## New Early Devonian gastropods from the Plectonotus (Boucotonotus) - Palaeozygopleura Community in the Prague Basin (Bohemia)

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#### Contents

Abstract	1
Zusammenfassung	2
1. Introduction	2
2. Geological setting	3
3. Subclass Archaeogastropoda Thiele, 1925	
4. Order Vetigastropoda Salvini-Plawen, 1980	5
4.1 Morphogroup Trochomorpha	5
4.2 Morphogroup Selenimorpha	17
5. Order Stylogastropoda nov.	18
6. Order Uncertain, Superfamily Peruneloidea	25
Acknowledgements	31
References	31

#### Abstract

A detailed study based on the shape of the early whorls of some Early Devonian gastropods from the *Plectonotus* (*Boucotonotus*) - *Palaeozygopleura* Community of the Prague Basin (Bohemia) enables the reevalution of their higher taxonomic position. The *Plectonotus* (*Boucotonotus*) - *Palaeozygopleura* Community consists of a highly diversified (several tens of species), small-sized fauna derived from deeper-water, mainly micritic Early Devonian limestones of the Prague Basin. Among gastropods from this community, the genera *Katoptychia* Perner, 1907, *Stylonema* Perner,

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gastropods. This is due to ignorance of the importance of the shape of the initial whorls in classification and due to the destruction of this early delicate portion of the shell during diagenesis. It now became possible to collect and study a species-rich fauna of Early Devonian gastropods from the vicinity of Prague in which the early shell portions are preserved. It has also been possible within the last few years to characterize living gastropods according to the shape of their early shells (protoconchs) in connection with their teleoconchs in such a way that a taxonomy based on anatomy can be understood by looking at shell morphology. The different subclasses of the Gastropoda can thus be characterized by shell shape, and within these groups can be recognized and traced through the fossil record. It has thus been possible to trace the extant subclasses of the Gastropoda, namely Archaeogastropoda, Neritimorpha, Caenogastropoda and Heterostropha through the Mesozoic and into the Permian/Carboniferous (Bandel 1991, 1992, 1993, 1995, 1996). As more detailed knowledge about the character of protoconchs from Lower Devonian gastropods from the Prague Basin has been elucidated, it was quite apparent that tracing these lineages became more difficult. While we had only a few problems in recognizing Archaeogastropoda, we failed to notice members of the other three subclasses of the Gastropoda, even though they should be recognizeable due to protoconch preservation. In this study, we present the fauna and begin to resolve its taxonomy by suggesting connections to lineages which have survived to modern times. It has become apparent that many of the seemingly well established larger taxa of Paleozoic gastropods are artificial groups in which convergent, but unrelated, species have been grouped.

## 2. Geological setting

The studied gastropods come from the Plectonotus (Boucotonotus) - Palaeozygopleura Community (FRYDA & MANDA, 1997) of the Praha (Pragian, middle Early Devonian) and Daleje -Třebotov (late Emsian, late Early Devonian) formations occurring in the SW neighbourhood of Prague. The Plectonotus (Boucotonotus) - Palaeozygopleura Community consists of a highly diversified (several tens of species), small-sized fauna containing both epifaunal and infaunal elements. This community comes from deeper-water, mainly micritic Early Devonian limestones of the Prague Basin. The Plectonotus (Boucotonotus) -Palaeozygopleura ranges the entire Lower Devonian (early Lochkovian - late Emsian). The connection of the Plectonotus (Boucotonotus) - Palaeozygopleura Community with specific microfacies of the highly diversified sediments of the Prague Basin is studied. The oldest occurrence of the Plectonotus (Boucotonotus) - Palaeozygopleura Community is in the Lochkov Formation (Lochkovian) where it is represented by Plectonotus (Boucotonotus) sp. and Palaeozygopleura chlupaci Frýda, 1993 (Frýda & Manda, 1997). In the Praha Formation (Pragian) this community involves the Kodymites - Diplozone - Palaeozygopleura assemblage described by Horný (1992) and is represented by Plectonotus (Boucotonotus) snajdri Horny, 1963 and Palaeozygopleura alinae alinae (Perner, 1907) and by other species of Palaeozygopleura (see Horný, 1955). This community is known from many outcrops of the Praha Formation (see HORNÝ, 1992). The youngest occurrence of the Plectonotus (Boucotonotus) - Palaeozygopleura Community is known from the uppermost part of Třebotov Limestone (latest Emsian) of the Daleje-Třebotov Formation where it is represented by Plectonotus (Boucotonotus) mareki Horny, 1963 and Palaeozygopleura alinae multicostata Horný, 1955 and by other species of Palaeozygopleura (see Horný, 1955). A detailed study of the *Plectonotus* (*Boucotonotus*) - *Palaeozygopleura* Community with a complete list of all gastropod species is being prepared.

Some limestone beds of the Praha and Daleje-Tøebotov formations have become deeply weathered and decomposed probably in pre-Quaternary times. The small, commonly well preserved gastropod shells were obtained by washing these decomposed limestones. Perner (1903, 1907, 1911) had not known this kind of preservation and thus did not describe gastropods from such occurrences. Subsequently a large part of such fauna represents undescribed taxa. This fauna has since been collected by a number of workers, but it has not been systematically studied. Horný (1992) established some new genera of gastropods and presented rather short descriptions without going into detail regarding their comparison with other known species or classification. The ongoing study of the Devonian gastropods of Europe carried out by us (especially J.F.) has also been focused on these Bohemian localities. Some new gastropod taxa, especially those with well preserved protoconchs found in this material, are described in the present paper. A more detailed account on the stratigraphic positions of the localities as well as the complete faunal list is in preparation. Material used in present study is based to a large part on that collected during 1982-1996 by one of us (J.F.), but also on some material from the older collections. A detailed description of the geological setting and a list of references have been presented by CHLUPÁÈ et al. (1992). The specimens described here are deposited in the collection of J. FRYDA, Èeský geologický ústav, Prague.

## 3. Subclass Archaeogastropoda Thiele, 1925

D is cussion: The protoconch of Archaeogastropoda consists of a little less than one whorl that is succeeded by the teleoconch. There is no addition of a larval shell that is constructed by a planktotrophic veliger as may be present in species of other subclasses of the gastropods living today. In the case of plankton feeding as may be present in some of the modern Docoglossa (an order of the Archaeogastropoda), the protoconch is still of the same type as in the modern Vetigastropoda (another order of the Archaeogastropoda), where the swimming stage in ontogeny relies on a yolk provided by the maternal animal and does not feed on plankton (Bandel 1982). The protoconch also commonly still reflects in its morphology the formation from a bilaterally symmetrical, originally unmineralized shell that before its transition to the benthic animal was deformed mechanically and subsequently mineralized.

R e m a r k s: Thiele (1929) included in his Archaeogastropoda also the Neritoidea (now Neritimorpha). Later, Wenz (1939) modified Thiele's concept and included in addition some fossil groups like the Tryblidoidea (now belonging to the class Monoplacophora) and the Bellerophontoidea (a disputed group of bilaterally symmetrical molluscs). Bandel (1982) redefined the subclass Archaeogastropoda using protoconch characters as stated above. Based on the construction of the nervous system, Haszprunar (1993) suggested inclusion also of the Neritimorpha and the architaenioglossate groups (Cyclophoroidea and Ampullaroidea) into his concept of the Archaeogastropoda. Bandel (1992) considered the Neritimorpha to represent an independent subclass characterized by its own typical protoconch and being detected in fossil record at least from the Middle Devonian. The architaenioglossate groups have been regarded as members of the Caenogastropoda (Bandel 1993). To include archaeogastropod groups that have no surviving species Bandel & Fryda (1996) and Bandel & Geldmacher (1996) suggested the use of the more neutral terms

Selenimorpha for archaeogastropods with a slit and selenizone and Trochomorpha for those without a slit following the suggestion of NAEF (1911). These taxa are not considered as formal taxonomic terms, but just as preliminary aids in grouping fossil archaeogastropods until they may be placed in a more appropriate taxonomic position.

## 4. Order Vetigastropoda Salvini-Plawen, 1980

D i a g n o s i s: This group includes species with selenimorph or trochomorph shells with an archaeogastropod protoconch (Bandel, 1982) that can be connected to modern species with anatomical features as designated by Salvini-Plawen & Haszprunar (1987) and Haszprunar (1988).

D is cussion: Among modern members of the order Vetigastropoda there are larger taxa such as the Seguenzioidea or the Scissurelloidea that unite species with shells having or lacking slits. Modern species of slit-bearing and slit-less species of these groups are connected to each other by features of their anatomy (Marshal, 1983, 1993). An example from the fossil record was provided within the superfamily Cirroidea, a group of probable Vetigastropoda that lived from the Late Silurian to the Late Cretaceous (Bandel, 1993; Frýda, 1997; Frýda & Blodgett, in print). In fossil members of the Vetigastropoda 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 this case, Bandel & Frýda (1996) and Bandel & Geldmacher (1996) suggest it should be included in a group of the Trochomorpha or the Selenimorpha.

#### 4.1 Morphogroup Trochomorpha

Remarks: Trochomorpha include all species of the extant Trochoidea as defined by Hickman & McLean (1990). But it also includes all similar fossil Archaeogastropoda that can not be analysed anatomically and have no clearly visible relation within modern forms. For these Naef (1911) suggested the term Trochomorpha. This concept was elaborated by Bandel & Geldmacher (1996) and it is used here as well.

## 4.1.1 Trochomorph group Eucochlis

Description: Small turbiniform shells having an ornament of fine transverse costae and a straight, oblique outer lip of the aperture. The first whorl is smooth, and ornamentation arises gradually on the second whorl.

R e m a r k s: Bandel & Geldmacher (1996) included in their trochomorph group *Eucochlis* the Carboniferous genera *Eucochlis* Knight, 1933, *Kyndalynia* Yoo, 1994 and perhaps *Microcochlis* Yoo, 1994 as well as the Triassic genus *Lanascala* Bandel, 1992. We add here the Devonian genus *Hawletrochus* n. gen. The Early Carboniferous *Kimina* Yoo, 1994 may belong here, but the features of the protoconch/teleoconch transition are not quite clear in the material presented by Yoo (1994).

## Genus Hawletrochus n. gen.

Type species: Hawletrochus pragensis n. sp.

Derivation ominis: The genus is named in honor of the Czech paleontologist IGNAC HAWLE, co-author of the "Prodrom einer Monographie der böhmischen Trilobiten" published in 1847.

Diagnosis: Small turbiniform shells with rounded whorls; whorl profile between sutures symmetrically convex; sutures impressed; shell base wide, minutely phaneromphalous or anomphalous; outer apertural lip prosocline and sigmoidal; margin of outer lip leaving the upper suture at first with a slight backward obliquity, then continually curving in a much steeper inclination up to the whorl periphery where it again curves forwards forming a wide and shallow arch; shell ornament consisting of collabral, regularly spaced threads; apex of shell formed by protoconch of archaeogastropod type.

C o m p a r i s o n: The new genus Hawletrochus resembles the genera Eucochlis KNIGHT, 1933, Elasmonema FISHER, 1885, Microcochlis Yoo, 1994, and Kyndalynia Yoo, 1994 in its general shell shape. The genus Eucochlis is based on the Late Carboniferous species Eucochlis perminuta Knight, 1933. The Early Devonian Hawletrochus n. gen. is distinguished from the latter by the general shape of its shell and different shape of its outer apertural lip. In Hawletrochus the outer lip is sigmoidally curved in contrast to that of Eucochlis Knight, 1933, which has a straight outer lip. In the latter genus the pleural angle of the shell is distinctly lower than that of the shell of Hawletrochus. In addition, the latter has convex shell sides, while in the former they are nearly straight. The genus Elasmonema FISHER, 1885 is based on Loxonema bellatula HALL, 1861 and comes from the Middle Devonian of Ohio. Hawletrochus differs from Elasmonema in having a smaller shell, more slowly expanding whorls and a more convex whorl profile between sutures. The genus Elasmonema represents the type genus of the family Elasmonematidae KNIGHT, 1956 into which Knight et al. (1960) also tentatively placed the genus Eucochlis Knight, 1933. You (1994) described the new genus Kyndalynia based on the Early Carboniferous species Kyndalynia inflata YOO, 1994 and placed his genus also in the family Elasmonematidae KNIGHT, 1956. Hawletrochus is distinguished from Kyndalynia by a different shape of its outer apertural lip. The genus Microcochlis Yoo, 1994 is based on the Early Carboniferous Microcochlis parva Yoo, 1994, and also resembles Hawletrochus pragensis, but the latter species differs by the shape of its outer apertural lip, by its convex whorl profile between sutures and by its elevated protoconch.

#### Hawletrochus pragensis n. sp.

(pl. 1, figs. 1-3)

Holotype: Pl. 1, figs. 1-3; CGU JF 360.

Derivatio nominis: pragensis, after the capital of the Czech Republic, Praha (latin, Praga).

Type locality: Holyně near Prague, central Bohemia.

Type horizon: The uppermost part of the Třebotov Limestone, Daleje-Třebotov Formation; late Emsian, late Early Devonian.

Diagnosis: Because of monotypy, see that of genus.

Description: A small, dextrally coiled, turbiniform shell consisting of at least 4 whorls; shell height approximately equal to its width; whorl profile between sutures

symmetrically convex; sutures moderately deep, impressed; shell base wide, minutely phaneromphalous or anomphalous; outer apertural lip strongly prosocline and sigmoidally curved, with margin leaving the upper suture at first with a slight backward obliquity, then curving continually more steeply towards the whorl periphery; from there it bends forwards again, forming a wide and shallow arch; inner shape of the axial section of aperture nearly circular; shell ornament consists of collabral, regularly spaced threads, with distance between them slightly increasing during shell ontogeny; protoconch of archaeogastropod type having a diameter of 0.2 mm.

Remarks: The archaeogastropod-type protoconch of *Hawletrochus pragensis* n. gen., n. sp., places this early Devonian genus into the subclass Archaeogastropoda. According to new observations (Bandel, personal observation), the protoconch in the type species of the genus *Eucochlis* Knight, 1933 is also that of an archaeogastropod and, thus, placement of *Hawletrochus* n. gen. into the trochomorph group *Eucochlis* is suggested.

Material: CGU JF 360-370.

#### Genus Kimina Yoo, 1994

Type species: Kimina globosa Yoo, 1994.

R e m a r k s: The genus Kimina Yoo, 1994 is based on the Early Carboniferous species Kimina globosa Yoo, 1994, from eastern Australia. Besides the type species Yoo (1994) described two further species of Kimina, K. australis Yoo, 1994 and K. minor Yoo, 1994, coming also from the Early Carboniferous sediments. Yoo (1994) tentatively placed his Kimina into the "Heterogastropoda" because he found a slightly deviated protoconch consisting of one and a quarter whorls in Kimina species. He also pointed out the similarity of his Kimina with the recent genus Rissoella. The teleoconch of Kimina yooi n. sp. described here fits well with morphological range of the genus Kimina. However, the protoconch of our species seems to be of archaeogastropod-type. Nevertheless, if Kimina can be shown conclusively to belong to the Heterostropha with the protoconch coiling sinistrally at first, then our species most probably represents an archaeogastropod and a new genus must be established for our species.

## Kimina yooi n. sp.

(pl. 1, figs. 4-6)

Holotype: Pl. 1, figs. 4-6; CGU JF 371.

Derivation nominis: The genus is named in honor of the Australian paleontologist E. K. Yoo, who greatly contributed to our knowledge of Carboniferous gastropods.

Typelocality: Praha - Barrandov, central Bohemia.

Type horizon: Praha Formation; Pragian, middle Early Devonian.

D i a g n o s i s: Species of *Kimina* with relatively low whorls; pleural angle about 35°; shell apex formed by slightly elevated protoconch; diameter of the first whorl about 0.3 mm.

Description: Small, dextrally coiled, turbiniform shell consisting of at least 6 whorls with a straight shell sides; height of the shell about twice that of its width; pleural angle about 35°; whorl profile between sutures strongly and symmetrically convex; sutures deeply impressed; shell base rounded, deeply phaneromphalous; circular aperture bearing

no sinus or slit; distance between the sutures about one half of whorl width; shell surface smooth; protoconch elevated; diameter of the first whorl is about 0.3 mm.

C o mp arison: Kimina yooi n. sp. is distinguished from the type species of Kimina by its lower whorls and by the shape of its protoconch. The protoconch in Kimina yooi is more elevated than that of Kimina globosa (Yoo, 1994, pl. 20, fig. 6). The latter character distinguishes Kimina yooi also from Kimina australis Yoo, 1994 and Kimina minor Yoo, 1994. The shape of the protoconch and teleoconch of Kimina yooi resembles that of the genus Palaeoalvania Yoo, 1994 based on Palaeoalvania talenti Yoo, 1994. But in contrast to the members of the genus Kimina, the monotypic Palaeoalvania has a shell ornament of spiral cords.

Material: CGU JF 371-377.

## Trochomorph group Araeonema

D e s c r i p t i o n: High spired, trochomorph shells with a simple aperture and ornament of spiral ribs. The inner shell is nacreous and the protoconch is of archaeogastropod type.

R e m a r k s: Bandel & Geldmacher (1996) placed the following genera in this group: *Araeonema* Knight, 1933, *Rhabdotocochlis* Knight, 1933, and *Yunnania* Mansuy, 1912. We add the genera *Australonema* Tassell, 1980 and *Omphalonema* Grabau, 1936.

#### Genus Australonema Tassell, 1980

Type species: Cyclonema australis Etheridge, 1890

Remarks: Tassell (1980) established the new genus Australonema for gastropods with numerous, closely spaced spiral elements of ornamentation and placed it to the subfamily Gyronematinae KNIGHT, 1956 of the family Holopeidae Wenz, 1938. According to Knight et al. (1960) this family belongs to the superfamily Platyceratoidea HALL, 1859. TASSELL (1980) considered his Australonema to belong to Gyronema-Yunnania lineage together with Cinclidonema KNIGHT, 1945 and Omphalonema GRABAU, 1936. Six species from Early Silurian to Early Devonian age strata of Australia were described or transferred to the genus Australonema by TASSELL (1980). This author also suggested placement of the Wenlockian age Cyclonema carinatum var. multicarinatum Lindström, 1884 to the Australonema. Later, Gubanov & Yochelson (1994) described an additional new species of Australonema, Australonema varvarae, from the Wenlockian of Siberia. These authors also questioned the higher taxonomy of Australonema and suggested a similarity of this genus with Oriostoma Munier-Chalmas, 1876. Gubanov & Yochelson (1994) pointed out that a presence of the shallow but distinct umbilicus in Oriostoma distinguishes Australonema from latter genus. However, as shown by TASSELL (1980), the shells of Australonema species including the type species, Australonema australis (ETHERIDGE, 1890), also have developed umbilici. Yochelson & Linsley (1972) described and illustrated a specimen of Cyclonema lilydalensis Etheridge, 1891 (=Australonema lilydalensis) with an in situ paucispiral operculum. A paucispiral operculum was also found in Australonema varvarae Gubanov & Yochelson, 1994.

Both species, Australonema blodgetti Fryda & Manda, 1997 (early Lochkovian) and Australonema havliceki n. sp. (late Emsian, ? Pragian), have an archaeogastropod-type protoconch which places this genus within the subclass Archaeogastropoda. Unfortunately, this important shell character is unknown in the type species of Australonema, Australonema australis (Etheridge, 1890).

## Australonema havliceki n. sp.

(pl. 2, figs. 1-6)

Holotype: Pl. 2, figs. 1, 3, 5-6; CGU JF 378.

Derivatio nominis: havliceki, in honor of the Czech paleontologist VLADIMÍR HAVLIČEK for his great contribution to our knowledge of paleontology and stratigraphy of the Prague Basin.

Typelocality: Holyně near Prague, central Bohemia.

Type horizon: The uppermost part of the Třebotov Limestone, Daleje-Třebotov Formation; late Emsian, late Early Devonian.

D i a g n o s i s: Species of Australonema with a small shell; shell ornamented by twelve or more acute spiral cords; distance between the cords same or greater than width of the cords; shell ornament developed on all whorls except protoconch; protoconch of archaeogastropod type; its length about 0.3 mm.

Description: Gastropods with small turbiniform shells having at least six whorls; whorl profile between the sutures convexly arched with maximum convexity slightly above the mid-whorl; height of the adult shell about 1.5 times greater than its width; pleural angle about 70°; whorl joins the preceding whorls below their periphery; sutures deep, impressed; whorls slightly shouldered close to the upper suture; lateral sides of whorls rounded; shell ornament consists of distinct acute spiral cords; their distance of separation greater than cord width; three distinct spiral cords appear on the first whorl; during shell ontogeny their number increases so that the last whorl bears about 15 cords; protoconch clearly of archaeogastropod type (pl. 2, figs. 3-5).

Comparison: Early Devonian Australonema havliceki is distinguished from the type species of Australonema, A. australis (Etheridge, 1890), in having a smaller shell that is ornamented by about 15 spiral cords of about the same size. In A. australis, the ornament consists of two orders of regularly spaced spiral cords covering the entire outer whorl surface. This shell character, as well as the naticiform shell shape of Australonema melbournensis Tassell, 1980, from the Early Devonian of Australia, distinguish the latter from Australonema havliceki n. sp. The Early Devonian age Australonema wellingtonensis (Etheridge, 1898) has the most similar shell ornamentation to Australonema havliceki n. sp. among Australian species of Australonema. Australonema havliceki n. sp. may by distinguished from Australonema wellingtonensis by its smaller shell with a lower value of its pleural angle. The Wenlockian (Silurian) age Australonema varvarae Gubanov & Yochelson, 1994 differs from Australonema havliceki n. sp. in having wider pleural angle and fewer spiral cords.

The Emsian age Australonema havliceki n. sp. differs from the early Lochkovian age Australonema blodgetti Frýda & Manda, 1997 by the lower pleural angle of its shell and by its shell ornamentation. Australonema blodgetti differs in having a lower number of spiral cords and smooth shell base. Three distinct spiral cords appear at the end of the archaeogastropod-type protoconch in Australonema havliceki n. sp. and their number increases to about 15 on the last whorl. On other hand, the shell of the early Lochkovian Australonema blodgetti has the first three whorls smooth. In the latter species, three distinct spiral cords appear at the end of the third whorl. Further spiral cords are developed during subsequent shell ontogeny. Seven spiral cords occur on sixth whorl of which five spiral cords are situated on whorl surface between the upper suture and the whorl periphery, one

cord forms the whorl periphery and one lowermost cord occurs below the whorl periphery. The rest of whorl base in *Australonema blodgetti* is smooth.

R e m a r k s: The species *Australonema havliceki* n. sp. belongs to very common elements of the *Plectonotus* (*Boucotonotus*) - *Palaeozygopleura* Community coming from the upper part of the Třebotov Limestone (Daleje-Třebotov Formation, late Emsian, Early Devonian). Several poorly preserved shells belonging to the genus *Australonema* Tassell, 1980 were also found in the Praha Formation (Pragian, Early Devonian). This species is very similar to the Emsian *Australonema havliceki* n. sp. Unfortunately, up now it is not clear whether both species are conspecific or represent two different species.

Material: CGU JF 378-395.

Genus Omphalonema GRABAU, 1936

Subgenus Omphalonema (Globulonema) n. subgen.

Type species: Omphalonema globosum Horný, 1992

Derivatio nominis: Globulonema, after its globular shell shape.

D i a g n o s i s: Subgenus of the genus *Omphalonema* with a small, globular shell; whorl joins the preceding whorl above its whorl periphery; shell ornament consisting of spiral cords intercalated with 3 to 5 thinner spiral cords on upper whorl surface; basal whorl surface ornamented by spiral cords of similar size; early whorls smooth.

R e m a r k s: The genus *Omphalonema* Grabau, 1936 is based on the Early Permian species *Omphalonema multispiralis* Grabau, 1936 from China. The Early Devonian species of the subgenus *Omphalonema* (*Globulonema*) differ from those of subgenus *Omphalonema* (*Omphalonema*) Grabau, 1936 by their much smaller size and more globular shell shape. The height of the shell in the Permian age *Omphalonema* (*Omphalonema*) multispiralis Grabau, 1936 is about 27 mm while both Early Devonian species are only about 4 mm high. Licharev (1977) described and figured an unnamed species that probably belongs to *Omphalonema* Grabau, 1936 from the Early Carboniferous of Middle Asia, but it also shows some resemblance with the genus *Australonema*.

The shell Omphalonema (Globulonema) also closely resembles the Early Carboniferous species Pleurotomaria portlockiana Koninck, 1834 that has been placed in the genus Gosseletina Fisher, 1887 by Batten (1966). In this species Batten (1966) found the selenizone to be ornamented by spiral cords similar to the rest of the outer whorl surface. The shell of the Early Carboniferous Gosseletina portlockiana is more similar to the Early Devonian Omphalonema (Globulonema) in its globular shell ornamented by spiral cords than to the large, smooth shell of the type species of the genus Gosseletina Fisher, 1887.

Included species: Omphalonema (Globulonema) globosum (Horný, 1992) from the uppermost Třebotov Limestone (late Emsian) and Omphalonema (Globulonema) sp. from the Praha Formation (Pragian).

Omphalonema (Globulonema) sp.

(pl. 3, figs. 1-2)

Description: Omphalonema (Globulonema) with a small, globular shell; whorl joins the preceding whorls above their whorl periphery; shell ornament consisting of spiral cords; two orders of regularly spaced spiral cords are developed on upper whorl surface; less numerous, stronger cords separated by more numerous thinner spiral cords; basal whorl surface ornamented only by small sized spiral cords; early whorls smooth.

Remarks: The type species of the new subgenus is represented by *Omphalonema globosum* Horný, 1992 which was based on five specimens coming from the uppermost Třebotov Limestone (late Emsian). Some shells that belong to the subgenus *Omphalonema (Globulonema)* were also discovered in the Praha Formation (Pragian). Of these only one complete specimen is up to now available for study and reveals some differences in its ornamentation from younger *Omphalonema (Globulonema) globosum (Horný*, 1992). Because of poor knowledge of the variability of both Early Devonian species we keep the Pragian species in open nomenclature.

M a t e r i a l : Only one complete shell from the quarry "Kantina" near Holyně, Prague; Dvorce-Prokop Limestone, Praha Formation (Pragian, middle Early Devonian). CGU JF 396.

## Trochomorph group "Holopea"

Description: Smooth, trochomorph shells with circular aperture and umbilicate shell base. Included in this group are species of the still enigmatic genus *Holopea* Hall, 1847 from different Paleozoic levels and members of the genus *Krasopea* Horný, 1992 from the Early Devonian.

R e m a r k s: The genus *Holopea* Hall, 1847 is based on the Middle Ordovician *Holopea symmetrica* Hall, 1847 from North America. During last 150 years, quite a number of species have been described as belonging to this genus from Ordovician to Carboniferous rock of North America, Europe and Asia. The smooth turbiniform shell of *Holopea* provides only a few shell characters and for this reason it is difficult or impossible to differentiate many of these species from each other. Moreover, many from these species were poorly described and figured and usually no information on their early ontogenetic shell forms exists, so that they may very well belong to different subclasses.

## Genus Holopea HALL, 1847

Type species: Holopea symmetrica HALL, 1847

R e m a r k s: The new species here described are tentatively placed into the genus Holopea and may in the future be recognized to represent synonymous species of earlier described species or may be placed in a different genus when the type species of Holopea is better known. The genus Holopea as understood here is very common among the gastropods from the Plectonotus (Boucotonotus) - Palaeozygopleura Community of the Prague Basin and for this reason we establish a new species name for it here.

## Holopea kettneri n. sp.

(pl. 3, figs. 3-5)

Holotype: Pl. 3, figs. 3-5; CGU JF 397.

Derivation ominis: kettneri, in honor of the Czech geologist R. Kettner for his great contribution to our knowledge of geology of the Prague Basin.

Typelocality: Praha - Barrandov, central Bohemia.

Type horizon: Praha Formation, Pragian, Early Devonian.

D i a g n o s i s: Small species of *Holopea* with smooth whorls; pleural angle of about 70°; whorls near upper suture slightly shouldered; shell base rounded, phaneromphalous; shell apex formed by slightly elevated protoconch of archaeogastropod type; its diameter of about 0.35 mm.

Description: Small, dextrally coiled, turbiniform shells consisting of at least 5 whorls; shell sides straight or very slightly convex; pleural angle about 70°; whorl profile between sutures strongly convex; sutures deep, impressed; shell base rounded, deeply phaneromphalous; whorl profile leaves the upper suture abaxially forming flat shoulder and then turns roundly over the whorl periphery onto the rounded base; aperture circular, slightly prosocline; outer shell surface smooth; apex of the shell formed by protoconch of the archaeogastropod-type; protoconch length about 0.35 mm.

Comparison: The Early Devonian Holopea kettnerin. sp. is distinguished from the Middle Ordovician Holopea symmetrica Hall, 1847 by its smaller shell size and shouldered whorl profile.

R e m a r k s: The protoconch of the archaeogastropod-type recognized in *Holopea kettneri* n. sp. places this species within the subclass Archaeogastropoda. Unfortunately, this important shell character is not known in the type species of *Holopea*. *H. kettneri* differs from the all species placed into the genus *Holopea* by Perner (1907) by its small shell with slightly shouldered whorl profile. Several of these species do not belong to the genus *Holopea* and they need to be revised.

Material: CGU JF 397-420.

Genus Krasopea Horný, 1992.

Type species: Krasopea solaris Horný, 1992.

R e m a r k s: The genus Krasopea Horný, 1992 is based on Krasopea solaris Horný, 1992 from the uppermost part of the Třebotov Limestone (Daleje-Třebotov Formation; late Emsian, late Early Devonian). Horný (1992) suggested that the shape of the columellar excavation extending over the parietal region to the juncture of the parietal and outer lips and down to the base of the aperture is evidence for the existence of an operculum. Horný also recognized that the higher taxonomic position of this genus remains unresolved. He suggested that it might be related to the neritopsids, since some of these have similar apertures. New species Krasopea glabra from the Praha Formation (Pragian, Early Devonian) appears to have an archaeogastropod-type protoconch, but the preservation of the early whorls in all studied specimens is not very good. The genus Krasopea Horný, 1992 is thus only tentatively placed within the subclass Archaeogastropoda.

Krasopea glabra n. sp.

(pl. 3, figs 6-7)

Holotype: Pl. 3, figs. 6-7; CGU JF 421.

Derivatio nominis: glabra, after its smooth shell.

Type locality: Požáry near Prague, central Bohemia.

Type horizon: Praha Formation (Pragian, Early Devonian).

D i a g n o s i s: Species of *Krasopea* with more expanded whorls; radially arranged riblets not developed around the umbilicus; shell base anomphalous or cryptomphalous; sutures shallow.

Description: Gastropods with small, turbiniform shells consisting of about five whorls; shell base anomphalous or cryptomphalous; whorl profile between the sutures gently convex; height and width of the adult shell measures about 4 mm; sutures shallow; whorl joins the preceding ones near their periphery; whorl profile curves from the upper

suture onto the shell base without angulation; outer apertural lip slightly prosocline, straight; columellar excavation extends over the whole parietal region and down to the base of the aperture; shell surface smooth.

Comparison: The Pragian species Krasopea glabra n. sp. is distinguished from Krasopea solaris Horný, 1992 by its shallower sutures, more expanded whorls and the absence of radially arranged riblets around the umbilicus. In Krasopea glabra n. sp. the whorls join the preceding whorls at their periphery forming shallow sutures; while in Krasopea solaris they join below the shell periphery to produce deeper sutures. The whorl expansion rate in shells of Krasopea glabra is distinctly greater than that in Krasopea solaris. The radial ornament of a small periumbilical callus is not developed in Krasopea glabra in contrast to the type species, K. solaris. The same shape of the columellar excavation in both species unites them into a single genus.

Material: CGU JF 421-425.

#### Trochomorph group Purkynespira

Description: Small, dextrally coiled turbiniform shells having a flat apex with a protoconch situated in the central depression; first whorl coils planispirally or slightly sinistrally; teleoconch being higher than wide; whorl profile convex; sutures deep and impressed; ornament consists of collabral cords crossed by thinner spiral cords forming a reticular pattern.

R e m a r k s: Among Paleozoic gastropods this shell shape is very unusual and thus we establish its own trochomorph group *Purkynespira* for it.

Genus Purkynespira n. gen.

Type species: Purkynespira reticulata.

Derivatio nominis: *Purkynespira*, in honor of the Czech biologist J. E. Purkyně.

D i a g n o s i s: Small, dextrally coiled shells with a flat apex having a concave apical depression in its center; first whorl planispirally or slightly sinistrally coiled; whorl profile between sutures strongly convex; sutures deep, impressed; outer apertural lip strongly prosocline and slightly sigmoidal; shape of aperture nearly circular in axial section; shell ornament consisting of collabral cords crossed by thinner spiral cords forming a reticular pattern.

R e m a r k s: The coiling of the first whorl in *Purkynespira reticulata* appears to be slightly sinistral. The dextral coiling starts slightly after beginning of the second whorl and the remainder of the shell is also dextrally coiled. Among the Archaeogastropoda, the members of the fossil superfamily Cirroidea Cossman change the mode their coiling during their ontogeny (Bandel, 1992; Fráda, 1997; Fráda & Blodgett, in print). However, in cirroidean gastropods the early whorls are dextral and the teleoconch is sinistrally or planispirally coiled and, thus, their shell coiling is opposite to the shell coiling of *Purkynespira reticulata* n. sp. Among the Archaeogastropoda, also the selenimorph genera, such as *Wortheniella* Schwardt, 1992 and *Lukesispira* Fráda & Manda, 1997, have a planispirally coiled initial part. The change in shell coiling from sinistral in the protoconch to dextral in the teleoconch is characteristic of members of the Heterostropha Fischer, 1885 (Bandel, 1991, 1995, 1996). However, members of the subclass Heterostropha develop a planktotrophic larva shell and their protoconch always has more whorls than are present

in the Archaeogastropoda. Unfortunately, the boundary between the protoconch and the teleoconch is not well preserved in any of the studied individuals of *Purkynespira reticulata* n. sp. and thus the higher taxonomic position of this genus is still somewhat doubtful.

In cluded species: Purkynespira reticulata n. sp. from the Praha Formation (Pragian, middle Early Devonian) and probably Purkynespira? parvula (=Auriptygma parvula Horný, 1992) from the uppermost Třebotov Limestone (Třebotov-Daleje Formation; late Emsian, late Early Devonian).

Purkynespira reticulata n. sp.

(pl. 4, figs. 1-5)

Holotype: Pl. 4, figs. 1-5; CGU JF 426.

Derivatio nominis: reticulata, after reticulate shell ornamentation.

Typelocality: Praha - Barrandov, central Bohemia.

Type horizon: Praha Formation, Pragian, Early Devonian.

Diagnosis: same as for the genus.

D e s c r i p t i o n: Small, dextrally coiled, turbiniform shells consisting of at least five whorls; flat apex of the shell formed by the first whorl that is planispirally or slightly sinistrally coiled; umbilicus of the first whorl forms a concave apical depression (pl. 4, fig. 5). The shell is higher than wide and its pleural angle amounts to about 40°. The whorls between the deep and impressed sutures are strongly and symmetrically convex. The rounded base is minutely phaneromphalous or anomphalous. The outer apertural lip is weakly sigmoidal and leaves the suture with a slight backward obliquity and then continues in a more prosocline curve downward. In cross-section the aperture is nearly circular. Ornament consists of collabral, slightly irregularly spaced cords with the distance between them increasing somewhat during the shell growth. Collabral cords are crossed by thinner spiral cords forming a reticulate pattern. The diameter of the first, planispirally coiled whorl is slightly more than 0.3 mm.

R e m a r k s: Horný (1992) described his species, *Auriptygma parvulum*, from the uppermost Třebotov Limestone (late Emsian) of the Prague Basin, but presented few details. It may well belong also to *Purkynespira*. Horný (1992) noted that his species may not belong to *Auriptygma* because of its strongly prosocline labrum.

C o m p a r i s o n: Purkynespira reticulata n. sp. differs from the genus Auriptygma Perner, 1903 based on the Silurian Auriptygma fortis Perner, 1903 by a more inclined aperture and by its more than ten-times smaller shell size. Auriptygma parvulum Horný probably represents a species of the genus Purkynespira because of its greater similarity with Purkynespira reticulata than with the type species of Auriptygma, Auriptygma fortis Perner, 1903. The Pragian age P. reticulata n. sp. may be distinguished from the Emsian age Purkynespira? parvula (Horný, 1992) by its reticular shell ornament and more convex, symmetrically arched whorl side in younger whorls.

Material: CGU JF 426-429.

#### Trochomorph group Anomphalus

D e s c r i p t i o n: Rotelliform to sub-lenticular shells with a low spire, a rounded periphery, deeply embracing whorls, shallow sutures and a slightly flattened umbilicate base; umbilicus commonly filled by callus. Whorls are rounded and ornament consists of

growth lines only. The aperture is rounded and the outer lip oblique. The inner shell layer is nacreous.

R e m a r k s: Bandel & Geldmacher (1996) involved in their trochomorph group *Anomphalus* the following genera: *Anomphalus* meek & Worthen, 1867, *Isonema* Meek & Worthen, 1866, *Antirotella* Cossmann, 1918, *Tychonia* Koninck, 1881, *Turbinilopsis* Koninck, 1881; we add *Eiselia* Dietz, 1911. These Paleozoic fossils closely resemble the modern *Umbonium* Link, 1807.

#### Genus Eiselia DIETZ, 1911

Subgenus Eiselia (Eoeiselia) n. subgen.

Type species: Eiselia (Eoeiselia) minutula n. sp.

Derivation ominis: *Eoeiselia*, using the combination of Eo (=early) and the generic name *Eiselia*.

Diagnosis: Species of *Eiselia* with smooth shells; whorl periphery rounded; shell base deeply umbilicate; whorl profile between sutures convex; protoconch of archaeogastropod-type and about 0.35 mm in diameter.

C o mp arison: The monotypic genus Eiselia is based on E. dyadica Dietz, 1911 from the Permian of Germany. It differs from Eiselia (Eoeiselia) by not having a rounded whorl periphery and a smooth shell. The shell ornamentation in E. (E.) dyadica consists of transverse costae which are strongest at the subangular whorl periphery, where they are angularly node-like (Knight, 1941).

Discussion: The subgenus Eiselia (Eoeiselia) n. subgen. is based on E. (Eoeiselia) minutula n. sp. from the Praha Formation of the Prague Basin and resembles Eiselia (Eiselia) Dietz, 1911, in its general shell shape and its size. The monotypic subgenus Eiselia (Eiselia) is based on Eiselia dyadica Dietz, 1911 from the Permian of Germany and it is a very poorly known shell. The rounded whorl periphery and its smooth shell distinguish the new species from the Permian age Eiselia dyadica Dietz, 1911. For this reason, we tentatively place our new species into a new subgenus of the genus Eiselia. The Early Devonian species may belong to its own genus, but this problem can only be solved when the Permian Eiselia (Eiselia) dyadica Dietz, 1911 becomes better known. Knight et al. (1960) placed this genus questionable into the family Anomphalidae Wenz, 1938. Its protoconch is still unknown.

Eiselia (Eoeiselia) minutula n. sp.

(pl. 4, figs. 5-6)

Holotype: Pl. 4, figs. 5-6; CGU JF 430.

Derivationominis: minutula, (= very small) according to its very small shell.

Type locality: Požáry near Prague, central Bohemia.

Type horizon: Praha Formation (Pragian, Early Devonian).

Diagnosis: Because of monotypy, see that of subgenus.

Description: A very small, rotelliform and dextrally coiled shell having at least 4 whorls. The width of the shell is about twice that of its height. The whorl profile between sutures is convex and in the last whorl continues into the rounded and deeply umbilicate base. The sutures are sharp but shallow and the outer shell surface is smooth. The protoconch is of archaeogastropod-type and measures 0.35 mm in diameter.

C o m p a r i s o n: The Early Devonian Eiselia (Eoeiselia) minutula n. sp. differs from the Permian Eiselia (Eiselia) dyadica Dietz, 1911 by its rounded whorl periphery and its smooth shell. In the latter species the whorl profile at the periphery is distinctly subangular with a shoulder developed next to upper suture (see Knight, 1941, pl. 63, fig. 5). The presence of an archaeogastropod-type protoconch places Eiselia (Eoeiselia) minutula in the Archaeogastropoda.

Material: CGU JF 430-440.

## Trochomorph group Cordaspira

Description: Small, dextally coiled shells having a flat upper surface and concave lateral sides with the shell periphery formed by a protruding keel. The widely umbilicate base is bounded by a large, protruding periumbilical keel. Otherwise shell surface is smooth.

R e m a r k s: The shell shape is very unusual among the Paleozoic gastropod genera and thus, we establish its own trochomorph group *Cordaspira* for it.

Genus Cordaspira n. gen.

Type species: Cordaspira enigma n. sp.

Derivation ominis: The genus is named in honor of the Czech paleontologist August Josef Corda, co-author of the "Prodrom einer Monographie der böhmischen Trilobiten" published in 1847.

D i a g n o s i s: Small, dextally coiled shells having a flat, slightly concave upper surface; shell periphery formed by large protruding keel situated at boundary between flat upper surface and lateral side of the whorl; widely umbilicate base bounded by a large periumbilical keel; lateral side of the whorl between peripheral and perumbilical keels strongly concave with abapical inclination; shell surface smooth.

C o m p a r i s o n: The shell of *Cordaspira* n. gen. is quite unusual in shape and no closely similar shell form occurs among Paleozoic gastropods. A resemblance may only be noted with the genera *Planotectus* Yochelson, 1956 and *Straparollus* (*Amphiscapha*) Knight, 1942. Both genera differ from *Cordaspira* n. gen. by having a more simple base and less convex whorl sides. The widely umbilicate base of *Cordaspira* n. gen. is bounded by a large periumbilical keel, but it is rounded in *Planotectus* and *Amphiscapha*. Also the convex lateral sides of the whorls in the latter two genera contrast with the strongly concave whorl sides in *Cordaspira* n. gen.

R e m a r k s: KNIGHT et al. (1960) placed the both genera, *Planotectus* Yochelson, 1956 and *Straparollus* (*Amphiscapha*) KNIGHT, 1942, in the family Euomphalidae KONINCK, 1881, which differ from the archaeogastropods in regards to the shape of their protoconchs (Bandel & Frýda, in preparation). The protoconch of *Cordaspira enigma* n. sp. is not well preserved, but seems to be of archaeogastropod type.

Cordaspira enigma n. sp.

(pl. 5, figs. 1-4)

Holotype: Pl. 5, figs. 1-4; CGU JF 441.

Derivationominis: enigma, according its mysterious shell shape.

Type locality: The quarry "Kantina" near Holyně, Prague, central Bohemia.

Type horizon: Praha Formation, Dvorce-Prokop Limestone (Pragian, middle Early Devonian).

Diagnosis: Because of monotypy, see that of genus.

Description: Small dextrally coiled shells having a flat upper surface; shell twice as wide as high. The upper shell surface is bounded by a large protruding keel situated on the periphery between the upper surface and lateral side of the whorl. The upper whorl profile is flattened except near the suture where it is convex. The shell base is widely umbilicate and bears a large periumbilical keel. The lateral whorl sides between the protruding peripheral and periumbilical keels are strongly concave. The whorl sides have a strong abapical inclination of about 35°. The shell surface is smooth.

R e m a r k s: Cordaspira enigma n. sp. represents a very rare species in the Pragian age gastropod fauna of the Plectonotus (Boucotonotus) - Palaeozygopleura Community. The initial part of the shell is preserved only in the holotype and even here the preservation is poor. The diameter of the smooth, initial cap of the protoconch measures about 0.1 mm and appears to be only very slightly coiled. Unfortunately, it is impossible to solve whether this represents a primary character or if it is the result only of poor preservation and diagenesis.

Material: CGU JF 441-445.

## 4.2 Morphogroup Selenimorpha

R e m a r k s: Bandel & Frýda (1996) and Bandel & Geldmacher (1996) have started to unite fossil gastropods with slit and selenizone into morphologically similar, but somewhat differing groups of Selenimorpha. This concept is followed here. Modern Selenimorpha can be classified into well differentiated superfamilies such as the Pleurotomarioidea Swainson, 1840, Haliotioidea Rafinesque, 1815, Seguenzioidea Verrill, 1884, Scissurelloidea Gray, 1847 and Fissurelloidea Fleming, 1922. These taxa can be traced back faithfully only into the Mesozoic Era, but not further to include Paleozoic Selenimorpha. Modern related groups show much variety regarding shell shape and a major division regarding shell wall composition. As long as the ancient Paleozoic groups can not be connected successfully with the modern groups, we here follow the concept of tracing interconnected species assemblages of basically Paleozoic occurrence in selenimorph groups and not the classical taxa established by Wenz (1939) or Knight et al. (1960).

## Selenimorph group Gosseletina

Description: Rounded shells having a selenizone situated high on the whorl.

R e m a r k s: The following genera were placed in this group: Gosseletina Bayle, 1885 with type from the Visé of Belgium and with similar species in existence up to the Triassic (Bandel, 1991), Rhaphischisma Knight, 1936 with the type Rotellina planorbiformis Koninck, 1881 from the Tournai of Belgium, Platyloron Oehlert, 1888 with its type species from the Middle Devonian of Germany, Planozone Perner, 1907 and Umbotropis Perner, 1903, both of the latter from the Lower Devonian of the Prague Basin.

#### Genus Umbotropis Perner, 1903

Type species: Umbotropis albicans Perner, 1903

R e m a r k s: The type species, *Umbotropis albicans* Perner, 1903, comes from the Early Devonian of the Prague Basin. Knight (1941) designated the holotype as the specimens

shown by Perner (1903) as figures 6-7 on pl. 42 derived from the neighbourhood of the village Měňany. The type horizon of this species is not clearly established, but it probably comes from limestones of Pragian age. Besides the type species, the Emsian age *Umbotropis mesoni* Tassell, 1982 from the "Receptaculites" Limestone of the Australia is the only additional described species of this genus.

Umbotropis rihai n. sp.

(pl. 5, figs. 5-7)

Holotype: Pl. 5, figs. 5-7; CGU JF 446.

Derivationominis: rihai, in honor of the Czech palaeontologist A. Říha, who studied Paleozoic gastropods.

Type locality: Požáry near Prague, central Bohemia.

Type horizon: Praha Formation (Pragian, Early Devonian).

D i a g n o s i s: Small species of *Umbotropis* having a pleural angle about 135°; upper suture near lower margin of the selenizone; whorl profile between the upper suture and selenizone slightly convex; below selenizone whorl profile nearly parallel with shell axis and continually curving onto umbilicate shell base; diameter of archaeogastropod-type protoconch about 0.35 mm.

Description: Gastropods with small, rotelliform shells consisting of at least five whorls; shell base deeply phaneromphalous; whorl profile between the sharp and shallow sutures gently convex; ornament consists of a revolving cord developed close to the upper suture and otherwise the shell is smooth; whorls join the preceding whorls at the lower margin of the selenizone; selenizone flat, adapically inclined; its width about one third of the distance between the upper suture and upper margin of selenizone; selenizone bounded by two spiral threads; below the selenizone whorl profile nearly parallel with the shell axis; far below the selenizone the whorl profile curves onto the shell base without any angulation; outer apertural lip slightly prosocline, straight; deep umbilicus is funnel shaped; archaeogastropod-type protoconch measures slightly more than 0.35 mm in diameter.

C o m p a r i s o n: *Umbotropis rihai* n. sp. is distinguished from the type of the genus, *U. albicans* Perner, 1903, by its lower pleural angle, the position of its selenizone above the suture, the less arched shape of the lateral whorl side and its smaller shell size (see Knight, pl. 27, fig. 6). The pleural angle of the shell of *Umbotropis albicans* is about 155°. The Emsian *Umbotropis mesoni* Tassell, 1982 has a similar pleural angle as *Umbotropis rihai* n. sp., but it differs in having the selenizone bordered on both sides by a distinct depression.

R e m a r k s: The upper whorl in the holotype of *Umbotropis rihai* bears two circular hollows with diameter about 0.3 mm which may be traces of borings applied by some predator. Similar holes have also been etched into the shells of some other Early Devonian gastropods and they will be described in more detail in a future paper.

Material: CGU JF 446-449.

#### 5. Order Stylogastropoda nov.

D i a g n o s i s : Slender high-spired shells of *Loxonema* or *Palaeozygopleura* type associated with a protoconch of Archaeogastropoda-type.

Derivationominis: A combination of the words stylus (=pin) and gastropoda.

Comparison: Carboniferous members of the Pseudozygopleuridae KNIGHT, 1930 as well as members of the Triassic Polygyrinidae Bandel, 1991 may have a very similar teleoconch to that of members of the Stylogastropoda, but differ by having a larval shell added to the embryonic shell and, in the case of lecithotrophic development, an embryonic shell that is larger than one whorl. The protoconch of Stylogastropoda, in contrast, consists of less than one whorl with a lateral fold and without a larval shell, as is the case among the Archaeogastropoda in general.

R e m a r k s: Among Early Devonian gastropods, members of Katoptychia Perner, 1907, Stylonema Perner, 1907, Palaeozygopleura (Palaeozygopleura) Horný, 1955, Palaeozygopleura (Palaeozyga) Horný, 1955, and Palaeozygopleura (Bohemozyga) n. subgen. developed no shell that could reflect the presence of a planktotrophic larva during their early ontogeny. Their protoconch has typical characteristics of the archaeogastropod protoconch (Bandel, 1982). The protoconch in all members of the above mentioned genera consists of less than one whorls and is comparatively large, measuring more than 0.25 mm in diameter and showing the characteristic fold of the embryonic shell of archaeogastropods. This protoconch on a slender turriform shell, which otherwise is rather exceptional among Archaeogastropoda, resembles that seen in the turriform Triassic genus Eucycloscala described by Bandel (1993). Here, a nacreous layer within the shell clearly supports placement within the Vetigastropoda.

## Superfamily Loxonematoidea ? Koken, 1889 Family Loxonematidae ? Koken, 1889

R e m a r k s: Knight et al. (1960) placed the superfamily Loxonematoidea Koken, 1889, which included the families Loxonematidae Koken, 1889, Palaeozygopleuridae HORNÝ, 1955, Pseudozygopleuridae KNIGHT, 1930, and Zygopleuridae WENZ, 1938 in the Caenogastropoda Cox, 1959. The Carboniferous and Permian members of the family Pseudozygopleuridae developed a planktotrophic larval shell as was noted by Knight (1930) and repeatedly from there onwards. Bandel (1991) placed the families Pseudozygopleuridae KNIGHT, 1930, and Zygopleuridae WENZ, 1938, together with his new family Protorculidae into the newly established superfamily Zygopleuroidea of the order Ctenoglossa within the subclass Caenogastropoda Cox, 1959. All of these have larval shells or simplified shells that reflect lecithotrophic development. In contrast to this, the Devonian members of the family Palaeozygopleuridae have a typical archaeogastropod-type of protoconch and thus, no larval shell formed during their ontogeny. For this reason the members of Palaeozygopleuridae do not fit into the Caenogastropoda, but appear to be members of the subclass Archaeogastropoda. The initial part of the shell in the Silurian age type species of the genus Loxonema Phillips, 1841 is unknown. Due to this ignorance, it may be rather difficult to resolve the subclass-level position of the family Loxonematidae Koken, 1889. Some of the Early Devonian genera like Katoptychia Perner, 1907 and Stylonema Perner, 1907 which closely resemble Loxonema regarding the shape of the teleoconch developed the same type of the protoconch as is found in the members of the family Palaeozygopleuridae. Thus, at least some genera of the family Loxonematidae Koken, 1889 belong to the subclass Archaeogastropoda. On the other hand, BANDEL (1991) showed that the Triassic Polygyrina lommeli (Munster, 1841) being the type species of the genus Polygyrina Koken, 1892, developed a planktotrophic larva and belongs to the subclass Caenogastropoda. In addition, BANDEL (1994) pointed out that the Middle Devonian "Loxonema" monilifera Goldfuss has a heterostrophic protoconch and belongs into the subclass Heterostropha Fischer, 1885. The above mentioned data suggest that members of three different gastropod subclasses have been placed into the family Loxonematidae.

Genus Katoptychia Perner, 1907

Type species: Katoptychia alba Perner, 1907.

Comparison: Katoptychia is easily distinguished from other Devonian loxonematid gastropod genera by its smooth teleoconch with flat whorls and shallow sutures.

R e m a r k s: The type species *Katoptychia alba* Perner, 1907, comes from Early Devonian limestones, most probably those of the Pragian age. Besides the type species, Perner (1907) described a second species, *Katoptychia fugitiva* Perner, 1907, and stated that it comes from the same type locality and horizon as the type species. Karczewski (1989) noted the occurrence of the genus *Katoptychia* also in Devonian of Poland, but his large, sinistrally coiled shells probably belong to a different genus.

Katoptychia holynensis n. sp.

(pl. 6, figs. 1-4)

Holotype: Pl. 6, figs. 1-2; CGU JF 450.

Derivatio nominis: holynensis, after the type locality.

Typelocality: Holyně near Prague, central Bohemia.

Type horizon: The uppermost part of the Třebotov Limestone, Daleje-Třebotov Formation; late Emsian, late Early Devonian.

D i a g n o s i s: Small species of the genus *Katoptychia* having slightly convex sides of the shell; pleural angle of first eight whorls larger (about 23°) than pleural angle of later whorls (about 19°); shell surface smooth; protoconch length more than 0.3 mm.

Description: Small gastropods having a high-spired, dextrally coiled shell with up to 11 whorls; shell sides very slightly convex; whorl profile flat or gently convex; sutures sharp but very shallow; whorls curve uniformly onto the rounded and anomphalous base without angulation; pleural angle of the first eight whorls about 23° while in later whorls it changes to about 19°; outer shell surface smooth; outer apertural lip is not well preserved in any of the studied specimens but it seems to be opisthocline; large and smooth protoconch very similar to that of *Palaeozygopleura*; its length more than 0.3 mm.

C o m p a r i s o n: Katoptychia holynensis differs from K. alba by its smaller shell size, slightly convex shell sides and smooth shell.

R e m a r k s: The late Emsian age *Katoptychia holynensis* represents a descendent of the Pragian *Katoptychia alba* Perner, 1907. *Katoptychia fugitiva* Perner, 1907 is poorly known but may represent synonym of *K. alba*.

Material: CGU JF 450-465.

Genus Stylonema Perner, 1907

Type species: Loxonema (Stylonema) potens Perner, 1907.

R e m a r k s: Perner (1907) included in his subgenus *Loxonema (Stylonema)* the genotype *Loxonema (Stylonema) potens* and 18 additional species from the Silurian and Devonian of the Prague Basin. Some of these species obviously belong to other genera. For example, *Loxonema (Stylonema) pollens* Perner, 1907 and *Loxonema (Stylonema)* 

solitarium Perner, 1907, have a very different general shape of the shell than is found in Loxonema (Stylonema) potens. Other species, as for example Loxonema (Stylonema) libens Perner, 1907 and Loxonema (Stylonema) transiens Perner, 1907, develop a distinct sinus in their outer apertural lip that contrasts to the shape of the outer lip of Loxonema (Stylonema) potens, and more closely resembles the subgenus Loxonema (Loxonema) Sowerby than Stylonema (see Perner, 1907). A reticulate ornament is found on shells of the species Loxonema (Stylonema) arachne Perner, 1907 and Loxonema (Stylonema) benevolum Perner, 1907 and these species also have to be placed in a different genus.

Outside of Europe, *Stylonema* (Perner, 1907) has been reported from the Early Devonian of the North Pribalkhash region, central Kazakhstan (Rohr et al., 1979), from Alaska (Blodgett et al, 1988) and from the Middle Devonian of Nevada (Blodgett & Johnson, 1992).

Stylonema parvula n. sp.

(pl. 6, figs. 5-6; pl. 7, figs. 1-4)

Holotype: Pl. 6, fig. 6; pl. 7, figs. 1-4; CGU JF 466.

Derivatio nominis: parvula (Latin) according to its very small shell.

Type locality: Praha - Barrandov, central Bohemia.

Type horizon: Praha Formation, Pragian, Early Devonian.

Diagnosis: Very small species of the genus Stylonema having straight shell sides; pleural angle of about 10°; shell surface smooth; protoconch length about 0.3 mm.

Description: Small high-spired, dextrally coiled shells consisting of at least 11 whorls; shell sides straight; whorl profile slightly convex with maximum convexity slightly below mid-whorl; sutures shallow; shell base rounded and anomphalous; pleural angle of spire about 10°; outer shell surface smooth; outer apertural lip not well preserved in any of the studied specimens; protoconch large, smooth, similar to that of *Palaeozygopleura*; its length about 0.3 mm.

Comparison: Stylonema parvula differs from the Silurian type species, Stylonema potens Perner, 1907, by smaller shell size and by its whorl profile being slightly convex with the maximum of convexity slightly below the mid-whorl. The small shell size and its smooth surface distinguishes S. parvula from all other species that have been described up to now.

R e m a r k s: Many of the nineteen species placed by Perner (1907) into his subgenus Loxonema (Stylonema) have very large shells, often more than 25 times larger than the micromorphic shell of Stylonema parvula. Some of these species clearly belong to the other, still undescribed genera and a revision of Perner's species is needed.

Material: CGU JF 466-480.

Family Palaeozygopleuridae Horný, 1955

(emended by Knight, Batten, Yochelson & Cox, 1960)

R e m a r k s: Horný (1955) established the family Palaeozygopleuridae to include his new subfamily Palaeozygopleurinae and the subfamily Pseudozygopleurinae Knight, 1930. The latter had formerly been considered to be part of the family Loxonematidae by Knight (1930). Knight et al. (1960) emended the family Palaeozygopleuridae and proposed to divide the superfamily Loxonematoidea into four families: Loxonematidae Koken, 1889;

Palaeozygopleuridae Horny, 1955; Pseudozygopleuridae Knight, 1930; and Zygopleuridae WENZ, 1938. The subfamily Palaeozygopleurinae Horny was erected for taxa in which the teleoconch features are similar to those species of the subfamily Pseudozygopleurinae KNIGHT, 1930 with equal type of ornament present on all whorls, but in which the pseudozygopleurid type of protoconch is not developed. Horný (1955) included in the Palaeozygopleurinae two genera, Palaeozygopleura Horný, 1955 and Devonozyga Horný, 1955, from the Early and the Middle Devonian of Bohemia which he had proposed along with the three previously established genera Platyconcha Longstaff, 1933, Eoptychia Longstaff, 1933, and Microptychis Longstaff, 1912. Hoare & Sturgeon (1980) found no pseudozygopleurid type of protoconch in Hemizyga (H.) elegans Girty, which represents the type species of the genus Hemizyga. Thus, they proposed the placement of Hemizyga in the family Palaeozygopleuridae. Subsequently, they erected the new genus Gamizyga for species of Hemizyga in which the pseudozygopleurid type of the protoconch is developed. For the same reasons HOARE (1980) placed the genera Spiromphalus HAYASAKA, 1939, Sturgeonospira HOARE, 1980 and Anozyga HOARE, 1980 in the Palaeozygopleuridae, since they prossess simple protoconchs. On the other hand, HOARE & STURGEON (1981) proposed to exclude the genera Microptychis Longstaff and Eoptychia Longstaff from the family Palaeozygopleuridae, where these genera had been placed by HORNÝ (1955).

Hoare & Sturgeon (1978) studied the protoconchs of many Pennsylvanian representatives of the family Pseudozygopleuridae and expressed the opinion that the Pseudozygopleuridae illustrate a remarkable consistency in the nature of the protoconch which readily differentiates it from other families of Loxonematoidea. They suggested that the pseudozygopleurid protoconch presents clear evidence that the members of the Pseudozygopleuridae had a planktotrophic protoconch and that all belonged to the subclass Caenogastropoda. The possibility of pairs of species within a genus in which one had planktrotrophic development while the other had lecithotrophic development was suggested by Bandel (1991) in case of the Pseudozygopleuridae. This kind of differentiation is found among most modern marine gastropod groups and its results in the formation of a larval shell in one case, and a simplified enlarged embryonic shell in the other case present in the protoconch. Palaeozygopleuridae were thus suggested to represent Pseudozygopleuridae with lecithotrophic development, exemplified with Carboniferous species as described by Anderson et al (1985).

FRÝDA (1993) discussed the characters such as type of shell ornamentation, general shape and size of the shell, and the form of the outer apertural lip. All these have been used to distinguish the families Loxonematidae and Palaeozygopleuridae by Horný (1955). It appeared that neither of the above-mentioned characters of the teleoconch, which had been used in the differentiation of the families Loxonematidae and Palaeozygopleuridae can be used for a reliable distinction of these two families. These data are now substituted with new facts about protoconch type. In contrast to Pseudozygopleuridae, the species of the genus *Palaeozygopleura* always have a protoconch of the archaeogastropod type, and this is also true regarding species of the genera *Katoptychia* and *Stylonema*. The latter two genera were considered to represent members of the family Loxonematidae by Perner (1907) and this position was accepted by Wenz (1938) and Knight et al (1960). Even though the protoconch of the type species of the genus *Loxonema* is still unknown, it is quite reasonable to assume that it had the same type of protoconch as the contemporaceous genera *Katoptychia*, *Stylonema* and *Palaeozygopleura*. If this is so, then the family Palaeozygopleuridae represents a junior synonym of the family Loxonematidae.

## Genus Palaeozygopleura Horný, 1955

T y p e s p e c i e s: *Zygopleura alinae* Perner, 1907; Early Devonian, Pragian; Dvorce-Prokop Limestone, Praha Formation, Prague Basin, Barrandian area, Bohemia.

R e m a r k s: The genus *Palaeozygopleura* Horný, 1955, is known from marine strata of the Devonian and Carboniferous of Europe (Horný, 1955; Batten, 1966, Frýda, 1993), Asia (Licharev, 1968, 1971), Australia (Tassell, 1982), and North America (Linsley, 1968; Rollins et al., 1971; Thein & Nitecki, 1974; Gordon & Yochelson, 1987; Blodgett et al., 1988). The oldest hitherto known representatives of this genus are known from the early Lochkovian (Early Devonian) of Europe (Frýda, 1993; Frýda & Manda, 1997).

Horný (1955) established three subgenera within the genus Palaeozygopleura: Palaeozygopleura (Palaeozygopleura), Palaeozygopleura (Palaeozyga), and Palaeozygopleura (Bojozyga). Many new species have become known during the last 40 years. It became quite evident that there are species with transitional characters connecting these three subgenera. Intrageneric classification of the genus Palaeozygopleura thus is of doubtful use (see Batten, 1966, Frýda, 1993, Licharev, 1968, 1971, Linsley, 1968; Rollins et al., 1971). We still use the original subgeneric placement here to also demonstrate that the protoconch characteristics within genus Palaeozygopleura are the same. But we also establish here a new subgenus Palaeozygopleura (Bohemozyga) n. subgen. based on Palaeozygopleura (Palaeozygopleura?) kettneri Horný, 1955. This species differs from all known species of Palaeozygopleura and it shows transitional shell characters between Palaeozygopleura and Katoptychia.

The following five species of *Palaeozygopleura* have been analysed and demonstrated the large archaeogastropod-type protoconch: *Palaeozygopleura* (*Palaeozygopleura*) alinae (Perner, 1907), *Palaeozygopleura* (*Palaeozyga*) bohemica Horný, 1955, *Palaeozygopleura* (*Palaeozyga*) prantli Horný, 1955, *Palaeozygopleura* (*Palaeozyga*) hanusi Horný, 1955, and *Palaeozygopleura* (*Bohemozyga*) kettneri (Horný, 1955).

Subgenus Palaeozygopleura (Palaeozygopleura) Horný, 1955

Type species: Zygopleura alinae Perner, 1907.

R e m a r k s: Along with the type species, HORNÝ (1955) placed four additional species from the Devonian of the Prague Basin into the subgenus Palaeozygopleura (Palaeozygopleura). Palaeozygopleura (P.) devonicans (Perner, 1907) and Palaeozygopleura (P.?) bouskai HORNÝ, 1955 are known from limestones of Pragian (middle Early Devonian) age. The latter species based on only one poorly known specimen. Palaeozygopleura (P.) vesna HORNÝ, 1955 is based on the holotype and two fragments coming from the Choteč Limestone (early Eifelian?, early Middle Devonian). The fourth species is Palaeozygopleura (Palaeozygopleura?) kettneri HORNÝ, 1955 which is here transferred into the new subgenus Palaeozygopleura (Bohemozyga).

Within the type species of *Palaeozygopleura*, Horný (1955) established three subspecies, *Palaeozygopleura* (*P.*) alinae alinae Horný, 1955, *Palaeozygopleura* (*P.*) alinae planicostata Horný, 1955 and *Palaeozygopleura* (*P.*) alinae multicostata Horný, 1955. The second subspecies, represented by only a single specimen, comes from the same locality as the first subspecies, and may simple represent only an anomalous shell. On other hand, according to Horný (1955), the third subspecies comes from the Choteč Limestone (early Eifelian?, Middle Devonian).

## Palaeozygopleura (Palaeozygopleura) alinae (PERNER, 1907)

(pl. 7, figs. 5-6; pl. 9, fig. 2)

Typelocality: Dvorce, Praha, central Bohemia.

Type horizon: Praha Formation, Early Devonian.

Description: Small gastropods with a high-spired, dextrally coiled shell consisting of at least 9 whorls; shell sides straight or very slightly convex; lateral sides of the whorl moderately convex and slightly adpressed; sutures shallow, but distinct; pleural angle about 15°; base of whorl smooth, rounded and anomphalous; lateral part of the outer whorl sides curves uniformly onto the basal part without any angulation; shell ornament consists of prominent, slightly arched costae; protoconch of archaeogastropod type, smooth; its length is more than 0.3 mm high; all whorls succeeding the protoconch are ornamented by characteristic costae (see HORNÝ, 1955, pl. II, fig. 2).

Material: CGU JF 481-510.

Subgenus Palaeozygopleura (Palaeozyga) Horný, 1955

Type species: Palaeozygopleura (Palaeozyga) bohemica Horný, 1955.

Remarks: Horný (1955) established the subgenus *Palaeozygopleura* (*Palaeozyga*) based on *Palaeozygopleura* (*Palaeozyga*) bohemica Horný, 1955. Along with the type species, he placed five additional species into this subgenus. One of them, namely *Palaeozygopleura* (*Palaeozyga*) svobodai Horný, 1955 comes from the Praha Formation (Pragian). The remaining four species are all from the same locality near the village Holyně and stratigraphically close to boundary of the Třebotov Limestone (Emsian) and the Choteč Limestone (Eifelian). The Choteč Limestone was regarded as the type horizon by Horný (1955). The material studied here was collected from the same locality, but from the uppermost part of the Třebotov Limestone (Daleje-Třebotov Formation; late Emsian). The shells studied here give evidence for the existence of transitional forms connecting *Palaeozygopleura* (*P.*) bohemica Horný, 1955, *Palaeozygopleura* (*P.*) prantli Horný, 1955 and *Palaeozygopleura* (*P.*) hanusi Horný, 1955. (see also Horný, 1955, Tab. VI). The latter two species thus may represent synonyms of the first species.

Palaeozygopleura (Palaeozyga) bohemica Horný, 1955

(pl. 8, figs. 1-6; pl. 9, figs. 3-4)

Type locality: Holyně near Praha, central Bohemia.

Type horizon: Choteč Formation, early Middle Devonian.

D e s c r i p t i o n : Small gastropods with a high-spired, dextrally coiled shell consisting of up to 11 whorls; shell sides nearly straight; whorl profile slightly convex; sutures moderately deep; mean spire angle about 20°; lateral part of the outer whorl sides curves uniformly onto the basal part, with a smooth curvature lacking any angulation; shell base smooth, rounded and anomphalous; ornament consists of prominent, slightly arched costae; protoconch of archaeogastropod type, smooth; its length more than 0.3 mm; all whorls succeeding the protoconch are ornamented by characteristic costae (HORNÝ, 1955, pl. II, fig. 5)

Material: CGU JF 511-540.

Subgenus Palaeozygopleura (Bohemozyga) n. subgen.

Type species: Palaeozygopleura (Palaeozygopleura?) kettneri HORNÝ, 1955

D i a g n o s i s: Subgenus of the genus *Palaeozygopleura* with a large, protruding protoconch; outer apertural lip straight, without sinus and inclined strongly obliquely forward from the upper suture (=opisthocline); whorl sides slightly convex; shell ornament consists of a fine collabral costae.

C o mp a rison: The subgenus Palaeozygopleura (Bohemozyga) is distinguished from all other species of Palaeozygopleura by its large, protruding protoconch and by the shape of outer apertural lip. The size of the protoconch in Palaeozygopleura (Bohemozyga) is about 50% larger than that found among the known representatives of the other subgenera of Palaeozygopleura. The outer apertural lip of Palaeozygopleura (Bohemozyga) is straight bearing no sinus and strongly oblique forward in inclination (= opisthocline). This shape of the outer apertural lip resembles that of the type species of the genus Katoptychia Perner, 1907. The shape of the initial part of the shell of Katoptychia holynensis n. sp. is very similar to that found in Palaeozygopleura (Bohemozyga) kettneri, but the protoconch is smaller. Species of Katoptychia may also be distinguished from Palaeozygopleura (Bohemozyga) by their nearly straight whorl sides.

R e m a r k s: According to Horný (1955), Palaeozygopleura (Palaeozygopleura?) kettneri differs from species of Katoptychia by its more elongate shell, shape of the "nuclear region" and by the presence of costae in the ornament. He stated that costae of Palaeozygopleura-type are never observed in representatives of the genus Katoptychia. Perner (1907) never described or figured the initial parts of the shell of species of Katoptychia. The initial part of the shell is also not preserved in holotype or paratypes of the type species, Katoptychia alba Perner, 1907 (see Knight, 1941).

Palaeozygopleura (Bohemozyga) kettneri Horný, 1955

(pl. 8, fig. 7; pl. 9, figs. 1, 5-7)

Type locality: Holyně near Praha, central Bohemia.

Type horizon: Choteč Formation, early Middle Devonian.

Description: Gastropods with high-spired, dextrally coiled shells having straight lateral sides; mean spire angle about 17°; slightly convex whorl sides with a shallow, but distinct sutures; lateral part of the outer whorl sides curves uniformly onto basal part without forming any angulation; shell base rounded, smooth and anomphalous; outer apertural lip straight, bearing no sinus and having a strongly obliquely forward inclination from the upper suture (=opisthocline); protoconch smooth, large and protruding (pl. 9, figs. 5-7), its length more than 0.4 mm; ornament of the shell consists of fine collabral costae.

Material: Nineteen complete shells. CGU JF 541-559.

#### 6. Order Uncertain

Superfamily Peruneloidea nov.

D i a g n o s i s: Gastropods with small dextrally coiled shells having the first whorl openly coiled; first whorl planispirally or dextrally low-spired; initial part of the shell with a non-archaeogastropod protoconch; shell surface smooth or ornamented by collabral costae.

R e m a r k s: The superfamily Peruneloidea unites the four genera, *Perunela* n. gen., *Smichovia* n. gen., *Chuchlina* Frýda & Manda, 1997, and *Zenospira* n. gen., from the Lower Devonian of the Prague Basin. All these genera have the same type of initial whorl which is always openly coiled. The first about 0.1 mm of the first whorl is formed by a straight to weakly cyrtocone tube that latter begins dextral coiling. Thus, the early part of the shell is clearly different from an archaeogastropod-type protoconch (Bandel, 1982). This openly coiled type of initial whorl was also observed in several undescribed small gastropods coming from the Lower and Upper Silurian of the Prague Basin (Frýda, personal observation).

The relation of the superfamily Peruneloidea to any of the modern gastropod subclasses that bear a coiled larval shell is still uncertain. Its relation to older gastropod species is also uncertain because of the poor knowledge concerning the initial shells in the majority of the Paleozoic gastropods. The teleoconch characters of members of the family Chuchlinidae n. fam., that is considered to belong to the Peruneloidea n. superfam., resemble those of some genera which have traditionally been placed in the superfamily Subulitoidea Lindström, 1884. No information exists about the morphology of the protoconch of the type species of the genus *Subulites* Emmons, 1842, *Subulites subelongatus* (Orbigony, 1950), and thus the possible relation between these two taxa remains enigmatic.

Included families: Perunelidae n. fam. and Chuchlinidae n. fam.

Family Perunelidae n. fam.

Type genus: Perunela n. gen.

D i a g n o s i s: Members of Peruneloidea with smooth shells; shell base rounded, phaneromphalous; first whorl low-spired; protoconch openly coiled.

C o m p a r i s o n: Members of the family Perunelidae differ from those of the family Chuchlinidae in having a smooth shell with a rounded, phaneromphalous shell base.

R e m a r k s: Perunela n. gen. has an unusual shell with a tendency for disjunct coiling of the final whorl. This tendency is caused by increasing the growth rate in the axial direction from the initially low-spired, first whorl to that of the nearly disjunct final whorl. The genus Smichovia n. gen. is placed in the superfamily Peruneloidea because of its openly coiled protoconch, smooth adult shell, and phaneromphalous shell base of the teleoconch. Nevertheless, the differences in the general shape of the teleoconch found in Perunela and Smichovia make the placement of the genus Smichovia only tentative.

Included genera: Perunela n. gen. and Smichovia n. gen.

Genus Perunela n. gen.

Type species: Perunela bohemica n. sp.

Derivationominis: Perunela, according to Perun (Slavic god of thunders).

D i a g n o s i s: Gastropods with small, dextrally coiled shells; shape of teleoconch resembling that of *Hydrobia*; shell apex formed by first whorl being openly coiled and having low-spired coiling; shell with a concave apical depression; sutures impressed; aperture circular; whorl profile strongly convex; later whorls very loosely coiled; outer shell surface smooth.

C o m p a r i s o n: The shell shape of *Perunela* n. gen. is a very uncommon one among Paleozoic gastropods known up to now. The teleoconch of *Perunela* has a distinct tendency to disconnect the final whorl from the high-spired shell due to an increase of the

growth rate in the axial direction. A similar teleoconch character is known in some euomphalid genera, the pseudozygopleurid genus *Helminthozyga* Knight, 1930, and the onychochilid genus *Voskopiella* Frýda, 1992. However, Carboniferous and Permian members of the family Pseudozygopleuridae Knight, 1930 belong to the subclass Caenogastropoda Cox, 1959, with dextrally coiled protoconchs commonly bearing a larval shell that succeeds the embryonic shell. Members of the superfamily Onychochiloidea have a sinistrally coiled shell quite different to that of the Archaeogastropoda (Frýda, 1995). Their protoconch is sinistral and closely coiled. The gastropod species of the genus *Euomphalus* and relative genera usually also have openly coiled protoconchs as found in the genus *Perunela* and its relatives, but in the former group the protoconch is much larger (Bandel & Frýda, in preparation).

Perunela bohemica n. sp. (pl. 10, figs. 1-2)

Holotype: Pl. 10, figs. 1-2; CGU JF 560.

Derivatio nominis: bohemica, after Bohemia.

Type locality: Barrandov, Prague, central Bohemia.

Type horizon: Praha Formation, Pragian, Early Devonian.

Diagnosis: Because of monotypy, see that of genus.

D e s c r i p t i o n : Gastropods with very small, dextrally coiled shells bearing a concave apical depression; shell with tendency for disjunction of the last whorl; shell with 4 whorls is about 2.5 mm high; whorls very loosely coiled, their sides convex; spire with a pleural angle about 45°; sutures very deep, impressed; whorl profile between sutures strongly convex with maximum convexity slightly below mid-whorl; outer shell surface smooth; whorl profile runs from the upper suture uniformly onto the shell base, forming a smooth arch without any angulation; shell base rounded and minutely phaneromphalous; outer apertural lip without any slit or sinus; columellar lip thin; in axial section whorl interior nearly circular; aperture bears no parietal structures; protoconch consists of an openly coiled first whorl; shell apex with a concave depression in its middle; the first about 0.1 mm of the protoconch is a nearly straight tube, which subsequently begins dextral coiling; diameter of the first, openly coiled whorl is slightly less than 0.5 mm.

C o m p a r i s o n: The shape of the teleoconch of *Perunela bohemica* n. sp. resembles that of  $Kimina\ yooi\ n.$  sp., but the latter species has a closely coiled shell with an acute shell apex formed by the protoconch.

Material: CGU JF 560-561.

Genus Smichovia n. gen.

Type species: Smichovia inepta n. sp.

Derivatio nominis: Smichovia - according to Praha-Smíchov, a suburb of town Praha.

D i a g n o s i s: Gastropods with very small, dextrally coiled, low-spired, lenticular shells; first whorl openly coiled; shell base phaneromphalous; whorls adpressed; whorl slightly convex between weak and shallow sutures; whorl joints the previous whorls above its periphery; outer shell surface smooth.

R e m a r k s: The genus *Smichovia* represents an unusual element in the Early Devonian gastropod fauna of the Prague Basin. Its presence was discovered in the basal

part of the Lochkov Formation (Lochkovian; FRÝDA & MANDA, 1997) as well as in the Praha Formation (Pragian). *Smichovia* is placed into the superfamily Peruneloidea because of the shape and size of its protoconch. We also place *Smichovia* n. gen. in the family Perunelidae because of its smooth shell surface and the phaneromphalous shell base of the teleoconch. Nevertheless, there exists quite some differences regarding the general shape of the teleoconch found in *Perunela* and *Smichovia*.

Smichovia inepta n. sp.

(pl. 10, figs. 3-4)

Holotype: Pl. 10, figs. 3-4; CGU JF 350.

Derivatio nominis: according to ineptus (latin) = inept, unable.

Typelocality: The section "Nad rokli", Prague, central Bohemia.

Type horizon: Monograptus uniformis Biozone, early Lochkovian, early Early Devonian.

Diagnosis: Because of monotypy, see that of genus.

Description: Very small gastropods with dextrally coiled, lenticular shells that are about twice as wide as high and widely umbilicate; outer shell surface smooth; upper shell sides convexly arched; whorl profile between the weak and shallow sutures slightly convex; lateral rounded whorl sides continue uniformly onto the shell base without angulation; whorls joins the previous whorls above their periphery; maximum convexity of the whorls is situated at the whorl periphery; outer apertural lip not well preserved, but bearing no slit or sinus; inner lip is thin, slightly oblique and inclined forward; openly coiled protoconch forms the first whorl of about 0.3 mm in diameter; its initial portion consists of an about 0.1 mm long, straight tube after which dextral coiling begins.

D is cussion: Smichovia inepta occurs in the Lochkov Formation (Monograptus uniformis graptolite Biozone, early Lochkovian, Early Devonian), but a species belonging to this genus was also found (pl. 10, figs. 5-6) in the Praha Formation (Pragian). At the moment it is not clear whether both species are conspecific or represent two different species.

Material: CGU JF 350-354.

Family Chuchlinidae n. fam.

Type genus: Chuchlina Frýda & Manda, 1997

D i a g n o s i s: Members of the Peruneloidea with a subulate teleoconch; shallow sutures being weak; shell ornamentation consisting of collabral costae; whorls adpressed; protoconch having planispiral or low-spired coiling, always openly coiled.

C o m p a r i s o n: Members of the family Chuchlinidae are distinguished from the members of the family Perunelidae by their subulate teleoconch with anomphalous base, shallow and weak sutures as well as by a shell ornamentation consisting of the collabral costae.

R e m a r k s: The teleoconch characters in the two genera *Chuchlina* and *Zenospira* of the family Chuchlinidae resembles that of some genera which are traditionally placed in the superfamily Subulitoidea Lindström, 1884. The type species of *Subulites*, representing the type genus of the family Subulitidae, is based on the Middle Ordovician *Subulites* subelongatus (Orbigny, 1850), that has a large, slender, spindle-shaped and smooth shell.

No information exists on the protoconch of this species and, thus, the relation of the family Chuchlinidae to the subulitoidean gastropods remains unsolved.

Included genera: Chuchlina Fryda & Manda, 1997 and Zenospira n. gen.

Genus Chuchlina FRYDA & MANDA, 1997

D i s c u s s i o n: The monotypic genus *Chuchlina* is based on *Chuchlina minuta* Frýda & Manda, 1997 from the Lochkov Formation (early Lochkovian, Early Devonian) of the Prague Basin.

C o m p a r i s o n: The teleoconch of *Chuchlina* resembles such members of the family Subulitidae Lindstrom, 1884 as *Bulimorpha* Whitfield, 1882, *Soleniscus* Meek & Worthen, 1861, *Fusispira* Hall, 1872, and *Cyrtospira* Ulrich in Ulrich & Scofield, 1897. The teleoconch of *Chuchlina* is distinguished from the type species of *Bulimorpha*, *B. bulimiformis* (Hall, 1858), by a differently formed columellar lip, by its smaller shell size, shell width and ornamentation. The columellar lip of the aperture in *Chuchlina* is parallel to the shell axis while it runs sideways in *Bulimorpha*. The shell height of *Chuchlina* is about twice its width, but three times its width in *Bulimorpha*. The outer shell surface of *Bulimorpha* is smooth but ornamented by collabral costae in *Chuchlina*. *Soleniscus* differs by being larger and having a siphonal canal and a parietal fold that is not present in *Chuchlina*. The latter differs also from the type species of *Cyrtospira* by its wider and ornamented shell. The type species of the *Fusispira*, the Middle Ordovician *Fusispira ventricosa* Hall, 1872, is poorly known. Nevertheless, *Chuchlina* differs from the latter genus by having a very small shell, a wider aperture and straight sides of its spire. *Fusispira ventricosa* is more than twenty times larger and has distinctly concave sides of its spire.

Chuchlina minuta Frýda & Manda, 1997 (pl. 11, figs. 5-6)

Description: Gastropods with a very small fusiform, high-spired shell having at least 6 whorls; sides of the spire slightly convex and contain an angle about 40°; sutures shallow and indistinct; whorl profile between the sutures symmetrically convex; the whorl profile runs from the upper suture uniformly onto the shell base, forming a smooth curvature without any angulation; shell base conical and anomphalous; outer apertural lip straight and orthocline; columellar lip thickened and parallel with the shell axis; the aperture bearing no parietal structures; shell ornament consists of fine collabral costae; the first, low spired whorl forming a flat apex on the shell; the first about 0.10 mm of the first whorl is formed by a straight tube that subsequently starts coiling dextrally; the first openly coiled whorl has a diameter of about 0.20 mm.

D is c ussion: The shape of the first whorl in Chuchlina minuta Frýda & Manda, 1997 resembles that found in Zenospira pragensis n. sp. The first whorl in the latter species is planispirally coiled and more distinctly shows open coiling than Chuchlina minuta. Nevertheless, the openly coiled early whorl places both genera, Chuchlina and Zenospira, into the same protoconch morphogroup. Their teleoconch characters also suggest a similar conclusion.

Material: CGU JF 356-359. Holotype CGU JF 356.

Genus Zenospira n. gen.

Type species: Zenospira pragensis n. sp.

Derivation ominis: The genus is named in honor of Franciscus Zeno, Czech Jesuit and author of the first notes about Bohemian Paleozoic fossils published in 1770.

D i a g n o s i s: Small gastropods with dextrally coiled, subulate shells; flat shell apex with concave depression in its center formed by the planispirally coiled protoconch; whorls of teleoconch strongly adpressed; outer lip straight, slightly opisthocline, without slit or sinus; shell ornamentation consisting of collabral costae.

Comparison: Zenospira n. gen. resembles Chuchlina Fryda & Manda, 1997 by the shape of its protococh and by the ornament and fusiform shape of its teleoconch. The former genus is distinguished from the latter by its more adpressed whorls, wider shell, shape of its aperture and by the shape of the initial whorl. The shell of Zenospira is slightly higher than wide, but in Chuchlina it is about twice as high as it is wide. In axial section the inner shape of the aperture in Zenospira is nearly circular, while it is considerably elongated in the axial direction in Chuchlina. The protoconch in Zenospira is planispirally coiled, while it is low-spired in Chuchlina. The shape of the teleoconch and the ornamentation in Zenospira resembles that of an undescribed species of "Fusispira" Hall, 1872 from the Praha Formation (Pragian) of the Prague Basin, which has a tightly coiled protoconch (Fryda, personal observation). Zenospira also resembles the genus Sinospira Yin, 1932, which is based on the Late Carboniferous Sinospira ornata Yin, 1932 from China. The latter genus was suggested to belong to the genus Leptoptygma Knight, 1936 by Knight et al. (1960). Zenospira differs from both Sinospira and Leptoptygma by its much smaller shell size and shallower sutures.

Zenospira pragensis n. sp.

(pl. 11, figs. 1-4)

Holotype: Pl. 11, figs. 1-4; CGU JF 562.

Derivatio nominis: pragensis, after the capital of the Czech Republic, Praha (Latin Praga).

Typelocality: Barrandov, Prague, central Bohemia.

Type horizon: Praha Formation, Pragian, Early Devonian.

Diagnosis: Because of monotypy, see that of genus.

Description: Gastropods with small, dextrally coiled, subulate shells having a flat apex; sides of the spire very slightly convex having the pleural angle about 60°; sutures between strongly adpressed whorls shallow; whorl profile between sutures symmetrically convex and in final whorl continuing uniformly onto the shell base forming a smooth arch; shell base conical and anomphalous; ornament consists of collabral costae; outer apertural lip straight and slightly opisthocline; columellar lip thickened and parallel with the shell axis; there are no parietal structures; in axial section the aperture is nearly circular; protoconch forms the flattened shell apex with a central depression; protoconch is planispirally and openly coiled; the initial about 0.1 mm of the first whorl consists of a nearly straight tube before dextral coiling begins; diameter of the first, openly coiled whorl forming the protoconch is slightly less than 0.5 mm.

R e m a r k s: The shape of the initial whorl of *Zenospira pragensis* resembles that of a group of still undescribed small shells coming from the Early Silurian of the Prague basin (FRÝDA, personal observation). The future study of these shells may also show the presence of the genus Zenospira in sediments of Silurian age.

Material: CGU JF 562-564.

## Acknowledgements

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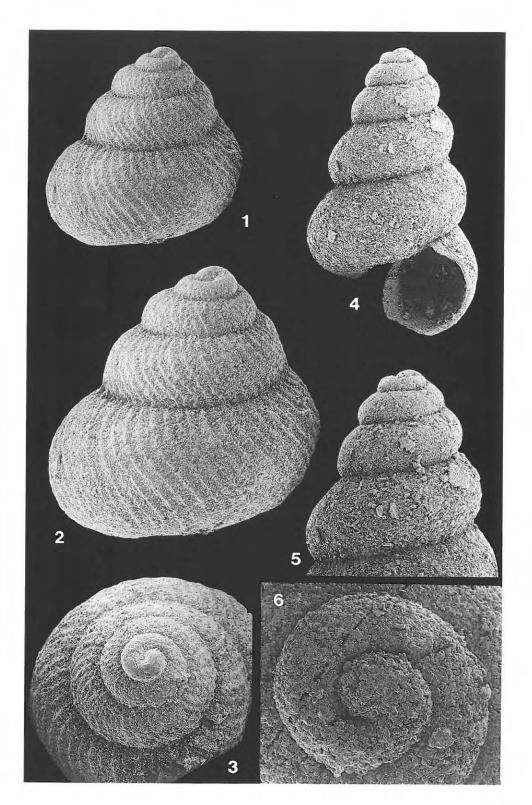
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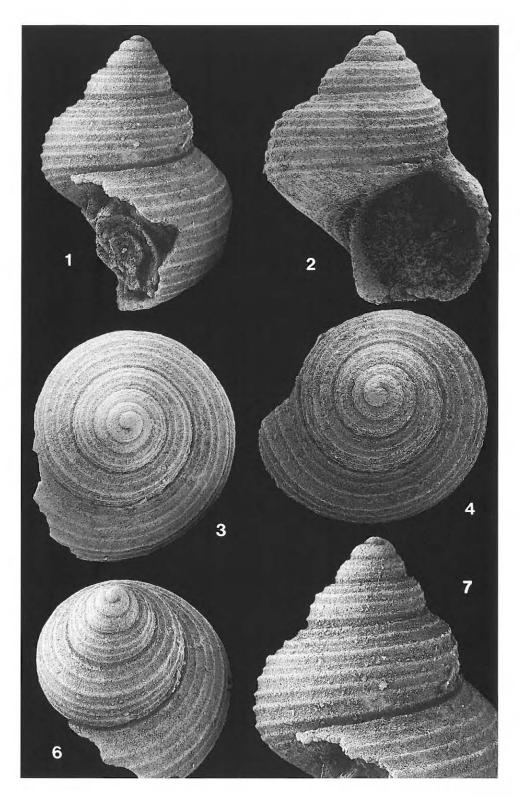
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#### Plate 1

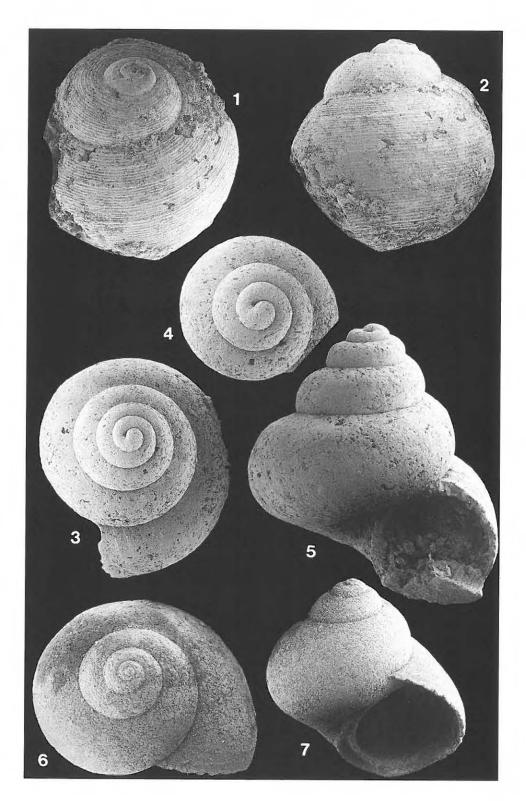
- Fig. 1: *Hawletrochus pragensis* n. sp. from the uppermost part of the Třebotov Limestone, Daleje-Třebotov Formation, Holyně near Prague; late Emsian, Early Devonian; oblique view of holotype, CGU JF 360, x 36.
- Fig. 2: Hawletrochus pragensis n. sp., same view, CGU JF 360, x 50.
- Fig. 3: Hawletrochus pragensis n. sp., oblique view showing the protoconch of archaeogastropod type, CGU JF 360, x 50.
- Fig. 4: *Kimina yooi* n. sp. from the Praha Formation, Barrandov; Pragian, Early Devonian; apertural view of holotype, CGU JF 371, x 33.
- Fig. 5: Kimina yooi n. sp. from the Praha Formation, Barrandov; Pragian, Early Devonian; view of early whorls, CGU JF 371, x 46.
- Fig. 6: Kimina yooi n. sp., apical view of protoconch, CGU JF 371, x 160.



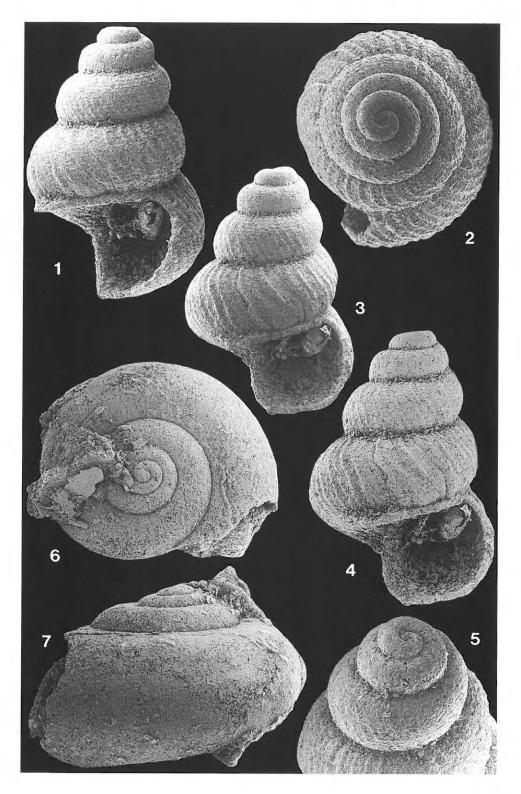
- Fig. 1: Australonema havliceki n. sp. from the uppermost part of the Třebotov Limestone, Daleje-Třebotov Formation, Holyně near Prague; late Emsian, Early Devonian; lateral view of holotype, CGU JF 378, x 14.
- Fig. 2: Australonema havliceki n. sp. from the uppermost part of the Třebotov Limestone, Daleje-Třebotov Formation, Holyně near Prague; late Emsian, Early Devonian; lateral view, CGU JF 379, x 19.
- Fig. 3: Australonema havliceki n. sp., apical view of holotype showing the protoconch of archaeogastropod type, CGU JF 378, x 16.
- Fig. 4: Australonema havliceki n. sp., apical view showing the protoconch of archaeogastropod type, CGU JF 379, x 18.
- Fig. 5: Australonema havliceki n. sp., oblique view of holotype showing the protoconch of archaeogastropod type, CGU JF 378, x 16.
- Fig. 6: Australonema havliceki n. sp., lateral view of holotype showing the shell ornamentation, CGU JF 378, x 20.



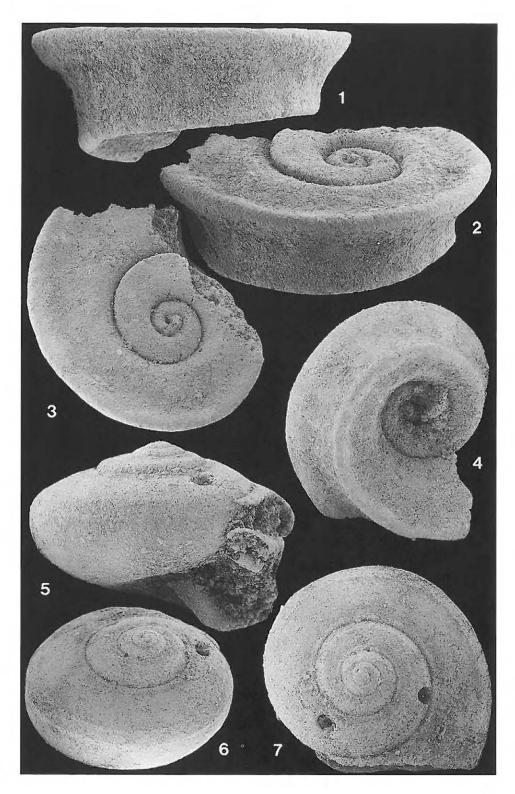
- Fig. 1: Omphalonema (Globulonema) sp. from the Dvorce-Prokop Limestone, Praha Formation, quarry Kantina near Holyně; Pragian, Early Devonian; oblique view, CGU JF 396, x 13.
- Fig. 2: Omphalonema (Globulonema) sp., lateral view, CGU JF 396, x 13.
- Fig. 3: *Holopea kettneri* n. sp. from the Praha Formation, Barrandov; Pragian, Early Devonian; apical view of holotype, CGU JF 397, x 22.
- Fig. 4: Holopea kettneri n. sp., detail view of shell apex showing the protoconch of archaeogastropod type, CGU JF 397, x 30.
- Fig. 5: Holopea kettneri n. sp., apertural view of holotype, CGU JF 397, x 23.
- Fig. 6: Krasopea glabra n. sp. from the Praha Formation, Požáry; Pragian, Early Devonian; oblique view of holotype, CGU JF 421, x 18.
- Fig. 7: Krasopea glabra n. sp., lateral view of holotype, CGU JF 421, x 15.



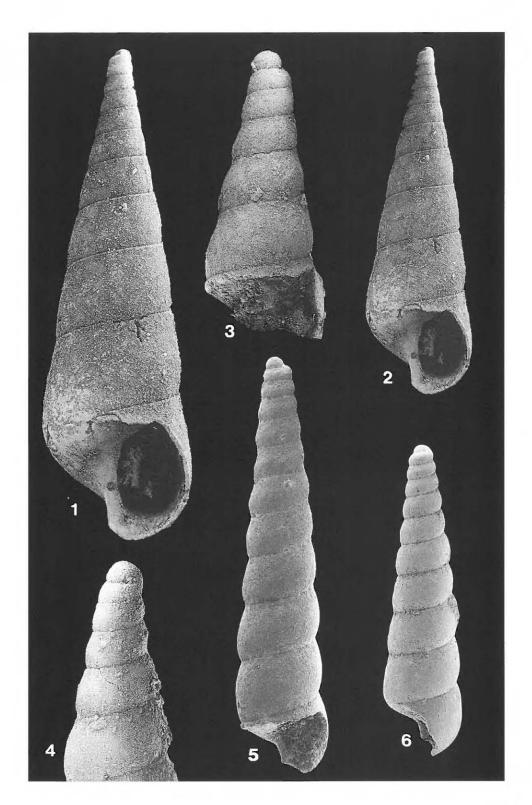
- Fig. 1: Purkynespira reticulata n. sp. from the Praha Formation, Barrandov; Pragian, Early Devonian; lateral view of holotype showing the reticulate shell ornamentation, CGU JF 426, x 36.
- Fig. 2: Purkynespira reticulata n. sp., apical view of holotype, CGU JF 426, x 40.
- Fig. 3: Purkynespira reticulata n. sp., lateral view of holotype, CGU JF 426, x 32.
- Fig. 4: Purkynespira reticulata n. sp., lateral view of holotype, CGU JF 426, x 36.
- Fig. 5: Purkynespira reticulata n. sp., oblique view of holotype showing the planispirally or slightly sinistrally coiled first whorl, CGU JF 426, x 47.
- Fig. 6: Eiselia (Eoeiselia) minutula n. sp. from the Praha Formation, Požáry; Pragian, Early Devonian; apical view of holotype showing the protoconch of archaeogastropod type, CGU JF 430, x 16.
- Fig. 7: Eiselia (Eoeiselia) minutula n. sp., lateral view of holotype, CGU JF 430, x 19.



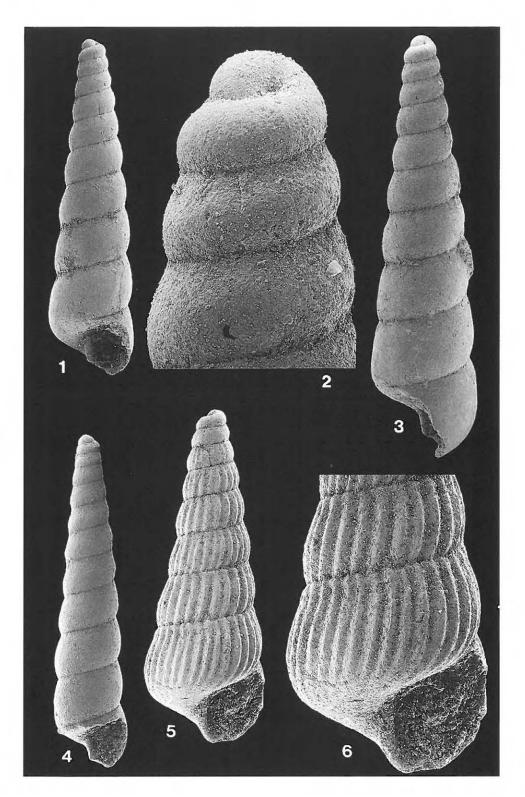
- Fig. 1: Cordaspira enigma n. sp. from the Dvorce-Prokop Limestone, Praha Formation, quarry Kantina near Holyně; Pragian, Early Devonian; lateral view of holotype showing the whorl profile, CGU JF 441, x 43.
- Fig. 2: Cordaspira enigma n. sp., oblique view of holotype, CGU JF 441, x 45.
- Fig. 3: Cordaspira enigma n. sp., apical view of holotype, CGU JF 441, x 38.
- Fig. 4: Cordaspira enigma n. sp., umbilical view of holotype, CGU JF 441, x 32.
- Fig. 5: *Umbotropis rihai* n. sp. from the Praha Formation, Požáry; Pragian, Early Devonian; lateral view of holotype, CGU JF 446, x 21.
- Fig. 6: *Umbotropis rihai* n. sp., oblique view of holotype showing the selenizone, CGU JF 446, x 16.
- Fig. 7: Umbotropis rihai n. sp., apical view of holotype showing the protoconch of archaeogastropod type, CGU JF 446, x 18.



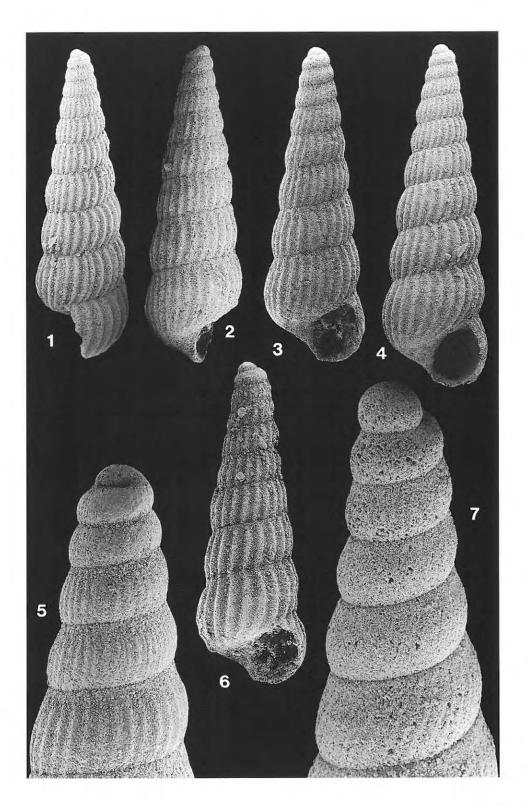
- Fig. 1: Katoptychia holynensis n. sp. from the uppermost part of the Třebotov Limestone, Daleje-Třebotov Formation, Holyně near Prague; late Emsian, Early Devonian; lateral view of holotype, CGU JF 450, x 13.
- Fig. 2: Katoptychia holynensis n. sp., same view as Fig. 1, CGU JF 450, x 9.
- Fig. 3: *Katoptychia holynensis* n. sp. from the uppermost part of the Třebotov Limestone, Daleje-Třebotov Formation, Holyně near Prague; late Emsian, Early Devonian; lateral view of early whorls, CGU JF 451, x 18.
- Fig. 4: Katoptychia holynensis n. sp., lateral view of early whorls, CGU JF 451, x 18.
- Fig. 5: Stylonema parvula n. sp. from the Praha Formation, Barrandov; Pragian, Early Devonian; lateral view, CGU JF 467, x 23.
- Fig. 6: Stylonema parvula n. sp. from the Praha Formation, Barrandov; Pragian, Early Devonian; lateral view of holotype, CGU JF 466, x 20.



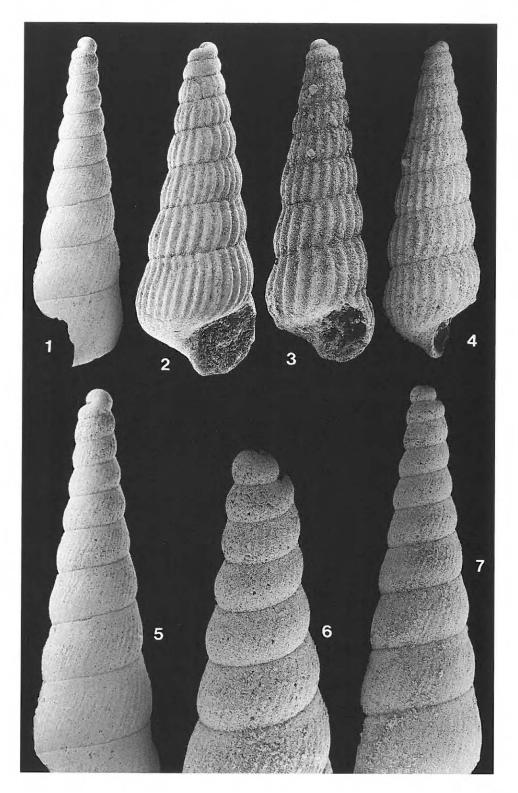
- Fig. 1: Stylonema parvula n. sp. from the Praha Formation, Barrandov; Pragian, Early Devonian; lateral view of holotype, CGU JF 466, x 20.
- Fig. 2: Stylonema parvula n. sp., lateral view of holotype showing the early shell whorls, CGU JF 466, x 125.
- Fig. 3: Stylonema parvula n. sp., lateral view of holotype, CGU JF 466, x 27.
- Fig. 4: Stylonema parvula n. sp. from the Praha Formation, Barrandov; Pragian, Early Devonian; lateral view, CGU JF 467, x 23.
- Fig. 5: Palaeozygopleura (Palaeozygopleura) alinae (Perner) from the Praha Formation, Barrandov; Pragian, Early Devonian; lateral view, CGU JF 481, x 20.
- Fig. 6: Palaeozygopleura (Palaeozygopleura) alinae (Perner), detail view of te shell ornamentation, CGU JF 481, x 33.



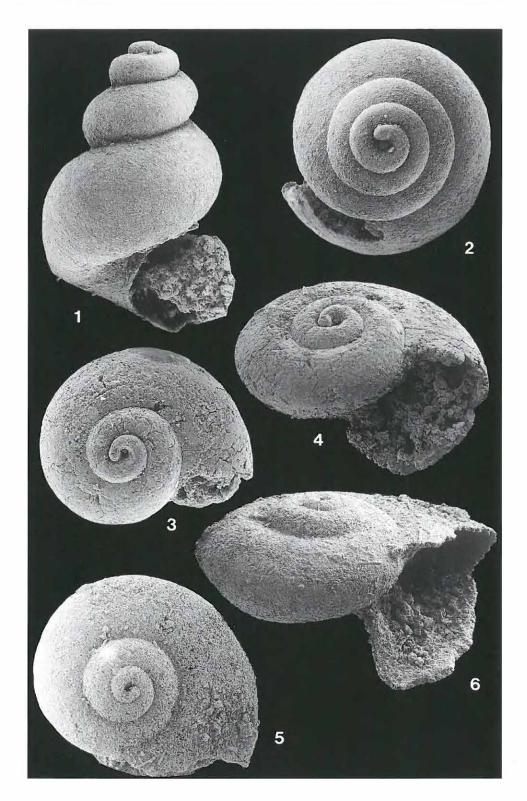
- Fig. 1: Palaeozygopleura (Palaeozyga) bohemica Horný from the uppermost part of the Třebotov Limestone, Daleje-Třebotov Formation, Holyně near Prague; late Emsian, Early Devonian; lateral view, CGU JF 511, x 18.
- Fig. 2: Palaeozygopleura (Palaeozyga) bohemica Horný from the uppermost part of the Třebotov Limestone, Daleje-Třebotov Formation, Holyně near Prague; late Emsian, Early Devonian; lateral view, CGU JF 512, x 18.
- Fig. 3: Palaeozygopleura (Palaeozyga) bohemica Horný from the uppermost part of the Třebotov Limestone, Daleje-Třebotov Formation, Holyně near Prague; late Emsian, Early Devonian; lateral view, CGU JF 513, x 20.
- Fig. 4: Palaeozygopleura (Palaeozyga) bohemica Horný, lateral view, CGU JF 511, x 19.
- Fig. 5: Palaeozygopleura (Palaeozyga) bohemica Horný from the uppermost part of the Třebotov Limestone, Daleje-Třebotov Formation, Holyně near Prague; late Emsian, Early Devonian; detail view showing the early whorls, CGU JF 514, x 50.
- Fig. 6: Palaeozygopleura (Palaeozyga) bohemica Horný from the uppermost part of the Třebotov Limestone, Daleje-Třebotov Formation, Holyně near Prague; late Emsian, Early Devonian; lateral view, CGU JF 515, x 22.
- Fig. 7: Palaeozygopleura (Bohemozyga) kettneri Horný from the uppermost part of the Třebotov Limestone, Daleje-Třebotov Formation, Holyně near Prague; late Emsian, Early Devonian; detail view showing the early whorls, CGU JF 541, x 50.



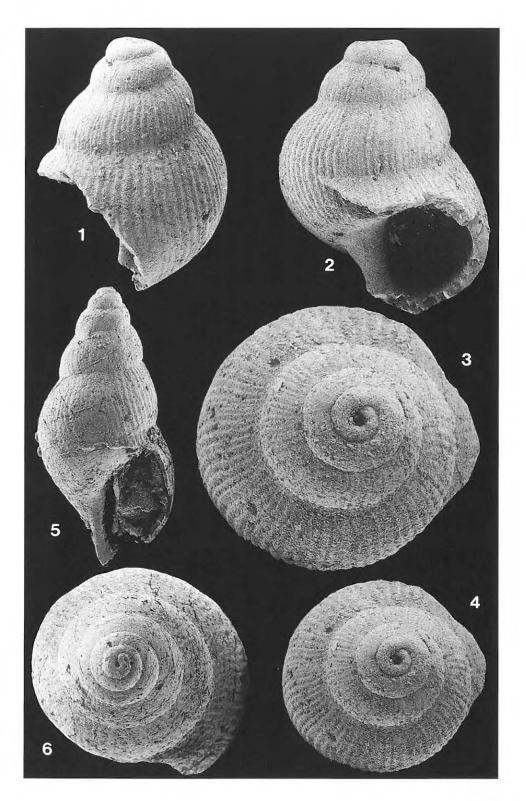
- Fig. 1: Palaeozygopleura (Bohemozyga) kettneri Horný from the uppermost part of the Třebotov Limestone, Daleje-Třebotov Formation, Holyně near Prague; late Emsian, Early Devonian; lateral view, CGU JF 542, x 50.
- Fig. 2: Palaeozygopleura (Palaeozygopleura) alinae (Perner) from the Praha Formation, Barrandov; Pragian, Early Devonian; lateral view, CGU JF 481, x 20.
- Fig. 3: Palaeozygopleura (Palaeozyga) bohemica Horný from the uppermost part of the Třebotov Limestone, Daleje-Třebotov Formation, Holyně near Prague; late Emsian, Early Devonian; lateral view, CGU JF 512, x 18.
- Fig. 4: Palaeozygopleura (Palaeozyga) bohemica Horný from the uppermost part of the Třebotov Limestone, Daleje-Třebotov Formation, Holyně near Prague; late Emsian, Early Devonian; lateral view, CGU JF 515, x 22.
- Fig. 5: Palaeozygopleura (Bohemozyga) kettneri Horný from the uppermost part of the Třebotov Limestone, Daleje-Třebotov Formation, Holyně near Prague; late Emsian, Early Devonian; lateral view showing the large and protruding protoconch, CGU JF 542, x 19.
- Fig. 6: Palaeozygopleura (Bohemozyga) kettneri Horný from the uppermost part of the Třebotov Limestone, Daleje-Třebotov Formation, Holyně near Prague; late Emsian, Early Devonian; detail view showing the large and protruding protoconch, CGU JF 541, x 36.
- Fig. 7: Palaeozygopleura (Bohemozyga) kettneri Horný, lateral view, CGU JF 541, x



- Fig. 1: Perunela bohemica n. sp. from the Praha Formation, Barrandov; Pragian, Early Devonian; lateral view of holotype, CGU JF 560, x 36.
- Fig. 2: *Perunela bohemica* n. sp. from the Praha Formation, Barrandov; Pragian, Early Devonian; apical view of holotype showing the openly coiled first whorl, CGU JF 560, x 42.
- Fig. 3: Smichovia inepta n. sp. from the Monograptus uniformis graptolite Biozone, bed 13, Nad roklí section, Lochkov Formation; early Lochkovian, Early Devonian; apical view showing the openly coiled first whorl, CGU JF 350, x 50.
- Fig. 4: Smichovia inepta n. sp., oblique view of holotype, CGU JF 350, x 60.
- Fig. 5: Smichovia sp. from the Praha Formation, Barrandov; Pragian, Early Devonian; apical view, CGU JF 355, x 45.
- Fig. 6: *Smichovia* sp. from the Praha Formation, Barrandov; Pragian, Early Devonian; oblique view, CGU JF 355, x 50.



- Fig. 1: Zenospira pragensis n. sp. from the Praha Formation, Barrandov; Pragian, Early Devonian; oblique view of holotype, CGU JF 562, x 27.
- Fig. 2: Zenospira pragensis n. sp. from the Praha Formation, Barrandov; Pragian, Early Devonian; apertural view of holotype, CGU JF 562, x 30.
- Fig. 3: Zenospira pragensis n. sp., apical view of holotype showing the openly coiled first whorl, CGU JF 562, x 42.
- Fig. 4: Zenospira pragensis n. sp., same view of holotype, CGU JF 562, x 42.
- Fig. 5: *Chuchlina minuta* Frýda & Manda, 1997 from the *Monograptus uniformis* graptolite Biozone, bed 13, Nad roklí section, Lochkov Formation; early Lochkovian, Early Devonian; lateral view of holotype, CGU JF 356, x 25.
- Fig. 6: Chuchlina minuta Frýda & Manda, 1997, apical view showing the openly coiled first whorl, CGU JF 356, x 40.



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