Review of palaeozygopleurid gastropods (Palaeozygopleuridae, Gastropoda) from Devonian strata of the Perunica microplate (Bohemia), with a re-evaluation of their stratigraphic distribution, notes on their ontogeny, and descriptions of new taxa

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Abstract

Review of all species of the family Palaeozygopleuridae Horný, 1955 (Gastropoda) known from the Perunica microplate (Bohemia) is presented with a description of three new species, Palaeozygopleura lukesi sp. nov., Cimrmaniela sveraki gen. et sp. nov. and Cimrmaniela smoljaki gen. et sp. nov. The stratigraphic distributions of the most of Bohemian palaeozygopleurid species are either corrected or refined, based on new records or modern stratigraphic studies. A complete list of the geographic occurrences of all known palaeozygopleurid gastropods from the Perunica microplate is also given together with notes on their ontogeny.

Key words: Gastropoda, Palaeozygopleuridae, Palaeozygopleura, Cimrmaniela gen. nov., Devonian, Europe, Perunica, new taxa

Introduction

Palaeozygopleurids represent a distinctive gastropod group, which occurred in the Devonian strata of Variscan Europe (Horný 1955; Frýda 1993, 1999, 2000; Blodgett et al. 1999; Frýda & Bandel 1997; Heidelberger & Bandel 1999; Heidelberger 2001, 2007; Krawczyński 2002, 2006; Frýda et al. 2008), northern Gondwana (De Baets et al. 2010), Laurentia (Linsley 1968; Rollins et al. 1971; Blodgett & Johnson 1992), Alaskan terranes (Blodgett 1992; Frýda & Blodgett 2004), central Asia (Gubanov et al. 1995) and Australia (Tassell 1982; Cook 1995; Cook & Camilleri 1997; Cook et al. 2003). Blodgett et al. (1988, 1990) interpreted this gastropod group as a typical element of the Old World Realm of Early Devonian age. The oldest (and only) Silurian species of palaeozygopleurid gastropods belongs to the genus Medfrazyga Frýda & Blodgett, 2004, and was found in the Heceta Formation in the Alexander terrane on Prince of Wales Island, south-eastern Alaska (Rohr et al. 2008). Recent palaeobiogeographic studies indicate that the Alexander terrane is faunally most similar to Siberia (Blodgett et al. 2002, 2003; Pedder 2006), notably its eastern portion. It is now considered that this terrane most likely originated as a rifted block of the eastern Siberian palaecocontinent, probably breaking away in the later part of the Devonian (Blodgett et al. 2010). Silurian Bivalvia from Chichagof Island, Southeast Alaska (Alexander terrane), seem to be very similar to the homologous and analogous late Wenlockian Bivalvia communities described from Gotland, Sweden and Baltica (Kříž et al. 2011). The fauna of the Alexander terrane is altogether different in species composition from the NW part of the non-accretionary portion of North America (i.e., Laurentia), although both regions belong to the Old World Realm. Hitherto no palaeozygopleurid gastropod was recorded from the non-accretionary portion of North America, belonging to the Western Canada Province, established by Blodgett et al. (2001), although the latter province clearly belongs to the Old World Realm (Frýda et al. 2002, 2008, 2011). The family Palaeozygopleuridae probably originated in the Old World Realm (Frýda 1993).
Hitherto, the highest biodiversity of this family was recorded in the Lower Devonian strata of the Perunica microplate (Fig. 1B). Later, in the Middle and Late Devonian, palaeozygopleurid gastropods also occurred in the Eastern American Realm, not only in the Old World Realm. Late Paleozoic palaeozygopleurid gastropods are poorly known, the youngest palaeozygopleurid belongs to the same genus, *Medfrazyga*, as the oldest one (see discussion in Nützel & Nakazawa 2012).

Generally, palaeozygopleurid gastropods were restricted to warm to tropical environments with carbonate sedimentation. The phylogenetic relationships of the palaeozygopleurid gastropods are still unsettled (Bandel 1991; Frýda & Bandel 1997; Nützel 1998; Frýda et al. 2008). The most discussed topics are on the nature of their ontogenetic strategy, as well as their relationships to their living environment.

All of the palaeozygopleurids described and reviewed here come from the Early Devonian strata of the Prague Basin (Fig. 1A), which is the only basin with Early Devonian strata preserved in the Perunica microplate. The Prague Basin represents a rift type basin, located at the northern margin of peri-Gondwana on the Perunica microplate (Fig. 1B), which drifted across the south subtropical and tropical zones during the Silurian and Early Devonian (Krůž et al. 2003). Ordovician, Silurian, and Early Devonian marine faunal communities of the Perunica microplate contain many endemic taxa, which was due to the geographic position of the Perunica microplate (Ebbenstad et al. 2013).

In this short paper, all species of the gastropod family Palaeozygopleuridae (including three new species) from the Perunica microplate are reviewed, and their stratigraphic distributions are corrected or refined, based on new records or modern stratigraphic studies. Special attention is also paid to their protoconch morphology and its interpretation.

**Material and methods**

The new taxa described here come from weathered beds of the Early Devonian Koněprusy Limestone (Praha Formation) of Pragian age found by one of us (LF) at the Císařský lom quarry (Fig. 1; Frýda & Ferrová 2011). These weathered beds contain a rather highly diversified gastropod fauna, which is under study. SEM-images of the first several whorls were used for measurement of protoconch size as well as for documentation of shell morphology (Figs 2, 3). Shells of all the newly described species (both figured and unfigured) are deposited in the Czech Geological Survey (Prague) under numbers (UUG JF 907–959). Abbreviations: NMP—National Museum, Prague, UUG JF—Czech Geological Survey (Prague).

**Localities of Bohemian palaeozygopleurids**

Intensive research on the Lower Devonian sections in the Barrandian area during the last decades has yielded much new stratigraphic and paleontological data, which makes possible a re-evaluation of the stratigraphic and geographic distributions of the Bohemian palaeozygopleurid gastropods. Hitherto published data on the stratigraphic distribution of the most of the Bohemian palaeozygopleurid species are incorrect (or not exact). In the following sections, all known localities of the Bohemian palaeozygopleurid gastropods (Fig. 1) are listed in alphabetical order including their revised occurrences. The Devonian strata of the Barrandian area were intensively folded in the Late Paleozoic (Chlupáč et al. 1992). Therefore, one has to keep in mind that short distances of Recent localities do not necessarily mean that were close in the past.

**Barrandov I**—Abandoned locality in weathered strata belonging to the Dvorce-Prokop Limestone of Pragian age. The locality was opened in a road cut in a SW portion of Prague (50°2′11.677″N, 14°23′59.722″E, locality number JF217).

**Barrandov II**—Road cut section in a SW portion of Prague (50°2′8.268″N, 14°23′32.921″E, locality number JF201), exposing late Emsian and Eifelian strata of Daleje-Třebotov and Chotět formations. Palaeozygopleurid gastropods were collected by two of us (JF and BF) from weathered strata of the uppermost part of the Třebotov Limestone (Daleje-Třebotov Formation). These strata belong to tentaculite [Nowakia (*Dmitriella*) *sulcata sulcata* (Roemer, 1843)] and conodont (*Polygnathus costatus costatus* Klappler, 1971) biozones indicating an early Eifelian age of the palaeozygopleurid gastropods (see Lukeš 1989; Zuzková 1991; Berkyová 2009; Vodrážková et al. 2013).
Čeřinka hillside section—Section south of Bubovice (49°58'1.973"N, 14°10'28.353"E, locality number JF8). Occurrence of palaeozygopleurid gastropods is restricted to *Nowakia barrandei* Bouček & Prantl, 1959 and *Nowakia elegans* (Barrande, 1867) tentaculite biozones (mid-Emsian) of the Chýnice Limestone (Frýda *et al.* 2008, 2009; Mergl & Ferrová 2009; Ferrová 2010; Ferrová *et al.* 2012).


*Císařský lom*—Quarry S of the village of Koněprusy (49°54'59.739"N, 14°3'37.580"E, locality number JF189). Palaeozygopleurid gastropods were collected by one of us (LF) from weathered Koněprusy Limestone at the fourth floor (No. 345) of the Císařský lom quarry (Frýda & Ferrová 2011).

*Dvorce*—Old quarry (50°3'4.323"N, 14°25'2.879"E, locality number JF218) in a suburb S of Prague. The complete section, exposing Late Silurian and Early Devonian strata, has been known as an important fossil locality for more than 200 years (Zeno 1770), and is protected as the Podolí Section Nature Monument. Palaeozygopleurid gastropods come from weathered strata at the boundary of the Slivenec and Dvorce limestones of the Praha Formation (more details in Kríž 1999).

*Hlubočepy*—Suburb SW of Prague (50°2'24.549"N, 14°24'0.039"E, locality number JF220), where there are several old quarries, which mainly belong to the Třebotov Limestone of the Daleje-Třebotov Formation.

*Holyně*—Section in a small quarry NE of the village of Holyně and W of the Prastav quarry (50°1'57.627"N, 14°21'5.471"E, locality number JF5) at SW suburb of Prague in the Daleje-Třebotov and Choteč formations. In the last century, this locality yielded very rich fauna of about 350 species (Bouček 1931) from weathered strata of the uppermost part of the Daleje-Třebotov Formation. A recent detailed study of the microfacies and conodont biostratigraphy in the Prastav quarry (about 100 m E of the locality) with the same succession (Berkýová 2009) suggests that the weathered beds belong to the *Polygnathus costatus partitus* Klapper, Ziegler & Mashkova, 1978 conodont Biozone of the early Eifelian age. However, some workers have interpreted the age of the weathered beds as late Emsian because of the absence of ammonoid species *Pinacites jugleri* (Roemer, 1850) and the presence of three species of ammonoid genus *Anarcestes*, *An. simulans* (Barrande, 1865), *An. plebeius* (Barrande, 1865), and *An. latissimus* Chlupáč & Turek, 1983 [= *An. crassus* (Barrande, 1867)]. Occurrence of the latter species is not evidence for the Emsian age, because they are known to occur also in the lowermost Eifelian (e.g., Klug 2002;
Ebbighausen et al. 2012). The section is preserved as a part of the U Nového mlýna National Nature Monument (see Krňíž 1999).

**Klukovice**—Old quarry “Červený lom” (50°2′10.417″N, 14°21′14.373″E, locality number JF2 and JF3) in a suburb SW of Prague, in Early Devonian strata of the Praha Formation. This important fossil locality is protected as part of Opatříka—Červený lom Nature Monument (more details in Krňíž 1999). Palaeozygopleurid gastropods come from two different stratigraphic levels of weathered limestones: from Slivenec and Dvorce limestones in the western part of the quarry, and from the uppermost layers of the Prokop limestone in the eastern part of the quarry.

**Konvárka**—Old quarry (50°37′850″N, 14°24′17.779″E, locality number JF219) in a suburb S of Prague, in Early Devonian strata of the Praha Formation. Palaeozygopleurid gastropods come from weathered Slivenec and Dvorce limestones of the Praha Formation.

**Koukolová hora**—Old quarry on top of a hill (49°55′18.346″N, 14°1′13.357″E, locality number JF219) in a suburb SW of Prague, in Early Devonian strata of the Praha Formation. Palaeozygopleurid gastropods come from two different stratigraphic levels of weathered limestones: from Slivenec and Dvorce limestones in the western part of the quarry, and from the uppermost layers of the Prokop limestone in the eastern part of the quarry.

**Konvárka**—Old quarry (50°37′850″N, 14°24′17.779″E, locality number JF219) in a suburb S of Prague, in Early Devonian strata of the Praha Formation. Palaeozygopleurid gastropods come from weathered Slivenec and Dvorce limestones of the Praha Formation.

**Květnice**—Natural section on the western slope of the Květnice hill (49°57′45.549″N, 14°10′50.217″E, locality number JF216) south of the village of Bubovice in the Chýnice Limestone.

**Pod Kotýsem**—Road cut (49°54′53.004″N, 14°2′44.031″E, locality number JF17) W of the village of Koněprusy exposing limestones of the lowermost part of the Lochkov Formation, belonging to the Monograptus uniformis graptolite Biozone (see map and description in Frýda & Manda 1997).

**U kantiny**—Old quarry (50°1′54.268″N, 14°2′22.246″E, locality number JF149) in a suburb SW of Prague, in Early Devonian strata of the Praha and Zlíčov formations. Palaeozygopleurid gastropods come from weathered limestones of the upper part of the Dvorce-Prokop Limestone of the Praha Formation.

**Za kapličkou section**—Trench (49°57′45.549″N, 14°10′50.217″E, locality number JF216) south of the village of Bubovice in the Chýnice Limestone.

**Review of the Devonian Palaeozygopleuridae of Bohemia**

Global diversity of the palaeozygopleurid gastropods is poorly known even though they are easily recognizable by their typical shell ornamentation among another high-spired Paleozoic gastropods. Except of one Silurian species (Rohr et al. 2008), they are known from Devonian, Carboniferous and Permian strata of many paleocontinents. Rapid radiation of the post-Devonian pseudozygopleurid gastropods, having similar teleoconchs but developing true larval shell in contrast to the palaeozygopleurids, has complicated determination of the post-Devonian palaeozygopleurids (see discussion in Nützel 1998). Present data, however, suggest that the palaeozygopleurids reached the highest global diversity during interval from the Pragian to Givetian (i.e., from middle Early Devonian to late Middle Devonian), from which almost one hundred species were described (Frýda unpubl. data). Many of those palaeozygopleurid species are still hidden under wrong generic names (mostly as Loxonema). In addition, many of palaeozygopleurid species are still undescribed from the Devonian strata of Europe, North Africa, Middle Asia, Australia and North America (Frýda unpubl. data), probably because of their rather small shell size. Description or re-description of those taxa should be completed prior to new analysis of their phylogeny or evolution of their global diversity.

In the following section, all known members of family Palaeozygopleuridae Horný, 1955 (including three new species and one new genus) from the Devonian strata of Perunica microplate (Bohemia) are reviewed and their stratigraphic distributions are re-evaluated. Genera as well as individual species within each genus are ordered alphabetically.
Class Gastropoda Cuvier, 1797

Superfamily Loxonematoidea Koken, 1889
Family Palaeozygopleuridae Horný, 1955

Remarks. Since establishment of the family, its phylogenetic position has been unsettled (Horný 1955; Licharew 1970; Hoare & Sturgeon 1978; Hoare 1980; Bandel 1991; Frýda & Bandel 1997; Nützel 1998; Blodgett et al. 1999; Frýda 1999; Frýda & Blodgett 2004; Frýda et al. 2008). They have been considered to be Archaeogastropoda, Caenogastropoda or Heterobranchia (see discussion below). The most discussed topic is their protoconch morphology and its interpretation (Frýda 2012). Here we follow the taxonomic position of the family Palaeozygopleuridae as presented by Bouchet et al. (2005).


Bohemozyga Frýda and Bandel, 1997


Remarks. Frýda and Bandel (1997) established the taxon Bohemozyga as a subgenus of the genus Palaeozygopleura. However, as the latter authors noted, its morphology distinguishes it from the range typical for another species belonging to Palaeozygopleura. For this reason, it was probably elevated in rank to genus within Palaeozygopleuridae by Wagner (2011). This classification is also used here.

Composition. There are only two species assigned to this genus: the early Eifelian (Middle Devonian) type species, Bohemozyga kettneri (Horný, 1955), and the Frasnian (Late Devonian) Bohemozyga pyritica Jagt-Yazykova, Krawczyński & Rakociński, 2006, from the Holy Cross Moutains (Poland).

Bohemozyga kettneri (Horný, 1955)

Holotype. NMP 34872 (Horný 1955: pl. IV, fig. 1).
Paratypes. NMP 34873–5 (Horný 1955: pl. IV, fig. 2).

Type locality. Section in small quarry NE of the village of Holyně and W of the Prastav quarry (50°1’57.627”N, 14°21’5.471”E).

Type horizon. Uppermost part of the Třebotov Limestone (Daleje-Třebotov Formation); the latest Emsian to early Eifelian, Middle Devonian.

Remarks. Horný (1955) described this species based on about 30 specimens, collected earlier by amateur palaeontologists R. Ružička and F. Hanuš. Frýda and Bandel (1997) studied additional 19 specimens from the type locality and described the large protruding protoconch in this species.

Stratigraphic and geographic distributions. This species is only known from its type horizon and locality.

Bojozyga Horný, 1955

Type species. Palaeozygopleura (Bojozyga) parallela Horný, 1955 (OD).

Remarks. Horný (1955) described Bojozyga as subgenus Palaeozygopleura (Bojozyga). Later it was synonymized with Palaeozygopleura by Knight et al. (1960); however, recently it was re-ranked as an independent genus within Palaeozygopleuridae by Wagner (2011).

Composition. Only two species Bojozyga mira (Horný, 1955), and Bojozyga parallela (Horný, 1955).
Bojozyga mira (Horný, 1955)

Holotype. NMP 34878 (Horný 1955: pl. III, fig. 5).

Type locality. Barrandov I section (50°2'11.677"N, 14°23'59.722"E), SW portion of Prague.

Type horizon. Dvorce-Prokop Limestone, Praha Formation of Pragian age (Early Devonian).

Remarks. Horný (1955) described this species based on fossil material collected by Mr. J. Bouška from a weathered bed of the Dvorce Limestone, containing only one almost complete shell (holotype) and eight fragments. No additional material has been gathered since from the type locality.

Stratigraphic and geographic distributions. Bojozyga mira was recently found in fossil material from the Malá Chuchle locality (Praha Formation), which is the second locality for this rare species.

Bojozyga parallela (Horný, 1955)

Holotype. NMP 34877 (Horný 1955: pl. III, fig. 6).

Type locality. Hlubočepy, Prague 5 (50°2'24.549"N, 14°24'0.039"E).

Type horizon. Třebotov Limestone (Daleje-Třebotov Formation); upper Emsian-early Eifelian, Devonian.

Remarks. This species is based on fossil material collected by Mr. J. Bouška and its exact age is unknown. Only two shell fragments were gathered; a fragment having four whorls was selected as holotype. Horný (1955) noted the Choteč Limestone (Eifelian) as the type horizon for the species. However, Chlupáč (1959) later re-evaluated its stratigraphic position and noted that this species came from the Třebotov Limestone of the Daleje-Třebotov Formation (upper Emsian-early Eifelian).

Stratigraphic and geographic distributions. Bojozyga parallela is only known from its type locality and horizon.

Cimrmaniela gen. nov.

Type species. Cimrmaniela sveraki sp. nov.

Diagnosis: Palaeozygopleurid with small, very slender, high-spired, multiwhorled shell having straight sides, narrow apical angle; whorl profile very convex; whorls ornamented by regularly spaced, opisthocyrt or orthocline costae; large protruding protoconch.

Comparison: Species of Cimrmaniela differ from all other palaeozygopleurid species by their small and very slender, high-spired and multiwhorled shells. Only species of Bojozyga have such slender shells (i.e., having a very narrow pleural angle). Whorls in both known species of Bojozyga are only gently convex and they are distinctly appressed, forming a typical sutural band (see Horný 1955: pl. III, figs 5, 6), in contrast to the shells of Cimrmaniela. Except for the latter characteristics, the species of Cimrmaniela differ from those of Bojozyga in having much smaller shells. Species of Cimrmaniela differ from Pragozyga Frýda, 1999, by their very slender, high-spired shells (compare Fig. 2 with fig.1a in Frýda et al. 2008).

Etymology: Cimrmaniela, in honour of Jára Cimrman, who was one of the greatest Czech universal scientists and artists of the 19th and early 20th century.

Species included: Cimrmaniela sveraki sp. nov. and Cimrmaniela smoljaki sp. nov.

Cimrmaniela smoljaki sp. nov.

Holotype. UUG JF 907 (Figure 2G–I, M).

Paratypes. UUG JF 908–913 (Figure 2J–L and 5 additional shells).

Type locality. Císársky lom quarry (49°55'00.99"N, 14°3'36.420"E), S of the village of Koněprusy.

Type horizon. Middle part of the Koněprusy Limestone, Praha Formation.

Etymology: smoljaki, in honour of Ladislav Smoljak (1931–2010), one of the preeminent biographers of Jára Cimrman.
**FIGURE 2.** *Cimrmaniela sveraki* sp. et gen. nov. (A–F) and *Cimrmaniela smoljaki* sp. et gen. nov. (G–M) from middle Early Devonian (Pragian) age strata of the Koněprusy Limestone (Praha Formation) in Barrandian, Czech Republic. A–D. Holotype (UUG JF 914), E–F. Paratype A (UUG JF 915). G–I and M. Holotype (UUG JF 907), J–L. Paratype (UUG JF 908). Shell height: A–D—3.2 mm, E, F—2.1 mm, H, I—4.2 mm, J–L—2.1 mm, figure height of shell detail: G—1.9 mm, M—1.8 mm.

**Diagnosis:** Species of *Cimrmaniela* ornamented by opisthocline costae, having regularly arched whorl side, narrow pleural angle.

**Description:** High-spired, narrow, multiwhorled, dextrally coiled shells, with up to 13 whorls; shell sides straight with pleural angle of 7 degrees; apical angle of first three whorls about 10 degrees; lateral whorl sides very convex, symmetrically arched; sutures relatively deep; sutural slope angle about 22 degrees; base of whorls rounded, anomphalous; external surface of whorls ornamented by regularly spaced costae; beginning at lower suture, costae run in opisthocline direction (also parallel with shell axis) across lateral whorl side, only just below upper suture gradually curving in an orthocline, then in prosocline direction; distance of costae about double their width (Fig. 2J–M); diameter of first half of shell whorl about 0.26 mm; first costae preserved from end of second whorl; preservation of shell not allowing for determination of exact position of protoconch/teleoconch boundary.

**Comparison:** Shells of *C. smoljaki* sp. nov. are ornamented by opisthocline costae, in contrast to *C. sveraki* sp. nov. (the only other species of *Cimrmaniela*) shells, which bear orthocline costae. In addition, the sides of whorls in *C. smoljaki* are regularly arched, but the whorl side in *C. sveraki* is distinctly flattened below the upper suture, and strongly arched in a mid-whorl position. The apical angle of first three whorls is about 10 degrees in *C. smoljaki*, and is much wider in *C. sveraki* - about 22 degrees (Fig. 3).

**Stratigraphic and geographic distributions.** *Cimrmaniela smoljaki* is only known from its type locality and horizon.
Cimrmaniela sveraki sp. nov.

Holotype. UUG JF 914 (Figure 2A–D).

Paratypes. UUG JF 915–921 (Figure 2E–F, and 6 additional shells).

Type locality. Císařský lom quarry, S of the village of Koněprusy (49°55′00.99″N, 14°3′36.420″E).

Type horizon. Middle part of the Koněprusy Limestone, Praha Formation.

Etymology: sveraki, in honour of Zdeněk Svěrák, one of the preeminent biographers of Jára Cimrman.

Diagnosis: Species of Cimrmaniela ornamented by orthocline costae; whorl side is distinctly flattened below the upper suture and strongly arched in mid-whorl position; diameter of embryonic shell about 0.17 mm, and diameter of the first half of whorl about 0.30 mm.

Description: High-spired, multiwhorled, dextrally coiled shell, with up to nine whorls present; shell sides slightly convex with pleural angle 9 degrees; initial shell having more convex sides than adult shell; apical angle of first three whorls about 22 degrees; lateral whorl sides distinctly flattened below upper suture, strongly arched in mid-whorl position; sutures relatively deep; sutural slope angle in juvenile shell about 13 degrees, about 17 degrees on adult whorls; base of whorls rounded, anomphalous; aperture circular; external surface of whorls ornamented by regularly spaced, orthocline costae; distance of costae about double their width (Fig. 2); diameter of first shell whorl about 0.30 mm; diameter of large embryonic chamber about 0.17 mm; first costae preserved on second whorl; preservation of shell not allowing for determination of exact position of protoconch/teleoconch boundary.

Comparison: Differences of both of the known species of Cimrmaniela are described in the section on C. smoljaki.

Remarks. The protruding and large embryonic chamber in C. sveraki (Fig. 2E–F) fits well in the morphological range of the protoconchs of other palaeozygopleurid genera.

Stratigraphic and geographic distributions. Cimrmaniela sveraki is only known from its type locality and horizon.

Devonozyga Horný, 1955

Type species. Devonozyga perneri Horný, 1955 (OD).

Remarks. Horný (1955) established Devonozyga for two Early Devonian species from the Barrandian (D. perneri and D. diversicostata), and for Loxonema arduum Kirchner, 1915, from Germany. Heidelberger (2007) added Devonozyga bandeli Heidelberger, 2007, from the Givetian (Middle Devonian) of Sötenich (Germany).

Devonozyga diversicostata Horný, 1955

Holotype. NMP 34890 (Horný 1955: pl. V, fig. 1).

Type locality. Section in small quarry NE of the village of Holyně and W of the Prastav quarry (50°1′57.627″N, 14°21′5.471″E).

Type horizon. Uppermost part of Třebotov Limestone (Daleje-Třebotov Formation); the latest Emsian to early Eifelian, Middle Devonian.

Remarks. This species is based on single shell collected by Dr. F. Prantl at the same locality and stratigraphic level as the type species D. perneri. It differs from the latter species only by an absence of collabrals ribs on the lower part of its last whorl (probably caused by abrasion or by subsequent fossilization). Small differences of both Bohemian species of Devonozyga probably only represent intraspecific variability. However, very limited material was available for study (six, mostly poorly preserved specimens in the case of D. perneri; one in the case of D. diversicostata), making an analysis of shell variability difficult. Future analysis based on new fossil material from the Holyně locality, which will be newly collected during on-going project of the Grant Agency of the Czech Republic (P210/12/2018), probably will solve that problem.

Stratigraphic and geographic distributions. This rare species is only known from its type horizon and locality.
Devonozyga perneri Horný, 1955

**Holotype.** NMP 34888 (Horný 1955: pl. V, fig. 2).

**Paratypes.** One numbered paratype (NMP 34889; Horný 1955: pl. V, fig. 3) and four additional unnumbered paratypes deposited in the same collection.

**Type locality.** Section in small quarry NE of the village of Holyně and W of the Prastav quarry (50°1'57.627"N, 14°21'5.471"E).

**Type horizon.** Uppermost part of Trébotov Limestone (Daleje-Trébotov Formation); the latest Emsian to early Eifelian, Middle Devonian.

**Remarks.** Horný used material collected by Dr. F. Prantl, and no additional specimens of this species have been found since.

**Stratigraphic and geographic distributions.** This rare species is known only from its type horizon and locality.

Palaeozygopleura Horný, 1955

**Type species.** Zygopleura alinae Perner, 1907 (SD: Horný 1955: 29).

**Remarks.** Devonian species of this genus were recorded from Europe, North America, North Africa and Australia. Blodgett *et al.* (1988, 1990) showed an Old World Realm distribution of the *Palaeozygopleura*, which most probably arose in the Rhenish - Bohemian Region of the Old World Realm, where the majority of the Early Devonian species (and also the oldest species) of this genus occur (Frýda 1993). Horný (1955) divided the genus *Palaeozygopleura* into three subgenera, *P.* (*Palaeozygopleura*), *P.* (*Palaeozyga*), and *P.* (*Bojozyga*). Knight *et al.* (1960) synonymized *P.* (*Palaeozyga*), and *P.* (*Bojozyga*) with *Palaeozygopleura*. In addition, the subgenera were not used for the majority of the newly described species of *Palaeozygopleura* (Linsley 1968; Rollins *et al.* 1971; Tassell 1982; Blodgett *et al.* 1988; Frýda 1993; Heidelberger & Bandel 1999; Heidelberger 2001, 2007; Krawczyński 2002, 2006; De Baets *et al.* 2010). Frýda (1993) discussed the usage of subgenera in *Palaeozygopleura* and concluded that their revision was needed. Frýda & Bandel (1997) transferred *Palaeozygopleura* (*Palaeozygopleura?*) kettneri into the new subgenus *Palaeozygopleura* (*Bohemozyga*). Later Frýda (2000) established the additional subgenus *Palaeozygopleura* (*Rhenozyga*) for some Early and Middle Devonian species (Frýda & Blodgett 2004). Recently, Wagner (2011) elevated some subgenera of *Palaeozygopleura* to genera (i.e., *Bojozyga*, *Bohemozyga*, *Rhenozyga*) within Palaeozygopleuridae. This classification is used here.

**Palaeozygopleura alinae** (Perner, 1907)

**Lectotype.** Specimen NMP ČF 857 selected as lectotype by Horný (1955) and figured by Perner (1907: pl. 110, figs. 5–6) and by Horný (1955: pl. 1, fig. 3).

**Paralectotypes.** NMP 348665–7. Three shells selected by Horný (1955: pl. II, figs 1–3) as paralectotypes were collected by J. Bouška at Barrandov I.

**Type locality.** Dvorce, a suburb of Prague (50°3'4.323"N, 14°25'2.879"E).

**Type horizon.** Lower Devonian, Pragian; Dvorce-Prokop Limestone, Barrandian area, Bohemia.

**Remarks.** Horný (1955) divided this species into three subspecies - *Palaeozygopleura* (*P.*) *alinae alinae* (Perner, 1907), *Palaeozygopleura* (*P.*) *alinae planicostata* Horný, 1955, and *Palaeozygopleura* (*P.*) *alinae multicoastata* Horný, 1955. The subspecies *Palaeozygopleura* (*P.*) *a. planicostata* is based on a single shell coming from the type locality of *Palaeozygopleura* (*P.*) *a. alinae*. In contrast to the holotype of the latter subspecies, *Palaeozygopleura* (*P.*) *a. planicostata*, was collected by R. Růžička from the Slivenec Limestone (thus from a different facies of the Praha Formation, than the holotype of the nominal subspecies). However, *Palaeozygopleura* (*P.*) *a. alinae* was also found in the Slivenec Limestone at the type locality. Both subspecies probably are synonyms. In constrast, *Palaeozygopleura* (*P.*) *alinae multicoastata* comes from much younger strata (uppermost part of the Trébotov Limestone, Daleje-Trébotov Formation, the latest Emsian to early Eifelian) at the Holyně
locality. This subspecies is based on a single specimen collected by F. Prantl. No additional specimens of this subspecies have been found and thus, an evaluation of its morphological variability is impossible.

**Stratigraphic and geographic distributions.** *Palaeozygopleura alinae* (Perner 1907) was recorded from the Slivenec Limestone at Dvorce, Klukovice, and Konvárka sections, from the Dvorce Limestone at Dvorce, Barrandov, and Konvárka as well as from the Třebotov Limestone at Holyně section.

**Palaeozygopleura bohemica** Horný, 1955

**Holotype.** NMP 34884 (Horný 1955: pl. VI, fig. 1).

**Paratypes.** NMP (Horný 1955: pl. VI, fig. 2), and an additional 200 unnumbered shells deposited in the same collection.

**Type locality.** Section in small quarry NE of the village of Holyně and W of the Prastav quarry (50°1'57.627"N, 14°21'5.471"E).

**Type horizon.** Uppermost part of Třebotov Limestone (Daleje-Třebotov Formation); the latest Emsian to early Eifelian, Middle Devonian.

**Remarks.** This species is one of the most common of all early Eifelian Bohemian palaeozygopleurids. Horný (1955) based the description of this new species on a large amount of material collected earlier by F. Hanuš. Frýda and Bandel (1997) described the protoconch morphology in this species and noted that it is formed by half a whorl, which is smooth and its diameter is slightly more than 0.3 mm. All whorls succeeding the protoconch are ornamented by characteristic costae, as had already been shown by Horný (1955: pl. II, fig. 5).

**Stratigraphic and geographic distributions.** Horný (1955) mentioned the type locality Holyně as the only occurrence of *P. bohemica*. Recently, a rich occurrence of the latter species was recorded in the same stratigraphic level at the Barrandov II section, SW part of Prague, where this species was found together with other gastropods in the uppermost part of Třebotov Limestone (early Eifelian).

**Palaeozygopleura bouskai** Horný 1955

**Holotype.** NMP 34876 (Horný 1955: pl. IV, fig. 6).

**Type locality.** Quarry named “U kantiny”, E of the village of Řeporyje, SW of Prague (50°1'54.268"N, 14°20'22.464"E).

**Type horizon.** Upper part of the Dvorce-Prokop limestone (Praha Formation).

**Remarks.** Horný (1955) described this species based on the only known specimen collected by J. Bouška. Since then, no additional shells of *P. bouskai* have been found.

**Stratigraphic and geographic distributions.** This species has hitherto only been known from its type horizon and locality.

**Palaeozygopleura chlupaci** Frýda, 1993

**Holotype.** UUG JF 50 (Frýda 1993: figs 2.1–2.3, 2.6, 2.7).

**Paratypes.** UUG JF 51–54 (Frýda 1993: figs 2.5, 2.6).

**Type locality.** Koukolová Hora hill near Beroun, Barrandian area, central Bohemia (49°55'18.346"N, 14°1'13.357"E).

**Type horizon.** *Monograptus uniformis* graptolite Biozone, Early Lochkovian, Early Devonian.

**Remarks.** *Palaeozygopleura chlupaci* is hitherto the oldest species of the genus. The first occurrence of *Palaeozygopleura* is connected with a period of global increase of δ¹³C in the marine ecosystem, known as the Klonk Event (Manda & Frýda 2010), which was followed by a rapid occupation of the free water column by different animal groups, an increase of free-swimming predators as well as distinct changes in the plankton composition (Nützel & Frýda 2003; Berkyová et al. 2007; Klug et al. 2010).

**Stratigraphic and geographic distributions.** Besides from its type locality and the "Nad roklí" section near Černá rokle Gorge (SW Prague; Frýda & Manda 1997), this species has been newly recorded from the Pod Kotýsem section (W of the village of Koněprusy).
Palaeozygopleura devonicans (Barrande in Perner, 1903)

**Lectotype.** Unnumbered specimen figured by Perner (1907: pl. 60, figs 16–17), designated by Horný (1955: 34, pl. 1, fig. 1), NMP.

**Parallectotypes.** Two unnumbered specimens, NMP. One of those was figured by Perner (1907: 351, text-fig. 255), and by Horný (1955: pl. 1, fig. 2).

**Type locality.** Area between the villages of Měňany and Koněprusy (49°54′25″–49°55′01″N, 14°5′32″–14°3′36.4″E), about 5 km SE of Císařský lom locality (Fig. 1).

**Type horizon.** Vinařice Limestone (Praha Formation) or Suchomasty Limestone (Daleje-Trebotov Formation).

**Remarks.** Barrande in Perner (1907) described this species as *Z. devonicans* but had already figured and named it in *Barrande in Perner* (1903) (explanation of pl. 60, figs 15–17). Another specimen was figured by Perner (1907: text-fig. 255). However, none of Barrande in Perner’s (1903) syntypes agree exactly with his (1907) figures, maybe because of oversimplification of the figures. Nevertheless, all figured specimens come from the same syntype series and are conspecific. Horný (1955) selected the most complete shell from three of Perner’s syntypes as the lectotype of *P. devonicans* and figured it on plate 1, fig. 1.

Perner (1903) used the name *Z. devonicans* Barr. in an explanation of plate 60 for two specimens figured under numbers 15–17 and noted that they both came from Dlouhá hora hill. However, later, Perner (1907: 352) mentioned that *Z. devonicans* only occurs in reddish limestones with crinoids and listed Koněprusy and Měňany as its localities without any comment about the previously noted Dlouhá hora locality. The latter locality is known as an area from which Barrande had described many Silurian species (see description of Kosov area in Ktůž *et al.* 1992), but no occurrence of reddish limestones with crinoids has been reported from there. On the other hand, reddish limestones with crinoids form two stratigraphically different horizons in the area between Koněprusy and Měňany, specifically the Vinařice Limestone (Praha Formation) of Pragian age, and the Suchomasty Limestone (Daleje-Trebotov Formation) of upper Emsian age (Chlupáč *et al.* 1992). The Suchomasty Limestone only occurs in the Koněprusy-Měňany area, and this lithostratigraphic unit was incorrectly considered to represent the stratigraphical equivalent of the Slivenec Limestone of the Praha Formation sixty years ago (Chlupáč 1955). This is why Horný (1955) mentioned the Slivenec Limestone as the type horizon for *P. devonicans*. As already noted by Horný (1955: 36), it is impossible to determine which one of those two different horizons provided *P. devonicans*.

According to Perner (1907), Barrande in unpublished manuscript used the name *Turritella s. Zygoopleura devonicans* for the species described by Barrande in Perner as *Z. devonicans*, and the name *Turritella devonica* for additional species described by Perner (1907: 352) as *Z. alinae*. The latter species comes from localities near Prague. Perner (1903, 1907, 1911) used a large fossil collection gathered earlier by Barrande and his collectors and had no direct information on their localities. Therefore, it is possible that this is the reason for the mistake he made in 1903 in the locality name.

**Stratigraphic and geographic distributions.** *Palaeozygopleura devonicans* has hitherto only known from six specimens (Horný 1955) coming from its type locality (area between the villages of Měňany and Koněprusy). Its stratigraphic position is unclear (see above).

Palaeozygopleura hanusi Horný, 1955

**Holotype.** NMP 34886 (Horný 1955: pl. VI, fig. 3).

**Paratype.** NMP 34887 (Horný 1955: pl. VI, fig. 4) plus 30 unnumbered specimens, NMP.

**Type locality.** Section in small quarry NE of the village of Holyně and W of the Prastav quarry (50°1′57.627″N, 14°21′5.471″E).

**Type horizon.** Uppermost part of Trebotov Limestone (Daleje-Trebotov Formation); the latest Emsian to early Eifelian, Middle Devonian.

**Remarks.** *Palaeozygopleura hanusi, P. prantli* and *P. bohemia* come from the same stratigraphic level at their type locality. Frýda and Bandel (1997) noted occurrences of transitional forms among these species and they concluded that the species may represent synonyms. Detailed morphometric analysis of these taxa is a subject of on-going master thesis.

**Stratigraphic and geographic distributions.** This species has hitherto only been known from its type horizon and locality.
FIGURE 3. Palaeozygopleura luklesi sp. nov. from middle Early Devonian (Pragian) age strata of the Koněprusy Limestone (Praha Formation) in Barrandian, Czech Republic. A–C, H, and I. Holotype (UUG JF 922), D. Paratype A (UUG JF 923), E, F, Paratype B (UUG JF 924). G. Paratype C (UUG JF 925), J, M. Paratype D (UUG JF 926), K. Paratype E (UUG JF 927), L, N. Paratype F (UUG JF 928). All samples are from the type locality. A—shell width 1.5 mm, shell height: B, C—4.6 mm, D—3.9 mm, E, F—3.8 mm, K—3.6 mm, L—5 mm, figure height of shell detail: G—1.1 mm, H—1.5 mm, I—1.6 mm, J—5.6 mm, M—2.8 mm, N—2.1 mm.
**Palaeozygopleura lukesi** sp. nov.

Fig. 3A–N

**Holotype.** UUG JF 922 (Fig. 3A–C, H, and I).

**Paratypes.** The shells figured herein as Figure 3D (paratype A; UUG JF 923), Figure 3E,F (paratype B; UUG JF 924), Figure 3G (paratype C; UUG JF 925), Figure 3J,M (paratype D; UUG JF 926), Figure 3K (paratype E; UUG JF 927), Figure 3L,N (paratype F; UUG JF 928), and 32 unfigured specimens (UUG JF 929–960). All paratypes come from the type locality.

**Type locality.** Císařský lom quarry, S of the village of Koněprusy (49°55'00.99"N, 14°3'36.420"E).

**Type horizon.** Middle part of the Koněprusy Limestone (Praha Formation), at the same level as *Konepruselia*.

**Etymology.** After our friend Pavel Lukeš, who has contributed considerably to our understanding of the Devonian stratigraphy of the Barrandian area (Bohemia).

**Diagnosis.** *Palaeozygopleura* with slightly convex sides, convex whorl profile; whorls symmetrically arched, ornamented by prominent, regularly spaced, asymmetrically curved opisthocyrt costae; costae covering lateral as well as basal surface of whorls (Fig. 3F); collabral costae culminating slightly above mid-whorl; angle between costae and lower as well as upper suture about 45 degrees; pleural angle of adult shell about 15 degrees; apical angle at first three whorls about 28 degrees; diameter of first half of whorl about 0.27 mm.

**Description.** High-spired, multiwhorled dextrally coiled shell with up to 10 whorls; sides of shell slightly convex; pleural angle about 15 degrees, sutural slope angle about 17 degrees; lateral whorl sides between sutures very convex and symmetrically arched; sutures relatively deep; base of whorls rounded, anomphalous; lateral, basal parts of whorls ornamented by prominent, asymmetrical arched costae; costae forming wide asymmetrical arched sinus; sinus culminating above middle of whorl; angle between costae, lower as well as upper suture about 45 degrees; distance between costae about double that of costae; protruding protoconch relatively large; diameter of first half of whorl about 0.27 mm, that of embryonic chamber about 0.14 mm; first preserved costae from end of first whorl; preservation of shell not allowing for determination of exact position of protoconch/teleoconch boundary.

**Comparison.** The deep, asymmetrically arched costae differ *P. lukesi* from the majority of the species of genus *Palaeozygopleura*, which have either a straight or symmetrical arched costae. Only three Early Devonian palaeozygopleurid gastropods: *P. devonicans*, *Bojozyga mira*, and *P. chlupaci* Frýda, 1993, have distinctly asymmetrically arched costae. Shells of *P. lukesi* have very convex lateral sides of the whorls, in contrast to *P. devonicans*, where the moderately convex whorls are flattened in their median region (Horný 1955: pl. 1, figs 1, 2). Shells of *P. lukesi* have a much wider pleural angle than *B. mira*. In addition, *B. mira* has less convex whorls, which are rather flat below the upper suture, and a much finer, and less arched costae. The Pragian aged *P. lukesi* resembles the Lochkovian *P. chlupaci* by the shape of its costae, but it differs from the latter species by much lower whorls, a wider apical angle, and symmetrically arched whorl side between sutures.

**Pathology.** An anomalous development of the ornamentation was found on the lateral whorl in one specimen (UUG JF 928: Fig. 3N), which was most likely caused by shell repair after a failed predation attack. Similarly damaged shells of other species of *Palaeozygopleura* were described in the Pragian *P. alinae* (see Horný 1955: pl. III, fig. 4), in the Lochkovian *P. chlupaci* (see Frýda 1993: fig. 2.6), and also occur in the Emsian *P. vaneki* Frýda, Ferrová, Berková and Frýdová, 2008 (this study).

**Stratigraphic and geographic distributions.** *Palaeozygopleura lukesi* is only known from its type locality and horizon.

**Palaeozygopleura prantli** Horný, 1955

**Holotype.** NMP 34882 (Horný 1955: pl. VI, fig. 5).

**Paratype.** NMP 34883 (Horný 1955: pl. VI, fig. 6), 80 unnumbered specimens, NMP.

**Type locality.** Section in small quarry NE of the village of Holyně and W of the Prastav quarry (50°1'57.627"N, 14°21'5.471"E).
**Type horizon.** Uppermost part of the Třebotov Limestone (Daleje-Třebotov Formation); the latest Emsian to early Eifelian, Middle Devonian.

**Remarks.** Horný (1955: 128) considered *P. prantli* to be closely related and a younger form of *P. bohemica*. However, *P. prantli* comes from the same stratigraphic level as *P. bohemica*. In addition, both species have hitherto only been known from their type locality from where the fossil material collected by Mr. V. Plas and Mr. F. Hanuš was later used by Horný (1955). Detailed morphometric analysis of the both taxa is a subject of on-going study.

**Stratigraphic and geographic distributions.** This species is only known from its type horizon and locality.

**Palaeozygopleura svobodai** Horný, 1955

**Holotype.** NMP 34879 (Horný 1955: pl. V, fig. 6).

**Paratypes.** NMP 34880 (Horný 1955: pl. V, fig. 5), and 20 unnumbered specimens, NMP.

**Type locality.** Červený lom quarry near Klukovice, SW part of Prague (50°2'10.417″N, 14°21'14.373″E).

**Type horizon.** Dvorce-Prokop Limestone, Praha Formation of Pragian age (Early Devonian).

**Remarks.** Horný (1955) used for a description of this species fossil material collected by Mr. R. Růžička from weathered beds of Prokop Limestone (microfacies of the Dvorce-Prokop Limestone). He also mentioned the occurrence of this, or a similar species, in the Dvorce Limestone (another microfacies of the Dvorce-Prokop Limestone) at the Barrandov I road cut section.

**Stratigraphic and geographic distributions.** *Palaeozygopleura svobodai* seems to occur in the upper part of the Dvorce-Prokop Limestone, and is only know from the above-mentioned localities.

**Palaeozygopleura tenuicostata** Horný, 1955

**Holotype.** NMP 34881 (Horný 1955: pl. IV, fig. 5).

**Paratypes.** Horný (1955) did not establish any paratype, even though he had about 120 unnumbered specimens of this species in his type series, all of which should be now considered to represent paratypes (ICZN 72.4.1.1).

**Type locality.** Section in small quarry NE of the village of Holyně and W of the Prastav quarry (50°1'57.627″N, 14°21'5.471″E).

**Type horizon.** Uppermost part of the Třebotov Limestone (Daleje-Třebotov Formation); the latest Emsian to early Eifelian, Middle Devonian.

**Remarks.** Horný (1955) described this species based on about 120 specimens collected earlier by Mr. F. Hanuš, and suggested that this species developed from *P. svobodai* of Pragian age. He also mentioned that this morphologically variable form is closest to *P. prantli*. However Frýda and Bandel (1997) noted that transitional forms of *P. hanusi*, *P. prantli*, and *P. bohemica* are present in the same stratigraphic level of the type locality and they can represent synonyms.

**Stratigraphic and geographic distributions.** This species is only known from its type horizon and locality.

**Palaeozygopleura vaneki** Frýda, Ferrová, Berkyová, and Frýdová, 2008

**Holotype.** UUG JF 851 (Frýda et al. 2008: fig. 1F–H).

**Paratypes.** UUG JF 852–891.

**Type locality.** Čeřinka hillside (49°58'1.973″N, 14°10'28.353″E), south of Bubovice, Barrandian; locality description with a list of the hitherto known fossils can be found in Chlupák et al. (1979), Havlíček & Vaněk (1996), and Ferrová et al. (2012).

**Type horizon.** The Chýnice Limestone, *Novakia elegans* Zone, middle Emsian, late Early Devonian.

**Remarks.** *Palaeozygopleura vaneki* is extremely abundant in strata belonging to the *Novakia barrandei* Bouček & Prantl, 1959—*N. elegans* (Barrande, 1867) Subzone of the *N. elegans* tentaculite Biozone (Ferrová 2010; Ferrová et al. 2012).
Stratigraphic and geographic distributions. *Palaeozygopleura vaneki* is a common species only at its type locality. It was also found on the west slope of the Květnice hill, NE of Hostim (about 20 km SW of Prague), also from the Chýnice Limestone. An additional occurrence of *P. vaneki* was recently recorded by Radek Labuta (pers. comm.) in the Chýnice Limestone of the Za kapličkou section near Bubovice. De Baets et al. (2010) reported an occurrence of *P. vaneki* from the early Emsian strata of Morocco.

**Palaeozygopleura vesna** Horný 1955

**Holotype.** NMP 34871 (Horný 1955: pl. III, fig. 3).

**Paratypes.** Two specimens NMP unnumbered.

**Type locality.** Section in a small quarry NE of the village of Holyně and W of the Prastav quarry (50°1'57.627"N, 14°21'5.471"E).

**Type horizon.** Uppermost part of Třebotov Limestone (Daleje-Třebotov Formation); the latest Emsian to early Eifelian, Middle Devonian.

**Remarks.** Only three incomplete shells of this species are known; they were collected by F. Prantl from weathered beds in uppermost part of the Třebotov Limestone. Its shell morphology shows some resemblance with the older *P. vaneki*, but the latter differs from *P. vesna* by a higher number of costae, which are also more asymmetrically curved. *Palaeozygopleura vesna* has two-edged costae (Horný 1955: 38, pl. 3.3), but costae in *P. vaneki* have a triangular profile (Frýda et al. 2008: fig. 1H).

**Stratigraphic and geographic distributions.** This rare species is only known from its type horizon and locality.

**Pragozyga** Frýda, 1999

**Type species.** Pragozyga costata Frýda, 1999 (OD).

**Remarks.** Frýda (1999) originally placed *Pragozyga* into the superfamily Loxonematoidea Koken, 1889, and discussed its similarity with some members of families Loxonematidae Koken, 1889 and Palaeozygopleuridae Horný, 1955. Diagnoses of the both families need detailed revision (see discussion in Frýda 1993). Increase of morphologic disparity of palaeozygopleurid shells described during the last twenty years led independently Frýda et al. (2008) and Wagner (2011) to placement of *Pragozyga* into the Palaeozygopleuridae. Wagner (2011) recently transferred *Loxonema jerseyense* Weller, 1903 from the Lochkovian strata of Maine (northeastern US) to the genus *Pragozyga*. Poor preservation of shell on the latter species coming from sandstone strata makes this placement unsafe.

**Composition.** *P. costata* Frýda, 1999, and *P. ? jerseyense* (Weller, 1903).

**Pragozyga costata** Frýda, 1999

**Holotype.** UUG JF 756 (Frýda 1999: fig. A,B,D,E).

**Paratypes.** UUG JF 757–769.

**Type locality.** Malá Chuchle, old quarry (50°1'30.399"N, 14°22'46.758"E), a suburb SW of Prague.

**Type horizon.** Dvorce-Prokop Limestone (Praha Formation); Pragian, Early Devonian.

**Remarks.** The large and smooth protoconch of *P. costata*, with diameter slightly more than 0.35 mm, is formed only by half of the first whorl. All whorls succeeding the protoconch are ornamented by collabral threads (Frýda 1999: fig. 3D,E).

**Stratigraphic and geographic distributions.** This rare species is only known from its type horizon and locality.
Protoconch morphology of palaeozygopleurids

The family Palaeozygopleuridae was placed into the superfamily Loxonematoidea Koken, 1889 together with families Loxonematidae Koken, 1889, Pseudozygopleuridae Knight, 1930, and Zygopleuridae Wenz, 1938 (Knight et al. 1960). Many opinions have been given on the phylogenetic position of the latter superfamily, which has been placed in the Archaeogastropoda, Caenogastropoda, or Heterobranchia (Wenz 1938; Horný 1955; Knight et al. 1960; Golikov & Starobogatov 1975; Ponder & Warén 1988; Bandel 1991; Frýda & Bandel 1997; Nützel 1998; Frýda 1999; Frýda et al. 2008). Discussion on the phylogenetic relationships of loxonematoidean gastropods has mainly focused on the nature of their protoconchs, which differ from typical caenogastropod-like protoconchs. Frýda & Bandel (1997) reported that Early Devonian members of the Loxonematidae and Palaeozygopleuridae have large protoconchs formed by less than one whorl. No member of the Loxonematidae and Palaeozygopleuridae is known to develop a true larval shell (protoconch II). In contrast, the Late Paleozoic pseudozygopleurids and the Triassic zygopleurids, developed typical planktotrophic as well as large non-planktotrophic protoconchs, and without doubt they belong to the Caenogastropoda, probably to the Ptenoglossa lineage (Bandel 1991; Nützel 1998). This fact complicates the placement of pseudozygopleurids, palaeozygopleurids, and loxonematids into one phylogenetic group.

The following facts and morphological features are important for a re-evaluation of the phylogenetic position of the palaeozygopleurid gastropods: (1) the oldest loxonematids are known from the Ordovician (Frýda & Rohr 2004), palaeozygopleurids from the Silurian (Rohr et al. 2001), and pseudozygopleurids from the Carboniferous (Bandel 1991; Nützel 1998); (2) there is a transition in “typical” teleoconch features among members of the Loxonematidae and Palaeozygopleuridae (Frýda 1993), and there is a strong similarity in teleoconch features (including characteristic ornamentation) among the palaeozygopleurid and pseudozygopleurid gastropods (Nützel 1998; it is noteworthy that even Late Paleozoic caenogastropod family Palaeostylidae have a convergent teleoconch morphology - see also Nützel & Nakazawa 2012); (3) pseudozygopleurid gastropods developed typical planktotrophic as well as large non-planktotrophic protoconchs (Bandel 1991; Nützel 1998); (4) all known protoconchs in the Loxonematidae and Palaeozygopleuridae have the same morphology, and are formed by a large shell having less than one whorl (Horný 1955; Frýda & Bandel 1997; Frýda 1999); and, (5) pseudozygopleurid gastropods belong without doubt to the Caenogastropoda, probably to the Ptenoglossa lineage (Bandel 1991; Nützel 1998).
In this context, three different interpretations of these above-mentioned facts have been advanced—(1) the palaeozygopleurid protoconch is formed by embryonic and larval shells being reduced because of a lecitotrophy strategy (Nützel 1998); (2) the palaeozygopleurid and loxonematid protoconchs only consist of a large embryonic shell, and these families are not closely related to the pseudozygopleurid gastropods (Frýda & Bandel 1997); and (3) palaeozygopleurid gastropods only developing a large embryonic shell, and might represent a grade before adaptation to a new planktonic food source (Frýda et al. 2008). During the Devonian some palaeozygopleurids might have adapted to this food source, extending their larval stage and starting to build a larval shell (protoconch II). These ontogenetic changes might also have been linked with the general reorganisation of the Devonian marine ecosystem and increases of the predation pressure (see discussion in Nützel & Frýda 2003; Berkyová et al. 2007; Klug et al. 2010; and Seuss et al. 2012). On the other hand, the latter interpretation suggests a multiple origin of planktotrophy in different gastropod lineages; however, this is not in conflict with the fossil record (see Frýda 1999, 2012; Frýda et al. 2008; but also see Nützel et al. 2006, 2007a,b).

Even though the present study did not contribute data that could resolve the above-mentioned problem, it adds important observations. Nützel (1998) analysed in detail the classification and evolutionary history of the Ptenoglossa, and interpreted the superfamily Zygopleuroidea as a parataxon. He also suggested that large non-planktotrophic protoconchs of the Devonian Palaeozygopleuridae could indicate that they live in a deeper-water environment. The discovery of palaeozygopleurid gastropods in the shallow environment of an Early Devonian reefal system (i.e., in the Koněprusy Limestone of Pragian age) with well-preserved protoconchs refutes this deeper water hypothesis. The diameter of the first half of whorl in these new palaeozygopleurids (in P. lukesi it is about 0.27 mm, and about 0.30 mm in C. sveraki), as well as diameter of their embryonic shells (in P. lukesi it is about 0.14 mm, and about 0.17 mm in C. sveraki) are rather large, and this morphological characteristic suggests their non-planktotrophic early ontogeny. Thus, the new data does not support the hypothesis that non-planktotrophic protoconchs of the Devonian Palaeozygopleuridae are linked with life in a deeper-water environment. Nevertheless, for a final determination of the phylogenetic position of the superfamily Loxonematoidea (including also the family Palaeozygopleuridae) we need to collect more data on their early shell ontogeny.

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