Higher classification of Paleozoic gastropods inferred from their early shell ontogeny

Výšší klasifikace paleozoických gastropodů odvozená z ontogenese jejich rané schránky
(Czech summary)

(7 text-figs.)

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The presence of six natural groups (Amphigastropoda, Archaeogastropoda, Mimospirina, Cyrtoneritimorpha, Euomphalomorpha, and Perumelomorpha) 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 sinistral 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 cyrtococon 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 Perumelomorpha, with an open, trochospiral protoconch, evolved larvae which secreted their typical larval shell. The Perumelomorpha may represent an ancestral group of the Caenogastropoda and Heterostropha. The uncoiled protoconchs found in Cyrtoneritimorpha, Euomphalomorpha and Perumelomorpha 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.

Key words: Paleozoic, Gastropoda, evolution, shell ontogeny, protoconch

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 distinct higher taxonomic categories like the Bellerophonita, Macluritina, Euomphalina, and Paragastropoda, which have been established for Paleozoic gastropods. The relationships of these megat taxa to extant gastropod groups are uncertain and often mysterious. Recent gastropods have been placed in one of four gastropod megataxes (=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 (Fryda 1995, 1997, 1998a–e, 1999a, b; Fryda – Bandel 1997; Fryda – Blodgett 1998; Fryda – Manda 1997; Bandel – Fryda 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 Plecto bellus (Boucoticonus) – Palaeozygoploidea Community (Fryda – 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 Perumelomorpha) 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 bellerophoniform molluscs, as well as about their shells with well preserved muscle scars, were published (see Horný 1992, Pecl 1991a, b, and Wahlman 1992 for review). However, interpretation of these data has divided paleontologists, who have variously argued that bellerophoniform molluscs were untorted, exogastrically oriented monoplacophorans, or torted, endogastrically oriented gastropods, or a polyphyletic combination of both (see Horný 1992, Pecl 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 Anphineura and Bellerophonatae. For this reason Wenz (1940, 1943) placed Cyttonella together with Tryblidiidae and Bellerophon-like molluscs into the new subclass Amphigastropoda. Wenz thus emended the Amphigastropoda of Simroth, who had used this name only for bellerophonid molluscs. Wenz also placed the subclass Amphigastropoda together with the subclasses Prosobranchia (=Streptonura) 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 Sinuites and Bellerophon and interpreted them as evidence that these genera were torted gastropods. He also agreed with Wenz’s conclusion that the genus Cyttonella 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 bellerophonid molluscs were placed within the suborder Bellerophontina Ulrich and Scofield, 1897 of the order Archaeogastropoda Thiele, 1925. The Bellerophonidae have been considered to be torted, in contrast to Cyttonella and its relatives which were placed in the order Tryblidioida Lemeche, 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 Lemeche, 1957 is the only order placed into this subclass. According to Horný, the subclass Cyclomya includes two orders: Archinacellida Knight and Yochelson, 1958 and Cytonellida Horný, 1963.

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

On the basis of the discovery of symmetrically disposed multiple muscle scars in the Devonian bellerophoniform species Sinuites acutilib. Rollins and Batten (1968) noted that such a character as a sinus or slit can no longer 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 Bellerophontinae). 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 bellerophoniform 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 bellerophoniform and pleurotomarioid 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: Cyttonellida, Tryblidiida, and Bellerophontida.

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

Salvini-Plawen (1980) analyzed the higher taxonomy of the Mollusca and also discussed the taxonomic position of bellerophoniform 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 bellerophoniform molluscs earlier than torsion (the primary character of the Gastropoda). Thus the presence of a dorsal sinus in bellerophoniform molluscs could not be taken as evidence for torsion of their soft body. Bellerophoniform 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 (Perser, 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, Cyrtoneillina, 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 Sylvrostrophaera 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 Cyrtoneillida 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. Bellerophontoidea 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 Echscholtz 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 Bellerophontoididea 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 bellerophonoides nor gastropods. According to Yochelson (1984) the Bellerophontoididea originated from pleurotomariaeans.

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 unsorted symmetrical univalved molluscs. Members of the class Tergomya Peel, 1991b (= Tergomya Horňý, 1965 + Cyclomya (in part) Horňý, 1965) are considered to be exogastric molluscs in contrast to the Helcionelloida 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 (Neottiephora, Caenogastropoda and Heterostropha). 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; Fryda 1998a–e, 1997–1999). 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 Monolophocera is still poor. Leneche and Winslow (1960) wrongly described and figured a protoconch of Neoportula galathea as a helicoid protoconch. According to Haszprunar and Schaefer (1997) the neopilitid protoconch is known only in small species and is bowl shaped. The shell apex of these living Monolophocera shows two distinct zones (Varén, 1988; Uroporina - Trouncos, 1994). This fact may indicate the existence of a true larval shell (i.e., protoconch II; Haszprunar - Schaefer, 1997). According to Varén (in Haszprunar - Schaefer, 1997) it is not known how the protoconch of nepilinids is lost after metamorphosis.

Dzik (1981) described and figured early shells of the bellerophontiform genera Simulopsis and Modiostoma which are bilaterally symmetrically coiled. The early shell of Modiostoma 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 Fryda (1988) in Modiostoma mergi from the Ordovician strata of Bohemia.

Horňý (1993) described the early shell of a cyrtocelid species Neocyclostomites advena (Perner, 1903) (= Cyclostomella 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.
in cyrtonellid 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 (Fryda 1998a, b; Bandel – Fryda, 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

Fig. 2. Archaeogastropoda – Coccoidea. 1 – apertural view of *Alaskiella medroensis* from the late Early Devonian (Emsian) of the west-central Alaska, x25; 2, 3 – *Alaskanerita bandeii* 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 – *Perneriterita sinistrorsus* from the Late Silurian of the Prague Basin (Bohemia), apical view, x4; 5 – *Barrandeiceras filamentis* from the *Prionopelis archiaci – Arrypeideos modesta* Community (late Ludfordian, Ludlow, Silurian; Prague Basin), apical view of the sinistrally coiled teleoconch with deeply concave apical depression formed by the umbilicus of dextrally coiled initial portion of shell, x8.
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 cyrtellids (like *Sinuitopsis*; Dzik, 1982) as well as from living nopolinids (Haszprunar – Schaefer, 1997). Thus, these data suggest that bellerophoniform 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 studies, 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 Clisopiridae 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 Macluritoida and Clisopiridae 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 Clisopiridae 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 unifying the Onychochilidae (including Clisopiridae and Onychochilidae), Macluritidae, and possibly the Euomphaloidae in a new order Hyperstrophida of a new class Paragastropoda. The class Paragastropoda has been considered to represent untor-ted molluscs. However, the quite different early shell ontogeny of members of the Onychochilidae and Euomphaloidae (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 Macluritoida, and “sinistral hyperstrophiic” Ordovician *Mimospira* is mentioned as their possible example. However, there is no evidence that Ordovician *Mimospira* and related genera belonging to the superfamaly Onychochilidae were “sinistral hyperstrophiic”. In addition, there is no data about the protoconchs of any members of the superfamaly Macluritoida. The teleoconch shapes of macluritoidan gastropods are far from those of the early Heterostropha of Early Carboniferous age. In summary, the Cambro–Devonian Mimospirina (Clisopiridae 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 determinati-on 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).
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 teleconch shell characters in Paleozoic gastropods. Recent studies (Friýa – Bandel 1997; Friýa – Manda 1997; Friýa 1998a, b, c; Bandel – Friýa 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 – Friýa 1996; Bandel – Gelmacher 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 Scissurelloida (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 Trochoidea 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 Porcellidiidae (Bandel 1993). The oldest representatives of the Cirroidea are known from the Paleozoic, the oldest representatives of the Porcellidiidae 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 Porcellidiidae bearing a slit evolved during the Triassic into members of the Cirridae that lacked a slit. However, the discovery of Alaskanthus bandelli Frýda and Blodgett, 1998, coming from the late Early Devonian (Emsian) of Alaska has changed our view on the early phylogeny of the family Cirroidea, 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 Porcellidiidae (planispirally coiled teleoconch and dextrally coiled early shell), but in contrast they bear no selenizone. The discovery of these gastropods (Alaskanthus and Pavlodiscus) has suggested that the family Cirridae separated from the family Porcellidiidae 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 species 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, unpublished 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 Wärén (1988). On the other hand, Golikov and Starobogatov (1975) placed the Loxonematoidea, together with the superfamilies Achioidae, 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 Protorculidae (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 (Kotyphchia and Stylolena) and Palaeozygopleuridae (Palaeozygopleura) had a large archaeogastropod-type protoconch and thus no larval shell formed during their ontogeny (Frýda – Bandel 1997; Frýda unpublished 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-
logastropoda Fryda 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 Neritoidae, Hydrocenoidae, Titiscanioidea, and possibly also the Cocculinoidea. Salvini-Plawen and Haszprunar (1987) placed the Neritopsisina (=Neritimorpha), together with the Docoglossa, Cocculiniforma, Vetigastropoda, Seguziina, and Architaeniglossa, in the Archaeogastropoda which they considered to be a paraphyletic group. Later, Haszprunar (1993) again suggested placing the Neritimorpha and the architaeniglossate groups (Cyclophoroidea and Ampullarioidae) 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 Biggeelaar and Haszprunar (1996), who characterized this large gastropod taxon by its cleavage patterns. The results of this study suggest that the Neritimorpha forms a gastropod group which is far removed from the Docoglossa (=Patello gastropoda) 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; Fryda unpubl, data) seems to be conformable with this view. However, new discoveries of well-preserved early shells in the members of the family Platyceratidae (Fryda 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 (Fryda 1998a, b, c; Bandel – Fryda, 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 – Vitaviella reticulata from the Monograptus uniformis graptolite Biozone (Lochkov Formation; early Lochkovian, Early Devonian; Prague Basin), 2 – protoconch of Vitaviella reticulata, x65; 3 – oblique view of juvenile shell, x38; 4, 5 – lateral and oblique views showing a reticulate ornamentation, 4 – x25, 5 – x28.

Eumphalomorphida

Koninck (1881) established his family Eumphalidae 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 eumphalid gastropods to be related with the members of the Pleurotomarioida because he observed a morphological convergence among both groups. He thus concluded that the Pleurotomarioida and the Eumphalidae arose from the same stock. Wenz (1938) placed the family Eumphalidae, together with the families Omphalocirridae, Platyceridae, Cirridae, Oriostomatidae, Puleumitidae and Macluritidae, within the superfamily Eumphalaceae (= Eumphalidoidea). All members of the Eumphaloida were considered by Wenz to belong to the Archaeogastropoda. Yochelson (1956) interpreted the Eumphaloida to have been derived from the Macluritoida in the Early Ordovician and he placed three families, Eumphalidae, Helicotomidae and Omphalostrochiidae 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 Eumphalidoidea. For this reason McLe-
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 Clisopilidae 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 cyrtococonic and planispiral, openly coiled protoconch in the Devonian and Carboniferous genera *Euomphalus, Strapatollia, Serpulospira, Phymatifer, Schizostoma*, and *Nodeuomphalus* that form the core group of the superfamily Euomphaloidea Koníček, 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 Heterostropha. 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 megat taxa like the Archaeogastropoda, Euomphalomorpha, Neritimorpha (Cycloneritimorpha and Cyrtoneritimorpha), Caenogastropoda and Heterostropha. For this reason, these gastropods have been placed in a new order Perunelo-
morphe based on the superfamily Peruneloidea which unites two families, the Perunelidae and Chucilinidae (Fryda – Bandel 1997; Fryda 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 (Fryda 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 Heterostropha. 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 planospirally) coiled early shells unlike the Euomphalomorpha. Secondly, Perunelomorpha have a smaller and less bulbous initial shell portion that is found in any euomphalomorph gastropods studied so far (Bandel – Fryda 1998). The members of the Cytoneeritimorpha, 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 (Bockelie – Yochelson 1979; Dzik 1994; Fryda – Bandel 1997; Fryda – Manda 1997; Fryda 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 (Fryda, unpubl. data).

A new model of gastropod evolution

On the basis of protoconch morphology, the presence of six natural groups (Amphigastropoda, Archaeogastropoda, Mimospirina, Cytoneeritimorpha, 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), Salmi-Piianen (1980), and Bandel and Geldmacher (1996) that the Amphigastropoda represent gastropods in which torsion of the soft body occurred, only after complete embryogenesis when the shell was mineralized. However, the question of whether the Amphigastropoda were rotated 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 mesotoblast formation in this group in comparison with those in subclasses Neritimorpha, Caenogastropoda and Heterostropha. All these facts together with evidence for the same pattern of early ontogeny in the Archaeogastropoda during the last 400 million years (Fryda – Manda 1997) suggest that this group represent a very old, independent gastropod group.

The members of the subclass Euomphalomorpha and the orders Cytoneeritimorpha and Perunelomorpha had an openly coiled early whorl. As noted by Bandel and Fryda (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 Cytoneeritimorpha and Perunelomorpha. The members of the order Cytoneeritimorpha are considered to be related 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 Cytoneeritimorpha and extant Neritimorpha (= Cycconeritimorpha). 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 Heterostropha (Bandel 1997, Fryda 1998a–c). The similarity of teleoconch shapes of the Devonian Perunelomorpha (Zenospira and Chuchilina; Fryda – Bandel 1997; Fryda – Manda 1997) with those of the oldest undoubted Caenogastropoda and Heterostropha (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 Heterostropha. In addition, an uncoiled planktotrophic larval shell was present in some Carboniferous caenogastropods (e.g., Globozoga mediocris; Nützel 1997, Pl. 34 A–C).
**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 (Cycloneritimorpha, Perunelomorpha, and Euomphalomorpha; Fryda – Bandel 1997; Fryda – Manda 1997; Bandel 1997; Bandel – Fryda 1998, 1999; Fryda 1998a, b, c). The Ordovician–Permian Cycloneritimorpha 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 – Fryda 1998). Thus, uncoiling of protoconchs found in the above-mentioned groups may represent a very old shell feature (Fryda 1998c). In contrast to these groups, the latter feature is not known among the members of the subclasses Archaeogastropoda and Amphigastropoda (Belleroaphon 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 phyletic 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 (Fryda 1995, 1997, 1998a–e, 1999b; Fryda – Bandel 1997; Fryda – Blodgett 1998; Fryda – Manda 1997; Bandel – Fryda 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 warenti Fryda, 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 (Fryda 1999, in prep.).
Conclusions

1. The nature of the early shells in the core genus Bellerophon (Amphigastropoda) does not belong to the subclass Archaeogastropoda. In addition, the early shells in Bellerophon differ from those of sinuate cyrtocelids 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 Cyrtoteritimorpha (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 cyrtocoonic and planispirally openly coiled protoconch of Euomphalus and related taxa (Euomphaloida) distinguishes them from members of the other four extant subclasses of the Gastropoda (Bandel & Frýda 1998). The subclass Euomphaloidea forms an independent gastropod group, known only from the Paleozoic (Cambrian–Permian). The non-archaeogastropod type of protoconch in Euomphaloida 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 Perumelomorpha, with an open, trochospheric protoconch, can be traced from the Early Ordovician to the Early Devonian and so the group existed for about 100 Ma. The Perumelomorpha evolved planktotrophic larvae which secreted their typical larval shell. This fact, together with the similarity of teleconch shapes in Devonian Perumelomorpha and the oldest undoubted Caenogastropoda and Heterostropha of Carboniferous age, suggests that the Perumelomorpha may represent their ancestral group.

7. The uncoiled protoconchs found in Cyrtoteritimorpha, Euomphaloida and Perumelomorpha may represent a very old shell feature. This fact suggests that the higher gastropods (Caenogastropoda, Heterostropha, and Neritimorpha), as well as the extinct Euomphaloida, 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


— (1999): Notes on the evolution and higher classification of the subclass Neritimorphia (Gastropoda) with the description of some new taxa. — Geol. Tidschr. 80, 1–6.


(1940): Ursprung und frühe Stammesgeschichte der Gastropoden. – Archiv für Molluskenkunde, 72, 1–10.
Vyšší klasifikace paleozoických gastropodů odvozená z ontogeneze jejich rané schránky


Německá stratigrafická komise při Německé unii geologických věd si převedla dlouhodobý a nenechý klíš: postupně publikovat obsažné monografické stratigrafické lexikony, které by obsahly jed- notlivé úseky geologické minulosti ve stratigrafickém a regionálně geologickém pořadí. Předložený svazek je věnován svrchnímu proterozoïkum (říjfen a vendú), kambr a ordiviku oblasti Duryńska, Sasky a východního Bavorska.


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

Každá regionálně geologická jednotka je uvedena úvodním stavbou o zásadách stratigrafického dělení. Jížem jsou pak stručně a výsítkém charakteristiky jednotlivých litostatigrafických jednotek, které vždy obsahují definici jednotky (odkazy na definice dřívější i definici nynější), litologickou charakteristiku, rozšíření, zastoupení v jiných regionálně geologických celcích, charakteristiku svrchní a spodní hranice, močnost, další podrobnější dělení (spolu s údaji o nižších členech), upozornění na zvláštní korelace, horizonty, litol- ogicko-facilitní zvláštnosti, podmínky vzniku, magnatismus, palaeo- ontologickou charakteristiku, data o deformacích, metamorfózy radiometrickém střídání (často chybějící), chronostatigrafické zařazení (sváděné jako "Stratigraphisches Alter") a odkazy na hlavní literaturu. Všechny tyto údaje jsou uvedeny i v případě, kdychy data chybějí, např. s poznánkou "Keine", nebo "Bisher unbekannt".

Tím, že je zachován jednotný plán u všech jednotek, je zajištěna jasná a snadná orientace a vystičení i stopu současných znalostí i s jeho mezerní.


K textu je připojeno 50 kreslených mapek a stratigrafických sché- mat, důležité zakončují velmi přehledné korelační tabulky pro jednotli- vé útvary, které obsahují i údaje o litologii, charakteru vyučování, výskytu zkamenělin a užitkových ložiscích. Výcet literatury zapřímu- je 26 stran a nechybí v něm ani citace českých autůr.

Jako celek jde o důležité hodnotné, přehledné a mnohostranné potřebné. Rodné bývá mělo být známe a přístupné všem pracovní- kům, kteří se zabývají sasko-durinskou oblasti. Jde dálší důležitou monografické řady jsou plánovány svazky o prevariských jednotkách Schwarzwaldu, předšleských jednotkách sředosaské krystal- nicí zóny i severního a západního Německa. Na počátku vzdále- nějších oborů se rychle a monografie o německém útvaru. Z jížem je zřejmé, že Stratigrafická komise Německa má nejen rozsáhle, ale i v daných podmínkách uskutečnitelné plány, které odrážejí a pochopení významu stratigrafie jako jednoho ze základních oborů geologických věd vyššími misty, což se v našich poměrech zatím nedaří prosadit.