

Systematic position of Cyrtoneritimorpha within the class Gastropoda with description of two new genera from Siluro-Devonian strata of Central Europe

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Abstract. In this short paper two new cyrtoneritimorph gastropod genera are described from the Late Silurian of Bohemia and Middle Devonian of Germany. The oldest known cyrtoneritimorph genus, *Krameriella* gen. nov., is placed within a new subfamily, Krameriellinae subfam. nov., of the Vltaviellidae. Ordovician-Permian Cyrtoneritimorpha are considered to be a gastropod group of uncertain systematic position. New taxa: *Krameriella hornyi* gen. et sp. nov., and *Eifelcyrtus blodgetti* gen. et sp. nov.

Abstrakt. V této krátké práci jsou popsány dva nové rody cyrtoneritimorfních gastropodů ze svrchního siluru Čech a středního devonu Německa. Nejstarší známý cyrtoneritimorfní rod, *Krameriella* gen. nov., je umístěn do nové podčeledi čeledi Vltaviellidae. Ordovicko-permská zástupci řádu Cyrtoneritimorpha jsou považováni za skupinu nejistého systematického postavení. Nové taxony: *Krameriella hornyi* gen. et sp. nov., a *Eifelcyrtus blodgetti* gen. et sp. nov.

Key words: Mollusca, Gastropoda, Neritimorpha, new taxa, Silurian, Devonian, Europe.

Introduction

Ongoing studies of protoconch morphology in early and middle Paleozoic gastropods yielded new data for evaluation of their higher classification. One of the most interesting results of these studies is the observation that many Paleozoic gastropod groups are difficult to connect to any of the post-Paleozoic groups (Frýda 1999, Frýda and Rohr, in press, and references therein). These “problematic” taxa include groups like Cyrtoneritimorpha, Perunelomorpha, and Euomphalomorpha developing openly coiled protoconchs. Relatively frequent occurrences of their isolated protoconchs suggest that they were an important component of early and middle Paleozoic gastropod communities. On the other hand, finds of their shells with well-preserved protoconchs are rare. For this reason, our knowledge of these Paleozoic gastropods is very limited (Frýda and Rohr, in press). In this short paper we report exceptional findings of two new cyrtoneritimorph gastropods with well-preserved protoconchs, one from the Late Silurian of Bohemia, and the other from the Middle Devonian of Germany, and discuss the systematic position of the Cyrtoneritimorpha within the class Gastropoda.

Systematic position of Cyrtoneritimorpha

The taxon Cyrtoneritimorpha was introduced by Frýda (1998a) within the subclass Neritimorpha for Ordovician-Permian “platyceratids” with openly coiled, fish hook-like protoconchs. The Neritimorpha represent a very successful gastropod group with an extremely rich fossil record, found

in almost all marine, freshwater and terrestrial environments. Marine Neritimorpha may be characterized by a typically strongly convolute protoconch (Bandel 1982). This protoconch type was reported from many post-Paleozoic gastropods and the oldest occurrences come from the Triassic strata (Bandel 1992). Bandel (1992), on the basis of his discovery of a neritimorph protoconch in the Triassic *Capulus alatus* Laube, 1869 [= *Pseudorthonychia alata* (Laube, 1869)], also suggested that the Paleozoic Platyceratidae belong to the Neritimorpha. However, in contrast to this presumption, Frýda and Manda (1997) found an unusual openly coiled, fish hook-like protoconch in their platyceratid-like gastropod *Vltaviella reticulata* Frýda and Manda, 1997, from the Silurian/Devonian boundary beds of the Prague Basin. Moreover, a detailed analysis of this discovery has shown that similar protoconchs were reported in the late Paleozoic species of *Orthonychia* (Knight 1934, Yochelson 1956), and isolated protoconchs of the same type were also found in the Ordovician (Bockelie and Yochelson 1979, Dzik 1994) and Silurian (Frýda, unpubl. data) strata. Frýda (1998a, b, 1999) interpreted these facts as evidence that these Paleozoic gastropods (“platyceratids” with openly coiled, fish hook-like protoconchs) represent an independent, long-lived gastropod group with a range of about 250 million years. For this reason Frýda (1998a, b) united them within a new gastropod group Cyrtoneritimorpha, which he considered to be related with the post-Paleozoic Neritimorpha. He introduced a new name Cycloneritimorpha for the post-Paleozoic Neritimorpha with strongly convolute protoconchs. Frýda (1999) pointed out that the Paleozoic Cyrtoneritimorpha gave rise to modern Cycloneritimorpha probably during the Devonian. This model was

later used by Bandel and Frýda (1999), who established two new families, Vltaviellidae and Orthonychiidae, within the Cyrtoneritimorpha. On the other hand, they considered the Paleozoic Platyceratoidea to belong to Cycloneritimorpha, i.e. to the Neritimorpha with strongly convolute protoconchs as we know in extant Neritimorpha. Bandel and Heidelberg (2001) established a new superfamily Nerrhenoidea for Paleozoic gastropods with naticoid teleoconchs bearing a low and spirally arranged protoconch and having a sinistrally coiled, spiral operculum. Bandel and Heidelberg (2001) placed their new superfamily within the Cycloneritimorpha. Recently, Bandel (2002) reported the same protoconch morphology (i.e., closely coiled, but not convolute protoconchs) from the Carboniferous *Naticopsis ventrica* (Norwood and Pratten, 1855). In addition, ongoing study of juvenile specimens of *Praenatica* and *Platyceras* from Siluro-Devonian strata of the Prague Basin (Frýda, unpubl. observ.) has revealed that their early shells also have a similar shape as those in the Nerrhenoidea (i.e., closely coiled, but not convolute protoconchs). These facts complicate our interpretation of early evolution of the Neritimorpha, which now seems to be much more complex. On the other hand, the discovery of the oldest member of the cyrtoneritimorph gastropods, the Silurian *Krameriella hornyi* gen. et sp. nov., with a highly turbiniform teleoconch has shown that the Cyrtoneritimorpha were much more diversified than we previously thought. The latter group now unites gastropods with different teleoconchs but with very stable morphology of their protoconchs. Because of this and the fact that new data on early evolution of Neritimorpha are incompatible, we consider the Cyrtoneritimorpha as a gastropod group with uncertain higher systematic position.

Systematic paleontology

Subclass uncertain
Order Cyrtoneritimorpha

Remarks: Bandel and Frýda (1999) established two new families, Orthonychiidae and Vltaviellidae, within the Cyrtoneritimorpha. The first unites gastropods with loosely coiled or limpet-like teleoconchs and the other those with naticiform teleoconchs. Family Vltaviellidae was hitherto represented only by a monotypic genus *Vltaviella* Frýda and Manda, 1997, from the *Monograptus uniformis* graptolite biozone of the Lochkov Formation (Early Devonian) of the Prague Basin. The discovery of the late Middle Devonian *Eifelcyrtus blodgetti* sp. nov. provides evidence that the stratigraphic range of this evolutionary lineage was much longer (being now more than 30 m.y.). A longer stratigraphic range of the Vltaviellidae was earlier presumed on the basis of the common occurrence of isolated cyrtoneritimorph protoconchs in Ordovician and Silurian strata (Bockelie and Yochelson 1979, Hynda 1986, Dzik 1994, Frýda 1999). This inter-

pretation now becomes much more difficult with the discovery of the early Late Silurian cyrtoneritimorph *Krameriella hornyi* sp. nov., which has a highly turbiniform teleoconch, quite different from those of *Vltaviella* Frýda and Manda, 1997, *Eifelcyrtus* gen. nov., and *Orthonychia* Hall, 1843. The systematic position of *Krameriella* gen. nov. within the Cyrtoneritimorpha is uncertain, and the genus may represent a quite independent phylogenetic lineage of the Cyrtoneritimorpha in addition to the limpet-like Orthonychiidae and naticiform Vltaviellidae. We leave its higher systematic position open and place it tentatively in a new subfamily Krameriellinae of the Vltaviellidae.

Family Vltaviellidae Bandel and Frýda, 1999
Subfamily Vltaviellinae Bandel and Frýda, 1999 comb. nov.

Diagnosis: Members of Vltaviellidae with naticiform teleoconchs.

Remarks: The rarity of Paleozoic gastropods with well-preserved protoconchs has considerably limited their recognition amongst other Paleozoic gastropods. Judging from the common occurrence of isolated cyrtoneritimorph protoconchs in the Ordovician, Silurian, and Devonian strata, the early and middle Paleozoic Cyrtoneritimorpha were probably a highly diversified gastropod group. We interpret the Middle Devonian *Eifelcyrtus* gen. nov. as closely related to the Early Devonian *Vltaviella* Frýda and Manda, 1997, representing the same evolutionary lineage of the Cyrtoneritimorpha.

Included genera:

- *Vltaviella* Frýda and Manda, 1997 – Lochkovian
- *Eifelcyrtus* gen. nov. – Givetian

Genus *Eifelcyrtus* gen. nov.

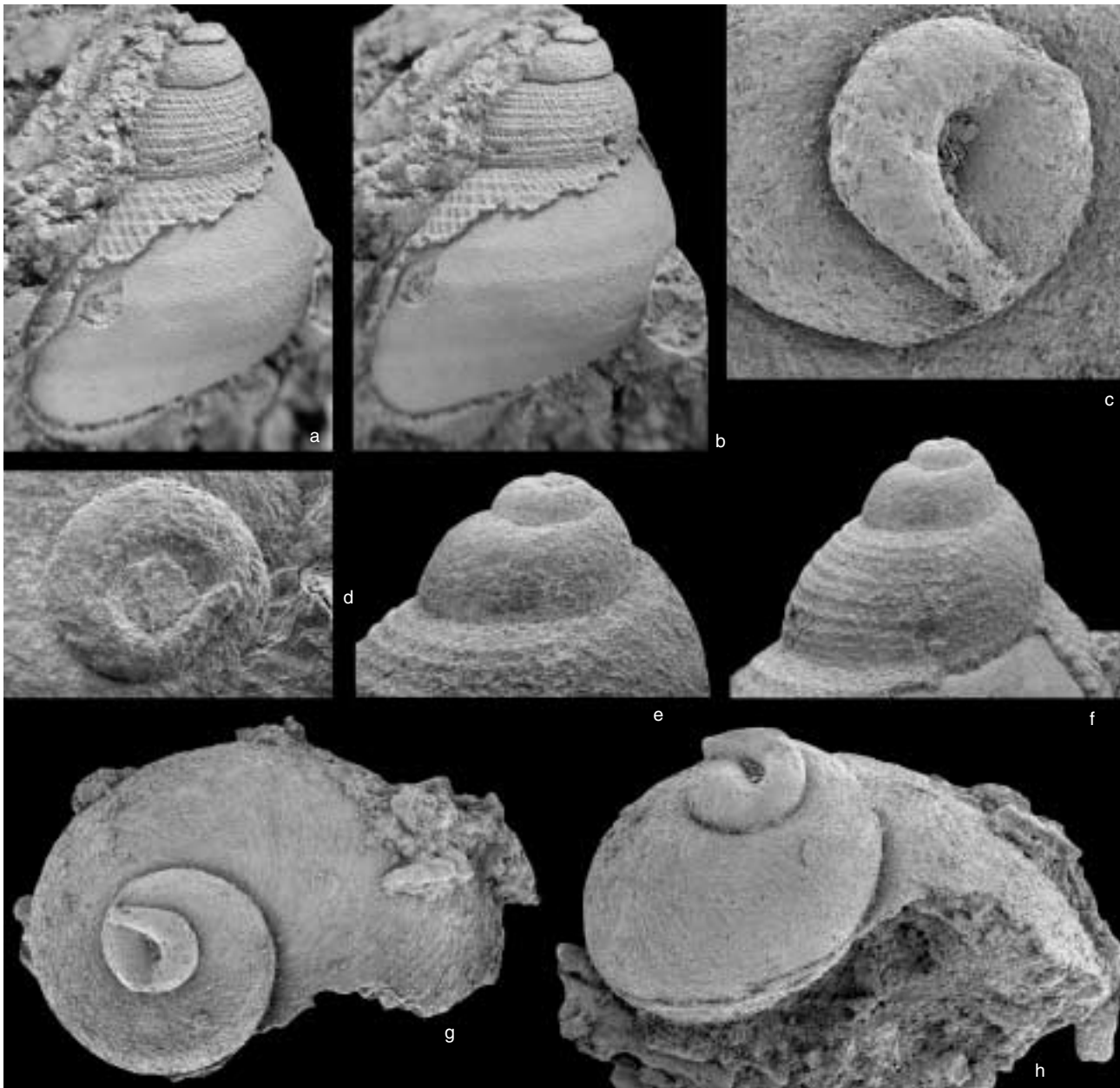
Type species: *Eifelcyrtus blodgetti* gen. et sp. nov.; early Givetian (late Middle Devonian); Eifel, Germany.

Etymology: *Eifelcyrtus*, after the Eifel area (Germany) where this genus was found for the first time.

Diagnosis: Naticiform shell similar to *Vltaviella* Frýda and Manda, 1997, but with small cyrtoneritimorph protoconch; teleoconch ornamented only by prosocline growth lines.

Relationships: Among the known cyrtoneritimorph genera, the Givetian (late Middle Devonian) *Eifelcyrtus* gen. nov. is closest to the Lochkovian (early Early Devonian) *Vltaviella* Frýda and Manda, 1997. *Eifelcyrtus* may be distinguished from the latter genus by its much smaller protoconch, which is also more closely coiled (Fig. 1c). Another feature distinguishing both genera is their shell ornamentation; the shells of *Vltaviella* bear distinct reticulate ornamentation, while *Eifelcyrtus* has only prosocline growth lines.

Species included: Only its type species is presently known.



Figs 1a, b, d–f. *Krameriella hornyi* gen. et sp. nov. from the Kopanina Formation (Gorstian, early Ludlow, early Late Silurian; Prague Basin); holotype ČGU JF 815; a – oblique lateral view, $\times 17$, b – lateral view, $\times 17$, d – detailed view of protoconch, $\times 80$, e, f – oblique lateral views on shell apex, e $\times 39$, f $\times 25$. Figs 1c, g–h. *Eifelcyrtus blodgetti* gen. et sp. nov. from the Scheid Member of the Cuerten limestone (early Givetian, late Middle Devonian; Soetenicher Mulde); Holotype SMF XII 3566; c – detailed view of protoconch, $\times 140$, g – apical view, $\times 42$, h – oblique apertural view, $\times 50$.

Eifelcyrtus blodgetti sp. nov.

Holotype: Specimen figured here as Figs. 1 c, g-h and deposited in the Senckenberg Museum in Frankfurt/M (SMF XII 3566).

Type locality: quarry “Am Wachtberg” (Soetenicher Mulde, Nordeifel, MTB Mechernich, R ^{2540 000/ H} ^{5598 700}), Eifel, Germany.

Type horizon: Cuerten strata, Scheid Member, Set γ ; early Givetian, late Middle Devonian.

Etymology: *blodgetti*, in honour of our friend, the American paleontologist Robert B. Blodgett who has contributed much to our knowledge of Devonian gastropods.

Diagnosis: Because of monotypy, see that of genus.

Description: A naticiform shell (maximum diameter about 1.6 mm) with rapidly increasing whorls; rounded whorls ornamented by prosocline growth lines; shell apex formed by smooth, fish-hook like protoconch (Fig. 1c); straight tube forming initial part of cyrtoneritimorph protoconch about 0.2 mm long and its apical diameter

about 0.05 mm; boundary between protoconch and teleoconch obscured.

Remarks: *Eifelcyrtus blodgetti* sp. nov. is a very rare element in the micromorph gastropod community derived from the Scheid Member of the Cuerten limestone (early Givetian; per. comm. P. Lütte). Its shell was found at the classical locality “Am Wachtberg” near Soetenich, described by Kirchner (1915) and Heidelberg and Bandel (1999).

Subfamily *Krameriellinae* subfam. nov.

Type genus: *Krameriella* gen. nov.

Diagnosis: Members of Vltaviellidae with highly turbiniform teleoconchs.

Remarks: At present we consider the placement of *Krameriellinae* subfam. nov. within the Vltaviellidae as the best, but rather uncertain, alternative, because the teleoconch shape of *Krameriella* gen. nov. is different from that of other members of the Cyrtoneritimorpha. On the other hand, its cyrtoneritimorph protoconch (Fig. 1d) clearly testifies for its placement somewhere amongst the Cyrtoneritimorpha. Comparison of *Krameriella* gen. nov. with all known Paleozoic gastropods with openly coiled protoconchs (i.e., members of Cyrtoneritimorpha, Perunelomorpha, and Euomphalomorpha) has brought to our attention the Givetian (late Middle Devonian) gastropod *Soetenichia girzenbergense* (Kirchner, 1915) from the Eifel area of Germany. This species also has a high turbiniform teleoconch similar to that of *Krameriella* gen. nov., and was interpreted as a member of the Perunelloidea Frýda and Bandel, 1997 (Heidelberg and Bandel 1999). However, the initial part of its protoconch seems to be straight (see Heidelberg and Bandel 1999, fig. 42), which is one of the features distinguishing cyrtoneritimorph and peruneloid protoconch types (compare plates 10 and 11 in Frýda and Bandel 1997, with those in Bandel and Frýda 1999). We, therefore, suggest that the Givetian *Soetenichia* Heidelberg and Bandel, 1999, might be another member of *Krameriellinae* subfam. nov.

Included genera:

- *Krameriella* gen. nov. – Ludlow, early Late Silurian
- ? *Soetenichia* Heidelberg and Bandel, 1999 – Givetian, late Middle Devonian

Genus *Krameriella* gen. nov.

Type species: *Krameriella hornyi* gen. et sp. nov.; Ludlow (early Late Silurian); Bohemia.

Etymology: *Krameriella*, in honour of the Czech humanist and publisher Václav Matěj Kramerius (1753–1808), who was born 250 years ago.

Diagnosis: Rather high turbiniform shell with rounded whorls and cyrtoneritimorph protoconch; outer apertural lip strongly prosocline; shell ornamented by numerous, regularly spaced, spiral and collabral ribs forming

reticulate pattern; diameter of openly coiled cyrtoneritimorph protoconch about 0.4 mm.

Relationships: The new genus can easily be distinguished from all known genera of Cyrtoneritimorpha by its highly turbiniform teleoconch. The other cyrtoneritimorph taxa have naticiform (*Vltaviella* Frýda and Manda, 1997, *Eifelcyrtus* gen. nov.) or limpet-like (*Orthonychia* Hall, 1843) teleoconchs. The Middle Devonian *Soetenichia* Heidelberg and Bandel, 1999, differs from the Late Silurian *Krameriella* gen. nov. in its lack of a distinct reticulate shell ornamentation as well as its slightly different whorl profile.

Species included: Only the type species is presently known.

Krameriella hornyi sp. nov.

Holotype: Specimen ČGÚ JF 815, figured here as Figs 1a,b,d,e,f deposited in the collection of J. Frýda, Czech Geological Survey, Prague.

Paratype: Specimen ČGÚ JF 816.

Type locality: Amerika (= Liščí lom) quarry, Mořina, Prague Basin, Bohemia.

Type horizon: Kopanina Formation; Gorstian, early Ludlow, early Late Silurian.

Etymology: *hornyi*, in honour of the Czech paleontologist Radvan Horný, who published the first study on the Silurian gastropod community, from which *Krameriella hornyi* sp. nov. was collected, precisely 50 years ago.

Diagnosis: Because of monotypy, see that of genus.

Description: Small, highly turbiniform shell with pleural angle of about 50°; whorls between sharp suture rounded; dome-like shell apex (Fig. 1e, f) formed by cyrtoneritimorph protoconch 0.43 mm in diameter (Fig. 1d); outer apertural lip prosocline; shell ornamented by numerous, regularly spaced, spiral and collabral ribs forming reticulate pattern (Fig. 1a, b); collabral ribs meet suture at an angle of about 60°; protoconch and first teleoconch whorl seem to be smooth.

Remarks: The shell of *Krameriella hornyi* sp. nov. is rather thin (about 0.06 mm in the most adult whorl of a shell about 3.8 mm high), and traces of spiral ornamentation are seen on internal moulds of its outer whorls (Fig. 1b). *Krameriella hornyi* sp. nov. comes from a shallow-water, highly dynamic environment. Its thin shell may therefore suggest that it was living in some sort of protected mode of life (among algae, within the interstices of rubble, or that it was infaunal).

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