, Caenogastropoda, and Heterostropha) have an uncoiled shell? – Abstracts, 13th International Malacological Congress, Washington DC, R. Bieler & P. M. Mikkelsen (eds.), 107, Washington.
- (1998d): Higher classification of the Paleozoic gastropods inferred from their early shell ontogeny. – Abstracts, 13th International Malacological Congress, Washington DC, R. Bieler & P. M. Mikkelsen (eds.), 108, Washington.
- (1998e): Some new and better recognized Devonian gastropods from the Prague Basin (Bohemia): part II. – *Věst. Čes. geol. Úst.*, 73, 4, 355–363. Praha.
- (1999a): Taxonomic position of suborder Jinonicellina. – *Věst. Čes. geol. Úst.*, 74, 1, 27–29. Praha.
- (1999b): Three new gastropod genera from the Early Devonian of Bohemia. – *Věst. Čes. geol. Úst.*, 74, 1, 31–38. Praha.
- Frýda, J. – Bandel, K. (1997): New Early Devonian gastropods from the *Plectonotus* (*Boucotonotus*) – *Palaeozygopleura* Community in the Prague Basin (Bohemia). – *Mitt. Geol.-Paläont. Inst. Univ. Hamburg*, 80, 1–58. Hamburg.
- Frýda, J. – Blodgett, R. B. (1998): Two new cirroidean genera (Vetigastropoda, Archaeogastropoda) from the Emsian (late Early Devonian) of Alaska with notes on the early phylogeny of Cirroidea. – *J. Paleont.*, 72 (2), 265–273.
- Frýda, J. – Manda, Š. (1997): A gastropod faunule from the *Monograptus uniformis* graptolite Biozone (Early Lochkovian, Early Devonian) in Bohemia. – *Mitt. Geol.-Paläont. Inst. Univ. Hamburg*, 80, 59–122. Hamburg.
- Frýda, J. – Rohr, D. M. (1999): Taxonomy and Paleobiogeography of the Ordovician Clisospiridae and Onychochilidae (Mollusca). – *Acta Univ. Carol. geol.*
- Golikov, A. N. – Starobogatov, Y. I. (1975): Systematics of prosobranch gastropods. – *Malacologia*, 15, 1, 185–232.
- (1988): Problems of Phylogeny and System of the Prosobranchiate Gastropods. – *Trudy Zoolog. Inst. AN SSSR*, 176, 1–77.
- Harper, J. A. – Rollins, H. B. (1982): Recognition of Monoplacophora and Gastropoda in the fossil record: A functional morphological look at the bellerophont controversy. – North American Paleontological convention, Montreal, Proceedings, 1, 227–232.
- Haszprunar, G. (1985): The Heterobranchia – a new concept of the phylogeny of the higher Gastropoda. – *Zeitschrift für zool. Systematik u. Evolutionsforschung*, 23, 1, 15–37.
- (1985): The fine morphology of the osphradial sense organs of the Mollusca. I. Gastropoda, Prosobranchia. – *Philosophical Transactions of The Royal Society of London Series B – Biological Sciences*, B 307, 457–496.
- (1988): On the origin and evolution of major gastropod groups, with special reference to the Streptoneura (Mollusca). – *J. Mollusc. Studies*, 54, 367–441.
- (1988): A preliminary phylogenetic analysis of the streptoneurous Gastropoda. 7–16. In: W. F. Ponder: Prosobranch Phylogeny, Malacological Review Supplement.
- (1993): The Archaeogastropoda. A clade, a grade or what else? – *Amer. Malacol. Bull.*, 10, 165–177.
- (1995): On the evolution of larval development in the Gastropoda, with special reference to larval planktotrophy. – *Notiz CISM, XVI*, 5–13.
- (1996): The Mollusca: coelomate turbellarians or mesenchymate annelids? 3–28. In: J. D. Taylor: Origin and Evolutionary Radiation of the Mollusca. Oxford University Press, New York.
- Haszprunar, G. – Schaefer, K. (1997): Monoplacophora. 415–457. In: I. Wiley-Liss: Microscopic Anatomy of Invertebrates, Mollusca.
- Hickman, C. S. (1988): Archaeogastropod evolution, phylogeny and systematics: a re-evaluation. 17–34. In: W. F. Ponder: Prosobranch Phylogeny, Malacological Review Supplement.
- Horný, R. (1964): New Lower Paleozoic gastropod genera of Bohemia (Mollusca). – *Čas. Nár. Muz., Ř. přírodověd.*, 133 (4), 211–216. Praha.
- (1965): O systematické příslušnosti měkkýše *Cyrtolites* Conrad, 1838 (Mollusca). – *Čas. Nár. Muz., Ř. přírodověd.*, 134, 8–10. Praha.
- (1992): Vývoj názorů na klasifikaci cyklomyarňích měkkýšů (Mollusca, Monoplacophora). – *Čas. Nár. Muz., Ř. přírodověd.*, 157, 1–4, 13–50. Praha.
- (1993): Shell morphology and mode of life of the Lower Devonian cyclomyar *Neocyrtolites* (Mollusca, Tergomya). – *Čas. Nár. Muz., Ř. přírodověd.*, 162, 1–4, 57–66. Praha.
- (1994): Muscle attachment areas in the Silurian Bellerophonacean gastropods *Bellerophon scaber* (Perner) and *Bubovicus tardus* (Barrande in Perner). – *Sbor. Nár. Muz. Praha, Ř. B.*, 50, 1–4, 13–24. Praha.
- (1996): A further specimen of *Bellerophon scaber* (Perner) (Gastropoda) with preserved retractor muscle scars (Silurian, Bohemia). – *Čas. Nár. Muz., Ř. přírodověd.*, 165, 1–4, 59–62. Praha.
- Hynda, V. A. (1986): Melkaja bentosnaja fauna ordovika jugo-zapada Vostočno-Evropskoj platformy. 1–153. S.I. Pasternak, editor. Akademia Nauk USSR – Naukova Dumka, Kiev.
- Knight, J. B. (1947): Bellerophon muscle scars. – *J. Paleont.*, 21, 3, 264–267.
- (1952): Primitive fossil gastropods and their bearing on gastropod classification. – *Smithsonian misc. Coll.*, 117, 13, 1–56.
- Knight, J. B. – Cox, L. R. – Myra, A. – Batten, R. L. – Yochelson, E. L. – Robertson, R. (1960): Systematic descriptions (Archaeogastropoda). 169–324. Treatise on Invertebrate Paleontology. Geological Society of America, Inc. and University of Kansas Press, Lawrence, Kansas.
- Knight, J. B. – Yochelson, E. L. (1958): A reconsideration of the relationships of the Monoplacophora and the primitive gastropoda. – *Malacol. Soc. London, Proc.*, 37–48.
- Koken, E. (1889): Über die Entwicklung der Gastropoden vom Cambrium bis zur Trias. – *Neu. Jb. Mineral. Geol. Paläont.*, 6, 305–484.

- (1897): Die Leitfossilien, ein Handbuch für den Unterricht und das Bestimmen von Versteinerungen. 1–848. Leipzig.
- Kollmann, H. A. – Yochelson, E. L. (1976): Survey of Paleozoic gastropods possibly belonging to the subclass Opisthobranchia. – Ann. Naturhist. Mus. Wien, 80, 207–220.
- Koninck, L. G. d. (1881): Faune du Calcaire Carbonifère de la Belgique, Gastéropodes. – Ann. Mus. Roy. Hist. Natur. Belgique, VI, 1–170.
- (1883): Faune du calcaire carbonifère de la Belgique 4 partie, Gastéropodes (suite et fin). – Ann. Mus. Roy. Hist. Natur. Belgique, 8, 1–240.
- Kříž, J. – Lukeš, P. (1974): Color patterns on Silurian *Platyceras* and Devonian *Merista* from the Barrandian area, Bohemia, Czechoslovakia. – J. Paleont., 48, 1, 41–48.
- Lemche, H. – Wingstrand, K. G. (1959): The anatomy of *Neopilina galathea* Lemche, 1957 (Mollusca, Tryblidiacea). – Galathea Rep., 3, 9–71.
- Linsley, R. M. – Kier, W. M. (1984): The Paragastropoda; a proposal for a new class of Paleozoic Mollusca. – Malacologia, 25, 1, 241–254.
- Marshall, B. A. (1983): Recent and Tertiary Seguenziidae (Mollusca: Gastropoda) from the New Zealand region. – N. Zealand J. Zool., 10, 235–262.
- McLean, J. H. (1981): The Galapagos rift limpet *Neomphalus*; relevance to understanding the evolution of a major Paleozoic–Mesozoic radiation. – Malacologia, 21, 1–2, 291–336.
- (1984): A case for derivation of the Fissurellidae from the Bellerophonacea. – Malacologia, 25, 1, 3–20.
- Naef, A. (1911): Studien zur generellen Morphologie der Mollusken. – Ergebn. Fortschr. Zool., 3, 73–164.
- Nützel, A. (1997): Über die Stammesgeschichte der Ptenoglossa (Gastropoda). – Berlin. Geowissensch. Abh., E, 26, 229 pp.
- Peel, J. S. (1980): A new Silurian retractile monoplacophoran and the origin of the gastropods. – Proc. Geol. Assoc., Parts 1–2, 91–97.
- (1982): Muscle scars in *Bellerophon recticostatus* (Mollusca) from the Carboniferous of Ireland. – J. Paleont., 56, 5, 1307–1310.
- (1986a): Muscle scars in *Porcellia* (Gastropoda; Pleurotomariacea) from the Carboniferous of England. – Meddr. Dan. Geol. Foren., 35, 1–2, 53–58.
- (1986b): Systematics and mode of life of a new Silurian *Clisospira* (Mollusca). Rapp. Grond. geol. Unders. 128, 65–74.
- (1991a): Functional morphology of the class Helcionelloida nov., and the early evolution of the Mollusca. 157–177. In: A. Simonetta – M. S. Conway: The early evolution of Metazoa and the significance of problematic taxa. Cambridge Univ. Press and Univ. Camerino, Cambridge.
- (1991b): The classes Tergomya and Helcionelloida, and early molluscan evolution. – Bull. Groenlands Geol. Unders., 161, 11–65.
- Phillips, J. (1841): Figures and descriptions of the Palaeozoic fossils of Cornwall, Devon, and West Somerset. 1–231. Longman, Brown, Green et al. editors. Longman, Brown, Green, and Longmans, London.
- Ponder, W. F. – Lindberg, D. R. (1996): Gastropod phylogeny-challenges for the 90s. 135–154. In: J. D. Taylor: Origin and Evolutionary Radiation of the Mollusca. Oxford University Press, New York.
- (1997): Towards a phylogeny of gastropod molluscs: an analysis using morphological characters. – Zool. J. Linnean Soc., 119, 83–256.
- °Ponder, W. F. – Warén, A. (1988): Classification of the Caenogastropoda and Heterostropha – a list of the family-group names and higher taxa. 288–326. In: W. F. Ponder: Prosobranch Phylogeny, Malacological Review Supplement.
- Rollins, H. B. – Batten, R. L. (1968): A sinus-bearing monoplacophoran and its role in the classification of primitive molluscs. – Palaeontology, 11, 1, 132–140.
- Runnegar, B. (1981): Muscle scars, shell form and torsion in Cambrian and Ordovician univalved molluscs. – Lethaia, 14, 4, 311–322.
- (1983): Molluscan phylogeny revisited. – Mem. Ass. Australas. Palaeontols., 5, 121–144.
- (1996): Early evolution of the Mollusca: the fossil record. 77–88. In: J. D. Taylor: Origin and Evolutionary Radiation of the Mollusca. Oxford University Press, New York.
- Runnegar, B. – Jell, P. A. (1976): Australian Middle Cambrian molluscs and their bearing on early molluscan evolution. – Alcheringa, 1, 2, 109–138.
- Runnegar, B. – Pojeta, J. J. (1974): Molluscan phylogeny; the paleontological viewpoint. – Science, 186, 4161, 311–317.
- Salvini-Plawen, L. v. (1980): A reconsideration of systematics in the Mollusca (phylogeny and higher classification). – Malacologia, 19, 249–278.
- Salvini-Plawen, P. L. – Haszprunar, G. (1987): The Vetigastropoda and the systematics of streptoneurous gastropods (Mollusca). – J. Zool., A 211, 747–770.
- Simroth, H. (1906): Mollusca. In: H. G. Bronn: Klassen und Ordnungen des Tier-Reichs, ed. 2, 3, 85–89.
- Starobogatov, Y. I. (1970): K sistematike rannepaleozoyskikh Monoplacophora. – Paleontol. Zh., 3, 6–17.
- Taylor, D. W. – Sohl, N. F. (1962): An outline of gastropod classification. – Malacologia, 1, 1, 7–32.
- Thiele, J. (1929): Handbuch der systematischen Weichtierkunde. Gustav Fischer Verlag, Jena.
- Urgorri, V. – Troncoso, J. S. (1994): A second record of *Laevipilina rolani* Warén and Bouchet, 1990 (Mollusca: Monoplacophora) from the Northwest of Spain. – J. Moll. Stud., 60, 157–163.
- Wahlman, G. P. (1992): Middle and Upper Ordovician symmetrical univalved mollusks (Monoplacophora and Bellerophonina) of the Cincinnati Arch region. – U.S. Geol. Surv. Profess. Pap. 1066-O, O1–O203.
- Wängberg-Eriksson, K. (1979): Macluritean gastropods from the Ordovician and Silurian of Sweden. Sver. Geol. Unders., Serie C, 72, 1–33.
- Warén, A. (1988): *Neopilina goesi*, a new Caribbean monoplacophoran mollusk dredged in 1869. – Proc. Biol. Soc., Washington, 101, 676–681.
- Warén, A. – Hain, S. (1992): *Laevipilina antarctica* and *Micropilina arntzi*, two new monoplacophorans from the Antarctic. – The Veliger, 35, 165–176.
- Wenz, W. (1939–1943): Gastropoda, Handbuch der Palaeozoologie, 1–6, 1–1639. O. H. Schindewolf.
- (1940): Ursprung und frühe Stammesgeschichte der Gastropoden. – Archiv für Molluskenkunde, 72, 1–10.
- Wingstrand, K. G. (1985): On the anatomy and relationships of Recent Monoplacophora. – Galathea Rep., 16, 7–94.
- Yochelson, E. L. (1956): Euomphalacea, Trochonematacea, Pseudophoracea, Anomphalacea, Craspedostomatacea, and Platyceratacea, Permian Gastropoda of the southwestern United States. – Bull. Amer. Mus. Nat. Hist., 110, 173–275.
- (1967): Quo Vadis, *Bellerophon*? 141–161. In: R. C. Moore: Essays in paleontology and stratigraphy. Kansas Univ. Dept. Geology.
- (1978): An alternative approach to the interpretation of the phylogeny of ancient mollusks. – Malacologia, 17, 2, 165–191.
- (1984): Historic and current considerations for revision of Paleozoic gastropod classification. – J. Paleont., 58, 1, 259–269.
- Yochelson, E. L. – Kříž, J. (1974): Platyceratid gastropods from the Oriskany Sandstone (Lower Devonian) near Cumberland, Maryland; synonymies, preservation and color markings. – J. Paleont., 48, 3, 474–484.
- Yoo, E. K. (1988): Early Carboniferous Mollusca from Gundy, Upper Hunter, New South Wales. – Rec. Austr. Mus., 40, 3–4, 233–264.
- (1994): Early Carboniferous Gastropoda from the Tomworth Belt, New South Wales, Australia. – Rec. Austr. Mus., 46, 63–120.

Vyšší klasifikace paleozoických gastropodů odvozená z ontogeneze jejich rané schránky

Studium morfologie protokonch u silurských a devonských gastropodů z pražské pánve odhalilo přítomnost šesti přirozených skupin (Amphigastropoda, Archaeogastropoda, Mimospirina, Cyrtoneritimorpha, Euomphalomorpha, and Perunelomorpha). Charakter protokonchy u rodu *Bellerophon* dokazuje, že taxon Amphigastropoda nepatří do podtřídy Archaeogastropoda a tvoří nezávislou skupinu se značným stratigrafickým rozsahem (kambrium–trias). Velmi malá velikost bilaterálně symetrické protokonchy u rodu *Bellerophon* (Amphigastropoda) naznačuje přítomnost planktotrofního larvalního stadia. Vyšší taxonomická pozice kambro–devonského taxonu Mimospirina, který sdružuje paleozoické gastropody se sinistrálně točenou schránkou nesoucí velkou, sinistrálně točenou protokonchu, je dosud nejistá. Objev archaeogastropodového typu protokonchy u raně devonských gastropodů dokazuje, že podtřída Archaeogastropoda měla stejný typ rané ontogeneze během posledních 400 miliónů let (devon–recent) a reprezentuje velmi starou, nezávislou skupinu gastropodů. Raně ordovičtí až pozdně permští zástupci řádu Cyrtoneritimorpha (Neritimorpha) s charakteristickou hákovitou protokonchou pravděpodobně dali vznik moderním zástupcům řádu Cycloneritimorpha (Neritimorpha). Euomphalomorpha se planispirální, otevřeně točenou protokonchou tvoří nezávislou skupinu gastropodů, která je známa pouze z paleozoika (kambrium–perm). Raně ordovičtí až raně devonští zástupci řádu Perunelomorpha s otevřenou, trochospirálně točenou protokonchou měli planktotrofní larvu, která sekretovala jejich typickou larvální schránku. Řád Perunelomorpha může reprezentovat předky podtřídy Caenogastropoda a Heterostropha. Otevřeně točená protokoncha nalezená u taxonů Cyrtoneritimorpha, Euomphalomorpha a Perunelomorpha je pravděpodobně velmi starým znakem. Vyšší gastropodi (Caenogastropoda, Heterostropha a Neritimorpha) jakož i fosilní Euomphalomorpha se mohli vyvinout ze společného předka s otevřeně točenou, tubulární schránkou, a tedy nikoliv přímo z paleozoických zástupců podtřídy Archaeogastropoda a/nebo Amphigastropoda.

RECENZE

Stratigraphische Kommission Deutschlands: Stratigraphie von Deutschland II. Ordovizium, Kambrium, Vendium, Riphäikum. Teil I: Thüringen, Sachsen, Ostbayern. – Courier Forschungsinstitut Senckenberg, 200, 437p. ISSN 0341-4116, ISBN 3-929907-43-7. Frankfurt a. M. 1997.

Německá stratigrafická komise při Německé unii geologických věd si předsevzala dlouhodobý a nelehký úkol: postupně publikovat obsažené monografické stratigrafické lexikony, které by obsáhly jednotlivé úseky geologické minulosti ve stratigrafickém a regionálně geologickém pořádku. Předložený svazek je věnován svrchnímu proterozoiku (rifeji a vendu), kambriu a ordoviku oblasti Durynska, Saska a východního Bavorska.

Na sestavení svazku se podílelo celkem 24 autorů, mezi nimiž nechybějí i u nás dobře známí badatelé, jako E. a P. Bankwitz, H. Brause, O. Elicki, F. Falk, G. Geyer, G. Hirschmann, G. Stettner a K.-A. Tröger. Látka je uspořádána podle regionálně geologických jednotek – např. Schwarzburské antiklinorium, Fransko-durinské břidličné pohoří, münchberský komplex, Smrčiny a Oberpfälzer Wald, Vogtland, Erzgebirge (Krušné hory), Středosaské granulitové pohoří, Labská zóna, Lužický masiv, Severosaské břidličné pohoří, sz. Sasko, veserské synklinorium, zóna Erbsdorf-Vohenstrauß a Bavorský les.

Uvnitř regionálně geologických jednotek je pak látka poněkud neobvykle uspořádána od mladších jednotek ke starším, v zásadě podle geologických útvarů. Jádrem celé monografie jsou podrobné charakteristiky jednotlivých litostratigrafických jednotek, mezi nimiž se rozlišují skupiny (Gruppe), souvrství (Formation) a Folge (sledy odpovídající souvrstvím nebo členům naší terminologie).

Každá regionálně geologická jednotka je uvedena úvodní statí o zásadách stratigrafického dělení. Jádrem jsou pak stručné a výstižné charakteristiky jednotlivých litostratigrafických jednotek, které vždy obsahují definici jednotky (odkazy na definice dřívější i definici nyníější), litologickou charakteristiku, rozšíření, zastoupení v jiných regionálně geologických celcích, charakteristiku svrchní a

spodní hranice, mocnost, další podrobnější dělení (spolu s údaji o nižších členech), upozornění na zvláštní korelační horizonty, lito-logicko-faciální zvláštnosti, podmínky vzniku, magmatismus, pale-ontologickou charakteristiku, data o deformacích, metamorfóze radiometrickém stáří (často chybí), chronostratigrafické zařazení (uváděné jako „Stratigraphisches Alter“) a odkazy na hlavní literaturu. Všechny tyto údaje jsou uvedeny i v případech, když data chybějí, např. s poznámkou „Keine“, nebo „Bisher unbekannt“.

Tím, že je zachován jednotný plán u všech jednotek, je zajištěna jasná a snadná orientace a vystižení i stupeň současných znalostí i s jeho mezerami.

Některé jednotky zasahují i na naše území, např. Brambach Gruppe je dělena na souvrství Oloví, Aš-Krajková a Mokřiny se zachová-ním českého pravopisu (zásada zachování jména podle země původu, zakotvená v International Stratigraphic Guide, je většinou dodržo-vána, což je jistě sympatické). Protože jednotek zasahujících na naše území je zejména v oblasti Krušných hor větší počet, je dílo význam-né i pro naše pracovníky, kteří se věnují sasko-durynské oblasti.

K textu je připojeno 50 kreslených mapek a stratigrafických sché-mat, dílo zakončují velmi přehledné korelační tabulky pro jednotli-vé útvary, které obsahují i údaje o litologii, charakteru vyvřelin, výskytu zkamenělin a užitečných ložiscích. Výčet literatury zaplňu-je 26 stran a nechybějí v něm ani citace českých autorů.

Jako celek jde o dílo velmi hodnotné, přehledné a mnohostranně potřebné. Rozhodně by mělo být známé a přístupné všem pracovní-kům, kteří se zabývají sasko-durynskou oblastí. Jako další díly mo-nografické řady jsou plánovány svazky o prevariských jednotkách Schwarzwald, předsilurských jednotkách středoněmecké krystal-i-nické zóny i severního a západního Německa. Na poněkud vzdále-nějším obzoru se rysuje i monografie o německém siluru. Z díla je zřejmé, že Stratigrafická komise Německa má nejen rozsáhlé, ale i v daných podmínkách uskutečnitelné plány, které odrážejí i po-chopení významu stratigrafie jako jednoho ze základních oborů geologických věd vyššími místy, což se v našich poměrech zatím nedaří prosadit.

Ivo Chlupáč