Acta Zoologica Academiae Scientiarum Hungaricae 69(4), pp. 337–352, 2023
DOI: 10.17109/AZH.69.4.337.2023
http://zoobank.org/6836FC88-636F-412E-850C-26F8C1A6294B

FERUSSINA PETOFIANA SP. N. (GASTROPODA, CAENOGASTROPODA, CYCLOPHORIDAE), THE OLDEST REPRESENTATIVE OF ITS SUBFAMILY FROM THE LATE CRETACEOUS OF ROMANIA

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The terrestrial gastropod *Ferussina petofiana* Páll-Gergely sp. n. is described from uppermost Cretaceous (Maastrichtian) deposits from the Haţeg Basin, Romania. It represents the first properly diagnosed and described snail taxon from these deposits, despite numerous earlier reports of gastropod occurrences. This new species is characterized by a depressed, mostly smooth shell, three spiral carinae on the ventral side (inside the umbilicus), and an upward-turning aperture. The last feature characterizes two European fossil snail genera, the cyclophoroidean *Ferussina*, and the stylommatophoran *Strophostomella*. The new species is classified in the former group due to its nearly circular aperture, and the presence of conspicuous spiral carinae. In contrast, the aperture of most stylommatophoran genera (including *Strophostomella*) is semilunar, and if raised sculptural elements are present, they are mostly radially oriented. The identification of this new taxon in the uppermost Cretaceous of Romania represents an important range extension for the genus *Ferussina*, and adds it to the brief list of European clades that appear to have survived the mass extinction event at the Cretaceous-Paleogene boundary.

Key words: Maastrichtian, *Strophostomella*, Anostomopsidae, Paleogene, K-Pg boundary

INTRODUCTION

Ferussina Grateloup, 1827 is to date considered to be a Western European Paleogene land snail genus, reported from Middle Eocene (Lutetian) to Upper Oligocene (Chattian) deposits of France, Germany, northern Italy, and

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Switzerland; a further dubious record comes from presumably Lower Miocene strata of southern France (Degrange-Touzin 1892). *Ferussina* species are characterised by an upward-turning aperture, i.e., its last quarter whorl turns towards the apex of the shell instead of away from it (termed "anostomy" by Nordsieck 1986). Currently, the genus contains seven species and two subspecies as follows: *Ferussina anomphalus*, *F. anostomaeformis* Grateloup, 1827, *F. globosa* Dumas, 1876, *F. lapicida* Leufroy, 1828, *F. praeglobosa* (Roman, 1904), *F. striata* (Deshayes, 1828), and *F. tricarinata* (M. Braun, 1838).

During fieldwork aiming to collect vertebrate fossils from uppermost Cretaceous continental deposits of the Haţeg Basin, Romania, a few fossil land snails were also found. Among them was a single shell, which is described herein, and included in the genus *Ferussina*. Accordingly, this occurrence is the oldest, as well as the easternmost representative of its genus.

Geological setting

The fossil gastropod specimen reported in this work was discovered in uppermost Cretaceous deposits cropping out in the neighbourhood of Vălioara village, in the northwestern corner of Haţeg Basin, in western Romania (Fig. 1A, B). These deposits are primarily known for their fossil vertebrate fauna which includes dwarf dinosaurs first described more than a century ago (e.g., Nopcsa 1915, 1923; see also Weishampel *et al*. 1991, Benton *et al*. 2010, Csiki-Sava *et al*. 2015), although rare invertebrates and plants have also been reported from them.

These fossiliferous continental deposits are distributed widely, albeit patchily, across the western and central areas of the Haţeg Basin (Fig. 1B), and are represented mainly by recurring cycles of various siliciclastic deposits formed in a fluvially dominated palaeoenvironment (Grigorescu 1992, Csiki-Sava *et al*. 2016). They were laid down within an actively subsiding intermountain basin surrounded by uplifting segments of Southern Carpathians (e.g., Willingshofer *et al*. 2001). This entire area of continental sedimentation was part of an isolated, insular area towards the eastern end of the Late Cretaceous European Archipelago (Benton *et al*. 2010, Csiki-Sava *et al*. 2015).

The fossiliferous uppermost Cretaceous continental beds exposed in the neighbourhood of Vălioara belong to the Densuș-Ciula Formation (Fig. 1B) that groups similar deposits from the northwestern part of the Haţeg Basin (e.g., Grigorescu 1992), one of the roughly synchronous lithostratigraphic units that are separated within the Haţeg Basin (Grigorescu 1992, Csiki-Sava *et al*. 2016; Fig. 1B). More precisely, they belong to the lower part of the Middle Member of this formation, characterized by coarse- to fine-grained siliciclastic, fluvial and floodplain deposits that vary from dominantly reddish to grey-green in colour, with a minor amount of reworked volcaniclasts present. The presence of these deposits in the surroundings of Vălioara was first re-

ported by Nopcsa (1905), and their relatively richly fossiliferous nature was first established by the excavations undertaken by Kadić (1916). The sedimentary make-up and fossil record of these beds was most recently reviewed by Botfalvai *et al*. (2021).

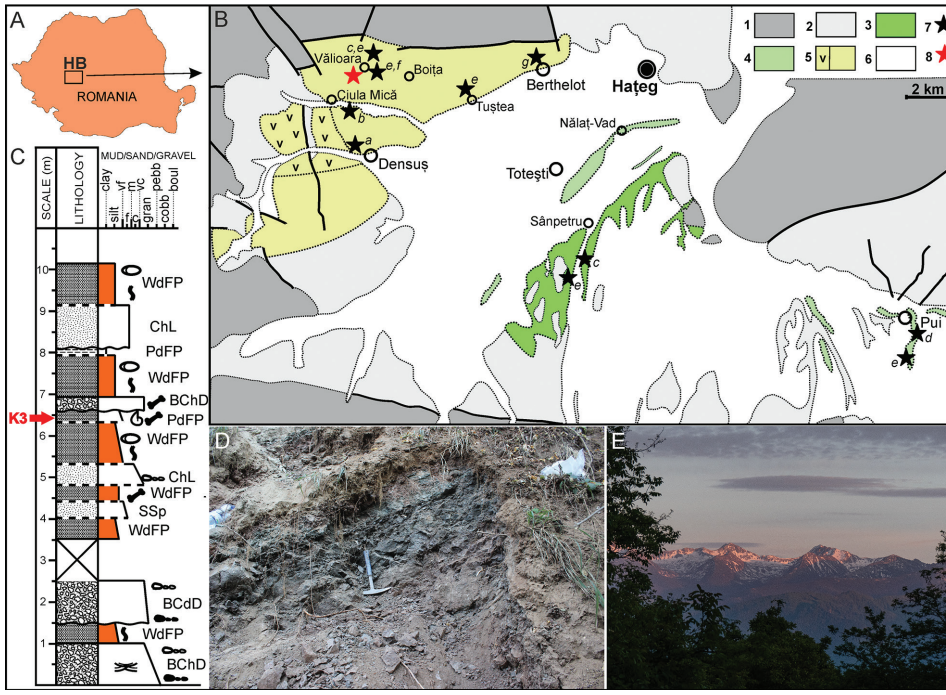

Fig. 1. Geological setting of the type locality of *Ferussina petofiana*. A = Position of the Hațeg Basin (rectangle; HB) within Romania. B = Simplified geological map of the Hațeg Basin, highlighting the distribution of the uppermost Cretaceous continental deposits (shades of green). Legend: 1 – surrounding metamorphic basement, 2 – units of the sedimentary basin infill (mostly marine), 3-5 – fossiliferous Maastrichtian continental deposits, with 3 – Sînpetru Formation, 4 – Densuș-Ciula Formation (v – volcaniclastic beds), and 5 – Sînpetru Formation-correlative units (see Csiki-Sava *et al*. 2016), 6 – Quaternary cover, 7 – sites with gastropod assemblages (*a* – Schafarzik 1909, *b* – Rădulescu *et al*. 1976, *c* – Antonescu *et al*. 1983, *d* – Grigorescu *et al*. 1985, *e* – Pană *et al*. 2002, *f* – Csiki *et al*. 2008, *g* – Vasile *et al*. 2011; see text for details), 8 – site K3 of Vălioara, the type locality of *Ferussina petofiana* (from Botfalvai *et al*. 2021). C = Synthetic lithological column near site K3 (marked by red arrow), modified from Botfalvai *et al*. (2021). Lithofacies abbreviations: BChD – braided channel deposits, mainly conglomerates, ChL – sandstone channel lag, SSp – sandstone sheet-splay, PdFP – poorly drained floodplain deposits, mainly grey-greenish silts and muds, WdFP – well-drained floodplain deposits, mainly red silts and muds. For more details, see Botfalvai *et al*. (2021). D. View of site K3 in the Pârâul Neagului ravine, located in grey-greenish fine-grained floodplain deposits (near handle of hammer). E. The Retezat Mountains overlooking the Hațeg Basin from the south (photo by Gergő Konecsni), mentioned by the Petőfi poem written during his 1849 visit in the area (see Etymology), as seen from the plateau overlying site K3

While attempting to relocate the old excavation sites of Kadić, Botfalvai *et al*. (2021) also identified several new vertebrate accumulations, including the K3 site (Fig. 1 B, C, D) that is located in the close proximity of the old excavation site III of Kadić (1916) in the Pârâul Neagului ravine. This site yielded mainly fragmentary, indeterminate vertebrate fossils, described from a bluish-greyish mudstone, in association with plant and gastropod remains; this bed was interpreted as a poorly drained floodplain deposit. A few other fossil remains were reported to come from an underlying red paleosol horizon (Botfalvai *et al*. 2021). The gastropod specimen reported here (LPB III g 10021) was recovered in 2019 from a poorly drained greyish brown mudstone horizon a few centimetres below the main fossiliferous bed. Judging from its good preservational state (Fig. 2), as well as from the sedimentological nature (mudstone) and palaeoenvironmental (floodplain) interpretation of the source deposits, the specimen is most probably autochthonous. Based on its relative stratigraphic position, combined with the available age constraints for the Densuș-Ciula Formation (synthesized by Csiki-Sava *et al*. 2016 and Botfalvai *et al*. 2021), the age of the K3 site, and thus that of the specimen of the new taxon, is early Maastrichtian (most probably the early part of this interval, approximately 71 Ma).

Although vertebrate remains discovered in the uppermost Cretaceous continental beds from the Haţeg Basin received the most scientific attention, the presence of gastropods in these beds was also noted at an early stage by Nopcsa (1905), and in close proximity of Vălioara, at Densuș, by Schafarzik (1909). However, none of these records were described in detail, and the current whereabouts of any gastropod fossils collected during these early excavations are unknown. Subsequently, Rădulescu *et al*. (1976) mentioned the presence of an assemblage of gastropods from the Densuș-Ciula Mare area (south of Vălioara; Fig. 1B). Meanwhile, Antonescu *et al*. (1983) reported the discovery of a gastropod assemblage from Vălioara (as well as from Sânpetru; Fig. 1B), which the authors considered to support a latest Cretaceous (Maastrichtian) age of these deposits. None of these specimens were described in detail or figured, and their whereabouts remain unknown, so the taxonomic assignments recorded by these authors cannot be confirmed. Gastropod remains are also known from other outcropping areas of the uppermost Cretaceous continental beds; Grigorescu *et al*. (1985) noted the presence of cf. *Bauxia*, cf. *Cyclophorus*, and *Lychnus* in the red beds from Pui (Fig. 1B), whereas Grigorescu *et al*. (1999) generally noted the widespread presence of gastropods in the microvertebrate fossil sites they surveyed, including from around Vălioara. Subsequently, Pană *et al*. (2002) reported on the relatively diverse gastropod assemblages from these different sites, but none of the cited taxa had been properly diagnosed, described and/or figured, thus their identity remains unsubstantiated. Following up on Pană *et al*. (2002), Csiki *et al*. (2008) have reported the pres-

ence of a continental gastropod assemblage at the Budurone microvertebrate fossil site southeast of Vălioara, consisting of freshwater and terrestrial taxa. Finally, Botfalvai *et al*. (2021) also mentioned the presence of mainly indeterminate gastropods from the surroundings of Vălioara, including the type locality of the new taxon reported here. Outside of the Haţeg Basin, Vremir *et al*. (2015) mentioned the occasional presence of indeterminate gastropods in the coeval continental beds of the southwestern Transylvanian Basin, and Vasile and Csiki-Sava (2012) described gastropod assemblages similar to those known from the Haţeg Basin from the nearby Rusca Montană Basin, as well.

By way of comparison, presence of gastropod fossils from uppermost Cretaceous continental beds from western (southern France, northern Spain; e.g., Matheron 1832) and central Europe (Austria, Hungary; Bandel & Riedel 1994, Ősi *et al.* 2021) were first reported much earlier than in Romania, and have been the subject of more research since (e.g., Sigé *et al*. 1997, Garcia *et al*. 2000, Turin 2017). These faunas appear, however, to be less taxonomically diverse than those from the Haţeg Basin and surrounding areas. This purported high local diversity is now further augmented with our report of a new continental gastropod taxon from the K3 site near Vălioara.

MATERIAL AND METHODS

The shell was imaged using a Nikon SMZ25 digital microscope with Nikon Nis-Elements software and measured with a Vernier caliper.

We aimed to compare the new species with type specimens of *Strophostomella* species, but these were not found in the Natural History Museum, Vienna and the GeoSphere Austria (Mathias Harzhauser and Irene Zorn, pers. comm., 2023 April). Nevertheless, the information available in the literature provided sufficient evidence that the newly collected specimen is a new species.

Abbreviations: LPB: Laboratory of Palaeontology, Faculty of Geology and Geophysics, University of Bucharest (Bucharest, Romania); NHMW: Naturhistorisches Museum Wien (Vienna, Austria).

RESULTS

Systematic description
Superfamily Cyclophoroidea Gray, 1847
Family Cyclophoroidea Gray, 1847
Subfamily Ferussininae Wenz, 1923 (1915)

Remarks: *Ferussina* Grateloup, 1827 has been classified in its own family, the Ferussinidae Wenz, 1923 (1915), in the superfamily Cyclophoroidea Gray, 1847 (Bouchet *et al.* 2017) due to the upward-turning aperture. Although this character is rare among land snails, it has evolved at least six times in Eupulmonata and three times in Cyclophoroidea (Páll-Gergely & Neubauer 2020).

This suggests that the systematic position of *Ferussina* should not be based on the upward-turning last quarter whorl alone but should also include the general morphology of the shell. Thus, its systematic position has been re-evaluated, and currently Ferussininae is treated as a subfamily of the Cyclophoridae (Páll-Gergely & Neubauer 2020).

Genus *Ferussina* Grateloup, 1827

Ferussina Grateloup, 1827: 5.
Type species: *Ferussina anostomaeformis* Grateloup, 1827, by monotypy.

Ferussina petofiana Páll-Gergely sp. n.
https://zoobank.org/6B11BD85-C451-43E6-BE23-7F467AE8B276
(Figs 2–3)

Type material: Holotype (Fig. 2). LPB III g 10021, in the collections of the Faculty of Geology and Geophysics, University of Bucharest, Romania. The single available shell is relatively well preserved, but the dorsal side, and partly the ventral side of ca. half whorl of the body whorl is missing.

Type locality/stratum/age: K3 fossiliferous site, Neagului Creek, Vălioara, north-western Hațeg Basin, Hunedoara County, Romania (see Botfalvai *et al*. 2021). The site is located in the basal part of the Middle Member of the Densuș-Ciula Formation (Grigorescu 1992, Csiki-Sava *et al*. 2016), estimated to have an age of early early Maastrichtian.

Diagnosis: A small *Ferussina* species with a predominantly smooth sculpture, an oval aperture, and three sharp spiral carinae on the ventral side.

Description: Shell depressed with flat base, domed dorsal surface, and rounded or slightly shouldered body whorl; last ca. quarter whorl turns upright, elevating higher than apex; whorls 4.25, separated by a deep suture; protoconch (Fig. 2G) consisting of ca. 1.25 whorls, smooth, protoconch-teleoconch boundary conspicuous, teleoconch predominantly smooth, with inconspicuous, irregular radial growth lines, last ca. quarter whorl near the suture finely ribbed, and this fine ribbing is also visible between the spiral carinae on the ventral side (Fig. 2H); umbilicus blocked with sediment that could not be removed, therefore it is not clear whether it is open or closed (but very probably open); last ca. half whorl strongly enlarged in diameter, bears three elevated, main spiral carinae inside umbilicus (Fig. 2D, H); carinae continuous, run until peristome (see Fig. 2E), not interrupted with radial ribs; area between the outermost and the middle carinae finely ribbed (Fig. 2H); a fourth, much lower carina is also visible; aperture oval (Fig. 2E), parietal side convex (not concave due to penultimate whorl); peristome is incomplete (the adult peristome is missing), therefore its morphology remains unknown.

Measurements: Shell diameter: 10.8 mm, shell height: 4.4 mm.

Differential diagnosis: All currently known *Ferussina* species are larger than 2 cm (Grateloup 1827, Deshayes 1828, Leufroy 1828, Dumas 1876, Sandberger 1870–1875, Sacco 1886, Roman 1904, Wenz 1938–1944, Salvador *et al*.

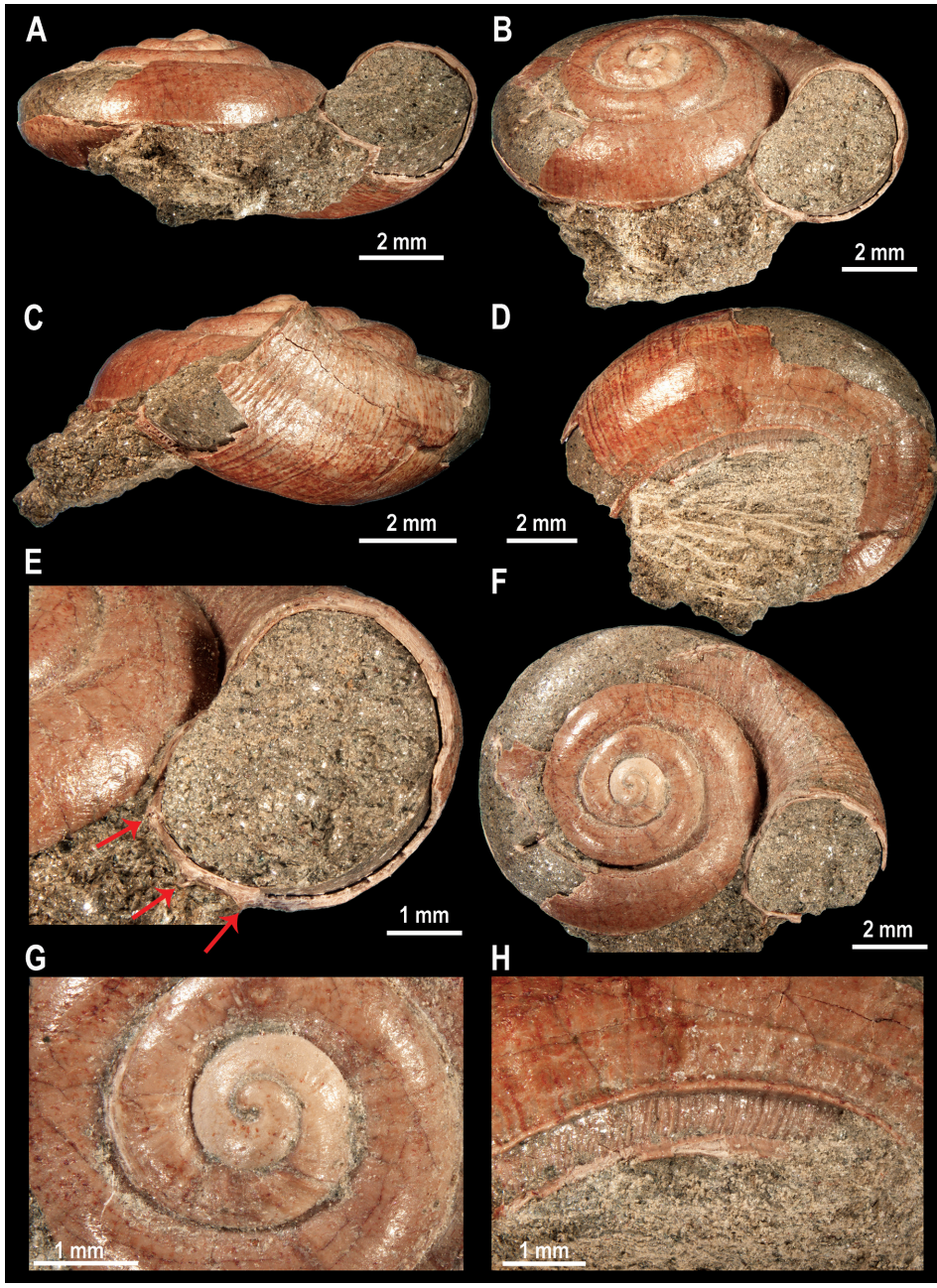

Fig. 2. Holotype and only specimen of *Ferussina petofiana* Páll-Gergely, sp. n.: A–D, F = various views of the shell; E = aperture; G: protoconch and first teleoconch whorls; H = Arrows on Fig. E indicate the positions of the spiral carinae

2016, Páll-Gergely & Neubauer 2020), with the exception of *Ferussina tricarinata* from the Upper Oligocene in Germany (see Kadolsky 2008), which is the only known species that can be as small as ca. 1 cm. However, that species has a stronger radial sculpture, presents only a single elevated spiral carina inside the umbilicus, and it also has one carina running along the edge of the body whorl (Kadolsky 2008, Páll-Gergely & Neubauer 2020), differing in these respects from the Vălioara specimen discussed herein.

The species of the genus *Strophostomella* P. Fischer, 1883, known from Hungarian [*S. cretacea* (Tausch, 1886), *S. fragilis* (Tausch, 1886)] and Austrian [*S. reussi* (Stoliczka, 1860)] uppermost Cretaceous deposits, possess semilunar apertures (Stoliczka 1860, Tausch 1886, Bandel & Riedel 1994). Moreover, none of the three known *Strophostomella* species possesses elevated spiral carinae on their ventral (=umbilical) sides, and they have much stronger radial sculpture than the new species (Stoliczka 1860, Tausch 1886, Bandel & Riedel 1994).

Etymology: This new species is dedicated to and named after Sándor Petőfi (1823–1849), the National Poet of Hungary, to commemorate the bicentenary of his birth but also his presence in the Hațeg Basin roughly 174 years before the identification and description of the new taxon reported in this contribution. Petőfi apparently visited Hațeg in 14 April 1849 (Kristóf 1944), and even wrote a poem while being there (Vajdahunyadon = At Hunedoara, transl. from Hungarian in original) (Dávid & Mikó 1972: 223). It is worth emphasiz-

Fig. 3. Artistic reconstruction of *Ferussina petofiana* Páll-Gergely, sp. n. (artwork by Márton Zsoldos)

ing that lines of this poem (albeit otherwise referring to an important Medieval historical character from Transylvania, János Hunyadi) are incidentally also highly evocative of the site of discovery of *F. petofiana*. These allude to a setting 'from where I'm staring at the past' and which 'Is hidden from the eyes of the world/… not seen by others than,/from far away, the white-capped head of/ the mountains' elder, the ancient Retezat' (transl. from Hungarian in original), altogether forming a remarkably fitting description of site K3 near Vălioara where the holotype specimen was excavated, close to the foothills of, and overlooked from the distance by, the Retezat Mountains (Fig. 1E).

DISCUSSION

Two fossil genera of land snails are closely comparable to the newly collected shell from the Haţeg Basin, both characterized by an upright turning aperture: the cyclophorid *Ferussina* Grateloup, 1827 (see Páll-Gergely & Neubauer 2020) and *Strophostomella* P. Fischer, 1883 (type species: *Boysia reussi* Stoliczka, 1859, by monotypy) (see, e.g., Bandel & Riedel 1994). The latter genus was included in the carnivorous, mostly tropical family Streptaxidae by Wenz (1940) due to its similarity with *Tonkinia* Mabille, 1887 (see Páll-Gergely *et al.* 2020). Later, Nordsieck (1986) transferred *Strophostomella* to a new stylommatophoran family, the Anostomopsidae. The latter decision can be debated, because all other genera assigned to Anostomopsidae possess apertural folds (see, e.g., *Gosavidiscus* Hrubesch, 1965, *Proterocorilla* Hrubesch, 1965) that are not present in *Strophostomella*. Nevertheless, we agree with the previous assessment that the species of *Strophostomella*, due to their semilunar aperture, are stylommatophorans, whereas the genus *Ferussina*, with rounded aperture, is a member of Cyclophoridae.

Ferussina is, so far, only known from Paleogene (Middle Eocene to Upper Oligocene and maybe to Upper Miocene) deposits of Western Europe (France, Germany, Switzerland, northern Italy; Páll-Gergely & Neubauer 2020), while *Strophostomella* was reported from Upper Cretaceous Austrian and Hungarian (Ajka) sites (Bandel & Riedel 1994). Based solely on their known stratigraphic ranges, the placement of the new species into the genus *Strophostomella* would thus appear to be more likely. In fact, *Strophostomella* has already been mentioned from Maastrichtian deposits of the Haţeg Basin (e.g., Antonescu *et al*. 1983), but it is very likely that this refers to the new *Ferussina* species described herein. However, in the absence of specimens and good quality illustrations, such a possibility can neither be ascertained, nor dismissed.

Nevertheless, the aperture of the new species is oval (nearly rounded), suggesting that it is instead a member of Cyclophoroidea. In contrast, the apertures of the known *Strophostomella* species are semilunar (i.e., the parietal side follows the shape of the penultimate whorl, resulting in a concave apertural shape), suggesting that they were stylommatophorans instead of operculate

snails. Due to the nearly circular cross section of the whorls, they do not (or very slightly) overlap in the Cyclophoroidea, and species belonging to that group are generally characterized by a deep suture. In contrast, the whorls of low-spired stylommatophoran snails more strongly overlap, and thus are divided by a generally shallower suture. These traits also suggest that the new species is a cyclophorid and not a stylommatophoran. Furthermore, multiple, strong, parallel, continuous (not interrupted) spiral carinae are only present in some groups of Cyclophoroidea (e.g., *Gassiesia* Clench, 1949: Solem 1961 and *Hirsuticyclus canaliculatus* Yu, 2022, but also in *Ferussina tricarinata*, see Páll-Gergely & Neubauer 2020), but not in Stylommatophora, with the exception of a single periumbilical keel or a keel on the body whorl. Instead, elevated, conspicuous sculptural elements are nearly always present as radial ribs in Stylommatophora, while such radial ribs are absent in the new species (Schileyko 1998–2007).

Accordingly, we classify the Vălioara specimen (LPB III g 10021) into the cyclophorid genus *Ferussina*. Furthermore, based on the differences between our specimen and the currently known species of *Ferussina*, we describe it as a new species, *Ferussina petofiana*. While doing so, we are nevertheless aware of the fact that our systematic placement has palaeobiogeographic and evolutionary implications, as outlined below, and thus we caution that these rely heavily on the currently proposed systematic status of the new species. We also note here that the widespread presence of cyclophoroidean gastropods in the uppermost Cretaceous deposits of the Haţeg Basin has already been reported by several sources (e.g., Antonescu *et al*. 1983, Grigorescu *et al*. 1985, Pană *et al*. 2002), although these previous claims were largely unsupported by clear evidence (excepting, in part, Pană *et al*. 2002), and the specimens upon which these were made are usually unavailable for direct comparisons. We also mention that some of the most commonly occurring gastropod remains from these beds, and that were customarily referred to cyclophoroideans, are roughly circular opercula that are frequently found especially in red-coloured fine-grained dry floodplain deposits (e.g., Pană *et al*. 2002, Vasile *et al*. 2011). However, calcified opercula are rare among extant Cyclophoroidea, and probably represent remains of Littorinimorpha.

The identification of a new, latest Cretaceous species of *Ferussina*, a genus that was until now recorded only from Paleogene beds of Western Europe, represents a significant range extension for this genus, both temporally and palaeogeographically. Its occurrence in layers of Maastrichtian age (Bojar *et al*. 2011, Csiki-Sava *et al*. 2016, Botfalvai *et al*. 2021), represents a minimum chronostratigraphic range extension of about 23 million years for this genus. Furthermore, its presence in western Romania during the latest Cretaceous also implies an important geographic range extension eastward compared to its Paleogene area of distribution that covers parts of Western Europe (Páll-Gergely & Neubauer 2020). Based on currently available data, it appears that the geographic

distribution of the genus shifted westward over time, which is in agreement with the fact that Cyclophoridae are of Asian origin, although such a picture may represent at least in part the result of its somewhat patchy fossil record.

The most important implication of the discovery of *Ferussina petofiana* in the uppermost Cretaceous of the Hațeg Basin is that the resulting extended chronostratigraphic range of the genus (and that of its parent subfamily, the Ferussininae) crosses the Cretaceous-Paleogene (K-Pg) boundary which coincides with one of the most devastating mass extinctions of the Phanerozoic (e.g., Raup & Sepkoski 1982, MacLeod *et al*. 1997). The end-Cretaceous mass extinction had extremely severe effects on the composition of the latest Cretaceous ecosystems, both marine and continental, eliminating a large number of groups of organisms, including iconic Mesozoic taxa such as the non-avian dinosaurs, flying pterosaurs, and ammonites (e.g., MacLeod *et al*. 1997, Archibald 2011). The extinction was also highly selective, with certain taxa less affected by the K-Pg boundary events whereas others were more severely impacted or even completely erased (e.g., Sheehan & Hansen 1986, Sheehan & Fastovsky 1992, Wilson 2013).

Mapping the effects of the K-Pg boundary events on the latest Cretaceous European continental ecosystems is still in its infancy compared to North America, where the fossil record is both more complete and temporally better constrained (e.g., Hunter *et al*. 1997, Nichols 2007, Mitchell *et al*. 2012, Fastovsky & Berkovici 2016), although important advances in this field had been made in recent years (e.g., López Martínez *et al*. 1999, Riera *et al*. 2009, Puértolas-Pascual *et al.* 2016). The latest review concerning the patterns of extinction of European continental vertebrates (Csiki-Sava *et al*. 2015) showed that a high percentage of latest Cretaceous higher-level vertebrate taxa disappeared near/at the K-Pg boundary, with only a small number of clades surviving into the Paleogene. Our knowledge concerning patterns of continental invertebrate extinction and survival is lagging well behind, although recently Neubauer *et al*. (2021) have surveyed the fate of European freshwater gastropods across the K-Pg boundary. They have identified that 9.5% (average value) of genera has gone extinct at the end of the Cretaceous. Comparable statistics are unfortunately unavailable for terrestrial gastropods such as cyclophoroids, but nonetheless the land snail subfamily Ferussininae can now be added to the list of K-Pg boundary extinction survivors in Europe. It is also clear that long-term morphological conservatism characterizes the Ferussininae, similar to a pattern that had been noted previously in the case of other cyclophorid clades crossing the K-Pg boundary (Hirano *et al*. 2019, Neubauer *et al.* 2019).

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Acknowledgements – We are grateful to Alexander Lukeneder and Mathias Harzhauser (both NHMW) and Irene Zorn (GeoSphere Austria) for their information on

Strophostomella types, and to Norbert Flórián (Institute for Soil Sciences, Centre for Agricultural Research, Budapest, Hungary) for his help in photographing. We are also grateful to the two reviewers (Tom White and Thomas Neubauer) whose insightful and detailed comments helped us improve the previous versions of the manuscript.

This study was supported by the Hungarian Research Fund (OTKA FK 135262; OTKA PD 131557) and the Bolyai Research Scholarship of the Hungarian Academy of Sciences to BPG and GB, as well as the Romanian Ministry of Research, Innovation and Digitalization (CNCS–UEFISCDI grant PN-III-P4-ID-PCE-2020-2570, within PNCDI III) to ZCsS. This project has received funding from the HUN-REN Hungarian Research Network. This is HUN-REN–MTM–ELTE Paleo contribution No. 375.

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Submitted April 24, 2023; accepted September 21, 2023; published October 6, 2023

Academic editor: Csaba Csuzdi