A new Early Devonian palaeozygopleurid gastropod from the Prague Basin (Bohemia) with notes on the phylogeny of the Loxonematoidea

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Palaeozygopleurid gastropods represent a distinctive group of Middle Paleozoic gastropods (Fig. 1) occurring in Devonian strata of Europe, North America, Australia, and central Asia (Horný 1955; Linsley 1968; Rollins et al. 1971; Kesling & Chilman 1975; Tassell 1982; Blodgett 1992; Blodgett & Johnson 1992; Frýda 1993, 1999b, 2000; Frýda & Blodgett 2004; Cook 1995, 1997; Cook & Camilleri 1997; Cook et al. 2003; Cook & Nützel 2005; Gubanov et al. 1995; Blodgett et al. 1999; Heidelberger & Bandel 1999; Heidelberger 2001, 2007; Amler & Heidelberger 2003; Heidelberger & Koch 2005; Krawczyński 2002, 2006). Early Devonian palaeozygopleurids are considered to be a typical element of the Old World Realm (Blodgett et al. 1988, 1990). Later, in the Middle and Late Devonian, palaeozygopleurid gastropods also occurred in another biogeographic realm (the Eastern American Realm). Generally palaeozygopleurid gastropods were restricted to warm to tropical environments. Despite the fact that palaeozygopleurid gastropods are easily recognized by their shell characters, their phylogeny is still poorly known. In this short paper we describe a new Early Devonian palaeozygopleurid gastropod from Bohemia and briefly discuss the phylogeny of the Loxonematoidea and the origin of planktotrophy.

Bohemian palaeozygopleurids

Palaeozygopleurid gastropods were initially recognized as a separate group of the Paleozoic gastropods by Horný (1955) in Devonian strata of Bohemia. Gastropod faunas of the Prague Basin (Bohemia) hitherto contained 19 species and subspecies, which belong to Palaeozygopleura (Palaeozygopleura) Horný, 1955, Palaeozygopleura (Palaeogyga) Horný, 1955, Palaeozygopleura (Bojozyga) Horný, 1955, Palaeozygopleura (Bohemozyga) Frýda & Bandel, 1997, Devonozyga Horný, 1955, and Pragozyga Frýda, 1999b (Fig. 1). The vast majority of Bohemian species were described by Horný in 1955 and they were derived mainly from several older fossil collections. During the last 50 years intensive field studies better specified the stratigraphic position of many of these localities. The oldest hitherto known Bohemian palaeozygopleurid gastropod, Palaeozygopleura chlupaci Frýda, 1993, comes from the early Lochkovian Monograptus uniformis Biozone (Early Devonian; Frýda & Manda 1997; Carls et al. 2007). This species was considered to be the oldest member of the family, but recently the first Silurian palaeozygopleurid gastropod belonging to the genus Medfrazyga Frýda & Blodgett, 2004 (Fig. 1) was discovered from Ludlow strata of the Silurian Heceta Formation of Prince of Wales Island, Alaska (Rohr et al. 2008).
Palaeozygopleura chlupaci is the only palaeozygopleurid gastropod in the Lochkov Formation of the Prague Basin. Diversity of palaeozygopleurid gastropods increased during the Pragian and early Emsian (Praha Formation). Six species and subspecies belonging to Palaeozygopleura (Palaeozygopleura), Palaeozygopleura (Palaeozyga), Palaeozygopleura (Bojozyga), and Pragoozyga are known from the Praha Formation (Horný, 1955, Frýda & Bandel 1997; Fig. 1C, E, J, K). On-going study of the Basal Choteč event (SB, unpublished data; see also Zusková 1991) reveals that the majority of these taxa are from the Polygnatus costatus partitus Biozone, and thus they are of earliest Eifelian age. Chlupáč (1959, p. 478) mentioned an occurrence of a new species of Palaeozygopleura from the Eifelian Acanthopyge Limestone on southern slope of the Zadní Kobyla Hill (Koněprusy area). However, this species was never described or figured and the material no longer exists. In contrast to a high diversity of palaeozygopleurids in the earliest Eifelian strata below the Basal Choteč event, there is no reliable record for any occurrence of palaeozygopleurid gastropod above this event in the overlying Eifelian Choteč Formation. The latter event thus crucially influenced the evolution of Bohemian palaeozygopleurid gastropods, which were considered to be typical elements of the Early Devonian Plactonotus (Boucotonotus)-Palaeozygopleura Community Group for almost 20 my.

Systematic paleontology

Class Gastropoda Cuvier, 1797
Superfamily Loxonematidea Koken, 1889
Family Palaeozygopleuridae Horný, 1955

Remarks. – Knight et al. (1960) included four families, Loxonematidae Koken, 1889, Palaeozygopleuridae Horný, 1955, Pseudozygopleuridae Knight, 1930, and Zygopleuridae Wenz, 1938, in the superfamily Loxonematoidea. Teleoconch and protoconch data suggest that the Loxonematidae are a sister taxon of the Palaeozygopleuridae. Phylogenetic relationships of the latter families to the Pseudozygopleuridae and Zygopleuridae are uncertain (see discussion below and classification of Bouchet et al. 2005).

Diagnosis. – Species with markedly convex whorl profile; whorls ornamented by rounded fine costae with triangular profile; about 50 to 60 asymmetrical curved costae per revolution on adult whorls; costae contain an angle about 60 degrees with the lower suture and meet the upper suture in an opisthocline direction.

Description. – Palaeozygopleura vaneki has a small high-spired, dextrally coiled shell with slightly convex sides; the pleural angle is about 18 degrees. The whorls are slightly adpressed on preceding whorls (Fig. 1F); the whorl profile is markedly convex and the sutures relatively deep. The shell base is smooth and anomphalous; the whorls are ornamented by fine rounded costae with a triangular profile (Fig. 1G, H); the width of the costae is smaller than their distance of separation; there are about 50 to 60 asymmetrical curved costae per revolution on adult whorls; the costae run almost straight in a prosocline direction to the middle of whorl and contain an angle of about 60 degrees with the lower suture; costae above the middle of the whorl curve in an opisthocline direction and meet the upper suture at an angle of about 80 degrees (Fig. 1G); the costae disappear slightly below the lower suture.

Discussion. – The teleoconch morphology of Palaeozygopleura vaneki sp. nov. is close to that in Palaeozygopleura (Palaeozygopleura) vesna Horný, 1955. The latter species is known only from three shells coming from uppermost layers of Třebotov Limestone (Emsian/Eifelian boundary beds), Holyně near Prague. Palaeozygopleura vaneki has a higher number of costae, which are also more asymmetrically curved, than Palaeozygopleura (P.) vesna. Costae in Palaeozygopleura vaneki have a triangular profile in contrast to the two-edged costae in Palaeozygopleura (P.) vesna (Horný 1955, tab. 3.3, p. 38). In the latter species the distance of costae separation is equal to their width, but this distance is about double in Palaeozygopleura vaneki (Fig. 1H).

Occurrence. – Palaeozygopleura vaneki is a common species at the type locality and has also been found NE of Hostim (about 20 km SW of Prague) in the Chýnice Limestone (coll. L. Ferrová).

Notes on phylogeny of Loxonematoidea and origin of planktotrophy

Many opinions have been given on the phylogeny of the superfamily Loxonematoidea (including Palaeozygopleuridae) and this superfamily 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) suggested that the Loxonematoidea represents a polyphyletic group and placed the families Pseudozygopleuridae and Zygopleuridae together with his new family Protorculidae into the newly established superfamly Zygopleuroidea of the Ctenoglossa. On the other hand, the Loxonematoidea together with his new family Polygyrinidae were placed into the Mesogastropoda. Frýda & Bandel (1997) pointed out that Early Devonian members of the Loxonematoidea and Palaeozygopleuridae have large protoconchs formed by less than one whorl. They interpreted these large protoconchs as being formed only by the embryonic shells and mentioned the similarity of early shell ontogeny (absence of the larval shell) in loxonematoidean gastropods to that found in members of the Archaeogastropoda and Patello-gastropoda. Nützel (1998) analyzed 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 reflect their living in a deeper-water environment. However, Frýda (1999b) later noted that these gastropods lived in other habitats including relatively shallow-water environments.

Discussion on the phylogenetic relationships of loxonematoidean gastropods has focused on the nature of the protoconch. There are two different interpretations of this feature – (1) the protoconch represents the embryonic and larval shell (Horný 1955), simplified by lecithotrophic development (Nützel 1998); and, (2) the palaeozygopleurid protoconch is formed only by the embryonic shell (Frýda & Bandel 1997). The first interpretation means that they might belong to the Caenogastropoda whereas the second interpretation suggests their affinity with groups like the Archaeogastropoda, Euomphalomorpha, and Patello-gastropoda. The very close similarity of the teleoconch characters of Devonian palaeozygopleurid and Late Paleozoic pseudozygopleurid gastropods seems to strongly support the placement of both groups in the Caenogastropoda because the pseudozygopleurid protoconch is without doubt of caenogastropod type (Knight 1930; Bandel 1991, 2002a; Nützel 1998). Taken together, the basic question is whether or not palaeozygopleurid gastropods developed a larval shell (protoconch II) like many groups of “advanced” gastropods. The development of larval shells is considered to be linked with the origin of planktotrophy.

The origin of planktotrophy within the Class Gastropoda has been a frequently discussed problem and one of most important and still unsolved questions is whether planktotrophy originated once or several times (see Haszprunar 1995, Frýda et al. 2008). Some palaeontological data suggest that planktotrophy was present even in the Ordovician (see discussion in Chaffee & Lindberg 1986; Frýda & Rohr 2004; Nützel et al. 2006, 2007; Freeman & Lundelius 2007; Runnegar 2007).
exist several groups among Ordovician and Silurian gastropods that developed larval shells (i.e. protoconch II), such as the Ctryoniniterimorpha, Perunelomorpha, and Mimospirina; see detailed discussion in Frýda 1999a, Frýda & Rohr 2004, and Frýda et al. 2008. Among extant gastropods development of protoconch II (larval shell) is present only in the Neritimorpha, Caenogastropoda and Heterobranchia, which can have a planktotrophic or a lecitotrophic strategy. Planktotrophic taxa that use external food sources during their larval stage typically have small embryonic shells. Lecitotrophic taxa have large embryonic shells and their larval shells are typically reduced in the number of whorls. These facts strongly suggest that the development of the larval shell is closely connected with a strategy to extend early ontogeny and to use the external food source before metamorphosis. Thus, small embryonic shells and the development of larval shells in some Early Paleozoic gastropods does not mean that those gastropods had a planktotrophic strategy but may only suggest that they used an external food source before metamorphosis. The oldest gastropods having a larval shell of the same morphology as living marine gastropods are known from the Devonian but become more frequent since the Carboniferous (Frýda 2001; Nützel 1998; Nützel & Bandel 2000; Nützel & Mapes 2001; Nützel & Pan Hua-Zhang 2005; Bandel 2002a, b, 2007; Frýda et al. 2008 and references hereina). Frýda (1998, 1999a) found open-coiled protoconchs in several unrelated gastropod lineages and pointed out that this morphological state might represent a plesiomorphic feature. He also noted that open-coiled protoconchs were apparently lost in multiple, unrelated gastropod lineages. Later Nützel & Frýda (2003) quantitatively documented this macroevolutionary trend showing decreasing proportions of open-coiled protoconchs throughout the Paleozoic. They also hypothesized that this distinct change in protoconch morphology (i.e. from open-coiled to closely coiled) was probably the result of increasing predatory activity. Predation on Devonian plankton was recently documented by Berkyová et al. (2007). An accompanying trend toward smaller embryonic shells was observed in Silurian and Devonian gastropods (Frýda 2004). This morphological change coincided with the invention of larval planktotrophy and was followed by the Late Paleozoic radiation of Neritimorpha, Caenogastropoda, and Heterobranchia. Frýda (2004) suggested that fundamental changes in biogeochemical evolution of the Paleozoic oceans, linked to a pronounced increase in nutrient input to surface sea waters during eutrophication episodes, triggered both the inception of larval planktotrophy and the diversification of groups with such larva.

In this context, we can re-evaluate observed data on palaeozygopleurid gastropods. The most important facts are as follows: (1) there is a transition in "typical" teleoconch features between members of the Loxonematidae and Palaeozygopleuridae (Frýda 1993); (2) 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 1999a); (3) there is a strong similarity in teleoconch features (including characteristic ornamentation) among the palaeozygopleurid and pseudozygopleurid gastropods; and, (4) pseudozygopleurid gastropods belong without doubt to the Caenogastropoda, probably to the Ptenoglossa lineage (Bandel 1991, Nützel 1998).

As mentioned above, two different interpretations of these facts have been published – (1) the palaeozygopleurid protoconch is formed by embryonic and larval shells being reduced because of lecitotrophy strategy, and (2) the palaeozygopleurid protoconch consists of only a large embryonic shell. The first interpretation suggests that the Palaeozygopleuridae may represent an ancestral or sister group of the Pseudozygopleuridae (Horný 1955), whereas the second interpretation results in an opinion that both groups are not closely related. However, there is also another possible interpretation. Palaeozygopleurid gastropods developing only a large embryonic shell might represent a grade before adaptation to a new planktonic food source. 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). If so, then the palaeozygopleurid protoconch is not a secondarily reduced larval shell, but rather a large embryonic shell. Nevertheless, palaeozygopleurid and pseudozygopleurid gastropods may be closely related groups as suggested by Horný (1955) on the basis of their teleoconch similarities. Even though a multiple origin of planktotrophy in different gastropod lineages seems to be less probable and parsimonious than a single origin, it is not in conflict with the fossil record (see Frýda 1999a, Frýda & Rohr 2004, Frýda et al. 2008). This process might have been linked to the Paleozoic plankton revolution (Nützel & Frýda 2003). The evolutionary advantage of a planktotrophic strategy over simple lecitotrophy (as seen for example in vetigastropods) may be illustrated by the increasing portion of gastropod groups developing larval shells during the last 400 My. Such gastropods form the vast majority of living species in modern marine faunas.

Acknowledgements

The work was supported by grants from the Czech Academy of Science (KJB307020602), the Grant Agency of the Czech Republic (205/08/0062), and the Czech-American Cooperation Programme (Kontakt ME08011). The authors thank Robert B. Blodgett (Anchorage) and Štěpán Manda (Prague) for their helpful reviews.
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